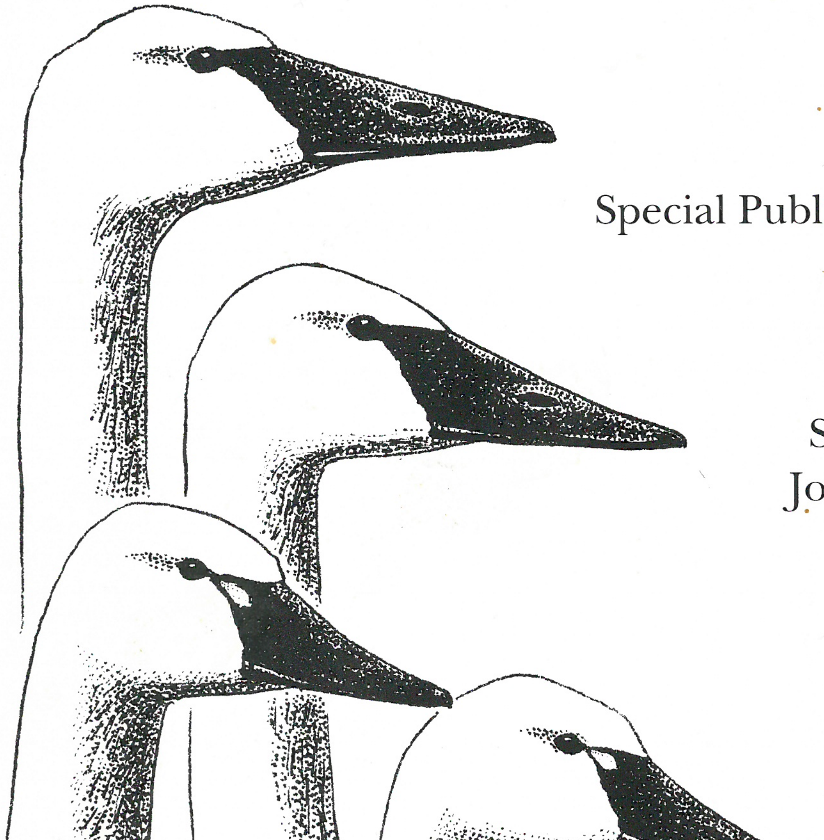
WATERBIRDS

Proceedings of the Fourth International Swan Symposium 2001



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Edited by
Eileen C. Rees
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13-18 FEBRUARY 2001

AIRLIE CONFERENCE CENTER, WARRENTON, VIRGINIA, USA

EDITED BY

EILEEN C. REES, SUSAN L. EARNST AND JOHN C. COULSON

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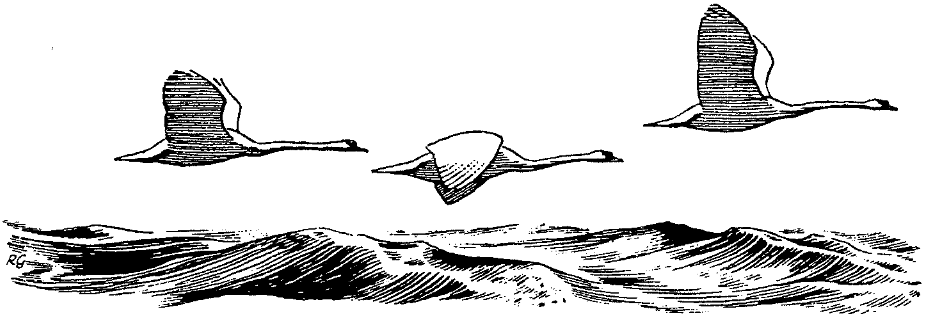

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Foreword

The Fourth International Swan Symposium was held at the Airlie Conference Center, near Warrenton, Virginia, USA from 13–18 February 2001, and was held concurrently with the Eighteenth Trumpeter Swan Society Conference. International swan symposia, which have been held at approximately10-yearly intervals since 1971, provide the main forum for members of the Swan Specialist Group (SSG), and other interested parties, to discuss the most recent results of their swan research programs, to identify gaps in knowledge with a view to encouraging new projects in these areas, and to facilitate the development of collaborative studies where appropriate. The SSG forms part of the Wetlands International/IUCN-Species Survival Commission Specialist Group network. As such, it is charged with providing the sound scientific basis for advising on swan management and conservation issues, especially at flyway or international levels. The 62 papers and 26 posters presented at the Symposium provided valuable new data on the status and ecology of swan species, generated since the Third International Swan Symposium in 1989, and we are proud to publish 54 of these papers here to provide an information source for scientists and reserve managers. Of the eight swan species and sub-species in the world, new data were presented for seven (Trumpeter Swan, Tundra Swan, Whooper Swan, Bewick's Swan, Mute Swan, Black-necked Swan and Coscoroba Swan), with only the Black Swan missing on this occasion.

Swans are truly a global family; they are widespread in North and South America, Europe, Asia and Australia/New Zealand, with smaller numbers occurring in Africa, and Black-necked Swans have even been recorded as vagrants in Antarctica. Since two swan symposia have been held in Europe (at Slimbridge, UK, in 1971 and at Oxford, UK, in 1989) and one in Asia (at Sapporo, Japan, in 1979), it therefore seemed appropriate that the fourth swan symposium should be held, for the first time, in the Americas. The offer by William J. ("Bill") Sladen, on behalf of Environmental Studies at Airlie, to host the meeting was particularly appropriate given Bill's lifetime devotion to swan research and conservation. The Swan Specialist Group is most grateful to the Environmental Studies at Airlie for their hospitality at a most successful meeting, particularly to Donielle Rininger for undertaking the substantial logistical arrangements needed to ensure that the 143 participants from 16 countries were all in the right place at the right time. The exceptional facilities provided by Airlie Conference Center, and efficient time-keeping by those chairing each session, resulted in the intensive program of talks and field excursions being enjoyable, as well as informative and on schedule.

In preparation for the meeting, the Swan Specialist Group's Regional and Species Coordinators acted as the Scientific Committee for the symposium: Eileen Rees, Roberto Schlatter, Carl Mitchell, Susan Earnst, Roland Limpert, Jan Beekman, Olafur Einarsson, Bjarke Laubek, Bert Coleman, Maria Wieloch, Ming Ma, Richard Kingsford and Murray Williams. The Scientific Committee reviewed abstracts to decide on the acceptance of oral and poster presentations, with valuable additional input from Ruth Shea on behalf of the Trumpeter Swan Society. In addition to the invaluable financial support provided by the Co-Sponsors and Patrons of the symposium and proceedings, without which neither the symposium nor the proceedings would have been possible, we are indebted to many others for their help in various ways: Pelle Andersen-Harild, Jon Bart, Vincent van den Berk, Jeff Black, Eric Bolen, John Bowler, Mark Brazil, Cindy Bronson, Preben Clausen, Bert Coleman, Jim Cooper, Ruth Cromie, Mike Daw, Simon Delany, Dirk Derksen, Andy Douse, Craig Ely, Tony Fox, Mark Fuller, Carol Gilbert, Todd Grant, Kim Head, Baz Hughes, Gary Ivey, Joe Johnston, Greg Justice, Janet Kear, Jim King, Richard Kingsford, Mel Kershaw, Steve Kohl, Bjarke Laubek, Konstantin Litvin, James Lovvorn, Carl D. Mitchell, Bart

Nolet, Mark O'Connell, David Parkin, Christopher Perrins, John Quinn, James Robinson, Marcus Rowcliffe, David Salmon, Joel Schmutz, Dafila Scott, Lady Scott, Jane Sears, Jerry Serie, Marcel Silvius, Dorothy Simpson, Chris Spray, Alan Thomson, Richard Ubels, Maria Wieloch, Murray Williams and Freddy Woog. We also thank first authors for submitting and amending their manuscripts, and for acting as reviewers for other papers in the proceedings.

The Symposium was opened by a welcome from Kim Head (President, Airlie Foundation), with introductory talks by Gerard Boere (International Conservation Officer, Wetlands International) on '*Wetlands International and its Specialist Group Network*', Harvey Nelson (President, The Trumpeter Swan Society) on the development of Trumpeter Swan management programs and John Turner (past Director of the U.S. Fish and Wildlife Service, and current President of the Conservation Fund) on '*U.S. Involvement with Swan Conservation and Research*'. In his speech John Turner observed that '*swans bring people together*', and this was particularly true of the Fourth International Swan Symposium, with participants attending from across the globe and from a variety of backgrounds, including scientists, amateur and professional ornithologists, reserve managers and animal welfare organizations.

Several major research projects have been developed within the SSG in the last decade, including energetics studies, assessment of population monitoring and trends and collaborative studies of birds breeding in the Russian arctic. The program of the Symposium therefore was organized into several thematic sessions to reflect the range of activity by swan researchers in the last decade: (1) population trends and dynamics; (2) ecology of migration; (3) breeding biology and demography; (4) feeding ecology and energetics; (5) management and conservation; and (6) general biology (including taxonomy, biometrics, animal health and molecular studies). The papers published here are grouped under similar thematic headings.

Finally, as co-editors of the symposium proceedings, we would like to acknowledge the major contribution made by our third editor, Dr. John Coulson, and to his wife Becky who provided invaluable support in checking and correcting the proofs. John is well known for his studies of seabirds, especially Kittiwakes, but his analytical brain and editorial pen have been invaluable in ensuring that scientific standards were maintained in the publication of these proceedings.

Eileen C. Rees and Susan L. Earnst
Wetlands International/IUCN-SSC
Swan Specialist Group

Census of Trumpeter Swans on Alaskan Nesting Habitats, 1968-2000

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Abstract.—In Alaska, hundreds of hours were flown by many survey crews during late summer in seven years to conduct a census of all occupied Trumpeter Swan (*Cygnus buccinator*) habitat (range 46,729 km^2 in 1968 to 123,857 km^2 in 2000). The total number of adult Trumpeter Swans increased from 1,924 to 13,934 between 1968 and 2000, a 624% increase. Population trends varied among eleven distinct geographical areas. Swan numbers increased in both high quality core habitat as well as in peripheral habitat added during the survey period. Although the Trumpeter Swan population summering in Alaska continues to grow, a comprehensive Alaska Trumpeter Swan Management Plan is needed to ensure that swans remain well distributed and a complete census every five years is recommended at least until the Alaska summering population stabilizes.

Key words.—Aerial survey, Alaska, *Cygnus buccinator*, population trend, summer population, Trumpeter Swan.

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Trumpeter Swans (*Cygnus buccinator*) summer in Alaska in the forested wetlands of the interior and along the coastal plain from Cook Inlet south to southeastern Alaska (Fig. 1). They historically wintered in estuaries and freshwater lakes and streams from Cook Inlet to the Columbia River in Washington and perhaps as far south as California (Bellrose 1976). Records of Trumpeter Swans in Alaska go back to the 1860s (Dall and Banister 1869; Banko 1960), but a breeding population was not described until 1954 (Monson 1956). Soon thereafter, additional nesting areas were identified on the Kenai Peninsula, the Gulkana Basin and the Minto Flats near Fairbanks. An attempt to count Trumpeter Swans from the air found 1,124 birds in 1959 (Hansen *et al.* 1971), but poor quality maps precluded a comprehensive census. Undertaken because of concern about their population status, the first census of Trumpeter Swans in Alaska was completed in 1968 when topographic maps became available for the entire Alaskan nesting habitat. The U.S. Fish and Wildlife Service has monitored the summering population in Alaska with a census every five years since 1975 in concert with the North American range-wide Trumpeter Swan survey (King 1976; King and Conant 1981; Conant *et al.* 1986, 1991, 1997).

METHODS

Most surveys were conducted during August (range 24 July–14 September) in each census year when young were flightless, large enough to be easily seen and prior to fall migration. Most surveys were conducted in either a specially modified, turbine-powered de Havilland Beaver, or Cessna 206s and 185s, or Piper Supercubs. Generally, a system of irregular, parallel tracks were flown at 150-180 m above ground over all known or suspected Trumpeter Swan summer habitat in a pattern that convinced the pilot that all swan habitat was searched (King 1973). Observations were recorded directly on 1:63,360 scale (2.54 cm = 1.61 km) topographic maps, or into on-board computers in 2000. Typically, pilot-biologists and one observer recorded all observations. In a few cases, non-biologist pilots and a second observer were used.

Alaska was separated into eleven Trumpeter Swan nesting units on the basis of significant geographical features such as large drainages and mountain ranges (Fig. 1). Censuses were begun in units 1–6 in 1968. Units 7-10 were added in 1975 and unit 11 in 1980. The area (km^2) searched in each unit (1–11) has changed through time: (1) 5,084–5,146; (2) 127–150; (3) 12,524–13,789; (4) 4,019–4,095; (5) 12,947–14,794; (6) 12,027–25,284; (7) 7,164–12,631; (8) 10,380–16,483; (9) 840–25,087; (10) 93–505; (11) 2,269–5,900; and all units combined 46,729-123,857. Survey units were added and surveyed areas within units were expanded if swans were known or suspected to have moved into this adjacent habitat. While a relatively small number of swans could have been present outside the census area in early years, biologists routinely flew over adjacent areas with suitable habitat without seeing swans. Thus, the results represent a census of the population even though the amount of habitat surveyed has increased.

A sigmoid curve was fit to the annual data within each nesting unit and for the eleven units combined with SigmaPlot by SPSS, Inc., and the regression coefficients and significance levels given below are based on these sigmoid curves.

RESULTS AND DISCUSSION

The number of adult Trumpeter Swans increased substantially during 1968-2000 ($r_5 = 0.99$, $P < 0.0001$; all units combined, Table 1, Figs. 2 and 3). The number of adults counted increased from 1,924 in 1968 to 13,934 in

Table 1. Number of adult and young Trumpeter Swans counted during late summer censuses in Alaska.

Year	Adults in pairs	Adults as singles	Adults in flocks	Cygnets	Total swans	Average brood size	Percentage cygnets
1968	1,320	108	496	923	2,847	3.6	32
1975	2,102	151	740	1,177	4,170	3.1	28
1980	3,324	169	1,766	2,437	7,696	3.6	32
1985	5,120	449	2,204	1,686	9,459	2.9	18
1990	7,056	647	2,039	3,595	13,337	3.2	27
1995	7,946	859	3,184	3,834	15,823	3.1	24
2000	9,986	899	3,049	3,221	17,155	2.8	19
Mean						3.2	26

2000, a 624% increase. The population trend varied among the eleven nesting units (Fig. 3). The population increased in the Gulkana, Cook Inlet, Lower Tanana, Kuskokwim, Koyukuk, Yukon Flats, Southeast Mainland, and Upper Tanana units ($r_5 = 0.96$ to 0.99, all $P < 0.01$), but not in the Gulf Coast ($r_5 = 0.74$, n.s.), Copper Canyon ($r_5 = 0.0$, n.s.), or Kenai units ($r_5 = 0.87$, $P = 0.06$). Among all units, swan numbers have increased in both the core habitat covered in every census and in the peripheral habitat that has been added to the census in more recent years (Fig. 4).

The census is an exhaustive attempt to find all swans irrespective of survey crew composition or aircraft type. Although swans are easily seen from the air, several factors including poor light, pilot and observer fatigue, poor

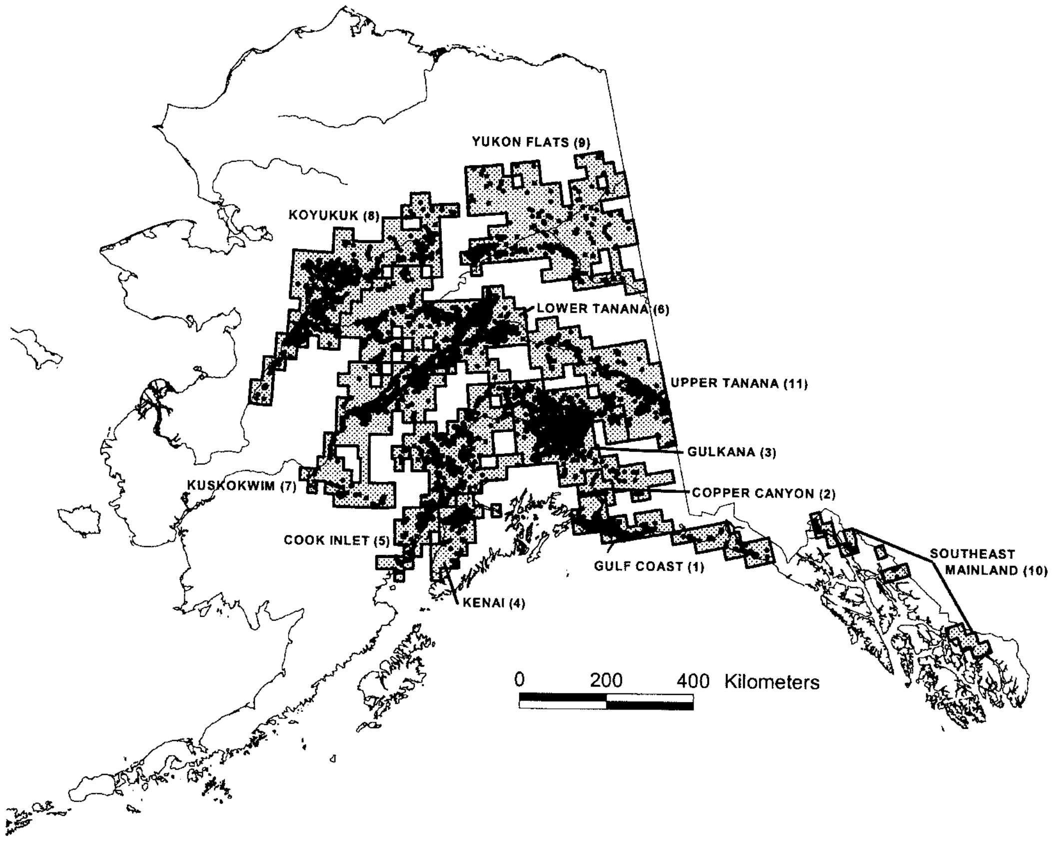

Figure 1. Area covered during Trumpeter Swan breeding ground censuses in Alaska in 2000. Each of the 6,422 dots represents a swan observation.

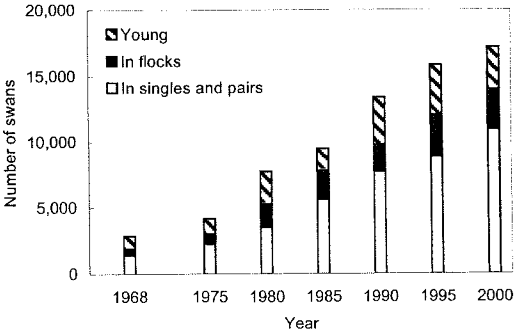

Figure 2. Number of Trumpeter Swans recorded in Alaska during state-wide, late summer censuses, 1968-2000.

weather conditions, and heavy cloud cover can cause swans to be missed. Onboard computers, first used in 2000, increased time available for observations and reduced observer fatigue. Poorer flying weather in 2000 may have reduced the number of swans observed.

Detection rates may vary with aircraft type, and increased flocking behavior throughout the survey period could affect results (Spindler *et al.* 2000). Spindler *et al.* (2000) speculated that if swans were forming flocks during the survey period, some counted early in the period could be counted again in a staging area. Likewise, swans could be missed due to such movements. To minimize differences among years, censuses were conducted on similar dates and in a similar sequence each year. Many different aircraft and crews were used in the first effort in 1968 and in the last four in 1985, 1990, 1995 and 2000. One crew and aircraft was used for essentially the whole census in 1975 and 1980. Repetitive fixed-wing surveys, helicopter surveys or ground surveys could help evaluate the number of swans missed on a single fixed-wing aerial survey. In spite of these concerns, we believe it is unlikely that the population growth rate of 624% is due to improved equipment or coverage.

The summering population of Trumpeter Swans in Alaska continues to increase (all units combined, Fig. 3), and although the increase can not be sustained indefinitely, it is not clear when or where the population will stabilize. The habitat appears to be saturated with swans in some areas (Gulf Coast). The density of swan use in some of the better-looking habitat is still increasing (Lower Tanana) while peripheral, previously empty habitat in the higher latitudes and altitudes is still being pioneered, noticeably on the Yukon Flats and the Upper Tanana areas. Human use of habitat is thought to be limiting swan use in the Cook Inlet area (Timm and Wojeck 1978).

The range and habitats of Trumpeter Swans and Tundra Swans (*C. columbianus columbianus*) overlap in the census area and species are not differentiated from the air. In Alaska, Trumpeter Swans mostly summer in the south coastal and interior boreal forest and taiga habitat, while Tundra Swans summer mainly on the western and northern coastal tundra. The line separating the two ranges is not distinct. There is evidence that Tundra Swans are present in some Trumpeter Swan census areas, but sampled areas tended to be small and were non-randomly selected during sporadic ground surveys in 1985–1987 (Loranger and Lons 1988) or 1986–1998 (R. J. King, pers. comm.) or during ground and helicopter surveys in 1989 (Wilk 1993). Tundra Swan numbers appeared to be proportionally higher in the northwestern fringe of the Koyukuk unit than elsewhere and comprised 89% of 70 swans (Loranger and Lons 1988) and 42% of 60 swans (Wilk 1993). Tundra Swans comprised 19% of 116 swans (Loranger and Lons 1988)and <1% of 600+ swans (R. J. King, pers. comm.) in the Lower Tanana unit and none of 200+ swans in the Gulkana unit (R. J. King, pers. comm.). A few Trumpeter Swans can probably be found in pockets of habitat within the traditional Tundra Swan range. It is possible that Trumpeter Swans have displaced Tundra Swans in some places as the numbers of Trumpeter Swans have increased (Loranger and Lons 1988). The Western Population of Tundra Swans, which breeds in western Alaska and winters along the west coast of the continental USA (Bellrose 1976), has increased 168% since 1964 based on spring breeding ground surveys (Conant and Groves 2001). Thus, the degree and location of overlap between the species is not surprising or static. Extensive ground surveys, distributed randomly or systematically throughout the Trumpeter Swan census units, are needed to clarify the proportion of Tundra Swans within each.

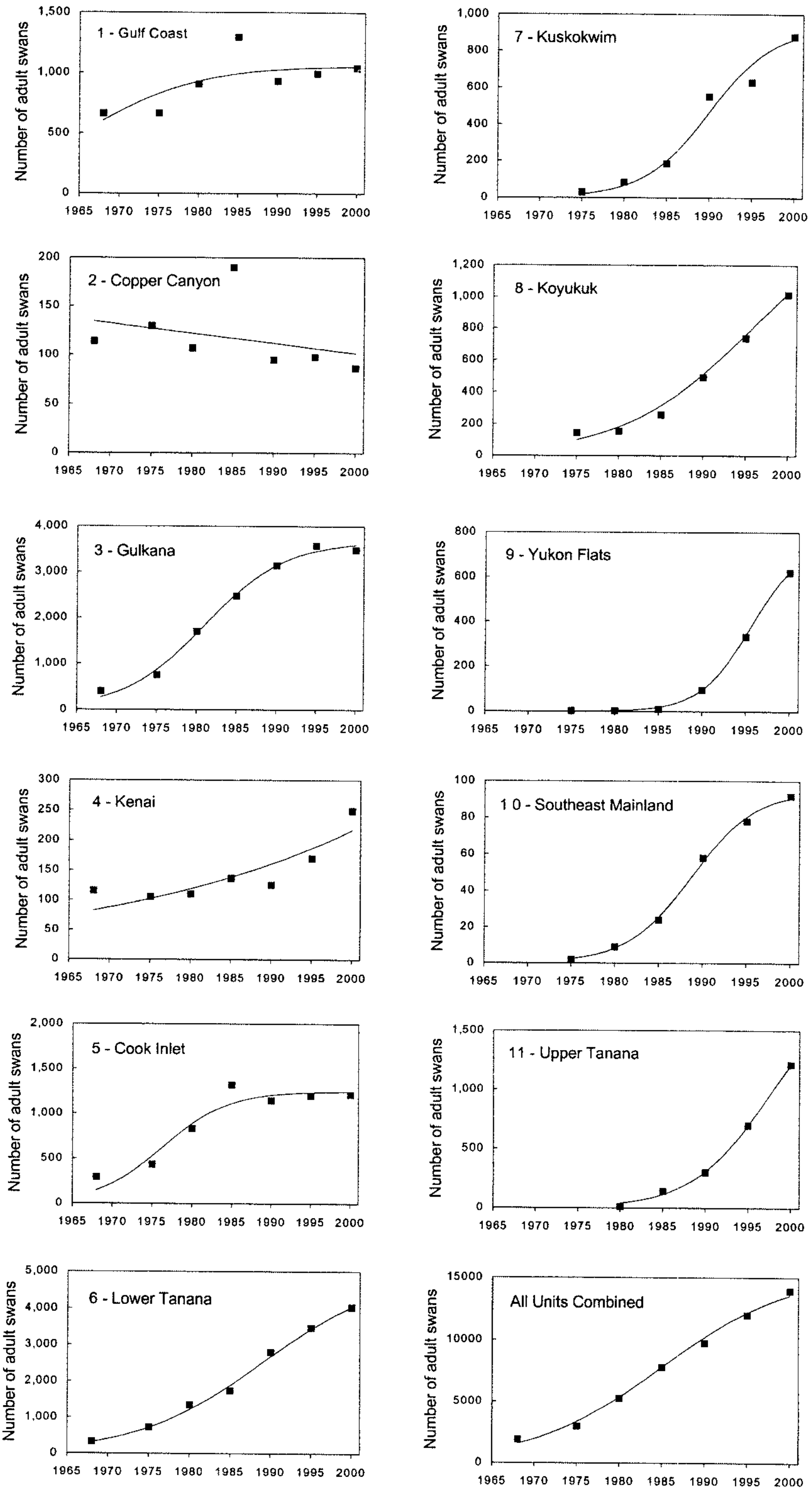

Figure 3. Trends in numbers of adult Trumpeter Swans recorded in Alaska during state-wide, late summer censuses for each of eleven survey units and all units combined. When a sigmoid curve was fit to the annual data, $r_5 = 0.96$ to 0.99 (all $P < 0.01$) for individual units, except unit 1 ($r_5 = 0.74$, n.s.), unit 2 ($r_5 = 0.0$, n.s.) and unit 4 ($r_5 = 0.87$, $P = 0.06$). For all units combined, $r_5 = 0.99$, $P < 0.0001$.

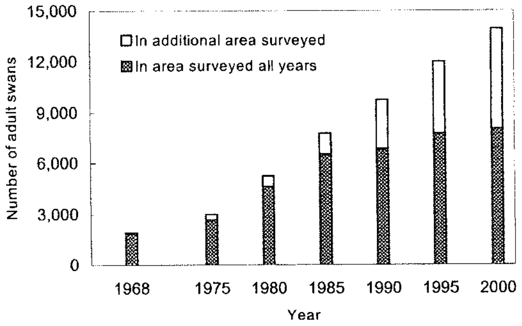

Figure 4. Increase in the numbers of adult Trumpeter Swans recorded in Alaska during state-wide, late summer censuses in areas surveyed each year, which typically have high densities of swans, and areas added since 1968, which are typically peripheral habitats.

In spite of these concerns, it is practical to monitor Trumpeter Swans summering in Alaska with this census method. The results are a detailed documentation of the pattern of occupation (or perhaps reoccupation) of Trumpeter Swan summer habitat. Factors that will limit the population size are not readily apparent. On the wintering grounds, a rapidly increasing human population is modifying the natural habitat at an alarming rate (King 1984). Swans have adapted to agricultural habitat on the wintering grounds but the future of this habitat is unclear and its use by swans causes conflicts with humans. Censuses at five year intervals, at least until the Alaska summering population stabilizes, seem warranted, and adoption of a comprehensive Alaska Trumpeter Swan management plan is recommended to ensure that swans remain well-distributed.

ACKNOWLEDGMENTS

We thank the many U.S. Fish and Wildlife Service pilots and observers, the U.S. Forest Service, the U.S. Geological Survey-Biological Research Division, the U.S. Army and Alaska Biological Research, Inc. observers and the commercial pilots who flew hundreds of hours gathering detailed swan observations. Surveys would not have been possible without the dedicated support of many aircraft maintenance personnel. We especially thank the administrators of the Alaska Region of the U.S. Fish and Wildlife Service for their enthusiastic support.

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Trumpeter Swan Numbers and Distribution in Western Canada, 1970–2000

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Abstract.—During the period 1970–2000, substantial efforts were made to document the distribution and number of Trumpeter Swans (*Cygnus buccinator*) in western Canada. Breeding surveys have expanded from covering less than 20,000 km^2 in the Grande Prairie region of Alberta to cover 780,000 km^2, perhaps one-third of northwestern Canada. Aerial surveys involving total or partial counts have been used in most areas. Since 1995, sample-based surveys have been used in Yukon Territory and extreme northern British Columbia. Between 1970 and 2000, breeding surveys have documented a dramatic increase in both breeding distribution and numbers in western Canada (100 to more than 3,700). Winter surveys in British Columbia have corroborated an increase in numbers on the southern coast (from 1,000 to at least 7,100) and in the southern interior (from 0 to 504), and also documented changes in the wintering distribution. Most, if not all, the increase in wintering numbers on the southern coast has been in agricultural areas on Vancouver Island and in the delta and lower valley of the Fraser River.

Key words.—Alberta, British Columbia, *Cygnus buccinator*, Northwest Territories, survey techniques, Trumpeter Swan, Yukon Territory.

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The Trumpeter Swan (*Cygnus buccinator*) continues to enjoy a remarkable comeback from the brink of extinction in the early part of the 20th century. Most populations in North America have been growing steadily and expanding their ranges for at least the past 30 years (Mitchell 1994) due to natural expansions and active restoration programs. Currently, western Canada has breeding Trumpeter Swans from the Pacific Coast Population in the Yukon Territory and British Columbia, from the Interior Canada Subpopulation of the Rocky Mountain Population in Yukon Territory, British Columbia, Northwest Territories, and Alberta, and from the Interior Population in Saskatchewan and possibly Manitoba (Fig. 1). The exact dividing line between the Pacific Coast Population and Rocky Mountain Population in the Yukon Territory is not known; its location in Fig. 1 is based on the observed patterns of eastward expansion of breeding swans from the extreme western part of the Territory and westward expansion from the extreme southeastern portion during the past 15 years. Wintering Trumpeter Swans from the Pacific Coast Population are found in large numbers on and near the coast of British Columbia, while smaller numbers, likely also from

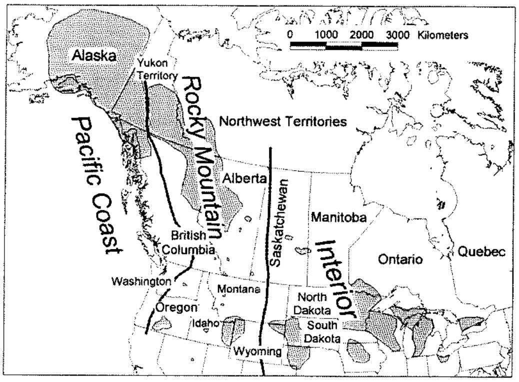

Figure 1. Current (2000) breeding range of the Trumpeter Swan shown as shaded areas. Bold lines delineate the three recognized populations: Pacific Coast, Rocky Mountain, and Interior.

the Pacific Coast Population, are found in the central and southern interior of British Columbia (Howie 1994; Corbould 2001). Trumpeter Swan numbers in parts of western Canada have been discussed previously (McKelvey *et al.* 1983; McKelvey *et al.* 1988). This paper presents results from surveys for Trumpeter Swans throughout western Canada from 1970 to 2000. Results are presented from breeding, winter, and migration surveys in western Canada, including Yukon Territory, Northwest Territories, British Columbia, Alberta, Saskatchewan, and Manitoba.

METHODS

Breeding Surveys

Survey areas are indicated in Fig. 2 and surveys are described in Table 1. The earliest dedicated breeding surveys, in the Grande Prairie area of Alberta, have been conducted nearly every year since 1953 (Turner 1981; MacKay 1988; Olson 2001). The Cypress Hills area of southwestern Saskatchewan has been surveyed since 1971 (Killaby 1991); all other areas have been surveyed only since 1980 or later. The most widespread and coordinated breeding survey is the North American Trumpeter Swan Survey, which has evolved into a regular effort every five years across the entire breeding range (Anonymous 1986; Anonymous 1994; Caithamer 1996, 2001). Parts of western Canada have been included in this survey since its inception in 1985 (Olson 2001).

Breeding surveys have been conducted from June to mid-September. June surveys coincide with incubation, while later surveys coincide with brood-rearing of flightless young. The North American Trumpeter Swan Survey is flown in late summer or early autumn (August-September) and much of western Canada has been regularly surveyed only in that season. Most surveys use small fixed-wing aircraft or helicopters flown at altitudes up to 300 m above the ground. When swans are seen, a lower pass is made to determine the number of adults, cygnets, nests, and eggs. Locations are recorded on topographic maps of 1:250,000 or 1:50,000 scale. During the 2000 surveys, the Alberta, northern British Columbia and Yukon surveys used moving map software and global positioning systems to record automatically aircraft flight tracks and the coordinates of observations.

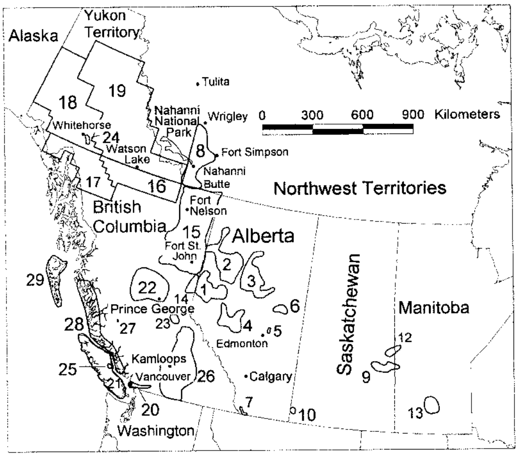

Figure 2. Areas surveyed for breeding, wintering, and migrating Trumpeter Swans in western Canada, 1970–2000. Numbered polygons correspond to areas in Table 1.

Three types of survey design have been used. Total counts are surveys that attempt to count all swans within specified polygons, and assume no swans are present outside these polygons. Partial counts are surveys in which selected wetlands are searched within delineated survey areas, with some attempt to sample the same wetlands each year. In partial counts, there is no attempt to account for birds present within the survey areas on wetlands that are not searched. Many surveys began with this method when only a few swans were present, but evolved gradually into total counts on all suitable wetlands within each delineated area. A more primitive variation of the partial count lacks delineated survey areas. Instead the aircraft is flown along pre-determined tracks, which are usually arranged to cover the most promising areas, especially those known to have swans in the past.

The third type, sampling survey, was first implemented in Alaska in 1986 for Trumpeter Swans (Conant *et al.* 1991). It uses a stratified random sampling procedure with optimal allocation (Cochran 1977) to attempt to minimize variance for a fixed "cost" (i.e., aircraft flight time). In Canada, this type of design was implemented in 1995 (Hawkings 2000) and continued in 2000 in the Yukon and northern British Columbia surveys (Fig. 2 areas 16–19). The protocol involves total counts within sample units chosen at random within different density strata. Sample units are assigned to density strata according to the number of swans likely to be present in each unit, based on previous knowledge of the area. Individual 1:50,000 maps are used as sample units in Canada. The total population and variance is estimated within each density stratum and the totals are added to obtain an overall estimate for the survey area (Cochran 1977). Post-stratification estimation procedures are used to estimate swan numbers in different geographic units (Fig. 2 areas 16–19) that separate populations (Rocky Mountain vs. Pacific Coast) and provinces (Yukon vs. British Columbia). This approach has often been used in large, remote areas in which swan breeding locations are poorly known.

Winter Surveys

In western Canada, the Pacific Coast Population winters mostly along the coast of British Columbia, and also in parts of the interior with suitable open water (McKelvey and Burton 1983). Banded swans from the Rocky Mountain Population also have been sighted in the southern interior, suggesting it may be a shared wintering area (King 1994; Howie 1997; Shea and Drewien 1999). Figure 2 shows the areas covered by regular winter surveys in western Canada. Numbers in parentheses in this section and others refer to numbered polygons in Fig. 2.

On the coast of Vancouver Island (21), aerial surveys have been conducted several times in the 1970s, again in 1988, and every three years since then (McKelvey *et al.*

Table 1. Parameters of Trumpeter Swan surveys in western Canada, 1970-2000. Winter surveys are identified by the autumn calendar year of each winter, i.e., a survey in January 1999 would be identified with the 1998 winter season. Only the most recent estimate given for winter surveys.

Season, Jurisdiction	Subregion		Popu-lation^{a}	Survey design^{b}	Survey method^{c}	Range of survey years	Years surveyed	Estimate of total swans				References^{d}
	No. in Fig. 2	Name						1985	1990	1995	2000	
Breeding Surveys												
Manitoba	9	Porcupine Hills	IP	PC	FW	2000	1				0	1
	12	The Pas	IP	PC	FW	2000	1				0	1
	13	Lake Manitoba—Shoal Lakes	IP	TC	FW	2000	1				0	1
Saskatchewan	9	Porcupine Hills	IP	PC	FW, H	1990–2000	7		2	26	49	1,2
	10	Cypress Hills	IP	TC	FW	1971–2000	26?	4	3	1	0	1,2,3
	12	Pasquia Hills	IP	TC	FW	2000	1				0	1
Alberta	1	Grande Prairie, Valleyview	RMP	PC, TC	FW, H	1953–2000	41+	285	321	533	608	1,4,5,6,7,32
	2	Peace River, High Level^{e}	RMP	PC	FW	1985–2000	6	16	73	199	224	1,5,6
	3	Utikima Lake—Peerless Lake	RMP	TC	FW	1990–2000	2		5		72	1
	4	Edson—Whitecourt	RMP	PC	FW	1983–2000	6	23	26	28	32	1,5,6
	5	Elk Island National Park	RMP	TC	FW, G	1987–2000	14		4	11	13	1,5,7
	6	Lac La Biche	RMP	PC	FW	1985–2000	5	0	14	2	9	1,7,8
	7	Southwest Alberta	RMP	PC	H	1985–2000	5+	6	21	21	37	1,5,6
Northwest Territories	8	Fort Liard—Nahanni—Tetcela	RMP	PC, TC	FW, H	1984–2000	7	75	182	220	294	1,2,5,9,10,11
British Columbia	14	Western Alberta Upland	RMP	PC	FW	1985–2000	6	36	67	51	101	1,3,5,6,12
	15	Fort St. John—Fort Nelson	RMP	PC	FW	1981–2000	4	66	197	259	363	13,14,15,6
	16	Taiga Plains	RMP	PC, SRS^{f}	FW	1985–2000	4	11	24	122^{g} (38)	260 (52)	13,16,17,18
	17	Coast Mountains	PCP	PC, SRS^{f}	FW	1985–2000	4	9	24	145 (68)	91 (7)	13,14,17,18,19
Yukon Territory	18	Southwest Yukon	PCP	PC, SRS^{f}	FW	1985–2000	4	33	89	347 (114)	305 (17)	13,14,17,18,20
	19	Eastern and Central Yukon	RMP	PC, SRS^{f}	FW	1980–2000	6	108	171	646 (185)	1,266 (214)	3,13,14,17,18,20
Winter Surveys								Most recent estimate of total swans				
British Columbia	21	Entire Vancouver Island										
		Aerial Surveys	PCP	TC	FW	1971–2000	9	4,700				15,21,22
		Christmas Bird Counts^{h}	PCP	TC	G	1980–2000	31	3,489				25
	25	Comox Valley	PCP	TC	G	1983–2000	16	1,689				23,24,34
	20	Fraser River Delta and lower valley										
		Aerial surveys	PCP	TC	FW, G	1987–2000	14	1,028				26,22
		Christmas Bird Counts^{i}	PCP	TC	G	1970–2000	31	2,088				25

Table 1. (Continued) Parameters of Trumpeter Swan surveys in western Canada, 1970-2000. Winter surveys are identified by the autumn calendar year of each winter, i.e., a survey in January 1999 would be identified with the 1998 winter season. Only the most recent estimate given for winter surveys.

Season, Jurisdiction	Subregion		Population[a]	Survey design[b]	Survey method[c]	Range of survey years	Years surveyed	Most recent estimate of total swans	References[d]
	No. in Fig. 2	Name							
		Central Interior							
	22	Fraser Basin and Fraser Plateau							
		Aerial surveys	PCP	PC	H	1990–2000	3	1,281	28,33
		Christmas Bird Counts[j]	PCP	TC	G	1970–2000	31	142	25
	23	Bowron Lake Park	PCP	TC	G	2000	1	12	25
	26	Southern Interior (Thompson—Okanagan)							
		Ground counts	PCP?	TC	G	1974–2000	27	258	29,33
		Christmas Bird Counts[k]	PCP?	TC	G	1972–2000	29	83	25
	27	Lonesome Lake	PCP	TC	G	1931–1975	45	360	30
	28	Mainland Inlets	PCP	TC?	FW	1975–1977	2	575	30
	29	Queen Charlotte Islands							
		Aerial counts	PCP	TC?	FW	1974–1976	2	117[l]	30
		Christmas Bird Counts[m]	PCP	TC	G	1982–2000	19	40	25
Migration Surveys									
Yukon Territory	24	Marsh Lake	PCP	TC	G	1978–2000	21	1,577[n]	31,17

[a] IP = Interior Population, RMP = Rocky Mountain Population, PCP = Pacific Coast Population.

[b] PC = Partial Count, TC = Total Count, SRS = Stratified Random Sample.

[c] FW = Fixed-wing aerial survey, H = Helicopter aerial survey, G = Ground count.

[d] References: (1) Norton and Beyersbergen 2000; (2) Beaulieu 1999; (3) Olson 2001; (4) Turner 1981; (5) Beyersbergen and Shandruk 1994; (6) Shandruk 1986; (7) Beyersbergen and Kaye 2000; (8) Shandruk 1991; (9) McCormick 1986; (10) Shandruk and McCormick 1991; (11) Caithamer 1996; (12) Beyersbergen, G., unpubl. data; (13) McKelvey 1986; (14) McKelvey and Hawkings 1990; (15) Breault, A., unpubl. Data; (16) McKelvey, R., unpubl. data; (17) Hawkings, J., unpubl. data; (18) Hawkings 2000; (19) Conant *et al.* 2002; (20) McKelvey *et al.* 1983; (21) McKelvey *et al.* 1991; (22) Breault, A. and S. Boyd, unpubl. data; (23) Innes 1994; (24) Buffet 2001; (25) Anon. 2001; (26) Boyd 1994; (27) Boyd, S., unpubl. data; (28) Corbould 2001; (29) Howie 1994; (30) McKelvey 1981; (31) Hawkings and Hughes 1994; (32) MacKay 1988; (33) Howie 2000; (34) Morrisson 1988.

[e] Includes Otter Lakes, Russell Lake and Chinchaga River area.

[f] Prior to 1995 all surveys were partial counts. 1995 and 2000 surveys were based on stratified random sample designs.

[g] Estimate (Standard Error). Figures from 1995 differ slightly from those reported in Hawkings (2000) due to modifications in the estimation procedure.

[h] Counts from Comox, Nanaimo, Deep Bay (1987–2000), Campbell River, Victoria, Sooke, Bamfield, Port Alberni (1993–2000), Parksville—Quallicum Beach, Duncan (no counts 1996–1999).

[i] Counts from Vancouver, Pitt Meadows, White Rock, Ladner, Abbottsford—Mission (2000 only), Chilliwack.

[j] Counts from Terrace, Fort St. James (1987–2000), Burns Lake—Francois Lake (1990–1998, 2000), Kitimat (1978–2000).

[k] Counts from Kamloops, Vernon, Vaseaux Lake, Oliver—Osoyoos, Shuswap Lake, Salmon Arm.

[l] 1974/1975 count. The 1976/1977 count (47) experienced bad weather that probably influenced results.

[m] Counts from Massett (1982–2000), Port Clements (1984–2000), Skidegate Inlet (1989–2000).

[n] Peak count from spring 2000 (15 April).

1991). A fixed-wing aircraft was flown along the entire coastline and any large, unfrozen freshwater areas. Flocks larger than 30 birds were photographed to provide more accurate estimates of numbers and ages (McKelvey *et al.* 1991; Boyd 1994). Weekly ground counts of swans in the Comox Valley (25) on Vancouver Island have been conducted since autumn 1983 (McKelvey 1981; Morrisson 1988; Innes 1994; Buffet 2001). Annual aerial surveys in the intertidal, outer portion of the Fraser River Delta (20) have been conducted since 1987 (Boyd 1994; Breault 1998). Occasionally, usually in combination with the triennial mid-winter surveys around Vancouver Island, swans are counted further inland along the lower Fraser River valley from Ladner to Hope. Elsewhere on the British Columbia coast, there were winter aerial counts along parts of the mainland coast (28) and Queen Charlotte Islands (29) from 1974 to 1977 (McKelvey 1981).

In the central interior of British Columbia, specific wintering sites in the Fraser Basin and Fraser Plateau (22), including Stuart River, Francois Lake and Crooked River (McKelvey 1981; Howie 1994), have been surveyed during localized ground counts by naturalist groups since 1990 (Howie 2000), and by several aerial surveys of lakes and rivers likely to have open water. The first widespread, dedicated surveys in the Fraser Basin and Fraser Plateau were in 2000 and 2001, although a partial survey was done in March 1990 (Corbould 2001). Perhaps the best known interior wintering site is Lonesome Lake (27), where there was a feeding program from 1931 to 1971 and regular ground counts from 1931 to at least 1976.

In the southern interior of British Columbia, the major wintering sites in the Thompson Okanagan region (26) are along the South Thompson River and in parts of the Okanagan Valley, where winter ground counts by naturalist groups have been conducted since 1974 (Howie 1994, 2000).

Audubon Christmas Bird Count data (Anonymous 2001) have been gathered for many years in various British Columbia communities using standard protocols. Many of these counts (Table 1) cover habitats used regularly by Trumpeter Swans.

Migration Surveys

Migration counts of Trumpeter Swans and Tundra Swans (*Cygnus columbianus columbianus*) have been conducted at a spring migration area at Marsh Lake, Yukon (24) beginning in 1978, and every spring since 1986. Ground counts from one or two selected vantage points were gathered at one to four day intervals during April and the first two weeks of May. Beginning in 1994, counts were made daily from the first week of April to mid-May. Numbers of one-year old (gray-plumaged) Trumpeter Swans and estimates of species composition (Trumpeter or Tundra Swans) of white-plumaged swans were recorded.

Annual Growth Rates

Annual growth rates were calculated using an exponential growth model, $N = N_0 (1 + r)^t$, where N_0 is the initial population size, N is the final size, t is the number of years, and r × 100% is the annual growth rate. Because only the endpoints (N_0 and N) of the trend were used, and a constant growth rate was assumed during intervening years, the resulting growth rate is an approximation.

RESULTS

Breeding Surveys

For each area, survey results from 1985, 1990, 1995 and 2000 surveys are shown in Table 1. Trends in total Trumpeter Swan numbers for each Province or Territory for the Rocky Mountain Population and the Pacific Coast Population are shown in Figures 3a and 3b, respectively.

Manitoba. Areas 13, and parts of 9 and 12, were surveyed only during the 2000 range-wide survey, and no swans were found, although unconfirmed sightings were reported from surveyed areas (Norton and Beyersbergen 2000). More swans were counted on South Dakota wintering grounds than were accounted for on breeding grounds, indicating that additional breeding locations have yet to be located.

Saskatchewan. The number of swans in the Cypress Hills area (10), surveyed annually since 1971, has dwindled from three pairs with one cygnet in 1971, to one adult in 1992 through 1995 (Beaulieu 1999), to no birds in 2000 (Norton and Beyersbergen 2000). Trumpeter Swans were discovered in the Greenwater Park-Porcupine Forest areas (9) of eastern Saskatchewan in 1986 and were surveyed annually during 1991–1995 and again in 2000 (Beyersbergen and Shandruk 1994; Beaulieu 1999; Norton and Beyersbergen 2000). Part of the increase between 1995 and 2000 was attributed to increased survey coverage.

Alberta. Grande Prairie—Valleyview (1) has been surveyed beginning with ground counts in 1944 and the first aerial survey in 1953 (MacKay 1988). The aerial survey was standardized in 1956 and continued until 1975. Survey coverage and intensity have increased since then, but the area covered and number of lakes surveyed each year have been recorded. The number of individuals recorded has gradually increased from 100 in 1970, to 285 in 1985 (185% total, 7% annual increase), and to 608 in 2000 (113% total, 5% annual increase 1985–2000). Virtually all the increase since 1990 was due to increased breeding density, as shown by a comparison of 1990, 1995, and 2000 results when differ-

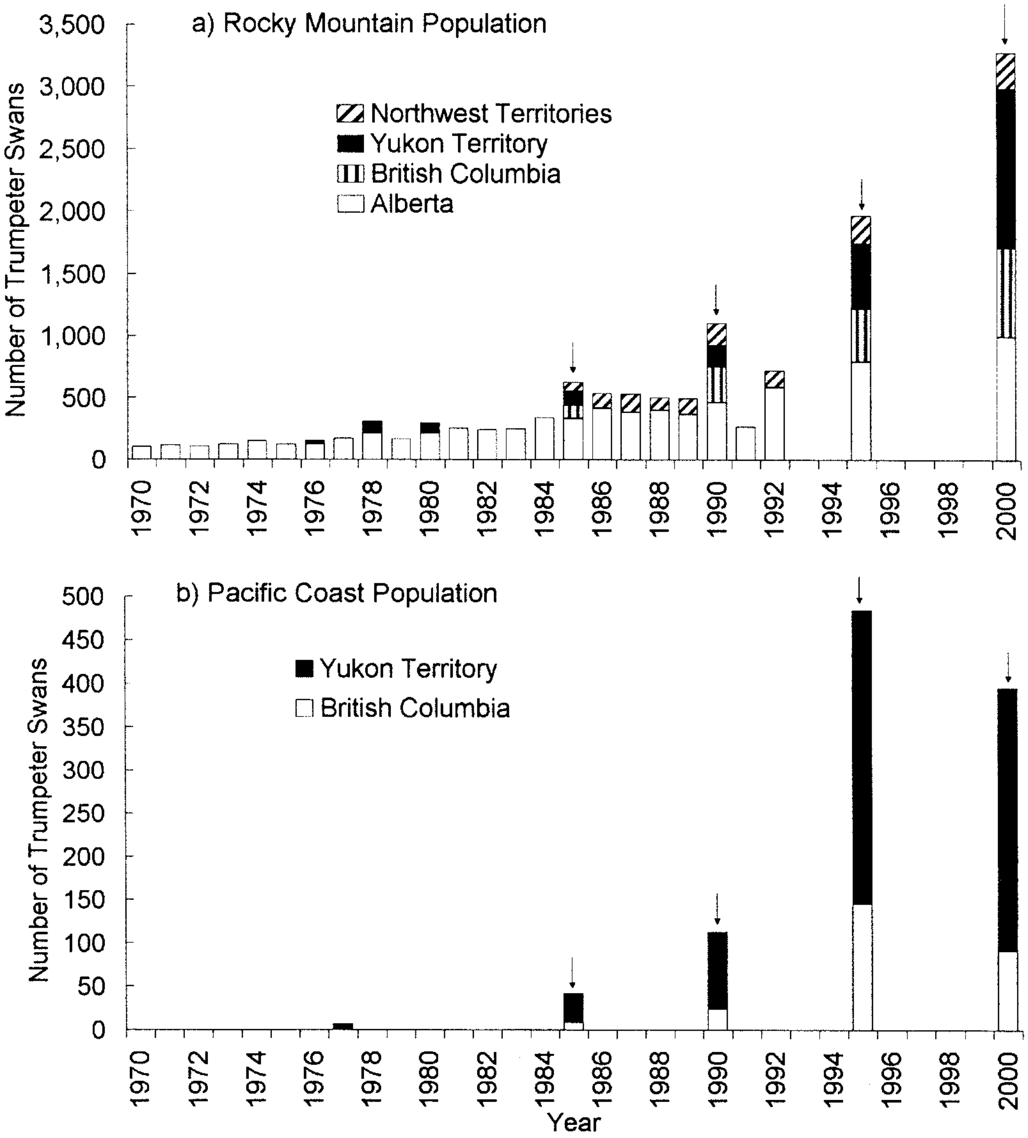

Figure 3. Results of breeding season surveys of (a) the Rocky Mountain Population and (b) the Pacific Coast Population of Trumpeter Swans in Alberta, British Columbia, Yukon Territory, and Northwest Territories, 1970–2000. Arrows indicate years with comprehensive, range-wide surveys in North America (1985, 1990, 1995, 2000).

ences in survey coverage were corrected (Norton and Beyersbergen 2000). This analysis yielded identical counts to those in Table 4, except for a slight change in 1990 (314 instead of 321). Additional results are presented in Turner (1981), Shandruk (1986), MacKay (1988), Holton (1988), Shandruk (1991), Beyersbergen and Shandruk (1994), and Beyersbergen and Kaye (2000).

Peace River—High Level (2) was first surveyed in 1985, when 16 swans were counted (Shandruk 1986). Since then the coverage has expanded as numbers increased to 199 in 1995 and 224 in 2000 (Beyersbergen and Shandruk 1994; Norton and Beyersbergen 2000). It is assumed that this represents an increase in swan numbers, but existing data cannot separate this likelihood from an increase in survey area. Additional confirmed reports of Trumpeter Swans outside this area in the far northwestern corner of Alberta (e.g., Bistcho Lake) suggest that additional breeding areas have yet to be discovered. Utikima Lake—Peerless Lake (3) was first surveyed in 2000 when 72 swans were observed. Few swans had been reported previously in this area, and it is unknown how long it has been occupied by Trumpeter Swans (Norton and Beyersbergen 2000). Edson—Whitecourt (4) survey coverage has expanded and intensified (a fourfold increase in effort from 1995 to 2000). Despite this, the number counted has remained about the same at about 30. The Elk Island National Park (5) flock began as a reintroduction program in 1987 and has been monitored annually. The first successful nests hatched in 1990, but the first successful fledging of cygnets was not until in 1998. By 2000, there was a total of 13 birds including two successful breeding pairs. Lac La Biche (6) was surveyed in 1985, but no swans were observed until 1990 when 14 were counted (Beyersbergen and Shandruk 1994). Although survey coverage was expanded in 2000, only nine swans were observed (Beyersbergen and Shandruk 1994; Norton and Beyersbergen 2000). Southwestern Alberta (7) was surveyed more than twice as intensively (i.e., more search effort in the same polygon) in 2000 than in 1990 or 1995, with a total of 37 swans counted (Norton and Beyersbergen 2000).

Northwest Territories. Fort Liard—Nahanni—Tetcela (8) was first surveyed in 1984 (McCormick 1986). Trumpeter Swans became established in the Northwest Territories in the late 1970s in what was to become the Nahanni National Park Reserve, and the first confirmed nesting was in 1977 (McKelvey *et al.* 1988). The 1984 survey covered areas of suitable habitat both within the Park Reserve and at several sites within 25 km. In 1985, the survey was broadened to include a large area bounded by the Mackenzie River to the east, Wrigley to the north, the Yukon border to the west and the British Columbia border to the south, but excluding much of the Park Reserve except for the extreme east and west ends. A survey in 1986, with similar coverage but increased effort in some wetland complexes, yielded more swans (120 compared to 75), an increase attributed to the more intensive survey effort. Surveys in 1987–1992 documented an increase to 182 swans. Anecdotal reports in the early 1990s suggested that Trumpeter Swans were established well north of Fort Simpson along the Mackenzie Valley. Surveys in 1995 and 2000, although differing in extent and intensity, recorded 220 and 294 swans, respectively. Correcting for differences in survey coverage yielded totals of 179 and 257 swans for 1995 and 2000, respectively (Norton and Beyersbergen 2000), a 43% (7.5% annual) increase. Sightings of swans on previously unoccupied wetlands within the survey area, as well as numerous sightings outside the surveyed areas, suggest that considerable numbers of swans were uncounted in the Northwest Territories in 2000. Reputable observers have reported isolated pairs and individuals as far north as Tulita in the Mackenzie Valley in the late 1990s. In addition, small groups were reported in 1999 from four locations much farther north in the lower Peel River drainage of northeastern Yukon, adjacent to the lower Mackenzie Valley (C. Eckert, Yukon Department of Renewable Resources, unpubl. data).

British Columbia. Western Alberta Upland (14) is adjacent to the Grande Prairie—Valleyview area in Alberta, and the two have generally been surveyed together. The coverage in British Columbia has varied, but has generally expanded as numbers have increased. The number of birds counted increased from 36 in 1985 to 101 in 2000 (180% total, 7% annual increase).

Fort Nelson—Fort St. John (15) was first surveyed in 1981 (Olson 2001). Survey effort in 1985 and 1990 (7.4 h and 10 h respectively) was considerably less than in 1995 and 2000 (25+ h in 2000). The greater effort occurred mostly south, east, and north of Fort Nelson. Swan numbers increased during 1990–1995 by 31% (6% annual), and during 1995–2000 by 40% (7% annual).

Taiga Plains (16) has not been well surveyed. The eastern portion is at the extremity of the survey flights currently based in Fort Nelson, Nahanni Butte, and Watson Lake. The western half appears to be virtually unoccupied by swans. The results of 1985 to 2000 surveys suggest annual growth rates of 15% to 30%.

Coast Mountains (17) were very poorly surveyed prior to 1995, primarily because there was little evidence of swans there. The northeastern part is still not occupied, though there have been increases in the areas closest to the coast, for example the lower Taku River near Juneau, Alaska. As in the Taiga Plains, numbers increased from nine to 24 to 145 birds in 1985, 1990 and 1995, respectively, suggesting substantial annual growth rates (>30%).

Yukon Territory. Southwest Yukon (18) was first surveyed in 1985, although breeding records go back to at least 1970. The increase in number of Trumpeter Swans seems to parallel that for the upper Tanana Valley in Alaska (Conant *et al.* 2002). Coverage was most intensive in 1995 and declined slightly in 2000 due to bad weather during the survey. With the exception of 1995–2000, the results suggest annual growth rates ranging from 9% (1985–2000) to 23% (1990–1995).

Eastern and Central Yukon (19) is the major breeding ground of the Rocky Mountain Population in Yukon Territory. Most survey effort prior to 1995 was south of 62°N, particularly in the southeast Yukon east of Watson Lake (McKelvey *et al.* 1983; McKelvey and Hawkings 1990; Hawkings 2000; Olson 2001). The results suggest an annual growth rate of 19% (1995–2000).

Areas 16–19 had a dramatic change in survey design beginning with the 1995 survey. The 1985 and 1990 surveys used a partial count design with no survey polygons delineated. In 1995 and 2000, a stratified random sample design was used (55 of 591 units in 1995, a 9.3% sample; 47 of 591 units in 2000, a 7.95% sample). This change in design was the primary cause of a substantial increase (366%, or 36% annual growth) in the estimates for these areas combined between 1990 (271) and 1995 (1,265). The increase from 1995 to 2000 (1,922) was more modest at 51.9% (8.7% annual growth). On 14 individual survey units that were counted in both 1995 and 2000, there was a 13.1% (2.5% annual) increase (169–191 swans) on ten units in the Rocky Mountain Population range, and a 25% (4.5% annual) increase (72–90 swans) on four units in the Pacific Coast Population range.

Overall, these breeding survey data (Table 1, Fig. 3) suggest that, in Canada, the Rocky Mountain Population increased from 626 in 1985 to 3,279 in 2000, an increase of 424% (12% annually), while the Pacific Coast Population increased from 42 in 1985 to 396 in 2000 (842% total, 16% annual growth). Trends within individual survey areas are difficult to assess because of changes in survey coverage. Norton and Beyersbergen (2000) compared 1995 and 2000 estimates in areas (Fig. 2 areas 1,2,5,7,8, and 9) where they could sufficiently standardize the area of survey coverage, notwithstanding some differences in search intensity. Their results differ little from those in Table 1 (their growth rates were slightly higher for area 8 and slightly lower for areas 2 and 9). Thus, the documented increase in these areas apparently is largely due to increased breeding density rather than increases in survey coverage.

Winter Surveys

Recent winter surveys (Table 1, Figs. 4 and 5) show that Vancouver Island (21) and the Fraser River Delta and lower valley (20) have the largest concentrations of wintering Trumpeter Swans. On Vancouver Island (Fig. 4a), combined Christmas Bird Count data suggest an 8% to 9% annual increase for the 5, 10, 15, and 20 years prior to 2000 (the apparent stabilization during 1992–1999 is due partly to lack of a count at one of the major count circles, Duncan, during 1996–1999). Aerial surveys (Fig. 4a) indicate an annual increase of 7% since 1977. On the Fraser River Delta and lower valley, aerial surveys indicate an increase from 377 in 1987 to 2,411 in 1998 (Fig. 4b), an increase of 539% (18.4% annually). Christmas Bird Counts (Fig. 4b) also show increasing numbers, but the trend since 1994 is less clear. In the southern interior of British Columbia, winter numbers have also increased (Fig. 5a). Ground counts in the Thompson-Okanagan region (26) show an increase of 784% (16% annually) from 57 in 1985 to 504 in 2000. Christmas Bird Counts show an increase over the same period from 18 to 83 (361% total, 11% annual). Further north, in the central interior of British Co-

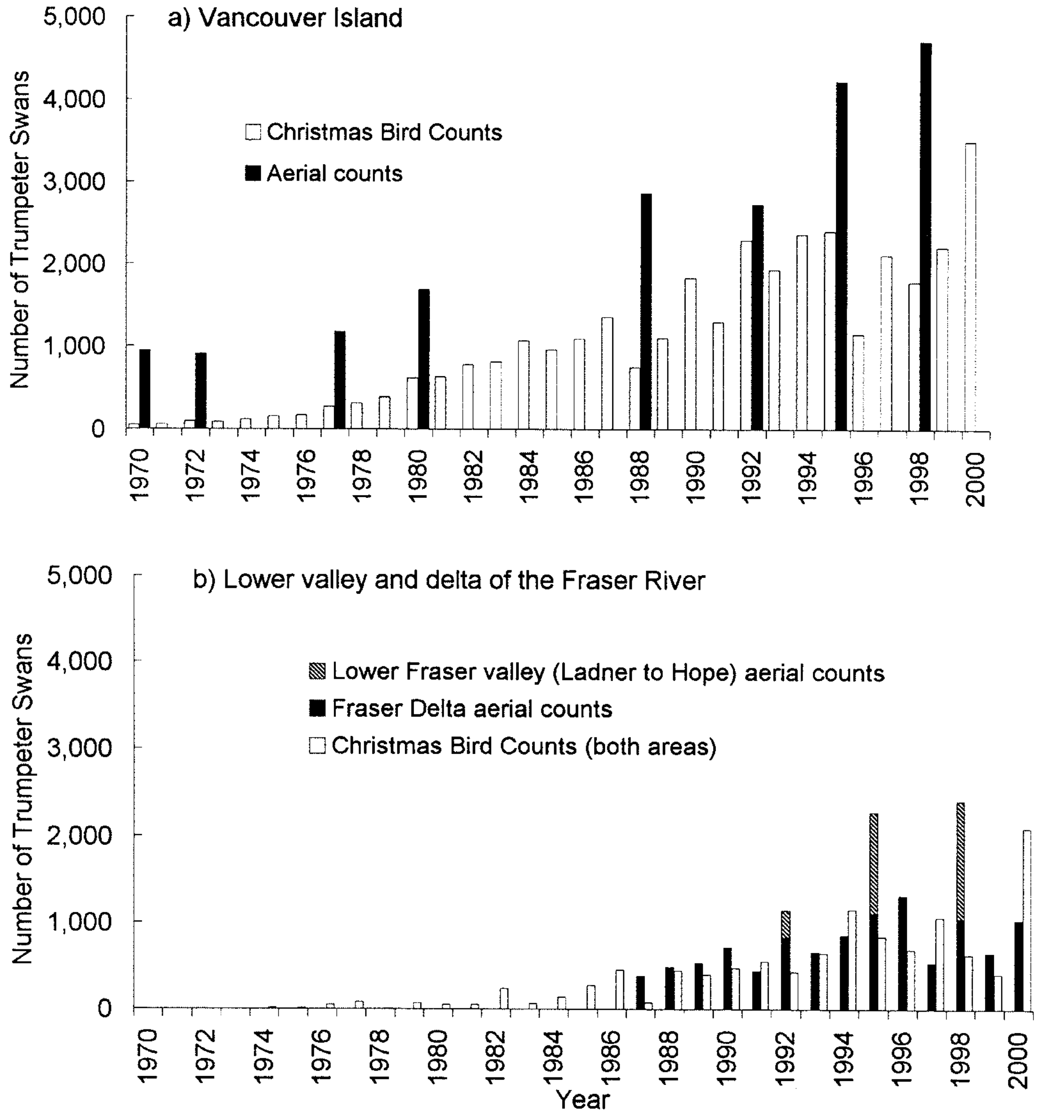

Figure 4. Trumpeter Swan winter counts during 1970-2000 from (a) Vancouver Island, and (b) the lower valley and delta of the Fraser River. Values for year refer to the calendar year of the autumn (e.g., 1970 refers to the winter of 1970–1971). See Table 1 for details of Christmas Bird Counts.

lumbia, aerial surveys in 1989 and 2000 in the Fraser Basin and Fraser Plateau (22) suggest an increase in numbers (Fig. 5b), however the 1989 survey was conducted in mid-March when some spring migrants may have been included. Christmas Bird Counts suggest an increase in the late 1980s, but the trend since the early 1990s is not clear. The most complete Christmas Bird Count data (Terrace and Kitimat) show an increase in the 1980s followed by fluctuations during the 1990s (Fig 5b). On the mainland coast (28), the only extensive count is 575 swans counted during the 1976 aerial survey. For the Queen Charlotte Islands (29), winter numbers appear stable or perhaps declining slightly based on Christmas Bird Counts since 1984, and the only good aerial survey, from 1974, suggests 120 individuals present.

Migration Surveys

At Marsh Lake, Yukon (24), Trumpeter swans arrived in late March (Fig. 6). Numbers

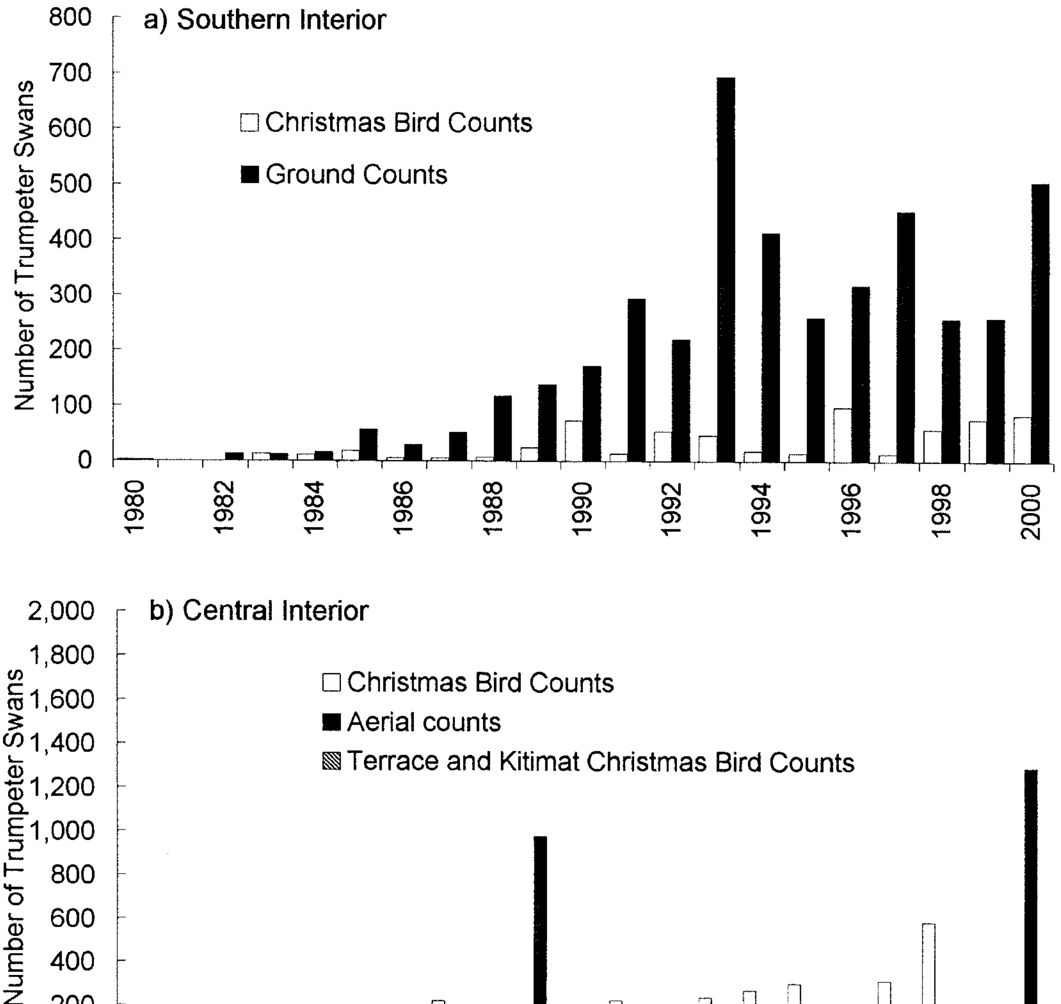

Figure 5. Results of Trumpeter Swan winter surveys in (a) the southern interior (Thompson Okanagan), and (b) the central interior (Fraser Basin and Fraser Plateau) of British Columbia. Values for year refer to the calendar year of the autumn (e.g., 1970 refers to the winter of 1970–1971). See Table 1 for details of Christmas Bird Counts.

increased and they were joined by Tundra Swans beginning approximately 15–22 April. Numbers of Trumpeter Swans (as indicated by immature plumaged birds) usually peaked during 10–20 April and most were gone by mid-May. More Trumpeter Swans were present in the first half of April during 1991–1995 than in 1985–1990, and more in 1985–1990 than in 1978–1983. There has been no obvious change in numbers recorded since 1995.

DISCUSSION

Breeding Surveys

Breeding survey data suggest that Canadian-breeding segments of both the Rocky Mountain Population (i.e., the Interior Canada Subpopulation) and the Pacific Coast Population have grown at substantial rates in most of the breeding range. In Alberta,

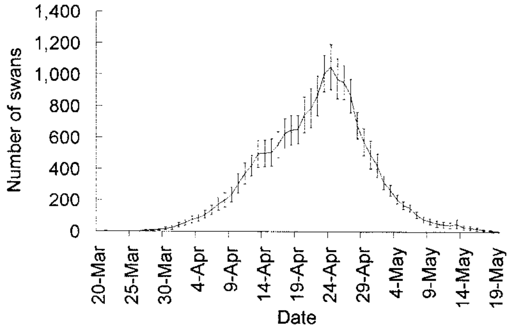

Figure 6. Mean (± SE) daily counts of Trumpeter Swans and Tundra Swans during spring migration at Marsh Lake, Yukon, 1978–2000.

Saskatchewan and Northwest Territories, standardized comparisons showed that most of the documented growth was due to increased breeding density within established breeding areas (Norton and Beyersbergen 2000), for example, Grande Prairie. Other survey and anecdotal data from Yukon and Northwest Territories indicate also that there was considerable growth due to expansion into previously unoccupied areas. This is similar to well-documented patterns of growth in Alaska since 1968 (Conant *et al.* 2002).

Another set of population estimates for the Interior Canada Subpopulation of the Rocky Mountain Population has been derived annually by subtracting the breeding (September) survey totals for the Tri-state Subpopulation from midwinter (February) survey totals of the entire known Rocky Mountain Population wintering area (Olson 2001). These estimates have increased from 1,019 birds during the winter of 1985–1986, to 3,494 during the winter of 2000–2001. The breeding survey data from Canada account for a much higher proportion of this midwinter estimate in 2000 (94%) than in 1985 (61%). The winter 2000–2001 estimate of 3,494 is remarkably close to the summer 2000 estimate of 3,279 for the Canadian-breeding segment of the Rocky Mountain Population.

With the exception of 1990–1995 when survey design changed in areas 16–19, none of the annual growth rates suggested for Canadian breeding areas are unreasonably high. Two regions of Alaska that are adjacent to the Yukon Territory (Upper Tanana River and Yukon Flats) have well-documented annual growth rates as high as 21% over a five-year period (Conant *et al.* 2002).

Breeding Survey Design: Strengths, Weaknesses, and Recommendations

Thirty years ago breeding Trumpeter Swans were relatively uncommon in western Canada, and surveys were sufficient to delineate the breeding range, provide a minimum estimate of numbers, and demonstrate growth in numbers. However, Trumpeter Swans are more numerous and more dispersed now, making surveys more difficult. Conant *et al.* (2002) recognized this problem and suggested a continental breeding survey based on the stratified sampling protocol followed in Alaska.

The stratified sampling protocol, used in the western Canada areas 16–19 beginning in 1995, sampled areas with an intensity proportional to their expected swan density. The initial estimates from 1995 were imprecise because of ineffective stratification, specifically because high numbers of swans unexpectedly appeared in low-density strata. Precision improved as more knowledge of swan distribution resulted in better stratification for the 2000 survey; further improvements can be expected in future surveys. The 2000 survey used four density strata: Stratum 0 where swans were considered highly unlikely due to the lack of suitable habitat, and in which no surveys were conducted; Stratum 1 where no swans were expected based on past history, but some suitable habitat was present; Stratum 2 where 1–10 swans per 700 km^2 were expected (700 km^2 is the area encompassed by a 1:50,000 map used as a sampling unit); and Stratum 3 where 11+ swans per 700 km^2 were expected. The advantage of a stratified random design, in which areas are sampled in proportion to their expected swan density, over those of partial or total counts, is the ability to estimate total numbers and to estimate the uncertainty (i.e., the standard error) of the estimate.

In areas where a stratified sampling design is not used, it would be beneficial to undertake complete surveys of all suitable habitat within specified survey polygons. This would solve the existing problem of interpreting increases in swan numbers where search intensity (proportion of suitable habitat searched) has also increased.

Winter Surveys

The results of winter surveys show that swan numbers are increasing steadily on Vancouver Island, the Fraser River Delta and lower valley, and in the southern interior of British Columbia. On Vancouver Island, most of the increase since 1970 has occurred in agricultural areas in the southwest quadrant (Campbell *et al.* 1990; McKelvey *et al.* 1991). Likewise, there have been dramatic increases in the agricultural areas of the Fraser River Delta and lower valley. Numbers in non-agricultural areas of the coast seem to be relatively stable. In the southern and central interior of British Columbia, where wintering swans are limited to aquatic feeding (i.e., non-agricultural settings), there were increases in the 1980s, followed by fluctuations in the 1990s. Howie (2000) suggested that water levels and the extent of open water, which ultimately influence the availability of aquatic vegetation, appear to be affecting swan numbers in the Thompson-Okanagan region.

Established winter surveys have attempted to monitor local wintering numbers on parts of the Pacific Coast and in the British Columbia interior. On Vancouver Island and the Fraser River Delta the surveys also provide information with which to manage conflicts between swans and agriculture. Frequent ground counts (for example in the Comox Valley) provide inexpensive but vital data on productivity and the phenology of arrival and departure, and allow a better assessment of winter numbers than do one-time counts. Christmas Bird Counts are useful to indicate general long-term trends, but many were initiated as late as the 1980s. Missing data, especially for sites with potentially high numbers of swans and varying winter (open water) conditions, make the data difficult to interpret compared to annual dedicated ground counts such as those in the Thompson-Okanagan region. Except for Vancouver Island and the Fraser River Delta and lower valley, aerial surveys have been too infrequent to be useful indicators of trends.

Winter surveys need to be able to adapt to changes in distribution, such as the expansion of wintering swans inland from the Fraser River Delta. In addition to continuing surveys in agricultural areas, more winter surveys are required in natural wintering habitats (mainland inlets, Queen Charlotte Islands, central interior) to determine if increasing numbers of swans are using these areas. If not, it may be that these areas have reached their carrying capacity, and further increases in the Pacific Coast Population will have to be accommodated by expansion of the winter range (likely to the south) and further increases in numbers in agricultural areas where conflicts with farming interests already occur (Wareham and Fowler 1994).

Migration Surveys

Migration surveys provide information on the timing of migration, migration routes, and the importance of stopover habitats. Age ratio and brood size data gathered in the spring complement similar measures from the previous summer and winter (Hawkings and Hughes 1994). To be most useful, counts at migration areas should be complemented by data on the numbers of birds arriving at and departing from staging areas. This would allow estimation of how many individuals use the area and how long they stay (i.e., turnover rates). As both the Pacific Coast and Rocky Mountain Populations increase, the ability of existing migration habitats to support more swans is a question that should be considered.

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Population Trends and Productivity of Tundra Swans on the Central Arctic Coastal Plain, Northern Alaska, 1989–2000

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Abstract.—Population trends and productivity of Tundra Swans (*Cygnus columbianus columbianus*) were monitored by two annual aerial surveys (June and August) in the Kuparuk Oilfield and adjacent areas on the Arctic Coastal Plain of Alaska during 1989-2000. Tundra Swan numbers increased significantly at an annual rate of 4.8% based on June counts of adults, and at 2.9% based on August counts of adults. Individuals in pairs composed 81% and 72% of adults in June and August, respectively. Young swans composed 25% of all swans recorded in August. Numbers of nests varied substantially among years ($\bar{x}$ = 79, range = 44–116), and did not increase significantly over the study period. The density of nests was low ($\bar{x}$ = 0.04 nests·km^{-2}), but except for higher densities on deltas, was comparable to other sections of the Arctic Coastal Plain. Mean annual nesting success (i.e., total broods per total nests) was 83% (range 64%–100%) and mean brood size was 2.5 young per brood. The number of nests was positively correlated with cumulative thaw degree-days (cumulative number of degrees per day above freezing) during spring (15 May–15 June). No similar relationship was found for the total number of adults present in June or brood size in August. Abundance and productivity are compared to other Tundra Swan surveys in northern and western Alaska.

Key words.—Aerial survey, Alaska, Arctic Coastal Plain, *Cygnus columbianus columbianus*, Kuparuk Oilfield, nesting success, population trends, productivity, Tundra Swan.

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Prior to 1989, Tundra Swans (*Cygnus columbianus columbianus*) in northern Alaska, which makes up part of the summer range of the Eastern Population, were monitored primarily during annual U.S. Fish and Wildlife Service waterfowl breeding-pair surveys conducted along an extensive series of transects across the region (Mallek and King 2000). Breeding-pair surveys during 1986–2000 included estimates of the total individuals (breeders and non-breeders), the number of nests, and the relative distribution of Tundra Swans, but did not include data on nesting success, productivity, brood numbers and distribution, nor site-specific information necessary for habitat analyses.

In the late 1980s, the need for site-specific data on swans, including the monitoring of swans around growing oilfield infrastructure, led to intensive regional surveys on the Colville River Delta (Campbell and Rothe 1990), in the Kuparuk and Prudhoe Bay oilfields (this study), and in the Arctic National Wildlife Refuge (Brackney 1989). In particular, because swans are long-lived and traditional in their selection of breeding areas (see Einarsson and Rees 2002; Stickney *et al.* 2002), nesting areas merited special attention during the mapping of sensitive wildlife habitats for the U.S. Fish and Wildlife Service and the U.S. Army Corps of Engineers permitting process for oilfield development.

In 1989, we initiated annual surveys of Tundra Swans during nesting and brood-rearing in the Kuparuk Oilfield and adjacent areas on the Central Arctic Coastal Plain of Alaska (Anderson *et al.* 2001). The goal of these surveys was to describe the annual distribution, abundance and productivity of Tundra Swans in the Kuparuk Oilfield and adjacent areas. Specific objectives were to (1) estimate trends in abundance of nests and adults during early incubation; (2) estimate trends in nesting success, productivity, and abundance of adults and young during brood-rearing; and (3) conduct spatial analyses of nest distribution relative to oilfield development (e.g., pads, roads) and natural terrain features (e.g., lakes, coastline). This paper addresses the first two objectives, and Stickney *et al.* (2002) addresses the third.

STUDY AREA

The Kuparuk Oilfield study area, which lies between the Kuparuk and Colville Rivers, encompasses about 2,250 km^2, is primarily composed of wetlands, and is typical of the flat, slowly rising Arctic Coastal Plain (Gallant *et al.* 1995; Fig. 1). The study area encompasses both the Kuparuk and Milne Point oilfields and currently includes 13 km^2 of oilfield infrastructure (gravel road and pads), which has increased incrementally during oilfield development since about 1980. Most of the study area (about 74%; 1,668 km^2) still is relatively undisturbed, as it is outside the zone of greatest disturbance by oilfield activities, which we have defined as the 582 km^2 within a 1-km buffer zone around (and including) all oilfield structures.

The study area is underlain by thick permafrost and, because of poor soil drainage and saturated soils, much of the area is covered by moist and wet tundra communities and numerous thaw-lakes. Oriented thaw-lakes, basin-wetland complexes, polygonal ground and peat ridges are common. Moist tussock tundra occurs on sites with better drainage, especially on the south side of the study area near the foothills of the Brooks Range. About half of the area is bisected by roads, pipeline and powerline corridors, and numerous facilities and gravel pads associated with the oilfields.

The highest nesting densities of swans on the Arctic Coastal Plain occur on large river deltas or in complex wetlands such as basin-wetland complexes. However, swans sometimes nest on tundra distant from water, especially on habitat features that become snow-free first, including sand dunes, natural mounds and upland relief such as tussock tundra (Ritchie and King 2000; Stickney *et al.* 2002). Tundra Swans are among the first spring migrants to arrive on the Arctic Coastal Plain of Alaska in mid-May. They leave the region just prior to the freezing of wetlands in late September–October

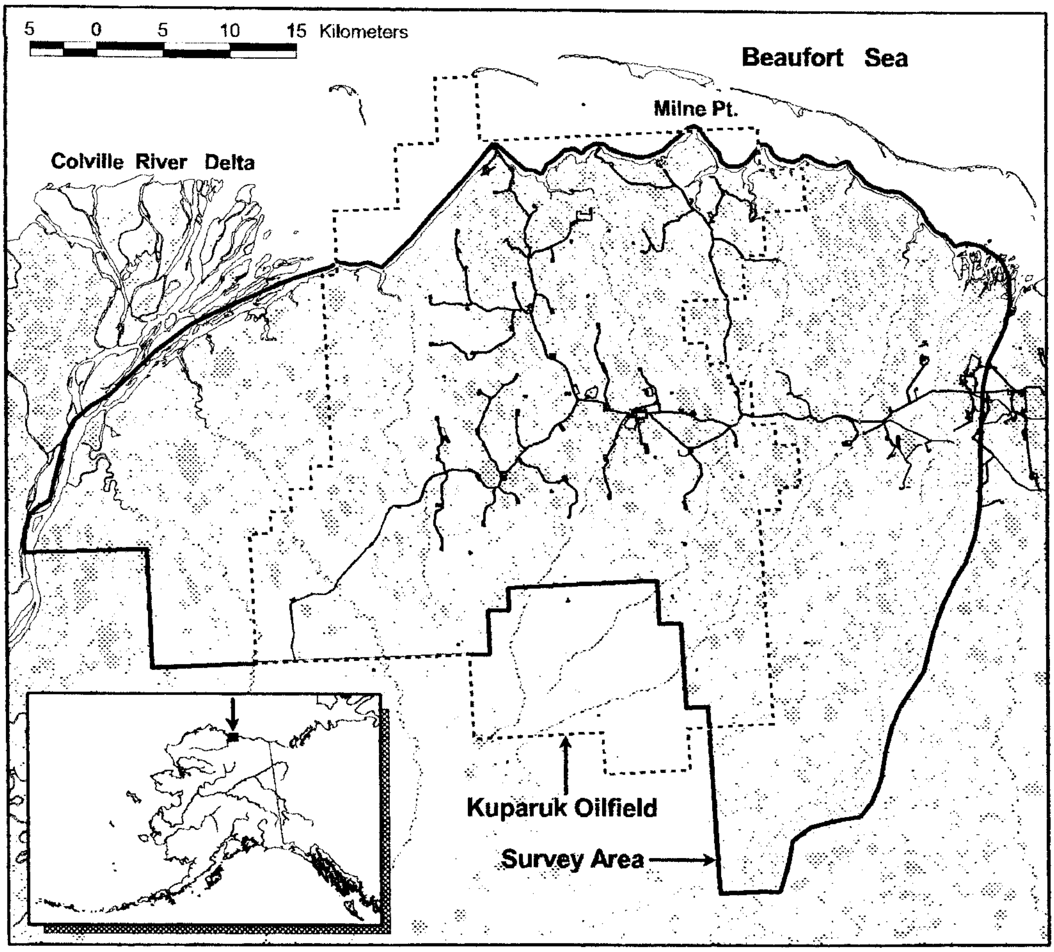

Figure 1. Study area for the annual breeding (June), and brood-rearing (August) aerial surveys for Tundra Swans in the Kuparuk Oilfield area, Central Arctic Coastal Plain, Alaska, 1989–2000.

(Ritchie and King 2000) and winter on the east coast of the United States (Sladen 1973).

METHODS

Data Collection

Aerial survey methods followed the U.S. Fish and Wildlife Service Tundra Swan Survey Protocol (USFWS 1987, 1991). Timing of surveys in June and August (1989–2000) was consistent among years and coincided with mid to late incubation (14–26 June) and late brood-rearing when young were about 6 weeks old (16–24 August).

A Cessna 185 airplane was used to fly along fixed-width (1.6-km wide), east-west transects that were oriented along township and section lines, providing complete coverage of the study area. The pilot maintained a speed of 145 km·hr^{-1} at an altitude of 150 m above ground level. Each of two observers scanned a transect approximately 800 m wide on his/her side of the aircraft, using binoculars when necessary, while the pilot navigated and scanned ahead of the aircraft. The pilot consistently provided information on swans directly in front of the aircraft to both observers.

Locations of adults, nests and broods were recorded on 1:63,360 (inch = mile) U.S. Geological Survey maps. Adults were counted and categorized as singles, pairs, singles or pairs with nests or broods, or flocks (i.e., ≥3 adults). The aircraft sometimes left the transect to allow observers to accurately map and photograph nests and to count young in broods. After each diversion, the aircraft returned to the point of departure and the survey continued.

Data Analysis

Data were entered onto digital topographic maps with a geographic information system. For each survey, we tallied all adults (white birds), as well as young (gray birds) during the August survey. No correction factors were used to adjust counts of nests or individuals, although preliminary research indicated that some swans were missed (e.g., >27% of nests were missed on one June survey; Stickney *et al.* 1993). Correction factors for visual counts of swans have not been well-established or applied to other aerial surveys of swans in Alaska.

To facilitate comparisons with other surveys in Alaska, the estimated number of individuals in pairs was defined as the sum of all individuals in pairs with or without nests or broods, plus twice the number of single swans with nests or broods. The number not in pairs equaled the total number of swans observed minus the estimated number in pairs. This estimate of pairs is comparable to the estimate of "indicated breeding pairs" used in other aerial surveys in Alaska such as the U.S. Fish and Wildlife Service breeding-pair surveys, and can be thought of as the potential breeding component.

Annual nesting success per year was calculated as the number of broods observed in August divided by the number of nests recorded in June. Linear regression was used to investigate temporal trends in counts of adults, mean brood size and nesting success. Changes in swan numbers over time were evaluated by an exponential ($\log_e$) regression of the annual June and August counts of adults and a calculation of the annual growth rate (annual percent increase = [exp(slope) – 1] × 100).

Effects of Timing in Spring

To assess the effect of temperature on nesting effort, the number of thaw degree-days for 15 May to 15 June was calculated for each year, a period corresponding to typical swan arrival, nest initiation and early incubation (Ritchie and King 2000). Thaw degree-days were calculated as the cumulative number of degrees the daily mean temperature was above freezing (0° C) summed for all days between 15 May and 15 June. Higher thaw degree-days were assumed to reflect warmer spring conditions and possibly earlier snow melt. Linear regression was used to evaluate the effect of thaw degree-days on the number of nests, nesting success (arcsine transformed) and brood size. Multiple regression was used to evaluate the effect of year and thaw degree-days on the number of nests and total swans recorded in June. Statistical analyses were conducted with SPSS software.

RESULTS

Breeding Surveys

The number of swans observed during June increased over the 12-year sampling period at a mean rate of 4.8% per year (r^2_{10} = 0.54, $P < 0.01$; Fig. 2a). The mean number of swans during June in the Kuparuk Oilfield area was 387 ± 26 (Table 1) and the estimated number of individuals in pairs was 312 ± 20 swans (or 156 pairs) per year, equivalent to 81% of all swans recorded. The density of all swans recorded in June was 0.17 ± 0.01 birds·km^{-2}.

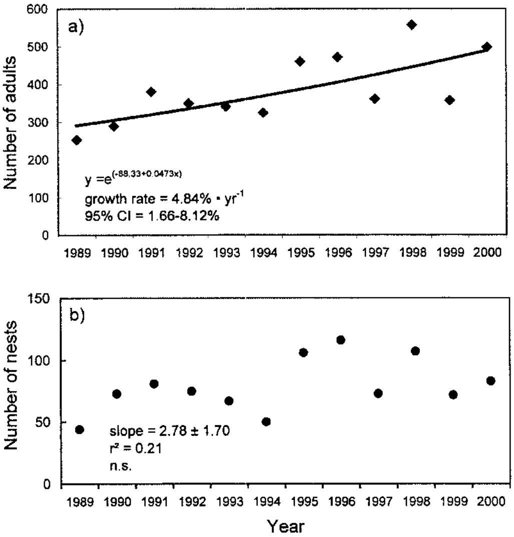

Figure 2. Trends in numbers of (a) adult Tundra Swans (breeding and non-breeding) and (b) nests in the Kuparuk Oilfield area, Alaska, in June 1989–2000.

Table 1. Numbers of Tundra Swans recorded during aerial surveys in the Kuparuk Oilfield, Alaska, in June 1989–2000.

Year	Nests	Individuals in pairs[a]	Individuals not in pairs[a]	Total adults	Percentage in pairs
1989	44	206	47	253	81.4
1990	73	246	43	289	85.1
1991	81	302	78	380	79.5
1992	75	262	87	349	75.1
1993	67	298	43	341	87.4
1994	50	244	80	324	75.3
1995	106	386	74	460	83.9
1996	116	374	97	471	79.4
1997	73	320	41	361	88.6
1998	107	430	127	557	77.2
1999	72	286	71	357	80.1
2000	83	384	114	498	77.1
12-yr mean	79	312	75	387	80.8
SE	6.3	19.9	8.2	26.3	1.3

[a] The estimated number of individuals in pairs was defined as the sum of all individuals in pairs with or without nests or broods, plus twice the number of single swans with nests or broods. The number not in pairs equaled the total number of swans observed minus the estimated number in pairs.

The number of swan nests per year ($\bar{x}$ = 79 ± 6.4, Table 1) has not increased significantly since 1989 (r^2_{10} = 0.21, n.s.; Fig. 2b), and has shown high interannual variability. Mean annual nest density was 0.04 ± <0.01 nests·km^{-2}.

Brood-rearing Surveys

The number of adults observed during August also increased significantly during 1989-2000 ($r^2_9 = 0.55, P < 0.01$) at a mean rate of 2.9% per year (Fig. 3a). The mean number of adults and young during August in the Kuparuk Oilfield area was 662 ± 26 (Table 2), including 357 ± 13 birds in pairs and 139 ± 14 not in pairs. Young in broods composed an average of 25% of all swans. The number of young per year has not increased significantly since 1989 (r^2_9 = 0.04, n.s., Fig. 3b). Mean densities (birds·km^{-2}) of adults in pairs, adults not in pairs, and young were 0.16 ± 0.01, 0.06 ± 0.01, and 0.07 ± 0.01, respectively. Mean density of all Tundra Swans recorded in August was 0.29 ± 0.01 swans·km^{-2}.

Mean nesting success was 83%, but varied substantially among years (range 64–100%), and declined significantly during the study period (r^2_9 = 0.84, $P < 0.001$, Fig. 4a). Although our measure of nesting success (number of broods observed divided by number of nests observed) is useful in assessing relative productivity among years, it may have a positive bias because broods likely have a higher detection rate than nests. Mean brood size was 2.5 ± 0.1 (Table 2). The

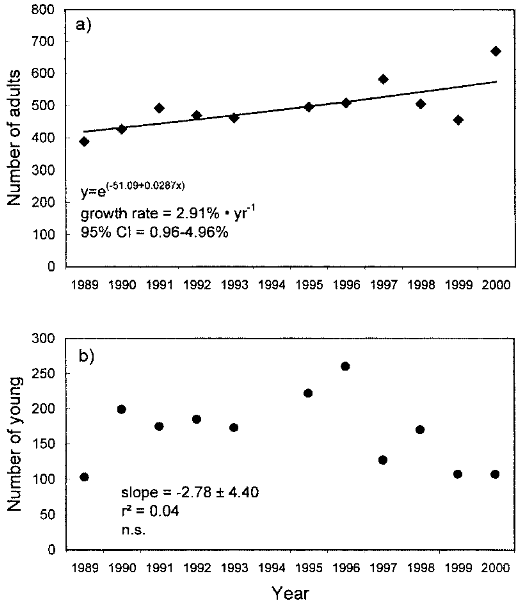

Figure 3. Trends in numbers of (a) adult and (b) young Tundra Swans in the Kuparuk Oilfield area, Alaska, in August 1989–2000.

Table 2. Numbers and productivity of Tundra Swans, determined from aerial surveys in the Kuparuk Oilfield (2,250 km^2), Alaska, in August 1989–2000.

Year	Individuals in pairs	Broods	Young	Individuals not in pairs	Total swans	Percent young	Mean brood size	Nest success (%)[a]
1989	330	45	103	58	491	21.0	2.3	100
1990	310	72	199	116	625	31.8	2.8	99
1991	350	69	175	142	667	26.2	2.5	85
1992	304	68	185	165	654	28.3	2.7	91
1993	362	69	173	99	634	27.3	2.5	100
1994	—	—	—	—	—	—	—	—
1995	372	82	222	124	718	30.9	2.7	77
1996	378	95	260	130	768	33.9	2.7	82
1997	372	57	127	210	709	17.9	2.2	78
1998	386	73	170	120	676	25.1	2.3	68
1999	312	47	107	144	563	19.0	2.3	65
2000	448	53	107	222	777	13.8	2.0	64
11-yr mean	357	66	166	139	662	25.0	2.5	83
SE	12.7	4.5	15.4	14.1	25.5	1.9	0.1	4.1

[a]Sample size of broods and nests given in Table 1. Nest success calculated as number of broods observed during the August survey divided by number of nests observed during the June survey.

linear trend in annual brood size was not significant ($r^2_9 = 0.30$, n.s., Fig. 4b); however, in the last four years of surveys, brood sizes have been lower than the 11-year mean and, with the exception of 1989, have been the smallest recorded.

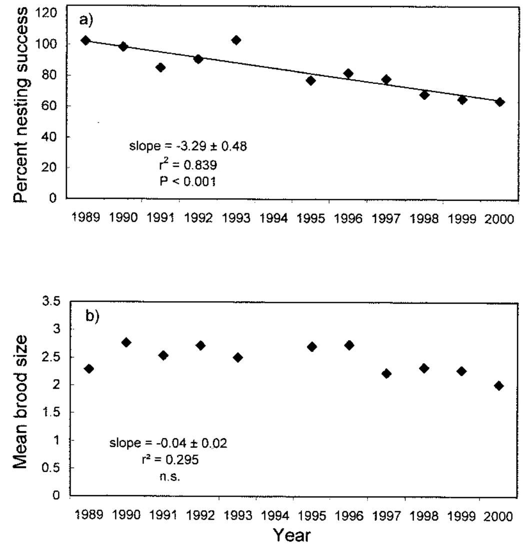

Figure 4. Trends in (a) estimated nesting success (broods per nest) and (b) mean brood size for Tundra Swans in the Kuparuk Oilfield area, Alaska, 1989–1993 and 1995–2000 (no survey conducted in 1994).

Effects of Timing in Spring

The number of nests was positively related to total thaw degree-days in each year ($r^2_{10} = 0.50$, $P < 0.01$; Fig. 5 and Table 3). This significant trend was driven primarily by the two years (1996 and 1998) when cumulative thaw degree-days were the highest (Table 3). Similarly, in a multiple regression analysis, number of nests increased with number of thaw degree-days ($F_{1,9} = 7.32$, $P < 0.05$), but not with year ($F_{1,9} = 1.48$, n.s.; overall $F_{2,9} = 5.84$, $P < 0.05$). In a multiple regression on total swan numbers in June, number of thaw degree-days was not a significant predictor of swan numbers ($F_{2,9} = 3.87$, n.s.), but the number of swans increased with year ($F_{2,9} = 9.90$, $P < 0.05$; overall $F_{2,9} = 9.45$, $P < 0.01$). Nesting success and mean brood size were not affected by thaw degree-days ($r^2_{10} = 0.17$ and $r^2_9 = 0.12$, n.s., respectively).

DISCUSSION

Population Trends

The number of Tundra Swans in the Kuparuk Oilfield and adjacent areas of the Central Arctic Coastal Plain between the Colville and Kuparuk Rivers has increased

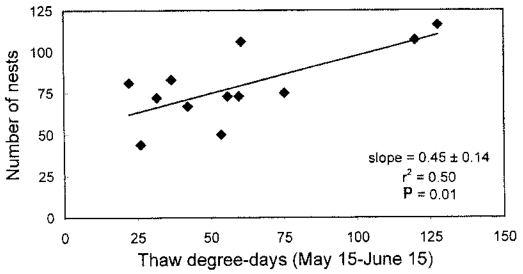

Figure 5. Number of nests by year in relation to cumulative thaw degree-days between 15 May–15 June in the Kuparuk Oilfield area, Alaska, 1989–2000.

significantly since at least 1989. The total number of adults in the region in 2000—both during nesting (June) and brood-rearing (August)—was approximately twice the number recorded on our first surveys in 1989. The number of nests also may be increasing, but high interannual variability, due in part to spring weather conditions, obscures the trend.

During the same period, Tundra Swans appeared to be increasing across the Arctic Coastal Plain, including our study area, based on data from two U.S. Fish and Wildlife Service aerial surveys: one conducted in mid-June during 1992-2000, primarily to count breeding Spectacled Eiders (*Somateria fischeri*) but also other waterfowl (Larned *et al.* 2001), and one conducted during late June–early July each year (1986–2000) to count all waterfowl (standard breeding pair survey; Mallek and King 2000). Population indices of adult Tundra Swans showed a nonsignificant increase during the 1992-2000 surveys (Larned *et al.* 2001), and an increase from about 6,700 to >17,000 swans during the 1986–2000 surveys (Mallek and King 2000; E. Mallek, USFWS, pers. comm.). Number of nests also increased during that period (Mallek and King 2000). The annual rate of increase in swan numbers was 1.0% during 1992–2000 (Larned *et al.* 2001), and 7.4% during 1989–2000 (our calculations based on data in Mallek and King 2000), compared to 4.8% from our June surveys during 1989–2000.

Tundra Swan numbers in our study area and elsewhere on the Arctic Coastal Plain may have been increasing before 1989. Early references suggested a scattered distribution and low numbers (Bailey *et al.* 1933; Dixon 1943; Gabrielson and Lincoln 1959). As late as 1969, most Tundra Swans on the Arctic Coastal Plain were considered either nonbreeders or unsuccessful breeders (Bartonek 1969), and total numbers were estimated at only about 800 swans (King 1970). More intensive surveys between the Sagavanirktok and Colville Rivers after 1970 reported more birds and broods than had

Table 3. Monthly mean temperatures (°C) and daily range in the Kuparuk Oilfield, May and June 1989–2000, compared to the 12-year average, and the thaw degree-days for 15 May–15 June 1989–2000.

	May		June		
Year	Mean	Range	Mean	Range	Thaw degree-days[a]
1989	-7.7	-21.7–5.6	4.3	-3.3–18.9	26
1990	-2.8	-18.9–6.7	5.7	-4.4–20.6	56
1991	-2.5	-12.2–5.0	4.5	-5.0–28.5	22
1992	-5.7	-27.8–10.0	4.6	-4.4–17.8	75
1993	-4.4	-20.6–6.7	4.2	-3.9–23.3	42
1994	-6.3	-16.7–3.3	3.0	-8.3–18.3	54
1995	-2.6	-11.7–2.2	4.7	-3.9–18.3	59
1996	-2.7	-27.8–12.8	6.9	-4.4–22.2	128
1997	-4.8	-20.0–10.0	4.5	-10.0–22.2	60
1998	-2.1	-22.8–13.3	7.0	-2.8–26.7	120
1999	-5.0	-18.9–4.4	3.1	-4.4–13.3	32
2000	-9.3	-25.0–1.1	6.6	-7.2–24.4	37
12-year mean	-4.6		4.9		

[a] Thaw degree-days are calculated as the cumulative number of degrees above freezing (0°C) per day; negative values are not summed.

previous studies, with the highest densities on or adjacent to major river deltas (Gavin 1972; Welling and Sladen 1978).

An increase in Tundra Swans in northern Alaska (part of the breeding grounds of the Eastern Population) is not surprising because the index of wintering Eastern Population swans has increased significantly, nearly doubling during 1955–1989 (Serie and Bartonek 1991) and continuing to increase through 2000 (Serie *et al.* 2002).

The density of Tundra Swans recorded in this study is representative of other low-density areas used by Tundra Swans on the Arctic Coastal Plain (Table 4). Higher densities of breeding swans are thought to occur where lakes are abundant, in areas closer to the coast and, more importantly, on river deltas (Ritchie and King 2000) (Table 4). In upland habitats and farther inland, where lakes generally are less abundant, Tundra Swans are less common; an exception to this pattern is the lower Itkillik River valley, where densities regularly exceeded 0.03 nest·km^{-2} (Stickney *et al.* 1994). The highest densities of both Eastern and Western Population Tundra Swans occur on river deltas throughout their range (Limpert and Earnst 1994). River deltas may provide better food resources and a longer period of open water than do non-delta coastal areas and inland habitats (McLaren and McLaren 1984; Monda *et al.* 1994).

Productivity

Although the number of adult Tundra Swans has increased in the study area, annual nesting success has declined. Still, the estimates of nesting success in this study are within the range of values from other aerial surveys in northern Alaska (Table 4). Ground-based survey data also support relatively high nesting success for swans in the region: 83% for a small sample of nests in the Prudhoe Bay area in 1985–1989 (Murphy and Anderson 1993) and 76% over three years (range 58–84%) in northeastern Alaska (Monda *et al.* 1994).

Brood sizes in this study also appear to be similar to or higher than brood sizes for other Eastern Population Tundra Swans nesting in northern Alaska (Table 4) and northwestern Canada (McLaren and McLaren 1984; Stewart and Bernier 1989). In contrast, Eastern Population productivity appears to be lower than for Western Population Tundra Swans breeding in western Alaska, where annual mean brood size ranges from 2.9–3.7 young (Lensink 1973; Wilk 1988; Spindler and Hall 1991). This difference may suggest that Eastern Population swans breeding in northern Alaska are near their ecological limits (King 1970; Lensink 1973; Bart *et al.* 1991). These northern-breeding swans of the Eastern Population nest farther north, their migration route is longer, and their breeding season is shorter than for Western Population swans breeding in western Alaska and wintering in western North America.

Possible explanations for suggested declines in nesting success include the influence of survey biases (i.e., sightability differences), spring conditions, and other factors (e.g., predation, effects of increased territorial conflicts as habitats reach capacity, oilfield disturbance), which are not easily addressed using aerial survey data. In regard to survey biases, we are confident that broods are detected more often than nests during aerial surveys; however, this bias should not produce an overall decline in nesting success (Fig. 4). If the timing of snow melt had become later during the 1989–2000 survey period, resulting in more snow present during June surveys, the poor detectability of nests in snow might have produced the observed decline in nesting success. However, our personal observations for the period indicate that this has not been the case. We address other possible explanations for declines in productivity in the next two sections.

Effects of Timing in Spring

Spring weather has been suggested as a primary factor influencing Tundra Swan productivity. For example, late springs resulted in fewer nesting attempts and smaller broods among Tundra Swans in Canada (McLaren and McLaren 1984). In northeastern Alaska, earlier snow-melt was associated with larger clutch sizes and earlier nest-initi-

Table 4. Regional comparison of adult and nest densities and productivity of Tundra Swans at six locations on the Arctic Coastal Plain, Alaska (1983–2000).

	Nests·km^{-2}		June adults·km^{-2}		Brood size		Nest success (%)		
Location	$\bar{x}$	(range)	$\bar{x}$	(range)	$\bar{x}$	(range)	$\bar{x}$	(range)	Years
Kuparuk Oilfield	0.04	(0.02–0.05)	0.17	(0.11–0.25)	2.5	(2.0–2.8)	83	(64–100)	1989–2000[a]
Oil/Gas Lease Area 54	0.03	(0.02–0.03)	0.15	(0.14–0.17)	2.7	(2.1–2.9)	66	(56–77)	1988–1992[b]
Prudhoe Bay Oilfield	0.03	0	0.13	(0.11–0.15)	2.5	(2.2–2.8)	98	(85–100)	1990–1991[b]
Sagavanirktok Delta	0.09	0	0.35	0	3.2	0	69	0	1992[c]
Colville Delta	0.06	(0.05–0.12)	0.43	(0.36–0.50)	2.3	(1.9–2.6)	79	(52–97)	1983–1989[d]
	0.06	(0.03–0.08)	0.35	(0.11–0.53)	2.4	(2.0–3.7)	73	(66–100)	1992–2000[e]
Arctic Natl. Wildl. Ref.	0.03	(0.02–0.05)	0.16	(0.13–0.20)	2.6	(2.3–2.8)	77	(64–100)	1983–1989[f]

[a] This study.

[b] Stickney *et al.* 1992. Oil and Gas Lease Area 54 borders the Kuparuk Oilfield to the southwest and extends south between the Colville and Itkillik Rivers. Prudhoe Bay Oilfield borders the Kuparuk Oilfield to the east.

[c] Stickney *et al.* 1993. The Sagavanirktok River Delta forms the eastern border of the Prudhoe Bay Oilfield. The survey area extended 8 km to the east.

[d] Campbell and Rothe 1990. The Colville River Delta borders the Kuparuk Oilfield on the west.

[e] Johnson *et al.* 1999; ABR unpublished report.

[f] Brackney 1989. Arctic National Wildlife Refuge is located 150 km east of the Kuparuk Oilfield between the Canning River and the Canadian border.

ation dates (Monda *et al.* 1994). Similarly, on the Yukon-Kuskokwim Delta, in subarctic western Alaska, environmental conditions in spring (e.g., late, cool springs that delay ice break-up and snow-melt) were the most important factors affecting the productivity of Tundra Swans, reducing clutch sizes and the proportion of swans that nested (Lensink 1973; Dau 1981).

Our weather data are limited, but also suggest that the timing of snow and ice melt can affect annual Tundra Swan productivity. In the Kuparuk Oilfield, more Tundra Swans nested during warmer springs (i.e., those with higher thaw degree-days). Whether cold springs with delayed snow and ice melt and/or cool temperatures affect annual or long-term productivity of swans in the Kuparuk Oilfield is not clear, as we found no significant relationship between cold spring temperatures (cumulative thaw degree-days) and nesting success or brood size, although some declines in nesting success and brood size do appear to coincide with colder springs.

Effects of Oilfield Development

Numbers and productivity of Tundra Swans potentially could be affected by oilfield infrastructure and activities. Mechanisms include long-term and temporary habitat loss and associated changes in habitat use, disturbance-induced changes in behavior, collisions with powerlines and oilfield structures, increased mortality and/or decreased productivity due to possibly elevated predator levels, and contamination associated with spills of hydrocarbons and other compounds in the oilfields (Ritchie and King 2000). Some site-specific impacts, such as lower productivity of swan nests near roads and pads, have been inferred (Murphy and Anderson 1993), and a few instances of direct mortality have been documented (Ritchie and King 2000).

Our aerial surveys during 1989–2000, a period of slow oilfield expansion, do not indicate a negative regional impact on swan numbers. Analyses of mean minimum distances of swan nests from various oilfield structures within the Kuparuk Oilfield suggest that territoriality and nest-site availability may be more important in nest-site selection than facility avoidance (Stickney *et al.* 2002). However, the apparent declines in some measures of productivity warrant closer investigation. Most importantly, a number of features of oilfield development, such as potential increases in predators attracted to human activities, and their cumulative impacts on Tundra Swans, need to be assessed and may require some level of ground-based study.

This study presents a substantial baseline of data on Tundra Swans from extensive and consistent annual aerial surveys in the Kuparuk Oilfield area. Although gaps in our knowledge still persist, and biases and limitations are associated with aerial surveys (Bart *et al.* 1991), our surveys effectively monitor population trends, brood size, and habitat-specific nest and brood locations for Tundra Swans using the Kuparuk Oilfield area.

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Population Trends, Productivity, and Harvest of Eastern Population Tundra Swans

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Abstract.—Population indices from the Midwinter Waterfowl Survey show that the number of Eastern Population Tundra Swans (*Cygnus columbianus columbianus*) has more than doubled since 1955 and currently exceeds 100,000. Numbers of swans wintering in Maryland, in the vicinity of Chesapeake Bay, continue to decline while numbers wintering further south along coastal North Carolina steadily increase. North Carolina winters an average of about 70% of the Eastern Population, while Maryland has 20%, Virginia 6%, New Jersey 3% and elsewhere 1%. No long term productivity trends are evident in the observed age-ratios and numbers of young per family. Currently, Montana, North Carolina, North Dakota, South Dakota, and Virginia issue up to a total of 9,600 swan hunting permits annually (one swan per permit). The percentage of the population harvested was lowered in 1996 from 10% to 5% to stimulate population growth. Presently, nearly 4,000 birds are taken by hunters annually (40% success rate). Although population growth has slowed since the initiation of hunting in 1984, the trend remains positive and appears to be increasing after lowering the harvest rate. Thus, at current population levels, we believe that the Eastern Population is capable of sustaining a limited harvest while still ensuring future growth, ecological integrity, and other recreational opportunities to benefit society.

Key words.—*Cygnus columbianus columbianus*, Eastern Population, harvest management, population trends, productivity, Tundra Swans, waterfowl.

Waterbirds 25 (Special Publication 1):32–36, 2002

Tundra Swans (*Cygnus columbianus columbianus*) are managed as Eastern and Western Populations, based on migration or wintering tendencies (EP Tundra Swan Committee 1998). Banding studies have found little interchange between these populations (Limpert *et al.* 1991). Eastern Population Tundra Swans migrate from traditional breeding areas in tundra coastal regions of Alaska and the central Canadian arctic across North America to winter primarily along the Atlantic coast (Fig. 1; Bellrose 1976). The purpose of this paper is to update the population trends, productivity, and harvest information for Eastern Population swans previously reported by Serie and Bartonek (1991a, 1991b). Comparable information for Western Population swans is not provided here but can be obtained from Trost and Drut (2001).

METHODS

Eastern Population swans are monitored annually by the Midwinter Waterfowl Survey (Crissey 1975), a set of aerial surveys conducted during a one or two week period in early January. This survey is a cooperative effort between state and federal wildlife agencies to obtain a complete count of waterfowl on key wintering areas (U.S. Fish and Wildlife Service 1989). It has continued on a comparable basis since 1955 with the same areas surveyed each year. These data provide a reasonable index of population size and long-term trends. Productivity indices are derived from counts of gray-plumaged young and white-plumaged adults or sub-adults, and from number of young per family group. These counts are obtained using ground observations and aerial photographs at the same locations each winter in New Jersey, Maryland, Virginia, and North Carolina in late November and December (U.S. Fish and Wildlife Service 1977).

Goals and strategies for maintaining the desired population level and distribution of Eastern Population swans are described in a management plan first approved in 1988 and revised in 1998 (EP Tundra Swan Committee 1998). This plan was developed cooperatively by states and provinces and federal wildlife agencies in Canada and the United States and adopted by the four Flyway Councils. An accompanying hunt plan sets harvest objectives and guidelines (EP Tundra Swan Committee 1998).

RESULTS

From 1995-2000, the Eastern Population more than doubled and presently exceeds 100,000 birds (Table 1). Since the mid-1980s, the index has fluctuated between 80,000 and 100,000 birds. Numbers fell sharply in 1993, but have since recovered to

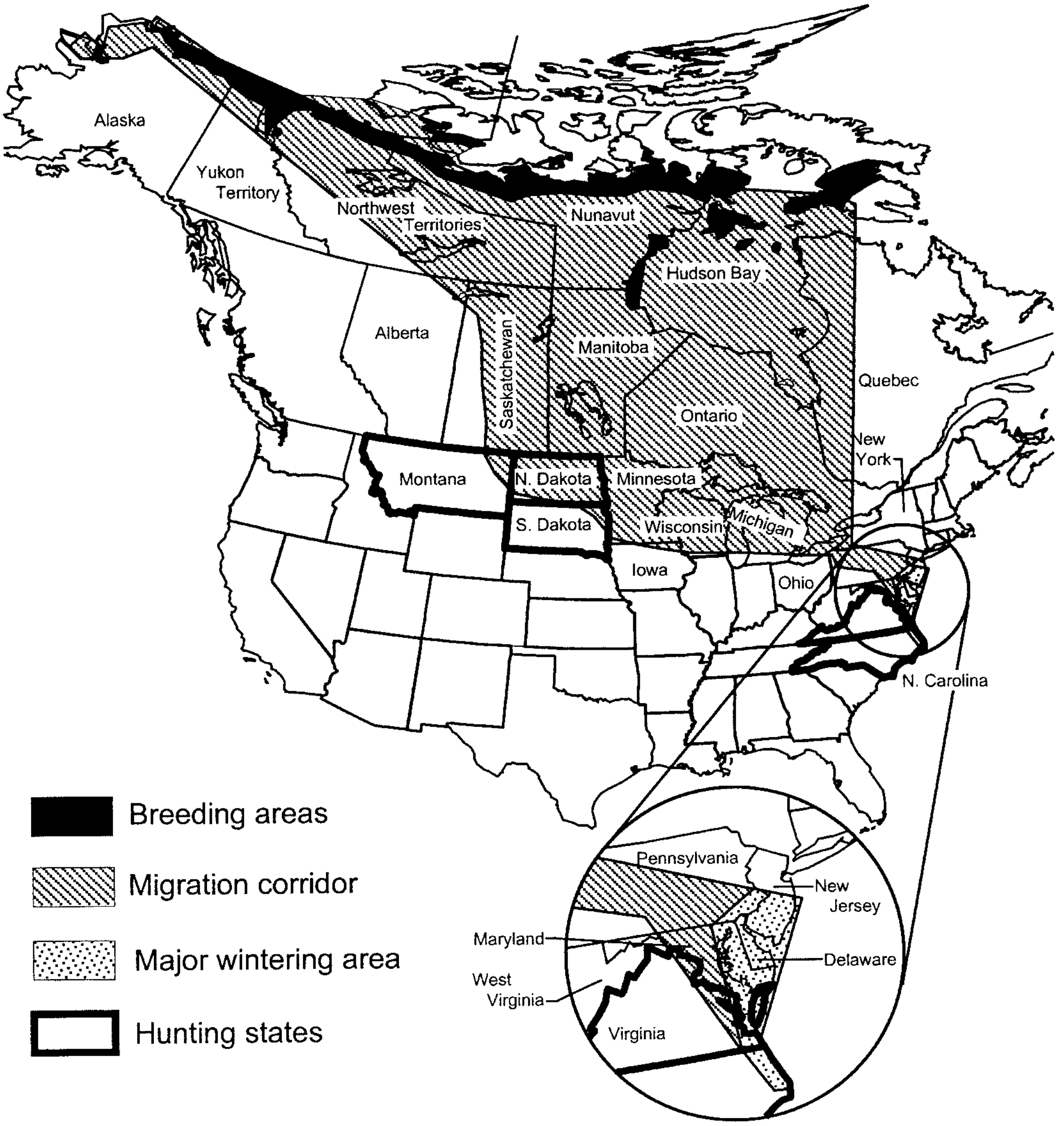

Figure 1. Map of Eastern Population Tundra Swan breeding, migration, and wintering range and states with swan hunting seasons.

100,000. The percentage of Eastern Population swans wintering in Maryland, in the vicinity of Chesapeake Bay, has declined since the 1960s from 65% to 20% while the percentage wintering further south along coastal North Carolina has increased steadily from 25% to 70% (Serie and Raftovich 2001). Virginia (6%), New Jersey (3%), and elsewhere (1%) make up the remaining 10%. The population in North Carolina has increased at an average annual rate of more than 12% ($P < 0.01$) since 1955.

The number of young per adult shows no apparent trend from 1984 to present (Table 1). The unweighted long-term average is 13% with considerable annual variability. The number of young per family averages 1.5 and also shows no long-term trend (Table 1).

Currently, 9,600 hunting permits are authorized annually (one swan per hunter) in Montana (500), North Dakota (2,000), South Dakota (1,500), North Carolina (5,000), and Virginia (600). Since 1995, an average of nearly 4,000 birds has been taken

Table 1. Population and productivity data for the Eastern Population of Tundra Swans, 1984-2000.

		Estimates of productivity[b]			
Year	Mid-winter Index[a]	No. families	Young/family	Total birds	Percent young
1984	81,235	240	2.2	8,913	19.8
1985	93,909	716	2.0	11,394	23.6
1986	90,766	235	1.3	11,903	8.7
1987	94,504	109	1.6	8,210	9.8
1988	77,110	247	1.9	10,260	14.8
1989	90,150	461	1.7	13,836	15.2
1990	90,593	297	1.9	11,604	10.3
1991	97,424	139	1.6	3,719	12.3
1992	109,788	125	1.6	11,800	4.1
1993	76,593	434	1.0	13,320	15.0
1994	84,527	497	1.3	5,214	19.2
1995	80,222	234	1.1	9,720	8.1
1996	79,021	922	1.2	15,290	10.0
1997	86,120	846	0.8	11,552	7.5
1998	96,544	1,411	1.2	13,042	15.7
1999	109,041	700	1.6	13,660	10.4
2000	103,082	676	0.9	7,229	10.2
Average	90,625	488	2.5	10,627	12.6

[a] Mid-winter Index is the number of individuals counted during aerial surveys conducted over the same areas each January.

[b] Estimates of productivity based on ground counts and aerial photographs taken at the same locations each year in late November and December.

each year (Table 2). Success rates (percentage of permit holders that harvest a swan) average nearly 40%. In 1996, the number of authorized permits was reduced to lower the harvest rate (i.e., percentage of population killed) from 10% to 5% because the Midwinter Survey estimates appeared to be declining and nearing the objective level of 80,000 (Fig. 2). Since permit numbers were readjusted in 1996, harvest rates have dropped and population indices have rebounded to nearly 100,000. However, overall population growth rates seem to have slowed since hunting was first authorized in 1984 (Fig. 2).

DISCUSSION

The management goal is to maintain Eastern Population swans at a population level and distribution that provide resource benefits for society consistent with habitat availability and international treaty responsibility (EP Tundra Swan Committee 1998). Management objectives include (1) sustaining a population above 80,000 based on a 3-year average of Midwinter Survey; (2) maintaining geographic and temporal distributions; (3) providing recreational (including hunting) and subsistence use; and (4) improving databases for management. A population objective of 80,000 birds is subjectively based upon the level perceived to support public enjoyment of this resource and the desire to maintain or expand distributions of Eastern Population swans. This population level is thought to be sufficient to support both subsistence and sport harvest without adversely affecting viewing, aesthetics, or future population viability. Management agencies have agreed to cooperatively manage the population within a range of 60,000 to 100,000 through adjustments in harvest rates and hunting regulations.

Tundra Swans are highly valued by society throughout their range and as a result, management actions that tend to redistribute their numbers should appropriately consider potential affects. In some localized areas of the Atlantic Flyway (e.g. North Carolina), Eastern Population swans winter in large concentrations and depredation of agricultural crops is a concern. In these isolat-

Table 2. Hunting permit and harvest information for the Eastern Population of Tundra Swans, 1984-2000.

Year	Permits issued	Number harvested[a]	Success rate (%)[b]	Harvest rate (%)[c]
1984	1,108	357	32.2	0.5
1985	6,120	2,802	45.8	3.2
1986	6,170	2,620	42.5	3.0
1987	6,139	3,152	51.3	3.4
1988	7,094	3,109	43.8	3.6
1989	7,211	3,153	43.7	3.6
1990	8,262	4,296	52.0	5.0
1991	9,804	4,769	48.6	5.1
1992	10,280	5,063	49.3	5.1
1993	10,112	4,629	45.8	4.9
1994	10,332	5,578	54.0	6.2
1995	10,391	4,574	44.0	5.7
1996	9,207	3,462	37.6	4.3
1997	9,041	4,088	45.2	5.0
1998	9,245	3,631	39.3	4.2
1999	8,895	3,675	41.3	3.8
2000	8,884	3,885	43.7	3.8
Average	8,135	3,697	44.7	4.1

[a] Number of swans killed, both those retrieved and unretrieved.

[b] Percentage of permit holders that successfully harvest a swan.

[c] Percentage of the Eastern Population harvested by hunting.

ed instances, swan hunting may help to alleviate complaints of local crop damage problems (Serie and Bartonek 1991b). To minimize conflicts with farming interests, management actions should encourage the availability and use of natural aquatic foods rather than increased dependence on agricultural crops. Declining numbers wintering in the Chesapeake Bay region of Maryland, despite lack of hunting, are thought to have resulted from decreased levels of submerged aquatic plants (Munro 1981). If numbers of Eastern Population swans increase substantially in the future, management actions should encourage a wider wintering distribution. Further research is needed to better understand spatial and temporal movement patterns, site fidelity, sub-population units or affiliations, and to monitor survival rates. Assessment of these parameters is essential to making informed management decisions and alleviating potential conflicts.

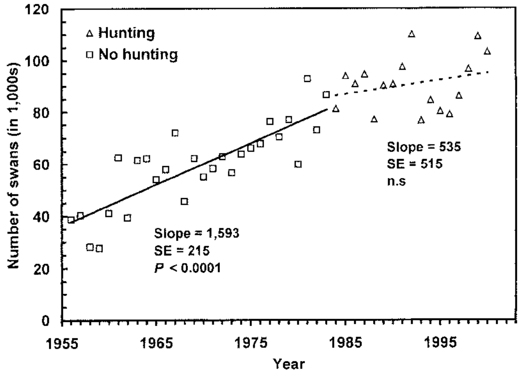

Figure 2. Eastern Population Tundra Swan Midwinter Waterfowl Survey population indices and trends for pre-hunting and post-hunting years.

Sport hunting of Tundra Swans in North America is provided for by the Migratory Bird Treaty Act of 1918, but swan hunting evokes strong emotion and considerable public sentiment (Serie and Bartonek 1991b). Those opposed to the hunting of swans feel that swans are too beautiful and symbolic to warrant killing (Sladen 1991), while those favoring hunting believe numbers are adequate to biologically justify a limited harvest. However, this use must be closely monitored and regulated to meet the other demands of society (Serie and Bartonek 1991b). The revision of the harvest objective from 10% to 5% harvest rate in 1996 seems to have resulted in a positive population response to more desired levels. Although hunting may have slowed the growth rate, the population is still trending upwards. Since productivity indices show no apparent trend, likely because of environment variability, it would appear that the existing combination of survival and productivity rates is sufficient to sustain the population. Hunting appears to be the primary mortality factor (Bartonek *et al.* 1991). For comparison, the current trend in the Western Population, based on midwinter data from the Pacific Flyway (Trost and Drut 2001), is also positive (slope = 1,162 ± 153[SE]; $P < 0.0001$) despite it having been hunted since 1962. Thus, at current population levels, we believe that the Eastern Population is capable of sustaining a limited harvest while still ensuring future growth, ecological integrity, and other recreational opportunities to benefit society.

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The Status and Distribution of the Icelandic Whooper Swan Population: Results of the International Whooper Swan Census 2000

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Abstract.—The Icelandic-breeding Whooper Swan (*Cygnus cygnus*) population winters almost exclusively in Ireland, Britain and Iceland. A coordinated census of Whooper Swans in these countries was undertaken in January 2000, following previous coordinated censuses in 1986, 1991 and 1995. Of the 20,856 birds recorded, 43% were in the Republic of Ireland, 18% in Northern Ireland, 19% in England, 14% in Scotland and 6% Iceland, with the combined totals for Wales and the Isle of Man accounting for <1%. Age assessments revealed 16.8% cygnets, with a mean brood size of 2.3; cygnet distribution was highly consistent between countries and regions in Britain and Ireland, but the proportion of young was lower and more variable between regions in Iceland. The census total was the highest to date, and represents an increase in numbers of 32% since 1995. There is little evidence that immigration of birds from the population wintering in continental northwest Europe is sufficient to explain the increase. The increase of 32% in population size between 1995 and 2000, together with productivity levels of 18.1% cygnets *per annum*, suggests an average annual mortality rate of 11.8% over the period. The increase in numbers occurred mainly in Ireland and England. This resulted in an increase in the number of flocks, and also in flock size, in both Northern Ireland and the Republic of Ireland. In England, birds appear to have become concentrated at traditional sites, and particularly at the two principal sites, Martin Mere and the Ouse Washes. Most birds were found on grassland habitats (although the proportion varied between countries) and on permanent water. As in previous censuses, the proportion recorded on arable habitats was low and, although higher in Britain, is localized there.

Key words.—Britain, *Cygnus cygnus*, Iceland, Ireland, population census, Whooper Swan.

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Whooper Swans (*Cygnus cygnus*) have a widespread Palearctic breeding distribution, mainly between 50°N and 70°N, extending eastwards more or less continuously from Iceland to the Bering Sea (Scott and Rose 1996). Five populations are recognized: (1) the Iceland-breeding population which winters in the United Kingdom, Republic of Ireland and Iceland; (2) the Northwest Mainland European population which breeds in Scandinavia and Russia and winters mainly around the Baltic Sea; (3) the West Siberian/Black Sea/East Mediterranean population which breeds in Siberia and winters around the Black Sea; (4) the West and Central Siberian/Caspian population which breeds in west Siberia and winters around and to the east of the Caspian Sea; and (5) the Central Siberia/East Asian population which breeds in Siberia and winters in Japan, Korea and China (Rose and Scott 1997). Banding programs have shown that the majority of Whooper Swans wintering in Britain and Ireland are from the Icelandic-breeding population (Gardarsson 1991; McElwaine *et al.* 1995; Rees *et al.* 2002), although a small number of birds marked in Finland have been recorded in southeast England, Scotland and Northern Ireland (Laubek *et al.* 1998; G. McElwaine, unpub. data). Of 197 birds marked with neck bands in Iceland in 1984 and 1985, 166 were resighted or recovered in the wintering range, of which six (4%) were reported in mainland Europe (two in Norway, two in Denmark and two in The Netherlands) suggesting that 400–600 birds wintered on the continent at that time (Gardarsson 1991; Cranswick *et al.* 1996). Around 500–1,300 Icelandic birds remain in Iceland throughout the winter (Gardarsson and Skarphedinsson 1985).

Indices generated from generalized waterbird monitoring schemes in the United Kingdom and Ireland show numbers of Whooper Swans wintering in Britain to have been relatively stable between the mid 1960s and mid 1990s, but with elevated levels in the early and late 1990s (Kirby *et al.* 1995; Pollitt *et al.* 2000). In contrast, there was an overall decrease in Northern Ireland between 1987 and 1998, and an increase followed by a decrease in the Republic of Ireland between 1995 and 2000 (Pollitt *et al.* 2000; Colhoun 2001). However, only about half of wintering Whooper Swan numbers are covered by these waterbird monitoring schemes, since they focus primarily on daytime counts of permanent wetlands; many swans on non-wetland sites or in more remote areas are missed. Consequently, the status and distribution of Whooper Swans is best assessed by a species-specific survey (Ruger *et al.* 1986).

Boyd (1963) estimated that 5,000–7,000 Whooper Swans wintered in Britain and Ireland in the early 1960s. Numbers were presumed to remain broadly similar until autumn censuses, primarily in Iceland, put the population size at 12,500 birds in 1982, 13,700 in 1984 and 14,250 in 1985 (Gardarsson and Skarphedinsson 1984, 1985; Gardarsson 1991; published estimates of 10,000–11,000 in 1982 having been revised upwards following subsequent surveys, A. Gardarsson unpubl. data). The first coordinated survey of Whooper Swans in Britain, Ireland and Iceland estimated 16,700 birds in January 1986 (Salmon and Black 1986), increasing to 18,000 in 1991 (Kirby *et al.* 1991), although it is believed that some double-counting may have overstated the true number in the latter survey. The estimate fell to 16,000 in 1995 (Cranswick *et al.* 1996).

The fourth international census of Whooper Swans in Britain, Ireland and Iceland was undertaken as part of the Europe-wide Whooper and Bewick's Swan census in January 2000. This paper describes the results of the census and thus provides an update of the size and winter distribution of the Icelandic Whooper Swan population. Data collected on productivity and habitat use is compared with those recorded in previous censuses.

METHODS

The census of Whooper Swans wintering in Ireland, Britain and Iceland in 2000 was organized by The Wildfowl & Wetlands Trust, BirdWatch Ireland, the Irish Whooper Swan Study Group, the University of Iceland and the Icelandic Institute of Natural History. The recommended count dates, 15 and 16 January 2000, coincided with the annual International Waterbird Census made throughout Europe, and with the national waterbird monitoring schemes in the United Kingdom and the Republic of Ireland. Counts from any dates in January and, exceptionally, from December or February were included if no count was submitted for the census date and it was considered that the risk of double-counting (due to birds having moved from adjacent sites) was minimal. Sites in northern Iceland were covered in early March.

The census attempted complete coverage of all Whooper Swans in Ireland, Britain and Iceland. Whooper Swans generally winter at traditional sites, well known to local observers, and many of these are already covered by ongoing waterbird monitoring schemes, notably the Wetland Bird Survey (WeBS) in the United Kingdom and the Irish Wetland Bird Survey (I-WeBS) in the Republic of Ireland. As with previous censuses, observers were asked to visit additional areas, not well covered by existing schemes, but known or suspected to support Whooper or Bewick's Swans. These additional sites, which were identified from previous censuses, the Irish Wetland Bird Survey database, the Irish Whooper Swan Study Group database, and local knowledge gained by counters in the weeks prior to the census, included temporary wetlands and flooded areas, particularly in the more remote areas of Britain and throughout Ireland. Comprehensive coverage was thus achieved for Lough Foyle/Swilly and around Lough Neagh and Lough Beg in Northern Ireland, the Irish midlands, the Shetland and Orkney Islands, and northern, central and the border areas of Scotland known to hold Whooper Swans. An aerial survey of the Shannon, Suck and Little Brosna Callows and adjacent sites in central Ireland was carried out on 25 January. Extensive coverage of most major wetlands throughout Britain and Ireland, undertaken concurrently as part of the national waterbird monitoring schemes, is thought to have located the majority of birds that moved away from these traditional areas. The main omission was that parts of County Clare were not visited, and access to some areas in Counties Galway and Roscommon was limited due to flooding.

In Iceland, all areas known to hold Whooper Swans in winter were covered with the exception of streams in the west and marine bays in the northwest, where the small numbers present are widely scattered. Ground counts in Iceland were undertaken mostly on 9 January, coinciding with national mid-winter counts organized by the Icelandic Institute of Natural History, although the Myvatn-Laxa area in north Iceland was not covered until 4–8 March. The southern lowlands of Iceland were covered by aerial survey on 29 February. Since there is also thought to be little movement between flocks in different parts of Iceland in winter, double-counting was deemed unlikely.

Counts were coordinated locally to ensure complete coverage and minimize double-counting. Early morning counts were made of roosting birds at some of the most significant sites, before they dispersed to daytime feeding areas. Once submitted, count data were assessed by national and local experts to identify duplicate counts, either from the same site or of birds moving between adjacent sites, and those deemed to be duplicate counts of the same birds were omitted from the census total. For the few areas where no counts were undertaken in 2000, numbers were estimated from previous midwinter counts (44 birds in West Iceland and 150 in County Clare). Coverage therefore is considered comprehensive throughout the wintering range, and consistent with previous censuses.

Counts recorded for each site were grouped by region and country for analysis (Appendix 1). In addition to numbers of birds present, observers were asked to record the number of adults and cygnets, brood sizes, whether the site was used for roosting and/or feeding, and habitat use (habitat categories given in Table 4). The percentage of juveniles was determined from the number of cygnets counted in relation to the total number of birds aged at the site. At some sites, where ageing was not possible during the census count (e.g., at roost sites), age assessments were undertaken separately, usually at feeding sites later in the day. As with the census data, age assessments considered to be duplicates were omitted from the analyses. Age assessments and habitat data were provided for only some of the sites. Chi-squared tests were used to analyze the count data. One-way analysis of variance was used to test for differences in the percentage of young recorded at sites between countries and regions.

RESULTS

Coverage

In Northern Ireland, all 97 sites at which Whooper Swans were recorded were visited within the two-week period spanning the recommended count dates. Some 87% of the 315 sites with Whooper Swans in the Republic of Ireland (where 89% of swans counted in the Republic of Ireland were recorded), and 82% of the 214 sites in Britain (92% of the count in Britain) were surveyed during the same period. Although the survey in Iceland was carried out over a longer period (9 January to 8 March), counts within each region were made simultaneously, which reduced the potential for double-counting.

Numbers and Distribution

The census total of 20,856 consisted of 20,662 birds counted and a further 194 estimated as having been missed (Table 1). This indicated a 32% increase in population size since the 1995 census, when 15,842 birds were recorded. Approximately 61% of the swans counted in 2000 were in Ireland, with 43% in the Republic of Ireland and 18% in Northern Ireland. In Great Britain, the largest proportions were in England (19%) and Scotland (14%), with the combined totals for Wales and the Isle of Man accounting for <1%. About 1,200 birds (6%) were recorded in Iceland.

In Iceland, most Whooper Swans were found in three discrete regions in 2000: (1) in the southwest, on marine and coastal lakes; (2) in the southern lowlands, on freshwater rivers and springs; and (3) in north Iceland, mainly at Myvatn-Laxa (Fig. 1). In contrast, distribution was widespread throughout many areas of Ireland, particularly in the north, midlands and western half of the country (Fig. 2). Although a similar pattern was evident in the central belt of Scotland, the general pattern in Britain showed birds to be concentrated at relatively few sites, notably in Lancashire and Cambridgeshire/Norfolk.

Eleven sites each held 1% (209 birds; the threshold used to identify sites of international importance) or more of the population at the time of the survey: Ouse Washes (east-central England): 1,580; Loughs Neagh/Beg (Northern Ireland): 1,421; Upper Lough Erne (Northern Ireland): 1,252; Martin Mere (northwest England): 1,210; Lough Swilly (northwest Republic of Ireland): 551; Shannon Callows (all regions, Republic of Ireland): 507; North Central Galway Lakes (northwest Republic of Ireland): 338; Lough Oughter Complex (northeast Republic of Ireland): 338; River Foyle (northwest Republic of Ireland/Northern Ireland): 281; and Castleplunket Turloughs (northwest Republic of Ireland): 251.

Comparison with Distribution in 1995

The distribution of birds in Britain, Ireland and Iceland (Figs. 1 and 2) was broadly similar to that of the previous census in 1995; of the 15,842 birds recorded in 1995, 18% were in Northern Ireland, 45% in the Re-

Table 1. Numbers of Whooper Swans recorded in Ireland, Britain and Iceland, January 2000.

	Flocks	Birds		Flocks	Birds
Iceland			**Scotland**		
West[a]	1	60	Dumfries & Galloway	10	466
Southwest	4	390	Strathclyde	24	489
South	5	578	Borders	10	195
Southeast	1	7	Lothians	3	97
North	4	165	Central	8	96
Total	**15**	**1,200**	Fife	5	70
			Tayside	17	339
Northern Ireland			Grampian	2	15
Down	12	249	Highland	26	540
Antrim	14	723	Western Isles	6	230
Armagh	16	451	Orkney	16	231
Londonderry	10	855	Shetland	22	93
Tyrone	8	117	**Total**	**149**	**2,861**
Fermanagh	37	1,268			
Total	**97**	**3,663**	**Isle of Man**		
			Total	**1**	**14**
Republic of Ireland					
Donegal	26	943	**England**		
Leitrim	36	374	Gloucestershire	1	2
Sligo	20	362	West Sussex	1	2
Mayo	41	746	East Sussex	1	1
Roscommon	30	648	Kent	2	21
Longford	9	189	Essex	1	3
Galway	34	1,147	Northamptonshire	1	2
Clare[a]	9	552	Bedfordshire	1	2
Limerick	7	221	Cambridgeshire	4	321
Tipperary	8	252	Norfolk	7	1,339
Kerry	9	260	Lincolnshire	2	29
Cork	6	190	Leicestershire	1	2
Waterford	6	248	Nottinghamshire	1	3
Wexford	4	235	East Yorkshire	3	75
Laois	2	47	Hereford & Worcestershire	1	12
Offaly	8	699	Staffordshire	1	4
Kildare	4	114	Shropshire	2	5
Wicklow	2	54	Cheshire	1	8
Dublin	1	19	Merseyside	1	6
Meath	4	97	Greater Manchester	2	11
Westmeath	5	360	Derbyshire	1	1
Cavan	26	874	South Yorkshire	1	6
Monaghan	19	385	North Yorkshire	3	83
Louth	1	51	Northumberland	8	371
Total	**317**	**9,067**	Lancashire	4	1,274
			Cumbria	7	356
Wales			**Total**	**58**	**3,939**
Dyfed	2	10			
Gwynedd	1	23			
Clywd	3	79			
Total	**6**	**112**	**Grand Total**	**643**	**20,856**

[a] Includes estimates for missed birds of 44 in West Iceland and 150 in County Clare, Ireland.

public of Ireland 16% in Scotland, 14% in England, 1% in Wales and 6% in Iceland (Cranswick *et al.* 1996). There was a significant difference between 1995 and 2000 in the distribution of swans among countries ($\chi^2_4 = 141$, $P < 0.001$, on summing data for England, Wales and the Isle of Man). This was due to an increase in the proportion in

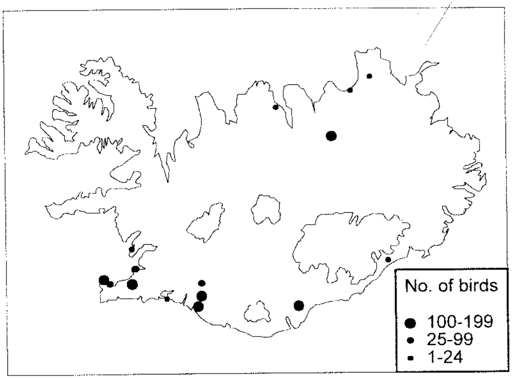

Figure 1. Distribution of Whooper Swans in Iceland in January 2000. Major glaciers are also depicted.

England and Wales relative to Scotland (χ^2_1 = 131, $P < 0.001$), rather than to changes in the proportion wintering in Northern Ireland relative to the Republic of Ireland (χ^2_1 = 0.60, n.s.), or in the proportion that over-wintered in Iceland rather than migrating to other parts of the range (χ^2_1 = 1.10, n.s.).

A comparison of the data presented in Table 1 with those for the 1995 census, presented by Cranswick *et al.* (1996), found that the proportional increase in numbers counted between 1995 and 2000 was most evident in England (+77%), with large increases in Northern Ireland (+32%), the Republic of Ireland (+28%) and Iceland (+24%) also, but only a moderate increase in Scotland (+10). Increases in just five counties (Lancashire, Norfolk, Cambridgeshire, Northumberland, and Cumbria) accounted for 85% of the increase in England. Although numbers fell in seven counties, these were vastly outweighed by gains in the other 21 counties (-45 and +1,755 birds, respectively). The increase of over 1,000 birds in Northern Ireland was reflected in higher counts in all counties except Tyrone; increases were greatest in Counties Armagh and Fermanagh primarily a result of large counts at Lough Neagh and Upper Lough Erne, respectively. The increase in the Republic of Ireland was evident throughout the country, with increases in 18 counties (+2,504 birds) and decreases in eight (-733 birds).

The increase in total numbers between 1995 and 2000 was accompanied by an increase in the number of flocks in the Republic of Ireland (+39%), Northern Ireland (+14%) and England (+35%), but not in Scotland (-9%) (Table 2). The increase in the proportion of flocks in the Republic of Ireland was significant (χ^2_1 = 6.01, $P < 0.02$), and the decrease in the number of flocks in Scotland was also significant (χ^2_1 = 7.71, $P < 0.01$, Table 2), in comparison with other parts of Britain and Ireland. Although numbers in England increased by 77% between the two censuses, the proportion of flocks recorded in England did not differ between 1995 and 2000 (χ^2_1 = 0.45, n.s., Table 2), and the proportion of flocks recorded in Northern Ireland also did not change between years (χ^2_1 = 0.08, n.s.). Average flock sizes did not differ between the two censuses (n.s. t-tests in Table 2). The most notable change appeared to be the number of swans in flocks of at least 1,000 birds in Great Britain in the January 2000 census (Fig. 3). In both 1995 and 2000, the number of birds observed in flocks of 500 or more occurred at just two sites, Martin Mere (Lancashire) and the Ouse Washes (Norfolk and Cambridgeshire). These two sites accounted for most of the increase recorded in Great Britain between 1995 and 2000, whereas in Ireland the increase in 2000 was recorded across a range of flock sizes (Fig. 3).

Age Structure and Brood Sizes

Over 70% of the birds counted were aged, and the overall proportion of first-winter (juvenile) birds was 16.8% (N = 14,627) (Table 3). Over 68% of birds were aged in each country except Scotland, where only 45% were aged. The overall proportion of juveniles was 17.5% in Ireland, 16.9% in Britain, 16.3% in Northern Ireland and 13.7% in Iceland. Variation between all six countries (Iceland, Northern Ireland, Republic of Ireland, Scotland, England and Wales) in the proportion of young recorded at sites in each country did not differ significantly ($F_{5,356}$ = 0.97, n.s.).

Within Iceland, proportions of young varied from 28.6% in the southeast to 7.7% in the north, but overall the variation be-

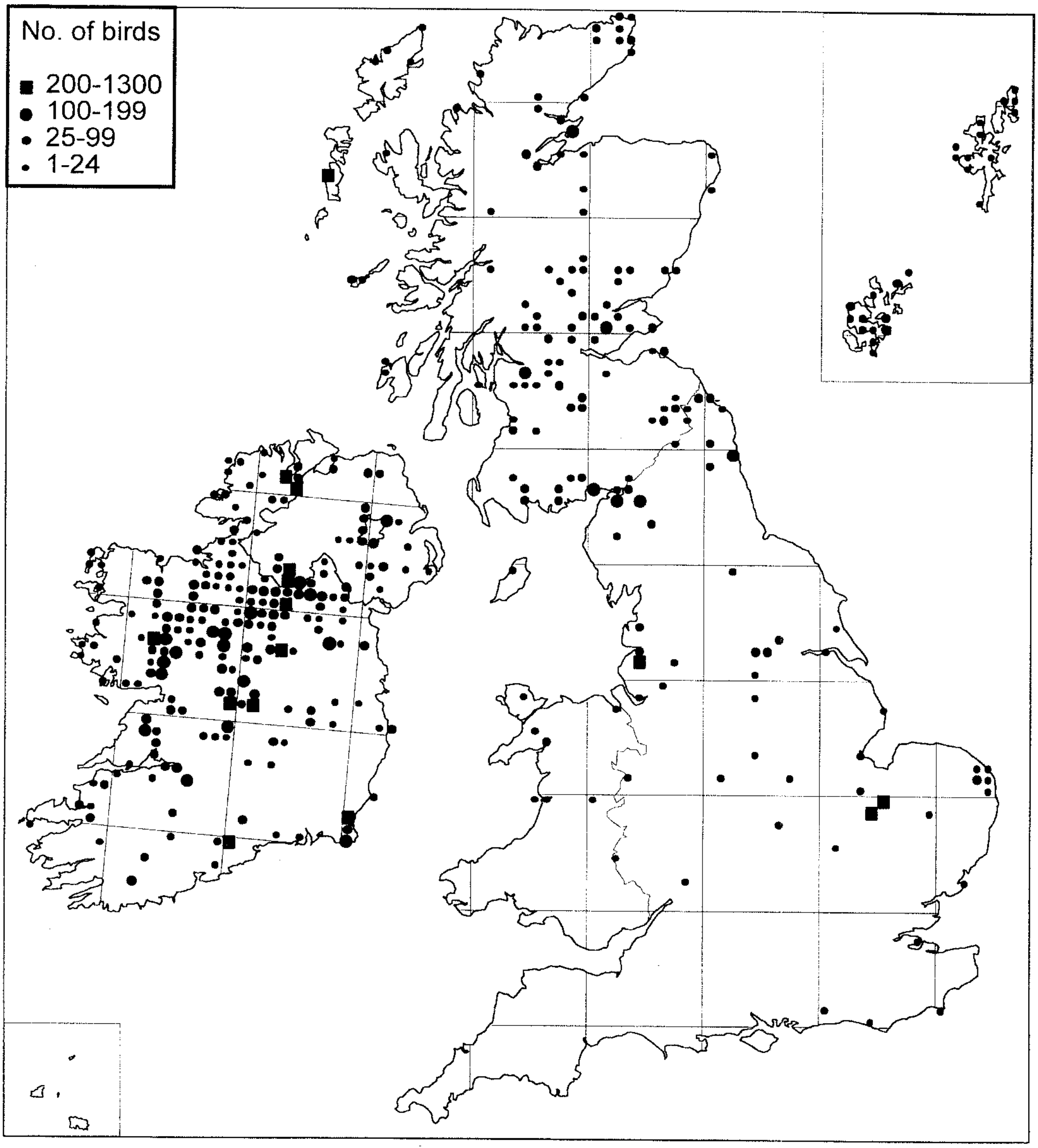

Figure 2. Distribution of Whooper Swans in Britain and Ireland in January 2000. Inserts illustrate Orkney and Shetland (top right) and the Channel Islands (bottom left). Counts of birds estimated for incompletely covered areas are not shown. Numbers are summed by 10-km square. The grid lines on the map are for 100-km squares.

tween regions in Iceland was not significant ($F_{2,12}$ = 2.87, n.s., small samples from west and southeast Iceland excluded; Table 3). In Ireland, proportions of young varied between 15.1% and 19.0%, the latter being the highest of any region away from Iceland. Similarly, in Britain, regional values varied between 16.1% and 18.1% (excluding northwest Scotland due to small sample size) except for a low of 13.9% in southwest Scotland (Table 3). None of the differences between regions within individual countries, however, was significant ($F_{8,58}$ = 1.67, n.s., and $F_{4,275}$ = 0.82, n.s., for Britain and all- Ireland respectively).

The overall mean brood size was 2.3 (N = 748) and differences between countries (excluding Iceland and Wales, due to small sample sizes) were not significant (range = 2.2–2.5, $F_{3,718}$ = 1.89, n.s., Table 3). In Britain and Ireland, excluding regions with samples of

Table 2. Number of flocks and average flock sizes during Whooper Swan censuses in 1995 and 2000. The proportion of flocks recorded in each country in 1995 was compared to that recorded in 2000 using χ^2, with d.f. = 1 when comparing each country with the rest of Britain and Ireland, and d.f. = 3 for the overall value. Independent t-tests were used to compare flock sizes recorded at sites, within each country and overall, between the two censuses.

		1995		2000					
	N	Mean flock size ± SE	N	Mean flock size ± SE	χ^2	P	t	d.f.	P
Northern Ireland	83	33.5 ± 5.9	95	38.2 ± 5.0	0.08	n.s.	0.60	176	n.s.
Republic of Ireland	226	31.3 ± 3.7	314	28.2 ± 2.5	6.01	<0.02	0.72	538	n.s.
Scotland	162	16.1 ± 1.7	148	17.9 ± 2.4	7.71	<0.01	0.64	308	n.s.
England	43	52.8 ± 27.0	58	67.9 ± 29.8	0.45	n.s.	0.37	99	n.s.
Wales	8	13.6 ± 4.6	6	18.7 ± 8.6	—	—	0.55	12	n.s.
Overall	522	28.4 ± 3.0	621	30.8 ± 3.2	9.05	<0.05	0.56	1144	n.s.

less than ten broods, regional variation in brood sizes was highly significant (range 1.8–3.2, $F_{12,731} = 2.74$, $P < 0.001$), with high values in Wales ($\bar{x} = 3.2$, N = 12) and southeast Ireland ($\bar{x} = 2.7$, N = 50), the latter also being the region where the highest proportion of juveniles was found (Table 3).

Brood size of one, two and three cygnets accounted for 84% of broods overall (30%, 33% and 22%, respectively). Broods of four (11%), five (3%), six (1%) and seven (0.1%) were infrequent. There was significant variation in the number of broods of each brood size between countries (when broods of four or more were combined into one category) ($\chi^2_{15} = 37.1$, $P < 0.01$) (Table 3). Brood sizes of one cygnet and of four or more cygnets were both more frequent in Northern Ireland (41% and 25%) than in other countries (range = 21%–34% and 6%–19%; $\chi^2_1 = 7.04$, $P < 0.01$ and $\chi^2_1 = 7.84$, $P < 0.01$, respectively, Table 3), and Scotland had a lower proportion of broods with four or more cygnets (6%) than did other countries ($\chi^2_1 = 7.59$, $P < 0.01$).

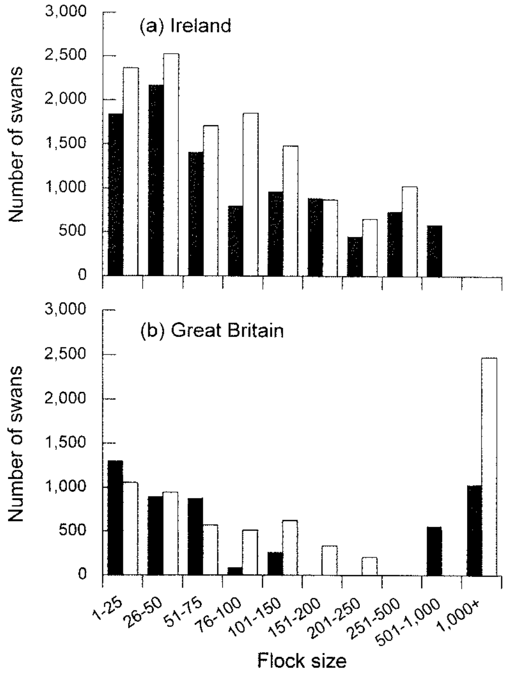

Figure 3. The number of Whooper Swans recorded in different flock sizes during censuses in 1995 (solid bars) and 2000 (open bars). Note that the flock size categories increase in range for the larger flocks.

Habitat Use

Swans were recorded in 24 habitats during the survey (Appendix 2), although the majority of birds (96%; N = 16,209) were recorded in 18 of these (Table 4). Distribution of swans across habitats was consistent between countries (Friedman test, $\chi^2_4 = 5.09$, n.s., Wales excluded due to small sample size). Use of permanent standing water was high in both Britain and Ireland, accounting for around 24% of all habitats used, although the smaller number of swans wintering in Iceland occurred mainly on rivers (59%) or coastal waters (27%), habitats that were infrequently used elsewhere in the wintering range. Terrestrial farmland habitats were also used in all regions, with 68% of birds in Britain and Ireland found on these habitats, but just 14% in Iceland. About half of all birds in Britain and Ireland were re-

Table 3. Age structure and brood sizes of Whooper Swans in Ireland, Britain and Iceland in January 2000 (see Appendix 1 for regional definitions).

			Brood size								
	N	% juveniles	7	6	5	4	3	2	1	Total	Mean
Iceland											
West	16	25.0	—	—	—	—	—	—	—	—	—
Southwest	223	24.2	0	0	1	1	3	1	2	8	2.7
South	412	9.7	0	0	0	2	5	5	2	14	2.5
Southeast	7	28.6	—	—	—	—	—	—	—	—	—
North	156	7.7	0	0	0	0	0	1	1	2	1.5
Total	**814**	**13.7**	**0**	**0**	**1**	**3**	**8**	**7**	**5**	**24**	**2.5**
Frequency (%)			0.0	0.0	4.2	12.5	33.3	29.2	20.8		
Northern Ireland											
Total	**3,215**	**16.3**	**1**	**3**	**2**	**20**	**16**	**20**	**43**	**105**	**2.3**
Frequency (%)			1.0	0.9	1.9	19.0	15.2	19.0	41.0		
Republic of Ireland											
Northwest	3,271	17.2	0	1	6	24	45	78	61	215	2.2
Northeast	1,611	18.1	0	0	3	5	23	37	32	100	2.1
Southwest	722	15.1	0	0	0	0	7	9	12	28	1.8
Southeast	970	19.0	0	3	0	11	12	15	9	50	2.7
Total	**6,574**	**17.5**	**0**	**4**	**9**	**40**	**87**	**139**	**114**	**393**	**2.2**
Frequency (%)			0.0	1.0	2.3	10.2	22.1	34.4	29.0		
Britain											
Northern Isles	188	16.0	0	0	0	2	3	4	4	13	2.2
NW Scotland	19	10.5	0	0	0	0	0	0	0	0	—
NE Scotland	261	18.0	0	0	0	1	3	6	9	19	1.8
SW Scotland	309	13.9	0	0	0	0	8	7	12	27	1.8
SE Scotland	426	18.1	0	0	1	1	10	13	5	30	2.3
Wales	102	17.7	0	0	3	2	2	4	1	12	3.2
NW England	1,579	17.6	0	1	6	15	22	44	25	113	2.4
NE England	344	16.3	0	0	1	1	5	2	9	18	2.1
EC England	795	16.1	0	1	0	0	2	1	0	4	3.5
S England	1	0.0	0	0	0	0	0	0	0	0	—
Total	**4,024**	**16.9**	**0**	**2**	**11**	**22**	**55**	**81**	**65**	**236**	**2.3**
Frequency (%)			0.0	0.9	4.7	9.3	23.3	34.3	27.5		
Grand Total	**14,627**	**16.8**	**1**	**9**	**23**	**85**	**166**	**247**	**227**	**758**	**2.3**
Frequency (%)			0.1	1.2	3.0	11.2	21.9	32.6	29.9		

corded in pastures, but this figure varied greatly between regions from 33% in Britain to over 76% in Northern Ireland. Except in Iceland, where no swans were recorded on pasture in winter, a high proportion of birds were recorded on improved pasture ($\bar{x}$ = 35% for Britain and Ireland). Dry grassland habitats, either improved or unimproved, held 41.3% of birds and wet pastures 11.4% of birds in Britain and Ireland, although within the Republic of Ireland the values were similar (26% and 28%, respectively). Arable habitats were used by less than 10% of birds in Ireland, but by 29% of birds in Britain. Almost 25% of birds in Britain were found on 'growing' crops (those which would not ordinarily have been harvested at the time of the census), largely Oilseed Rape (*Brassica napus*) and winter cereals.

DISCUSSION

The total of 20,856 Whooper Swans estimated for Ireland, Britain and Iceland in January 2000 is the highest recorded for the Icelandic-breeding population. Coverage in January 2000 was comprehensive and believed to be more thorough than achieved previous-

Table 4. Proportion of Whooper Swans among habitat types in January 2000.

Habitat type	Iceland	Northern Ireland	Republic of Ireland	Britain	Britain and Ireland
Number of swans	1,156	3,810	7,734	4,665	16,209
Permanent standing water	0	12.0	26.4	29.1	23.9
River	59.1	3.9	4.0	4.3	4.1
Coastal	26.5	<0.1	1.6	5.0	2.3
All pasture	0	76.1	53.8	33.0	52.7
improved dry	0	65.6	25.6	16.8	32.3
improved wet	0	4.3	12.9	8.3	2.7
rough dry	0	0	0.3	6.7	9.0
rough wet	0	6.2	15.0	1.2	8.7
All arable	14.4	8.0	9.9	28.6	15.2
waste	14.4	7.6	9.4	5.9	7.9
growing	0	0.4	0.5	22.7	7.3
Other	0	0	4.2	0	1.9

Definitions of the habitat categories are: (1) *Permanent standing water* = natural permanent lake, artificial lake/reservoir, gravel pit; (2) *River* = non-tidal river, freshmarsh; (3) *Coastal* = tidal river/estuary, saltmarsh, brackish lake, open coast; (4) *Improved pasture (dry)* = dry pasture managed to improve sward (e.g., fertilized, even, weed-free sward), may include dry reseeded pasture; (5) *Rough/unimproved pasture (dry)* = dry apparently unmanaged sward (e.g., longer, rank sward); (6) *Improved pasture (wet)* = improved pasture (flooded), reseeded pasture (wet), callow—improved; (7) *Rough/unimproved pasture (wet)* = rough/unimproved pasture (flooded), turlough—rough/unimproved, callow—rough/unimproved; (8) *Arable (waste)* = stubble, potatoes, carrots, sugar beet; and (9) *Arable (growing)* = winter cereal, oil seed rape.

ly. A combination of high levels of coordination at regional and local levels ensured detailed, systematic searches of nearly all known sites and subsequent checking of data minimized the potential biases and sources of error associated with duplicate or missed counts. Coverage was incomplete in only a few areas and is estimated to have missed only a small proportion of the census total (194 birds). Consequently, the census is believed to provide an accurate assessment of population size and distribution in January 2000. It is recommended that the population estimate is revised to 20,900 and that the 1% threshold (for identifying sites of international importance) should be adjusted to 209 birds.

The productivity assessment of 16.8% in January 2000 compares with a value of 17.9% recorded during the 1995 census and a mean of 18.1% for the breeding seasons 1995 to 1999 (Irish Whooper Swan Study Group unpubl. data, using methods similar to those used in the 2000 census). While there is a high degree of similarity between these estimates, it should be recognized that biases in age assessments are well known; adult to juvenile ratios increase with flock size (Brazil 1981), and Rees *et al.* (1997) demonstrated the interactive effects of habitat, geographical location and season on the distribution of family groups in the United Kingdom. Nevertheless, given that the sample for the 2000 census comprises 70% of the population, this gives reasonable confidence that the figure is close to the true proportion of young in January 2000.

The census total in January 2000 exceeds the previous highest count of 18,035 in 1991 (Kirby *et al.* 1992) by 16%, and represents a 32% increase since the last census in 1995 (Cranswick *et al.* 1996). Whereas the 1991 total is considered to be a slight overestimate, that of 1995 is believed to be representative of the population at that time (Cranswick *et al.* 1996). The increase in numbers between 1995 and 2000 equates to an average annual rate of increase of 6.3% during the period. Given average annual productivity during the period of 18.1% (Irish Whooper Swan Study Group, unpub. data), an average annual mortality of 11.8% for all birds over the period is required to account for the change in population size between the two censuses. This compares with a derived annual mortality estimate of 20% between 1991 and 1995, to account for the population decline between the two censuses in those years, and an observed average annual productivity of 16.7% for the period (Cranswick *et al.* 1996).

Possible confounding factors in these calculations are that the productivity assessments used in Cranswick *et al.* (1996) were derived from smaller sample sizes and from just three British sites (Wildfowl and Wetlands Trust Centers at Caerlaverock, Martin Mere and on the Ouse Washes), although they are consistent with other figures for the 1990s (generally between 16% and 18%). Further, the 1991 census total is considered to be an overestimate. Although this cannot be accurately quantified, the degree of error in census totals is believed to be relatively small and the decrease in population size between 1991 and 1995 is considered genuine. Lastly, the arrival of Whooper Swans from the population wintering in continental Europe, indistinguishable in the field from those in the Icelandic-breeding population, may have resulted in increased numbers counted in Britain and Ireland. Although evidence for or against this last argument is limited, the wintering distributions of the two populations are thought to be largely discrete; ringed birds from the European population have been recorded widely within Britain and Ireland but numbers of sightings remain low (Laubek *et al.* 1998). Moreover, there is little anecdotal information of Whooper Swans arriving in autumn from the east to the Ouse Washes which, given large number of birdwatchers in east-central England, would be expected if there was a substantial influx of Whooper Swans from the continental population. Whooper Swans banded in Iceland have been sighted on the continent in winter (Gardarsson 1991), but this suggests that only about 400–600 birds are involved. Any movements between populations in January 2000 have not been incorporated into the totals presented here.

Although not conclusive, it is thought that differences in the sources of productivity data, double-counting during the 1991 census, and the inclusion of birds from other populations in the census total have only a relatively minor influence on the these calculations. Consequently, it is believed that a decrease in mortality is likely to be the major factor responsible for the difference in the annual rate of change in population size between the periods 1991 to 1995 (-3.3%) and 1995 to 2000 (+6.3%). An independent measure of mortality, however, is necessary to confirm this assertion and determine the value more precisely. The development of standardized age assessment protocols, and the continued banding of the Icelandic and Northwest Mainland European populations to assess survival rates and the degree of intermixing of the populations on the wintering grounds are essential to the development of population models and better explanation of changes in abundance.

At a country level, the proportional increase between 1995 (data described in Cranswick *et al.* 1996) and 2000 was most evident in England, with large increases also in Northern Ireland, the Republic of Ireland and Iceland, but only a moderate increase in Scotland. Increases in just five counties (Lancashire, Norfolk, Cambridgeshire, Northumberland, and Cumbria) accounted for 85% of the increase in England. Although numbers fell in seven counties, these were vastly outweighed by gains in the other 21 counties. Increased numbers in the Republic of Ireland, Northern Ireland and England between 1995 and 2000 were accompanied by increases in the number of flocks (+39%, +14% and +35%, respectively), while there was a decrease in Scotland (-9%). Average flock sizes were broadly similar between the two censuses and, although those in England increased by 29%, none of the changes at a country level or overall were significant. The increase in numbers of flocks in England, however, largely reflected small numbers of birds in counties in which birds were not previously recorded. Thus, it appears that the overall increase in numbers in Ireland was evenly distributed among flock sizes, manifest as both the development of new flocks and, presumably, increases in the size of flocks at established sites (Fig. 3), whereas, in Britain, birds remained restricted to existing flocks with increasing concentration of the population particularly at the key sites, namely Martin Mere and the Ouse Washes (these two sites accounting for all birds observed in flocks of 500 or more).

While direct comparison of habitat use with previous censuses is made difficult due to the refinement of habitat classifications, the overall pattern of occurrence on farmland was similar in 1995 (67%) and 2000 (68%). Within this, however, the proportion of swans using arable habitats increased from 7% in 1995 to 15% in 2000, balanced by a decrease in birds using pastures from 62% to 53%. The proportion of birds using permanent standing water was 12% lower in 2000 also. Further examination of the type of arable crops exploited suggests that this development may not pose as great an agricultural problem as at first suggested. Only 5% of birds found on arable habitats in Ireland occurred on unharvested arable crops (i.e., winter cereal and Oilseed Rape). The equivalent proportion in Britain, though much higher (80%), involved only 1,060 birds, largely in northern England and southeast Scotland. There is, therefore, little evidence to suggest that the potential for agricultural conflict on arable habitats has increased as it has, for example, in parts of continental Europe (Laubek 1995). The use of grassland pastures is probably more significant in this respect, particularly given the large numbers of birds using this habitat and the consequent higher potential for damage, through loss in yield by defoliation and/or puddling (Colhoun and Day 2002). Such damage, however, is perhaps less noticeable due to the nature of the crop and the fact that birds using this habitat are generally widely dispersed at low density, lessening the chance of intensive damage in localized areas.

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Appendix 1. Regional definitions, by country.

Iceland

West: Vestur-Bardastrandarsysla to Kjosarsysla
Southwest: Reykjavik and Reykjanes Peninsula
South: Arnessysla, Rangarvallasysla, Vestur-Skaftafellssysla
Southeast: Austur-Skaftafellssysla, Sudur-Mulasysla
North: Sudur- and Nordur-Thingeyjarsysla

Northern Ireland

Down, Antrim, Armagh, Londonderry, Tyrone, Fermanagh

Republic of Ireland

Northwest: Donegal, Leitrim, Sligo, Mayo, Roscommon, Galway
Northeast: Longford, Westmeath, Cavan, Monaghan, Louth, Meath, Dublin
Southwest: Clare, Limerick, Kerry, Cork
Southeast: Tipperary, Offaly, Laois, Kildare, Wicklow, Wexford, Carlow, Kilkenny, Waterford

Scotland

Northern Isles: Orkney, Shetland
Northwest: Highland South West, Western Isles
Northeast: Grampian, Highland South East, Highland North
Southwest: Dumfries & Galloway, Strathclyde
Southeast: Borders, Lothians, Central, Fife, Tayside

Wales

Gwent, Mid Glamorgan, South Glamorgan, West Glamorgan, Dyfed, Powys, Gwynedd, Clwyd

England

Northwest: Cheshire, Merseyside Greater Manchester, Isle of Man, Lancashire, Cumbria
Northeast: Cleveland, Durham, Tyne & Wear, Northumberland
East Central: Northamptonshire, Bedfordshire, Cambridgeshire, Suffolk, Norfolk, Lincolnshire, Leicestershire, Nottinghamshire, Humberside, Warwickshire, West Midlands, Staffordshire, Shropshire, Derbyshire, South Yorkshire, West Yorkshire, North Yorkshire
South: Cornwall, Devon, Dorset, Somerset, Avon, Gloucestershire, Wiltshire, Hampshire, Isle of Wight, West Sussex, East Sussex, Kent, Surrey, Greater London, Essex, Hertfordshire, Buckinghamshire, Berkshire, Oxfordshire, Hereford & Worcester

Note that Britain comprises Scotland, Wales and England. The United Kingdom comprises Britain and Northern Ireland.

Long-term Trends in the Number of Whooper Swans Molting at Lake Myvatn, Iceland, 1974-2000

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Abstract.—The number of Whooper Swans (*Cygnus cygnus*) molting at Lake Myvatn, Iceland, was monitored for 27 years, from 1974 to 2000. For most of this period, Lake Myvatn held the largest concentration of Whooper Swans molting on freshwater in Iceland, although larger numbers are found on coastal bays and brackish lagoons. Two lakes less than 50 km from Myvatn that also receive molting Whooper Swans have been monitored since 1989. The numbers of Whooper Swans molting in the general region (4,500 km^2) were probably stable from 1974 to 1998. On Lake Myvatn, molting numbers averaged 470 ± 21 (SE) in the period 1974–2000. There was considerable short-term variation in numbers between years, perhaps for demographic reasons or because of changes in food availability. At Lake Myvatn, molting swans occurred mainly in two bays, with different bottom vegetation, and numbers on each bay varied inversely from year to year. Numbers molting on Lake Myvatn showed a linear declining trend, with an average loss of 10.5 individuals per year. This decline correlated significantly with a reduction in the size of the available habitat due to underwater strip-mining (diatomite extraction), which increased the depth of the macrophyte zone to a level that no longer supported the plant species mainly eaten by molting Whooper Swans.

Key words.—*Cygnus cygnus*, Iceland, monitoring, Myvatn, shallow lakes, waterfowl, Whooper Swan.

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Whooper Swans (*Cygnus cygnus*) molting at Lake Myvatn were counted in early August each year, for the years 1974–2000 inclusive, as part of a long-term waterbird monitoring program at the site. For most of this period, Lake Myvatn held the largest concentration of Whooper Swans molting on freshwater in Iceland, although larger numbers molted on shallow bays on the west coast and on brackish lagoons in the southeast (Gardarsson and Skarphedinsson 1984). The annual censuses of waterbirds at Lake Myvatn are part of a broad-based monitoring scheme, designed to provide up-to-date scientific information for advising on the conservation and management of this internationally important wetland (Gardarsson and Einarsson 2000).

Lake Myvatn is well known as a site of many unusual scenic, geological and biological features. The lake and its effluent river, the Laxa, have long been the basis of a rich fishery and the harvesting of wild duck eggs is traditional in the region (Gudmundsson 1979). Since about 1950, Lake Myvatn and the surrounding area has come under increasing human pressure, most notably: (1) widespread changes in farming and fishing practices; (2) increased local population, consumption, tourism and communications; (3) harnessing of hydroelectric and geothermal energy and; (4) the extraction of bottom sediments from the lake for the production of diatomite, which is used as an absorbent and in industrial filters. Other threats to waterbirds include the introduced American Mink (*Mustela vison*), which at present are heavily controlled. A law aimed at protecting the entire Myvatn region (about 6,000 km^2) from the deleterious effects of industry and tourism was enacted in 1973. The wetlands of the protected region, which total about 200 km^2, were afforded international protection under the Ramsar Convention in 1978.

The largest industrial activity in the Myvatn region today is the production of diatomite from sediment, which is mined from the bottom of the lake. Diatomite extraction began in 1967, six years before the area was protected by law. No environmental baseline studies were made before extraction began, but it has since been shown to have serious consequences for the lake ecosystem, resulting from mobilization of nutrients and from the change of bottom topography which causes sediment relocation (see review in Gardarsson and Einarsson 2000).

In this paper we describe long-term changes in the numbers and distribution of Whooper Swans molting at Lake Myvatn and at other sites in the vicinity. The results are discussed in relation to variation in water depth associated with diatomite extraction.

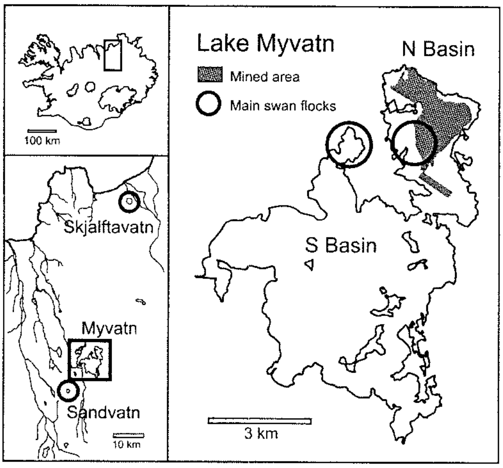

Figure 1. Map showing the location and main features of Lake Myvatn. Note the mined area in the year 2000 (shaded) and the two main molting areas on the lake (rings). Inset: (above) map of Iceland showing the location of the 4500 km^2 study region; (below) the three study areas in the region, where molting swans were counted annually in 1989 to 2000.

STUDY AREA

The main study area was Lake Myvatn (65°40'N, 17°00'W, area 37 km^2, altitude 277 m) and 18 km^2 of waterbodies lying in a shallow depression of about 400 km^2. The lake is divided into a North Basin (8 km^2) and a South Basin (29 km^2). The mean depth is 2.2 m, about 15 km^2 are less than 2 m deep and approximately half of that area is covered with vegetation. Most primary production in Myvatn is by benthic diatoms (Jonasson 1979). Blooms of blue-green algae occur in many summers. Important macrophytes in the shallow North Basin (0.8–2.5 m deep) are the Slenderleaf Pondweed (*Potamogeton filiformis*), a preferred waterfowl food, and the Spiked Water-milfoil (*Myriophyllum spicatum*), avoided by waterfowl at Myvatn, as well as green algae (*Cladophora* spp.). In the deeper South Basin of the lake (2.5–4 m), *Cladophora* covers an area varying from 4 to 16 km^2; and also occurs in shallow, sheltered bays. Midge larvae (Diptera: Chironomidae) and small crustaceans (Cladocera: Chydoridae) dominate the invertebrate bottom fauna. There are no herbivorous fish; only three fish species occur, Three-spined Stickleback (*Gasterosteus aculeatus*), Arctic Charr (*Salvelinus alpinus*) and Brown Trout (*Salmo trutta*). Some 10,000–15,000 pairs of waterbirds of about 20 species commonly breed at the site, the most abundant being Tufted Duck (*Aythya fuligula*), Greater Scaup (*A. marila*) and Eurasian Wigeon (*Anas penelope*).

From 1989 onwards, molting swans were counted annually over an area of 4,500 km^2 in northern Iceland (Fig. 1). In addition to Lake Myvatn, only two concentrations of molting swans were found. In the Kelduhverfi district, most swans molted at Lake Skjalftavatn (50 km north of Myvatn, surface area 4.7 km^2), which was formed by tectonic subsidence in 1975. Another flock was found at Lake Sandvatn (9 km southwest of Myvatn, area 2.4 km^2). Both are shallow lakes, but the bottom vegetation has not been surveyed.

METHODS

Numbers of Whooper Swans at molting sites are generally stable between 25 July and 20 August, while the birds are flightless (Gardarsson and Skarphedinsson 1984). In the main study area of Lake Myvatn and its surrounding wetlands, molting swans and other waterbirds were counted at least once annually in this period on all waters (55 km^2). During the 27-year study, from 1974–2000, the swans were counted between 3 and 15 August in 24 years; in 1982 and 1983 the counts were on 28 July and 29 July, respectively, and in 1977 on 10 September. From 1989 onwards, molting swans were also counted annually at Sandvatn and Skjalftavatn. Swans were usually counted from the ground, using telescopes, but sometimes from the air or from aerial photographs.

There is little direct information on long-term temporal variation in submerged bottom vegetation at Myvatn. However, diatomite has been extracted from the shallow North Basin since 1967. This underwater strip-mining has resulted in an increase in depth of shallow areas previously covered by rooted macrophytes to a level (>2 m depth) that no longer supports the plant species mainly used by molting Whooper Swans. Maps, aerial photographs and field measurements were used to plot the excavated area and to estimate changes over time in the area of shallow water and water exceeding 2 m in depth. Extensive ground surveys were carried out in 1977, 1983 and 2000 (North Basin only). The area of shallow habitat was estimated in nine years for which vertical aerial photographs were available: 1963, 1972, 1975, 1977, 1980, 1982, 1985, 1992 and 2000.

RESULTS

The total number of Whooper Swans molting regionally, on all three lakes, was 597 ± 28 (SE) in 1989 to 2000 (Fig. 2). The only regional total available before 1989 was for 1974 when an aerial survey of the region yielded 636 molting Whooper Swans, 106 of these in Kelduhverfi where the wetlands were changed by tectonic upheavals in 1975. Lake Sandvatn held no molting swans when surveyed in early August 1981. Thus there are indications that the regional number of

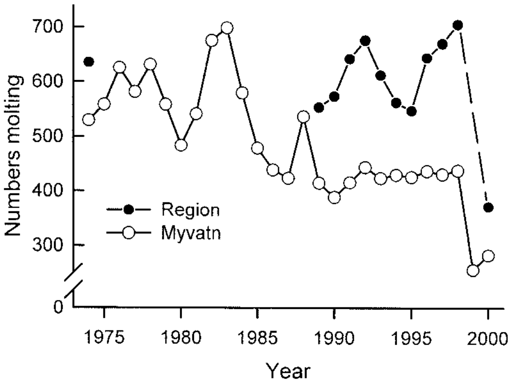

Figure 2. Numbers of Whooper Swans molting in the Myvatn study area (about 400 km^2) in 1974–2000 and in the region of North Iceland (4,500 km^2) where molting swans were monitored in 1989-2000.

Whooper Swans did not change greatly prior to the annual censuses of the region. Since 1989, mean numbers were 46 ± 9 (range 6–114, N = 12 years) at Sandvatn and 128 ± 21 (range 8–210, N = 11 years) on Skjalftavatn, corresponding to densities of 19 birds km^{-2} and 27 birds km^{-2}, respectively. A mean of 485 ± 21 (13 km^{-2}, or 32 km^{-2} if only shallow areas <2 m deep are considered) swans molted each year in the Myvatn study area. Of these, a mean of 470 ± 21 swans molted in the two main molting flocks on the lake itself, and an additional 15 in various marginal localities. Total numbers at Myvatn fluctuated considerably, with a peak of almost 700 in 1982–1983, generally low numbers of around 400 after 1985, and less than 300 in 1999 and 2000. The decline in the last two years is also seen at Skjalftavatn.

The two main molting sites on Lake Myvatn, which are separated by a low peninsula, only 1 km wide, differ in their benthic macrophyte vegetation. Most birds (380 ± 19, range 230–640) occurred in the western part of the North Basin over beds of pondweeds and *Cladophora* spp. The second flock molted in a sheltered bay of the South Basin, Neslandavik (91 ± 18, range 3–323), where the swans fed on *Cladophora* spp., which formed a loose carpet under Spiked Water-milfoil. Until 1990, the numbers of swans at the two main molting sites on Lake Myvatn varied in an inverse manner (Pearson correlation for 1974–1990, $r_{15} = -0.58$, $P < 0.05$), but few birds were found on the South Basin in subsequent years (Fig. 3), thus the inverse relationship was not apparent when all years were considered (Pearson correlation for 1974–2000, $r_{25} = -0.25$, n.s.).

Despite substantial annual variation, numbers of swans molting at Myvatn showed a significantly decreasing trend. Between 1974 and 2000, the numbers on Lake Myvatn decreased by 50%, from approximately 600 to 300. Because short-term fluctuations are so large, the trend was not evident until 1990. The density of molting swans on the lake was a linear function of the area of the bottom <2 m deep (Fig. 4). The shallow area of the North Basin has been reduced by about 10 ha per year, from 7 km^2 in 1963, before the start of mining, to 3 km^2 in 2000, fitting quite closely to the decline in the number of swans molting at the site. The number of molting swans per year was significantly related to the area (ha) of the bottom <2 m deep in that year ($Y = -76.26 + 1.20\ x$, where Y is the number of molting swans on Lake Myvatn and x is the area <2 m deep; $r^2 = 0.64$, $F_{1,5} = 9.10$, $P < 0.05$). Since there was little variation in the area of habitat lost each year, the relationship can also be expressed as a linear regression of molting swans over time ($Y = 623.30 - 10.52\ x$, where x is the number of years since 1974; $r^2 = 0.61$, $F_{1,25} = 36.62$, $P < 0.001$).

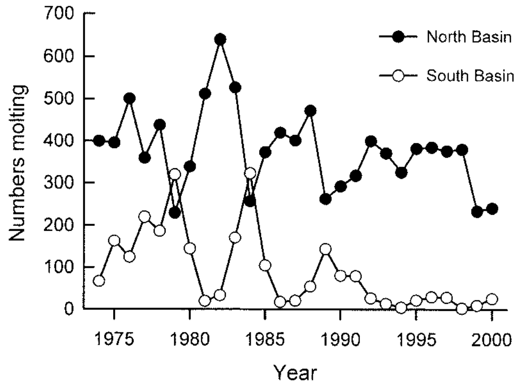

Figure 3. Numbers of Whooper Swans molting in the North Basin and the South Basin of Lake Myvatn in 1974–2000. A small number of birds molting elsewhere in the Myvatn study area are omitted.

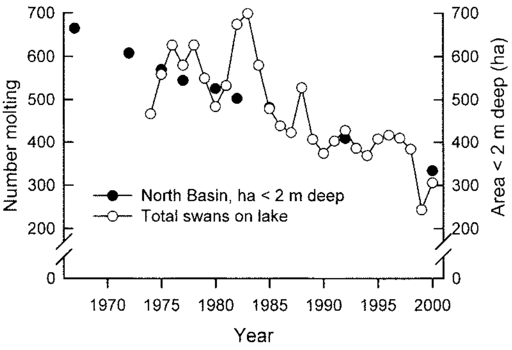

Figure 4. Total numbers of Whooper Swans molting in the North Basin plus the South Basin of Lake Myvatn in 1974–2000 compared with the area (ha) of shallow water (<2 m) in the North Basin.

DISCUSSION

A recent study of seven species of diving ducks at Myvatn has considered factors limiting the density of molting waterfowl. The ducks showed a range of responses, related to their life histories, but molt dispersal was often related to food levels on a local or regional scale (Einarsson and Gardarsson 2000). It seems reasonable that swans might be similarly influenced by food availability. The annual variation in distribution, with molting swans switching between two sites at Lake Myvatn with different food supplies, strongly suggests a nutritional response, but there are currently no data to support this hypothesis. Variation in disturbance also may affect the selection of a molting site, and this was observed in 1980 when corralling the birds for banding caused 124 of 145 flightless Whooper Swans to leave Neslandavik in the South Basin and swim to the North Basin.

The strongest case for food resources limiting the Whooper Swans' selection of Lake Myvatn as a molt site is the close association of molting numbers with the size of the area available for macrophyte growth, and hence for feeding, estimated from aerial photographs. The strength of this relationship is the simplicity and accuracy of the crude estimation of water depth for virtually the whole feeding area. Conventional sampling of the complex, mosaic bottom vegetation is likely to be limited by very large sampling error and high costs. The decline in the number of Whooper Swans molting at Myvatn is unlikely to be due to a decrease in the Icelandic population, because international censuses suggest an increase in population size between 1995 and 2000 (Cranswick *et al.* 2002).

Reasons for short-term fluctuations in numbers molting at Lake Myvatn and elsewhere are still not understood. The variation may be due to weather, especially through aquatic macrophyte production at the molting sites, and to current or previous breeding success of swans in the general region. These influences are not necessarily simple, and unless carefully studied over many years they can only be surmised.

Long-term monitoring studies are scientifically useful in that they help to formulate realistic questions leading to decisive experiments. In the case of the Myvatn swans, destruction of the feeding habitat is shown to have a strong effect on local density, but assessing the regional effect may take many years. Such is the post hoc nature of monitoring.

ACKNOWLEDGMENTS

This paper is based on long-term studies of the Myvatn ecosystem. Many scientists, students and members of the public, too numerous to list here, assisted in the field and laboratory. Research grants from the Iceland Science Fund and the University of Iceland Research Fund are gratefully acknowledged.

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Numbers of Mute Swans and Whooper Swans in Sweden, 1967–2000

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Abstract.—Mute Swans (*Cygnus olor*) and Whooper Swans (*Cygnus cygnus*) in Sweden have been monitored as part of the International Waterbird Census (IWC) since 1967. For the Whooper Swan, midwinter indices show fluctuations around a slowly increasing trend. Country-wide surveys in 1971–72, 1988–89, 1995 and 2000, however found a more substantial increase in numbers, with national totals estimated at 2,000, 4,000, 8,000 and 8,000 individuals, respectively. The difference between the trends indices and the results of the country-wide surveys is attributable to the birds using more terrestrial habitats since the early 1980s, which are less well covered by the IWC. In 1995, 33% of the swans were found on land, compared to 43% in January 2000. For the Mute Swan, the midwinter indices showed a significantly increasing trend from 1970 to 2000, whereas autumn indices from September counts fluctuated around a more or less stable level, but with a decrease in the last few years. Country-wide midwinter counts recorded about 8,000 Mute Swans in 1973, 13,000 in 1988–89 and over 15,000 in January 1993.

Key words.—*Cygnus cygnus*, *Cygnus olor*, distribution, field feeding, Mute Swan, population trend, south Sweden, Whooper Swan, winter numbers.

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At present, internationally important numbers of Mute Swan and Whooper Swan breed and winter in Sweden, with national winter totals accounting for at least 10% of the continental northwest European population (Delany *et al.* 1999). When regular waterfowl counts started at a national level in Sweden in 1959–60 (Nilsson 1976), the Mute Swan was a regular breeding species in the southern part of the country, whereas the Whooper Swan was still regarded as a rare breeding species of remote areas in the far north (Blomgren 1974). Large flocks of migrating Whooper Swans were a regular feature of some sites in southern Sweden at that time, but these had bred elsewhere, probably further east.

Numbers of both species of swan have been monitored in Sweden since 1967 as a part of the International Waterbird Census (IWC) coordinated by Wetlands International in mid January each year. For the Mute Swan, national counts in September have also provided autumn trends in numbers since 1973. As the proportion of Whooper Swans in Sweden covered by the IWC decreased markedly over the years, apparently due to a change in the swans' feeding habits from aquatic vegetation towards more terrestrial feeding (noted during the regular goose counts undertaken in south Sweden since 1977–78), additional country-wide midwinter surveys were organized in Sweden, as in a number of other European countries (Nilsson 1997; Laubek *et al.* 1999; Cranswick *et al.* 1997).

Whereas trends in wintering numbers have been monitored annually through the IWC, information about numbers breeding is less detailed. The general distribution of the two species in the country has been well described in the national Bird Atlas (Svensson *et al.* 1999). For the Mute Swan, some regional surveys have been published but there have been no national breeding surveys. For Whooper Swans, a national breeding survey was undertaken in 1997 (Axbrink 1999), with a less complete survey made in 1985 (Arvidsson 1987). Additionally, regional aerial surveys were made of the main Whooper Swan breeding areas in the north of the country in 1972–75 (Haapanen and Nilsson 1979; Nilsson *et al.* 1998).

The results of the midwinter counts (IWC) up to and including 1989 have been published previously (Nilsson 1975; Nilsson 1991), as has the 1995 national Whooper Swan survey (Nilsson 1997). In this paper, I analyze the whole series of midwinter Mute Swan and Whooper Swan counts, and thus update former analyses of swan trends in Sweden (Nilsson 1991; Nilsson 1997).

METHODS

The methods and coverage of the Swedish January IWC survey and September counts have been described in earlier publications (Nilsson 1975, 1991). Whereas January indices could be calculated for both species, September indices are only available for the Mute Swan. During the early years, the aim during the midwinter counts was to cover as many important sites as possible. After a two-year build-up phase, extensive coverage was obtained in 1969–78, and country-wide surveys aiming at near-complete coverage were undertaken in 1971–73. From 1979 onwards counts were undertaken annually on a sample of about 700 sites, dispersed across the southern part of the country, where areas of open water and wintering waterfowl were known to be present, the same sites being covered each year. The sites counted were selected to cover all areas with internationally important waterfowl concentrations (international importance being defined as 1% of the total population being counted at that site; c.f. Delany *et al.* 1999), and to obtain representative coverage of different wintering habitat for waterfowl in the country. For the Mute Swan, it is estimated that more than 50% of the numbers present in winter were covered annually in the January counts, whereas about 20% of Whooper Swans in Sweden were counted on the IWC sites in 2000 (L. Nilsson, unpubl. data). A new program of country-wide surveys was undertaken during the winters 1987–1989. September waterfowl counts were made at a sample of about 200 sites annually in the southern part of the country from 1973 onwards (Nilsson 1984). Their main aim is to monitor trends in numbers for species that leave the country during the winter, but they also provide for a series of September indices for the Mute Swan.

Indices were calculated by pair-wise comparisons of the totals for all sites counted in two consecutive years (Ruger *et al.* 1986; Nilsson 1975, 1991). The total for Year 2 was expressed as a percentage of the total for Year 1, and the percentage obtained was then recalculated in relation to an index of 100 set for the selected base year (1973). To avoid a bias towards extreme years, the series of primary indices were recalculated so that the means of the indices for the 34 years of the January IWC survey and for the 27 years of September counts, equaled 100 in each case.

In January 1995 and 2000, special surveys were organized to cover all aquatic and terrestrial sites holding Whooper Swans in Sweden (Nilsson 1997), as part of a coordinated international Whooper Swan census across Europe (Laubek *et al.* 1999; Cranswick *et al.* 2002). To achieve this, all former counters and many other ornithologists, including members of bird clubs and report committees were contacted. In 2000 information about the survey was also distributed by a special swan homepage on the Internet with links to all local bird clubs, web-pages and the media, and thus to the general public to obtain information about formerly unknown swan sites. During the special Whooper Swan counts, data on the habitat used by the birds was also collected.

RESULTS

Mute Swan

The Mute Swan is widely distributed over a large number of sites in southern Sweden, both during September and in January (Fig. 1a, b). September flocks include post-molt birds, which occur both inland, for instance at Lake Tåkern, and on the coast in the southern part of the Öresund. In January, most Mute Swans are found at the coasts both in the archipelagos and along areas of open coast, especially in areas with extensive growth of Eelgrass (*Zostera* spp.), one of their main foods.

The midwinter indices show a significantly increasing trend over the 34 year period of midwinter counts (linear regression analysis, $r = 0.82$, $b = 3.45 \pm 0.42$, $F_{1,32} = 67.8$, $P < 0.001$; Fig. 2), the level being around index 50 for the first five years, compared to indices fluctuating about the 150 level in the 1990s. Although the overall index series shows a significantly increasing trend since 1967, this increase can be divided into parts showing different stages in the development of Mute Swans wintering in Sweden. During 1967–1972 the index was more or less stable around a low level. A much higher index was noted during some of the mild winters of the 1970s, but a new low level occurred in the cold winter of 1979. Thereafter there was a steady increase to January 1990, followed by an unusually high index in 1991. During the 1990s fluctuations were more marked than in previous years. This increase was also reflected in the results of the country-wide surveys, which yielded 8,000 Mute Swans in 1973, 13,000 in 1988–89 and over 15,000 in the 1993 survey of water areas in Sweden.

The September indices however, describe a different pattern for the Mute Swan in Sweden (Fig. 2). The general trend for the period 1973–1999 is one of decline (linear regression analysis, $r = 0.57$, $b = -1.51 \pm 0.44$, $F_{1,25} = 11.9$, $P < 0.002$), with high indices recorded before the cold 1979 winter, fluctuations around a lower but stable level in the 1980s, then a marked decrease from 1994 to 1999. The September figures, however, are heavily influenced by counts of some large concentrations of post-molt swans, and the low indices in the last few years can be due to local changes on a few important sites. When comparing the distribution maps from the September and January counts, it should be

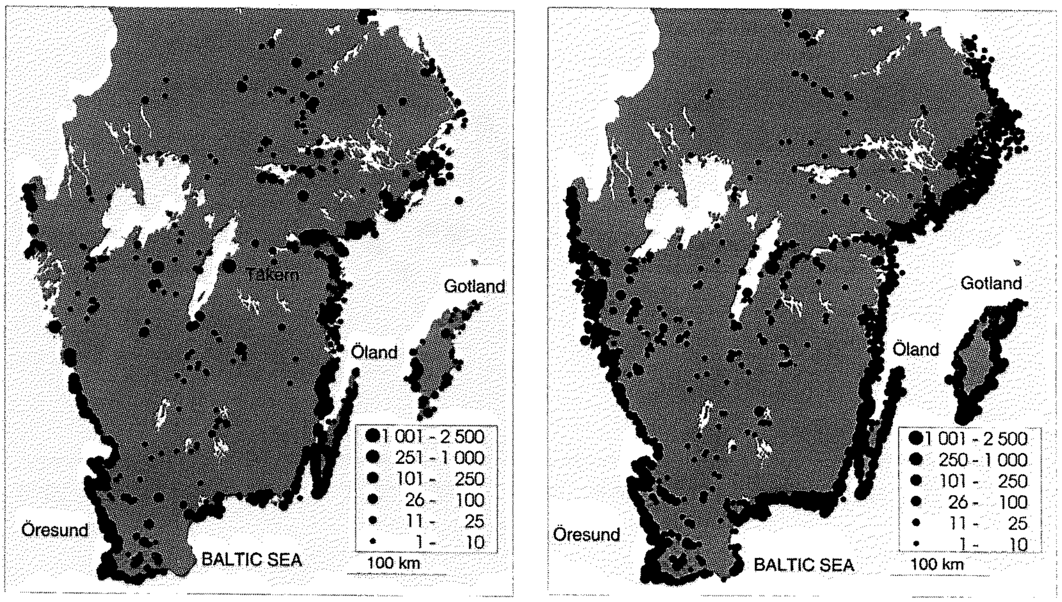

Figure 1. Maximum counts of Mute Swans on different sites in south Sweden in (a) September and (b) January.

noted that the January counts include a number of years with country-wide surveys, whereas the coverage in September is much less comprehensive, especially on the east coast.

Whooper Swan

In January, the Whooper Swan is widely distributed across Sweden (Fig. 3), occurring both in inland and coastal areas. In contrast to the Mute Swan (Fig. 1), the Whooper Swan has more or less been absent from the archipelagos on the east coast with the exception of the southeast corner, where the archipelago had different characteristics to the islands further north, with extensive areas of *Zostera* vegetation in shallow areas that often are ice-free in mild winters. Important concentration areas were found on the west coast and on the islands Öland and Gotland in the Baltic Sea. Further inland, there is also a marked concentration of Whooper Swans in the western part of the country, where flocks of several hundred swans are found along some of the rivers.

The midwinter indices show a significantly increasing trend over the study period (linear regression analysis, $r = 0.34$, $b = 0.76 \pm 0.37$, $F_{1,32} = 4.18$, $P < 0.05$), although the increase was slow and there were marked annual fluctuations in the indices. There is no consistent pattern in the relation to cold winters, however, with low indices being found in some cold winters, such as 1979 and 1982, whereas relatively high indices were found in other cold winters such as 1985 and 1987.

An increasing proportion of Whooper Swans have used terrestrial habitats in more recent winters and therefore were not covered by the IWC counts, which were confined to wetland habitats. During the first country-wide surveys in 1971–73, around 2,000 Whooper Swans were counted. The next survey in 1987–89 showed an increase with about 3,500 Whooper Swans counted in 1988 and the total numbers wintering in Sweden was estimated at 5,000 individuals taking uncovered sites into consideration (Nilsson 1997). In 1987, a very cold winter, about 2,500 were counted in a survey with good coverage. The IWC indices indicated fluctuations around a steady level for the period between 1987 and 1995, whereas the special country-wide survey in January 1995 showed a very marked increase in wintering numbers from about 5,000 to at least 8,000 birds (7,439 swans actually counted). The numbers counted in January 2000 was 7,022, giving an estimated total

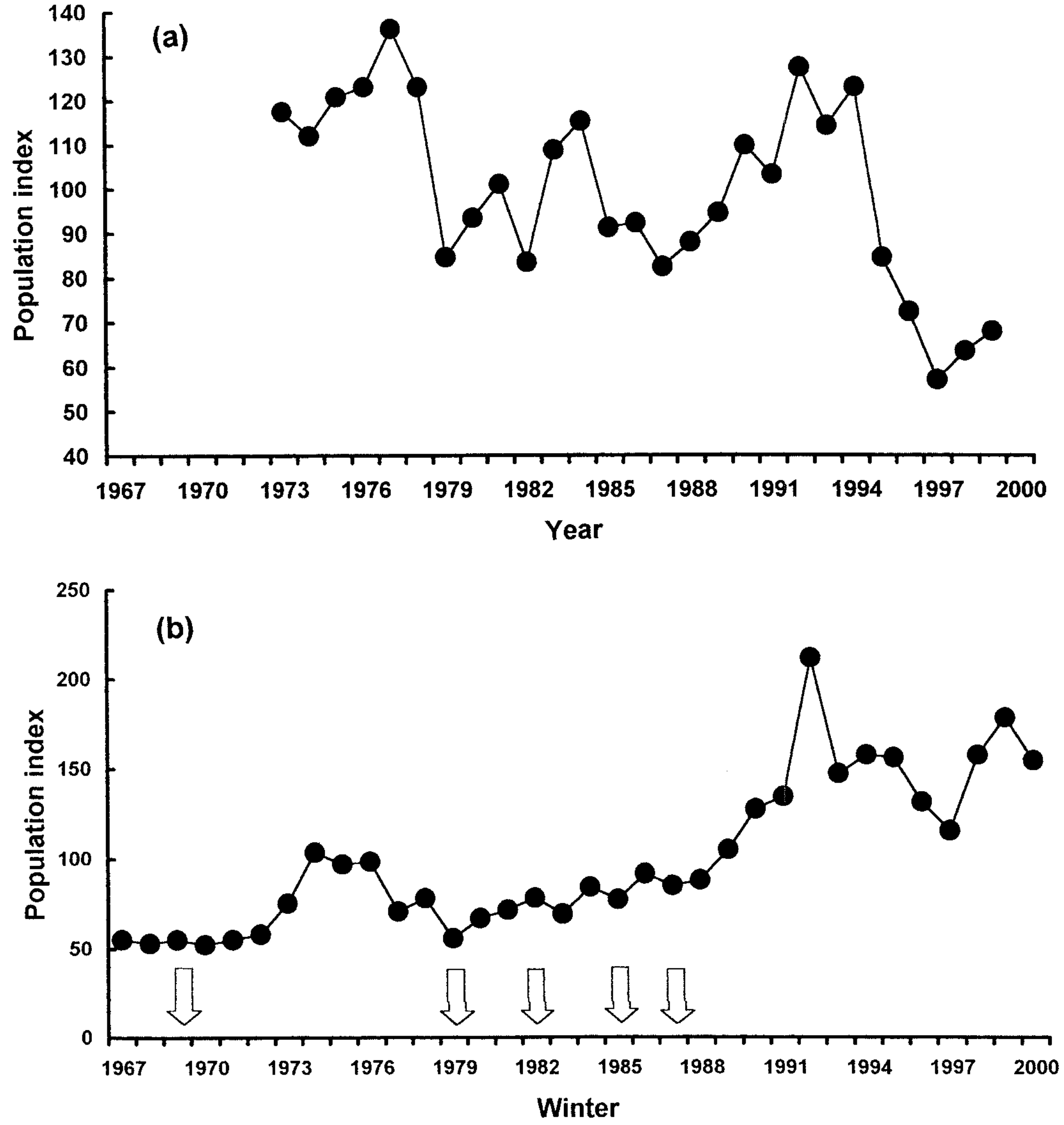

Figure 2. Population indices for Mute Swan in south Sweden: (a) September and (b) January. Cold winters (mean monthly January temperatures for a standard sample of ten stations in south Sweden <-5°C) are marked with arrows. Winter indicates the year in December for indices in the following January (i.e., 1967 indicates the 1967–68 winter).

of about 8,000 Whooper Swans in Sweden, similar figures to the previous country-wide survey in January 1995.

One of the reasons for the discrepancy between the Whooper Swan indices, based on the IWC, and the observed development of numbers wintering in Sweden was the relatively new tendency for Whooper Swans to feed in terrestrial habitats. In January 1995, about 30% of the Whooper Swans were found on terrestrial habitats (Nilsson 1997). In January 2000, which was also a mild winter, 43% of the Whooper Swans were found on the fields. When the waterfowl counts started, only small numbers of Whooper Swans were found on land and in these cases they were close to water (Nilsson 1997).

There was marked regional variation in field choice by Whooper Swans in both January 1995 and January 2000 (Fig. 5, Table 1). In Scania, the proportion using terrestrial habitats was lower in January 2000 than in

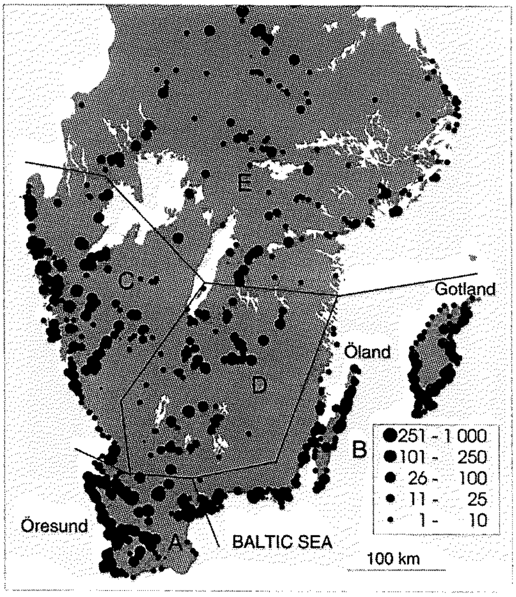

Figure 3. Maximum counts of Whooper Swans at different sites in Sweden in January. The map also shows the different regions used in the analysis of field choice in Table 1: A = Scania, B = Southeast, C = West coast, D = South inland and E = Central.

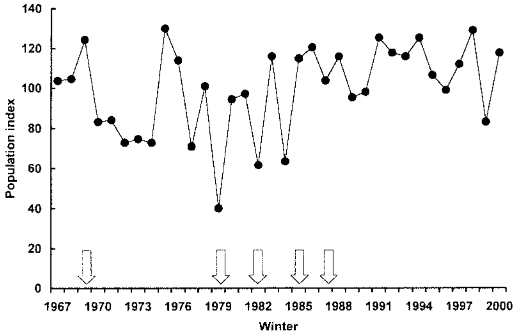

Figure 4. January indices for Whooper Swans in south Sweden. Cold winters (mean monthly January temperatures for a standard sample of ten stations in south Sweden < -5°C) are marked with arrows.

January 1995, (40% and 70% respectively), whereas in all other regions the proportion using terrestrial habitats was higher in 2000 than in 1995. The main field types used by the Whooper Swans were winter cereals, grassland and winter oilseed rape. Rape was used primarily in Scania, which is the main growing region for this crop.

DISCUSSION

The midwinter counts indicate increases in wintering numbers of both Mute Swans and Whooper Swans in Sweden from 1967–2000, this increase being part of a general increase in wintering populations for both species in northwest Europe (Delany *et al.* 1999). In the Mute Swan, this increase was also reflected in the results of the country-wide surveys, whereas in the Whooper Swan trends derived from the IWCs did not correspond to the four-fold increase in swans counted during the country-wide surveys from the early 1970s to 1995, or the doubling of numbers since the mid 1980s, probably because the increasing number of field-feeding Whooper Swans were not covered by the IWC counts.

Mute Swan

There have been no country-wide surveys of breeding Mute Swans with which to compare the indices from the September and January counts. The Swedish Bird Atlas (Svensson *et al.* 1999) gives some historical data, with an estimate of about 310 pairs for the region around Lake Mälaren in south central Sweden in 1921. There was then slow growth in the number of breeding pairs until a more substantial increase between 1950 and the mid 1970s, during which period there was also a marked spread in breeding distribution northwards. Recent reports indicate a decrease in inland breeding by Mute Swans during the 1980s and 1990s, whereas numbers breeding on the coast, especially in the archipelagos, has continued to increase (Svensson *et al.* 1999). According to the Bird Atlas (Svensson *et al.* 1999), numbers now breeding in Sweden are estimated at between 4,000 and 7,000 pairs.

The different trends for inland and coastal breeding, at least in some Swedish districts, can explain the discrepancy between the September and January Mute Swan indices. In January, most Mute Swans are concentrated on the coast, whereas only small numbers that do not have much influence on the indices, remain inland. Moreover, large areas especially in the inner archipela-

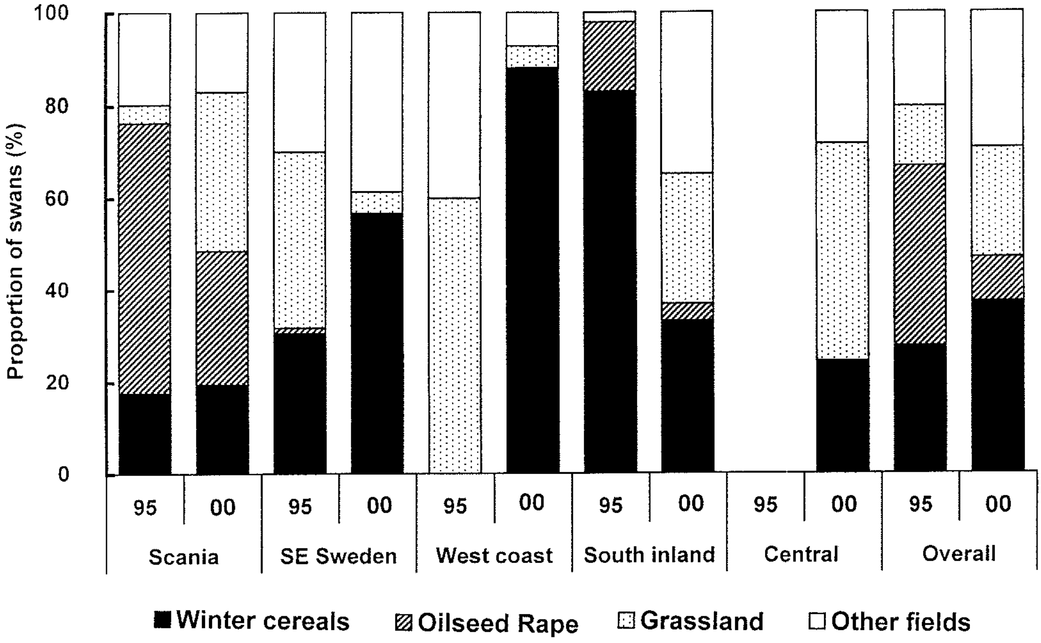

Figure 5. Field choice of Whooper Swans (as percentage of all Whooper Swans counted on land) at country-wide surveys in south Sweden in January 1995 and 2000. The different districts are shown in Fig. 3. The proportion of swans on terrestrial habitats is given in Table 1.

gos freeze in winter, and the swans then concentrate on areas of open water included in the IWC counts. The September counts, on the other hand, have a good coverage of inland areas and some coastal sites mostly used by post-molt swans, but the extensive archipelagos are not covered. Thus the September counts measure changes in the numbers breeding inland, whereas the January indices measure trends for all Mute Swans wintering in Sweden.

Whooper Swan

The increase in Whooper Swans wintering in Sweden is in line with an increase in the numbers breeding in Sweden (Arvidsson 1987; Axbrink 1999; Haapanen and Nilsson 1979; Nilsson *et al.* 1998), and with the increase in the northwest European population as a whole (Laubek *et al.* 1999). When the winter surveys considered here commenced, Whooper Swans bred only in the

Table 1. Field feeding by wintering Whooper Swans in different parts of south Sweden, recorded during the international swan censuses of January 1995 and January 2000. For the different areas in south Sweden see Fig. 3. The totals given here are lower than total counts for the regions because some observers did not report on habitat choice.

	January 1995		January 2000	
Area	Percentage of swans on land	Total swans counted	Percentage of swans on land	Total swans counted
A. Scania	68.1	2,214	40.5	2,076
B. SE Sweden	34.7	1,188	62.3	1,258
C. West coast	12.3	1,215	25.3	498
D. South Inland	19.0	1,773	46.7	2,031
E. Central	0.0	879	21.7	849
Overall total	33.1	7,269	43.0	6,712

northernmost parts of Sweden, with just a few occasional pairs found nesting further south (Nilsson *et al.* 1998; Axbrink 1999; Svensson *et al.* 1999). In 1972–75, aerial surveys were undertaken in the two northernmost provinces, Västerbotten and Norrbotten (118,000 km^2), constituting about a third of the total area of Sweden (Haapanen and Nilsson 1979). Numbers breeding in these two provinces was estimated at 310 territorial pairs (120 nests). A repeat aerial survey was made in 1997 (Nilsson *et al.* 1998), resulting in an estimate of 2,800 pairs (1,800 nests) for the same two provinces, with a marked spread of Whooper Swans from the inland core areas over the entire study area. In 1997 the Swedish Ornithological Society organized a survey of Whooper Swans breeding across Sweden, which yielded an estimate of 3,800 pairs for the country (Axbrink 1999), including the results of the aerial survey referred to above. Arvidsson (1987) had estimated that 500 pairs bred in Sweden in 1985, but this was certainly an underestimate, at least when the two northernmost core provinces are considered (Haapanen and Nilsson 1979), and numbers were probably closer to 700 pairs or more.

The five-fold increase in Whooper Swans breeding in Sweden between the mid 1980s and late 1990s thus appears to be much more substantial than the doubling in the numbers counted in winter over the same period. The main breeding area in Sweden is in the northernmost part of the country, however, and swans from these regions mostly migrate west to winter on the Norwegian coast (Mathiasson 1991; Preuss 1981), whereas banding programs in Finland indicate swans wintering in the south of Sweden are from breeding grounds further east (Laubek 1998).

During the first decades of the 20th century the Whooper Swan was a rare species with a restricted distribution in the large mires of northernmost Sweden. When the species was protected from hunting by a governmental act in 1926, numbers breeding in Sweden was estimated at only about 20 pairs. The increase in numbers following legislation to protect the birds was slow until the 1960s, with the swans still occurring mainly on large mires in the northern part of the country. Even if the main reason for the increase in Whooper Swan numbers in Sweden and in other parts of northern Europe is the protection that has allowed the species to spread south over the boreal forest zone and its lakes and mires, it is likely that the rate of increase in recent years has also been influenced by changes in agriculture which has provided new feeding areas for the swans (Nilsson 1997; Laubek *et al.* 1999) as well as for goose populations (Nilsson and Persson 2000).

ACKNOWLEDGMENTS

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Numbers and Distribution of Whooper Swans Breeding, Wintering and on Migration in Estonia, 1990–2000

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Abstract.—A large proportion of the Whooper Swans (*Cygnus cygnus*) that winter in continental northwest Europe stage in Estonia during migration. Spring staging areas often overlap with those of the Bewick's Swans (*Cygnus columbianus bewickii*) migrating to arctic Russia. Whooper Swans occur in internationally important numbers (>600 birds) at seven wetland sites in spring, and eight sites are of national importance (100–600 birds). During the 1990s, up to 5,700 and 3,900 swans were counted at the key staging sites of Matsalu Bay and Haapsalu Bay respectively. Flocks are smaller (often <50 birds) and more scattered during autumn migration but two wetlands, Haapsalu Bay and Matsalu Bay, again hold internationally important numbers, with up to 3,900 and 1,200 individuals at this time. The Whooper Swan is a regular but innumerous wintering species, occurring in low numbers in coastal areas. In hard winters up to 300 birds and in mild winters up to 1,000 birds have been recorded in Estonia. There is no clear trend in the number of swans present in winter. The first breeding attempt by Whooper Swans in Estonia was recorded in 1979, a steady increase in the number of breeding pairs was recorded during the 1990s and the number currently breeding is estimated at 30–40 pairs. Breeding habitats are natural and artificial pools (dyseutrophic lakes), raised bogs (43% of breeding attempts), eutrophic inland lakes (31%) and coastal lakes and bays (26%). Flocks of molting swans (mainly non-breeding birds) have been observed in western Estonia since 1993.

Key words.—Breeding distribution, *Cygnus cygnus*, habitat use, migration, non-breeding distribution, Whooper Swan, wintering.

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The Whooper Swan (*Cygnus cygnus*) has long been known to be an abundant migratory species in Estonia, occurring on the shallow bays of the west coast in large numbers in spring, and staging in generally the same areas for shorter periods in autumn (Leibak *et al.* 1994). It was a quarry species until the early 1950s with, according to hunting records from the late 19th and early 20th century, up to 23 swans (maximum) shot by a single hunter in one day (1891; Matsalu Bay) and 74 birds over a spring season (1930s; Matsalu Bay) (E. Kumari, personal archives). In 1957, legislation was introduced that banned the hunting of Whooper Swans, under the Act of Nature Conservation of the Estonian S.S.R., in order to protect the species.

Whooper Swans in Estonia are from the population that breeds in Fenno-Scandia and northwest Russia and winters in continental northwest Europe (Cramp and Simmons 1977). There are seven internationally and 14 nationally important wetlands for Whooper Swans staging in Estonia if 600 birds is taken as the threshold level (1%) for international importance (Laubek *et al.* 1999), and 100 birds for national importance. This is in accordance with the criteria established under the Convention on Wetlands of International Importance especially as Waterfowl Habitat (the "Ramsar" Convention), which states that a wetland should be considered internationally important if it regularly supports 1% of the individuals of a population of one species or subspecies of waterfowl. In the late 1970s, there were major changes in the swans' distribution and staging patterns in Estonia. Whooper Swan flocks were first seen feeding in fields in 1978 (Rootsmäe 1990), and in 1979 the first breeding attempt was recorded.

The main aims of this study were to describe sites of national and international importance for the migratory swans and to assess the expansion of the breeding range for the species in Estonia. This was with a view to promoting the conservation of important staging areas and breeding grounds.

METHODS

Distribution During Migration

Counts of birds made each year from 1990 to 2000 inclusive, by the research team of the Institute of Zoology and Botany as part of its swan-monitoring program, were used in the analyses of Whooper Swan migration. Earlier notes, and results from volunteer projects organized by the Estonian Ornithological Society, were not used because Whooper Swan counts were often combined with those of the Bewick's Swan (*Cygnus columbianus bewickii*). Sites known to have been used by one or both species were checked during the 1990–2000 surveys. Important staging sites used regularly by Whooper Swans were visited at least once during the peak migration period. Eleven spring (April–May) aerial flights made to count staging waterfowl between 1990 and 2000 (with some gaps in 1990–1995) gave valuable additional data on swan distribution, particularly for areas inaccessible by land. Autumn aerial surveys (October-November) were started in 1994 and were usually performed once every second year. Most of the ground observations were made at the swans' feeding areas. Telescopes were used to identify species, age structure and to check the birds for individual markers (leg bands and neck collars). A short description of the habitat, including the main food items available to the swans, was made at each site.

Winter Distribution

Results of the annual midwinter countrywide counts of waterfowl, undertaken by up to 150–200 volunteers each January since 1967, as part of the International Waterfowl Censuses (IWC) coordinated by Wetlands International, are much more reliable that the spring and autumn counts because the Bewick's Swan rarely winters in Estonia and >95% of yellow-billed swans counted in winter therefore are Whooper Swans. The accuracy of the winter ground counts also depends on the coverage of ice-free coastal areas, which varied between 60-80% in mid January each year for the years 1994-1999 inclusive (Pehlak *et al.* 2001). Whooper Swan flocks were never found at inland sites in winter—neither on fields nor on water-bodies. In January 1993, the ground counts were supported by an aerial survey.

Breeding Distribution

Data on breeding distribution are fragmentary because special countrywide surveys have not been undertaken in the breeding season. The main systematic source is a comprehensive survey of the birds on Estonian mires made from 1986–2001, during which 436 km^2 of treeless raised bogs (41% of the area surveyed), 402 km^2 of raised bogs with trees (38%) and 233 km^2 of treeless fens (22%) were studied by the Estonian mire bird study group (land coverage according to Meiner 1999).

Most breeding records were received through reports from volunteers (members of the Estonian Ornithological Society and local Bird Clubs), special questionnaires sent to a network of 150 volunteers active in waterfowl monitoring (in 1990–1992 and 2000) and aerial surveys in 1996–2000 (western Estonia). All breeding records, from the first report in 1979 to summer 2000, were used in the analyses. Doubtful records were first checked with the observers, then excluded from the database if not confirmed.

RESULTS

Distribution During Spring and Autumn Migration

The first flocks on spring migration arrive on the west coast of Estonia in the first half of March. During the 1990s, large flocks (>500 individuals) were observed throughout second half of March and April, with peaks counts recorded in first half of April. The last Whooper Swan flocks depart in the first week of May. Spring staging areas receiving over 100 birds are mainly in western Estonia, and these important migratory sites often overlap with those of the Bewick's Swan, which occur in greater numbers than the Whooper Swans in Estonia (Luigujõe *et al.* 1996). There are seven wetlands where Whooper Swans regularly concentrate in internationally important numbers (>600 individuals; Laubek *et al.* 1999) and eight sites of national importance (100–600 individuals) (Fig. 1). In the 1990s, the key staging sites were Matsalu Bay (500–5,700), Haapsalu Bay (500–3,900), Väike-Väin Strait (400–3,000), the Häädemeeste coast (100–1,500), Paldiski Bay (200–700), Audru polder (300–600) and the Kasari River delta (200–700).

Autumn migration starts in early October and most flocks leave by mid November. Peak numbers were recorded between the second half of October and the first week of November. The swans are more dispersed in autumn than in spring, with large numbers of small, scattered flocks using coastal areas and inland lakes. In the 1990s, the internationally important autumn staging sites were Haapsalu Bay (500–3,900 individuals) and Matsalu Bay (500–1,200). Sites of national importance were Väike-Väin, Lake Peipsi (both with 200–500) and a few sites (>100) found in southern Saaremaa (Fig. 1).

Winter Numbers and Distribution

The Whooper Swan is regular, but not a numerous wintering species, with marked annual variation in the numbers recorded during the mid January counts (Fig. 2). Wintering flocks are small and scattered on

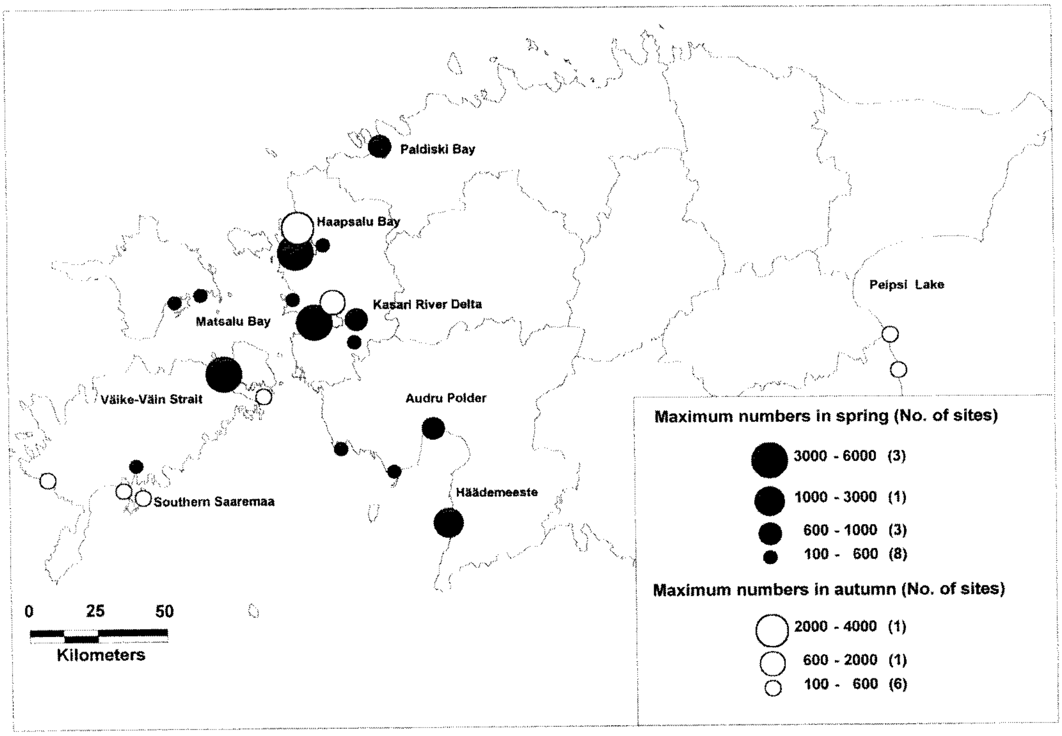

Figure 1. Spring and autumn staging sites of the Whooper Swan in Estonia, 1990–2000.

coastal waters. Only a few coastal bays on Saaremaa Island hold more than 100 individuals. The number of wintering swans fluctuated between 300 and 1,000 birds, depending mainly on mildness of the winter the extent of ice-cover on the coast. The peak numbers registered in1983, 1988, 1990–1992 and 1998 corresponded with extremely warm weather, with the mean air temperature recorded in Tallinn in January for each of these years (above 0°C in each case) being substantially higher than Tallinn's average mean January air temperature (-4°C).

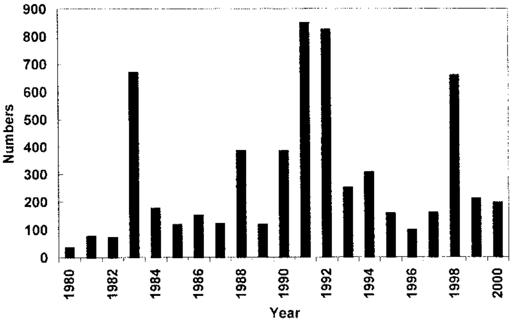

Figure 2. Number of Whooper Swans recorded in Estonia during mid winter (January) censuses from 1980–2000.

Breeding Distribution and Habitat Choice

Breeding attempts by Whooper Swans in Estonia have been known since 1979, and expansion of the breeding population probably has taken place in waves (Fig. 3). The most recent increase (from 1995–2000) was the most substantial, with 23 new breeding areas, bringing the total number of known breeding sites to 39 (Fig. 4). The species breeds across the country, but there is a concentration in the zoogeographical regions of Lowland Estonia (the western counties) and Intermediate Estonia. The latter is a zone of extensive forests and bogs, which covers the central part of Estonia from northeast to southwest.

Information on breeding habitats indicated that the birds nest mainly near eutrophic or dyseutrophic inland lakes (31%), bog lakes (43%) and coastal waterbodies

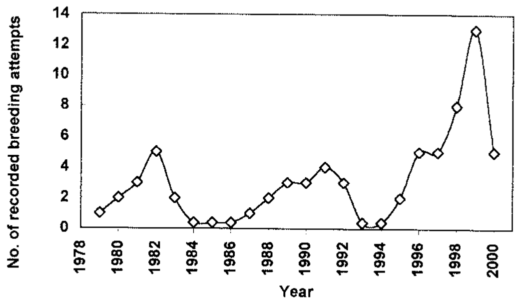

Figure 3. Number of Whooper Swan pairs recorded breeding in Estonia each year (1978–2000 inclusive).

(26%) (Table 1). Of all known breeding habitats, 21% were man-made waterbodies. The long bog-pits with island strips, created across Estonian raised bogs in the course of comprehensive peat mining projects since early 1950s until the end of 1980s, may provide suitable habitat for further breeding expansion. So far only few pairs has bred on large fishponds in Estonia, although this is a favorite breeding habitat for Whooper Swans in Latvia (Viksne 1983).

Flocks of molting Whooper Swans were first observed in Estonia in 1993, on the western coast of the country. Three molt sites have been recorded since 1998, including Matsalu Bay, which received up to 45 birds in 2001. The larger molting flocks consist mainly of non-breeding birds.

DISCUSSION

Whooper Swans wintering in continental Europe breed mainly in the Nordic countries and Russia (Cramp and Simmons 1977). Expansion of the Whooper Swans' breeding range to more southerly latitudes, around the Baltic Sea, has been attributed mainly to conservation efforts, which have enabled swans to re-establish breeding territories in the more productive waterbodies of southern Scandinavia (Ohtonen 1992). The higher reproductive success of swans nesting in the south has supported population growth and consolidated use of these sites by breeding pairs (Laubek 1998). Enlargement

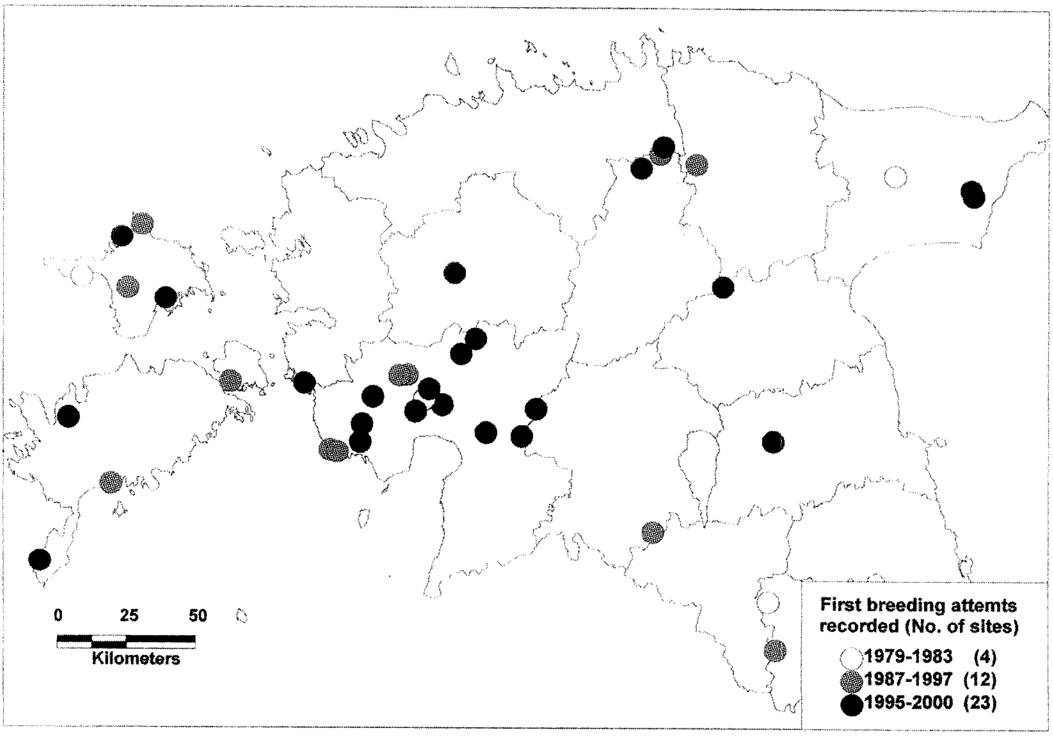

Figure 4. Breeding distribution of the Whooper Swan in Estonia.

Table 1. Breeding habitats for Whooper Swans in Estonia.

	Known breeding sites	
Type of waterbody (from Paal 1997)	Number	% territories
Dyseutrophic lake	5	13
Eutrophic lake	4	10
Eutrophic lake (man-made)	3	8
Dyseutrophic bog lake	12	30
Dyseutrophic bog pit (man-made)	5	13
Eutrophic coastal bay	5	13
Halotrophic coastal lake	5	13
Total	39	100

of the breeding range may be related to changes in feeding behavior, such as the wider use of nutrient-rich agricultural crops, which in turn may improve survival rates and body condition prior to breeding.

The development in the numbers of Whooper Swans breeding in Estonia follows substantial population growth and expansion of the species in northwest Europe over the last 50 years (Laubek *et al.* 1999). Increases in the numbers and densities of breeding pairs in the Fenno-Scandian sub-arctic regions were noted during the 1950s, and in the 1970s the breeding area expanded rapidly from Lapland to the boreal zone (Väisänen *et al.* 1998). First breeding attempts were recorded in Lithuania in 1965 (Svazas *et al.* 1997), Latvia and Poland in 1973 (Viksne 1983; Tomialojc 1990), Estonia in 1979 and Germany in 1994 (Profus 1999). Current estimates put numbers breeding in the southern Baltic at a minimum of 100–150 pairs, of which more than 30 are in Latvia (Kalnins 1997), 20–40 in Lithuania (Svazas *et al.* 1997), 30–40 in Estonia and 20–30 pairs in Poland and Germany respectively (Profus 1999). Numbers breeding in Sweden also increased substantially between the mid 1980s and the late 1990s (Nilsson 2002), and the most recent estimate for Whooper Swans breeding throughout Fenno-Scandia is 6,000 pairs (Väisänen *et al.* 1998).

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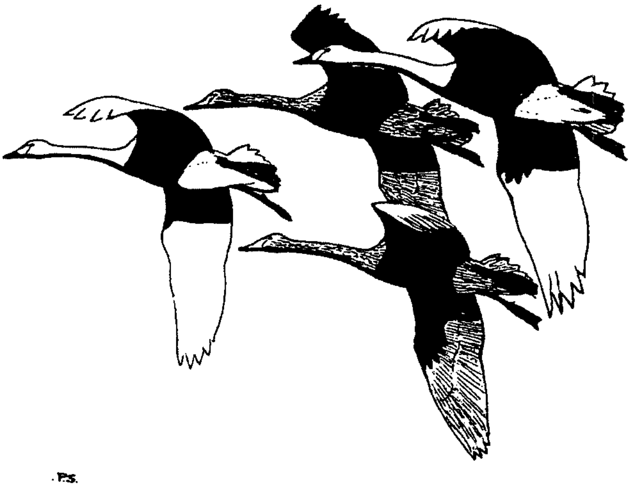

Reassessment of the Southern Limit for Whooper Swans Breeding in Northwest Russia

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Abstract.—This article reviews current and historical literature, and also original data, with a view to describing changes in the southern limit for Whooper Swans (*Cygnus cygnus*) breeding in northwest Russia. The swans were more numerous in the region, and their distribution more widespread, in the 19th century and first half of the 20th century than they are today. In the mid 20th century, increased human activity resulted in a substantial decline in numbers, with breeding pairs no longer occurring in parts of central Karelia, nor in the Leningrad region in southern Karelia. A gradual increase in numbers began in the 1980s, and their breeding distribution shifted southwards. The southernmost sites where Whooper Swans breed regularly are now at 62°10'N in west Karelia (on the Russian-Finnish border), much further north (at 63°20'N) in central Karelia, but further south again (at around 62°N) where Karelia meets the Arkhangelsk region. Further east, regular breeding occurs across the Kargopol district of Arkhangelsk, from 61°45'N in the west to 61°20'N at its southeast border with the Vologda region (at Lake Lacha). Irregular breeding occurs across southern Karelia and the northern part of the Leningrad region. The change in the southern limit of the swans' breeding distribution cannot, however, be considered an expansion of the breeding range because the swans have not yet fully returned to the range occupied in the first half of the 20th century.

Key words.—*Cygnus cygnus*, limit of breeding distribution, northwest Russia, population dynamics, Whooper Swan.

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The Whooper Swan (*Cygnus cygnus*) is widely distributed in forest tundra and taiga zones across Russia, from its borders with other European countries (particularly Finland) in the west to Chukotka and the Bering Sea in the east (Flint *et al.* 1996; Rees *et al.* 1997; Syroechkovski 2002). It breeds throughout central and eastern parts of Russia, and only in European Russia does the southern edge of the breeding range rise sharply to the north. In northwest European Russia, the southern border of regular nesting by the species is usually taken as being from Lake Ladoga to the upper reaches of the Volga River and the Ural Mountains and its surroundings (Isakov and Ptushenko 1952; Ivanov 1976; Riabitsev 2001). However, a lack of concrete data concerning Whooper Swan nesting distribution has resulted in all information being combined in describing its breeding range, with information from 50–100 years ago still being used despite more recent changes.

Since the early 1980s, inventory and monitoring work in northwest Russia has provided new information on the numbers and breeding distribution of avian species, including the Whooper Swan. This paper therefore reviews both original and published data to determine the Whooper Swans' current breeding distribution in northwest Russia, particularly the southern border of its range. It also aims, as far as is possible from published and archive sources, to give an overview of historic changes in the numbers and breeding distribution of Whooper Swans in the area.

MATERIALS AND METHODS

An inventory of the fauna (including birds) of Karelia and neighboring territories to the southeast was developed during the 1990s by the Karelian Research Center of the Russian Academy of Sciences, within a framework of programs studying biodiversity in the region. In different years these included a joint Finnish-Russian program entitled "Inventory and study of biodiversity in the Republic of Karelia" (Krutov and Gromtsev 1999), identifying Important Bird Areas (IBAs) as part of Birdlife International's assessment of important sites for birds in Europe (Sviridova 2000) and planning the protection of territories. Nine IBAs are listed for Karelia, most of which are important for waterfowl conservation (Hokhlova 2000; Sviridova 2000). Separate projects also contributing swan data were: (1) monitoring biodiversity in the European north of Russia (financed by the Ministry of Science and Technology of Russia), (2) autumn goose migration in Zaonezh'ye (for the Bird Conservation Union of Russia), (3) monitoring birds in the Kizi skerries (for the Kizhi Reserve Museum), and (4) making an inventory of birds in the Kenozero National Park (for the Kenozero National Park authorities). New data were recorded for territories not previously surveyed (i.e., central Karelia, the border of Karelia with Finland, and the Kargopol and Plesetsk districts of the Arkhangelsk). The status of existing reserves and potential sites for conservation on the White Sea, Lake Ladoga and Lake Onega was assessed. A major part of each of these studies was to describe bird fauna at different sites in the region and, whenever possible, to record numbers present, seasonal variation (i.e., whether a site was in a breeding, wintering or migratory area) and the main habitats used by the birds. During these studies, information on Whooper Swan locations, numbers and breeding status was sought mainly by individual interviews with local inhabitants, and subsequent verification of this information by ornithologists whenever possible. The study focused on determining the southernmost sites used by the swans, and confirming breeding by finding their nests or broods. Despite this effort, data are fragmentary for a large part of the region, particularly in the band between 61°N and 64°N, which is more inaccessible and sparsely populated than other parts of Karelia. Annual observations of swans by ornithologists were made only at existing reserves and, with over 60,000 lakes and marshes in Karelia, some areas difficult to reach have not been studied at all.

Published records and data held in the Karelian Research Center and the Kivach Strict Reserve archives were also used to determine not only current status but also changes in the southern distribution of Whooper Swans breeding in northwest Russia. All known data on swans breeding in Karelia before 1991 have been published previously (Zimin *et al.* 1993). Subsequent information is given in regional reports, which are not always readily available to other scientists, but which are included here.

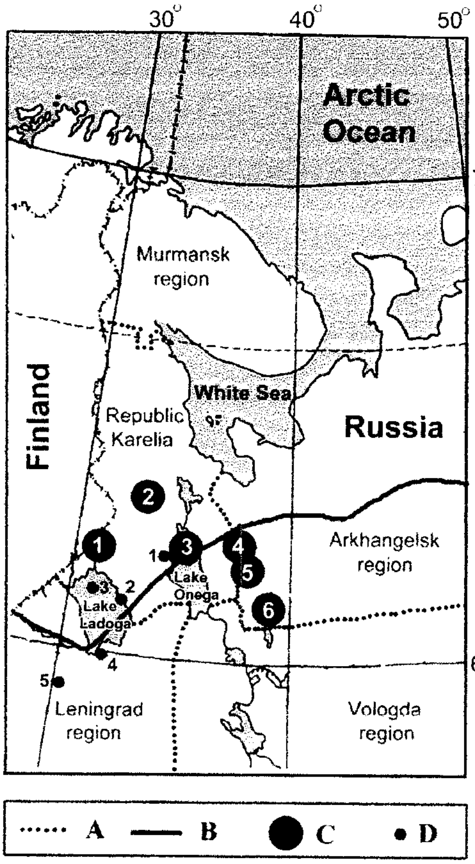

Figure 1. The southern limit for Whooper Swans breeding in northwest Russia. A = Boundaries of administrative areas of Russia. B = Southern edge of the Whooper Swans' regular breeding range in the 1950s–1960s (from Isakov and Ptushenko1952). C = Current most southerly regular nest sites mentioned in the text (1—Tolvojarvi; 2—Segozero; 3—Zaonezh'ye; 4—Vodlozerski National Park; 5—Kenozerski National Park; 6—Lake Lacha). D = Most southerly sites of occasional breeding mentioned in the text (1—Kivach Strikt Reserve; 2—Andrusovo; 3—Valaamski archipelago; 4—Island Ptilov; 5—Lake Vyalie).

STUDY AREA

The southern edge of the Whooper Swan's breeding range in northwest Russia is within the Republic of Karelia and the Kargopol region of the Arkhangelsk region (Fig. 1). It is an important breeding area for waterfowl, including Whooper Swans, and also provides staging sites for birds along the White Sea-Baltic migratory flyway. It is characterized by an extensive and complex network of waterbodies, low human population density, and the absence of an advanced road system. These are obstacles to efficient monitoring, but benefit the conservation of waterfowl and other taiga-breeding birds in the region.

Karelia is located along Russia's western border with Finland, extending from 60°40'N to the Arctic Circle (66°40'N, and with a total area of 180,520 km^2. More than half of Karelia is covered with forest (98,595 km^2), with open water occupying 23%, mires about 20%, and communities and road systems about 1.5%. Agricultural land accounts for only 1.1% of the area. The unique network of waterways consists of 26,700 different rivers and more than 61,000 lakes, including the largest freshwater lakes in Europe (Lake Ladoga and Lake Onega), and the western part of the White Sea. Mires are highly diverse and, together with swamp-forest, makes up 30% of Karelia (Karelian State Report 1998; Hokhlova 2000). The Karelian fauna is highly heterogeneous, and over 40% of species in the region are at the edge of their range (Zimin *et al.* 1993).

The study area in northwest Russia also included the Kargopol region in southwest Archangelsk, on Archangelsk's border with Karelia and Vologda. Kargopol covers an area of 10,110 km^2, and has a more continental climate. The major feature of region is the widespread carbonate rocks occurring close to the surface and "karst" landscape (i.e., karsten lakes, craters and caves). Most of Kargopol is covered with forests (70%), predominantly coniferous. There are many large open marshes and swamp forests, with different kinds of marsh occurring across two thirds of the region. Its territories east of River Onega are mainly natural marshes, many areas are inaccessible, and the wildlife has not yet been studied. Only 8.5% of Kargopol is open agricultural land, found in small areas around the villages (Pronicheva 2000). Settlements and farmland are predominantly in central Kargopol, mainly on the River Onega, around Lake Lacha and along several large roads. The network of waterbodies includes 96 rivers, with the largest (River Onega) flowing from Lake Lacha to the White Sea. Lacha is the largest freshwater lake in Archangelsk, but is also shallow with an average depth of less than 1 m. Almost half of the surface water is covered with reeds and aquatic vegetation. The lake and surrounding marshes is listed as an Important Bird Area (IBA) for its breeding birds and because it is a major staging area for waterfowl and marsh birds on migration (Skokova 1984; Hokhlova *et al.* 1998, 2000a).

RESULTS

Current Regular Nesting Areas

Surveys carried out in the 1990s found that Whooper Swans regularly breed across most of Karelia and Arkhangelsk. In Karelia, breeding was recorded annually in the Loukhi, Kalevala, Kem, Belomorsk, Muethersk, Segezha, Suojarvi, Medvezhegorsk and Pudos areas (Zimin *et al.* 1998; Sazonov 1995; Sazonov *et al.* 1998; Sazonov and Medvedev 1999; Hokhlova 1998; Hokhlova and Artemjev 1999, 2000; Hokhlova *et al.* 1998, 1999, 2000c). However the number of birds and nesting density was low in north Karelia, as well as in the south, and their distribution was not uniform. Up to ten pairs were recorded in the Kostomukshsa Nature Reserve (476 km^2), and no more than five pairs in the Paanoiarvi National Park (1,033 km^2) (Sazonov 1997). The most southern regular nesting sites are in the Suojarvi, Medvezhegorsk and Pudos areas of Karelia, and also in the Kargopol area of Arkhangelsk (Fig. 1). These sites are as follows:

1. *Southwest Karelia, on the border with Finland* (Suojarvi area). Here swans breed regularly on the Tolvojarvi Lake system (62°10'N, 31°30'E). Between 1930–1940 at least eight nest sites were known between Suojarvi and Suistamo (Koskimies 1979). In 1988–1989 swans were still nesting in the area, for example on Lake Raikonavolotskoe (Zimin *et al.* 1993), and also on neighboring territories in Finland (Haapanen and Koskimies 1998). The swans continued nesting in the vicinity of Tolvojarvi Lake during the 1990s (Zimin *et al.* 1998; Kolomitsev 2001)

2. *Central Karelia* (Medvezhegorsk area). Historically, the area to the north and northwest of Lake Onega was one of the main breeding areas for Whooper Swans in central Karelia (Sievers 1878; Marvin 1951; Gebel 1879). At present, local inhabitants report that the swans regularly hatch nestlings on remote wooded lakes to the west and southwest of Lake Segozero (a basin of the Voloma River; 63°22'N, 33°15'E) and on Lake Hizhozero (63°02'N, 34°45' E). There is insufficient data, however, to determine whether breeding density has declined in recent years.

3. *Zaonezh'ye skerries and the coast of northwest Lake Onega* (Zaonezh'ye IBA). Whooper Swans nested regularly in the northern part of Lake Onega from at least the 19th century until the middle of the 20th century (Bordzinski 1867; Kessler 1868; Sievers 1878; Marvin 1951). The last nesting record for the area was in the 1960s (reported by the inhabitants of Large Klimenetski island, Zaonezh'ye; Hokhlova 1998), until one pair started nesting regularly on a small lake overgrown with reeds on the Zaonezhski peninsula of the Azhepnavolok headland at Lake Hashozero (62°37'N, 35°00'E) during the 1990s (A. I. Kamaev, pers. comm.). We recorded swans here annually in 1998–2001 and in 1998 the pair was recorded with two nestlings (Hokhlova *et al.* 2000b).

4. *Southeast of Karelia* (Pudos area). In the 19th century, Whooper Swans commonly occurred in the vicinity of Lake Vodlozero (Kessler 1868). At present it occurs regularly in the Vodlozersky National Park (62°35'N, 38°35'E), which is a large protected territory of 4,683 km^2, most of which is in the Arkhangelsk region and only 1,306 km^2 in Karelia. Between 150 and 400 swans are present in the National Park in summer. At some sites within the reserve the density is as high as 20–30 birds per 100 km^2, but there are few breeding pairs. The most southerly site where Whooper Swans breed annually in the Pudos area is at Lake Korbozero (61°52'N, 37°45'E), close to the border with the Arkhangelsk region (Sazonov 1995). In 1997–1999, at least two pairs nested at small lakes in the area (V. V. Berdnikov, pers. comm.).

5. *Southwest Arkhangelsk, on the border with Karelia* (Kargopol and Plesetsk areas). This

territory was inspected for the first time in 1995. Local inhabitants report that not less than ten pairs occur in the Kenozerski National Park (1,392 km^2; 61°55'N, 38°07'E) and its environs (the Kenozer'ye IBA). We found broods on Lake Verkhnee on 7 July 1997 and on Lake Porgenskoe on 13 August 1999. Lake Lekshmozero (Kargopol area; 61°43'N, 38°05'E) is the most southerly site of regular, but not annual, breeding by Whooper Swans in the National Park (Hokhlova *et al.* 1999; Hokhlova and Artemjev 2000).

6. *Southeast Arkhangelsk.* Local inhabitants report that the swans have always bred in small numbers on marshes and small lakes in the vicinity of Lake Lacha (61°20'N, 38°35'E; the Lake Lacha IBA), and that they also stop here in large numbers (up to 1,000 individuals) during migration (Skokova 1984). One site where the birds have nested irregularly for at least the last ten years is the inaccessible Lake Lebiazhje, 5 km from the village of Nokola (Hokhlova *et al.* 1998, 1999; V. V. Prigodin pers. comm.).

Current Occasional Nesting Areas

During the 1980s and 1990s, Whooper Swans were also occasionally seen breeding in southern parts of Karelia and in the Leningrad region at sites that have been monitored over many years, and where breeding was not recorded in the 1950s–1970s (shown as irregular breeding sites in Fig. 1):

1. *Central Karelia, Kondopoga area.* A brood was observed on Lake Pandozero in the Kivach Strict Reserve (62°13'N, 34°0'E) in 1995 (M.Yakovleva, pers. comm.).

2. *South Karelia, Olonets area.* In summer 1980, a pair is thought to have nested on the Vazhinskoe bog (61°24' N, 33°28' E) and, in the mid-1990s, the same observer saw a brood on the Andrusovo gulf of Lake Ladoga (60°59'N, 32°07'E) (V. I. Ignatenko, pers. comm.).

3. *Lake Ladoga, Valaamski archipelago, South Karelia* (61°23'N, 31°10'E). An unsuccessful nesting attempt was recorded in 1997. The nest with eggs was destroyed, and swan eggshell was found under a Hooded Crow's (*Corvus corone cornix*) nest (Mikhaleva 1997).

4. *Southern Coast of Lake Ladoga, Leningrad region* (60°10'N, 31°54'E). A pair with three non-flying nestlings was seen near Ptilov Island in mid-August 1986. None were seen in the area in subsequent years (Vysotski 1998).

5. *Luga area, Leningrad region.* Whooper Swans nested on Lake Vyalie (59°10'N, 30°10'E) in 1999 after an absence of over 20 years. The nest was found on 7 May, and five nestlings aged 7–10 days were seen there on 12 June (Golovan and Kondratiev 1999). Lake Vyalie was a regular breeding site for the swans up to 1956 but, except for the 1999 observations, pairs have not been recorded there since 1967 (Malchevski and Pukinski 1983).

DISCUSSION

The results of the monitoring and inventory program indicate that the southernmost edge of the Whooper Swan's regular breeding range in northwest Russia is between 61°20'N and 63°20'N (Fig. 1). Within Karelia it follows the northern border of the state's warmest agro-climatic zone (Buginova 1974; Atlas Karelskoi ASSR 1989). The southern limit of the breeding range currently crosses the western frontier of Russia at 62°10'N (Tolvojarvi), rises sharply to the north (up to 63°20'N) in central Karelia (Segozero), then shifts to the south again (to around 62°N) at Karelia's eastern border with the Arkhangelsk region. Thereafter it crosses the Kargopol area of Arkhangelsk, from 61°45' in the west to 61°20' (Lake Lacha) at its southeast border with the Vologda region. Local inhabitants report that at several pairs of swans now nest regularly in the northeastern part of the Vologda region (Nikolaev 2000). Regular nesting areas have not been recorded in northwest Russia south of this line, although an estimated 100–150 pairs (minimum) now breed in the southern Baltic countries (Estonia, Latvia, Lithuania, Poland and Germany) (Luigujõe *et al.* 2002). Occasional breeding does, however, occur in southern parts of Karelia, the Leningrad region and in the Darvinski Strict Reserve in the Vologda region, were nesting swans were found for the first time in 1983 (Nemtsev 1988). It is interesting to note that records of occasional nesting appear to be in a northwest to southeast line, which coincides with the main flight-path for Whooper Swan migration in northwest Russia.

Information on the distribution Whooper Swans in northwest Russia in earlier years is rather fragmentary, because most of the northwest region was not surveyed before the 1990s. Nevertheless reports do indicate some variation in the breeding range. In the 19th century and first half of the 20th century the Whooper Swan apparently occupied a larger area, and numbers appeared to be much higher than today. It is known, for example, that up to the middle of the 20th century it regularly bred on Lake Onega. In the 19th century, broods were regularly seen in the northern gulfs of the lake (Bordzinski 1867; Kessler 1868; Sievers 1878). The Whooper Swan nested in small numbers on the Zaonezhski gulf of Lake Onega until 50 years ago (Marvin 1951) and, until the 1960s, on several inland lakes on the Zaonezh'ye peninsula and on the Kizhi skerries (reported by local inhabitants). In the first half of the 20th century, Whooper Swans also bred on Lake Ladoga and separate reservoirs in the Leningrad region (Malchevski and Pukinski 1983 and Fig. 1). However, by the 1950s, the swans completely ceased nesting in the Leningrad region (Malchevski and Pukinski 1983) and in the 1960s they also disappeared from Lake Onega (Hokhlova 1998).

A similar reduction in the swans' breeding range, to more northerly latitudes, was noted in both Finland and Sweden in the first half of the 20th century (Mericallio 1958; Fjeldsa 1972). Human activity such as illegal hunting and the taking of eggs and cygnets nearly eradicated breeding in Finland by the early 1950s (Haapanen *et al.* 1973; Rees *et al.* 1997). The species responded to conservation measures, however, and numbers increased gradually during the 1960s, more rapidly in the 1970s, and by the1980s–1990s the increase in Fenn-Scandian/Northwest Russian breeding population was evident in the countries of Fenno-Scandinavia and the Baltic region (Haapanen and Koskimies 1998; Laubek *et al.* 1999; Luigujõe *et al.* 2002; Nilsson 2002). After a long absence there are now reports of swans breeding in the Leningrad region and southern Karelia. Thus, the Whooper Swan breeding distribution also appears to have spread in northwest Russia, and the border of its breeding range has moved to the south. This cannot, however, be considered an expansion of the breeding range because the swans have not yet returned to the full range occupied in the 19th century and early 20th century.

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Numbers and Ecology of Swans Wintering in Japan

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Abstract.—The numbers of Whooper Swans (*Cygnus cygnus*) and Bewick's Swans (*Cygnus columbianus bewickii*) wintering in Japan have increased in recent decades. Annual winter counts show a steady growth in the last twenty years. Swans arrive in Japan from mid-October onwards, and up to 32,000 Whooper Swans and 31,000 Bewick's Swans have been recorded in mid-winter in the late 1990s. This is more than 50% of the East Asian populations of these two species. In addition, 150 feral Mute Swans (*Cygnus olor*) reside in Japan throughout the year. There is a long tradition of providing rice and bread for swans in Japan, and the number of supplementary feeding sites has increased since 1980. Food for swans and other waterfowl is now distributed at nearly 300 locations; about 55% of the wintering swans are found at these sites. Unlike in Europe and North America, no conflicts with farming interests have been reported.

Key words.—Bewick's Swan, *Cygnus cygnus, Cygnus columbianus bewickii, Cygnus olor,* Japan, Mute Swan, supplementary feeding, Whooper Swan.

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Asian waterfowl inhabit vast breeding areas, and many of the species migrate long distances to their wintering grounds. Studies of their annual movements between suitable wetlands have led to the recognition of two major flyways, the Central-South Asian Flyway and the East Asian Flyway (Miyabayashi and Mundkur 1999). All three Palearctic swan species, the Whooper Swan (*Cygnus cygnus*), Bewick's Swan (*Cygnus columbianus bewickii*) and Mute Swan (*Cygnus olor*), occur in eastern Asia. The Whooper Swan and Bewick's Swan are native species to Asia, breeding in central and northeastern parts of Russia, and in the highlands of central Asia (del Hoyo *et al.* 1992). Swans of the East Asian Flyway migrate via staging sites at traditional wetlands and lakes before arriving at the wintering grounds in northern Japan, southeastern Russia and Kamchatka, coastal China, and the Korean peninsula (Miyabayashi and Mundkur 1999). There is no evidence from banding and satellite-tracking programs initiated in Japan that central Asian swans visit Japan, although this may reflect greater banding and resighting effort in eastern than in central Asia. The current population estimates of the Whooper Swan and Bewick's Swan in the East Asian Flyway are 60,000 and 40,000 birds, respectively (Miyabayashi and Mundkur 1999).

The Whooper Swan is a regular and locally common winter visitor to Japan, where it occurs from October until April (Brazil 1984). Birds tracked by satellite from the Kominato coast in northernmost Honshu, migrated across the strait between Hokkaido in Japan and Sakhalin in Russia (Kanai *et al.* 1997), which is a well-known migration route of Whooper Swans between the two countries (Matsui *et al.* 1981). Another easterly route via the Kuril Islands has yet to be confirmed, although Whooper Swans have been observed migrating through this region (Ostapenko 1991). Bewick's Swans arrive earlier in October and November than do Whooper Swans, and generally spend the winter further south, before returning in April (Brazil 1991). They migrate between Honshu and Sakhalin via the north coast of Hokkaido (Yamashina Institute for Ornithology 1996; Kamiya and Ozaki 2002), and satellite-tracking has recently provided evidence of a more westerly migration route, direct from Honshu across the Sea of Japan (Kamiya and Ozaki 2002). Mute Swans have probably spread through Asia with help from humans, having been released or escaped from zoological collections, and local populations can now be found in East Asia (del Hoyo *et al.* 1992). Current numbers in Eastern Asia are estimated at 1,000-3,000 birds (Miyabayashi and Mundkur 1999). There is little historical information on the introduction (e.g., dates first occurred) and changing status of the Mute Swan in Japan before this species was included in the annual winter survey in 1988. Brazil (1991) stated that the introduction of the Mute Swan to Japan attracted surprisingly little interest, and that their status and their distribution were poorly known. Additionally, the Black Swan (*Cygnus atratus*) occurs in Japan. These individuals have escaped from waterfowl collections and are found at sites in temperate parts of Honshu and Kyushu. In Europe, the feral Black Swan is known to have bred in Austria, Slovenia and The Netherlands (Brugger and Tarborsky 1994; Snow and Perrins 1998) but this is not yet reported in Japan (M. A. Brazil, pers. comm.).

Supplementary feeding of swans started in the middle of the last century in Japan (Hatakeyama 1981; Ohmori 1981). It started as an aid to help the survival of birds in winter, and now this practice has spread to many traditional and man-made wintering areas. Government staff or local volunteers take responsibility for the distribution of food, and large numbers of waterfowl can be found at these sites. Artificial feeding sites attract birds, but also people, and the tourist and leisure industry often promotes this practice. Sites where swans occur are extremely popular as visitor attractions and, because feeding the birds is a major part of the attraction, swans that feed entirely on a natural diet are now something of a rarity (Brazil 1991).

This paper describes variation in the numbers of Whooper Swans, Bewick's Swans and Mute Swans in Japan, their current status and their ecology in winter. The tradition of supplementary feeding in Japan is described, and data is provided on the frequency of supplementary feeding since 1955.

METHODS

The primary means of investigation was a search of published reports and papers concerning swans in Japan. Most of the data on swan numbers come from annual censuses of wintering waterfowl, organized by the Environment Agency of Japan since 1970. The waterfowl counts take place on 15 January, or close to this date depending on logistics and weather. In this way, counting is coordinated (i.e., all counters counting at the same time, to avoid counting the same birds twice), and at the same time of year, to ensure that the between-winter data are comparable. Data were collected by environmental staff at government offices, by non-governmental organizations (ornithological societies, hunting associations, conservation associations), and by local volunteers. A total of 3,550 sites (covering a total area of 250,000 ha) were surveyed in 1970, while waterfowl were recorded at 8,987 sites (394,186 ha) in 1999 (Environment Agency of Japan 1999). The available data were not appropriate to use counts from key sites monitored in all years, rather than at all sites, in determining trends in swan numbers to control for variation in coverage (e.g., Delany *et al.* 1999). In response to the growing interest in swans, the Swan Society of Japan was established in 1978, and this provided the incentive for holding the 2nd International Swan Symposium at Sapporo in 1980. Since early 1980s, Swan Society members have made great efforts trough expertise and participation in the annual waterfowl censuses and the coverage has been regarded as good, especially for wintering swans. This ensures that the between-winter data are comparable from 1980 onwards. The different swan species have been recorded separately throughout the annual censuses, and swans were observed at 111 sites (32,075 ha) in 1970, whereas the number of recorded wintering sites of swans had increased to 488 (78,800 ha) by 1999 (Environment Agency of Japan 1999).

In 1999, 48 local government offices and volunteer groups responsible for supplementary feeding were sent a questionnaire inviting information on: (1) the year in which the feeding program was initiated; (2) type of food provided; (3) approximate weight of food provided each day, and; (4) the number of swans of each species occurring at the site. Unless otherwise stated, the data were grouped into five-year means if the available information made this possible. The other data describe the situation in mid-January 1999.

RESULTS

Population Trends

The number of Whooper Swans wintering in Japan has increased nearly three-fold, from 11,095 birds when the winter census was initiated in 1970, to an average of 31,000 over the last five years (1995–99; Environment Agency of Japan 1999; Fig. 1). There was a slight decrease in numbers between first half and second half of the 1970s, with the steepest growth in numbers occurring from early to late 1980s (Table 1). By the 1990s, numbers of Whooper Swans were still growing, but not so steeply. A total of 32,423 Whooper Swans was counted in mid-January 1999 (En-

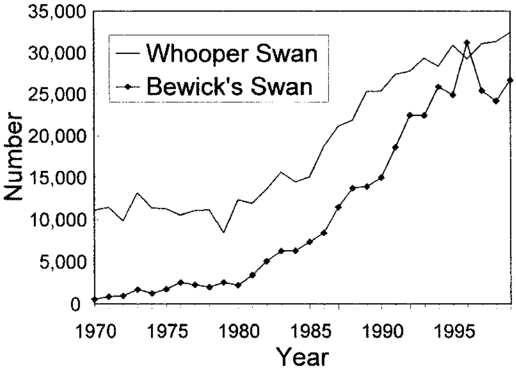

Figure 1. Trends in the number of Whooper Swans and Bewick's Swans recorded in Japan, mid-January 1970–1999.

vironment Agency of Japan 1999), the highest number recorded in Japan, exceeding the previous year's count by 1,119 birds.

The 1970 census recorded 542 Bewick's Swans in Japan (Fig. 1), and numbers counted have risen considerably since then. Over 100% increases in summed Bewick's Swan counts were recorded for each five-year period from the early 1970s to late 1980s inclusive, and trends continued to increase but at a slower rate from the early 1990s onwards (Fig. 1, Table 1). A total of 26,684 Bewick's Swans was observed during the winter count in January 1999 (Environment Agency of Japan 1999). This number was 2,505 higher than reported the previous year, and the second highest after the peak in 1996 when 31,198 individuals were counted. Bewick's Swan numbers may now be stabilizing, having fluctuated around an average of 26,000 birds over the last five years (Environment Agency of Japan 1999).

One Mute Swan, presumed wild, was recorded in the Izu Islands in 1933 (Brazil 1991). In mid 20th century the interest of introducing Mute Swans to scenic spots in Japan grew. An increasing number of popular tourist sites throughout Honshu introduced Mute Swans in the 1970s, and escaped individuals have formed a feral population (Brazil 1987, 1991). Seven birds escaped from Onuma Park, southwest Hokkaido, moved northeastwards and settled at Lake Utonai where they started breeding in 1978. Ten years later, numbers amounted to 90 individuals including 15 breeding pairs (Ohata 1987). The Environment Agency has monitored the wintering sites and numbers of the Mute Swan population since 1988. The number of birds has increased (Fig. 2), and the peak count was 178 birds in 1995. The population appears to have stabilized at around 150 individuals over the last five years (Environment Agency of Japan 1999).

Wintering Sites in Japan

The number of recorded swan wintering sites increased from about 100 in the early 1970s to about 200 sites in the mid-1980s (Fig. 3, Table 1). Since then, the number of sites increased more rapidly, although it started to stabilize at nearly 500 sites by the end of the 1990s. Japan is a contracting party to the "Convention on Wetlands of International Importance especially as Waterfowl Habitat" (more commonly known as the "Ramsar Convention"), and Wetlands International has recognized 43 internationally important staging and wintering sites for Whooper Swans and Bewick's Swans in Japan fulfilling the Ramsar criteria for designation (Figs. 4 and 5; Miyabayashi and Mundkur 1999). The Mute Swan is a feral species in Japan, so was not included when the list of international key sites was established.

Table 1. Change (%) in the number of swan wintering sites, Whooper Swans and Bewick's Swans recorded in Japan over five-year intervals.

Years	Wintering site	Whooper Swan	Bewick's Swan
1970-74 vs. 1975-79	28	-8	111
1975-79 vs. 1980-84	39	30	109
1980-84 vs. 1985-89	66	50	137
1985-89 vs. 1990-94	26	35	91
1990-94 vs. 1995-99	15	12	27

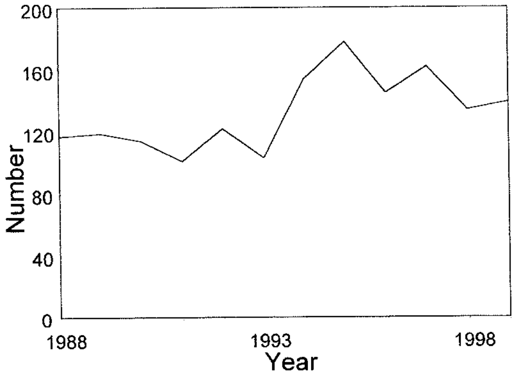

Figure 2. Trend in the number of Mute Swans recorded in Japan, mid-January 1988–1999.

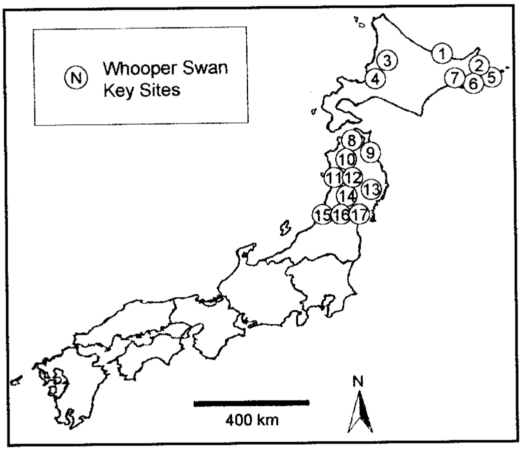

Figure 4. Sites of international importance for Whooper Swans in Japan, according to the Ramsar criteria for designation. 1 = Lake Notoro-ko, 2 = Notsuke Bay, 3 = Lake Fukurojinuma, 4 = Lake Miyajimanuma, 5 = Lake Furen-ko, 6 = Lake Akkeshi-ko, 7 = Kushiro Marsh, 8 = Mutsu Bay, 9 = Lake Ogawara-ko, 10 = Mawarizeki Reservoir, 11 = Hachirogata Rice Fields, 12 = River Tamagawa, 13 = Shin-tsutsumi Reservoir, 14 = River Omonogawa, 15 = River Mogami-gawa, 16 = Lakes Izunuma and Uchinuma, 17 = Lake Naganuma (derived from Miyabayashi and Mundkur 1999).

In the migration season, the largest concentrations of Whooper Swans can be found in Hokkaido, in the order from north to south, at Lake Tofutsu-ko, Notsuke Bay, Lake Furen-ko, Lake Akkeshi-ko and Lake Utonai-ko (Fig. 4; Brazil 1991), of which Lake Tofutsu-ko and Lake Utonai-ko have not fulfilled the Ramsar criteria for designation as a key site for Whooper Swans. Most of the birds in Hokkaido move south to Honshu when ice makes food inaccessible. During the 1990s, on average 15.3% (SD ± 2.4) of the total number of Whooper Swans in Japan remained in Hokkaido in mid-January (range = 13%–20% for the years 1990–1999; Environment Agency of Japan 1999). Whooper Swans can be found on natural habitats in mid-winter in Lake Akkeshi-ko (Fig. 6), while at other localities in Hokkaido limited numbers of birds remain at supplementary feeding sites. The main wintering areas in Honshu are in Mogami-gawa River (Yamagata Pref.), Tamagawa River (Akita Pref.), and Kitakami-gawa River (Iwate Pref.) (Fig. 6). Few birds are observed south of Niigata Prefecture on the east coast and south of Ibaragi Prefecture on the western side of the country (Environment Agency of Japan 1999).

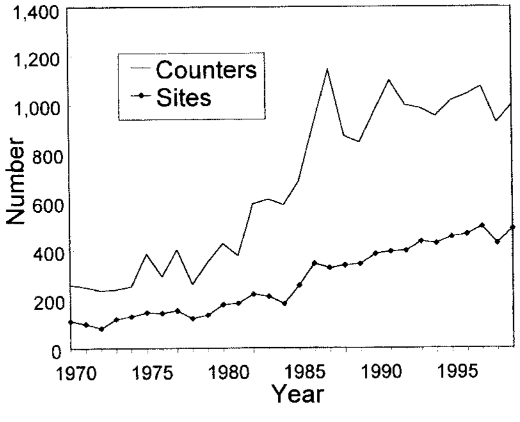

Figure 3. The number of counters and count sites where swans were observed in Japan during mid-January counts, 1970–1999.

Stop-over sites at Lake Kutcharo-ko and nearby Lake Onuma in north Hokkaido, may be visited by 20,000 Bewick's Swans, but ice formation forces them south by mid winter (Table 2). On average, only 3.5% (SD ± 1.6) of the total number of Bewick's Swans in Japan spend the winter in Hokkaido (range = 2%–7% for the years 1990–99, Environment Agency of Japan 1999). The main wintering areas are in Mogami-gawa River (Yamagata Pref.), Lake Hyoko (Niigata Pref.), around Niigata City and Toyosato town (Niigata Pref.), and Hazama-gawa River (Miyagi Pref.) (Fig. 7). Large numbers of swans can be found even further south, with about 2,000 birds wintering in the Tottori/ Shimane area of western Honshu (Environment Agency of Japan 1999).

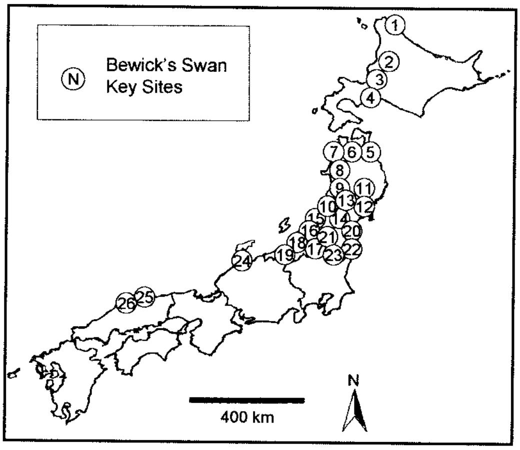

Figure 5. Sites of international importance for Bewick's Swans in Japan, according to the Ramsar criteria for designation. 1 = Lake Kutcharo-ko, 2 = Lake Fukurojinuma, 3 = Lake Miyajimanuma, 4 = Lake Utonai-ko, 5 = Lake Ogawara-ko, 6 = Ezogatate Reservoir, 7 = Mawarizeki Reservoir, 8 = Otomonuma Reservoir, 9 = Hachirogata Rice Fields, 10 = River Mogami-gawa, 11 = River Hasama-gawa, Wakayanagi Town, 12 = River Hasama-gawa, Toyosato Town, 13 = Kitashinbo-ooike Reservoir, 14 = River Shiroishi-gawa, 15 = Lake Fukushimagata, 16 = Lake Toyanogata, 17 = Lake Hyoko, 18 = Lake Sakata, 19 = River Shinano-gawa, 20 = River Abukuma-gawa, 21 = Lake Inawashiro-ko, 22 = Kamishigeoka Reservoir, 23 = River Natsui-gawa, 24 = Ouchigata Rice Fields, 25 = Lake Nakaumi, 26 = Nougi Rice Fields (derived from Miyabayashi and Mundkur 1999).

The data from the annual winter counts indicate that most of the Mute Swans spend the winter around Lake Kasumigaura (Ibaragi Pref.) (88 individuals; Environment Agency of Japan 1999). Other preferred wintering sites are in Lake Yamanaka-ko (Yamanashi Pref.), Teganuma Pond (Chiba Pref.), and Kamoike Pond (Niigata Pref.) with 15, 14, and ten individuals, respectively (Fig. 8).

Supplementary Feeding

The Environment Agency of Japan started recording the number of supplementary feeding sites in 1995, and the number of sites where waterfowl were provided with supplementary food increased between 1995–99 (154, 134, 138, 212 and 294 sites respectively, Environment Agency of Japan 1999). During those years, swans were observed at 100, 98, 101, 118 and 135 of these sites respectively (i.e., 46%–73% of sites where food was provided, Environment Agency of Japan 1999).

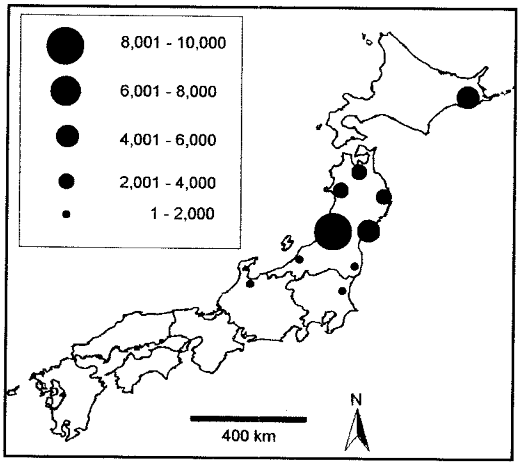

Figure 6. Whooper Swan wintering sites in Japan. Size of dots indicates total number of birds recorded in each prefecture in mid-January 1999, while the location of dots show the most important site in each prefecture.

In the period between 1995–99, on average 55.2% (SD ± 6.1) of the total number of swans wintering in Japan were counted at supplementary feeding sites (57%, 58%, 55%, 45%, and 61% respectively, Environment Agency of Japan 1999). In 1999, the 294 supplementary feeding sites were located in 37 prefectures (Environment Agency of Japan 1999). In 1999, 20,090 Whooper Swans, 16,090 Bewick's Swans, and 91 Mute Swans were counted at these sites, which is 62%, 60%, and 65% of each species recorded during the January 1999 census (Environment Agency of Japan 1999). The Environment Agency of Japan also noted, however, that the number of swans recorded at sites where food was provided was the total number present, and that the numbers using the supplementary food, as opposed to natural food sources, at these sites has not been estimated.

The request for information from local government staff and volunteer groups regarding their supplementary feeding program produced 18 responses out of 48 surveys. Since 63% of the surveys were not returned, this raises the question of whether those that returned the surveys provide a random sample of those approached. Since the responses indicated that there are large local differences in the extent of supplementary feeding, we accepted them as being rep-

Table 2. Whooper Swan and Bewick's Swan sites in Japan where supplementary food is provided. The data are for 18 sites where questionnaires were returned, out of 135 sites where swans were fed in Japan in 1999 (Whooper Swan = WS, Bewick's Swan = BS).

Prefecture	Location	Site	Started	Food type	Kg/day	Number of swans
Hokkaido	Hamatonbetsu town	Lake Kutcharo-ko	1973	Bread and unripe rice	60	Mid-January (481 BS)/Staging (12,000 BS)
Hokkaido	Wakkanai city	Lake Onuma	1995	Bread and barley	40	Mid-January (90 WS)/Staging (10,000 BS)
Hokkaido	Abashiri city	Lake Tofutsu-ko	1974	Bread	8	Mid-January (367 WS)/Staging (10,000 WS)
Hokkaido	Obihiro city	Tokachi-gawa River	1990	Barley	5	Mid-January (122 WS)/Staging (500 WS)
Aomori	Tenmabayashi town	Tsubo-gawa River	1993	Unripe rice	10	Mid-January (407 WS)
Aomori	Hiranai town	Asadokoro Beach	1987	Unripe rice	8	Mid-January (442 WS)
Iwate	Morioka city	Kitakami-gawa River	1978	Unripe rice	5	Mid-January (370 WS)
Miyagi	Shiroishi city	Shiroishi-gawa River	1988	Unripe rice	10	Mid-January (302 WS)
Miyagi	Wakayanagi town	Hazama-gawa River	1978	Unripe rice	10	Mid-January (263 WS + 928 BS)
Miyagi	Wakayanagi town	Lake Izunuma	1970s	Unripe rice	10	Mid-January (156 WS)
Miyagi	Kitakami town	Sarakai-gawa River	1990s	Unripe rice	7	Mid-January (54 WS + 46 BS)
Akita	Nakasen town	Tama-gawa River	1992	Unripe rice	25	Mid-January (1,312 WS)
Akita	Jumonji town	Minase-gawa River	1975	Unripe rice	15	Mid-January (332 WS)
Yamagata	Sakata city	Mogami-gawa River	1975	Unripe rice	20	Mid-January (5,550 WS + 2,820 BS)
Fukushima	Kagamiishi town	Koya Pond	1976	Unripe rice	15	Mid-January (288 WS + 10 BS)
Fukushima[a]	Fukushima city	Abukuma-gawa River	1974	Bread and unripe rice	320	Mid-January (234 WS + 680 BS)
Niigata	Suibara town	Lake Hyoko	1955	Unripe rice	30	Mid-January (132 WS + 3,452 BS)
Tottori	Yonago city	Yonago Bird Sanctuary	1980	Unripe rice	40	Mid-January (1 WS + 798 BS)

The mid-January numbers are from Environment Agency of Japan (1999), while the numbers for the staging period are estimated by local contacts.

[a] This site is a preferred wintering site for ducks, with 15,524 ducks counted in mid-January 1999 (Environment Agency of Japan 1999).

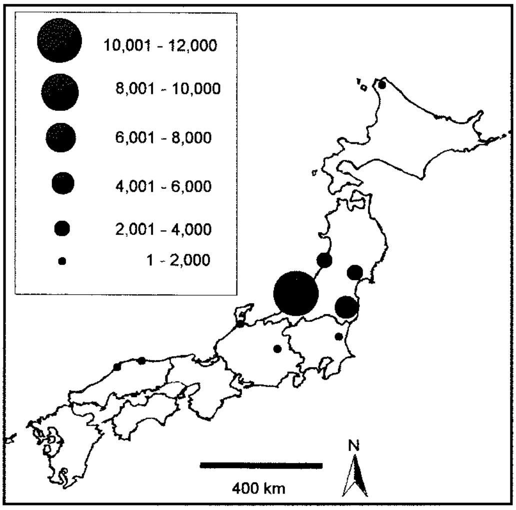

Figure 7. Bewick's Swan wintering sites in Japan. Size of dots indicates total number of birds recorded in each prefecture in mid-January 1999, while the location of dots show the most important site in each prefecture.

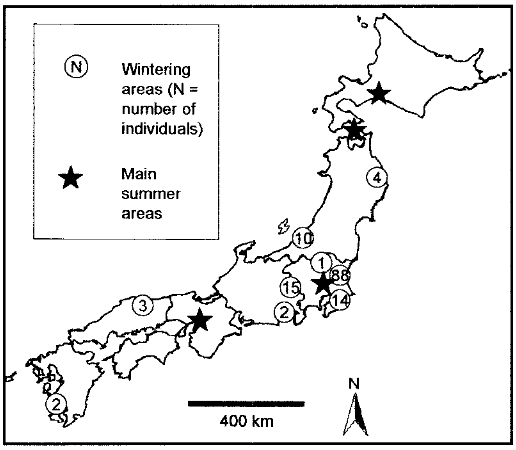

Figure 8. Mute Swan wintering sites in Japan. Numbers indicate the individuals recorded in mid-January 1999.

resentative of the feeding programs taking place in Japan, and assumed that the level of bias in the survey was low. Supplementary feeding data, indicating the average situation in mid-January between 1995–1999, are given in Table 2. At Lake Hyoko, the feeding program had already started in 1955, which to our knowledge is the earliest provisioned site for swans in Japan. Ten sites have been feeding birds since the 1970s (including at Lake Hyoko), and several sites have started feeding in more recent years (1990s). The surveys showed that unripe Rice (*Oryza sativa*), Barley (*Hordeum vulgare*) and bread were fed to waterfowl, and that the amount varied from 5–320kg/day (Table 2). The wintering number of swans at these sites varied from 90–8,370 individuals, and there were usually an unknown number of ducks and gulls also present. The highest recorded daily amount of food (320 kg/day) was provided at the Abukuma-gawa River feeding site (Table 2), which is a favorite site for wintering ducks, and usually receives about 1,000 swans in winter. Staging sites in the north of Hokkaido, at Lake Kutcharo-ko, Lake Onuma and Lake Tofutsu-ko, can hold up to 12,000 swans waiting to continue on their spring or autumn migration (Table 2). The relatively low amount of food per day issued at some sites in relation to swan numbers present indicates that the food provided almost certainly reaches only a small proportion of the birds present.

DISCUSSION

The data collected during thirty years of mid-January waterfowl censuses shows a substantial increase in the numbers of Whooper Swans and Bewick's Swans recorded wintering in Japan (Fig. 1). Horiuchi (1981) summarized the first ten years of censuses, and considered the total number of swans to be stable at around 13,500 individuals in the 1970s. From the early 1980s, the total numbers of swans wintering in Japan have shown an upward trend, with linear growth of approximately 1,900 individuals per year in the last decade (Environment Agency of Japan 1999).

Horiuchi (1981) did not treat the swan species separately between 1970–79, but Bewick's Swan counts were low in the beginning of that decade, and it is interesting to note that there was a four-fold increase in Bewick's Swan numbers recorded during the 1970s (Fig. 1). The increase in the Bewick's Swan numbers was not matched by a similar decrease in Whooper Swan numbers, because Bewick's Swans were only a small proportion of migratory swans recorded wintering in Japan at that time. Brazil (1991) mentioned that the ability to discriminate between the two species increased in the period after Bewick's Swan was first recognized, in the late 1940s (Austin 1949; Austin and Kuroda 1953), as a part of the Japanese avifauna. It is possible that misidentification influenced the ratio between Whooper Swan and Bewick's Swan recorded in the first decade of censuses. Founding the Swan Society of Japan in the late 1970s probably helped to improve species identification by census personnel, resulting in better quality of the swan data thereafter.

Some caution should be taken in interpreting the swan data from the first fifteen years of the study. In the 1970s, the number of persons participating in swan surveys varied at around 350 (Fig. 3) and, although the main wintering areas were covered, many small localities probably were not visited. In this period the number of recorded swan sites were stable. From the early 1980s onwards, the personnel involved increased each year, perhaps inspired both by the founding of the Swan Society of Japan, and by holding the 2nd International Swan Symposium at Sapporo in 1980. The increase in the number of recorded swan sites in the mid-1980s therefore may be a combined effect of more personnel and increased knowledge about wintering sites, and the increased coverage from 1970 to the mid-1980s may partly explain the increase in swan numbers recorded in this period. Since the mid-1980s, the number of participants has been quite stable, at about three times higher than a decade earlier, while the number of swan sites has continued to increase (Fig. 3). The Environment Agency of Japan has not evaluated the complete census coverage (i.e., the ratio of the number of sites covered to the total number of wetlands) but, due to the strong participation of prefecture offices and local expertise regarding wintering sites for waterfowl, the census coverage is now considered comprehensive, and the swan numbers in Japan are probably correctly estimated. Thus, the increase in the number of swan wintering sites since the mid-1980s may be an effect of the growing number of individuals dispersing to use new wintering sites, utilizing either new natural feeding areas or artificial feeding sites.

The Central Asian/East Asian Whooper Swan population is currently estimated at 60,000 individuals (Miyabayashi and Mundkur 1999), and the results from the annual waterfowl censuses show that about half of them winter in Japan (Environment Agency of Japan 1999). Wintering numbers in China and the Korean Peninsula are estimated at 10,000–15,000 and 4,000 birds, respectively (Miyabayashi and Mundkur 1999). The numbers wintering in Japan have increased, but for the rest of Central Asia and East Asia the trend is not known (Miyabayashi and Mundkur 1999). It is also not known whether the increase in numbers in Japan is partly due to displacement from wintering sites in China or Korea, but the limited data from banding programs does not support this theory. The aggregation of birds at wintering sites makes it relatively easy to monitor population development compared to the breeding grounds where swans are widely dispersed over large areas. Syroechkovski (2002) reports a northward shift in breeding localities in Yakutia and Taimyr, which may indicate an increase in Whooper Swan numbers breeding in the northern part of the breeding range, and this may be the source of the increased numbers wintering in Japan.

The Central Asian/East Asian Bewick's Swan population is estimated at 40,000 individuals (Miyabayashi and Mundkur 1999). About 65% (26,000 birds) of them winter in Japan, where they are increasing in number (Environment Agency of Japan 1999). As for the Whooper Swans, the trend for the whole of the Bewick's Swan population in Central Asia/East Asia is not known, but numbers wintering in China and on the Korean Peninsula are estimated at 10,000 and 500–1,000 birds, respectively (Miyabayashi and Mundkur 1999). Although Kamiya and Ozaki (2002) have recently described a more westerly migration route, when satellite-tracking Bewick's Swans from the south of Japan, there is no indication that swans previously wintering in China and Korea have been displaced to Japan. Reports from breeding areas in northeastern Russia partly confirm the increase in swan numbers observed at Japanese wintering grounds (Syroechkovski 2002). Although it is relatively easy to estimate numbers in Japan compared with the Russian arctic, studies in the breeding grounds found a similar trend. For instance, Kondratyev (1990) estimated that 300 Bewick's Swans occurred in Chaun Bay and 700 in the lower Kolyma River valley in the late 1980s, but aerial censuses in 1993–95 found a large increase in numbers, giving new estimates of 6,000–7,000 birds for Chaun Bay and 13,000–14,500 for the lower Kolyma River (Poyarkov *et al.* 2000). Increased numbers have also been reported further east, for the tundra areas of the Taimyr Peninsula (Kolpashikov 2001) and the Lena River delta (Pozdnyakov 2002).

The East Asian population of the Mute Swan was recently estimated at 1,000–3,000 individuals, and is thought to be in decline (Miyabayashi and Mundkur 1999). Nearly all are in China, although about 100 occur on the Korean Peninsula (Miyabayashi and Mundkur 1999). The feral Japanese Mute Swan is now stable at around 150 individuals (Environment Agency of Japan 1999). One explanation why Mute Swan numbers are relatively static may be that they are probably limited by the availability of suitable breeding locations. Another likely reason is predation on eggs and chicks by Red Fox (*Vulpes vulpes*) and Raccoon Dog (*Nyctereutes procyonoides*), which are quite common in Japan.

The Whooper Swan is found during winter at estuaries, bays, inland lakes, marshes and rivers (Brazil 1991). They can occasionally be seen on rice stubble fields, but rarely on other types of farmland (Brazil 1991). Nowadays they are often found at supplementary feeding sites (Environment Agency of Japan 1999). The Bewick's Swan is found in wetlands, bays, inland lakes, marshes and large rivers (Brazil 1991). They can regularly be observed feeding on fields in many areas (Brazil 1991), and are often found at sites with supplementary feeding (Environment Agency of Japan 1999). Neck-banding in the 1980s established a link between wintering birds at Lake Kasumigaura in Ibaragi Prefecture, Honshu, and the breeding site at Lake Utonai-ko in Hokkaido (Yoshi 1985; Ohata 1987). The birds start on their 1,000 km journey when the breeding area freezes between October and December and return in February–April. The fairly small number of Mute Swans is found in lakes, rivers and castle moats (Brazil 1991), and many of them use sites where supplementary feeding occurs (Environment Agency of Japan 1999).

The waterfowl censuses by the Environment Agency show that there is an overall difference in wintering locations between Whooper Swans and Bewick's Swans (Figs. 6 and 7). The Whooper Swan occurs predominately in the northern prefectures (Horiuchi 1981), and Brazil (1983) suggested that such division of the wintering areas might be related to energy expenditure due to the smaller size of the Bewick's Swan. There appears to have been a recent shift southward in the Whooper Swan's wintering areas. Horiuchi (1981) found that 53% of the Whooper Swans in Japan occurred in Hokkaido in midwinter, while Brazil (1991) mentions that more started wintering in Honshu from the mid-1980s onwards. The recent surveys by the Environment Agency support this trend, showing that now only 15% of Whooper Swans winter in Hokkaido. This may be due to the limited ice-free wintering sites in the north being occupied to their carrying capacity, forcing the growing number of Whooper Swans to shift south.

Supplementary feeding of waterfowl began in Japan as early as in 1955 at Lake Hyoko, Niigata Prefecture (Table 1). Ohmori (1981), who investigated supplementary feeding of swans, found 15 sites where swans were fed throughout the whole winter, and another three locations where swans were fed temporarily. The same 18 sites are still in operation today, but the number of supplementary feeding sites has increased considerably since Ohmori's investigation by the end of the 1970s. Providing food for swans started when local people became worried that the swans would not find enough natural food in their habitat (Hatakeyama 1981), and this practice grew after incidents where swans died due to starvation during cold winters in the mid 1970s. In particular, 500 Whooper Swans starved to death at Notsuke

Bay after a cold spell in 1976 (Ohmori 1981). As watching swans being fed became a recreational activity, the tourist industry supported the establishment of new feeding sites, and the increase between 1995-99 indicates that these are still growing in numbers (Environment Agency of Japan 1999). Ohmori (1981) described supplementary swan food as consisting mostly of rice or bread, but other types of food was also reported, including cereals, tea leaves, fruit rinds, oats, barley, corn, and apples. Rice and bread are still the major food items at current feeding sites (Table 1). Ohmori (1981) also reported that 400–500 g of food was given per swan each day. Both the numbers of swans wintering in Japan, and the numbers of feeding sites have increased, but the amount of food given per bird probably is considerably less in most places today. Three factors make it difficult to calculate the exact amount of food provided per swan: (1) all the swans visiting feeding sites do not necessarily eat supplementary food; (2) the large concentrations of waterfowl attract many sightseers, who bring additional food or buys food from stalls or vending machines at the feeding sites, and the volume of this kind of food is not known; and (3) it was not possible to calculate from this data how much was provided per swan due to the unknown numbers of ducks and gulls also eating the food provided.

There is reason to believe that supplementary feeding increases winter survival of swans in Japan, although this is certainly not the only reason. The practice started in an *ad hoc* way to help starving swans, and the large increase in the number of supplementary feeding sites seen since 1980 may perhaps be associated with the rapid growth in numbers observed over the same period. Bewick's Swan and Whooper Swan numbers were probably reduced by hunting to below the carrying capacity of their tundra and taiga habitats during the late 19th century and first half of the 20th century, and more recently may have responded to an increased winter food supply with more successful breeding. The positive trend in numbers for Whooper Swans and Bewick's Swans wintering in Japan is not symptomatic of the situation for swans elsewhere in the East Asian Flyway. In several countries in East Asia, for example China (Lu 1995), wetland habitat has been seriously damaged or reclaimed, and waterfowl are hunted illegally, causing a drastic decrease in the number of birds. Similar situations facing waterfowl on the Korean Peninsula have greatly reduced the number of wintering swans (Won 1981), and wetlands needs special attention in the future (Pak 1995; Won 1995). Wetlands International initiated the annual Asian Waterfowl Census, which will provide invaluable information on the waterfowl in the region, but it is difficult to obtain national data from other countries that are comparable to the consecutive 30-year waterfowl census data recorded by the Environment Agency in Japan. This lack of information from elsewhere in East Asia means that it is not possible to determine the extent to which the increase in swans wintering in Japan is due to a concentration of birds at an increasingly limited number of sites.

Whooper Swans have used agricultural land in Great Britain since the hard winters of the 1940s (Owen and Kear 1972), and Bewick's Swans have also used arable land since the 1970s (Rees *et al.* 1997). Field-feeding by waterfowl is an economic problem for the agriculture industry in some parts of Europe and the USA (Owen 1990; Patterson 1991). Lane *et al.* (1998) reviewed this subject in Japan and found that some non-migratory waterfowl species do affect crop-growing farms, because traditional agriculture involves growing rice during the summer months. Since rice is harvested before migrants return in autumn, there is currently no serious conflict between migratory waterfowl and rice farmers, but some grazing on winter-sown crops are reported. However, changing crop policies in Japan, in combination with growth in waterfowl populations, may cause problems in the future.

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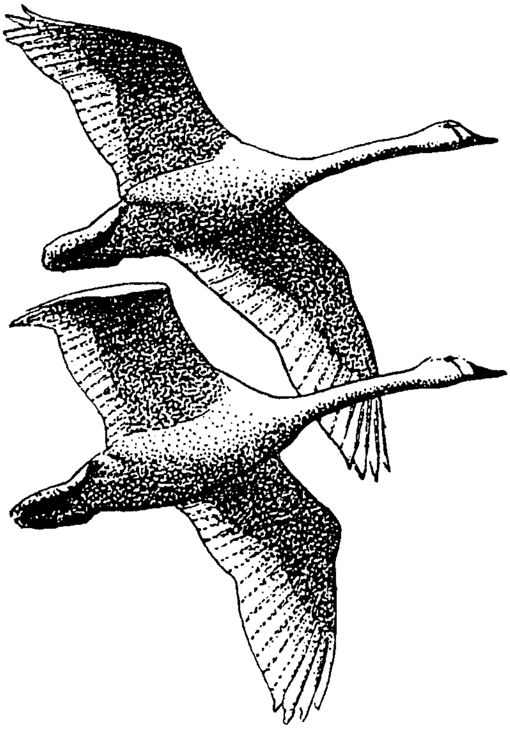

Annual Variation in the Proportion of Whooper Swans and Bewick's Swans Breeding in Northern European Russia

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Abstract.—Aerial surveys of breeding and non-breeding Bewick's Swans (*Cygnus columbianus bewickii*) and Whooper Swans (*Cygnus cygnus*) were made in north European Russia in 1980, 1981, 1991 and from 1996 to 2000. There was a significant increase in the density of territorial Whooper Swan pairs on the Pechora Delta over this period, whereas the density of Bewick's Swan pairs on open tundra on the Russkiy Zavorot Peninsula, some 50 km further north, was stable. Additional surveys of Whooper Swans breeding in forest tundra to the south of the main study areas showed that nesting density in this region was much lower than for the Pechora Delta. The proportion of territorial pairs with nests varied substantially between years for both species. In Whooper Swans, the ratio of territorial breeding pairs to non-breeding pairs also changed substantially between June and July, particularly in 1998 and 1999, but there was little seasonal variation in the proportion of territorial pairs breeding recorded for Bewick's Swans during the study. Extensive surveys conducted in 1980, 1981, 1991 and 1999–2000 indicated that 56%–73% of Whooper Swans and 54%–62% of Bewick's Swans in the region do not defend breeding territories in early summer, but congregate in non-breeding flocks.

Key words.—Arctic Russia, Bewick's Swan, *Cygnus columbianus bewickii, Cygnus cygnus*, Pechora Delta, proportion of breeding birds, trends in numbers, tundra, Whooper Swan.

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Bewick's Swans (*Cygnus columbianus bewickii*) breed on the tundras of arctic Russia, with birds from the western population migrating some 4,000 km each autumn to winter in northwest Europe (Rees *et al.* 1997a). In the wintering range, the ratio of paired birds to single swans, and of breeding pairs (accompanied by juveniles) to pairs without young, varies between years (Evans 1979). At a single wintering site, the proportion of adults recorded as paired ranged from 61%–89%, and averaged 73% over a 15-year period (derived from Evans 1979). Yearlings, which were excluded from the adult category, usually do not pair, and none have been recorded with young (Evans 1979; Rees *et al.* 1996). The proportion of paired birds that bred successfully also varied, with parents comprising 12%–66% of total pairs seen in winter. These figures were similar to the proportion of paired Western Population Tundra Swans (*Cygnus columbianus columbianus*) with broods in western Alaska ($\bar{x}$ = 31%, range = 15%–48% in August 1963–71; Lensink 1973), and also to the proportion of Eastern Population Tundra Swans pairs with broods at higher latitudes ($\bar{x}$ = 37%, range = 24%–50% in north Alaska in August 1989–2000, Ritchie *et al.* 2002; $\bar{x}$ = 34% in northern and eastern Alaska in August 1983–89, Bart *et al.* 1991). Annual variation in the percentage of juveniles recorded in the wintering population has been attributed to weather conditions during the short arctic summer (Poorter 1991), but the extent to which this variation is due to variation in the proportion of pairs attempting to breed, clutch size or cygnet survival cannot be determined without studies such as this one in the breeding range.

Whooper Swans (*Cygnus cygnus*) breed mainly in sub-arctic and taiga zones, at more southerly latitudes than the Bewick's Swans (Ogilvie 1972; Rees *et al.* 1997b). The percentage of adults accompanied by cygnets on the wintering grounds again varies substantially between years, ranging from 13%–30% in southwest Scotland (Black and Rees 1984). Moreover, observations on the breeding grounds in Iceland suggest that a high proportion of the Icelandic population (over 60%) does not defend breeding territories, but instead remains in non-breeding flocks in both spring and summer (Gardarsson and Skarphedinsson 1984; Rees *et al.* 1991; Einarsson 1996). Whooper Swans breeding in Iceland have shown little annual variation in the proportion of territorial pairs that laid a clutch, but the proportion of breeders that fail varies between years, frequently because of local flooding (Einarsson 1996; Einarsson and Rees 2002). The proportion of adults with cygnets in winter has not yet been described for the continental northwest European Whooper Swans, which breed in Fenno-Scandia and northwest Russia, but the proportion of non-breeding adults (i.e., swans in flocks and territorial pairs without nests or young) in Finland was high (71%–73%) in the late 1960s and early 1970s (Haapanen *et al.* 1973; Haapanen 1991).

Here we use aerial surveys to estimate annual variation in the proportion of the Bewick's Swans on the Russkiy Zavorot Peninsula, in northern European Russia, that hold territories. We consider the results in relation to environmental conditions. Similarly, annual and seasonal variation in the proportion of birds holding territories, and in the proportion of territorial pairs breeding, was estimated for Whooper Swans on the Pechora Delta, and the results considered in relation to water levels in the Pechora River. Whooper Swan surveys were extended to the forest tundra in two years, to determine whether the ratio of breeding pairs to non-breeders differed from that of the Bewick's Swans in an area where Whooper Swans are at the northern limit of their geographic range. Trends in breeding density recorded for both species since the early 1980s are described to determine whether they reflect trends recorded for the northwest European Bewick's Swan population and the continental northwest European Whooper Swan population over this period (Delany *et al.* 1999; Laubek *et al.* 1999).

STUDY AREA AND METHODS

The numbers and distribution of Bewick's Swans and Whooper Swans in the Nenetskiy State Nature Reserve (68°15'–69°N, 52°30'–54°E) and the northern Pechora Delta (67°30'–68°N, 53°–54°E) were recorded in 1980-1981, 1991 and 1996-2000. Within the Nenetskiy State Nature Reserve, the Russkiy Zavorot Peninsula has one of the highest breeding densities of Bewick's Swans in northeast European Russia (Mineyev 1991). Its open maritime (i.e., coastal) tundra habitat on the northern part of the peninsula includes a large number of lakes and pools of varying size, together with a complex network of rivers and channels. The predominant vegetation on maritime tundra is low-lying wet sedge-grass meadows and marshes, with a variable community structure, depending on the proximity of waterbodies and the extent of flooding. This habitat provides feeding for the birds in spring and early summer, whereas inland tundra to the south has more elevated areas with drier moss-lichen habitat and fewer marshes.

The Pechora Delta region, which lies to the south of the Russkiy Zavorot Peninsula, is an extensive river estuary, with the lower delta and adjacent coastal plain covering 15,000 km^2 (Rikhter 1946; Taskaev *et al.* 2000). The delta is dominated by shrub-marsh communities, alternating with trees and meadows (Leummens *et al.* 2000). To the north of the city of Nar'Yan-Mar, the delta reaches 45 km wide, with thousands of pools and lakes intersected by numerous river channels. Surveys by boat have shown that this area is used mainly by Whooper Swans, rather than by Bewick's Swans, during the breeding season (Mineyev 1995). Several settlements are situated on the banks of the largest channels, as are the huts of local fishermen and hunters. Human activity on the delta in summer includes fishing and mowing of hay on the delta islands, with transport being mainly by motorboat. The northern part of the delta has been designated a federal sanctuary (the Nizhnepechorsky zakaznik), adjacent to the Nenetskiy State Nature Reserve.

Aerial surveys were conducted in 1980–1981, 1991 and from 1996–2000. In June 1980 and June 1981, the survey included the northern coast of the Malozemelskaya and Bolshezemelskaya tundras (from Sengeiskiy Island in the west to the Medynskiy Zavorot Peninsula in the east), and also the Pechora Delta to the south, with six transects flown across the Russkiy Zavorot Peninsula (Fig. 1). There were no efforts made to differentiate between Bewick's and Whooper Swans in 1980 and 1981 (Shchadilov and Orlov 1987), but ground verification has since indicated that swans seen on the Russkiy Zavorot Peninsula and Bolshezemelskaya tundra were predominantly Bewick's Swans and that those on the Pechora Delta were Whooper Swans. In 1991, the aerial survey of the Russkiy Zavorot Peninsula was repeated, following the same six transects flown in 1980 and 1981, and attempts were made to separate the two species by body size. In June 1996–2000, and also in July from 1997–2000, both Whooper and Bewick's Swans in the Pechora Delta region were counted along a single-line transect between Nar'Yan Mar and the south coast of Korovinskaya Bay. Bewick's Swans on the Russkiy Zavorot Peninsula also were recorded along shorter single-line transects, between the north coast of Korovinskaya Bay (Cape Kostyanoi Nos) and Khabuicka on the same days from 1996 onwards (Fig. 1). In 1999 and 2000 additional aerial surveys of Whooper Swans were undertaken, with five transects covering the Pechora Delta from the north of Nar'Yan-Mar to Korovinskaya Bay, and a further five transects covering the forest tundra and taiga zones south of Nar'Yan-Mar to the southern border of the Nenetskiy Autonomous Okrug (Fig. 1).

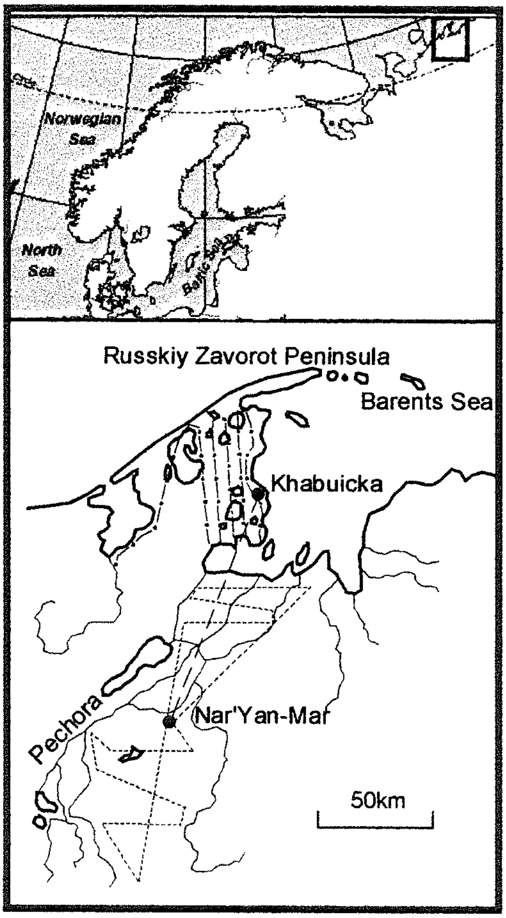

Figure 1. Map of the study area, showing transects flown during aerial surveys. Dot-dash lines indicate flights over the Russkiy Zavorot Peninsula in 1980–1981 and 1991. Dash lines indicate flights between Nar'Yan Mar and Khabuicka (crossing the Korovinskaya Bay, not labeled) from 1996–2000. Dotted lines indicate additional transects of the Pechora Delta north of Nar'Yan Mar and of forest tundra south of Nar'Yan Mar in 1999. Routes of additional transects of the Pechora Delta and forest tundra in 2000 are not shown, but were similar to those followed in 1999.

In 1980 and 1981 the surveys were made from an An-2 fixed-wing airplane, in 1991 in a Mi-8 helicopter and in other years by Mi-2 helicopter, at an altitude of 100 m and an average speed of 150 $km \cdot h^{-1}$ in all cases. Transect width was 500 m on either side of the aircraft. At least two persons recorded swans on each side of the aircraft, to verify observations. Swans were recorded as singles, territorial non-breeding pairs (discrete pairs without a nest), breeding pairs (with a nest in June, or with a nest or cygnets in July) and as non-breeding flocks. The distances covered by the transects were recorded to determine population density. The habitat in which each swan occurred also was recorded as maritime tundra, inland tundra, Pechora River delta or forest tundra.

One-way analysis of variance was used to assess the significance of variation in density between regions and habitats, and linear regression analysis was used to test for changes in swan density over time. In years where more than one survey was made over the same habitat in one month (i.e., July 1997), data for the more extensive survey was used in the regression analyses, unless otherwise stated, because the shorter survey covered part of the same ground. Variation in total swan density between surveys may be high for the shorter surveys, depending on whether the transects pass over non-breeding flocks, so this study focuses mainly on the density of territorial pairs in the region.

RESULTS

Whooper Swans on the Pechora Delta

Results of aerial surveys of Whooper Swans in the Pechora Delta are illustrated in Table 1. There was a significant increase in the density of territorial pairs recorded in June from 1980-2000 ($r_5 = 0.82$, $b = 0.04 \pm 0.01$, $F_{1,6} = 9.97$, $P < 0.05$; Fig. 2). There was no evidence, however, for an increase in the density of territorial pairs present in July 1996-2000 ($r_3 = 0.28$, $b = 0.05 \pm 0.09$, $F_{1,4} = 0.26$, n.s.). The more extensive surveys of the delta (June 1980, 1981 and 1991, and July 1999–2000) similarly found no evidence of a long-term trend in total numbers (range = 1.35–2.97 birds km^{-2}, Table 1; $r_3 = -0.17$, $b = -0.012 \pm 0.04$, $F_{1,4} = 0.08$, n.s.). The extensive aerial surveys also indicated that some 56%–73% of Whooper Swans recorded on the delta did not defend territories but congregated in non-breeding flocks in June, and that 45% were in non-breeding flocks in July 1999 (derived from Table 1). No non-breeding flocks were recorded during the July 2000 survey, but may have been missed since a smaller area was covered.

The proportion of Whooper Swan pairs with nests on the Pechora Delta in June varied significantly between years (range 23%–86%; $\chi^2_4 = 29.6$, $P < 0.001$; Fig. 3). By July, however, the proportion of pairs breeding (recorded with nest or young) had dropped substantially and was less variable (range 29%–36%); annual variation in the proportion of swans breeding at this stage of the season was not significant ($\chi^2_4 = 0.28$, n.s., including counts made during the shorter aerial survey in 1999, since this followed the track of the earlier surveys). The change in the proportion of territorial pairs breeding

Table 1. Densities (swans·km^{-2}) of Whooper Swans, and their breeding status, recorded during aerial surveys of the Pechora Delta. The total number of birds recorded is given in parentheses. Average density for territorial birds (excluding swans recorded as single or in flocks) was 0.98 swans·km^{-2} in June and 0.87 swans·km^{-2} in July. Similarly, average density for breeding birds (recorded with nests or cygnets) was 0.58 swans·km^{-2} in June and 0.23 swans·km^{-2} in July[a].

		Density of individuals observed as				
Date	Area surveyed (km^2)	Singles	Non-breeding pairs	Breeding pairs	Flocks	Overall (N)
June 1980	243		0.50[b]		1.38	1.88 (456)
Late June 1981	261		0.62[b]		0.78	1.40 (365)
Mid June 1991	70	0.10	0.49	0.31	2.07	2.97 (208)
June 1997	31.5	0.13	0.13	0.76	2.09	3.11 (98)
June 1998	31.5	0.16	0.82	0.32	1.37	2.67 (84)
June 1999	31.5	0.06	0.76	0.38	0.16	1.37 (43)
June 2000	15.7	0.19	0.64	1.15	2.87	4.85 (76)
July 1996[c]	31.5	0.10	0.57	0.32	0	0.98 (31)
July 1997	31.5	0.13	0.38	0.19	0	0.70 (22)
July 1998[c]	31.5	0.12	0.32	0.13	0	0.57 (18)
July 1999[c,d]	31.5	0.13	0.44	0.25	0	0.83 (26)
July 1999[c,e]	273	0.13	0.52	0.09	0.61	1.36 (372)
July 2000	124	0.16	0.79	0.40	0	1.35 (168)

[a] Data from the extended 7 July 1999 survey were excluded when calculating average density of territorial birds and breeding birds for the 1980–2000 study period, to avoid biasing the results towards 1999 data.

[b] Swans were classified as either in flocks (3+ birds) or not in flocks (singles and pairs) in the extended 1980 and 1981 surveys.

[c] Extensive flooding on the Pechora Delta, following snow melt into the upper reaches of the Pechora River.

[d] Whooper Swans counted while passing over the Pechora Delta, when returning from Khabuicka to Nar'Yan Mar, 5 July 1999.

[e] Whooper Swans counted during the extensive aerial survey of the Pechora Delta north of Nar'Yan Mar, 7 July 1999.

between June and July was significant for 1997 and 2000 ($\chi^2_1 = 13.2$, $P < 0.001$ and $\chi^2_1 = 9.2$, $P < 0.01$), but not in 1998 and 1999 ($\chi^2_1 = 0.00$ and $\chi^2_1 = 0.06$, n.s.). There was similar annual and seasonal variation in the density of breeding pairs, with high nesting density recorded in June 1997 and 2000 ($\bar{x} = 0.48 \pm 0.14$ SD pairs·km^{-2} for these two years, compared with $\bar{x} = 0.33 \pm 0.10$ pairs·km^{-2} for 1997–2000), but only average density of pairs with young by July ($\bar{x} = 0.15 \pm 0.07$ for 1997 and 2000, compared with $\bar{x} = 0.11 \pm 0.07$ families·km^{-2} for 1997–2000; Fig. 4). Moreover, the density of non-breeding pairs ap-

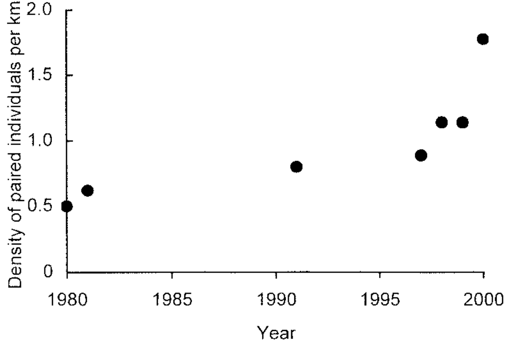

Figure 2. Density of territorial Whooper Swan pairs (with and without a nest) recorded on the Pechora Delta in June.

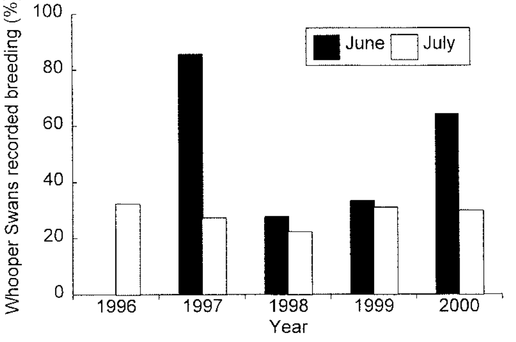

Figure 3. Percentage of discrete Whooper Swan pairs recorded as breeding in (a) June (with nest) and (b) July (with cygnets) from 1996–2000 inclusive. June surveys were not undertaken in 1996.

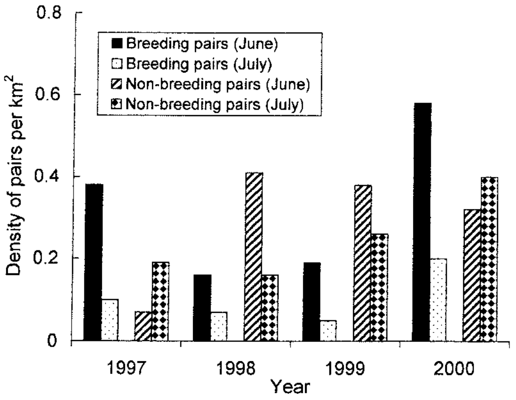

Figure 4. Density of Whooper Swan pairs (both with nest, and territorial pairs without nest) recorded during aerial surveys in 1997 to 2000.

peared to increase between June and July in 1997 and 2000, but to decline between months in 1998 and 1999 (Fig. 4).

Whooper Swans South of Nar'Yan Mar

Aerial surveys of the forest tundra to the south of Nar'Yan-Mar, undertaken in July 1999 and 2000 covered 295 km^2 and 65 km^2 respectively. Whooper Swan density in this region was very low, with a total of 36 birds recorded in 1999 and eight birds seen in 2000. The density of breeding (0.02 and 0.03 pairs·km^{-2}) and non-breeding (0.09 and 0.08 pairs·km^{-2}) pairs was low each year. Single swans were sighted (0.01 and 0.02 birds·km^{-2}), but no flocks were recorded in either year. The density of Whooper Swan pairs in the forest tundra was significantly lower than for Pechora Delta habitat to the north (Table 1) on the same days ($\chi^2_1 = 5.64$, $P < 0.02$ for breeding pairs; $\chi^2_1 = 8.14$, $P < 0.01$ for non-breeding pairs).

Bewick's Swans on the Russkiy Zavorot Peninsula

In 1980 and 1981, Bewick's Swan density on the Russkiy Zavorot Peninsula and Bolshezemelskaya tundra appeared to vary both between areas and across different habitats within the two regions (Table 2, derived from Shchadilov and Orlov 1987). When including densities recorded in the two years for different habitats as separate data points, the density of territorial birds, and also of all Bewick's Swans recorded, was lower on the Bolshezemelskaya tundra than the Russkiy Zavorot Peninsula (one-way ANOVA, $F_{1,8} = 9.48$ and $F_{1,8} = 9.52$ for territorial birds and all birds respectively, $P < 0.02$ in each case). Densities appeared higher on maritime tundra than on inland tundra for both the Bolshezemelskaya tundra and the Russkiy Zavorot Peninsula, but differences between habitats were not significant when data from the two sites were combined (one-way ANOVA, $F_{2,7} = 0.76$, n.s., for territorial swan density and $F_{2,7} = 1.60$, n.s., for total swan density). There was a significant correlation in swan distribution across region and habitat in 1980 and 1981 ($r_3 = 0.99$, $P < 0.01$ for all swans, but $r_3 = 0.873$, n.s. for territorial

Table 2. Variation in Bewick's Swan density by region and habitat in 1980 and 1981 (derived from Shchadilov and Orlov 1987).

				Density (individuals km^{-2})					
Region	Habitat	Area surveyed (km^2)		Territorial swans[a]		Grouped swans		Total swans	
Bolshezemelskaya tundra		1980	1981	1980	1981	1980	1981	1980	1981
	Maritime tundra	148	161	0.29	0.36	0	0.55	0.29	0.91
	Inland tundra	571	459	0.14	0.17	0	0.27	0.14	0.45
	Pechora Delta	105	44	0.22	0.40	0.19	0	0.41	0.40
Russkiy Zavorot									
	Maritime tundra	86	75	0.50	1.04	2.09	3.21	2.59	4.25
	Inland tundra	256	245	0.51	0.80	0.39	0.62	0.90	1.42

[a] Single swans, pairs without nests and pairs with nests were all classified as territorial swans in the 1980 and 1981 surveys.

swans). It seemed that relatively more Bewick's Swans occurred in flocks on maritime and inland tundras rather than on river deltas; of 1,661 swans counted during the 1980 and 1981 surveys, 509 were in flocks on the maritime tundra, 378 on inland tundra, and only 20 birds were in flocks on the Pechora Delta, compared with 223, 490 and 41 territorial birds on the tundra and delta habitats respectively ($\chi^2_2 = 120$, $P < 0.001$; Table 2).

The extensive surveys of 1980, 1981 and 1991 showed that 54%–62% of Bewick's Swans on the Russkiy Zavorot Peninsula occurred in non-breeding flocks (Table 3). The proportion of territorial pairs breeding in June was recorded in only 1991, 1998 and 1999, and showed substantial but statistically insignificant annual variation, at 65%, 71% and 20% respectively ($\chi^2_3 = 6.15$, n.s.). In July of 1996–1999, annual variation in the proportion of territorial pairs breeding (seen either still incubating or with downy young) was significant (range 20%-64%; $\chi^2_3 = 17.4$, $P < 0.001$; Table 3).

Unlike Whooper Swans, the density of territorial Bewick's Swans (breeders and non-breeders) in June did not increase from 1980-1999 ($r_3 = 0.02$, $b = -0.001 \pm 0.03$, $F_{1,4} = 0.001$, n.s.). Inclusion of July data for 1996 and 1997 (i.e., years with no June surveys) also gave no indication of a change in density ($r_5 = 0.38$, $b = 0.06 \pm 0.06$, $F_{1,6} = 0.83$, n.s.; Fig. 5), and there was no consistent trend in total Bewick's Swan density since the early 1980s ($r_5 = 0.06$, $b = 0.001 \pm 0.09$, $F_{1,6} = 0.02$, n.s.). An apparent decline in the density of territorial Bewick's Swans in recent years (1996-1999) was not significant ($r_2 = 0.86$, $b = -1.01 \pm 0.42$, $F_{1,3} = 5.81$, n.s.). There was also no evidence for a change in breeding pair density over this period ($r_2 = 0.76$, $b = -0.19 \pm 0.11$, $F_{1,3} = 2.70$, n.s.). The proportion of territorial pairs breeding did not differ significantly between June and July surveys in 1998 or 1999 ($\chi^2_1 = 0.28$ and $\chi^2_1 = 0.03$, n.s., respectively; Table 3). Overall, the density of territorial Whooper Swan pairs on the Pechora Delta in 1991 and 1996-2000 ($\bar{x} = 0.97 \pm 0.16$ SD) was lower than for Bewick's Swans on the Russkiy Zavorot Peninsula in the same years ($\bar{x} = 1.91 \pm 1.27$ SD), but the difference was not significant (paired-t test, $t_4 = -1.56$, n.s.).

DISCUSSION

Variation in the Proportion of Non-territorial Birds, and of Territorial Pairs that Breed

Aerial surveys indicate that a high proportion of Bewick's Swans (54%–62%) on the Russkiy Zavorot Peninsula and Whooper Swans (56%–73%) on the Pechora Delta do not hold breeding territories, but remain in non-breeding flocks. The Whooper Swan estimates are similar to those for the Iceland-breeding Whooper Swan population, where over 60% congregate in non-breeding flocks in spring and summer (Gardarsson and Skar-

Table 3. Bewick's Swan density (swans·km^{-2}) and breeding status, recorded during aerial surveys of the Russkiy Zavorot Peninsula. The total number of birds counted is given in parentheses.

		Density of individuals observed as				
Date	Area surveyed (km²)	Singles	Non-breeding pairs	Breeding pairs	Flocks	Overall (N)
1980	342	0.51[a]			0.82	1.33 (454)
1981	320	0.86[a]			1.23	2.08 (667)
June 1991	362	0.38	0.72	1.36	2.86	5.3 (1,923)
July 1996	7.5	0.13	3.20	0.80	0	4.13 (31)
July 1997	22	0.18	0.41	0.82	0.18	1.60 (36)
June 1998	22	0.14	0.45	1.09	0	1.68 (37)
July 1998	22	0.14	0.45	0.82	0.14	1.54 (34)
June 1999	11	0.36	0.54	0.18	0.27	1.36 (15)
July 1999	22	0.09	0.45	0.18	0	0.72 (16)

[a] In 1980 and 1981, density is given for singles and pairs combined.

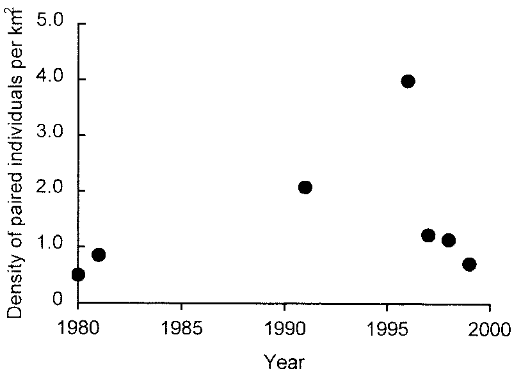

Figure 5. Density of Bewick's Swan pairs (breeders and non-breeders) recorded on the Russkiy Zavorot Peninsula in June 1980–81, 1991 and 1998–99, and in July 1996–97.

phedinsson 1984; Rees *et al.* 1991; Einarsson 1996). A large non-breeding component has also been reported for Tundra Swans during the breeding season (Bart *et al.* 1991; Ritchie *et al.* 2002). The proportion of Bewick's Swan adults recorded as paired in winter averages at 73% (from Evans 1979), which is much higher than the proportion of discrete singles and pairs recorded in summer in the present study, suggesting that some paired birds do not make a prolonged attempt to establish a breeding territory, if at all, but quickly join the non-breeding flocks. The substantial annual variation in the proportion of territorial pairs breeding (20%–71% for Bewick's Swans and 23%–86% for Whooper Swans in June), however, mirrors observations made of Bewick's Swans in the wintering range, where the proportion of paired birds with cygnets varied from 12%–66% (Evans 1979).

Habitat and Other Factors Influencing Breeding

Breeding density varied with habitat for Whooper Swans, being lower in the forest tundra than on the Pechora Delta, but not for Bewick's Swans. Although Bewick's Swan density was apparently higher on the open maritime tundra than on inland tundra, combining observations made on the Bolshezemelskaya tundra and the Russkiy Zavorot Peninsula may have resulted in significant regional differences over-riding any habitat effects. More detailed habitat monitoring is necessary to determine not only the habitat variables influencing breeding density but the reasons for the differences in densities between the two regions.

The relatively few years of data presented in the study makes it difficult to determine the biological reasons underlying annual variation in the proportion of territorial pairs that breed. A combination of factors may be involved, including the age structure of the population, the timing of the spring thaw influencing arrival and onset of nesting, and the body condition of birds arriving in the breeding areas. Nevertheless, the decrease between June and July in the proportion of territorial Whooper Swan pairs on the delta with nests or young in 1997 and 2000, and a corresponding increase in the density of non-breeding pairs, suggests that nest failure was higher in these years than in 1998 and 1999, when there was no difference between months in the proportion of territorial pairs breeding. The 1998 and 1999 seasons were both characterized by late flooding of the delta, which may explain the lower percentage of swans attempting to breed in these two years (Fig. 3). Average water levels in the Pechora Delta from 10–20 June, measured at the monitoring station near Nar'Yan Mar, were 5.25 m in 1998 and 5.34 m in 1999, compared with 3.63 m for the same period in 1997 (Nar'Yan-Mar hydrological station, pers. comm.). The number of breeding pairs present in July 2000 may be an underestimate because an early spring and very high temperatures in late June to early July resulted in early hatching and rapid vegetation growth on the delta, making cygnets more difficult to see. The density of breeding Whooper Swan pairs was low in both 1998 and 1999, which is likely to be due to the exceptionally high water levels recorded in the delta in these two years reducing the availability of suitable or traditional nest sites, but further studies are needed to confirm this point. Certainly Molochaev (1990) reported that breeding density for Whooper Swans and other waterfowl in the upper reaches of the Ob River varied between years, with nesting success observed to be lower in years of high and extensive flooding.

More detailed studies would be needed to explain variations in the proportion of territorial pairs that breed, both between and within years. One possible reason for within season variation is an influx in some years of pairs consisting mainly of young inexperienced birds, which would be more likely to have low breeding success. Breeding success in swans is known to increase both with pair duration (Rees *et al.* 1996) and with the dominance rank of the pair (Scott 1988). Moreover, there was a substantial increase in the continental European Whooper Swan population during the 1990s (Delany *et al.* 1999; Laubek *et al.* 1999), suggesting that the number of inexperienced breeders would have increased at this time. The proportion of birds joining the breeding population is not usually considered as a factor in explaining annual variation in breeding success, and this warrants further investigation.

Trends in Numbers

The study found an increase in the density of territorial Whooper Swans on the Pechora Delta since the early 1980s, despite regular human activity on the Delta in the last twenty years, and despite the Pechora Delta being at the northern reaches of the Whooper Swans' range. In other parts of Europe, notably Finland and Sweden, the Whooper Swans' breeding distribution is shifting southwards (Nilsson *et al.* 1999), where the swans appear to have higher breeding success than at more northern latitudes (Laubek 1998). This, combined with the very low nesting density recorded for Whooper Swans in the northern forest tundra, suggests that the Pechora Delta provides an exceptional habitat for the species and that Whooper Swans would not usually colonize areas this far north. The importance of the major river deltas is already recognized for Tundra Swans in Alaska, which occur there in higher densities than on mainland tundra, because they may provide better food resources and longer periods of open water than non-delta habitats (review in Ritchie *et al.* 2002). Substantial increases in numbers recorded for the continental northwest European Whooper Swan population in recent years (Laubek *et al.* 1999), and predictions of climate change in northern Eurasia linked to global warming, may result in further changes in the Whooper Swans' breeding distribution in future years.

In comparison, there was no significant increase in the density of territorial Bewick's Swans on the Russkiy Zavorot Peninsula since the early 1980s, despite an increase in the Bewick's Swan population wintering in northwest Europe during the 1980s and early 1990s (Beekman 1997; Delany *et al.* 1999). There is increasing evidence, however, that the Bewick's Swan population declined in the mid to late 1990s (Delany *et al.* 1999; SOVON Ganzen-en Zwanenwerkgroep 2001), which may account for the variation in Bewick's Swan breeding densities recorded on the Russkiy Zavorot Peninsula.

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Status and Breeding Ecology of Bewick's Swans in the Lena Delta, Yakutia, Northern Asia

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Abstract.—The Lena Delta is one of the key areas for Bewick's Swans (*Cygnus columbianus bewickii*) breeding in northern Asia. Aerial censuses, carried out during the period 1963–1994, showed that swan abundance decreased from 4,200 to 700 individuals between 1963–1983, then increased again to 6,000 individuals. The negative correlation between swan abundance and Reindeer (*Rangifer tarandus*) numbers over this period was not significant, but further monitoring of the possible effects of Reindeer numbers is warranted. During 1994–2000, swan distribution, numbers and breeding biology were studied on foot and by boat. The phenology of spring and autumn migration, seasonal distribution of breeding and non-breeding birds within the Lena Delta, breeding dates, features of nest biology and the potential relationship between breeding success and environmental factors are described. Mean brood size correlated with mean temperature during the pre-breeding period.

Key words.—Bewick's Swan, breeding, *Cygnus columbianus bewickii*, Lena Delta, trends in numbers, *Rangifer tarandus*, Reindeer, Yakutia.

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The Lena Delta is one of the key sites for Bewick's Swans (*Cygnus columbianus bewickii*) in northern Asia during the summer months. It is the largest delta in the Russian arctic, covering 28,500 km^2, and differs markedly from adjacent territories on mainland Russia. The delta is low-lying, with over 30,000 lakes and 6,500 channels in the area (Zalogin and Rodionov 1969). Much of the habitat is polygonized tundra with low-centre polygons (polygon pools), which provide good nesting habitat for swans. This paper presents the results of almost 40 years of monitoring swan abundance and seven years of monitoring Bewick's Swan breeding ecology in the Lena Delta.

METHODS

Studies of Bewick's Swans have been conducted in the Lena Delta for almost 40 years, with the first counts being made from aircraft in 1963 (Egorov 1965a). Aerial survey of swans and Reindeer (*Rangifer tarandus*) were undertaken simultaneously until 1990 (Perfiljev 1979; Blokhin 1984; Degtyarev 1990), and these data are used to test for an association between swan abundance and Reindeer numbers. The most recent aerial survey was conducted in 1994 (Hodges and Eldridge 1995). Coverage varied between surveys, ranging from 1.2–13.3% of the Lena Delta territory. Since, in some cases, the authors did not extrapolate the results to the whole delta, we describe swan abundance as density (individuals/100 km^2), rather than giving total numbers for the region.

Terrestrial surveys of Bewick's Swans were started in 1994. Counts were carried out by traveling along delta channels in a motor boat and recording swans within 1 km of the boat. Between 1994 and 2000, 13,982 km of channels were surveyed. Surveys were made at any time of day between 20 June and late July (when light for 24 h), and during daylight from 1 to 20 August. They were not carried out when the wind was more than 7 m/s, as in such weather the swans sheltered behind banks and therefore were less visible. Swans were recorded along the same channels each year. The results of the boat surveys are used to describe the zones with different swan abundance (Fig. 1).

To determine the mean temperature of the pre-breeding period we used mean daily temperatures recorded at the Stolb meteorological station, situated in the south of the Lena Delta. The pre-breeding period is taken as being from 21 May to 10 June. Most swans arrive in the Lena Delta and start laying between these dates.

RESULTS AND DISCUSSION

Distribution and Density

The terrestrial surveys, undertaken since 1994, indicated that Bewick's Swan distribution within the Lena Delta is uneven (Fig. 1).

Northeastern Delta. The highest density of swans (up to 45 individuals/100 km^2) was recorded in the northeast parts of the delta (east from 126°E and north from 72°30'N). Mean density (±SD) was also high (21.8 ± 14.3 individuals/100 km^2, N = 7) for the years 1994-2000. This is the lowest-lying part of the delta and is abundant in narrow, shallow, convoluted channels. The islands are covered by polygonal-marsh tundra with low-

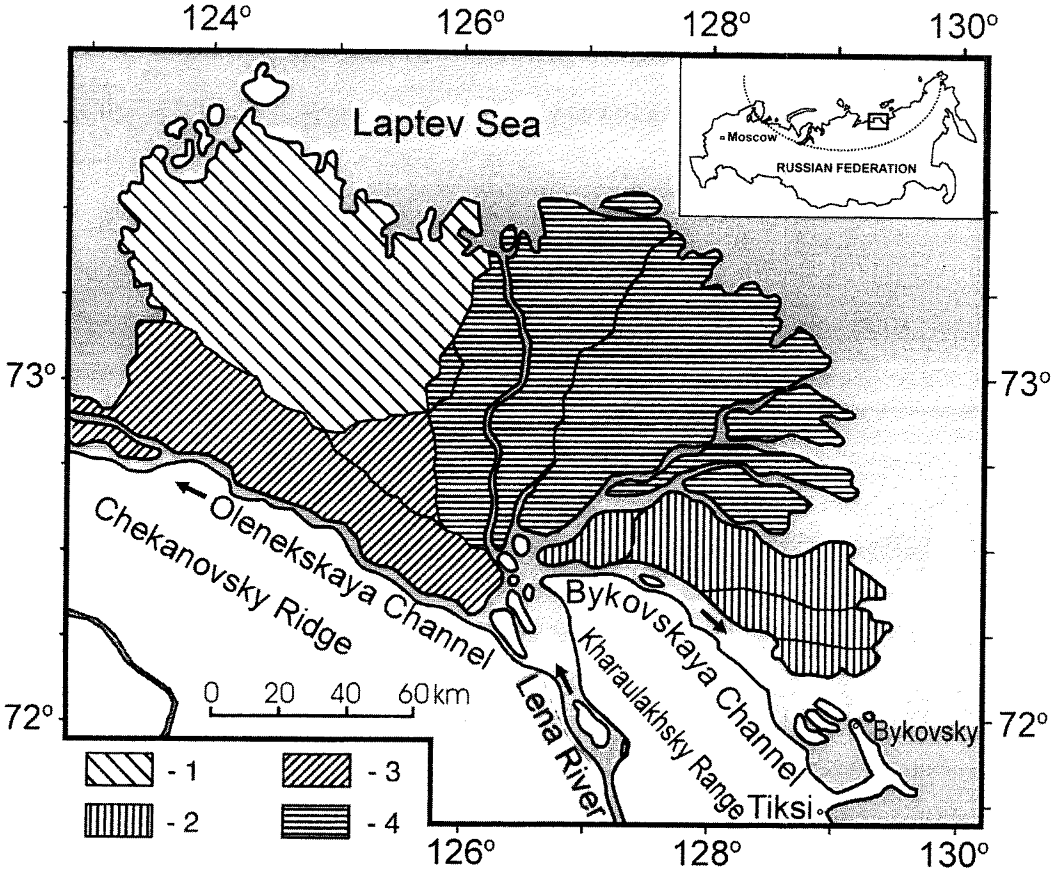

Figure 1. Map of the Lena Delta, showing Bewick's Swan densities recorded for different parts of the delta for the period 1994–2000. Mean density (individuals/100 km^2) is indicated as: 1 = 0.5–0.9; 2 = 1–4.9; 3 = 5–14.9; 4 = 15–45.

center polygons. Most non-breeding swans aggregate at coastal sites in this area.

Southwestern Delta. In the southwestern part of the delta, Bewick's Swan numbers did not exceed 15 individuals/100 km^2, and mean density was 7.3 ± 6.2 individuals/100 km^2 (N = 7) for the years 1994–2000. This area differs from the northeastern part of the delta in that large elevated islands are present, which are the outliers of an ancient maritime plain. These islands have few lakes suitable for nesting and, although swans are regularly present in this area, they occur in low numbers.

Southeastern Delta. This area supported a low density of swans (maximum of 5 individuals/100 km^2), with a mean density of 2.6 ± 2.3 individuals/100 km^2 (N = 5) between 1996 and 2000. It is adjacent to the main commercial shipping route, the Bykovskaya channel, which connects the Lena River with the Laptev Sea. An intensive movement of ships and motor boats occurs between the Tiksi and Bykovsky settlements and fishing sites in the southern part of the delta. Furthermore, there are many sandy islands without vegetation where swans were absent.

Northwestern Delta. The large Arga-Muora-Sise Island (about 5,000 km^2) occupies the western and northwestern part of the delta. It is the outlier of a marine terrace from the upper quaternary period. Swan distribution in the interior areas of this island was monitored during aerial censuses only. The density of swans in this region did not exceed one individual/100 km^2.

Trends in Numbers

Data collected during aerial censuses showed that the average abundance of Bewick's Swans in the Lena Delta declined from 17 to 2.5 individuals/100 km^2 during the period 1963–1983 (Egorov 1965a; Perfiljev 1979; Blokhin 1974), with a total of only 700–800 swans present in 1983. Since then numbers have increased, with this increase first being noted in 1988–1990 (Degtyarev 1990). Average swan density in the delta reached 28 individuals/100 km^2 in 1994, when a total of 6,100 swans were recorded (Hodges and Eldridge 1996). We suggest that swan numbers have continued to increase after 1994 but, due to the change in counting methods, there are no data suitable for comparison with the aerial surveys data.

We considered whether the number of Bewick's Swans in the Lena Delta was associated with trends in the numbers of wild Reindeer, because maximum declines in swan numbers appeared to occur in years when Reindeer numbers were increasing, and an increase in the numbers of swans occurred after Reindeer numbers had declined (Fig. 2). It is known that Reindeer sometimes feed on the eggs and chicks of birds, and trample on the nests of waterfowl (Egorov 1965b). Disturbance by Reindeer may also be a relevant factor. The negative correlation between swan abundance and Reindeer numbers was not significant (Spearman Rank, r = -0.37, N = 6, n.s., excluding 1975 and 1978 when swan densities were not recorded), but there were gaps of several years between sampling sessions in the early years of the study (Fig. 2) so further monitoring of this issue is warranted.

In the northeastern and southwestern regions of the study area, where the greatest swan numbers occur (Fig. 1), Reindeer density was 1.3 and 2.3 individuals/km^2 respectively, and total Reindeer numbers in the Lena Delta were 20,000 in 1963 (Egorov 1965b). By 1978, total Reindeer numbers had reached 35,200 for the whole delta (Safronov *et al.* 1999), with density almost doubling between 1963 and 1978. Following a decline in Reindeer numbers due to over-hunting in the 1980s (Safronov *et al.* 1999), swan numbers began to rise (Fig. 2). Reindeer appear in the delta earlier than swans, and feed on the abundant sedges and grasses near ponds (Egorov 1965b), at sites used by the swans for nesting. The interaction between swans and Reindeer therefore should be studied in greater detail, particularly whether disturbance by Reindeer herds limits the nesting habitat available to swans in spring.

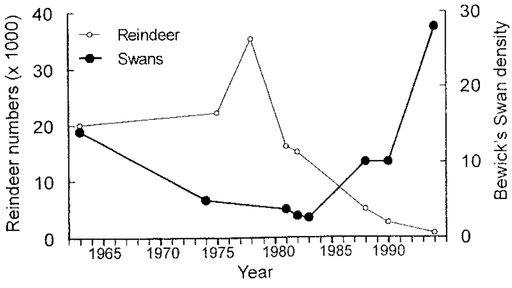

Figure 2. Numbers of Reindeer and Bewick's Swan population density (individuals/100 km^2) in the Lena Delta, 1963–1994.

Migration

Bewick's Swans arrive in breeding grounds on the Lena Delta during the second half of May. Arrival dates generally are associated with weather conditions, with swans observed in the delta much later in years with cold, late springs. The earliest arrival record was 15 May in 1995 and 2000. In the latest year, 1996, the swans were first recorded in the south of the delta on 30 May, and in the north of the delta on 9 June. The main migratory route passes along the Lena River valley (Labutin *et al.* 1988). After passing through this narrow river valley, migrating flocks start dispersing across the delta at a latitude of 71°40'N, with some birds flying northwest along the Bulkurskaya and Olenekskaya channels, whereas others cross the northern part of Kharaulakhsky range to move to the eastern part of the delta. In the interior areas of the delta, northward migration prevails. In the southern part of the delta, migratory flocks number up to 50 birds, which subsequently disperse as they move north.

Autumn migration begins in mid September. Breeding birds usually migrate in family groups, but non-breeders form flocks up to 60–70 birds. The latest date that swans were observed in the Lena Delta was 4 October 1995.

Habitats

Bewick's Swans breed across the whole of the Lena Delta territory, but prefer damp low-lying tundra abundant in small lakes with irregular, marshy and grassy banks, or moss polygonal-marsh tundra. Birds with broods are most often observed on small shallow and over-dried channels (59% broods occurred there during the aerial censuses; Degtyarev 1990). If there is enough food, the broods stay on the lakes of the delta islands. Non-breeders move into the whole delta territory but favor wetlands in maritime tundra and shallow sites at the mouths of the delta channels. In such sites, large flocks of up to 300–500 swans sometimes occur. They also molt there. Some pairs of birds occupy nesting territories but do not build nest mounds. These birds may join flocks of non-breeders to molt. Breeding adults molt in the presence of broods. Sometimes they leave non-flying young on the channels and move 1–2 km to island lakes; three broods without parents were seen on 14 August 1999, and one on 22 August 2000. The reason for them leaving the chicks is not known, but is considered unlikely to be due to human disturbance because there were no other people in the area prior to the survey.

Breeding

The period between the arrival of the first swans and the beginning of nesting lasts 5–10 days. A nest with five cygnets was found on 1 July 2000 so, since Bewick's Swan incubation is 29–30 days from laying of the last egg, and the eggs are laid at 48 h intervals (Evans 1975; Rees *et al.* 1997), the onset of laying for this clutch was about 20 May. The birds begin to build their nests on the first available snow-free patches. The nests are located near water on dry sites with good visibility. Usually, nest-sites are on the elevated (but not precipitous) banks of channels and small lakes, and also on the banks of low-center polygon pools. Older birds probably use the same breeding territories each year. Observations of individuals identified by leg bands, neck collars or natural marking show that Bewick's Swan pairs occupy the same breeding territories over several summers (Shchadilov *et al.* 1998). Usually birds build new nests, but sometimes they use old ones; in some parts of the delta two to four old nests that had been used in previous years were found near inhabited nests, at distances of 100–300 m from the new nest site. When re-using old nests, the swans add new nest material; such nests may be up to 300 m across at the base and 110 m high. The minimum size recorded for a new nest was 110 cm across the base and 30 cm high. Mean nest dimensions (±SD) were 182 cm (±64.8, range 110–300, N = 9) at the base and 57 cm (±28.0, range 30–110, N = 9) in height. To build the nest, birds pluck vegetation from 2–3 m around the nest.

The earliest onset of laying was recorded on 20 May, and the egg-laying period lasts until mid-June. Mean clutch size was 4.1 (range 3–5 eggs, N = 16), although maximum clutches may contain six eggs, since a brood of six cygnets was observed in 2000. Mean egg dimensions (±SD) were 103.7 (±5.09) × 66.4 (±2.98) mm (range 94.9–113.4 × 60.4–71.2; N = 35). Hatching occurred in late June and in mid July. A few days after hatching the parents lead young from islands to the channels. The earliest record of broods on the channels is 10 July. In mid-August, some parents leave their young on the channels and travel to the lakes on nearby islands. We suggest that brood aggregation may occur at this time, something rarely reported in swans. Brood aggregations of Whooper Swan (*Cygnus cygnus*) were observed in West Siberia (A. M. Antipov, pers. comm.). A mixed brood of eight young of two different age groups were seen without parents on 14 August 1999. Mean brood size (±SD) was 3.5 ± 1.03 (range 1-6 cygnets, N = 96). Between years, mean brood size varied between 2.5 ± 1.05 (N = 6) and 4.2 ± 0.69 (N = 27) (Fig. 3).

The relationship between brood size and climatic conditions during the pre-nesting period was investigated (Fig. 3). Average temperature at the beginning of the breeding period (from 21 May to 10 June) was positively correlated with brood size (Spearman

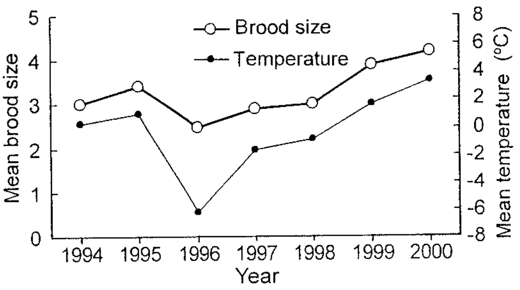

Figure 3. Average temperature during the pre-breeding period (i.e., from 21 May to 10 June) and mean Bewick's Swan brood sizes in the Lena Delta, 1994–2000.

Rank, r = 1.0, N = 6, P < 0.001). In years where the average temperatures were below zero, the mean brood size did not exceed three young (Fig. 3). It is known that Bewick's Swan clutch size is influenced by the timing of the snow melt (Shchadilov *et al.* 1998), and consequently on temperature during the pre-breeding period. Our data similarly suggest that Bewick's Swan breeding success may be prognosticated at the start of the breeding season, although it may be ameliorated by conditions later in the year. Future studies of Bewick's Swan ecology in the breeding range should focus on this and on the influence of Reindeer numbers on Bewick's Swan population trends.

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Distribution and Population Estimates for Swans in the Siberian Arctic in the 1990s

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Abstract.—The distribution of swan species in the Siberian Arctic, from the Gydan Peninsula to Chukotka, was studied between 1988 and 2000. Bewick's Swan (*Cygnus columbianus bewickii*) numbers increased in all areas from the Yamal Peninsula to Chukotka, and its previously fragmented range is now continuous. A total of about 66,200 Bewick's Swans spend the summer on Eurasian tundra, of which about 60% are in Siberia. The Whooper Swan (*Cygnus cygnus*) has expanded its range northwards and eastwards during the last ten years. Breeding concentrations occur further north than 30–40 years ago, and the species now nests on open tundra as well as in forest-tundra and taiga zones. The Tundra Swan (*Cygnus columbianus columbianus*) has expanded its breeding range to both west and south in Asia. They now occupy an area extending along 500 km of the north coast of Chukotka, and total numbers in Russia are estimated at 600–1,000 birds.

Key words.—Arctic, Bewick's Swan, breeding distribution, *Cygnus cygnus, Cygnus columbianus, Cygnus buccinator,* population trend, Russia, Tundra Swan, Whooper Swan.

Waterbirds 25 (Special Publication 1):100–113, 2002

The Siberian Arctic is a belt of tundra and forest-tundra habitat, 5,000 km long and 200–700 km wide, extending from the eastern slopes of the Ural Mountains to Chukotka in far eastern Russia. More then half of the world's Bewick's Swans (*Cygnus columbianus bewickii*) breed on tundra in the Siberian arctic. The Whooper Swan (*Cygnus cygnus*) nests mainly in taiga in Siberia, but extends into the arctic at the northern limit of its range. The Tundra Swan's (*Cygnus columbianus columbianus*) breeding range, which is mainly in North America, extends west into Russia to the Siberian tundra in Chukotka. The only report of a Trumpeter Swan (*Cygnus buccinator*) in Russia to date is of a single vagrant seen at Kanchalan Bay on the mouth of the Volchikha River, about 30 km from Anadyr, Chukotka, on 16–18 June 1991 (Dorogoy 1993). The Mute Swan (*Cygnus olor*) commonly occurs in Russia south of forested areas, and has been seen north of the arctic circle only in European Russia (K. Litvin, Yu. Mineev and E. Rees, pers. comm.); it still has not been reported in the Siberian Arctic.

The status of swans in Siberia was last reviewed in the Second All-Union Conference on Swans in the USSR in 1988 (Koshelev 1990). From the mid 1990s onwards, the Goose, Swan and Duck Study Group of Northern Eurasia has updated information on the waterfowl of Eastern Siberia, including swan species. This paper presents data on changes in swan distribution and population estimates, based on (1) field observations made during expeditions by the Russian Academy of Sciences and by the Goose, Swan and Duck Study Group of Northern Eurasia, and (2) a review of the recent Russian literature.

METHODS

The numbers, distribution and breeding status of swans were recorded at 5–6 sites each year for 13 field seasons (June-August, 1988–2000), the sites being in different parts of the Siberian Arctic, from the Gydan Peninsula to Chukotka. Each year several expeditions, involving a total of 10–15 ornithologists, recorded the distribution and biology of waterfowl at these sites, including swans. About 1,700–4,000 km of transects were covered on foot each year, and a further 500–1,500 km by boats and track vehicles ("vezdekhod"). Surveys were made from a network of temporary camps, and aimed to cover as large an area as possible. In the Taimyr and Yakutia, about 50 h of aerial surveys also were undertaken by helicopter in 1990, 1991, 1997 and 1998.

By 2001, swans had been recorded at 442 sites. Of these, 181 were of breeding and possible breeding bird locations, including 75 recorded after summer 1988. Previously unpublished data (including the author's own observations) and information from all available

Russian literature (including unpublished reports) are described in this review. The breeding range was estimated for each species by recording known breeding distribution on vegetation maps, then extrapolating from these to estimate breeding density for similar landscapes not yet surveyed (following Lappo 1996, 2000).

Population estimates presented in this paper are also derived from existing publications and unpublished data. These figures are based mainly on about 240,000 km of aerial census transects (calculation based on published papers) made throughout the Russian arctic in the last 25 years. Most of the aerial counts followed the standard methods of the Russian game management authorities (Kistchinski 1973; Kuz'min *et al.* 1984). Some differences in interpretation of count results are possible, depending on the width of transects counted for swans. Swan numbers may be underestimated by 10–20% if the transect counted is wider than 100 m each side of the aircraft (particularly in the southern tundra and forest-tundra; Kalyakin and Molochaev 1999), and if the count is for all waterfowl and reindeer rather than focusing on swans. Recent monitoring in northeast Asia has used different aircraft with better visibility, and American standards for counting birds and extrapolating aerial census data (Poyarkov *et al.* 2000), which differs from standard methods used in Russia (A. G. Degtyarev, pers. comm.). Although a systematic comparison of the two techniques should be undertaken, preliminary attempts on the Indigirka Delta indicate that the results are similar, at least for some groups of waterfowl such as eiders (*Somateria* spp.) (W. Eldridge, pers. comm.).

RESULTS

Bewick's Swan

The Bewick's Swan's breeding range in Siberia extends from the Yamal Peninsula in the west to Chaun Bay in the east, and covers most of the tundra zone (Fig. 1). The main breeding areas are usually not more then 50–100 km from the arctic coast, in large lowland areas, deltas and estuaries, although in some regions such as the Yamal Peninsula and Taimyr Peninsula they can breed up to 500 km inland. They are less numerous in the southern shrub tundra and rare in forest tundra. Breeding has also been recorded at a few sites in the large open wetlands of the northern taiga zone, however, in the eastern part of the west Siberian plain between the Turukhan River (a tributary of the Yenissey River) and Taz River (Syroechkovski *et al.* 2000), on the lower Lena River in Yakutia (Perfiliev 1987) and in the middle reaches of the Kolyma River (Pozdnyakov and Degtyarev 2001). In the western part of central Siberia, Bewick's Swans are said to be breeding in the southern taiga, in the extensive raised bogs of the upper Sym valley (A. P. Savchenko observations in Syroechkovski *et al.* 2000), but this report needs confirmation. Bewick's Swans normally do not breed in the northern part of the high Arctic (i.e., in Frantz-Josef Land, northern Taimyr, northern Novaya Zemlya, New Siberian Islands, Severnaya Zemlya and Wrangel Island). There are suitable lowlands and deltas in these areas, but the summer is perhaps too short to give the young time to fledge. Information on numbers and distribution over the

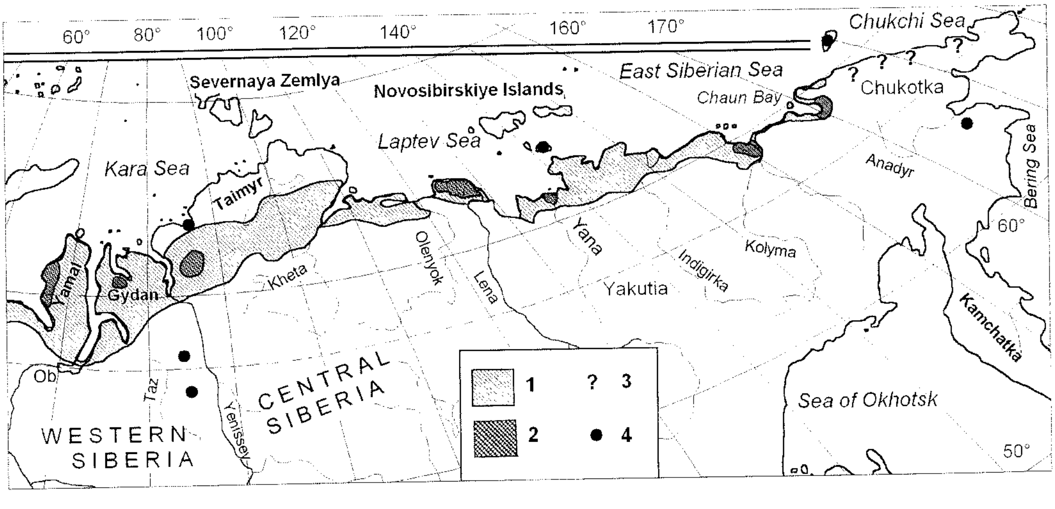

Figure 1. Bewick's Swan breeding range in the Siberian Arctic. 1 = breeding range; 2 = areas of high breeding numbers and non-breeding concentrations; 3 = areas where Bewick's Swans likely started breeding in the last decade, but not yet confirmed by ornithologists; 4 = breeding recorded outside of the main range.

last 30 years, for different breeding areas in the Siberian Arctic, is as follows:

Western Siberia (Yamal Peninsula and Gydan Peninsula). Extrapolation of swan counts recorded during aerial surveys in 1968–1969 gave an estimate of up to 5,600 Bewick's Swans in Western Siberia; 2,600 on the Yamal and 3,000 on the Gydan Peninsula (Uspenski and Kistchinski 1972). At least 10% of the swans counted are likely to have been Whooper Swans. The extensive aerial surveys were repeated in 1987, and total numbers were then put at 9,000–11,000 birds, with minimal estimates of 5,460 birds for the Yamal Peninsula, 2,290 for the Gydan Peninsula and 1,600 for the Tazovskiy Peninsula (Kalyakin and Molochaev 1990; Fig. 2). However, local ornithologists consider that these figures were overestimated, and that many flocks of non-breeding swans seen on the southern tundra were Whooper Swans (V. K. Ryabitsev, pers. comm.). Sources concur that major Bewick's Swan concentrations occur on the west Yamal lowlands and at the Yuribei basin on the Gydan Peninsula.

Taimyr. Estimates of the number of Bewick's Swans on the Taimyr Peninsula are derived from long-term aerial survey work (1966–2000), made mainly in western and central Taimyr (Kokorev 1995; Kolpashikov 2001). The area counted varied between years, from 3,000–8,000 km^2, and there were gaps of up to five years between censuses, so it is not possible to describe population trends precisely. Nevertheless, numbers were declining by the mid 1960s, and minimum levels were reached in the late 1970s, when only 260 birds, including both breeding and non-breeding birds, were recorded (Vinokurov 1987; Fig. 3). We think these figures may underestimate numbers for the whole of the Taimyr because eastern Taimyr and inner delta of the Yenissey River were not regularly or extensively covered by surveys before the 1980s. Since the early 1990s, numbers have started to increase, especially in

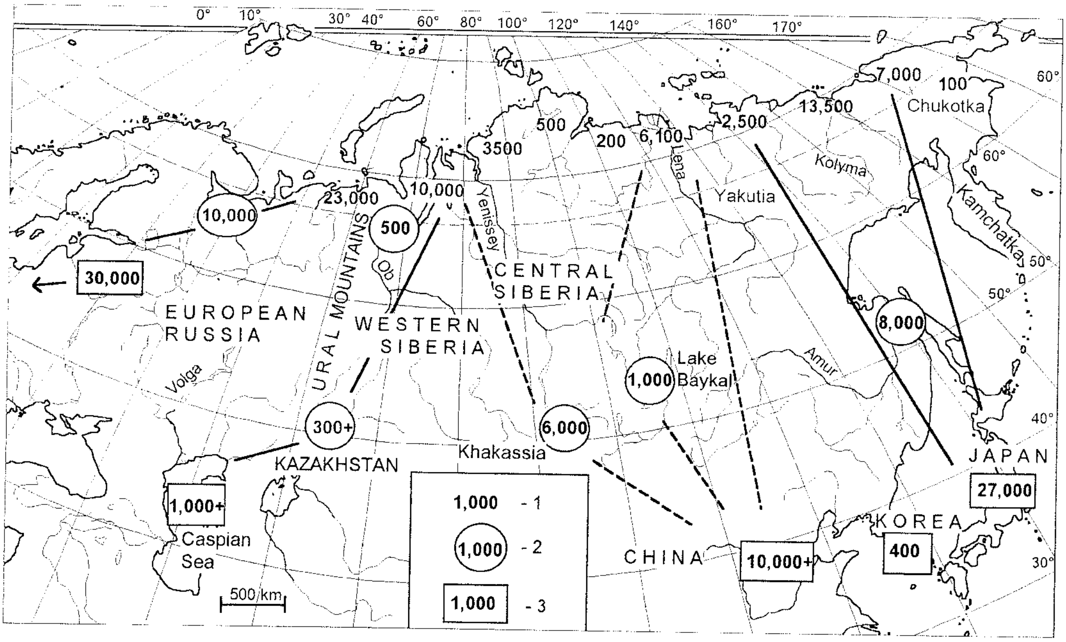

Figure 2. Bewick's Swan migration routes and population estimates, 1994–2000. Population estimates are derived from: A. I. Artyukhov, pers. comm.; Environmental Agency of Japan 1998; Babenko and Poyarkov 1998; Beekman 1997; Braude 1987; Gurtovaya *et al.* 1999; Golovatin and Paskhalny 1996; A. Degtyarev and V. Pozdnyakov, pers. comm.; Kolpashikov 2001; H. Lee, pers. comm.; Ma and Cai 2000; Melnikov in press; Mineev and Kondratiev 2001; Morozov 1996; Nolet *et al.* 2001; Poyarkov *et al.* 2000; Rees *et al.* 1997; Rose and Scott 1997; and Syroechkovski *et al.* 2000. 1 = numbers estimated in the breeding grounds; 2 = numbers estimated at stopover sites; 3 = numbers estimated in the wintering range. Solid lines indicate known migratory routes; dashed lines indicate possible migratory routes.

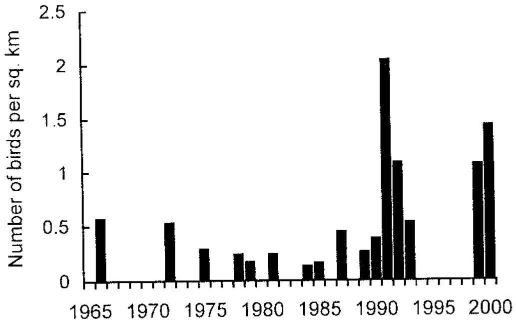

Figure 3. Bewick's Swan density in western and central Taimyr, 1966–2000 (from Kokorev 1995; Kolpashikov 2001).

southwestern Taimyr, and are now estimated at about 3,500 birds for western and central Taimyr (Kolpashikov 2001). Fieldwork on the Taimyr from the 1990s onwards found breeding birds and small non-breeding flocks at a number of sites in central and eastern Taimyr where birds where not reported during the 1980s, at Dudypta, Logata and the lower reaches of the Balakhnya River (Russian Academy of Sciences, unpub. data). These surveys suggest 400–500 swans on the eastern Taimyr, in addition to the 3,500 birds elsewhere on the Taimyr (Kolpashikov 2001; Fig. 2). Main breeding concentrations are in southwest Taimyr (upper Pyasina River and Pura Lakes) and in central Taimyr in the Verkhnyaya Taimyra River basin. The inner delta of the Yenissey River (Brekhovskie Islands), which was an important breeding and molting area in the beginning of the 20th century (Tugarinov and Buturlin 1911), saw a substantial decrease in numbers due to heavy pressure from human activity in the 1960s–1980s, and now only about 100–300 swans occur regularly during the summer (A. A. Vinkurov, pers. comm.; interviews with local inhabitants).

Yakutia. Bewick's Swans are more common in Yakutia than on the Taimyr, occurring in high densities in two main coastal areas, the Lena Delta and the Kolyma Delta, with small numbers breeding at other coastal sites. The detailed monitoring of swans on the Lena Delta is described elsewhere in this volume (Pozdnyakov 2002) but, to summarize, numbers in the area decreased from 4,000–5,000 birds in the early 1960s to 700–800 birds by the mid 1980s, then increased to 6,100 birds by the mid 1990s (Poyarkov *et al.* 2000; Figs. 1 and 2). Numbers on the Kolyma Delta were put at about 700 birds in the 1980s (Kondratyev 1990), but it seems likely that this was an underestimate because it would otherwise be difficult to explain how they rose to 13,000–14,500 by the mid -1990s (Poyarkov *et al.* 2000; Figs. 1 and 2). A third area with reasonable numbers of Bewick's Swans in Yakutia is the Yana Delta and its environs (Poyarkov *et al.* 2000; Russian Academy of Science unpub. data). A comparison of swan densities recorded by Yakutian game biologists during aerial surveys in 1982 and 1989 from the Yana Delta east to the Sellyakh River indicates no change, or a very small increase in numbers, over this period (A. Degtyarev and V. Pozdnyakov, pers. comm.). In 1994, about 2,000 birds were reported here (Poyarkov *et al.* 2000; Figs. 1 and 2), a five-fold increase on the 1982 level, when numbers for the same area were estimated at 400 birds (Labutin *et al.* 1984). It has not been possible to determine whether this was due to rapid population growth during the 1990s, or to slight variation in the methods used to count the swans and extrapolate data recorded in the surveys. Elsewhere in Yakutia, coastal lowlands between the Anabar and Olenyok estuaries held about 100 birds in 1983 (Labutin *et al.* 1984) and not more than 200 in 1991, 1994 and 1998 (Russian Academy of Science unpub. data). The Indigirka Delta and the Khroma estuary and surrounding area each received about 200 birds in 1994 (Poyarkov *et al.* 2000).

Chukotka. The Bewick's Swan's main breeding area in Chukotka is the lowlands at Chaun Bay. Numbers breeding there were estimated at 300 birds in the early 1980s (Kondratyev 1990), but this figure seems rather low because an aerial survey in July 1993 gave 6,000–7,000 birds for the Chaun Bay area, including Ayon Island (Poyarkov *et al.* 2000; Figs. 1 and 2). Kondratiev (1998) mentions a 50% increase in the breeding density of Bewick's Swans on the Chaun lowlands between 1984 and 1994, but information on numbers and densities are not provided. The eastern limit of the Bewick's Swan breeding range is along the north Chukotka coasts and, although this area is not well monitored, they were commonly seen nesting at Nolde Bay (173°30'W) in the early 1990s, with several breeding pairs as far east as the mouth of the Ekviatap River (179°E) (M. S. Stishov, pers. comm.). An aerial census of Chukotka in 1994, found the last Bewick's Swans as far west as near to the Pegtymel estuary (174°W) (Poyarkov *et al.* 2000), whereas in earlier times they occurred up to 500 km further east on the Amguema estuary and Koliuchin Bay (175°W) (Kondratiev 1998). Although the Bewick's Swan was not formerly recorded in southeast Chukotka (Anadyr basin) (Kretchmar *et al.* 1991), in the last decade it has become a regular visitor, especially on lowlands of the Anadyr Liman (estuary) (A. V. Kondratiev, P. S. Tomkovich and A. I. Artiukhov, pers. comm.; Russian Academy of Sciences, unpub. data), and a brood was seen on the southern coast of Onemen Bay in early August in 1990s (M. M. Shulga, pers. comm.). It is possible that, with the increase in numbers wintering in Japan, more birds are moving into the Anadyr lowlands of south Chukotka and that the establishment of a new breeding group is underway.

Numbers at stopover sites in Russia and Kazakhstan. There are only a few places in the former USSR where Bewick's Swans are monitored annually and accurately at their migratory sites, but these include important spring staging areas in the southern part of Central Siberia and in the upper Yenissey River. Two main flyways have been recorded. The first has stopover sites mainly in Khakassyia, where the number of swans counted has increased from 1,500 to 6,100 birds in the last 20 years (Figs. 2 and 4) (Syroechkovski *et al.* 2000). Eight sites are regularly used, the two largest being Ulug-Kol Lake (maximum count of 3,400 birds in last five years) and the Bele and Shira Lakes (maximum count of 4,400 birds on both lakes) (Yemelianov 1990; Savchenko and Yemelianov 1991; Yemelianov *et al.* 1995). The number of Bewick's Swans counted at these stopover sites easily exceeds the number of breeding birds recorded on the Taimyr Peninsula, the main breeding grounds in the northern part of Central Siberia. It is suggested (Yemelianov 1990; Savchenko and Yemelianov 1991) that most Bewick's Swans migrating through Khakassiya probably do not continue due north along the Yenissey valley in spring, since very few birds are observed there on migration (Rogacheva 1992), but that they head northwest and cross the eastern part of Western Siberia to breeding grounds on the Gydan and part of the Yamal Peninsula. The possibility that some swans migrate northeast from Khakassiya to reach northwest Yakutia, or even the Lena Delta, also cannot be excluded.

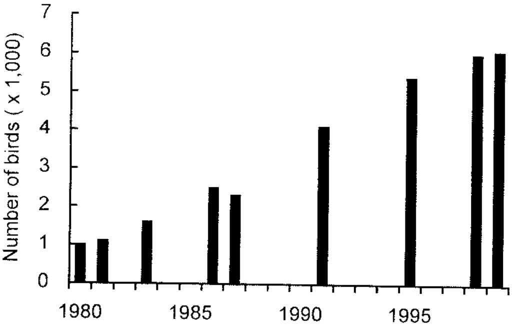

Figure 4. Numbers of Bewick's Swans counted in southern Central Siberia, 1980–1999 (from Savchenko *et al.* 1995; Yemelianov *et al.* 1996; Syroechkovski *et al.* 2000)

Fewer swans follow the second flyway through Central Siberia, arriving from the southeast from China in spring, and migrating across Lake Baykal where numbers on passage are estimated at about 1,000 birds (Melnikov, in press). In May they stop on the lower reaches of the Angara River, about 300–500 km northeast of the Khakassiya staging areas (Fig. 2). Some 300–400 birds use the site, with no trend in numbers over the last ten years (Yemelianov *et al.* 1996).

Staging by large numbers of Bewick's Swans at sites near the southern Urals, southern parts of Western Siberia and north Kazakhstan have not been noted in earlier years. Reviews of waterfowl data for different parts of Kazakhstan, written in the 1960s–1970s, often do not mention the species, or report only negligible numbers. Bewick's Swan sightings are evident in more recent publications, with up to 150 birds in the south Turgay depression in 1986 (Khrokov *et al.* 1990), a count of 230 Bewick's Swans in only two days in the Kustanav region in autumn 1999 (Gurtovaya *et al.* 1999), and less than one hundred Bewick's Swans across several wetlands in a small area west of Ural River estuary in 1996 (V. V. Morozov and V. P. Belik, pers. comm.). These sightings serve to identify some of the stopover areas used by swans migrating to and from wintering grounds on the Caspian Sea, thought to be the same birds seen migrating north along the Ob valley in spring (Braude 1987; Golovatin and Paskhal'ny 1997), although these sightings describe only a small part of the flyway. Surveys of wetlands in the Russian steppes and north Kazakhstan have not focused particularly on Bewick's Swans, and detailed coordinated counts of other waterbirds also have not been undertaken, so many birds may have been missed.

The only important spring stopover site identified for Bewick's Swans in far eastern Russia is the Amur Liman (estuary) and Tatar Strait, where more than 8,150 birds were counted in May 1991 (Babenko and Poyarkov 1998). The total number passing through the area may be much higher. Reports of local hunting inspectors show that this site is regularly used on migration, and birds marked in Yonago Estuary are also known to use this site on spring migration (Kamiya and Ozaki 2002).

Tundra Swan

Although a vagrant in northeast Chukotka during the 1950s and 1960s (Ptushenko 1952; Portenko 1972), the Tundra Swan was not reported breeding in Russia until 1974, when it was seen with a brood on Koliuchin Bay (Kistchinski *et al.* 1975) and on Neshkan lagoon (Lutsiuk and Sychev 1974). Ornithologists only occasionally visit the Chukotka Peninsula, so large-scale inventories and long-term monitoring of Tundra Swans have not been possible, but it was known to have bred subsequently in other parts of the Chukotka Peninsula during the 1970s and early 1980s (Tomkovich and Sorokin 1983). An increase in total numbers in the northern part of Koliuchin Bay was reported from the mid 1970s to 1980s (Tomkovich and Soloviev 2000), and at Neshkan lagoon in the late 1990s (Zheleznov and Naumkin 2000). Aerial surveys in 1993, and interviews with local people, found that the breeding range had expanded west and south of Koliuchin Bay, and that they occurred along north coasts of Chukotka as far as Nolde Bay (174°E) by the early 1990s (Poyarkov *et al.* 2000) (Fig. 5). By 2000, they also occupied suitable, undisturbed habitats in the Mechigmen lowlands (Russian Academy of Science, unpub. data) and, according to interview data, part of the Ioniveem River basin. Local sources describe an expansion of the breeding range southwest to Kresta Bay (65°30' N), but this has yet to be confirmed. A non-breeding Tundra Swan has been sighted at the Anadyr lowlands in south Chukotka, but further details were not provided (Kondratiev 1998).

The total number of Tundra Swans in Chukotka is not easy to estimate due to poor coverage of the area by ornithologists. Aerial surveys of the north Chukotka coastline in 1993 recorded about 230–240 birds (Poyarkov *et al.* 2000), but these counts covered only about 30% of the current range, mainly areas only recently colonized by the species. Some 600–1,000 birds therefore may occur in Chukotka in summer. In the western part of its range, the Tundra Swan's distribution overlaps with the eastern end of the Bewick's Swan's breeding range. A mixed Bewick's and Tundra Swan pair, with three young more than half-grown, was seen at Koliuchin Bay in the early 1970s (Kistchinski *et al.* 1975), and there was a mixed pair on the Ekviatap estuary (179°E) in 1990, although a nest was not found (M. S. Stishov, pers. comm.). Since 1990, 10–29 Tundra Swans have been observed each year at Bewick's Swan wintering sites in Japan (Environmental Agency of Japan 1998), and mixed Bewick's × Tundra Swan pairs have been reported wintering in Japan since the late 1980s (Mikami 1989).

Whooper Swan

The Whooper Swan's breeding range extends from the Russian tundra to the desert-

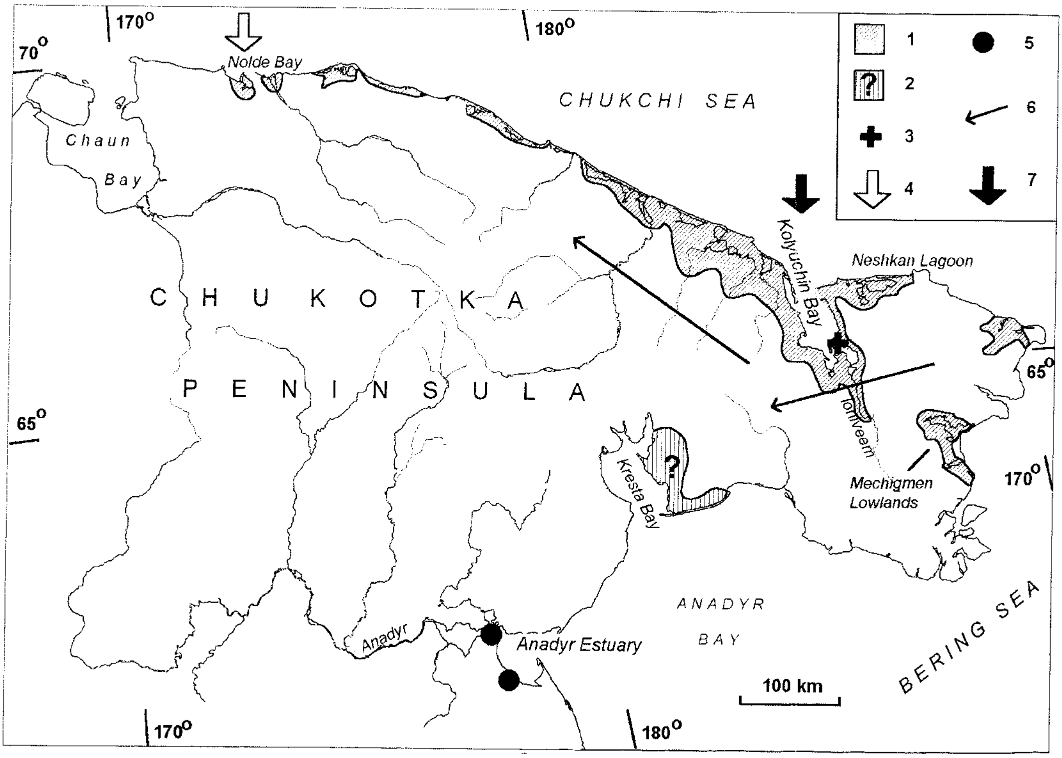

Figure 5. Tundra Swan breeding range in Chukotka, northeast Asia, in 2000. 1 = breeding range; 2 = breeding reported by local people, not yet confirmed by ornithologists; 3 = mixed Bewick's × Tundra Swan pair recorded; 4 = current western limit of breeding range; 5 = non-breeding Tundra Swan recorded outside main range; 6 = main direction of expansion of the breeding range in the last 20 years; and 7 = western limit of breeding distribution in the 1970s.

zone wetlands of China and Mongolia (Ptushenko 1952; Ma and Cai 2000), although the main breeding concentrations are on wetlands of the taiga zone. This paper describes only its northern distribution (Fig. 6), together with some changes in distribution in recent years. Population estimates are not provided because this would require data from outside the Siberian Arctic study area, and a much wider literature survey.

Western Siberia. Although Whooper Swans breed in the southern parts of the Yamal Peninsula and Gydan Peninsula, their main breeding and molting concentrations are further south in the Ob' valley and the vast plains of the West Siberian lowlands (Poyarkov and Johnson 1996; A. M. Antipov, pers. comm.). Surveys of the south Yamal in the late 1970s indicated that the swans were breeding further north than in the 1950s (Ptushenko 1952; Krivenko *et al.* 1987); no further changes in breeding distribution have been reported for the region since then. In the north of the West Siberian plain, Whooper Swans breed regularly in open landscapes within northern taiga and forest-tundra habitats on the lower reaches of the Nadym River and the Schutchya River valley. They breed irregularly and in low numbers in the shrub-tundra zone (Kalyakin and Molochayev 1990).

Central Siberia. Whooper Swans occur in lower densities in Central Siberia than in any other part of Siberia, and the only areas with reasonably high numbers is in the north taiga zone, between the Taz River (near the border with West Siberia) to the west and the Turukhan River and Yeloguy River to the east, and also near Makovskoe Lake (Rogacheva 1992; E. Kuznetsov, unpub. data). On the Taimyr Peninsula, the number of Whooper Swans at the Norilsk Lakes and the lower Yenissey River has decreased substantially, and only some tens of pairs now occur here

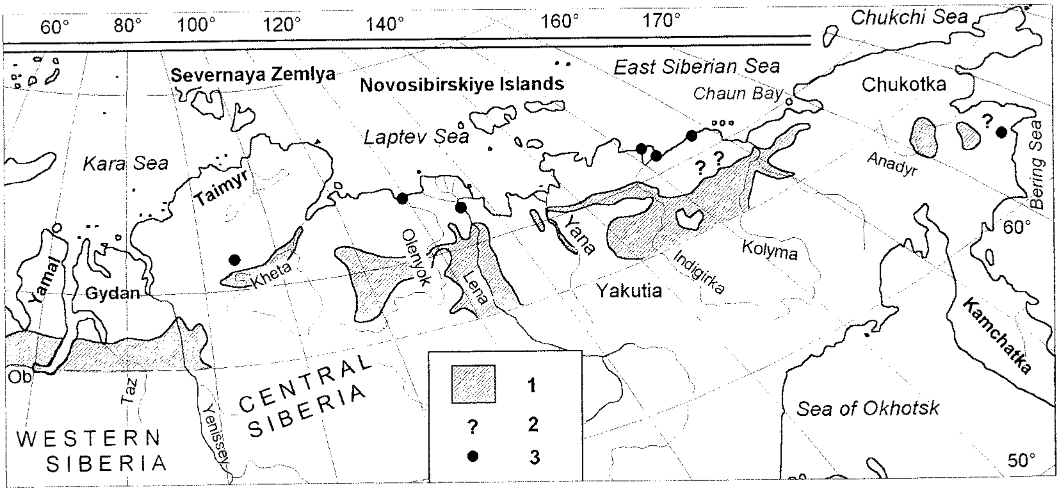

Figure 6. Northern part of the Whooper Swan's breeding range in Siberia. 1 = breeding range (southern part of the range is cut at the border of the arctic and boreal zones); 2 = areas where Whooper Swans are likely to have started breeding in the last decade, but observations by ornithologists are not yet available; 3 = breeding recorded outside of the main range.

(Rogacheva, 1992; Russian Academy of Science, unpub. data). The Putorana mountains have very low numbers, with no recent breeding records (Romanov 1996; A. V. Romanov, pers. comm.). The lowland forest-tundra of Central Taimyr, around Khatanga and along the Kheta River, also has very small numbers, but in the 1990s there was some evidence of an increase and expansion of the breeding range to the north. For instance, in 1995 non-breeding Whooper Swans were recorded in the southern tundra of the Dudypta basin (Russian Academy of Science, unpub. data) and local people observed a brood of this species. A Whooper Swan nest was found where forest-tundra becomes tundra habitat on the Boganida River in 1996 (A. I. Artiukhov, pers. comm.).

Yakutia. Up to the early 1960s, Whooper Swans in Yakutia bred only in the southern taiga zone, mainly in the Viluy River basin (Ptushenko 1952; Vorobiev 1963). During the 1960s and 1970s, the breeding range expanded to the north in two areas, along the Lena River valley and to the lowlands between the Kolyma River and Alazeya River (Perfiliev 1987). Molting and breeding concentrations were found in the lower Indigirka River during the 1980s (Degtyarev 1990), by which time the species had reached arctic latitudes and was breeding in the northern forest-tundra at 69–70°N. In the 1990s, Whooper Swans started occurring in arctic landscapes, where they were found breeding on the Olenyok Delta in 1997 and on the Indigirka Delta in 1999 (Russian Academy of Science, unpub. data). Flocks of molting non-breeding birds were regularly sighted on the Yana Delta in 1996 (Russian Academy of Science unpub. data). There is also evidence of Whooper Swans breeding on tundra in the lower reaches of the Alazeya River in the mid-1990s (A. G. Degtyarev, pers. comm.).

Chukotka. This region has fewer Whooper Swans than Yakutia and, up to the 1980s, most breeding sites were on wetlands of the mid Anadyr River valley within the taiga zone (Kretchmar *et al.* 1991). The breeding range expanded eastwards during the 1990s, from forested areas to coastal tundra, and Whooper Swans now breed at a number of sites in south Chukotka, such as along the Velikaya River in 2001 (A. I. Artiukhov, pers. comm.), the Vaamochka Delta in the Meinopylgeno River system (E. V. Golub' and A. P. Golub', pers. comm.) and, according to interview data, in several parts of the Anadyr lowlands, especially the Tymna River basin. The total number in the area is now at least 1,000 birds. The wintering grounds for Whooper Swans breeding in Chukotka are still unknown, but are probably in Japan, where Whooper Swan numbers increased substantially during the 1990s (Environmental Agency of Japan 1998; Fig. 7). The expansion of the breeding range into east Chukotka appears to have continued to North America, since Whooper Swans have recently been reported breeding on Attu, the westernmost of the Aleutian Island (Sykes and Sonneborn 1998).

DISCUSSION

Bewick's Swan

The Bewick's Swan was a common species of Russian tundra landscapes during the 19th and early 20th centuries (Ptushenko 1952), but numbers of the species decreased substantially in many parts of the Siberian Arctic during the 1950s–1970s. Data on the decrease in numbers both in the breeding grounds and on migration for the Yamal Peninsula, Taimyr Peninsula, Yakutia and Chukotka, as well as at staging sites along the Yenissey River, Ob' River and Lena River, have been presented in the proceedings of two swan conferences held in the USSR (Syroechkovski 1987; Koshelev 1990). The breeding range became fragmented, the species disappeared from many peripheral parts of the range, and was rarer even in some optimal habitats. Unlimited hunting, habitat loss, disturbance and lack of conservation programs in Russia, together with similar pressure on Bewick's Swan populations in the wintering grounds, were the main reasons for the declines. Since the 1970s, the Bewick's Swan has been included in the Red Data Book of the USSR (now the Red Data Book of Russia). Much effort has been directed towards conserving the species, both in the wintering grounds (Japan and Western Europe) and also in Russia, and numbers increased during the late 1980s and early 1990s. The review of recent data on the Bewick's Swans' distribution, numbers and trends on the breeding grounds, presented above, indicates an increase in numbers in most areas, and a return to much of its former range.

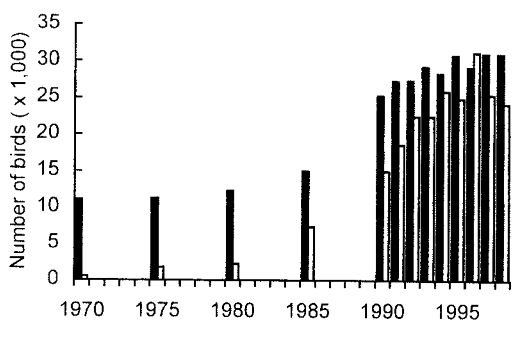

Fig. 7. Numbers of Whooper Swans and Bewick's Swans recorded in Japan, 1970–1998 (Environmental Agency of Japan 1998). Closed columns = Whooper Swans; open columns = Bewick's Swans.

Figure 2 illustrates total numbers estimated for Bewick's Swan populations, not only in the Siberian Arctic but throughout the range, including breeding grounds in European Russia, and data from the wintering grounds in both Europe and Asia (Morozov 1996; Beekman 1997; Rees *et al.* 1997; Rose and Scott 1997; Babenko and Poyarkov 1998; Environmental Agency of Japan 1998; Gurtovaya *et al.* 1999; Ma and Cai 2000; Mineev and Kondratiev 2001; Nolet *et al.* 2001; Syroechkovski *et al.* 2000; Melnikov, in press; A. I. Artyukhov, pers. comm.; H. Lee, pers. comm.; Russian Academy of Sciences unpub. data). Estimates of 30,000–36,000 birds for northeast European Russia in the late 1980s (Mineev 1991) seem to be an overestimate and therefore are not included in the calculations. The estimate of 23,000 for this part of the breeding range (Fig. 2) was calculated from published and unpublished data for European Russia, not presented in detail here because these birds occur outside the Siberian Arctic. Numbers on the breeding grounds therefore are estimated at about 66,400 in the late 1990s, determined mainly by extrapolating aerial counts of full-grown birds during the molt in July to early August, compared with about 69,000 swans including cygnets in the wintering range (Fig. 2). Winter population sizes are determined from total counts, rather than extrapolating from aerial transects, and these seem to be more accurate. An exception is China, where the sources of winter count data, national totals and methods used to estimate these totals are not very clear, and the status of swans wintering around the Caspian Sea also needs clarification. It should be noted that information from different parts of Russia giving rise to population estimates in the breeding range, as well as the comparison of population estimates made in summer and winter, includes data for different years within the 1994–2000 period. Nevertheless, given that population estimates in both summer and winter could easily be subject to a 10% error, the totals match reasonably well, and it seems that important Bewick's Swan breeding sites in the Siberian Arctic have not been overlooked.

The Bewick's Swans' status on wintering grounds around the Caspian Sea warrants further consideration. A figure of 6,500 swans reported for the area (Rose and Scott 1994) is known to have been a typing error, later corrected to 500 birds (Rose and Scott 1997), so issues raised by Morozov (1996) concerning wintering population estimates are now partly resolved. Nevertheless, albeit irregular sightings of Bewick's Swans migrating between the Caspian Sea and Western Siberia, in both autumn and spring, reinforce the view that this is a distinct Bewick's Swan population, which probably breeds in Western Siberia, and consistently winters on the Caspian Sea (Braude 1987; Khrokov *et al.* 1990; Samigullin *et al.* 1995; Azarov 1996; Golovatin and Paskhal'ny 1996; Davygora 1998; Gurtovaya *et al.* 1999). Suggestions that the size of this population has been underestimated (Kistchinski 1979; Morozov 1996) should be investigated because Bewick's Swans are likely to have been missed both at stopover and at wintering sites due to (1) misidentification, since only binoculars were used for counts in the 1960s to 1980s, and most censuses in Kazakhstan and the Caspian Sea area were by game management staff and wardens not trained in the identification of swan species; (2) wetland censuses over the last 30 years were irregular and often did not cover swan habitats; (3) most Bewick's Swan wintering grounds in the north Caspian are on open sea along the edge of the ice (Rusanov 1984) so, since censuses were mainly from a single engine AN-2 airplane officially not allowed to fly over open water, or lower then 100 m over ice, separating swan species on the water was not easy; and (4) special Bewick's Swan surveys have never been undertaken in the region. Thus, Bewick's Swans could easily be missed among the large number of Whooper Swans that migrate across the steppe wetlands to winter on the Caspian Sea, and there are currently insufficient data to make an accurate estimate of population size. A maximum count of 843 birds was recorded on the southern coast of the Caspian Sea in 1969 (Ferguson 1972) and, in view of the sightings derived from incomplete monitoring, the Caspian-West Siberian population probably exceeds 1,000 birds. Coordinated boat and terrestrial censuses of swans wintering on the Caspian Sea, especially in northern parts along the edge of the sea ice, would provide a better indication of population size.

Questions remain concerning the wintering grounds for the rest of the Bewick's Swans breeding in Western Siberia (Yamal Peninsula and Gydan Peninsula). Of about 100 recoveries in Russia of birds marked in Europe, all were reported west of the Urals and Vaigach Island (Moscow Bird Ringing Center, unpub. data), so there is no evidence for European wintering birds breeding on the Yamal Peninsula or further east. Yet numbers observed at the stopover sites in Kazakhstan and southern Central Siberia account for little more than half (6,500–7,000) of totals (9,000–11,000) estimated for the Yamal Peninsula and Gydan Peninsula. The source of the increasing numbers in west Taimyr also is unclear, but it is possible that they arrive from the southwest, across the Western Siberian plain, in spring. Several explanations can be given for the discrepancy in numbers for the breeding grounds, stopover sites and wintering sites in the central part of the range: (1) extrapolation of aerial counts on the West Siberian tundra overestimating numbers on the breeding grounds; (2) birds from European wintering grounds reaching the Yamal Peninsula, and therefore being included in numbers recorded for Western Siberia; (3) more birds from Western Siberia wintering on the Caspian Sea; and (4) many more swans from wintering grounds in China crossing the southern part of Central Siberia and Western Siberia to breed on the Yamal, but these being missed at the stopover sites. Future research will show the extent to which each of these explanations is correct. An exchange of swans between the European to the Caspian wintering populations has been discussed in the literature (Rees 1991), and at least four individuals marked in Europe have been recovered along the West Siberian to Caspian Sea flyway, at sites near the Urals, in Astrakhan' and as far south as Iraq (Rees *et al.* 1997). This suggests that some movement of birds from the European tundra to the Yamal Peninsula is possible, although it is not yet known whether this occurs.

The number of Bewick's Swans in Eastern Siberia (Lena Delta, Kolyma Delta and Chaun Bay) started to increase in the 1970–1980s (Mineev and Kondratyev 2000; A. Degtayrev and V. Pozdnyakov, pers. comm.), and this corresponded with an increase in numbers wintering in Japan (Environmental Agency of Japan 1998; Fig. 7). Marking programs in have shown that the Japanese wintering birds breed in East Siberia (Kistchinski 1979; Higuchi 1991), but it seems likely that birds from the more western areas (Lena Delta, Eastern Taimyr, Central Siberia) winter in China, with some perhaps migrating to Korea. However, there has been no report of a substantial increase in Bewick's Swans wintering in China over the last 15 years, even in a recent review of the status of swans in China (Ma and Cai 2000), so population trends and distribution in the far east should be addressed in further detail at a flyway level.

The following areas of research, aimed at separating and describing more precisely the Bewick's Swan populations in Siberia and the other countries of east Asia, therefore seem likely to be informative: (1) color marking and satellite tracking swans from stopover sites in south Siberian to confirm both the breeding areas and wintering sites for these birds; (2) coordinated boat and terrestrial censuses of swans wintering on the Caspian Sea, especially in northern parts along the edge of the sea ice, to provide a better indication of population size; (3) color marking and satellite tracking of swans molting on the Yamal Peninsula and Gydan Peninsula; (4) monitoring the progress of swans breeding in new areas in south Chukotka; and (5) more accurate counts, and development of a marking program, on wintering grounds in China.

Tundra Swan

The Tundra Swan has not been studied in detail in Asia, so any scientific information concerning the species in this part of the range is of value. Of particular interest is its interaction with the conspecific Bewick's Swans where their breeding ranges overlap, since this might resolve the taxonomy of these two forms. Russian specialists in avian taxonomy recognize Tundra Swans and Bewick's Swans as being two separate species (Stepanyan 1990), and further data on the frequency of hybridization would help to clarify the situation. Monitoring the numbers and distribution of both forms in Chukotka should be combined with comparative studies of their behavior, ecology and genetics in different part of the range. Color marking and satellite tracking is needed to describe their migration routes to wintering sites, and thus determine whether Tundra Swans breeding in Chukotka are from the Eastern Population or the Western Population in North America.

Whooper Swan

Whooper Swans have increased in numbers in Siberia, and their breeding range has expanded to the north and east. In the last decade, the species started breeding on open tundra and now nests regularly in the southern part of the Siberian Arctic. Much higher numbers also breed in the sub-arctic northern taiga zone (Degtyarev 1990; Poyarkov and Johnson, 1996) than in areas further south, and the core of the breeding range generally has shifted north.

The increase in numbers in some part of the breeding range can be partly attributed to conservation efforts in Japan, where swan populations have increased three-fold in 30 years (Environmental Agency of Japan 1998; Fig. 7). However, Japanese Whooper Swans are thought to breed mainly in the Kolyma River and Indigirka River basins of Yakutia (Kanai *et al.* 1997), whereas the tendency to breed further north was also noted in more western areas such as the Taimyr Peninsula and Western Siberia, which are very unlikely to receive birds wintering in Japan. Moreover, the northward expansion of Whooper Swans in Eastern Siberia was reported in the late 1960s to 1970s (Perfiliev 1987), much earlier than the increase in the Japanese wintering population which was not noted until the mid-1980s (Environmental Agency of Japan 1998; Fig. 7). Information on trends in numbers wintering in China could help to determine whether the changes in the breeding distribution recorded in Siberia were associated with population growth at this time.

The wintering grounds of Whooper Swans that started breeding in coastal areas of south Chukotka in the 1990s have not yet been determined. Tens of birds marked with neck bands on the middle reaches of the Anadyr River in the 1980s were not resighted in Japan, and therefore probably migrated to China (Kretchmar *et al.* 1991), at a time when the middle Anadyr River was the easternmost part of the breeding range. Wintering of some birds on ice-free wetlands of Kamchatka is also possible (Yu. Gerassimov, pers. comm.). More recently, birds have been breeding in coastal south Chukotka, about 200–400 km to the east and southeast, and the migratory routes from the two breeding areas may overlap, perhaps facilitating an exchange of birds between Japanese and Chinese wintering grounds. It is still not known whether the tripling of Whooper Swans counted in Japan since the early 1980s is due mainly to growth of the section of the population that winters in Japan, improved counting coverage in Japan, a redistribution of birds that previously wintered in China to protected and managed Japanese wintering sites, or to all three of these factors. Such a change in distribution may also have occurred for Bewick's Swans, White-fronted Geese (*Anser albifrons*) and other waterfowl species, which have increased substantially in numbers in Japan in recent years (Environmental Agency of Japan 1998). More detailed surveys of swans breeding in the middle Anadyr, coastal south Chukotka and north Kamchatka regions, together with satellite tracking and color marking programs, would serve to describe population distribution and trends for Whooper Swans in far east Asia.

An important issue currently being debated is whether to permit an open hunting season for Whooper Swans in Yakutia. The Yakutian Hunting Society and some representatives of the Yakutian Ministry of Nature Conservation take the view that Whooper Swans are very aggressive during the breeding season, and that this accounts for a decrease in the numbers of game waterfowl, mainly ducks. The hunting lobby is particularly strong in the Kolyma and Indigirka taiga, and in forest-tundra lowlands, which are thought to have high Whooper Swan densities in summer. An open season for Whooper Swan was permitted for one year in the middle 1990s, the only time that swan hunting has been legal in Russia over the last 30 years.

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Effects of El Niño Southern Oscillation on Numbers of Black-necked Swans at Río Cruces Sanctuary, Chile

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Abstract.—Population trends of Black-necked Swans (*Cygnus melancoryphus*) at Río Cruces Sanctuary are analyzed and discussed in light of annual and seasonal fluctuations at this Ramsar site. Aerial, boat or ground surveys of swans have been made every month since 1985. Pronounced annual and seasonal fluctuations in numbers, with lows during the wet autumn/winter and peaks during the dry spring/summer, characterize this population. Numbers of swans more than doubled during the La Niña periods of 1989–1991 and 1996–1997. These periods coincided with macro-regional droughts that forced swans to move nomadically in the southern cone of the Neotropic. Río Cruces is a stable wetland and a likely demographic source for Black-necked Swans in the region, where their distribution and numbers have increased in the last decade.

Key words.—Black-necked Swan, conservation, *Cygnus melancoryphus*, demography, ENSO, Neotropic southern cone, nomadism, mobility, Río Cruces, subpopulation.

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Migration is an adaptation that allows individuals to cope with seasonally and/or spatially fluctuating environments and resources (Alerstam 1990). Migration varies among species, populations, age groups and sexes, and may even vary within individuals over time (Alerstam 1990). Differences occur with respect to distances traveled, routes followed, timing of departure and arrival, and behavior during migration (Alerstam 1990; Berthold 1993). A more detailed knowledge of variation in migration, and its mechanisms and environmental correlates, is crucial for understanding the role of migration in a species' life-history.

The movement patterns of Neotropical breeders, especially waterbirds, have not been well described. The movements of waterbirds in southern South America seem to be different from those of birds in the Northern Hemisphere (reviewed in Alerstam 1990; Haig *et al.* 1998) and to be more similar to those of Australian birds (Ford 1989) whose movements are shaped by dry and wet seasons and the stability of wetlands in an otherwise arid region (the "boom and bust" systems described by Kingsford 1996 and Kingsford *et al.*1999).

Long-term studies have demonstrated that climatic fluctuations can produce changes in distribution and reproductive success of animal populations (Caughley 1994; Kingsford 1996). Stable climatic conditions, especially regular rainfall, are essential for maintaining stable populations and site fidelity (Alerstam 1990). One of the most important climatic phenomena is El Niño Southern Oscillation (ENSO), a non-periodic oscillatory event (Rasmusson 1987; Aceituno *et al.* 1993; Jacksic 1998). This phenomenon has a large effect in the Southern Hemisphere and also affects other parts of the globe. Although ENSO's effect on populations in tropical South America is unclear (de Souza *et al.* 2000), its effect along the southern Pacific coast has been documented in rodents (Lima *et al.* 1999), terrestrial birds (Jaksic and Lazo 1999), penguins (Boersma 1998), and other seabirds (Jahncke and Goya 2000).

Local numbers of Black-necked Swans fluctuate strongly in some years and their movements seem erratic. Swans move to southern Brazil (Menegheti *et al.* 1990), Uruguay (Vaz-Ferreira and Rilla 1991), and the tip of South America, with stragglers reaching the Antarctic Peninsula and adjacent islands (reviewed in Olavarría *et al.* 1999). A relationship between movements and the ENSO cycle has been proposed for Black-necked Swans (Schlatter *et al.* 1991a, 1991b; Schlatter 1998; Silva and Vilina 1999; Olavarría *et al.* 1999) and other aquatic birds (e.g., Podicipediformes) in central Chile (Vilina and Cofré 2000).

Since 1975, Schlatter *et al.* (1991a) have studied Black-necked Swans on two wetlands in central Chile, El Peral and Torca lagoons, and one wetland of southern Chile in particular, the Río Cruces Sanctuary. At Río Cruces, the total number of swans has increased in the last ten years, but numbers have fluctuated between seasons and years (Schlatter *et al.* 1991a, 1996; Schlatter 1998). The number of breeding swans has increased fairly steadily without major annual fluctuations (Schlatter 1998).

We suggest that Black-necked Swan numbers at Río Cruces fluctuate seasonally due to the regional rainfall patterns, and fluctuate between years due to ENSO (El Niño-La Niña) events. In particular, we predict that (1) the Río Cruces population peaks during dry years (La Niña) when swans on unstable, drying wetlands search for more stable wetlands; and (2) seasonal peaks at Río Cruces occur from spring to late summer (December-March), when declining water levels on surrounding wetlands push birds to more stable wetlands like Río Cruces. We relate our findings to the conservation management of Black-necked Swans in the Neotropics where this swan was previously considered endangered (Schlatter *et al.* 1991a) and is still classified as a vulnerable species in Chile, Brazil, and Uruguay.

STUDY AREA AND METHODS

The "Carlos Anwandter Nature Sanctuary" Ramsar site, also known as Río Cruces, is located between the forks of the Cruces and Cau-cau Rivers near the city of Valdivia, north of Teja Island (39°49'S and 73°15'W) and close to the village of San José de la Mariquina. It covers 4,877 ha and was designated by the Chilean Government as the first Neotropical wetland of International Importance on 27 July 1981 under the Convention on Wetlands (the "Ramsar Convention"; Schlatter 1998). The Cruces River is the main channel of this extensive wetland system, which includes adjacent floodplains and marsh areas inundated with water up to 2 m deep. Waters are slow-flowing in the main river channel which is 4–8 m deep and has a lime and sand substrate (Ramírez *et al.* 1991). Recently Río Cruces has been proposed as an official National Reserve that will include more than 6,000 ha of wetland (Schlatter and Mansilla 1998; CONAF-UACH 1999). The Río Cruces wetland originated by the sinking of lowlands and local endemic forest-scrub wetlands as a consequence of an earthquake in May 1960 (Weischet 1960). The site is estuarine in nature and is affected by tides from the nearby Pacific Ocean (Campos *et al.* 1974).

Central Chile, from 33°S in the north to Valdivia (40ºS) in the south, has a Mediterranean climate and rainfall regime that is humid and temperate with small thermal oscillations and mild winters (Huber 1975). The annual mean temperature is 11º C, and annual rainfall may reach 2,415 mm (Huber 1975). The region's aquatic flora comprises 80 species, 32% of which are exotics. Cryptophytes make up 27% of emergent aquatic plants, 14% of floating-leaf species, and 59% of underwater vegetation (Ramírez *et al.* 1991).

Each month, from October 1985 to December 1999, Black-necked Swans on the Cruces River Sanctuary were monitored by wardens according to an established protocol (see Schlatter *et al.* 1991a, Schlatter 1998). The monitoring procedure required an entire day. Additional aerial and ground censuses were carried out during November 1995 for mainland Chiloé and Chiloé Island (42°30'S and 73°55'W, north and east coast only) in northern Patagonia (R. P. Schlatter and L. A. Espinoza, unpubl. data), and Budi Lake (38°53'S and 73°18'W) during January 1996 in the Chilean Araucanian Lake district (R. P. Schlatter, pers. obs. 1996). The latter location was surveyed seasonally for Black-necked Swans from 1989 to 1994 (Saavedra 1994).

We classified all surveyed wetlands by their degree of within- and between-year stability and thus their suitability for Black-necked Swans. Stable wetlands had appropriate and stable water levels and submerged food (even during tidal fluctuations) throughout the year, adequate bulrushes (*Scirpus* spp.) for nesting (Corti and Schlatter 2002), sporadic or no human impact, and were in a protected system where swans breed regularly. Moderately stable wetlands had periodic years of drought and changes in water level (not considering tidal changes), moderate or periodic human impact (e.g., moderate erosion, sedimentation and summer tourism), and supported breeding swans only in years of rainfall. Unstable wetlands had irregular water levels, continuous human intervention (e.g., persistent erosion, wetland sedimentation and tourism), and either no breeding swans or only occasional breeders.

Climatic data for southern South America, specifically about El Niño Southern Oscillation (ENSO), were obtained from the Climate Prediction Center of the National Oceanic and Atmospheric Administration web service (www.cpc.ncep.noaa.gov). The Climate Prediction Center's classification of ENSO events in the tropical Pacific is essentially a subjective one based on a re-analysis of sea-surface temperatures by season (January–March, April–June, July–September, and October–December). This ENSO index ranks the intensity of events from 0 to 3, where 0 represents cold sea-surface temperatures, resulting in a dry La Niña event, and >2 represents warm sea-surface temperatures resulting in a rainy El Niño event.

Monthly counts of Black-necked Swans were analyzed using a classical time series model, as described by Netter *et al* (1988). The analysis was restricted to October 1985–December 1999, during which there were no gaps in the data. The model involved three steps. First, a linear regression model was fitted to estimate the population trend through time (Zar 1999). The assumptions of the linear regression were checked with residual, normality, and lack of fit plots (Zar 1999). Second, the observed values were then expressed as a percentage of the predicted value (percent of trend = observed count/predicted count * 100) where the predicted value was obtained from the regression of swan numbers on year. The effect of this step is to remove the trend from the time series and thereby clarify seasonal and annual fluctuations. Third, the Centered Moving Average (CMA) of the percent of trend was calculated using a 12-month window in order to remove the seasonal effect from the time series. The moving average corresponds to the seasonal cyclical component of the series, which was then related to the occurrence of warm ENSO events.

Differences between the number of swans counted during spring/summer and autumn/winter, from 1986 to 1999, were compared using a two-tailed paired t-test. Data from 1995 were excluded from analyses because of missing data in some seasons.

RESULTS

The number of swans in the Cruces River Sanctuary was highly variable, but a distinct increase in numbers is evident during the last 15 years (Fig. 1; $Y = 299.68x - 593676$, $r^2 = 0.24$ $N = 172$, $P < 0.001$). This positive trend explains 24% of the variance of the original series. The highest number of swans counted over a year was 95,630 in 1996, corresponding to a monthly average of 7,969 swans. The highest single count was 14,533 swans in April 1997, during a dry period without ENSO activity (Fig. 1). The lowest count, 640 individuals, was in February 1985 at the end of a long El Niño event characterized by high rainfall. The Central Moving Average of the percent trend, which removes effects of seasonal tendencies (Fig. 2) and clarifies the effect of ENSO events, shows clear peaks during 1988–1991 and 1995–1998 (Fig. 3).

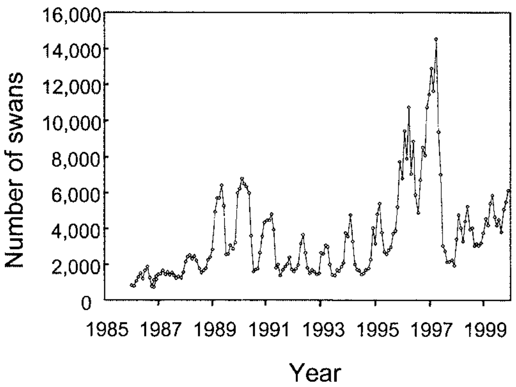

Figure 1. Numbers of Black-necked Swans at Río Cruces Sanctuary, Chile, from January 1986 to December 1999. Dots represent monthly counts.

Black-necked Swan numbers tended to be lowest in winter (Jun–Aug) and highest in summer (Dec–Mar) (Fig. 1), but there was considerable variability in the timing of peaks and troughs. Annual fluctuations showed important tendencies relative to the intensity of ENSO events. The time series (Figs. 2 and 3) shows two clear peaks in swan numbers, one during 1988–1991, and the other during 1995–1998. These peaks in swan numbers occurred during periods of La Niña (cold ENSO event) followed by a "normal" period (no ENSO activity). Seasonality, expressed as the difference between monthly averages (as shown by the vertical distance between solid lines in Fig. 3), was less pronounced during El Niño events than during intervening years, especially during the first and second El Niño events. Number of swans during spring/summer (September–March) was statistically higher than during autumn/winter (April–August) from 1986 to 1999 years (mean difference = 8319 ± 1742 [SE]; $t_{13} = 4.78$, $P < 0.001$).

Aerial and ground surveys performed sporadically at Chiloé during the last decade have shown an increase in colonization in several inlets, estuaries, mudflats, marshes,

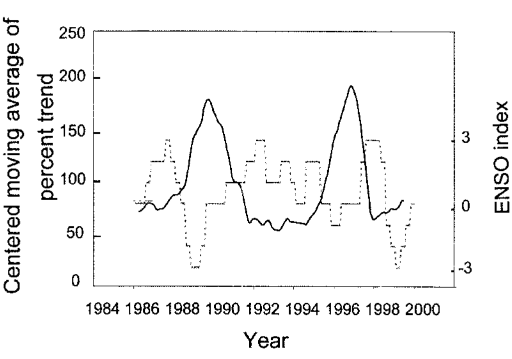

Figure 2. Annual fluctuations in Black-necked Swan numbers at Río Cruces Sanctuary, Chile, in relation to El Niño events. The solid line is the Centered Moving Average of the percent trend (observed/predicted based on linear regression) which serves to remove seasonal fluctuations and clarify annual fluctuations. The broken line is the quarterly El Niño index (El Niño events, index >2; La Niña events, index = 0).

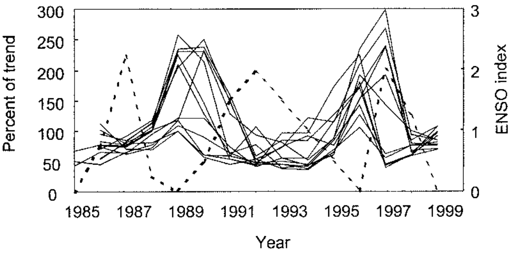

Figure 3. Seasonal fluctuations in Black-necked Swan numbers at Río Cruces Sanctuary, Chile. The twelve continuous lines represent swan numbers during each month across 15 years. Swan numbers are given as the percent of the linear regression trend (observed/predicted * 100). The broken line is the El Niño index (El Niño events, index >2; La Niña events, index = 0).

and slow flowing rivers (R. P. Schlatter and L. Espinosa, unpubl. data) with sporadic breeding by small numbers (R. P. Schlatter pers. obs.). The current estimate of swan numbers at Chiloé is 10,000 birds. North of Chiloé, between Chacao channel (41°50'S and 73°22'W) and Budi Lake, a similar number of swans have colonized several wetlands. At Budi lake, swans increased from a yearly average of 500 individuals during 1989–1993 to a yearly average of 2,000 birds during 1994–1996, with a maximum of 2,950 in May 1997. We estimate that the total number of Black-necked Swans in southern Chile (northern Patagonia and Araucanian Lake District) is approximately 25,000 birds.

Wetlands along the Chilean coast where swans were observed during the study period are presented in Figs. 4a and 4b. These sites are concentrated along or close to the Pacific shoreline. Numbers of swans and wetland size are smallest for the northernmost wetlands, which are unstable and occur in arid habitat. We noted that all stable (two sites) and all moderately stable wetlands (five sites) in Chile are protected, either by the government or private organizations. Only two of six unstable wetlands are protected (Reloca Estuary and Torres del Paine National Park).

DISCUSSION

Effects of El Niño

Black-necked Swans at Río Cruces have exhibited an increasing trend and substantial oscillations between and within years during the last 15 years. Swan numbers were higher during the dry spring/summer than during the wet autumn/winter. High rainfall in winter increases water levels at Río Cruces, resulting in swans, probably non-breeders, dispersing to other recently created waterbodies. In late summer and autumn at the end of the dry season, swans concentrate on the most stable wetlands on which water levels and food availability remain adequate, like Río Cruces in southern Chile, and Torca lagoon in coastal central Chile (Schlatter *et al.* 1991a; CONAF 1999).

ENSO has been shown to affect temperature in the southern cone of South America (see Rasmusson 1997; Rosenblüth *et al.* 1997). Temperature and precipitation are highly seasonal in Argentina and Chile, especially during autumn and winter months (Pittock 1980a, b). Black-necked Swan numbers at Río Cruces clearly peaked during La Niña events (dry years) and declined during El Niño events (rainy years). We suggest that during rainy years, and the rainy months of winter, that the increasing water level at Río Cruces causes submerged food to become less available to swans and that swans seek other wetlands with lower water, more available food, and less competition for food (Corti 1996). Similarly, we suggest that during dry years, swans in surrounding, drying wetlands move to more stable ones, including inland lakes, oligotrophic lakes, riverbeds, estuaries (such as the Río Cruces), and shallow seashores. Swans may then recolonize formerly dry wetlands if they are replenished during rainy years. This pattern is similar to that of waterbirds in arid Australia (Simpson and Day 1984; Ford 1989; Kingsford 1996; Kingsford *et al.* 1999).

A review of published surveys indicate several sites important to Black-necked Swans in the Southern Neotropics. Southern Neotropic sites with large numbers of Black-necked Swans, ranging from 5,000 to 50,000 birds, were Seno de Ultima Esperanza in Chile and Llancanelo Lake in Argentina (Blanco *et al.* 1996) (Fig. 4a). Wetlands supporting large numbers of breeding pairs were Río Cruces with 250–800 breeding pairs (Schlat-

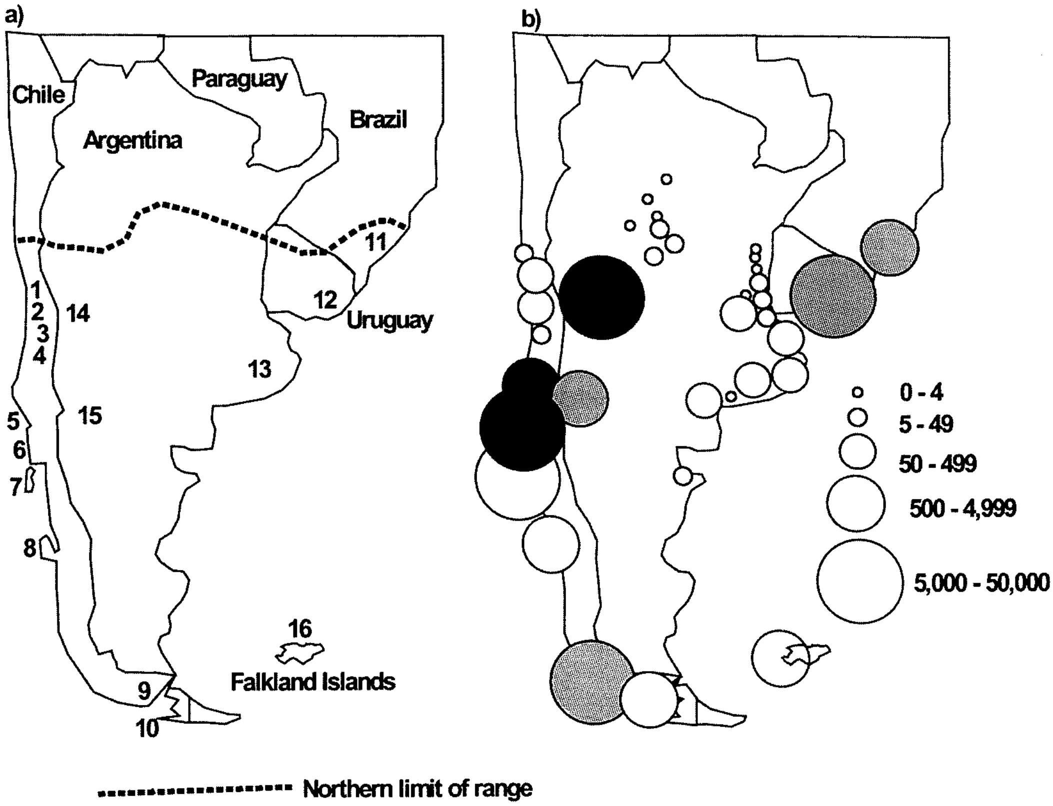

Figure 4. Distribution and numbers of Black-necked Swans in southern South America (Argentina, Brazil, Chile, and Uruguay) during 1990-2000. (a) Names of primary locations and maximum counts of Black-necked Swans recorded at each. Chile: 1—Punta Teatinos Point (> 4 swans); 2—El Peral Lagoon (>110); 3—Yali complex (>1,470); 4—Torca and Vichuquén Lakes (>1,150); 5—Budi Lake (>2,970); 6—Río Cruces Sanctuary (>14,500); 7—Chiloé island and surroundings (>5,000); 8—Laguna San Rafael (> 500) 9—Seno Ultima Esperanza and Torres del Paine National Park (>20,000); 10—Lago de los Cisnes, Tierra del Fuego (>2,000). Brazil: 11—Lagoa do Peixe. Uruguay: 12—Bañados del Este. Argentina: 13—Buenos Aires and La Pampa Lagoon complex; 14—Laguna Llancanelo, Mendoza; 15—Laguna Blanca, Neuquén. United Kingdom: 16—Las Malvinas. (b) Size of circle indicates the maximum number of Black-necked Swans recorded on each wetland. Black circles represent swans on stable wetlands; gray circles on moderately stable wetlands, and open circles represent swans on unstable wetlands. Figure derived and modified from Blanco *et al.* (1996).

ter *et al.* 1991b; this study), Llancanelo in Argentina (Martínez *et al.* 1997) with over 800 breeding pairs, and Laguna Blanca, north of Bariloche, Argentina, which occasionally supported up to 2,500 swans but <300 breeding pairs (Ramilo *et al.* 1993). Sites with fewer swans include Laguna de Rocha in Uruguay, and Chiloé, Maullín river estuary, El Yali, and Laguna Torca in Chile (Blanco *et al.* 1996; this study) (Fig. 4a,b).

Movements

Most descriptions of avian migrations in South America have dealt with typical long-distance, north-south movements between continents (e.g., Keast and Morton 1980). Recently, temperate-tropical migration within the Neotropics has been described (Chesser 1994; Joseph 1997). North-south and west-east movements have been demonstrated for some Anatidae, including Black-necked Swans and Coscoroba Swans (*Coscoroba coscoroba*) between the Argentinean Paraná and the Atlantic coast of southern Brazil and Uruguayan lagoons (Antas 1994; Antas *et al.* 1996; Nascimento *et al.* 2000). Similar movements have been reported for Chilean Flamingos (*Phoenicopterus chilensis*), Olivaceus Cormorant (*Phalacrocorax brasilia-*

nus), and White-faced Ibises (*Plegadis chihi*) (Antas 1994; Antas *et al.* 1996).

Black-necked Swans have been reputed as typically migratory (Blake 1977) or partially migratory (Antas *et al.* 1996), but only local movements have been documented (Belton 1984). Our data on large influxes of swans to Río Cruces during La Niña years, and the patterns described below of unusual influxes and movements of banded birds, indicate that Black-necked Swans undertake short, opportunistic, and erratic movements rather than classical long-distance migrations (Corti and Schlatter 2002).

Movements of individuals between sites can only be traced with a banding program, but data on banded Black-necked Swans is limited. Only 300 swans have been neck-collared in three different wetlands in central (Vilina *et al.* 1997) and southern Chile (Schlatter and CONAF unpubl. data). In Brazil, 23 of 422 banded Black-necked Swans have been resighted from rather short distances away; only one recovery indicated a long-distance movement (from Taim, Brazil, to Buenos Aires, Argentina; Antas *et al.* 1996).

Unusual influxes of swans at other sites also indicate short and erratic movements. The unusually high number of Black-necked Swans at Seno Ultima Esperanza in April 1995, when over 20,000 Black-necked Swans were recorded in shallow seawater (Vuilleumier 1997), must have resulted from an erratic movement due to a dry period in southern Patagonia (Blanco *et al.* 1996). Similarly, in 1970, Markham (1971) counted over 11,000 swans wintering here and south to Tierra del Fuego during a dry event (La Niña) in southern Patagonia. In contrast, in a typical winter there are few waterfowl in southern Patagonia because most inland ponds freeze at that latitude (51°S) (Garay *et al.* 1991). In southern Brazil, Black-necked Swan numbers show pronounced fluctuations between months and seasons (Menegheti *et al.* 1990). A similar trend has been observed in Uruguay, where swan numbers fluctuate in coastal lagoons without a defined pattern (Vaz-Ferreira and Rilla 1991). Another important cause of movements in need of further research is the molt migration, which has been preliminarily described for South American waterfowl by Weller (1968) and Nascimento *et al.* (2000).

Conservation Issues

Most Chilean wetlands that contained swans were located along the coast, from central Chile (Punta Teatinos) to Tierra del Fuego, and inland in Southern Patagonia. It is probable that these wetlands constitute a chain of suitable habitats and thus allow swans to easily move between them. The proximity of suitable habitat patches is probably important to Black-necked Swans, because the only resightings of banded swans indicate a tendency for local movements between wetlands rather than longer movements (Vilina *et al.* 1997; Schlatter and CONAF unpubl. data). Only three Neotropical sites have been identified as sufficiently stable to support regular breeding (Río Cruces, Llancanelo, and Laguna Blanca). It is possible that these sites serve as sources of swans that disperse to new, temporal or permanent, staging and breeding sites. For example, it appears that Río Cruces swans have colonized northward to Budi Lake and southward to mainland Chiloé and Chiloé island.

It is unclear whether this degree of wetland connectivity is sufficient to support the type of avian movements that have evolved in this climate where unstable wetlands are more common than stable ones (Haig *et al.* 1998). Given this uncertainty, Black-necked Swan population dynamics in Argentina need to be better assessed (see Fig. 4b) to ensure that this species is not endangered and to understand the extent and pattern of its erratic movements.

Black Swans (*C. atratus*) in New Zealand apparently comprise a series of regional populations, among which limited intermingling occurs and no interbreeding has been recorded (Williams 1981). We suspect that Black-necked Swans, instead of forming a series of discrete populations, are breeding in a demographic panmixia (Harrison 1991; Esler 1999). We also suspect that experienced breeders tend to remain on stable wetlands where they have bred previously and that provide adequate food and nest sites, whereas non-breeders frequently move between unstable and moderately stable wetlands. A proper multi-national banding program across this heterogenous landscape, and a population genetic analyses in terms of metapopulation theory, are needed to solve this puzzle (Nichols 1996; Stacey *et al.* 1997).

It is clear that Río Cruces has become an important staging area for Black-necked Swans during continental droughts and an important breeding site (Schlatter *et al.* 1991b, Schlatter, 1998). The productivity of Black-necked Swans at Río Cruces (>2.5 cygnets per pair/year) (Schlatter *et al.* 1991b; Schlatter 1998) and sporadically at Laguna Torca and El Yali, suggests significant recovery compared to 20 years ago in Central and South Chilean wetlands. However, the breeding wetlands have reached current conditions mostly by mismanagement of watersheds (deforestation, agricultural activities, erosion, pollution) resulting in an overabundance of sediments and/or nutrients, so they are limnologically rich and undergoing an accelerated ecological succession. In addition, these habitats are affected by tourism and recreational activities during the summer (Gibbs 2000). Thus the stability and future suitability of these important wetlands for Black-necked Swans, a recovering species in southern Chile, is uncertain.

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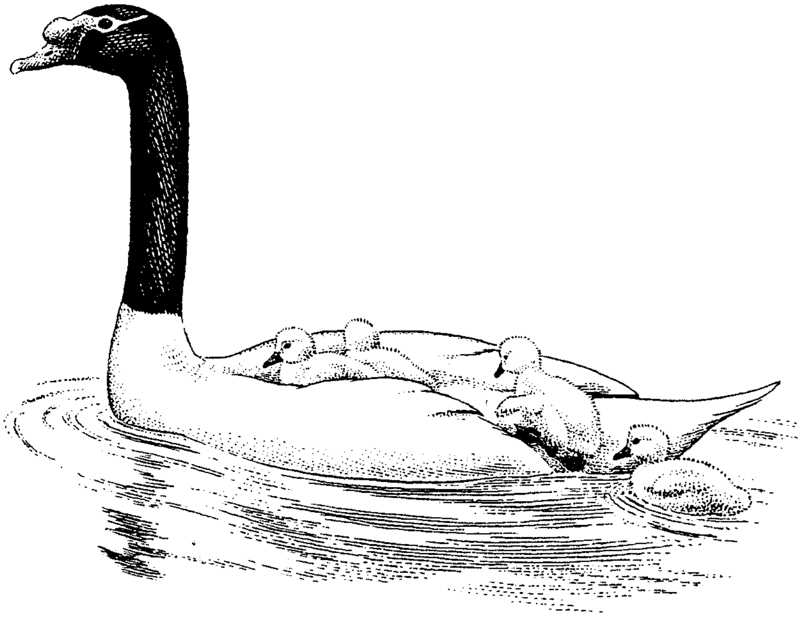

Effects of El Niño on Abundance and Breeding of Black-necked Swans on El Yali Wetland in Chile

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Abstract.—The El Niño Southern Oscillation (ENSO) phenomenon has frequently been associated with negative effects on bird populations. Here we analyze the effect of increased rainfall associated with an El Niño event on Black-necked Swans (*Cygnus melancoryphus*) at El Yali National Reserve, an important coastal wetland of the Mediterranean region of Chile. The Black-necked Swan is a regular winter visitor to the El Yali wetland but, during and after El Niño years, it increases markedly in number, stays longer (throughout the summer) and breeds. During and after El Niño years, El Yali has more swans and higher breeding productivity than at other known breeding sites in central Chile. Consequently, after El Niño events, the El Yali wetland may be a source from which swans colonize other wetlands in the Mediterranean and Austral regions of Chile.

Key words.—Black-necked Swan, breeding, Chile, conservation, *Cygnus melancoryphus*, El Niño Southern Oscillation, Mediterranean wetland.

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The El Niño-Southern Oscillation (ENSO) is a global phenomenon that has an extensive influence around the world (Arntz 1986; Glynn 1988; Grant *et al.* 2000; Holmgren *et al.* 2001). During an El Niño episode, rainfall dramatically increases in certain areas, whereas severe droughts occur in other regions. The next phase, known as La Niña, produces roughly the opposite climatic patterns to those found during an El Niño episode (see Fig. 1 in Holmgren *et al.* 2001).

Multiple ecological effects of El Niño have been noted in marine ecosystems of western South America (see reviews in Jaksic 1998, 2001). Effects include massive die-offs of plankton, macroalgae and marine animals, the occurrence of unusual pelagic and demersal animals, migrations to high sea by fishes of commercial concern, and many others (see Table 1 in Jaksic 2001). Among seabirds, the most obvious effects of El Niño are population declines due to migration of fish to the high seas (Boersma 1978, 1998; Schreiber and Schreiber 1984; Duffy and Merlen 1986; Hays 1986; Araya and Todd 1987; Boulanger 1987; Guerra *et al.* 1988; Duffy 1990; Vilina 1993). In contrast, effects on terrestrial and freshwater ecosystems in western South America have been poorly explored (Holmgren *et al.* 2001; Jaksic 2001). Only in recent years have results of long-term studies become available, revealing evidence that unusual rainfall, associated with El Niño events, strongly affects terrestrial ecosystems (Jaksic *et al.* 1996; Jaksic and Feinsinger 1998). Specifically, El Niño has been shown to affect the abundance and population trends of vertebrates such as small mammals (Meserve *et al.* 1995, 1999; Lima *et al.* 1999a, b), top predators (Jaksic *et al.* 1997) and land birds (Jaksic and Lazo 1999).

Few studies have investigated the effects of ENSO on populations and communities of waterbirds (Vilina and Cofré 2000). Here, we analyze the relationship among an ENSO event, the high rainfall during this disturbance, and changes in abundance, breeding occurrence and local distribution of Black-necked Swans (*Cygnus melancoryphus*). The Black-necked Swan is endemic to the southern cone of South America. Its population is estimated at approximately 100,000 individuals distributed among Chile, Argentina, Uruguay and southeastern Brazil (Schlatter *et al.* 1991).

STUDY AREA

The El Yali wetland is located at the mouth of the El Yali stream (33°47'S, 71°23'W), 20 km south-southeast of San Antonio, Chile. This sub-humid Mediterranean region has warm, dry summers and cold, rainy winters. The rainy period generally lasts from April to September (Di Castri and Hajek 1976). The mean annual rainfall during the last ten years recorded at Fundo Las Dos Puertas Meteorological Station (33°47'S, 70°40'W) was 371 mm (range 852–127 mm) (data of Ministerio de Obras Publicas, Chile). The mean annual temperature was 13.2°C (Di Castri and Hajek 1976). Due to the great diversity of its aquatic avifauna, this wetland has been declared a Ramsar site (under the Convention on Wetlands of International Importance especially as Waterfowl Habitat).

Within the El Yali wetland, five sites were surveyed: El Rey lagoon, Los Molles reservoir, El Yali stream, the Coastal lagoon and the El Convento saltmarsh. These sites were chosen because they are representative of the different habitats in the wetland. El Rey lagoon and Los Molles reservoir are large, seasonal wetlands (106 and 83 ha, respectively), and have large areas of emergent and submergent vegetation. El Yali stream (42 ha) is a permanent wetland with floating and submergent vegetation. The Coastal lagoon (94 ha) is a permanent habitat with a sand beach and floating vegetation only. Each of these four sites is eutrophic and shallow (<3 m). El Convento saltmarsh (60 ha) is flooded by rainfall from autumn to spring, and is artificially flooded during the summer. This saltmarsh is characterized by floating and submerged vegetation, brackish water and a shallow depth of <0.5 m.

METHODS

Data Collection and Statistical Analyses

From January 1993 to August 1999, we conducted 52 seasonal surveys (in at least one month per season) simultaneously in each of the five sites. The abundance of swans at each site was determined through direct counts along fixed transects using the methods and recommendations of Kauppinen *et al.* (1990). Censuses were conducted from 08.30 to 14.00 h. The observer was always the same for a given site, and used a spotting scope and binoculars. The effect of ENSO on swan distribution among the five sites was analyzed for all months (N = 52). These 52 months were divided into breeding months (January 1993 to April 1994, and June 1997 to February 1999; N = 21), and non-breeding months (November 1994 to May 1997, and March to August 1999; N = 31). During the last breeding season (June 1997 to February 1999), we also examined breeding phenology by recording the timing of courtship behavior, nesting, egg laying, and the appearance of chicks, fledglings and juveniles. Due to the sensitivity of Black-necked Swans to human presence, all observations were carried out from a distance (i.e., nest were not approached). Other data collected included the number of chicks (white down), number of pairs with chicks, and the number of chicks and fledglings (gray down) per pair. These data allowed estimation of productivity and numbers of swans at each of the five sites and at the overall El Yali wetland.

Linear regression was used to describe the relationship between annual cumulative rainfall and Black-necked Swan abundance during different seasons in the same, and in the following year, from 1993–1999. Likewise, linear regression was used to describe the relationship between the number of breeding months per year and cumulative rainfall in the previous year. Finally, a chi-square test was used to assess differences between sites in swan abundance during breeding and non-breeding periods (Sokal and Rolf 1995).

RESULTS

Abundance

At the El Yali wetland, Black-necked Swan numbers underwent strong annual and seasonal fluctuations (Fig. 1). In years between ENSO events, there was a clear seasonal pattern: swans were abundant during winter (June to August) and scarce or absent during summer (December to February), when they abandoned several of the lagoons that dried up completely. During El Niño years (1992 and 1997) there was an increase in rainfall during fall and winter. Toward the end of these two years and during the following year, Black-necked Swans stayed at the El Yali wetland throughout the year, and there was an increase in the number of adults both in winter and in summer. No relationship was found between annual rainfall and summer or winter abundance ($R^2_5 = 0.22$, n.s., and $R^2_5 = 0.04$, n.s., respectively). Similarly, annual rainfall was not related to summer abun-

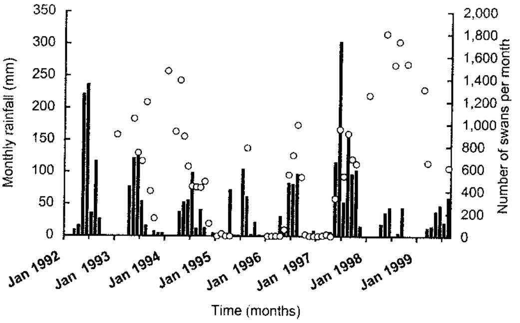

Figure 1. Monthly rainfall (columns) and monthly abundance of Black-necked Swans (open dots) at five sites in El Yali wetland, Chile, 1993–1999. For the monts with no rainfall bars, rainfall was 0 mm.

dance in the following year ($R_5^2 = 0.14$, n.s.). However, there was a positive and significant relationship between annual rainfall and swan abundance during the winter of the following year ($R_5^2 = 0.65$, $P < 0.05$, Fig. 2).

Breeding

Black-necked Swans bred opportunistically at the El Yali wetland. They bred only in those years with abundant rainfall (ENSO and post-ENSO years). There was a significant positive relationship between the number of months of breeding (0–12) and cumulative rainfall (and thus accumulation of water in wetlands) in the previous year ($R_5^2 = 0.74$, $P < 0.05$, Fig. 3). Both years of no breeding (1995 and 1996) were preceded by two years of dry conditions (total rainfall <325 mm per year).

During the 1997–1998 ENSO event, swans bred continuously from June 1997 to February 1999. Among the five sites studied, nesting occurred only at El Rey lagoon. During this period, a maximum of 30% of swans at El Yali bred (Fig. 4). Maximum numbers of breeding pairs (194) were recorded in February 1998, which was also the highest number of breeding pairs ever recorded for a Mediterranean wetland in Chile. We estimated that, during 1997–1999, 300 pairs bred and produced approximately 1,200 fledglings. Brood size ranged from one to nine chicks per breeding pair. Mean productivity varied among sites from 4.5 to 5.4 downy chicks and from 3.6 to 4.1 fledglings per breeding pair.

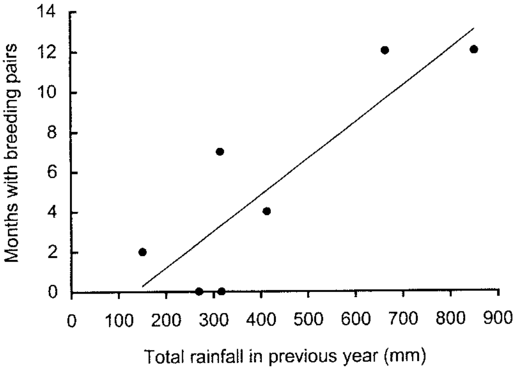

Figure 3. Linear regression ($R^2_5 = 0.691$; $P < 0.05$) between total annual rainfall in the previous year and number of months per year in which Black-necked Swans bred at El Yali wetland, Chile, 1993–1999.

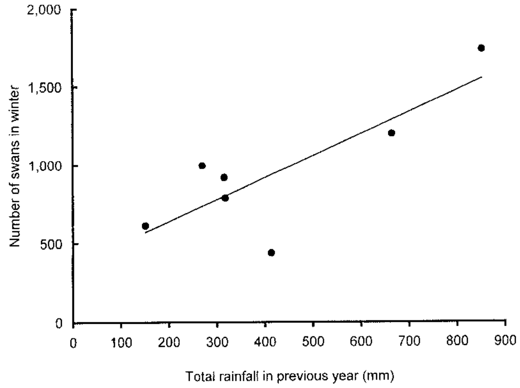

Figure 2. Linear regression ($R^2_5 = 0.65$; $P < 0.05$) between winter abundance of Black-necked Swans and total annual rainfall in the previous year at El Yali wetland, Chile, 1993–1999.

Differences in Abundance Among Habitats

The abundance of swans varied significantly among the five sites surveyed, both during breeding months ($\chi^2_4 = 36{,}552$, $P < 0.0001$), and non-breeding months ($\chi^2_4 = 1{,}953$, $P < 0.0001$). The differences in abundance were more pronounced during the breeding season, because of the substantial influx of swans to El Rey lagoon at this time (Fig. 5).

DISCUSSION

As in other species of vertebrates such as small mammals (Meserve *et al.*, 1995 1999; Lima *et al.* 1999a, b), landbirds (Jaksic and

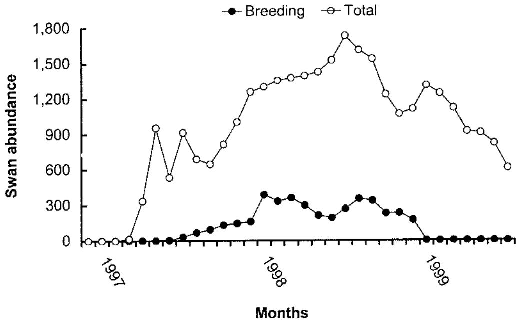

Figure 4. Total abundance and abundance of breeding Black-necked Swans at El Yali wetland during the ENSO event of 1997–1999.

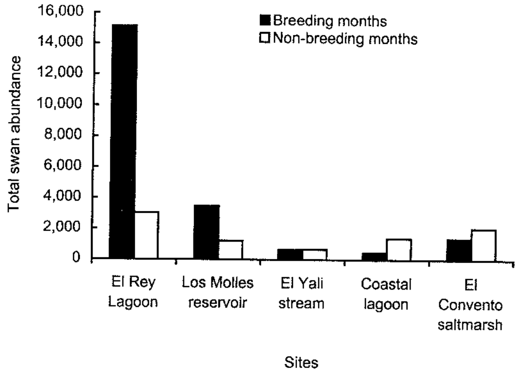

Figure 5. Total abundance of Black-necked Swans at five sites within El Yali wetland during breeding (January 1993 to April 1994, and June 1997 to February 1999, N = 21 months) and non-breeding months (November 1994 to May 1997, and March to August 1999, N = 31 months).

Lazo 1999), raptors (Jaksic *et al.* 1997), foxes (Jaksic *et al.* 1997) and grebes (Vilina and Cofré 2000), the local abundance of Black-necked Swans within the Mediterranean region of Chile is strongly influenced by ENSO events. Like some large rodents in semi-arid ecosystems (Meserve *et al.* 1995, 1999; Jaksic *et al.* 1997), Black-necked Swans take between six months and a year to exhibit increased abundance and productivity (Figs. 3 and 4). This delayed response can be explained because it is due not only to an increase in primary productivity (i.e., food), but also to increased water levels and increased availability of breeding habitats such as extensive beds of the reed *Scirpus californicus.*

During ENSO years (El Niño phase) the El Yali wetland has the largest breeding colony of Black-necked Swans in Chile's Mediterranean region. Birds raised in this wetland (source habitat) may colonize other wetlands where breeding does not occur or is scare (sink habitats). In addition, breeding productivity in the El Yali wetland is higher than that observed in other wetlands of central and southern Chile (Schlatter *et al.* 1991; Schlatter 1998). On the other hand, it is likely that during years between ENSO events, and especially in very dry years (La Niña phase), swans migrate to more stable wetlands that do not dry up and thus can sustain populations during summer months. These may be the wetlands of southern Chile (Schlatter 1998, Schlatter *et al.* 2002), as well as coastal bays and other wetlands in the southernmost part of South America (Blanco *et al.* 1996; Vuilleumier 1997), and even those on the South Shetland islands and Antarctic Peninsula (Olavarría *et al.* 1999).

In conclusion, unlike its effect on seabirds, in which ENSO events are associated with breeding crashes, in Black-necked Swans and other species of aquatic birds such as Silver Grebes (*Podiceps occipitalis*) (Vilina and Cofré 2000), Coscoroba Swans (*Coscoroba coscoroba*) and Black-winged Stilts (*Himantopus melanurus*) (Vilina *et al.* unpublished data), ENSO perturbations increase abundance by facilitating reproduction.

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Satellite Tracking of Bewick's Swan Migration from Lake Nakaumi, Japan

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Abstract.—The Bewick's Swan's (*Cygnus columbianus bewickii*) spring migration route from Lake Nakaumi, southern Japan, was studied using satellite telemetry in 1994 and 1997. Of four birds tracked in 1994, one crossed the Sea of Japan and covered 900 km in 13 h on 31 March. It reached the mainland near Vladivostock, then headed north via Khanka Lake and the Sanjiang Plain in China to the mouth of the Amur River in northern Russia. The distance from the wintering site to its summer site was about 2,000 km. The three other swans, followed for shorter periods in 1994, were recorded at various points along the Japanese Islands. Of a further four swans fitted with satellite transmitters in 1997, two crossed the Sea of Japan. One of these then headed north to the mouth of the Amur River, following a very similar route to the bird tracked in 1994. The other two swans followed a route along the islands of Japan, heading north until mid April when their transmitters failed. These observations suggest that Bewick's Swans wintering at Lake Nakaumi follow at least two migration routes in spring, one along Japanese islands, and the other directly across the Sea of Japan.

Key words.—Bewick's Swan, *Cygnus columbianus bewickii*, migration, satellite tracking, Yonago Waterbirds Sanctuary.

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Lake Nakaumi, on Honshu Island, is the most southerly lake regularly used by Bewick's Swans (*Cygnus columbianus bewickii*) wintering in Japan. Up to 1,000 swans are recorded at the Yonago Waterbirds Sanctuary (YWS) (133°17'N, 35°26'E) on the eastern side of the lake in winter.

The Bewick's Swan's migration route in Far East Asia has been studied by marking birds with neck bands since 1975. About 90 Bewick's swans with neck bands have been observed on migration at sites on the islands of Japan (Bird Migration Research Center, Yamashina Institute for Ornithology 1987), but only three sightings have been recorded in Russia (Kondrat'ev 1984).

Satellite telemetry was used in the early 1990s, when four birds were fitted with transmitters at Lake Kuccharo, a Bewick's Swan staging site in northern Japan, in 1990 (Higuchi *et al.* 1991). Different methods were used to attach the transmitters to the birds (three were attached with harnesses and one was glued to the swan's back with epoxy resin adhesive) and the transmitters also had differing pulse intervals. The four birds all followed a similar migratory route, flying north along Sakhalin, and staging in northern Sakhalin or the mouth of the Amur River (Higuchi *et al.* 1991). One bird arrived at the mouth of the Kolyma River within the breeding area on 17 May 1990.

Although Bewick's Swans staging at Lake Kuccharo probably migrate along the Japanese islands, ornithologists have seen swans wintering at the Yonago Waterbirds Sanctuary take a different route, heading north across the Sea of Japan. This study therefore uses satellite telemetry to track the spring migration route of Bewick's Swans from the Yonago Waterbirds Sanctuary, in southern Japan, to determine whether the birds use different migration routes from different parts of the country.

METHODS

The Bewick's Swans' migration was monitored in two years, in 1994 and 1997. On both occasions the swans were caught at the Yonago Waterbirds Sanctuary in spring. Five swans were caught on 10 March 1994, of which four were fitted with Toyocom T-2050 satellite transmitters and metal leg band. The transmitter was attached to the back of the swan using a Teflon harness. Each transmitter weighed 105 g, and was 93 mm × 36 mm × 19.5 mm in size, with a 200 mm antenna. The transmitters were heavier than those used by Higuchi *et al.* (1991)

because, in order to prolong the transmission period, ours used heavier batteries with a longer life-span. The transmitter cycle was 6 h active transmission followed by a 12 h inactive period, and the pulse interval was 60 s. The other swan was fitted with a metal leg band only.

Eleven swans were caught in 1997, of which four were fitted with transmitters (T-2050) on 5 March. Each transmitter weighed 89 g and was 92 mm × 36 mm × 24.5 mm in size, with a 200 mm antenna. The cycle for these transmitters was 8 h active transmission followed by a 40-h inactive period, with the longer inactive period (in comparison with 1994) making it possible to reduce the weight of the transmitters while still covering the spring migration. The pulse interval was again 60 s. The swans fitted with transmitters were not fitted with neck bands, but were marked with plastic and metal leg bands. The seven other swans caught were fitted with plastic neck bands and with plastic and metal leg bands. The neck bands were green with white codes, as used on Bewick's Swans elsewhere in Japan.

Data on the location of the swans with transmitters were obtained, almost daily, by computer link to the Argos Global Processing Center in Toulouse, France. The accuracy of each location was classified on a five-point scale.

RESULTS

Migration in 1994

The transmitters reported the swans' position for two to six months in 1994 (Table 1). One swan transmitter code 21410) crossed the Sea of Japan covering 900 km in 13 hours on 31 March (Fig. 1). It was tracked across the sea, arriving near Vladivostock (37°16'N, 136°50'E), then headed north to the mouth of the Amur River, via Khanka Lake (44°96'E, 132°86'N) and the Sanjiang Plain (46°17'N, 132°93'E) in China. Finally the swan reached the mouth of the Amur River (52°53'N, 139°50'E) on 22 June to spend the summer in the region, with local moving within a 50 km radius of this point, but occurring mainly on Udly Lake. The direct distance from the starting point to its summer site was about 1,900 km. This same swan started to move south on 24 October, and was tracked along the Amur and Ussuri Rivers to near Khabarovsk (47°96'N, 135°06'E), where it was last recorded on 5 November 1994. The transmitter ceased transmission because the life-time of the battery had expired.

The other three swans (21409, 21411 and 21412) were followed for only short periods and distances in 1994, either because the transmitter had fallen off the bird, or because the swan was sick or had died, but nevertheless were located at various points around Honshu Island in spring before the transmitters failed (Fig. 1). One swan, which reached Lake Hyoko (northeast Honshu) on 3 April, lost its transmitter near the lake. The second was last recorded on or over the Sea of Japan, apparently heading for Hokkaido or Sakhalin. The third swan may have been sick because it did not complete migration but was observed in Japan in June. In all cases, the swans seemed to migrate along the islands of Japan in spring.

None of the swans fitted with transmitters in 1994 were sighted in subsequent winters, but the swan marked with a metal leg band returned to the Yonago Waterbirds Sanctuary in winter 1994-95.

Migration in 1997

The four swans fitted with satellite transmitters in early March 1997 were tracked for one to eight months (Table 1). Two of the swans

Table 1. Bewick's Swan migration distance from the Yonango Waterbirds Sanctuary, Japan, recorded by satellite telemetry in 1994 and 1997. All birds were adult swans.

Year	Transmitter number	Sex	Start date	Date last recorded	Length of route tracked (km)
1994	21409	M	10 May	2 Jun	590
1994	21410	F	10 Mar	29 Oct	2,000
1994	21411	F	10 Mar	6 Jul	360
1994	21412	M	10 Mar	3 May	700
1997	06043	F	5 Mar	21 Apr	660
1997	06044	M	5 Mar	2 May	550
1997	06045	M	5 Mar	10 Apr	630
1997	06046	M	5 Mar	14 Nov	2,050

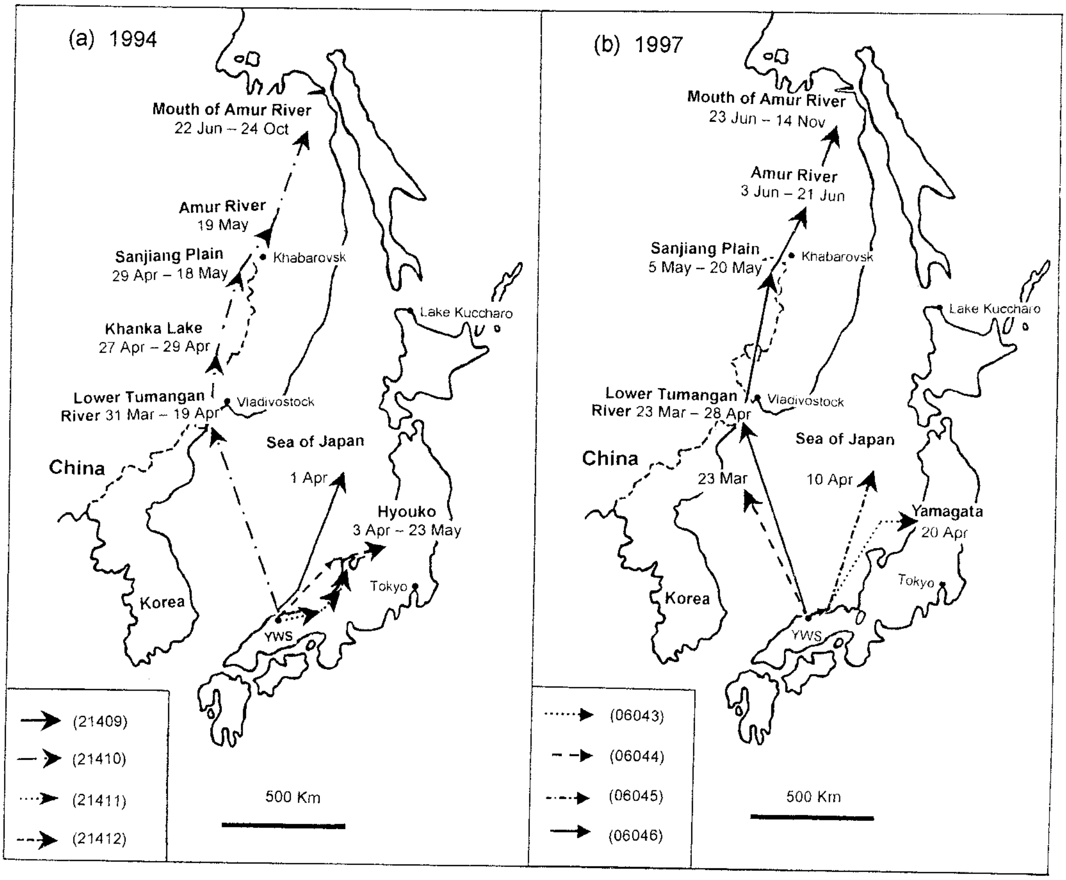

Figure 1. Migration routes taken by individual Bewick's Swans tracked by satellite telemetry in (a) 1994, and (b) 1997. YWS is the Yonago Waterbirds Sanctuary in the Tottori Prefecture, Japan, where the swans were fitted with transmitters. The dates indicate first and last records for each site. Southbound migration by swan 21410 in autumn 1994 is not illustrated but is described in the text.

(06044 and 06046) crossed the Sea of Japan between 21 and 23 March (Fig. 1), and one of these (06046) arrived at the lower Tumangan River (42°22'N, 130°37'E). The second swan (06044) was last recorded on or over Sea of Japan, probably because the transmitter became detached or failed. The swan recorded at the lower Tumangan River was heading north to the mouth of the Amur River, following a very similar route to the swan (21410) tracked in 1994 (Fig. 1). This bird (06046) also spent the summer (23 June–14 November) on Udly Lake (52°35'N, 140°48'E), near the mouth of the Amur River. The position of the swan was recorded every 2 days within a 100 km radius on the mouth of the Amur River, mainly on Udly Lake but sometime moving to the coastal part of Tataskiy Proliv (Mamiya strait).

The other two swans carrying satellite transmitters (06043 and 06045) followed a different route, along the north coast site of the Japanese Islands. These birds headed across the Sea of Japan, apparently towards stopover sites in northern Japan islands, but the transmitter both stopped transmitting while the swans were over the sea. One swan (06043) was subsequently caught, and found to be sick, in Yamagata (38°69'N, 139°67E) on 20 April 1997.

One of the neck-banded swans was sighted in Aomori (40°43'N, 140°36E) in northern Japan during the same season, on 23 March 1997, which was the last sighting of this bird. However, the four other neck-banded swans were observed in Japan during autumn migration that year. As in 1994, the swans with transmitters were not subsequently sighted, but had been marked with leg rings and not neck collars.

DISCUSSION

The observations of eight swans fitted with satellite transmitters suggest that Bewick's Swans wintering at Lake Nakaumi follow two different migration routes in spring, one along the north coast site of the Japanese Islands, and the other directly across the Sea of Japan. After crossing the sea, the swans' migration route followed the Usurri River and the Amur River, staging on the lower Tumangan River, Khanka Lake, the Sanjiang Plain and Udly Lake. The route along the Amur River had been followed by Bewick's Swans monitored in the early 1990s (Higuchi *et al.* 1991), and Whooper Swans (*Cygnus cygnus*) also use the mouth of the Amur River as a migratory site in spring (Kanai *et al.* 1997).

Satellite tracking of the Red-crowned Crane (*Grus japonesis*) migration from Khanka Lake (on the border of eastern China and Russia) found that, like Bewick's Swans, some of the cranes used the lower Tumangan River as a staging area (Higuchi *et al.* 1998). A further satellite tracking study, of White-naped Cranes (*Grus vipio*) from southern Japan, found that these birds migrated north through the demilitarized zone and the western coast of Korea to the Sanjiang Plain (Higuchi *et al.* 1992).

Although the cranes' migration routes were not directly across the Sea of Japan, they seem to use the same staging sites as Bewick's Swans. These areas on the border between east China and Russia have many important marshes for waterbirds on migration. Lake Khanka and the Sanjiang Plain, which are protected areas and listed as key sites supporting at least 20,000 waterfowl in the East Asian Flyway (Miyabayashi and Mundkur 1999), are located in this area.

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Teaching Migration Routes to Canada Geese and Trumpeter Swans Using Ultralight Aircraft, 1990–2001

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Abstract.—This paper summarizes eleven years (1990–2001) of experiments to teach Canada Geese (*Branta canadensis*) and Trumpeter Swans (*Cygnus buccinator*) pre-selected migration routes using ultralight aircraft. When Canada Geese were trained to follow an ultralight aircraft for southward autumn migrations of 680 or 1,320 km, 81% (83/103) returned on their own in the next spring to near their place of training. In contrast, none returned of 21 similarly raised geese that were transported south in a closed truck over a route of 680 km. Trumpeter Swans have proven more difficult to train. However, in two experiments in which Trumpeter Swans followed an ultralight for the entire pre-selected route, one of three and two of four returned close to their training area. A stage-by-stage method, in which swans were transported in trucks between stops, flown in the vicinity and penned with a view of the night sky, has shown some promise. So far an established migration route (north and south twice) has been confirmed in only two geese

Key words.—Ultralight, Trumpeter Swan, *Cygnus buccinator*, induced migration, restoration, Canada Goose, *Branta canadensis*.

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Young geese and swans learn traditional migration routes from their parents when they first fly south from their breeding grounds (Scott 1972). If deprived of this opportunity, they tend not to migrate but undertake sporadic movements. In an attempt to restore migration routes to the rare Trumpeter Swan (*Cygnus buccinator*), we taught swans to follow an ultralight aircraft, a technique first used with young Canada Geese (*Branta canadensis*) in 1988 (Lishman 1996). Experiments began in 1990 with six Trumpeter Swan × Tundra Swan (*C. columbianus columbianus)* hybrid cygnets that were reared and trained successfully to follow a float-equipped ultralight on the water but, before they could be led on migration, the swans were confiscated because of inadequate permits (Lishman 1996). After this initial abortive attempt with swans, Canada Geese were used in 1993–1995 experiments to ascertain the likelihood of success before using swans, and Trumpeter Swans were used from 1997 onwards.

Prior to European settlement, Trumpeter Swans were thought to have either bred or wintered throughout North America south of the arctic tundra to the Mexican border, with an estimated population of 130,000 (Lumsden 1984). It was believed to have been extirpated from eastern North America almost 200 years ago by commercial harvesting and hunting (Banko 1960).

This paper summarizes the successes, problems and possible new approaches of ultralight-induced migration, a technique that could prove useful in restoring migratory pathways for geese, swans and cranes.

METHODS

Rearing and Handling

Since 1990, several experiments with Canada Geese (1993–1995) and swans (1990, 1997–2000) have been performed to refine methods for teaching Trumpeter Swans pre-selected migration routes using an ultralight aircraft or a ground vehicle (Lishman *et al.* 1997; Sladen 1998; Sladen and Rininger 2000; Bezner Kerr 2001; Table 1).

In all Canada Goose experiments, eggs were taken from Ontario's wild non-migratory flock. In the 1997 and first 1998 Trumpeter Swan experiments, eggs were taken from captive (pinioned) parents at Airlie, near Warrenton, Virginia. All eggs taken had been incubated for 10+ days by natural parents and were then hatched

Table 1. Results of our motorized-induced migration experiments using Canada Geese and Trumpeter Swans, 1993–2000, and those of Bezner Kerr (2001).

Year	Method[a]	Species	No. start south	No. finished[b]	Origin (North)	Terminus (South)	Route length (km)	No. returned north/no. alive
1993[c]	U	Goose	18	18	Ontario	Virginia	640	13/16
1993[c]	T	Goose	5	5	Ontario	Virginia	640	0/5
1994[c]	U	Goose	36	35	Ontario	S. Carolina	1312	33/35
1995[c]	U	Goose	32	29	Ontario	S. Carolina	1312	20/29
1995[c]	U	Goose	29	29	Virginia	S. Carolina	672	15/23
1995[c]	T	Goose	16	16	Ontario	Virginia	640	0/16
1997[d]	U	Swan	3	3	Virginia	Maryland	170	1/3
1997[d]	T	Swan	2	2	Virginia	Maryland	170	0/2
1998[d]	U/S	Swan	18	16	New York	Maryland	530	0/13
1998[e]	U	Swan	5	4	Ontario	Indiana	1120	2/4
2000	U/T/U	Swan	14	13	New York	Maryland	530	0/12[f]

[a] Ultralight-led migration (U); Stage-by-stage (S); Transported in closed truck (T).

[b] Includes those that flew the route plus others that flew some of the route but were injured, sick, lost or uncooperative and were transported in a vehicle to terminus.

[c] Lishman *et al.* 1997; Ellis *et al.* 2001.

[d] Sladen and Rininger 2000.

[e] Bezner Kerr 2001.

[f] Results as of 31 January 2002.

in incubators. In 2000, Trumpeter Swan cygnets were captured in the Copper River Delta, Alaska, and in Bezner Kerr's 1998 experiment, cygnets were taken from a captive flock in Ontario (Bezner Kerr 2001). All cygnets were captured at age 10+ days and were reared by human handlers.

In all goose and the 1997 swan experiments, birds were reared where they would learn to follow the aircraft on autumn migration. In other swan experiments, birds were raised at Airlie and, when near fledging, were shipped in closed vehicles to a New York Department of Environmental Conservation facility at Basom, New York, for final training for the flight south.

During rearing, birds were confined to moveable wire pens on grass surrounded by an electric fence that protected them from predators. When being transported by vehicle, birds were confined to standard dog kennels tall enough for them to stand and lined with shredded newspaper.

Geese and swans were marked with a standard U.S. Fish and Wildlife Service metal tarsus band. In all experiments except Bezner Kerr's 1998 experiment, individuals were also marked with coded color neck bands (Sladen 1973). All swan neck bands had radio transmitters attached with a range of about 24 km. Antennae were incorporated into neck bands so there was no protruding object. In addition, in each of three swan experiments (1997, first 1998, and 2000), one dominant bird was harnessed with a satellite transmitter.

Aircraft and Training

Aircraft used were Cosmos or Airbourne Trikes fitted with Rotax 503 engines with an endurance of 2.5 h and speed of 40–100 km·hr^{-1} depending on type of wing used. Trikes fly like motorized hang-gliders. Propeller guards were fitted to Trikes used in all experiments except Bezner Kerr's 1998 experiment, in which birds were trained initially from water with floats and then from the ground (Bezner Kerr 2001). In all other experiments birds were trained entirely from the ground.

The 2000 swan experiment differed from former experiments in two respects. First, wild-caught, rather than incubator-hatched cygnets were trained. Second, a rigorous training program was initiated in which the handlers and pilots always wore a specific uniform. The uniform, designed to simulate a pilot's winter gear, was a black and white contrasting coverall, red face mask with amber-tinted goggles and black helmet. Handlers and pilots wore uniforms to make it more likely that birds would learn to recognize handlers, follow them only, and fear other people. Communication was restricted to a bicycle horn, resembling a swan call note, and a recording of the ultralight engine.

In addition to flights behind ultralights, a stage-by-stage method of transportation was used in the first 1998 experiment. This consisted of transporting swans by truck between pre-selected migration stopovers. At each stop, swans were flown within an 8-km radius at altitudes of up to 310 m and penned with a view of the night sky (Sladen and Rininger 2000).

RESULTS

Results of our experiments and those of Bezner Kerr (2001) are summarized in Table 1. Of 113 Canada Geese successfully led south by ultralights from Ontario to Virginia (680 km) or further south to South Carolina (1,320 km), at least 103 survived the winter. Of these, 83 (81%) returned on their own the following spring to their training area or to within 35 km.

The most convincing results occurred in 1994 when 34 of 35 geese led to South Carolina returned to Ontario. In contrast, of 21 geese not trained to fly with the aircraft, but raised under identical conditions and transported in a closed truck from Ontario to Virginia, none returned to their natal area. Instead, they remained in the wintering area, and two surviving females are now breeding there. At least two ultralight-led geese repeated the north-south migration the following season. However, none were re-sighted thereafter.

Geese proved easier to train and lead in large groups than swans. Geese fledged sooner than swans, and thus began following the ultralight by mid-July in contrast to swans that began following in late August. Cygnets captured in Alaska adapted to their human handlers more quickly and followed the ultralight approximately seven days earlier than cygnets hatched in incubators. Initially trained in groups of 5–7, geese could be amalgamated into larger flocks of up to 30 birds or more for the migration. For example, in 1995, after having been filmed for the movie “Fly Away Home” (Columbia Pictures, 1996, Sony Productions, Hollywood, CA), 32 geese followed two ultralights from Ontario to Virginia, where they were combined with additional ultralight-trained geese to comprise a flock of 61 that followed three ultralights to South Carolina (Table 1). Swans were also trained in groups of 3–6 birds of similar age. However, when groups were amalgamated, swans fought for dominance in the air, adding risk to birds and pilots. Thus, during migration swans were flown in their original groups. The most difficult time for the geese, swans and pilots was when the birds were learning to fly and during the first stage of migration south. In total, three geese and one swan were lost in plane-related accidents, and an additional two swans sustained non-lethal injuries during migration.

In 1997, three female Trumpeter Swans were led from Airlie over a 170 km route in early December and released for the winter on the eastern shore of the Chesapeake Bay, south of Cambridge, Maryland. Two males, not following the ultralight well, were transported in a closed vehicle over the same route (Fig. 1, Table 1). All five swans remained together as a group during winter and integrated well with the neighboring wild Tundra Swans and Mute Swans (*C. olor*). In spring, all three females returned on their own to about halfway to Airlie, deviating no more than 8 km from the route that they had been shown by ultralight. One returned to within 35 km of Airlie; a second was injured by a dog during movement towards Airlie and was then transported the remainder of the way to Airlie. The third backtracked to the wintering grounds. The two males stayed on the wintering area.

In the first 1998 experiment (Sladen and Rininger 2000) from Basom, New York, to the Wildfowl Trust of North America near Grasonville, Maryland, 5 of 18 swans flew the first two stops behind the ultralight at which time two non-lethal bird-aircraft strikes occurred. This prompted the stage-by-stage method in which swans were transported by truck between stops of about 65 km to their winter destination, 530 km to the south (Fig. 1). This method proved insufficient to initiate a return to New York in spring, thus the surviving 13 swans were transported by truck back to a suitable summering area close to their previous training ground. After six mortalities, four from illegal shooting, one from aspergillosis, one power line casualty, and one disappearance, five of the six remaining swans were captured in January after a severe freeze and transported to their former (1998–1999) wintering area in Maryland.

The only swan (male, marked R18) not captured was confirmed by its radio-neckband to be still in the New York study area on 5 January, but not on 6 January when the rest of the flock was captured. However, on 22 January, it was relocated near Altoona, Pennsylvania, approximately 160 km west of the previous year’s stage-by-stage route (Fig. 1). It had flown 340 km south, two-thirds of the total migration distance between New York and Maryland. It remained near Altoona for the winter. On 8 March, R18 was relocated near Rochester, New York having flown north to within 50 km of its previous training area (Fig. 1). Soon after, in accordance with our federal and state permits, R18 was captured and returned to Airlie. The remaining swans that wintered in Maryland did not ini-

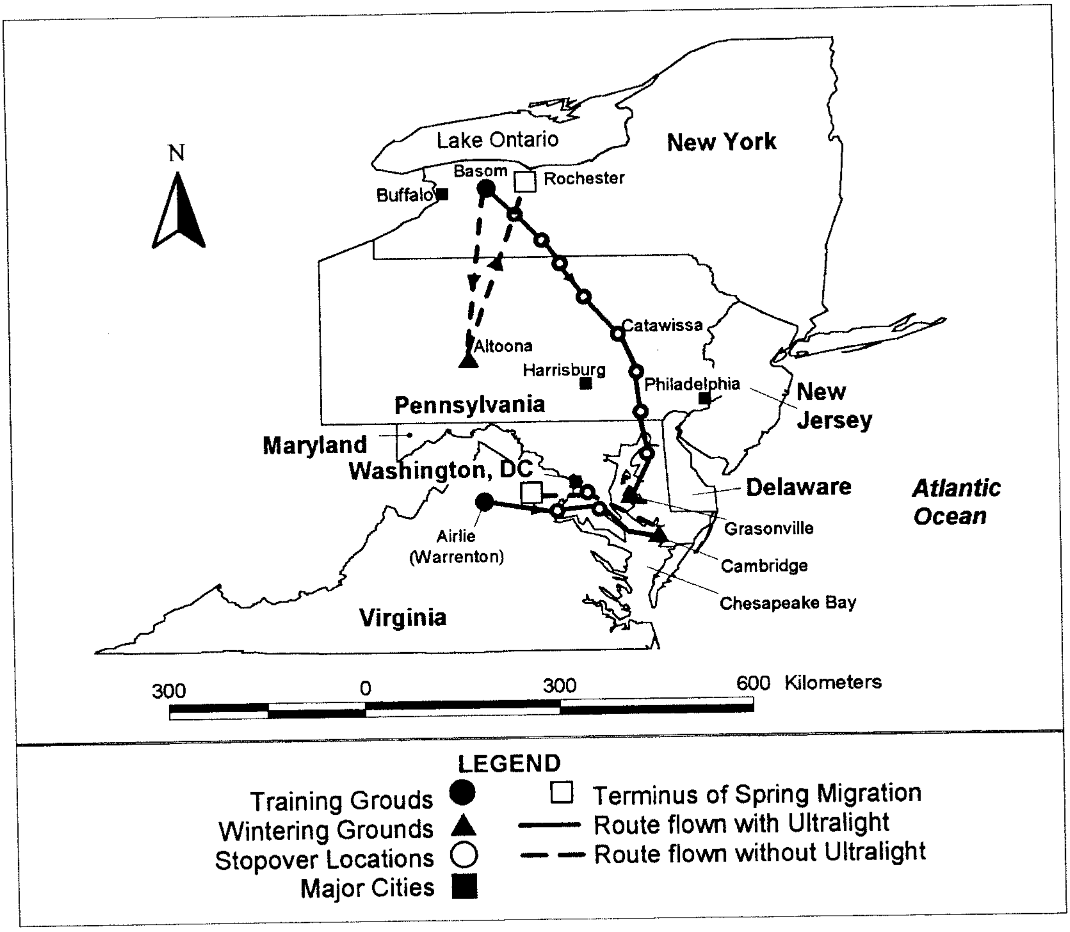

Figure 1. Routes taken by Trumpeter Swans during and after ultralight-led, stage-by-stage migrations during 1997, 1998, and 2000.

tiate a return migration in the spring and were also returned to Airlie.

Also in 1998, Bezner Kerr (2001) successfully led four Trumpeter Swans behind two ultralights over a pre-selected route of 1,120 km from Sudbury, Ontario to the Muscatatuck National Wildlife Refuge in Seymour, Indiana (Table 1). At least two of these returned close to Sudbury the following spring, identified by reading their metal bands, but none returned to Indiana (Bezner Kerr 2001).

In our 2000 experiment, 14 swans were again trained in Basom, New York and migration to Maryland began on 29 December. Nine swans that were not following the aircraft well were either left in New York (N = 6) or returned there (N = 3) after beginning the first leg, and one swan was killed after colliding with the ultralight. The remaining four completed the 64 km flight to the first stop. Because of bad weather, all swans were transported by truck 225 km across the Pennsylvania mountains to Catawissa, Pennsylvania. On 12 January, the five best fliers were led by ultralight over the last two legs to their wintering site in Maryland, covering 115 km nonstop. The remaining eight swans that did not follow the ultralight were transported by truck to Maryland. The birds, confirmed healthy (Olsen 2002), remained in the general wintering area but did not fly north in the spring of 2001. Thus, they were transported by truck back to their previous summer area in New York. At the time of writing (January 2002), in light of record warm temperatures and the persistence of open water and food, the swans had not attempted an autumn flight back to Maryland.

DISCUSSION

From our experiments with Canada Geese, it is clear that geese transported south in closed vehicles do not return to their site of training. However, if geese follow an ultralight aircraft along the entire route, the majority will return the following spring to near their place of training and first flight south (Lishman *et al.* 1997).

Studies of Sandhill Cranes (*Grus canandensis*) also show that the majority returned if they followed an ultralight on their original migration (Lishman *et al.* 1997; Ellis *et al.* 2001). For example, in 1997, six of seven (86%) cranes that followed ultralights from Ontario to Airlie, and that survived the winter, returned to within 32 km of their first flight south. None of the six that were transported by truck over the same route returned (Lishman *et al.* 1997; Ellis *et al.* 2001). Similarly, in 2000, nine of ten (90%) cranes that followed an ultralight over a 2,000 km route from Wisconsin to Florida, and that survived the winter, returned to their training area in the autumn (Ellis *et al.* 2001).

Trumpeter Swans, because of their weight and need for an uplifting wind, appear more reluctant to fly than geese or cranes, especially in the calm conditions required for ultralight flying. The 1997 experiment and Bezner Kerr's 1998 experiment (Bezner Kerr 2001), the only experiments that have led Trumpeter Swans over the entire route by ultralight, have confirmed that swans can learn a migratory route from the air. At least three of seven swans led to wintering areas in these experiments returned to their site of training. There seems also to be some promise that the stage-by-stage method used in the first 1998 experiment could work, as illustrated by swan R18.

To date, no swans and only two geese have been confirmed to have flown north in two successive springs and south again twice on their own, thus establishing a potential migration route. The small number of successful geese likely reflects both their tameness and hunting mortality. It is likely that mild winter weather contributed to the failure of Trumpeter Swans in the 1997 and 2000 experiments to return to their wintering site since Trumpeter Swans are reluctant to move when there is adequate unfrozen food (Gillette 1997).

Several problems remain to be overcome in teaching Trumpeter Swans migratory routes. Tameness of birds and later aggression toward people after release into the wild may be overcome by use of uniforms by handlers, especially if uniformed handlers exhibit dominance over birds similar to that exhibited by a natural parent, while non-uniformed persons haze the birds to illicit a fear response. Mortality due to illegal shooting, lead poisoning and power-line strikes may be reduced by increased public education and exposing birds to power-lines during early stages of training. The ultralight, at present the only way to show a route from the air, has severe limitations because it can safely fly with the birds only in calm conditions. Moreover, ultralights are not certified to fly at night. Although Ellis (2001) has had variable results in teaching cranes to migrate behind a truck, we believe that leading the birds from the air is more promising. There are two possibilities other than ultralights. First, a remote-controlled model aircraft could be used, but is unlikely to be successful because of its fragility and potential dominance interactions between birds and aircraft. Second, swans could be transported in an un-manned, self-propelled airship (similar to a blimp or durgible) that can fly safely day or night, in winds up to 50 km·hr^{-1} (Darlington, pers. comm.), and thus can cover the entire pre-selected migration route non-stop, more closely replicating a natural swan migration. The question is now whether birds learn best by expending effort to learn a route, for example by following an ultralight, or if they can be flown over a route passively in specially designed cages from which they can see both land and sky. We encourage more research into these techniques and believe that motorized-induced migration will prove to be a useful technique in Trumpeter Swan restoration throughout North America.

Since 1990, our experiments with geese, swans and cranes have focused on developing and improving techniques to restore migratory populations, especially of Trumpeter Swans. These techniques could be applied anywhere and are now being used for the endangered Whooping Crane (*Grus americana*) (Ellis *et al.* 2001). With assistance from the Trumpeter Swan Society, all flyways (Pacific, Mississippi and Central), except the Atlantic, have approved management plans for restoration of the Trumpeter Swan in North America. The delay in passing a management plan in the Atlantic is the result of at least two factors (Luszcz 2000; Jordan *et al.* 2000): first, the likelihood that Trumpeter Swans will be shot during the legal Tundra Swan sport hunt (Serie and Bartonek 1991; Sladen 1991; U.S. Fish and Wildlife Service 2001; Serie *et al.* 2002); and second, the desire to establish migratory swans to the Atlantic Flyway. Although the Atlantic Flyway Council has endorsed our experiments at restoring pre-selected migration routes by the ultralight technique, federal and state permits do not allow our experimental swans to be released into the wild until the management plan has been approved.

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Use of Winter Translocations to Expand Distribution of Trumpeter Swans in the Western United States

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Abstract.—During 1990–1996, Trumpeter Swans (*Cygnus buccinator*) were translocated from high-risk wintering sites in the Greater Yellowstone Region of Idaho, Wyoming, and Montana to potential new wintering areas in Idaho, Wyoming, Oregon, and Utah in an attempt to broaden winter distribution and reduce the vulnerability of the Western Canada and Greater Yellowstone breeding populations, which winter primarily in Greater Yellowstone. Survival and movements of 1,127 neck-banded swans translocated in 1990–1995 were monitored to determine their use of new wintering areas in years after translocation. Survival estimates were hindered by uneven resighting effort and lack of data on neck-band loss, however, at least 683 swans, including 71% of adults and 50% of cygnets, survived at least one year after translocation. Of these 683 swans, 62% subsequently wintered away from the monitored Greater Yellowstone winter habitats. By 1997, persistent use by >50 wintering swans existed at only two of eight release sites. We conclude that Trumpeter Swans would establish greater use of new wintering sites if winter translocations, primarily of juveniles, were made to sites (1) that have adequate ice-free food and low human disturbance, (2) that are situated directly south of currently occupied winter habitat, and (3) at which obvious mortality factors, such as shooting and power lines, are minimized.

Key words.—*Cygnus buccinator*, Greater Yellowstone Region, translocations, Trumpeter Swans, winter range expansion.

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Migrations of Trumpeter Swans (*Cygnus buccinator*) to southerly and relatively ice-free wintering areas were greatly reduced during the 18th and 19th centuries as the species was eliminated from most of North America. During the 20th Century, remnant breeding populations in western Canada and the Greater Yellowstone Region of Idaho, Wyoming, and Montana increased and became almost entirely dependent upon marginal winter habitat in Greater Yellowstone, where both breeding populations winter sympatrically. Due to their greatly diminished winter distributions, both populations are vulnerable to high mortality during severe winters when extensive ice cover reduces availability of aquatic vegetation (Gale *et al.* 1987; Pacific Flyway 1992, 1998; Shea 2000). In 1989, more than 100 Trumpeter Swans died in eastern Idaho when feeding areas froze and hundreds more were saved by emergency release of reservoir waters to thaw feeding sites on the Henry's Fork of the Snake River. Risks to the wintering birds heightened further in 1990 when aquatic vegetation at Harriman State Park, Idaho, the primary Henry's Fork wintering site, underwent massive decline (Vinson *et al.* 1992; Shea and Drewien 1999).

In 1990, federal and state wildlife agencies increased efforts to reduce the vulnerability of Trumpeter Swans wintering in Greater Yellowstone by expanding their winter distribution. The ensuing translocation effort described here was not designed as a research project. It was an emergency action to disperse large numbers of wintering Trumpeter Swans from high-risk sites and encourage use of more suitable wintering areas in future years (Pacific Flyway 1992, 1998; Shea and Drewien 1999). This paper describes the propensity of winter-translocated Trumpeter Swans to use new wintering sites in subsequent years.

METHODS AND STUDY AREA

During 1990–1995, Trumpeter Swans were captured in November to early January at high-risk wintering sites at Harriman State Park, Idaho, and Red Rock Lakes National Wildlife Refuge, Montana, 30–50 km west of Yellowstone National Park. Swans were placed individually in wooden boxes and moved by truck to potential winter-

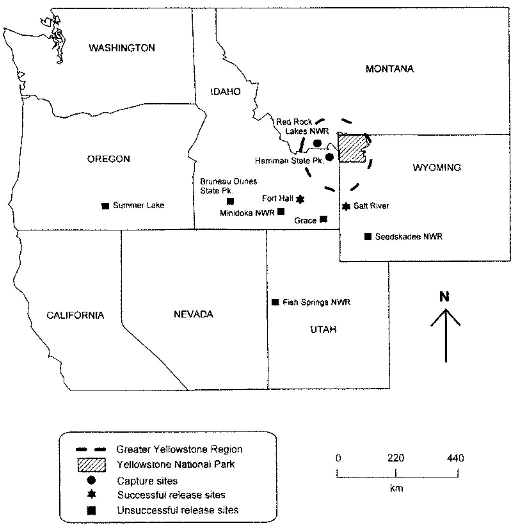

Figure 1. Map of the western United States, showing Greater Yellowstone Region, capture sites, and release sites for Trumpeter Swans translocated in winters 1990–1995. Abbreviations: National Wildlife Refuge (NWR) and Park (Pk).

ing sites in four states (Fig. 1). Most swans were captured at Harriman State Park by night-lighting during moonless nights in November and December (Drewien *et al.* 1999). Swans were weighed, measured, sexed, tarsal-banded, and marked with green neck bands with unique alphanumeric codes (white). Most were also conspicuously marked with yellow (picric acid) or red (rhodamine B) dye on a wing, neck, or tail, depending upon the release site (Drewien and Bouffard 1994). In 1993–1995, some swans released in Oregon were wing-clipped (and therefore flightless until the following summer molt) to increase release site fidelity. Survival and movements of the translocated swans were monitored from November 1990 to May 1997 in the western United States and Canada. Monitoring focused primarily within 150 km of capture sites, due to manpower limitations and logistical constraints. At more distant wintering locations, release sites, migration stopovers, and summer habitats, monitoring intensity varied greatly, was often opportunistic, and depended primarily upon reports from volunteer observers and agency personnel stationed in those areas. Adequate data to determine neck-band loss rates were not obtained. To assess use of new wintering areas, we identified neck-banded swans that survived at least one year after translocation and categorized the predominant wintering area used by each until its death, disappearance, or termination of the study in May 1997. We analyzed differences in performance of various groups using 2 × 2 contingency tables.

RESULTS

During 1990–1995, we captured and neck-banded 1,066 Trumpeter Swans for translocation to eight potential wintering sites in

Table 1. Characteristics of release sites, numbers of Trumpeters Swans translocated in winters 1990–1995, and subsequent peak numbers of wintering swans as of 1997.

Release site	No. released	Distance from capture site (km)	Peak no. ≥2 yrs. after last release	Comments
Bruneau Dunes, Idaho	229	350	23	Heavy boat traffic and waterfowl hunting on river, little secure foraging area, 6 found shot; far west of current migration route
Fort Hall, Idaho	185	160	63	Heavy waterfowl hunting and large security areas with excellent food; south of occupied habitat
Grace, Idaho	7	200	0	Small spring fed emergency site used only once during severe blizzard
Minidoka NWR[a], Idaho	16	210	6	Extensive ice by December caused termination of releases; boats and hunting on river
Summer Lake, Oregon	557	725	39	Heavy waterfowl hunting and large security areas; far west of current migration route; primarily resident swans remaining[b]
Fish Springs, Utah	49	500	0	Extensive ice in severe weather; distant and isolated desert wetland; *Histomonas* infection
Salt River, Wyoming	30	150	79	Moderate human activity and hunting; scattered secure areas with good food; directly south of occupied habitat
Seedskadee NWR[a], Wyoming	54	270	20	Moderate waterfowl hunting, shooting incident disrupted first release; east of current migration route

[a] National Wildlife Refuge (NWR).

[b] 52 potentially nonmigratory Trumpeter Swans from Red Rock Lakes National Wildlife Refuge, Montana, were also released at Summer Lake in summer 1992.

Oregon (557), Idaho (376), Wyoming (84), and Utah (49) (Table 1); 61 additional Trumpeter Swans were also captured and neck-banded at Red Rock Lakes National Wildlife Refuge and translocated to southern Idaho in 1991 by the U.S. Fish and Wildlife Service.

Of the 1,127 neck-banded swans (590 adults, 537 hatch-year birds, hereafter juveniles) translocated in 1990–1995, 12% (132) were known to have died and 28% (312) could not be found by the end of the first year after release. The latter category included swans that disappeared due to undocumented mortality, neck-band loss, and dispersal outside of monitored areas. Combined, these categories included 29% (173) of adults and 50% (271) of juveniles. If all swans that disappeared during the first year are presumed to have died, the minimum survival estimate for translocated swans one year after release was 0.71 for adults (including an unknown number of second-year birds) and 0.50 for juveniles, and was significantly higher for adults than for juveniles ($\chi^2_1 = 52.56, P < 0.001$).

Of the 683 individuals (61%) that were verified to have survived at least one year after release, 32% were confirmed to use wintering sites outside Greater Yellowstone until they eventually died, disappeared, or the study ended in May 1997, and 30% were identified during spring or fall migration but could not be found during winter; 38% were confirmed to winter in Greater Yellowstone in subsequent years (Table 2). Surviving juveniles (N = 266) were significantly more likely ($\chi^2_1 = 49.01, P < 0.001$) than surviving adults (N = 417) to use new wintering areas in subsequent years. The surviving wing-clipped swans were also significantly more likely to use new wintering areas in subsequent years than were the surviving unclipped swans (76%, N = 88 vs. 41%, N = 595; $\chi^2_1 = 25.75, P < 0.001$).

Documented mortality factors for 116 winter translocated swans were parasite related (32% in a single incident attributed to *Histomonas* sp.), power line and fence collisions (24%), shooting (23%), predation (10%), lead poisoning (5%), transport and neck-band injury (3%), and disease (3%). Most predation occurred among wing-clipped swans that were stranded during severe ice conditions at the Oregon release site.

DISCUSSION

Past studies of marked Canadian Trumpeter Swans that wintered primarily in the Greater Yellowstone Region (Turner and Mackay 1982) estimated that juvenile survival from fledging to June was 0.43, while subadult (second year) and adult survival from June to June was 0.71 and 0.82, respectively. In a study of local (nonmigratory) Trumpeter Swans in Wyoming, Lockman *et al.* (1987) estimated that juvenile survival from fledging to June was 0.60, while subadult (second year) and adult survival from June to June was 0.66 and 0.93, respectively.

During the current study, the minimum first year survival of 0.71 for combined adults and second-year birds was lower than previously estimated for Canadian and Wyoming adults, and comparable to previous survival estimates for second-year birds. Although

Table 2. Subsequent wintering areas of neck-banded adult (N = 417) and juvenile (N = 266) Trumpeter Swans known to have survived at least one year after translocation to potential new wintering areas.

	Age when translocated					
	Adult		Juvenile		All ages	
Subsequent wintering areas	Percentage	(N)	Percentage	(N)	Percentage	(N)
TOTAL confirmed at new wintering areas	23.7	(99)	45.5	(121)	32.1	(220)
Release site vicinity	16.0	(67)	25.6	(68)	19.7	(135)
Elsewhere outside Greater Yellowstone	7.7	(32)	19.9	(53)	12.4	(85)
Undetermined wintering area	28.8	(120)	31.2	(83)	29.7	(203)
Greater Yellowstone wintering area	47.5	(198)	23.3	(62)	38.1	(260)

previous studies estimated juvenile survival for different and shorter periods, the minimum survival of translocated juveniles one year after release (0.50) was similar to that estimated in previous studies of juveniles that had not been translocated.

Although 62% of the swans that were confirmed to have survived at least one year after release subsequently wintered away from the monitored Greater Yellowstone wintering sites until they died, disappeared, or the study ended, by 1997 recurrent use by over 50 swans had been established at only two release sites. In addition to winter-translocated individuals, swans subsequently using these new wintering areas also included their mates and cygnets, as well as other Trumpeter Swans that were attracted to these sites. Both successful release sites (Fort Hall, Idaho and Salt River, Wyoming) were within 100 km south of previously occupied habitat and contained substantial areas with adequate food and minimal human disturbance. We conclude that release site inadequacies were primarily responsible for the failure of winter translocations to establish substantial and persistent use at other sites. The main inadequacies were excessive distance from likely southern migration routes, human disturbance, and inadequate ice-free foraging areas. Release sites were deliberately selected to divert Trumpeter Swans away from Tundra Swan (*C. columbianus columbianus*) hunting areas in Utah and Nevada, where they might be killed or might complicate hunt administration (Aldrich 1997; Shea and Drewien 1999). This decision forced the majority (75%) of swans to be released far to the west or east of the most likely southward migration route, while key potential habitats directly south, including Bear River Migratory Bird Refuge, Utah, were unavailable for use as release sites due to Tundra Swan hunting.

At several release sites, managers were also unwilling or unable to modify existing human activities, particularly waterfowl hunting, to provide adequate security for translocated Trumpeter Swans. The lack of undisturbed, ice-free feeding habitat contributed to rapid scattering and mortality of newly translocated swans by powerboat traffic, illegal shooting, hunting, and other human activities, and to the shooting and dispersal of Trumpeter Swans that returned in subsequent winters. We conclude that Trumpeter Swans would demonstrate stronger and more persistent use of new habitat if winter translocations, primarily of juveniles, were made to sites that (1) have adequate ice-free food and low human disturbance, (2) are situated directly south of currently occupied winter habitat, and (3) if obvious mortality factors, such as shooting and power lines, were minimized.

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Population Trends and Habitat Use of Tundra Swans Staging at Long Point, Lake Erie

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Abstract.—Long Point, Lake Erie, is an important spring and autumn staging area for Eastern Population Tundra Swans (*Cygnus columbianus columbianus*). Habitat use and trend in numbers of Tundra Swans at Long Point were assessed using data from twelve Tundra Swans fitted with satellite transmitters and tracked locally, aerial surveys of swans on water (1971–1999), and roadside surveys of swans in fields (1998–2000). Mean peak autumn aquatic counts at Long Point increased from 442 Tundra Swans in the 1970s to 7,177 in the 1990s. The proportion of the Eastern Population of Tundra Swans using Long Point during peak one-day autumn counts increased from <1% in the 1970s to nearly 8% in the 1990s. In contrast, there was no change in peak spring aquatic counts. Tundra Swans were located in agricultural fields more often in spring (74% of diurnal satellite locations) than in autumn (9%). During spring, most (65%) swans using terrestrial habitats were observed in corn (*Zea mays*) fields, whereas during autumn, most (67%) were in winter wheat (*Triticum duriem*) fields. Seasonal differences in use of fields appeared to influence wetland habitat use; during spring, when agricultural fields were used extensively, Tundra Swans were located in those aquatic habitats that were closest to fields. However, during autumn, when aquatic plants were their primary forage, swans tended to use aquatic habitats closer to the tip of Long Point. Given the potential for Tundra Swans to influence the structure of waterfowl communities and aquatic habitats, and the overall lack of information about staging Tundra Swans, further research into the ecological importance and use of spring and autumn stopover sites is warranted.

Key words.—*Cygnus columbianus columbianus*, Great Lakes, habitat use, Lake Erie, Long Point, migration, population, staging, Tundra Swan, waterfowl.

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Eastern Population Tundra Swans (*Cygnus columbianus columbianus*) make extensive annual migrations between Atlantic coast wintering areas and arctic breeding areas, which extend from Baffin Island to the western edge of northern Alaska (Sladen 1973). However, Tundra Swans lose weight during winter and depart Atlantic coast wintering areas in spring at their lowest annual body mass (Bortner 1985). Further, due to the temporal and nutritional constraints of breeding at high latitudes, Tundra Swans are likely to arrive on their arctic breeding areas with most of the lipid and protein reserves necessary to begin breeding (Alisauskas and Ankney 1992). Consequently, Tundra Swans are replenishing and acquiring nutrient reserves when they are incurring substantial energetic costs associated with spring migration. During autumn migration, juveniles probably continue to grow, and adults are likely to be replenishing reserves used during reproduction and wing molt. Events and conditions at migratory stopover sites, therefore, are important for Tundra Swan reproductive success, growth and survival.

After being harvested commercially and non-commercially throughout the 1800s and early 1900s, Tundra Swans were given total protection under the Migratory Bird Treaty Act of 1916. Consequently, North American Tundra Swan populations rebounded; the Eastern Population has surpassed 100,000 birds (Serie *et al.* 2002) and a limited sport harvest was initiated in 1983 (Serie and Bartonek 1991). The steady increase in North America's Tundra Swan populations has also been attributed to their declining use of traditional aquatic foods and increased reliance on readily available, highly nutritious agricultural grains on wintering and staging areas (Munro 1981).

Despite the perceived importance of migratory stopover areas to Tundra Swans, and the substantial increase in the Eastern Population over the last half century, little is known about the habitat use or population status of this species at key spring and autumn staging areas (but see Earnst 1994; Thorson *et al.* 2002). Therefore, the objectives of this paper are to (1) document long-term trends in Tundra Swan numbers at Long Point, Ontario, (2) compare macrohabitat (aquatic versus terrestrial) use during spring and autumn migration, (3) describe seasonal differences in use of agricultural fields and (4) provide baseline information for subsequent studies of Tundra Swan staging ecology at Long Point and elsewhere.

STUDY AREA

Long Point is a 35-km sandspit extending into the eastern basin of Lake Erie (80°30'E, 42°35'N to 80°03'E, 42°33'N; Fig. 1). This spit partially encompasses and protects a 280,000-ha lacustrine embayment (Inner Bay) and 24,000 ha of palustrine wetlands. The Inner Bay is shallow (mean depth = 2 m), and over 90% of the bottom is covered by submerged aquatic vegetation (Wilcox 1994; Knapton and Petrie 1999).

Much of the area surrounding Long Point is a sand plain that is farmed intensively for tobacco which provides limited foraging opportunities for waterfowl. However, a 7,600-ha clay plain at the base of Long Point is farmed extensively for corn (*Zea mays*), winter wheat (*Triticum duriem*) and soybeans (*Glycine max*), which provide foraging opportunities for field-feeding ducks, geese and swans.

METHODS

Aerial Surveys (1971-1999)

Waterfowl were surveyed on Long Point's wetlands in the spring and autumn by the Canadian Wildlife Service during 1971, 1975, 1979, 1984, 1986 and 1988, and by the Long Point Waterfowl and Wetlands Research Fund from 1991 to 1999 (Fig. 1). All eight of Long Point's wetland complexes were surveyed extensively by two observers in a fixed-wing aircraft at an altitude of 100 m. Generally five or six survey flights were flown during each spring and autumn in each year. Observers identified and estimated the number of each waterfowl species along each transect. Seasonal waterfowl use was calculated by averaging the number of waterfowl counted during two consecutive surveys and multiplying the mean by the number of days between the two survey days (Dennis *et al.* 1984). Estimates were calculated for spring (1 March–15 May) and autumn (1 September–15 December), and these estimates were then summed to generate total use-days for each species.

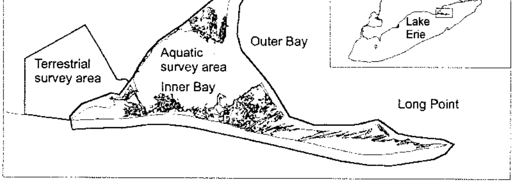

Figure 1. Geographic location of Long Point Bay, Lake Erie, and area covered by aerial aquatic (1971–1999) and ground-based terrestrial (1998–2000) waterfowl surveys.

To assess the total biomass-days of Tundra Swans (spring and autumn combined), relative to other waterfowl at Long Point, the average mass of each waterfowl species ([male + female]/2; from Bellrose 1980) was multiplied by the number of use-days for that species. Four one-way ANOVAs were used to determine if there were differences in total biomass-days (combined spring and autumn) between Tundra Swans and dabbling ducks (all spp. combined), diving ducks (all spp. combined), Canada Geese (*Branta canadensis*), or Mute Swans (*Cygnus olor*) for the period 1991–1999. All analyses were performed using SYSTAT (Wilkinson 1988).

To determine long-term trends in Tundra Swan use of Long Point, linear regression was performed on peak spring and peak autumn counts and on total Tundra Swan use-days. The percentage of the Eastern Population counted during peak daily counts (for each season) was calculated using data from the annual Midwinter Waterfowl Index (U.S. Fish and Wildlife Service 2000) and analyzed using linear regression. This enabled us to determine if the relative importance of Long Point to staging Eastern Population swans had changed since the 1970s. A Mann-Whitney U-test was used to determine if there were seasonal differences in the proportion of Tundra Swans using each of eight Long Point wetland units, and to determine if there were seasonal differences in number of swans using Long Point's wetlands (all wetland units combined).

Satellite Tracking

Satellite transmitters (Microwave Telemetry, Inc., Columbia, Maryland) were attached by backpack-harness (95 g transmitter) or by neck collar (30 g transmitter) to Tundra Swans captured at Long Point during spring 1998 (N = 4), autumn of 1998 (N = 3) and spring of 1999 (N = 5). Although transmitters were deployed as part of a separate study of migration, in this study we use locations recorded while birds were at Long Point to assess macrohabitat use (aquatic versus terrestrial). Transmitters deployed during 1998 (attached by backpack harness) were programmed to transmit 24 h per day for one month to optimize location information while birds were at Long Point. Transmitters deployed during 1999 (attached by neck collar) had a transmission frequency of 8 h per day during the first month of operation. Bird movements were monitored with the Argos satellite tracking system (Argos 1996). Satellite signals were converted to locations by Argos CLS (Landover, Maryland). Each location was assigned a class which depended on number and quality of messages received. Class 1 (estimated accuracy = 350 to 1,000 m), 2 (150 to 350 m), and 3 (<150 m) locations were included in the analysis of habitat use (Argos 1996). Each bird was considered a separate sampling unit and none of the birds were tracked for more than one season. ArcView and Ontario

Base Maps (1:50,000) were used to assign an aquatic or agricultural habitat type to each location.

Due to the possibility of assigning swan locations to the wrong habitat type, based on error estimates of satellite locations, a 1,000-m buffer zone was established along the aquatic-terrestrial interface and all locations occurring in this buffer were excluded from analysis. A Mann-Whitney U-test was used to determine if there were seasonal differences in the proportion of locations received for each bird in aquatic and agricultural habitats.

Terrestrial Roadside Surveys

Based on preliminary results of local satellite tracking, and known field use by swans at Long Point, a 100 km inland roadside survey route was established throughout the clay plain at the base of Long Point. The standardized survey route was driven by one observer 10-32 times per season during autumn in 1998 and 1999 and spring in 1999 and 2000. Starting points (north versus south) and times (between 08.00–16.00 h) were randomized. Flock size, time, field type and location were recorded for each flock observed during surveys. Seasonal comparisons in the number of birds observed (per survey) in agricultural fields were made using Mann-Whitney U-tests. The percentage of swans located in each crop type (corn, winter wheat, soybeans, plowed fields) is reported, but not analyzed statistically as values were not corrected for availability. Means ± SEs are given throughout.

Field reconnaissance was completed during spring and autumn 1998 to identify the total area of each crop type in the terrestrial survey area. Crops were identified and labeled on 1:10000 aerial photographs (1995), and field boundaries were then digitized into a geographic information system.

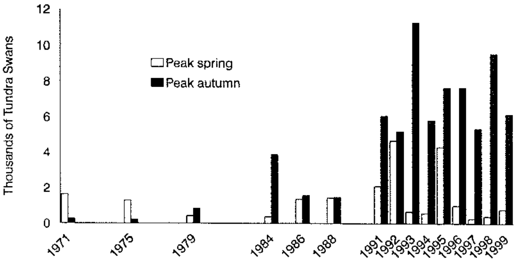

Figure 2. Peak annual spring and autumn counts of Tundra Swans at Long Point, Lake Erie, 1971–1999.

RESULTS

Peak autumn counts increased from an average of 442 Tundra Swans in the 1970s (i.e., 1971, 1975 and 1979) to an average of 7,177 in the 1990s (1991–1999 inclusive) ($b = 322 \pm 64.8$, $r^2_{13} = 0.66$, $P < 0.001$, Fig. 2). In contrast, there was no change in mean peak spring counts during that time ($b = 6.1 \pm 43.5$, $r^2_{13} = 0.002$, n.s., Fig. 2). Peak autumn counts represented 0.7% (442 of 61,167) of the Eastern Population of Tundra Swans in the 1970s, 2.4% (3,866 of 94,000) in the 1980s and 7.9% (7,177 of 92,500) in the 1990s ($b = 0.34 \pm 0.08$, $r^2_{13} = 0.57$, $P < 0.01$, Fig. 3). Annual Tundra Swan use-days (spring and autumn combined) increased from 40,888 use-days in 1975 to 269,448 use-days in 1999 ($b = 13,348 \pm 2,790$, $r^2_{12} = 0.66$, $P < 0.001$), corresponding to an increase in biomass-days from 278,035 kg-days in 1975 to 1,832,246 kg-days in 1999. Although, the estimate of Tundra Swan biomass-days was substantially lower than that for diving ducks ($F_{1,16} = 9.6$, $P < 0.01$), it was similar to the estimate for dabbling ducks ($F_{1,16} = 0.81$, n.s), and was greater than estimates for Canada Geese ($F_{1,16} = 36$, $P < 0.001$) and Mute Swans ($F_{1,16} = 30.6$, $P < 0.001$, Fig. 4).

During autumn, 198 satellite locations (class 1, 2 and 3) were received from three Tundra Swans at Long Point, and 80 locations were received from nine swans in spring (Fig. 5). Tundra Swans were located in agricultural fields less often during autumn ($\bar{x}$ = 5% of locations received, range = 1–11% for individual swans) than during spring ($\bar{x}$ = 38%, range = 25–56%, $U = 12$, $P < 0.05$). When only daytime locations (06.00–18.00 h) were included, 9% of autumn locations and 74% of spring locations were in agricultural habitats. Similarly, more Tundra Swans were counted in agricultural habitats during spring roadside surveys ($\bar{x} = 704 \pm 183$, $N = 24$) than during autumn roadside surveys ($\bar{x} = 78 \pm 23$, $N = 52$, $U = 310.5$, $P < 0.001$, Fig. 6). Conversely, more swans were counted in aquatic habitats during autumn aerial surveys ($\bar{x}$ =

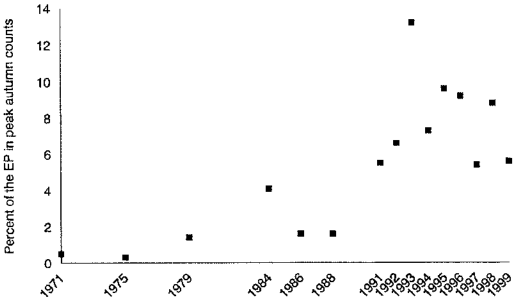

Figure 3. Percentage of Eastern Population (EP) Tundra Swans counted (peak daily count) at Long Point, Lake Erie, during autumn aerial surveys, 1971–1999.

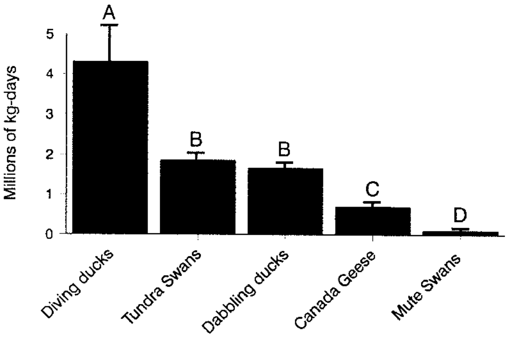

Figure 4. Mean annual biomass-day (± SE) of waterfowl staging at Long Point, Lake Erie, based on waterfowl days (spring and autumn) and average species mass, 1991–1999. Species and species groups not sharing the same letter are statistically different.

6,302 ± 1,094, N = 10) than during spring aerial surveys ($\bar{x}$ = 473 ± 139, N = 6, U = 86, P < 0.001, Fig. 6). With the exception of an 18% reduction in corn availability between spring and autumn in 1998, there were no between-season changes in the relative availability of agricultural crops in the study area (Table 1). During spring, 65% of birds observed in agricultural habitats were in corn, 24% were in winter wheat, 8% were in soybeans, and 2% were in plowed fields. During autumn, 67% were in winter wheat, 7% were in corn, 10% were in soybeans, and 16% were in plowed fields.

During spring, when swans spent considerable time feeding in terrestrial habitats, wetlands close to agricultural fields (Big Creek, U = 1,100, P < 0.001; Crown Marsh, U = 900, P < 0.05; Turkey Point Marsh, U = 911, P = 0.05) had higher proportional use than they did during autumn (Fig. 7). Conversely, those wetland complexes closer to the tip of Long Point (Long Point Company Marsh, U = 350, P < 0.001; Long Point National Wildlife Area, U = 340, P < 0.001; Tip of Long Point, U = 229, P < 0.001) had higher proportional swan use during autumn (Fig. 7).

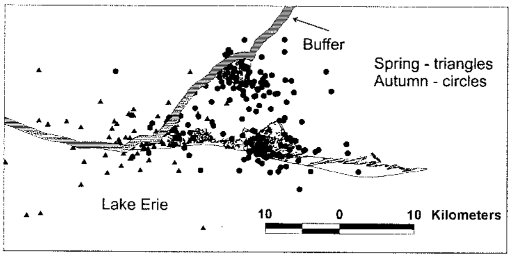

Figure 5. Locations of three Tundra Swans tracked in the autumn and nine in the spring at Long Point, Lake Erie, 1998–2000, using satellite telemetry. Locations within a 1,000-m buffer between aquatic and agricultural habitats are excluded.

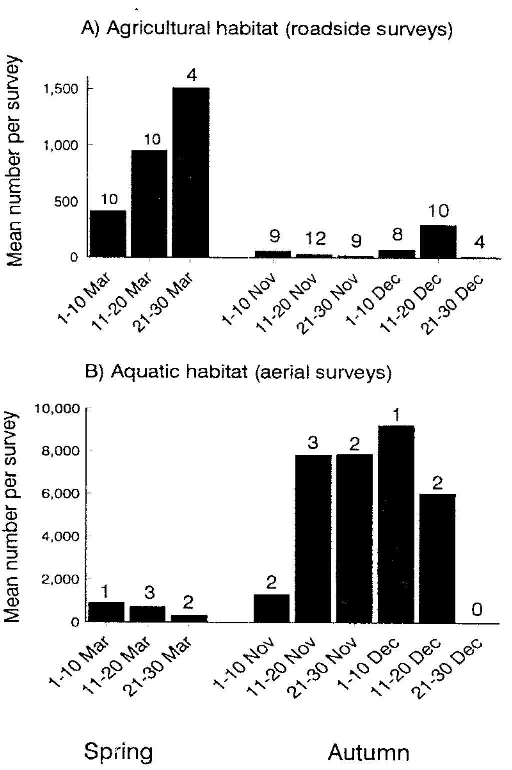

Figure 6. Mean number of Tundra Swans counted at Long Point, Lake Erie, during roadside agricultural (A) and aerial aquatic (B) surveys (1998–1999). Numbers above bars represent total number of surveys for that time period.

DISCUSSION

Population Trends

Long Point Bay is an important spring and autumn staging area for Eastern Population Tundra Swans (Petrie 1998) and autumn use of this area has increased substantially since the 1970s (Fig. 2). Eastern Population Tundra Swan numbers have doubled over the past 40 years (Serie *et al.* 2002) which probably contributed to their increased use of Long Point. However, because

Table 1. Relative availability (ha) of agricultural crops in the Long Point study area during spring and autumn, 1998.

Crop type	Spring	Autumn
Corn	1,720	1,403
Winter wheat	173	173
Soybeans	98	98

mean peak autumn counts increased from 0.7% of the estimated Eastern Population in the 1970s to 7.9% in the 1990s, other factors have probably contributed to the increased use of Long Point in recent years.

Colonization by filter-feeding Zebra Mussels (*Dreissena polymorpha*) and reduced phosphorus inputs to Lake Erie have resulted in increased light penetration, which has changed the aquatic macrophyte communities of Long Point Bay (Knapton and Petrie 1999; Petrie and Knapton 1999). This has resulted in increased abundance and availability of *Vallisneria americana* (Wild Celery), *Elodea canadensis* (Canadian Waterweed), and *Najas* spp. (Naiad), all important foods for waterfowl (Petrie 1998; Knapton and Petrie 1999). This increased availability of aquatic plant foods, most notably *V. americana* (S. S. Badzinski, pers. obs.), has probably increased the carrying capacity of Long Point's wetlands for Tundra Swans.

Temperature data from the National Oceanic and Atmospheric Administration meteorological station at Erie, Pennsylvania (42°05'N, 80°11'W), about 35 km south of Long Point, show that midwinter air temperature (1 November to 1 March) of the lower Great Lakes increased from an average of -1.28°C during 1970–1979 to +1.27°C during 1990–1999. These milder winters in recent years have probably enabled birds to remain at Long Point longer in autumn. Notably, the mean number of Tundra Swans counted during Christmas Bird Counts at Long Point increased from 62 birds during 1970–1979 to 1,819 birds during 1990–1999 (Butcher 1990).

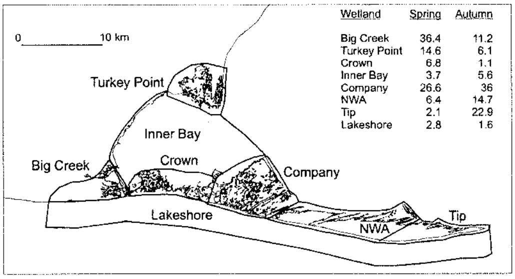

Figure 7. Percentage of Tundra Swans observed in each of eight Long Point, Lake Erie, wetland units during spring and autumn aerial waterfowl surveys conducted during 16 years between 1971 and 2000.

Tundra Swans began consuming cereal grains and the shoots of winter wheat in the 1960s and 1970s (Nagel 1965; Tate and Tate 1966; Munro 1981). This change in diet has quite possibly influenced migratory patterns as well as duration of stay at certain staging areas. There has been a 204% increase in corn production in Norfolk County since 1961 (Government of Canada, unpub. data). This increase may have also influenced duration of stay in the autumn since Tundra Swans appeared to spend more time in fields in late autumn (Fig. 6).

Lack of a long-term trend in peak spring counts may be attributed to more variability in the number of birds staging at Long Point in the spring than in the autumn, quite likely due to annual variation in spring thaw. Also, because Tundra Swans spend considerable time field-feeding in the spring, they are less dependant on large staging wetlands such as Long Point.

Biomass-days and Potential for Interspecific Competition

Tundra Swans were not the most numerous group of spring and autumn staging waterfowl at Long Point, but the estimate of their total biomass-days (i.e., biomass times use-days) was similar to that of all dabbling duck species combined. At Long Point, Tundra Swans and ducks (especially dabbling ducks) coexist on shallow cattail marshes (Petrie 1998; S. S. Badzinski, unpub. data), and rely on aquatic plant parts (Earnst 1994; Limpert and Earnst 1994; Petrie 1998). It has been proposed that swans influence the abundance of dabbling ducks (Oksanen *et al.* 1979), and increased use by Tundra Swans could change the waterfowl community structure at Long Point through interspecific competition (Nudds 1992).

Tundra Swans are large, gregarious birds that feed on submerged aquatic vegetation in shallow wetlands during migration (Earnst 1994; S. S. Badzinski, unpub. data). Because they uproot aquatic vegetation while foraging (Limpert and Earnst 1994), swans may reduce food resources for other waterfowl. Evidence suggests that tuber consumption by migrating swans may result in such dramatic declines in the tuber bank that plant re-growth is inhibited during the next season (Beekman *et al.* 1991; also see Mitchell *et al.* 1998). Further, exploitative competition may explain decreased use of agricultural fields by ducks following grazing by Bewick's Swans (*Cygnus columbianus bewickii*) (Rees 1990). Therefore, although Long Point is an important staging area for migrating Tundra Swans, they may affect the carrying capacity of aquatic and agricultural habitats for staging ducks and geese.

Seasonal Difference in Habitat Use

Whereas Tundra Swans make regular diurnal foraging trips to agricultural fields in spring, they rarely do so in autumn. As Tundra Swans are late autumn and early spring migrants, agricultural grain and winter wheat availability (per unit area) is similar during autumn and spring. Therefore, we suggest that seasonal differences in foraging strategies of swans are determined by an interplay of intrinsic and extrinsic factors unrelated to seasonal changes in availability or quality of agricultural forage. When Tundra Swans arrive at Long Point in autumn, they have large lipid stores (S. A. Petrie, unpub. data) and submerged aquatic vegetation is readily available (S. S. Badzinski, unpub. data). Conversely, when Tundra Swans arrive at Long Point in spring, they have small lipid reserves (S. A. Petrie, unpub. data), and autumn foraging, winter senescence and spring ice-cover would reduce the relative availability of submerged aquatic vegetation at that time. Therefore, we suggest that seasonal differences in field-feeding propensity are due to seasonal differences in submerged aquatic plant availability and may also be influenced by seasonal differences in size of lipid reserves upon arrival at Long Point.

Seasonal differences in propensity to feed in fields appear to influence wetland selection by Tundra Swans at Long Point. During spring, when swans spend considerable time in agricultural fields, they concentrate on wetlands closest to fields, presumably minimizing energetic costs of moving between fields and aquatic roosting sites. Conversely, in autumn, when Tundra Swans are foraging primarily on aquatic vegetation, they often use wetlands up to 30 km from agricultural fields. Use of aquatic habitats far from agricultural fields in autumn may be influenced by patterns of human disturbance (S. S. Badzinski, unpub. data) or by spatial differences in availability of submerged aquatic plants.

Future Research

Although Tundra Swans spend approximately half of their lives on staging areas (Ely *et al.* 1997; Petrie, unpubl. data), little is known about their dietary preferences or changes in body condition during migration. Also, Tundra Swan numbers increased substantially in the latter part of the twentieth century (Serie *et al.* 2002), and because they are large, gregarious birds, are capable of depleting aquatic plant foods at staging areas (Beekman *et al.* 1991; Nolet and Drent 1998; also see Mitchell *et al.* 1998). Therefore, further research into the staging ecology of Tundra Swans, as well as their ecological relationship with other waterfowl species is warranted.

ACKNOWLEDGMENTS

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Tundra Swan Use of the Upper Mississippi River during Autumn Migration

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Abstract.—The Upper Mississippi River is an autumn stopover site for the Eastern Population of Tundra Swans (*Cygnus columbianus columbianus*). A total of 37 aerial surveys and ten video surveys were conducted along 180 km of this river in the autumn of 1998 and 1999 to estimate swan numbers, percentage of young and brood sizes. Numbers peaked during late November and swans were present on the river in substantial numbers (>5,000) for nearly two months. Calculations suggest that 52% of the Eastern Population cygnets and about 25% of all Eastern Population swans used the study area during autumn migration. Video surveys indicated that breeders arrived later than non-breeders in autumn migration and that average brood size was 1.9 in 1999. Based on 43 radio-marked swans tracked every two to three days, the average length of stay was 33.6 days. The turnover rate (swans using the study area/peak number recorded in the study area) was low, 1.29 in 1998 and 0.94 in 1999. These findings suggest that the Upper Mississippi River is an important autumn stopover site for the Eastern Population of Tundra Swans, and may be especially important for cygnets.

Key words.—Aerial surveys, *Cygnus columbianus columbianus*, brood size, length of stay, migratory stopover site, percent young, radiotelemetry, Tundra Swan, Upper Mississippi River, videography.

Waterbirds 25 (Special Publication 1):150–156, 2002

The Eastern Population of Tundra Swans (*Cygnus columbianus columbianus*) increased at an average annual rate of 2.4% from 1955 to 1989 (Serie and Bartonek 1991a), but has experienced no significant growth since 1984 (Serie *et al.* 2002). The Eastern Population now exceeds the North American Waterfowl Management Plan goal of 80,000 birds (Serie and Bartonek 1991b). The Eastern Population nests from east of Point Hope, Alaska to Hudson Bay and winters primarily in North Carolina and Maryland (Limpert *et al.* 1991). In spring, Eastern Population swans stage primarily in the Susquehanna River Valley in Pennsylvania and Lake St. Clair in southern Ontario before moving through Wisconsin, Minnesota, North Dakota, and the southern Canadian prairies. Major autumn migration stopover sites include the Prairie Pothole area of North Dakota, the Upper Mississippi River in Minnesota, and the Long Point region of Lake Erie (Limpert and Earnst 1994; Petrie *et al.* 2002). Few studies have investigated the number of swans, percentage of young, brood sizes or length of stay at autumn stopovers.

About 90 Tundra Swans were first observed on the Upper Mississippi River in 1946 and use of the river in autumn appears to have increased through 1990, although survey data are incomplete. During this period, peak swan numbers reached 8,334 in 1972, 12,000 in 1984 and 8,780 in 1990. About 200,000 swan use-days (i.e., number of swans times days of use) were calculated for the autumns of 1972 and 1984 (E. Nelson, unpublished data). Swan use of the Upper Mississippi River has increased dramatically since 1990. Peak swan counts were as high as 20,000 in 1993 and swan use-days in autumn neared 620,000 in 1997 (Wetzel 1999).

The objectives of our study were to estimate (1) number of swans using the area, (2) brood size and percentage of young by week and for the autumn season, and (3) length of stay and turnover rates at this Upper Mississippi River autumn stopover site.

STUDY AREA

The Upper Mississippi River is one of three segments of the Mississippi River. It lies between the Headwaters segment and the Lower Mississippi River segment. The Mississippi River is one of the world's major river systems in size, habitat diversity and biological productivity, but has been extensively modified for commercial navigation and other human developments (Wiener *et al.* 1998). The Upper Mississippi River is currently managed to maintain a 2.7 m deep channel with locks and dams, which create pools within the river proper (Fremling and Claflin 1984). In general, upper portions of pools are similar to the river before impoundment, and contain a complex of bottomland forest and backwater sloughs, with relatively small ponds, lakes, and streams. Lower portions of pools resemble shallow reservoirs, and consist of large, open expanses of water, with scattered, small wooded islands (Fremling and Claflin 1984; Wiener *et al.* 1998).

The study area was a 180 km reach of the Upper Mississippi River covering 790 km^2 of the river and its floodplain (Fig. 1). It extended from Wabasha, Minnesota (44°22′N, 92°02′W) downstream to Harpers Ferry, Iowa (43°12′N, 91°09′W). This reach included a portion of Pool 4 and all of Pools 5, 5a, 6, 7, 8, and 9. Portions of the Upper Mississippi River National Wildlife and Fish Refuge and Trempealeau National Wildlife Refuge lie within our study area. The American Bird Conservancy recently designated these refuges as Globally Important Bird Areas. A major reason for this designation is the use of the area by waterfowl in autumn, which accounted for about 30 million annual use-days in recent years (Wetzel 1999).

In certain areas of the refuges, posted as closed areas, hunting and trapping of any species was prohibited for most of the autumn stopover period, but was not prohibited in open areas. Boating and fishing was allowed in both open and closed areas. The nine closed areas within the study area covered 14,100 ha (17.9% of the study area), were on average 1,567 ha in size, and at least one closed area occurred in each pool. Swans were not hunted in the three states (Minnesota, Wisconsin and Iowa) in our study area.

METHODS

The U.S. Fish and Wildlife Service and Wisconsin Department of Natural Resources aerial waterfowl surveys were conducted weekly from fixed-wing aircraft at an altitude of 45 m. These surveys estimated the total number of swans and other species of waterfowl present in all river pools and subpools in the study area by date. Subpools were delimited areas within pools that were categorized as either open or closed to hunting and trapping.

The University of Minnesota aerial swan surveys were also flown weekly and followed a protocol similar to the previously mentioned surveys, except that they focused on swans, made an ocular estimate of number of cygnets, and were flown at a higher altitude (150 m). Both aerial surveys provided nearly a complete census of swans on the study area because swans were conspicuous, occurred within a narrow linear area, and observations covered the entire width of the river.

Video surveys were flown at the same time as the University of Minnesota aerial swan surveys and in the same aircraft. A large representative sample of swans from non-overlapping transects was videotaped in each subpool (i.e., areas within pools delimited as either open or closed). Isolated flocks of <30 were generally not sampled by video recordings because they were difficult to target and record on video; however, no flocks were excluded in the regular aerial swan surveys. The definition of flock used for this study was all swans in a subpool at one point in time. This may differ from the definition for a social flock, but was necessary due to the instantaneous nature of our sample. Video recordings were taken through the floor port of a Cessna 172 aircraft at a ground speed of 160 km·h^{-1}. The camcorder was set with a shutter speed of 1/1000th of a second, on auto focus, with 8.4 mm focal length, and with date and time displayed (Sidle and Ziewitz 1990). Analog signals (color S-VHS video) were converted to digital video signals, and then saved as adjacent digital still images. Each image was interpreted to determine the total number of adults and cygnets, and the number of cygnets in each isolated family group (defined as two parents plus associated cygnets). Features in each image were tallied as cygnets when they were both smaller than nearby adults and gray in color (Serie and Bartonek 1991a). This is a conservative count of cygnets because some cygnets were larger than adults and appeared white on the images.

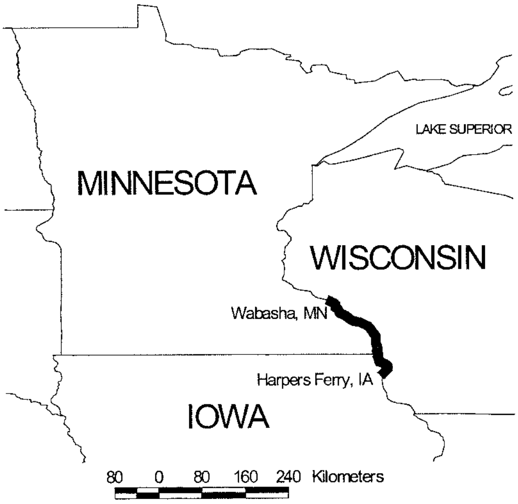

Figure 1. Reach of the Upper Mississippi River and its floodplain in southeastern Minnesota, northeastern Iowa, and southwestern Wisconsin in which Tundra Swans use was investigated in 1998–1999.

In total, 37 aerial surveys, 15 in 1998 and 22 in 1999, were flown to ascertain numbers of swans in Pools 4–9. Flights were conducted from early October through to the end of December; video surveys were conducted in conjunction with the first ten University of Minnesota surveys in 1999 (18 October–16 December).

Length of stay within the study area in autumn was estimated using data from 43 radio-marked adult Tundra Swans (27 males and 16 females). Swans were captured early in the stopover period during 1998 (N = 20) and 1999 (N = 23) using night-lighting techniques (Cummings and Hewitt 1964). Based on observations before or soon after capture, birds were categorized as breeders (N = 26) if accompanied by cygnets or as nonbreeders (N = 17). Transmitters emitted a signal for two field seasons and were attached to neck bands. Radio-marked birds were tracked from the ground or by aircraft every two to three days. Length of stay was defined as the interval in days between capture (or the first radio signal from swans marked in 1998 and returning in 1999) and the last radio signal recorded within the study area. The length of stay estimate was conservative because birds may have arrived several days before capture or before the first radio signal was recorded, and may have remained two to three days past the last radio signal recorded. Transmitter failures that we were not aware of would also lead to conservative estimates. More accurate length of stay estimates were calculated from returning radio-marked swans because these birds were marked prior to arrival.

Percentage of young was calculated by dividing the number of cygnets by the number of all swans and multiplying by 100. Total swan counts from all aerial surveys were used to calculate total swan use-days for each autumn. Use-days were calculated by summing the product of the average count of successive surveys and the number of days between successive surveys, for all survey intervals. For example, a 1 November University of Minnesota survey count of 5,000 and a 5 November U.S. Fish and Wildlife Service and Wisconsin Department of Natural Resources survey count of 10,000 would yield 30,000 swan use-days (7,500 swans times 4 days) for that survey interval. Total swan use-days were divided by the average length of stay to calculate the total number of swans that used the study area each autumn. For the purpose of this study, the turnover rate for each year was defined as the number of swans that used the area divided by the peak number of swans observed.

Two-sample t-tests were used to compare swan use-days, length of stay estimates and percentage of young between years. Percentage of young estimates from video and aerial surveys were compared using paired t-tests. One-way analysis of variance (ANOVA) was used to compare multiple means and, if significant, was followed by pairwise comparisons using the Tukey-Kramer HSD test. Means ± SEs are reported throughout the text.

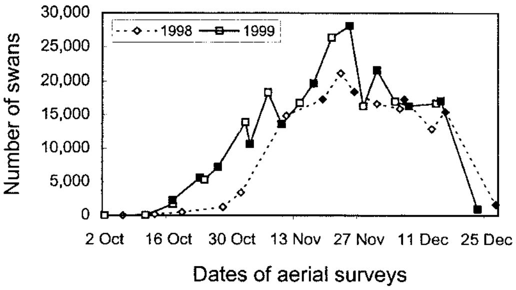

Figure 2. Number of Tundra Swans recorded during aerial surveys on the Upper Mississippi River, 1998–1999. Solid black markers represent University of Minnesota aerial swan surveys and open markers represent U.S. Fish and Wildlife Service and Wisconsin Department of Natural Resources aerial waterfowl surveys.

RESULTS

Swans were recorded during 35 of 37 aerial surveys. In both years, swans arrived starting in mid-October, peaked in late November, and departed by the end of December (Fig. 2). Peak numbers of 21,155 occurred on 24 November 1998 and 28,115 on 26 November 1999. Despite nearly complete ice cover by 21–22 December 1998 and 16–18 December 1999, large numbers of swans were still in the study area for the 28 December 1998 and 24 December 1999 surveys. Four seasonal periods were defined: an initial increase, a main increase, a main decrease, and a final decrease. The percentage of total swans found in open areas varied by seasonal period ($F_{3,31} = 24.8$, $P < 0.0001$, Fig. 3). Proportionately fewer swans used open areas during each of the first three seasonal periods than during the final (5–31 December) seasonal period (Tukey-Kramer, all $P < 0.01$). A total of 788,746 swan use-days were calculated for 1998 and 990,329 swan use-days for 1999. Using pools as the sampling unit, total swan-use days did not differ by year ($t_{12} = 0.42$, n.s.). Swan use-days per pool were divided by the area (km^2) of water in the pool to standardize comparisons between pools. Using survey interval as the sampling unit (N = 34), swan use-days·km^2 varied by pool ($F_{6,231} = 21.4$, $P < 0.0001$), with Pools 4, 7, 8, and 9 receiving significantly more swan use per area than Pools 5, 5a, and 6 (Tukey-Kramer, $P < 0.01$, Fig. 4).

From 1,369 relocations, 42 length of stay estimates were measured. Six of the 20 swans radio-marked in 1998 returned to the study area in 1999. Length of stay estimates did not differ for swans tracked in 1998 (N = 19, $\bar{x}$ = 28.8 ± 3.50 days) and 1999 (N = 23, $\bar{x}$ = 37.5 ± 3.12, $t_{40} = 1.85$, $P = 0.07$), for swans that

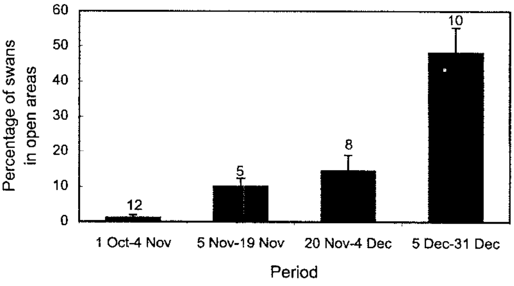

Figure 3. Percentage of Tundra Swans on the Upper Mississippi River using open areas (i.e., open to hunting and trapping) by seasonal period determined from aerial surveys, 1998–1999. Error bars represent SEs. Each aerial survey served as a sampling unit, and number of surveys per period is reported above each column.

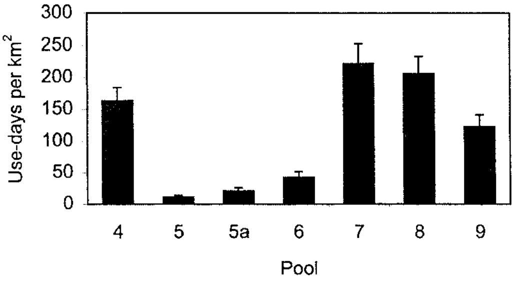

Figure 4. Tundra Swan use-days per km^2 of water in each pool of the Upper Mississippi River, 1998–1999. Error bars represent SEs and survey intervals were used as sampling units (N = 34).

returned in 1999 compared to those that were radio-marked in 1999 (t_{21} = -0.40, n.s.), or for breeders compared to non-breeders (N = 22 and 14, respectively, t_{34} = 0.28, n.s.). We estimated that 27,387 swans used the study area in 1998 (788,746 swan use-days/28.8 days) and that 26,408 swans used the study area in 1999 (990,329 swan use-days/37.5 days) based on use-days and length of stay estimates. The turnover rate (swans using the study area/peak number recorded in the study area) was 1.29 in 1998 and 0.94 in 1999.

A total of 48,888 swans were counted on 1,615 digital still images, and represented a large percentage of swans present on each video survey date (N = 10, $\bar{x}$ = 37.8% ± 4.33%, range 13%–62%). In 1999, 20.1% of swans present were cygnets. Percentage of young increased from 8.6% on 18 October to 22.4% on 18 November and then remained high with little variation through December (Fig. 5). The percentage of young was higher after 15 November for both the aerial surveys (t_9 = 3.33, $P < 0.01$) and the video surveys (t_8 = 2.81, $P < 0.05$), using the individual surveys as the sampling unit. Percentage of young declined with larger flock size categories ($F_{5,89}$ = 4.12, $P < 0.01$, Fig. 6), which has also been documented in other studies (Bart *et al.* 1991; Earnst 1994). There was greater variability in percentage of young in smaller flocks. In the 576 families detected on digital still images, average brood size was 1.9 ± 0.04 cygnets (range 1–5). Average brood size did not differ by survey date ($F_{9,566}$ = 0.82, n.s.) and ranged from 1.8–2.1 cygnets.

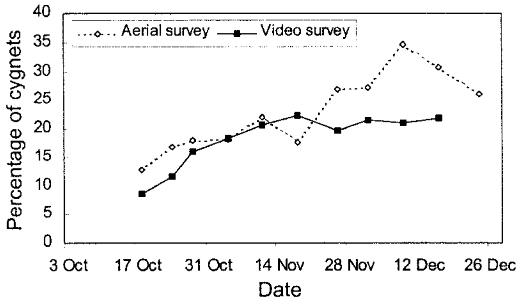

Figure 5. Trends in percentage of cygnets estimated from aerial swan surveys and video surveys for Tundra Swans on the Upper Mississippi River, 1999.

Direct comparison of percentage of young estimates from video surveys and aerial swan surveys was possible because the surveys were conducted on the same flocks at the same time. Overall, percentage of young estimates from aerial swan surveys were significantly larger than those from video surveys ($\bar{x}$ = 31.4% ± 1.3% and 22.2% ± 0.8%, paired t_{94} = 8.16, $P < 0.001$), when the sub-pool-survey was used as the sampling unit and only video surveys based on >10% of swans present were included. When surveys were split into an early and late period (before and after 20 November, respectively), an ANOVA indicated that significant differences existed among the means ($F_{3,16}$ = 12.0, $P < 0.001$). Estimates did not differ between survey types for the earlier period (n.s.), but estimates from aerial swan survey were significantly higher than those from video surveys during the latter period (Tukey-Kramer, $P < 0.05$, Fig. 5).

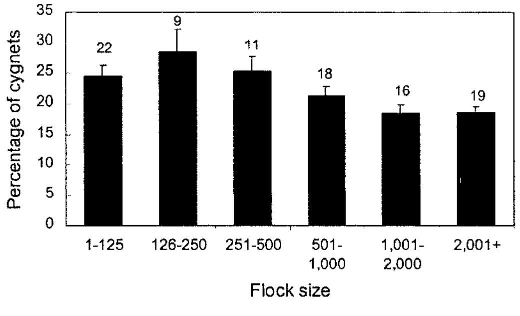

Figure 6. Mean percentage of cygnets from video surveys for Tundra Swan flock size categories on the Upper Mississippi River, 1999. Error bars represent SEs and sample size is reported above each column.

DISCUSSION

Annual Midwinter Waterfowl Surveys estimated the Eastern Population at 109,041 swans in January 1999 and 103,082 swans in January 2000 (Serie *et al.* 2002). The number of swans using the Upper Mississippi River each year was about 27,000 or 25% of the Eastern Population. Many thousand swans use the Prairie Pothole region each autumn and the peak numbers during autumn in the Long Point region of Lake Erie has been up to 12,000 swans (Earnst 1994; Petrie *et al.* 2002). The Upper Mississippi River probably holds more Tundra Swans than any other autumn stopover site used by the Eastern Population.

Swans tended to use open areas proportionately more later in the autumn and this is probably related to human disturbance and the availability of aquatic food resources. Open areas are used extensively for boating, fishing, trapping, and hunting, but little human disturbance occurs in closed areas during autumn. Early in the autumn, swans seemed to prefer undisturbed, closed areas. Later in the autumn, as human activity in open areas declined due to dropping temperatures and freezing of the river, swans appeared to move to unexploited food resources in open areas. This shift in swan use of open areas was probably not related to river freeze-up because no major difference in the timing of freeze-up between open and closed areas was observed.

There was a slight bimodality in autumn migration, with non-breeders arriving earlier than breeders, reflected by the low initial percentage of young estimates. Family groups are known to make many stops to rest and replenish body reserves during autumn migration (Ely *et al.* 1997) and are the last to leave the breeding grounds. This may explain why family groups arrived later to the Upper Mississippi River. The bimodality observed in this study was similar to that at an autumn stopover site in the Netherlands (Beekman *et al.* 1991), but different from that at a wintering site in Britain (Rees and Bacon 1996). The bimodality observed here was reversed and less pronounced than that observed in Whooper Swans (*Cygnus cygnus*) during spring migration, when families arrive earlier than non-breeders (Haapanen and Hautala 1991).

The Upper Mississippi River stopover site may be especially important to cygnets. Our estimate of 20.1% cygnets is much higher than the 10.4% cygnets reported on the wintering grounds for the 1999/2000 winter (Serie *et al.* 2002). An estimated 52% of cygnets and only 24% of adults in the Eastern Population used the study area in 1999. In both years, radio-marked birds stayed within the study area for a month or more. In the Western Population of Tundra Swans, satellite-marked swans also lingered in southern autumn migration areas, including Alberta, Saskatchewan, and Idaho (Ely *et al.* 1997). Turnover rates in the Upper Mississippi River were low for both years and most swans did not leave until freeze-up.

Swans may be attracted to the Upper Mississippi River because it has large extensive closed areas, abundant aquatic vegetation, and holds a desirable location within the migration corridor. Pools 4-9 have supported an abundance of submersed and emergent vegetation, including Arrowhead (*Sagittaria latifolia* and *S. rigida*), Sago Pondweed (*Potamogeton pectinatus*), and Wild Celery (*Vallisneria americana*) (Sladen 1973; Wiener *et al.* 1998). Arrowhead, thought to be the main food resource of Tundra Swans on the river, occurs in pure dense stands (Limpert 1974) and is an important part of the Upper Mississippi River's ecosystem (Clark and Clay 1985). Large numbers of other waterfowl are also attracted to the Upper Mississippi River. Autumn peak counts for single species have been over 400,000 for Canvasback (*Aythya valisineria*), 150,000 for Mallard (*Anas platyrhynchos*), 125,000 for Lesser Scaup (*Aythya affinis*), and 30,000 for Canada Geese (*Branta canadensis*) in recent years (Wetzel 1999).

Our findings and previous studies suggest that autumn stopover sites are vitally important, energetically, for cygnets. Tundra Swan cygnets are among the slowest of northern waterfowl to grow and they fledge at a smaller proportion of adult mass than geese (Bellrose 1980; Sedinger 1992). Cygnets are thus developmentally less mature than goslings at the beginning of migration and are probably less able to sustain long, uninterrupted flights (Ely *et al.* 1997). It is likely that cygnets require many stopover sites to rest, feed and develop. Cygnet mortality from exhaustion or starvation is known to occur during sustained migration (Bartonek *et al.* 1991). Cygnets may experience as much as a 48% mortality during their first autumn migration (mid-August to mid-December) (Bart *et al.* 1991). Based on brood sizes during 1999 on the breeding grounds (2.3, Ritche *et al.* 2002), our study site (1.9) and the wintering grounds (1.6, Serie *et al.* 2002), appreciable cygnet mortality probably occurs before swans reach the Upper Mississippi River and after they leave. The already high cygnet mortality would likely increase if critical autumn stopover sites were eliminated or their quality diminished.

In conclusion, autumn stopover sites can hold a significant proportion of Tundra Swan populations for an extended period and may be especially important to cygnets. Thus, the ecology of Tundra Swans at autumn stopover sites may warrant more conservation and research effort.

ACKNOWLEDGMENTS

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Sex Differences in the Movements and Mortality of Mute Swans

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Abstract.—Mute Swan (*Cygnus olor*) movements were examined in relation to sex. Movement patterns differed between the sexes, with females making longer movements, on average during the study, than males (46.3 km compared to 40.1 km). Females also moved further from their place of banding than males (46.9 km compared to 39.8 km). Although males appeared to undertake more frequent movements, it is likely that the frequency of movements by females was under-estimated since females moved further and a higher percentage of females than males went missing at all ages. Collisions with fixed obstacles accounted for at least 30% of all recorded deaths and 57% of mortality where the cause of death was known.

Key Words.—*Cygnus olor*, dispersal, life-expectancy, mortality, movements, Mute Swan.

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The Irish Mute Swan (*Cygnus olor*) population is estimated at around 10,000 birds (Scott and Rose 1996). Studies of marked individuals indicate that Mute Swans in Ireland do not breed until, on average, the age of five (Collins 1991), in contrast to swans in Britain which tend to breed earlier (Birkhead and Perrins 1986; Rees *et al.* 1996). The delay in breeding may be due to a shortage of suitable breeding territories (Collins and Whelan 1990). Later breeding and a shortage of territories may explain why swans move extensively within Ireland, with some also moving to Britain (Collins and Whelan 1994a).

Collision with a fixed obstacle is the most common cause of death (Collins and Whelan 1994b). In view of the vulnerability of swans to collisions, any differences in the extent of movement between the sexes might be expected to result in differing mortality rates. This paper examines movements, causes of death and mortality rates in relation to sex.

METHODS

Between 1983 and 2001, 1,508 Mute Swans were fitted with individually coded plastic leg bands and numbered metal bands in a 1,500 km^2 study area around Dublin, Ireland (53°20'N, 6°14'W). Birds were captured on breeding territories, in flocks and elsewhere within the study area. Cygnets were not captured for banding until they were at least three months old. The mates and offspring of banded swans breeding outside the study area, irrespective of the distance from the study area, were also marked.

Age and sex were determined using the methods described by Baker (1993). The sex of cygnets captured on the natal territories was not determined on banding but the sex of these birds was recorded if caught subsequently as adults.

Banded swans were tracked within the study area by regularly visiting flocks and breeding territories. Swan haunts outside the study area were visited less frequently, but sightings of banded swans were reported by members of the public. Such reports were verified before inclusion in the database. Annual survival rates were calculated from 1 April each year.

Swan deaths were investigated and post mortem examinations carried out where feasible, but the results were often inconclusive. Swans found dead close to overhead cables were considered to be collision victims.

In assessing movement and the distances traveled by individual swans, a single movement was deemed to have occurred between sites at which a swan was recorded on consecutive occasions. It was assumed that swans moved directly between observation points. Movements of less than 5 km (the length of the largest recorded territory) on the same water body were excluded.

Such methods can detect only minimal numbers of movements and minimal distances traveled. Many swans will have moved more frequently and covered greater distances than were recorded. Movements within the study area were more likely to be detected than those to remote locations. However, relative mobility between the sexes should be comparable.

RESULTS

Of the 1,508 swans banded during the study, 687 (46%) were male and 581 (39%) were female. In 240 (16%) cases, the sex was not determined. As of 1 April 2001, 368 deaths of fledged banded swans had been recorded. Of the swans found dead, 188 (51%) were males and 117 (32%) were females. The sex of 63 (17%) dead swans was not known.

On 1 April 2001, 48 males (7.0%) and 21 females (3.6%) were known to be still alive, a significantly greater percentage of males than of females ($\chi^2_1 = 6.3$, $P < 0.05$). However, the percentage of males known to be dead was also significantly higher; 188 males (27.4%) compared to 117 females (20.1%) ($\chi^2_1 = 8.6$, $P < 0.01$). The percentage of swans whose status was unknown on 1 April 2001, classified as "missing", was therefore much higher for females; 451 females (76.2%) compared to 443 males (65.6%) ($\chi^2_1 = 16.5$, $P < 0.01$). The numbers of swans of known age recorded alive, found dead or listed as "missing", from the ages of one to 18 years are given in Table 1. There were no significant differences between the proportions missing in each age category ($\chi^2_9 = 7.5$, n.s. for males; $\chi^2_9 = 11.8$, n.s. for females), indicating that the higher percentage of females missing was consistent for all ages. Moreover, there was no difference between the sexes in the proportion of birds recorded missing before reaching breeding age (i.e., up to and including age 4-5 years, Table 1) and after reaching breeding age (age 5–6 years onwards) ($\chi^2_1 = 0.24$, n.s.).

The cause of death was determined for 195 swans, including those of unknown age; 98 were males, 55 were females and in 42 cases the sex was not known (Table 2). Collision with a fixed obstacle was the principal cause, accounting for at least 30% of all recorded deaths, and 57% of deaths for which the cause was known. Collisions accounted for 31% of male deaths compared to 27% of female deaths. This difference was not statistically significant ($\chi^2_1 = 0.27$, n.s.). Oil pollution accounted for 26 deaths, 16 of them in a single incident.

Male swans were more frequently found dead in circumstances associated with territorial defense, or were killed by vandals, dogs and foxes; 12 of 98 males for which the cause of death was known died in such circumstances, compared to two out of 55 females (Table 2). Since only 16 such deaths (4% of the total) were recorded, however, this difference between the sexes was not significant ($\chi^2_1 = 2.2$, n.s.).

Males appeared to move more frequently than females, with 3,022 moves recorded for 494 males, 6.1 moves per bird (SD ± 6.1), compared to 1,953 for 405 females, 4.8 moves per bird (SD ± 5.0) ($t_{897} = 3.52$, $P < 0.001$).

The total distance traveled by males was at least 74,965 km, compared to 52,682 km for females. The average distance recorded for males was 151.8 km per bird (SD ± 170.60) compared to 129.8 km per bird (SD ± 136.9) ($t_{897} = 2.14$, $P < 0.05$). However, females moved a greater distance between consecutive sightings, on average, than did males ($\bar{x} = 46.3 \pm 42.9$ km and $\bar{x} = 40.1 \pm 28.1$ km respectively, $t_{897} = 2.51$, $P < 0.02$).

Table 1. Survival table for male and female Mute Swans of known age. Age, in years, is taken from 1 April each year. "Missing" denotes swans that had not been recorded on, or after, 1 April. "M" denotes males and "F" denotes females. The figures for the 10–18 age category are the cumulative annual totals for the period. The sample size for the 2–3 age category is higher than for the 1–2 age category due to the inclusion of swans caught for the first time as two year old birds.

	Sample		Survived		Died		Missing	
Age (years)	M	F	M	F	M	F	M	F
1 to 2	206	178	161	124	15	7	30 (15%)	47 (27%)
2 to 3	264	218	194	157	19	17	51 (19%)	44 (20%)
3 to 4	203	169	145	131	13	4	45 (22%)	34 (21%)
4 to 5	145	131	112	95	9	10	24 (17%)	26 (19%)
5 to 6	112	95	80	80	13	4	19 (16%)	11 (12%)
6 to 7	80	80	58	57	8	3	14 (18%)	20 (25%)
7 to 8	58	57	44	43	7	2	7 (13%)	12 (19%)
8 to 9	44	43	35	32	2	0	7 (18%)	11 (24%)
9 to 10	35	32	25	21	4	4	6 (10%)	7 (23%)
10 to 18	78	62	54	41	6	3	18 (23%)	18 (21%)

Table 2. Causes of death for Mute Swans, including deaths of fledged swans of known age, unknown age and of swans where the sex was not known.

	Total	Males	Females
Collision with fixed obstacle	111	58	32
Oil contamination	26	7	13
Struck by road vehicle	7	5	2
Shooting	7	6	1
Lead poisoning	7	2	3
Fights with conspecifics	7	6	1
Gut parasites; Echinuria	6		
Band entangled in artifact	5	3	1
Vandalism	4	3	
Dogs	3	2	
Foxes	2	1	1
Veterinary procedure	2	1	
Warfarin poisoning	2	1	
Other[a]	6	3	1

[a] Other causes of death include one case each of botulism (male), choking on bread (male), pneumonia/pulmonary failure (male), struck by train (female), starvation (sex not known) and aspergillosis (sex not known).

When the maximum distance recorded for each individual from the place of banding was examined, a similar result was obtained; females tended to move further from their banding site ($\bar{x}$ = 46.9 ± 44.0 km) than males ($\bar{x}$ = 39.8 ± 27.9 km respectively, t_{897} = 2.81, $P < 0.005$). When the maximum distance recorded from the banding location was grouped into four distance categories (Table 3), analysis of the numbers of birds recorded at increasing distances from their banding site again found that females tended to move further away than males ($\chi^2_3 = 13.2$, $P < 0.01$).

DISCUSSION

The study investigated whether movement rates differed between the sexes and, if so, whether this resulted in greater mortality rates in the more mobile sex. More male deaths were recorded, but since far more females went missing and the proportion of missing birds (of either sex) which were dead was not known, it was not possible to say whether there was an overall difference between the sexes in their mortality rates.

The greater number of missing females may be due either to (1) most of the missing females having died, with the cause of death making them less likely to be reported than males, or (2) the missing females having moved to locations where they were less likely to be reported, either alive or dead. In support of the first explanation, it can be claimed that male Mute Swans tend to be more aggressive than females (Birkhead and Perrins 1986). Fights between swans, or confrontations with vandals or dogs at the nest, would be more common among males and more males might be expected to die as a result of such conflicts. Deaths due to such activities are likely to be more visible to observers than those resulting from disease or starvation, and so the reporting rate for such deaths could be higher. However, very few deaths from such causes were recorded in this study. Also, if the explanation is correct, we would expect the proportion of birds missing to be higher for females than for males from breeding age (age five) onward, and not in their first few years but there was no difference between the sexes in the numbers missing before and after age

Table 3. Maximum distances from place of banding recorded for male and female Mute Swans, including swans of known and unknown age.

Distance category	Males	Females
5 to 50 km	314 (64%)	231 (57%)
50 to 100 km	160 (32%)	148 (36%)
100 to 150 km	19 (4%)	15 (4%)
Above 150 km	1	11 (3%)

five. Less conspicuous causes of death therefore seem unlikely to account for the higher proportion of missing females.

In favor of the second explanation, females undertook longer journeys than males and tended to move further from their banding locations. Swans in the study area were unlikely to remain unrecorded for long. However, as birds moved away from the area, the probability of their being recorded would have progressively declined. Many would be in places seldom visited in searches for banded birds, often in rural locations with few people to report band sightings. Since females tended to make longer movements, more females would have left the study area. Accordingly, movement by females to locations where they were less likely to be observed is a plausible explanation for the discrepancy between the proportions of missing males and females.

Female waterfowl are more likely than their male counterparts to return to their natal areas to breed (Greenwood 1980; Lessells 1985). Coleman and Minton (1979) found that Mute Swan pairs nest closer to the female's natal territory than to the male's. Collins (1993) found that median distances from natal origins to the location of a first nest, were lower for females than for males. The results here might seem to suggest the opposite. However, the study concerned movements in general, and was not confined to young birds dispersing from natal territories. Also, with swans not breeding until, on average, the age of five, a tendency to move further away does not exclude the possibility that swans return to the natal territories in due course.

Although more movements and greater cumulative distances were recorded for males, the data are subject to bias. Since more females went missing, the numbers of movements and overall distances traveled by them are likely to be under-estimated when compared to males. There is no compelling evidence, therefore, that males move more frequently and travel greater overall distances during their lives than females.

Collins and Whelan (1994a) showed that swans move most in their first two years of life, and progressively less as they grow older. Most of the swans in this study were banded as young birds. The age of a swan can seldom be determined more than two years after hatching and 16% of the swans studied were of unknown age. Many of these would be beyond the age of high mobility. Accordingly, although the actual difference in mobility between the sexes may be greater than the data here suggest, the maximum distances and frequency of movements per bird are well covered by this study, due to the high proportion of young birds included.

The data on causes of death are subject to several forms of bias and must be treated with caution. Cables (the main collision obstacle) tend to be located where there are people to report such deaths. A collision may cause a power failure, drawing attention to the swan. A collision death therefore is more likely to be reported than one from disease or poisoning. Also, the injuries following a collision will tend to make the cause of death evident, whereas, with poisoning or disease, a post mortem examination would be needed. These factors may give an exaggerated impression of the importance of collisions as a cause of death in swans. There was no significant difference between the sexes in the proportion of deaths due to collisions, suggesting that the more frequent movements recorded for males did not result in higher mortality from flying into cables. However, since females were more likely to move to outside the main study area, the frequency of female movements is likely to be under-estimated and the potential for collisions therefore could be similar for the two sexes.

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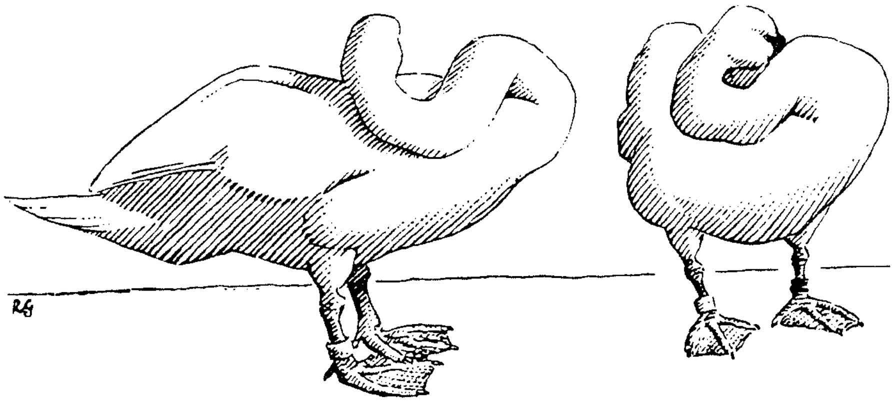

Effect of Tundra Swan Grazing on Winter Wheat in North Carolina

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Abstract.—Tundra Swans (*Cygnus columbianus columbianus*) grazing on winter wheat (*Triticum duriem*) were studied using 61 sets of paired plots (one exclosure, one subject to grazing) in fields near a major wintering area in North Carolina during 1995–1996. Aboveground biomass, number of seed heads, and seed head mass were determined for each plot and used as measures of grain yield; plant height and leaf damage on each plot were used to assess grazing intensity. Tundra Swans reduced aboveground biomass by 12% and seed head mass by 11% in grazed plots compared to exclosure plots. More blades were grazed and plant height was reduced in grazed plots compared to exclosure plots in each month after plot deployment, with the greatest reduction in plant height (28%) occurring in February, and a final reduction of 6% at the time of harvest in June. However, these differences in crop yield and plant height occurred only in plots on sanctuary fields, in which swans can feed without disturbance from farmers or hunters, but not in plots on non-sanctuary fields.

Key Words.—Crop damage, crop yield, *Cygnus columbianus columbianus*, effects of grazing, Tundra Swan, winter wheat.

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Tundra Swans (*Cygnus columbianus columbianus*) of the Eastern Population winter on the eastern coast of North America, from the Chesapeake Bay, Maryland, to North Carolina. Most of the population previously wintered on Chesapeake Bay in Maryland (Scott 1972; Wilmore 1974; Limpert and Earnst 1994). Today, however, more Tundra Swans winter in North Carolina than in any other state.

The change in the winter distribution of Tundra Swans brought corresponding changes in feeding habits. In Chesapeake Bay prior to the 1970s, swans fed primarily on aquatic vegetation and mollusks; grain was not a dietary staple (Stewart and Manning 1958; Stewart 1962; Wilmore 1974). In the 1970s, however, aquatic communities deteriorated in Chesapeake Bay, and with the loss of their natural foods, Tundra Swans began moving to North Carolina where they concurrently started feeding on agricultural crops (Bortner 1985; Limpert and Earnst 1994).

By 1990, about 65,000 Tundra Swans wintered in North Carolina, with Lake Mattamuskeet National Wildlife Refuge alone supporting 45,000 birds, or about 50% of the Eastern Population—a dramatic increase from the 3,000–4,000 swans wintering at the refuge in the 1950s (Yelverton and Quay 1959). During the same period, the acreage of winter wheat (*Triticum duriem*) also increased in North Carolina. The developing seedlings afforded Tundra Swans with easily accessible forage, and claims of crop damage soon followed.

The purpose of this study was to determine the effect of grazing by Tundra Swans foraging in wheat fields near Lake Mattamuskeet National Wildlife Refuge. Other studies on waterfowl, primarily Canada Geese (*Branta canadensis*), indicate that the effect of waterfowl grazing on winter cereals is variable. In some cases, geese damaged crops (Reed *et al.* 1977; Kahl and Samson 1984; Allen *et al.* 1985; Flegler *et al.* 1987; Conover 1988; Patterson *et al.* 1989), but other studies indicated little damage and some benefits, such as removing unwanted vegetation or accelerating nitrogen cycling with droppings (Kear 1965; Kear 1970; Marriott 1973; Newton and Campbell 1973; Cargill and Jefferies 1984). Damage, when it occurred, resulted from one or more activities: trampling, heavy grazing, and pulling up roots (Kear 1965; Conover 1988).

STUDY AREA

This study was conducted during the winter and spring of 1995–1996 in Hyde and Tyrrell Counties, North Carolina, where large number of Tundra Swans wintered at Mattamuskeet and Pocosin Lakes National Wildlife Refuges. Swans roosted on shallow lakes and impoundments at the two refuges and typically left during the day to forage elsewhere. Of some 57,700 ha of farmland in Hyde and Tyrrell counties, 15,800 ha (27%) were in wheat production during the winter of 1995–1996. Wheat fields selected for study were on farms regularly visited by feeding swans, and included some sites managed by the North Carolina Wildlife Resources Commission's Waterfowl Sanctuary Program (i.e., fields where hunting was prohibited and farmers were compensated for crop losses due to grazing). Four fields were studied in Hyde County: two sanctuary sites (Davis Field and Nebraska Field) and two others (Berry Field and Lake Landing Field). Four fields also were studied in Tyrrell County: Cherry Field, Timberlake Field, Frying Pan Field, and Foster Field, none of which were included in the sanctuary program. The study fields had similar topography, slopes (ranging from 0% to 2%), soil types, and rainfall. The fields were large, ranging in size from 125 ha to 175 ha. Yields of wheat in the study area typically ranged from 4.35 to 4.79 m^3 per ha (Tant 1988).

METHODS

Wheat fields were selected based on (a) previous observations of feeding swans within fields and (b) the cooperation of the landowner and/or farmer. Each of the eight fields contained smaller units known as cuts, the areas lying between drainage ditches. Cuts also were selected based on accessibility and historic use by swans, and 61 pairs of exclosure and control plots were placed in selected cuts as follows: Berry Field, one pair in each of two cuts; Cherry Field, one pair in each of seven cuts; Davis Field, 15 pairs across eight cuts; Foster Field and Frying Pan Field, each with one pair in each of eight cuts; Lake Landing Field, eight pairs across four cuts; Nebraska Field, one pair in each of six cuts; and Timberlake Field, one pair in each of seven cuts.

Exclosures were installed in fields when the wheat started to emerge, usually at a height of about 5 cm, in late November to late December. Each exclosure was located randomly within a cut using computer-generated coordinates, and an adjacent control plot was established at a distance of 20 m (i.e., a paired-plot design). No plot was within 50 m of an edge of a cut or within 100 m of another pair of plots.

Each exclosure was made of welded-wire fencing and enclosed a circular area of 3 m^2, of which only 1 m^2 in the center was sampled (i.e., an area beyond access of a swan reaching through the fencing). The mesh size, about 5 × 10 cm, permitted smaller animals access to the interior of each exclosure. Because the fencing was rusted and difficult to see at a distance, the exclosures were assumed to have minimal visual impact on swans.

Wheat plant height was measured when the paired plots were established in late November or December and again in the first week of each month until the wheat was harvested in June. Leaf damage was measured in February, March, April, and May (resulting in 6 height and 4 leaf damage measurements). At each visit, ten plants were randomly selected from the center 1 m^2 of each plot, and plant height was measured with a ruler from the ground to the tip of the longest blade. On the same ten plants, leaf damage was measured as the number of blades showing evidence of grazing. At harvest, plants in the center 1 m^2 of all plots were clipped at ground level to determine aboveground biomass. These samples were dried at approximately 38°C, then weighed, after which the seed heads were removed, counted, and weighed separately.

A paired t-test was used to compare paired grazed and exclosure plots. Independent two-sample t-tests were used to compare the difference between exclosure and grazed plots in sanctuary fields to that in non-sanctuary fields. Cuts were considered to be independent of one another due to their large size (6 ha to 9 ha) and the physical barriers (ditches and roads) separating them, which resulted in a tendency for a swan flock to use one cut at a time without substantial movement to adjacent cuts. Since most cuts contained only one pair of plots (61 pairs distributed among 50 cuts), pairs of plots were also considered to be independent.

Swan diets were determined from a small sample (N = 6) of gizzards collected from birds legally shot by hunters during the 1995-1996 hunting season. The contents of gizzards were separated into wheat and other food items, and the volume of each component was determined.

Field work occurred between early November 1995 and mid-June 1996. Tundra Swans were first observed in the study area at the beginning of November and in winter wheat fields on 24 November 1995. Most swans migrated from the study area about the middle of March and were last observed in wheat fields on 4 April 1996.

RESULTS

Total aboveground dry mass was 12% less in grazed plots than in exclosure plots when sanctuary and non-sanctuary fields were combined ($\bar{x}$ = 798 g and 907 g, t_{60} = 3.93, $P <$ 0.001, Fig. 1; Table 1). Seed head mass was 11% less in grazed plots than in exclosure plots ($\bar{x}$ = 472 g and 531 g, t_{60} = 3.66, $P <$ 0.0005), although the difference in number of seed heads was not significant ($\bar{x}$ = 554 g and 586, t_{60} = 1.89, P = 0.06, Fig. 1 and Table 1).

Wheat height was lower in grazed plots relative to exclosure plots in every month subsequent to deployment of the plots (paired t-tests, all P-values <0.05), with the greatest proportional difference occurring in February, when grazed plots were 28% shorter than exclosure plots (t_{60} = 8.75, $P <$ 0.0001, Table 2). By the end of the study (June), wheat height in all study fields was 6% lower in grazed plots than exclosure plots (t_{60} = 5.12, $P < 0.0001$). Grazed and exclosure plots did not differ (t_{60} = 0.67, n.s.) in plant height at the time of plot deployment in December and early January.

Leaf damage, or the number of blades showing evidence of grazing on ten plants, was measured in early February, March,

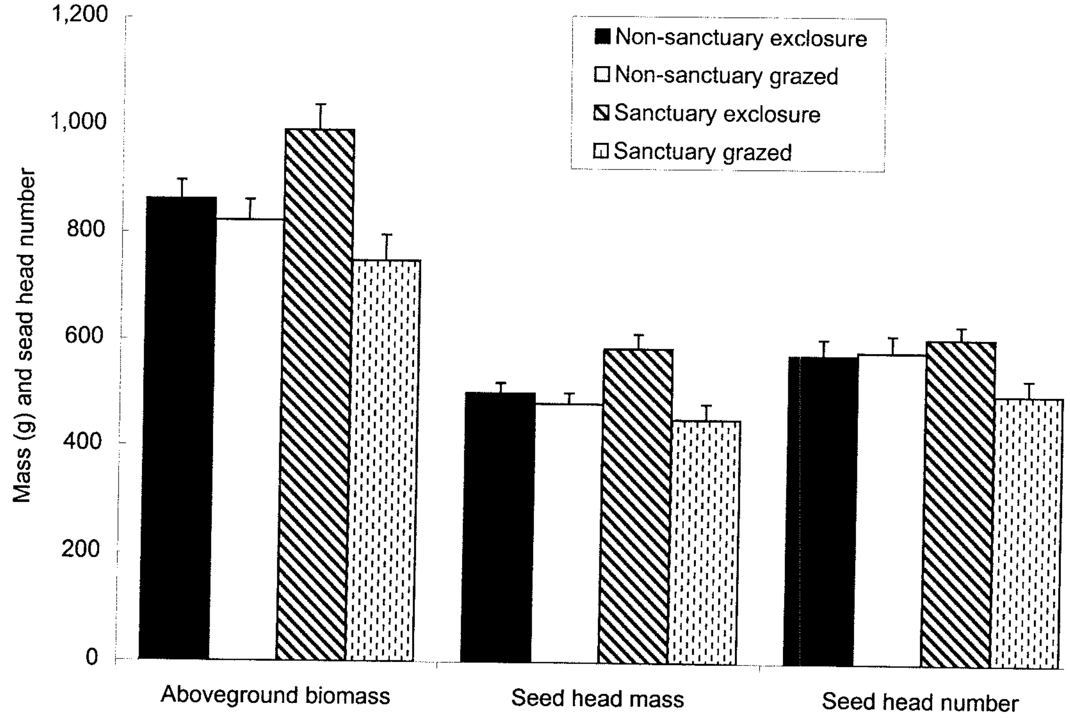

Figure 1. Average yield in aboveground biomass, seed head mass, and seed head number on grazed and exclosure plots in non-sanctuary vs. sanctuary fields in North Carolina. Error bars are one SE.

April, and May, which corresponds to grazing pressure in the preceding month. The number of blades grazed was greater in grazed plots than control plots in early February ($\bar{x}$ = 16.8 and 2.82 leaves, respectively, t_{60} = 9.63, $P < 0.0001$), March ($\bar{x}$ = 2.28 and 0.08 leaves, respectively, t_{60} = 4.31, $P < 0.0001$), and April ($\bar{x}$ = 1.16 and 0.0 leaves, respectively, t_{60} = 2.58, $P < 0.01$), corresponding to the months in which swans were present on the study site (January–March). Leaf damage occurring in April (i.e., the early May measurement) after swans had left the study area, did not differ on grazed and exclosure plots ($\bar{x}$ = 0.02 and 0.0 leaves, respectively, t_{60} = 1.0, n.s.).

Davis Field and Nebraska Field were part of the North Carolina Wildlife Resource Commissions' Waterfowl Sanctuary Program, in which swans and other waterfowl can feed without disturbances from either farmers or hunters. Grazing intensity, measured as the

Table 1. Difference in measurements of winter wheat yield attributed to grazing on 61 pairs of exclosure and grazed plots in Hyde and Tyrrell Counties, North Carolina. Waterfowl on sanctuary fields were protected from hunting and those in non-sanctuary fields were not. Statistical difference between exclosure and grazed plots within all plots, sanctuary and non-sanctuary columns was based on paired t-tests (df = 20 and 39, respectively). The difference between sanctuary and non-sanctuary plots was based on two-sample t-tests with d.f. = 59. SE of the difference given with the mean difference; ns = non-significant, *P < 0.05, **P < 0.01, ***P < 0.001.

	Mean difference in yield (exclosure—grazed)			
Measurement	All plots (N = 61)	Sanctuary (N = 21)	Non-sanctuary (N = 40)	Sanctuary vs. non-sanctuary, t-value
Aboveground mass (g per m^2)	109.0 ± 27.7***	242.7 ± 53.3***	38.8 ± 25.9^{ns}	3.88***
Seed head mass (g per m^2)	58.9 ± 16.2***	133.7 ± 31.6***	19.6 ± 14.9^{ns}	3.72***
Seed head number (per m^2)	32.0 ± 16.9^{ns}	106.4 ± 32.2**	-7.0 ± 16.7^{ns}	3.47***

Table 2. Grazing intensity, as measured by the difference in plant height (mm) on exclosure compared to grazed plots, in sanctuary and non-sanctuary fields. SE of the difference given with the mean difference; ns = non-significant, *P < 0.05, **P < 0.01, ***P < 0.001.

	Mean difference in plant height due to grazing (exclosure—grazed)			Sanctuary vs. non-sanctuary, t-value
	All plots[a]	Sanctuary[b] (N = 21)	Non-sanctuary[c] (N = 40)	
January[d]	-0.11 ± 0.17^{ns}	0.01 ± 0.38^{ns}	-0.17 ± 0.16^{ns}	0.51^{ns}
February	2.92 ± 0.33***	5.30 ± 0.28***	1.67 ± 0.35***	6.86***
March	4.60 ± 0.47***	6.60 ± 0.91***	3.55 ± 0.45***	3.35***
April	10.3 ± 1.13***	16.7 ± 2.0***	6.89 ± 1.01***	4.84***
May	4.91 ± 0.85***	9.78 ± 1.20***	2.35 ± 0.90**	4.87***
June	4.73 ± 0.92***	10.1 ± 1.67***	1.93 ± 0.82*	4.93***

[a] Student's t-values for January–June were 0.67, 8.75, 9.84, 9.10, 5.78, and 5.12, respectively.
[b] Student's t-values for January–June were 0.02, 19.23, 7.23, 8.23, 8.13, and 6.04, respectively.
[c] Student's t-values for January–June were 1.07, 4.73, 7.81, 6.79, 2.60, and 2.36, respectively.
[d] January measurements were taken at the time of plot establishment.

difference in plant height between grazed and exclosure plots, was greater on sanctuary plots than non-sanctuary plots in all months after plot establishment (Table 2). Likewise, the average difference in yield was greater for sanctuary fields than for non-sanctuary fields when measured as aboveground biomass (t_{59} = 3.88, $P < 0.0003$), seed head mass (t_{59} = 3.72, $P < 0.0005$) and number of seed heads (t_{59} = 3.47, $P < 0.001$, Table 1; Fig. 1). In fact, the difference between grazed and exclosure plots was significant for plots in sanctuary fields (aboveground biomass: t_{20} = 4.55, $P < 0.0002$; seed head mass: t_{20} = 4.23, $P < 0.0005$; and seed head number: t_{20} = 3.31, $P < 0.004$), but not for plots in non-sanctuary fields (aboveground biomass: t_{39} = 1.50, n.s.; seed head biomass: t_{39} = 1.32, n.s.; and seed head number t_{39} = 0.42, n.s., Table 1; Fig. 1). Loss of yield (ratio of seed head mass in exclosure compared to grazed plots) was related to grazing intensity (ratio of plant height, averaged for February–April, in exclosure compared to grazed) in sanctuary plots ($R = 0.26$, $F_{20} = 6.61$, $P < 0.001$) but not non-sanctuary plots ($R = 0.02$, $F_{39} = 0.67$, n.s.), suggesting that grazing was the factor reducing yield in sanctuary plots.

Four of the six gizzards contained 1 to 5 cc of winter wheat, and two gizzards contained no wheat. Overall, wheat comprised 75% of the volume of food items. The two gizzards with the largest amounts of wheat were from swans collected as they departed from fields.

DISCUSSION

Grazing reduced the yield of winter wheat, as shown by the 12% reduction in aboveground biomass and the 11% reduction in seed head mass in grazed plots compared to exclosure plots. Similarly, plant height at maturity was reduced by 6% in grazed plots. An analysis of a small number of gizzards confirmed that Tundra Swans consumed winter wheat, as did extensive observations of feeding behavior (Crawley and Parnell, unpublished data.). The study attributes the observed pattern of grazing to Tundra Swans, rather than other herbivores, for the following reasons. First, Tundra Swans were observed within the study fields during December to mid-March. Second, repeated visits to study fields, as well as time-activity budgets, conducted as part of a larger study on these and surrounding fields, indicated that Tundra Swans spent the majority of the day feeding when in fields (Crawley 1997). Third, geese and other herbivores were rarely encountered during these observations (Crawley 1997).

Grazing pressure (i.e., numbers of swans per unit of time) and duration are likely reasons for the difference in yields among fields. Conover (1988) found that Canada

Geese caused greater reductions in the growth of rye from repeated grazing in comparison with a single clipping, but Flegler *et al.* (1987) determined that Canada Geese could reduce wheat yields by as much as 30% in a single grazing event. In our study, wheat height showed the greatest proportional reduction in grazed plots during the month of February. In each successive month (March–June), the proportional difference in height between grazed and exclosure plots steadily lessened but nonetheless remained statistically significant. This suggests that grazing intensity was high initially, and that dormant winter wheat did not recover quickly, but that as temperatures increased later in the growing season, the wheat steadily recovered. Tundra Swans therefore may cause greater damage during cold winters, due to reduced recovery time for growth later in the season.

Patterson *et al.* (1989), studying Greylag Geese (*Anser anser*) and Pink-footed Geese (*Anser brachyrhynchus*) in Scotland, found that heavy grazing reduced yields of winter wheat and barley in half of the fields that they studied, whereas grazing pressure was insufficient to reduce yields in the remainder. Allen *et al.* (1985) and Percival and Houston (1992) similarly showed that grazing intensity of winter wheat by Canada Geese and Barnacle Geese (*Branta leucopsis*), respectively, was a determining factor affecting yield.

Spatial relationships between roosts and feeding areas may influence grazing intensity. For example, most Greylag and Pink-footed Geese feed within ten km of their roosts (Patterson *et al.* 1989). Davis, Lake Landing and Nebraska fields, those with the greatest reduction in yields, each were within five km of the major roosting area at Lake Mattamuskeet (e.g., 14,200 birds in the winter of 1995–1996). Also, this area contained fewer hectares of wheat compared to the area of Foster, Frying Pan, and Timber Lake fields.

Clark and Jarvis (1978) found that grazing by geese increased, rather than decreased, yields of rye grass seed. They attributed the variability in yields between fields to soil types and farming methods. Kahl and Samson (1984) reached a similar conclusion regarding the effects of geese on winter wheat yields, and attributed much of the difference to weather and soil rather than to grazing geese. In our study, soil types and weather were similar among fields and produced similar average wheat yields. Moreover, our experimental design of paired grazed and exclosure plots greatly reduced the chance that soil or weather contributed to differences in yield between grazed and ungrazed plots.

Geese at times may trample crops (Kear 1964; Kear 1970; Kahl and Samson 1984; Conover 1988). We did not observe Tundra Swans causing this type of damage in North Carolina, although this might occur during rainy periods on poorly drained soils.

Sanctuary fields showed a greater reduction in measurements of crop yield (aboveground biomass, seed head biomass, and seed head number) due to grazing than did non-sanctuary fields. In fact, the loss of yield was statistically significant in sanctuary but not in non-sanctuary fields. This suggests that sanctuary fields were grazed more heavily than non-sanctuary fields. Our measure of grazing intensity, the difference in plant height between grazed and exclosed plots, also indicated that sanctuary fields were grazed more heavily than non-sanctuary fields. In sanctuary fields, Tundra Swans were free from hunting pressure and other human disturbances. Although the Tundra Swan hunt in North Carolina is limited to 2,000 permits annually, it may have some effect on swan movements among fields. In this study, the activity of hunters and farmers was occasionally observed to cause birds to move to adjacent fields. There is evidence that the systematic disturbance of waterfowl may prevent their feeding in one field for too long or too often. For example, Hochbaum *et al.* (1954) and Kear (1963) concluded that one person could effectively reduce grain losses by occasionally chasing waterfowl from fields. Chemical repellents offer another option, but are often ineffective (Conover 1988).

Castelli and Applegate (1989), in their study of Tundra Swan depredations in cranberry bogs, suggested that some poorly producing bogs be set aside as sanctuaries to help reduce the loss of crops in other bogs. In our study, crop loss due to grazing was statistically significant only in sanctuary fields, and was greater in sanctuary fields than non-sanctuary fields. It is not known whether the presence of sanctuary fields reduced crop loss in other fields in this study. Additional studies are needed to compare crop loss in the presence and absence of sanctuary fields. We suggest also that further studies of Tundra Swan effects on winter wheat include counts of swans and other grazing waterfowl within study fields to assess grazing intensity more accurately, and that proximity to roost sites be incorporated into the experimental design and analysis.

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Effects of Grazing on Grasslands by Wintering Whooper Swans

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Abstract.—The effects of grazing by Whooper Swans (*Cygnus cygnus*) on agricultural grasslands in winter were investigated in northwest Ireland. Exclosure cages were used to compare aboveground biomass in ungrazed plots with those grazed by swans. Grazing intensity was measured by recording cumulative dropping densities in fixed plots. Measurements of aboveground biomass were made on three occasions: midwinter (January), early spring (late March) and late spring (late May) at two different study sites in different years. There were significant yield losses between grazed and ungrazed plots for each sampling period. These were highest in spring when losses of up to 65% were recorded. Swan grazing intensity was positively correlated with yield losses and aboveground biomass and the correlation was especially strong in late spring. Geese were also present in fields at one of the study sites and, while they also had a significant effect on biomass, swan grazing had a proportionately stronger effect. While the results illustrate the potential severity of grazing by swans, they should be interpreted with caution as previous studies have shown the interactive effects of a range of variables, including weather conditions, which make it difficult to predict the response of a sward to grazing.

Key words.—Agriculture, *Cygnus cygnus*, crop damage, grasslands, grazing, habitat, Whooper Swans.

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The effects of grazing by waterfowl on agricultural habitats has been subject to intensive study since the mid-1900s, largely in response to concern within the agricultural community about potential damage due to the grazing and trampling of crops. Geese have been the major focus of this work because of the relatively large numbers and range of species increasingly utilizing agricultural habitats, particularly in parts of northwest Europe and North America (Patterson 1991; Madsen 1991). In contrast, relatively little work has been undertaken on crop damage attributable to grazing by swans. It is likely that a number of factors including the relatively low numbers of swans involved, the relatively recent development of a field-feeding trait, and the more regional nature of any potential problems, have led to the effects of swan grazing being largely overlooked.

Terrestrial feeding by Whooper Swans (*Cygnus cygnus*) and Bewick's Swans (*Cygnus columbianus bewickii*) in the European wintering grounds is a relatively recent phenomenon. Whooper Swans were first recorded feeding on potatoes during severe weather in the 1940s, and the species has increasingly used arable habitats since the 1960s (Kear 1963; Sheppard 1981). MacMillan (1969) reported Bewick's Swans feeding on arable land in Britain in 1968. A similar trend towards field-feeding became evident in Denmark and The Netherlands at around the same time (Poorter 1991). The change in habit has been attributed to changes in agricultural practices in the British wintering grounds, particularly the shift towards arable cultivation and intensive drainage (Kear 1963). Laubek (1995) suggests that the increase in land area under arable crops, particularly Oilseed Rape (*Brassica napus*), coincident with the eutrophication of wetlands in the late 1970s and early 1980s, triggered the similar habitat switch in Denmark.

Rees *et al.* (1997), in a study of the distribution of swans in Britain in the 1990–1991 winter, reported that the majority of Bewick's Swans (74%) and only 26% of Whooper Swans were found on pasture and arable land. International censuses in 1995 (Cranswick *et al.* 1996) and 2000 (Cranswick *et al.* 2002) found that around two-thirds of Whooper Swans occurred on pasture and arable land in mid-January. Over 75% of Whooper Swans in Denmark fed in arable habitats in the early 1990s (Laubek 1995).

The increasing tendency towards grazing on agricultural land coincided with an increase in population sizes for all three swan species in Britain and northwest Europe during the 1980s (Dirksen and Beekman 1991; Kirby *et al.* 1994; Delany *et al.* 1999), which in turn increased the potential for conflict between swans and agricultural interests. A review by Madsen (1991) showed that swans (*Cygnus* spp.) have been implicated in causing crop damage in eight European countries, with both Mute Swans (*Cygnus olor*) and Whooper Swans causing damage in half of the countries in which they occur (Madsen 1991), although the level of damage was not quantified. Laubek (1995) reports a considerable increase in the number of complaints about swans made by farmers to the Danish government, particularly since the late 1980s.

This study assesses the effects of grazing (specifically defoliation) by Whooper Swans wintering on improved grasslands in Ireland. The loss in yield attributable to grazing is examined on two occasions when the quantity of food available in pastures is most crucial for farmers, (1) in late March/early April, when the availability of newly grown vegetation ("spring bite") is important for livestock in spring; and (2) in late April/May when the first cut of silage is taken.

STUDY AREA AND METHODS

The study was carried out at two sites in the north of Ireland, both of which regularly hold internationally important numbers of Whooper Swans from the Icelandic population (i.e., where the five-year mean of the maximum counts recorded each winter is at least 210 birds; Cranswick *et al.* 2002). Inch Levels on Lough Swilly (55°03'N, 07°27'W) is probably the most important site for the species in Ireland, holding on average 700 birds throughout the wintering period and frequently in excess of 1,500 birds in autumn (Colhoun 2001). The feeding areas comprise intensively managed mixed farmland adjacent to a large brackish lake used for roosting. Up to 2,000 Greylag Geese (*Anser anser*) and smaller numbers of Greenland White-fronted Geese (*Anser albifrons flavirostris*) and feral Canada Geese (*Branta canadensis*) also occur at the site. Toome (54°46'N, 06°28'W) is a much less extensive area of predominantly grassland habitat between Loughs Beg and Neagh. It holds around 200 Whooper Swans during the period from November through to March.

The study was carried out in different years at the two sites, during the 1995–1996 winter at Inch Levels and in 1996-1997 at Toome. In both cases, two recently reseeded fields (1–2 years old) were chosen, as these were the most important to agriculture, and also were selected preferentially by the swans (Colhoun 1998). The method, which followed those of several previous studies (Patton and Frame 1981; Summers 1990; Percival and Houston 1992), involved using exclosure cages to compare the aboveground biomass of grass in ungrazed areas with those in adjacent grazed control plots. The possible effect of the exclosures on plant growth had been investigated, and no significant difference in aboveground biomass, nor significant effects of other herbivores, were recorded (Colhoun 1998).

In all fields, four to eight exclosure cages were erected along two to three parallel transects, equidistant within fields, in early autumn after grazing livestock had been removed. Plot location appeared to be unbiased in that grazing intensity (measured by dropping density) was uniform across the study fields. Each exclosure was a 2 m × 2 m (4 m^2) structure, 1 m high, supported at each corner by 5 cm × 5 cm wooden paddock posts and enclosed by 5 cm × 5 cm mesh chicken wire. In order to deter geese or swans from entering from above, thin strings were tied across each diagonal. There was no evidence that the exclosures themselves affected grazing behavior as the birds were observed feeding at the edge of exclosures and, on a number of occasions where they had been partially damaged, within them. In such cases, data on the quantity of vegetation in the exclosures were excluded from the analyses.

The intensity of grazing was measured indirectly by counting the density of swan and goose droppings in permanent plots (Owen 1971); swan and goose droppings were separated by their size and mass. As Greylag Geese and Whooper Swans defecate at regular intervals of three to five min and ten to twelve min respectively (K. Colhoun, unpub. data), the cumulative number of droppings can be used as an index of the amount of time spent grazing in that area by each species. Permanent dropping density plots were located adjacent to exclosures, and also at 15–25 random locations in other parts of each field, to provide an assessment of grazing intensity. Each plot consisted of a small numbered peg, around which droppings within a 2 m radius (12.56 m^2) were counted and removed at 10–15 day intervals. This interval was less than the average decomposition rate of droppings, measured before the experiment and throughout the season. In addition, the validity of the dropping density technique as a measurement of grazing intensity was assessed by relating cumulative dropping densities to counts of birds in fields, made at least twice-weekly throughout the season. The number of swan-days between dropping density measures was calculated by interpolation of the swan counts, there normally being no more than two or three days between counts. Although it would have been preferable to remove exclosures immediately following cessation of swan and goose grazing, to minimize any sheltering effect on the growing crop, the exclosures remained in place until the late spring. Other herbivores, notably the European Rabbit (*Oryctolagus cuniculus*), probably would have exploited the relative abundance of grass in the exclosure plots if accessible.

Measurements of aboveground biomass were made three times during the winter/spring period, (1) in early January (Toome only); (2) in late March (Inch Levels and Toome), and; (3) in mid-May (Inch Levels only). The midwinter and early spring samples were taken at Toome to estimate amounts of vegetation removed up to this period and available for early season livestock grazing. At Inch, samples were taken in spring only as these fields were being managed for silage production.

On each occasion, samples were taken from within the paired ungrazed and grazed plots. A 25 cm × 25 cm (625 cm^2) quadrat was thrown randomly in each plot and vegetation within the quadrat was cut to ground level using hand-shears. Samples from grazed plots were taken from within a 2 m radius of the dropping density marker adjacent to exclosures, and the paired ungrazed sample was removed from within the exclosures. In both cases the quadrat was thrown at random and the point from which samples were taken was marked to avoid re-sampling on subsequent visits. Grass samples were sorted by hand into live and dead material, and the live material dried in an oven at 80°C for at least 24 h to constant mass. The dried material was then weighed and converted to dry live mass per m^2.

Yield loss was determined by calculating the difference in biomass between grazed and ungrazed plots, and the change in yield loss between the first and second sampling occasions was analyzed by using paired t-tests. Pearson correlations were used to test the association between aboveground biomass of vegetation and grazing intensity, with grazing measured as the cumulative sum of dropping densities recorded during the winter. Stepwise multiple regression was used to investigate the relative effects of swan- and goose-grazing on above-ground biomass and yield losses. Mean values are given with standard errors throughout.

RESULTS

Duration and Intensity of Grazing

The number of swan-days recorded for the study fields were highly correlated with swan dropping densities over the equivalent time periods (cumulative number of droppings·m^{-2}) (Pearson correlation, $r_{13} = 0.817$, $P < 0.01$, Fig. 1), permitting the use of dropping densities to describe grazing intensity. Droppings were found to have disintegrated within, on average, 20 ± 0.7 days (N = 54).

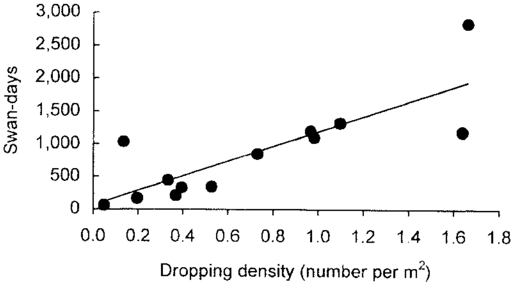

Figure 1. Relationship between swan dropping density (mean number of droppings per m^2) and the number of swans recorded in the field between samples (swan-days). The linear regression line is plotted (swan-days = 1,133 × dropping density + 64).

Grazing occurred on the two experimental fields at Inch Levels (field codes 3 and 49) from early December 1995 through to early April 1996 (median dates: 15 March and 28 February, respectively), and from early November 1996 to the end of January 1997 on the two fields at Toome (field codes 635 and 637; Table 1, Fig. 2). At Inch Levels, Field 49 was used more heavily than Field 3, and both fields were grazed most intensively from early February to late March. Early April was the only period during which Field 3 was grazed more than Field 49 (Fig. 2). At Toome, grazing intensity peaked in mid-December (median dates: 14 and 20 December, Table 1).

Geese utilized both experimental fields at Inch Levels, but were not present at Toome. At Inch, goose usage, determined by a combination of dropping density and actual counts, was higher in Field 49 throughout

Table 1. Total number of Whooper Swan (WS) and goose droppings (GG) counted in fixed plots, in two fields at Inch Levels (field codes 3 and 49) during the 1995–1996 winter, and in two fields at Toome in 1996–1997 (field codes 635 and 637; zero goose droppings). The dates on which 50% of the cumulative totals were counted (median) and the 25% and 75% inter-quartile periods are also shown.

			Cumulative number of droppings		Time of grazing	
Field	Season	Species	Mean	95% C.L.	Median	Inter-quartile period
3	1995-96	WS	4.2	3.8–4.6	15 Mar	2 Mar–28 Mar
		GG	4.3	3.5–5.1	2 Feb	25 Jan–11 Feb
49	1995-96	WS	6.5	5.6–7.4	28 Feb	5 Feb–23 Mar
		GG	1.0	0.7–1.3	15 Mar	11 Mar–19 Mar
635	1996-97	WS	5.7	5.2–6.1	20 Dec	12 Dec–28 Dec
		GG	0.0	—	—	—
637	1996-97	WS	4.3	4.0–4.6	14 Dec	9 Dec–19 Dec
		GG	0.0	—	—	—

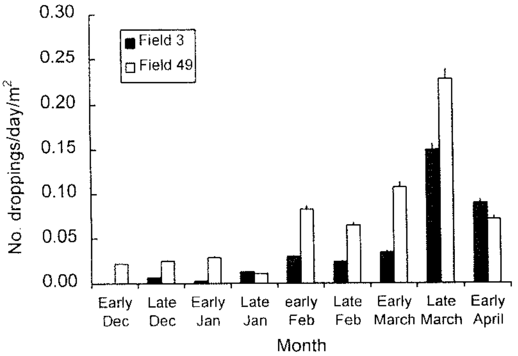

Figure 2. Seasonal usage by grazing Whooper Swans of experimental grasslands at Inch Levels in the 1995–1996 winter.

much of the 1995–1996 winter, with Field 3 being used principally in late March/early April (median dates: 2 February and 15 March, respectively, Table 1).

Effects of Grazing on Aboveground Biomass

Midwinter (late January) estimates of aboveground biomass and yield loss were recorded only at Toome. The aboveground biomass in grazed plots varied between 42.5 g·m^{-2} and 68.0 g·m^{-2} ($\bar{x}$ = 65.9 ± 5.6 g·m^{-2}) and was significantly lower than those of ungrazed areas by, on average, 31% (Table 2). Grazing intensity was positively correlated with both aboveground biomass (Pearson correlation: $r_8 = 0.807$, $P < 0.01$; Fig. 3a), and yield loss ($r_8 = 0.722$, $P < 0.05$; Fig. 3b) in January at Toome.

Grazing caused significant reductions in aboveground biomass at Inch Levels and Toome in early spring (late March) of between 31.6 g·m^{-2} (28%) and 140.5 g·m^{-2} (65%) (Table 2), and was greatest in the fields at Inch Levels where grazing intensity was highest at this time (up to 8 droppings·m^{-2}). The relationship between grazing intensity and aboveground biomass, and also with yield loss (measured as the difference between paired grazed/ungrazed plots), were both positive and significant ($r_{15} = 0.613$, $P < 0.01$ and $r_{15} = 0.718$, $P < 0.01$, respectively; Fig. 4a,b). Multiple regression analysis showed that 32.7% of the variation in aboveground biomass from grazed plots at Inch Levels in March was explained by swan grazing alone, and a further 13.8% was accounted for when goose grazing intensity was added as an explanatory variable (Table 3). Swan-grazing alone accounted for 47.8% of variation in the early spring reduction in aboveground biomass in the fields measured at Inch Levels, and the inclusion of goose-grazing intensity significantly improved the fit of the model by a further 21.6% (Table 3). Areas that were grazed most intensively tended to have significantly higher aboveground biomass ($r_{15} = 0.871$, $P < 0.01$; Fig. 5a), but there was no significant relationship between grazing intensity and aboveground biomass loss ($r_{15} = -0.277$, n.s.; Fig. 5b) when both fields at the Inch Levels were considered together. Separately, however, grazing intensity was positively correlated with aboveground biomass losses (Field 3: $r_8 = 0.92$, $P < 0.01$; and Field 49: $r_7 = 0.76$, $P < 0.01$). Swan grazing accounted for 83.8% of the variation in late spring yield and the addition of goose graz-

Table 2. Comparison of yields (dry weight aboveground biomass) in January (Toome), March (Inch and Toome) and May (Inch) of grazed control and exclosure plots, together with statistical comparison (paired t-test) and significance; *P < 0.05, **P < 0.02, ***P < 0.001.

		Yield g·m^{-2} (SE; N)			
Field	Date	Grazed	Ungrazed	Yield loss g·m^{-2} (%)	t
Toome 637	late Jan 1997	65.9 (5.6; 4)	95.7 (6.5; 4)	29.8 (31.1)	3.88*
Toome 635	late Mar 1997	80.2 (2.6; 4)	111.9 (5.3; 4)	31.6 (28.3)	4.37*
Toome 637	late Mar 1997	84.8 (3.2; 4)	168.2 (17.8; 4)	83.4 (49.6)	4.97**
Inch 3	late Mar 1996	81.3 (3.7; 8)	213.0 (13.5; 8)	131.7 (61.8)	12.37***
Inch 49	late Mar 1996	76.3 (17.4; 7)	216.8 (28.9; 7)	140.5 (64.8)	10.44***
Inch 3	late May 1996	288.1 (13.6; 8)	696.2 (48.3; 8)	408.1 (58.6)	11.02***
Inch 49	late May 1996	404.6 (22.6; 7)	687.6 (42.3; 7)	282.9 (41.1)	13.54***

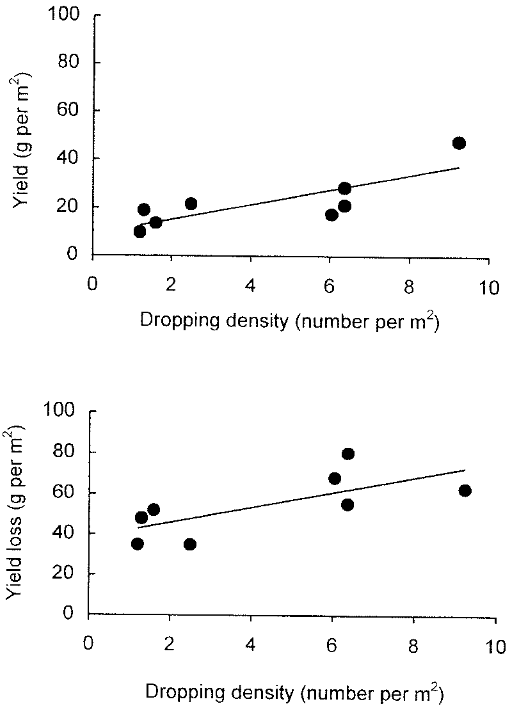

Figure 3. **Relationship between grazing intensity and (a) aboveground biomass (g·m^{-2}) and (b) yield loss (difference in aboveground biomass between adjacent grazed and ungrazed areas) (g·m^{-2}) in January 1997 at Toome. The linear regression lines are plotted (yield = 3.40 × dropping density + 8.2, $r = 0.81$, $P < 0.05$; and yield loss = 3.47 × dropping density + 39.2, $r = 0.72$, $P < 0.05$, respectively).**

ing intensity did not significantly improve the fit of the model (Table 3).

DISCUSSION

The results of this study indicate that grazing by mixed flocks of geese and swans caused significant reductions in aboveground biomass in grasslands, similar to previous studies which demonstrated significant yield reduction attributable to goose grazing in both early spring (Kuyken 1969; Groot Bruinderink 1989; Percival and Houston 1992) and early summer (Groot Bruinderink 1989; Ernst 1991; Percival and Houston 1992).

Although the primary objective of this aspect of the study was concerned with the impact of swan grazing, it was not possible to investigate this in isolation, since both species often used the same fields, either in single-species or in mixed flocks. Whooper Swans were, however, the predominant grazing species at all times and it appears likely that by far the greater contribution to yield loss was caused by this species. This argument is supported by the fact that the incorporation of goose grazing intensity as an explanatory variable in the damage model explained a relatively small, albeit statistically significant, proportion of the overall variability in yield and yield loss, and did not explain variation in the late spring yield. In the latter case, over 80% of the variance in yield was explained by swan grazing intensity alone. Assuming equal digestive efficiencies and a similar amount of time spent feeding by both species, it is likely that swans were removing by far the largest proportion of available biomass. Estimates of

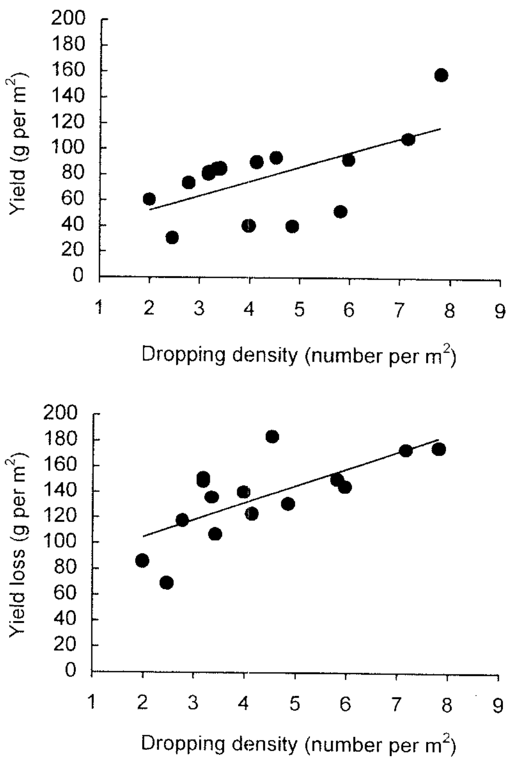

Figure 4. **Relationship between grazing intensity and (a) aboveground biomass (g·m^{-2}) and (b) yield loss (difference in aboveground biomass between adjacent grazed/ ungrazed areas) (g·m^{-2}) in March 1996 at Inch Levels. The linear regression lines are plotted (yield = 11.2 × dropping density + 30.0, $r = 0.61$, $P < 0.05$; and yield loss = 13.3 × dropping density + 78.4, $r = 0.72$, $P < 0.01$, respectively).**

Table 3. Results of multiple regression analysis showing the relative effects of swan and goose grazing on aboveground biomass (in grazed plots) and yield losses (difference between paired grazed/ungrazed plots) at Inch in early and late spring 1996; n.s. = not significant, *P < 0.05, **P < 0.01, ***P < 0.001; d.f. = 1,13 for swan grazing and d.f. = 2,12 for goose grazing.

Yield measurement	Field	Date	Variable	Regression coefficient	Cumulative R^2 (adj.)	F value
Yield	Inch 3 & 49	Mar 1996	Constant	3.55		
			Swan	14.52	0.327	7.81*
			Goose	8.44	0.465	7.01**
Yield loss	Inch 3 & 49	Mar 1996	Constant	45.77		
			Swan	17.37	0.478	13.81**
			Goose	10.00	0.694	16.89***
Yield	Inch 3 & 49	May 1996	Constant	65.77		
			Swan	48.46	0.838	73.54***
			Goose	2.70	—	0.24 n.s.
Yield loss	Inch 3 & 49	May 1996	Constant	316.23		
			Swan	19.41	—	2.46 n.s.
			Goose	-1.28	—	1.13 n.s.

consumption based on equal retention rates, mean dropping mass and cumulative dropping mass suggests that goose grazing accounted for 13% (Field 3) and 4% (Field 49) of all consumption by geese and swans (Appendix 1).

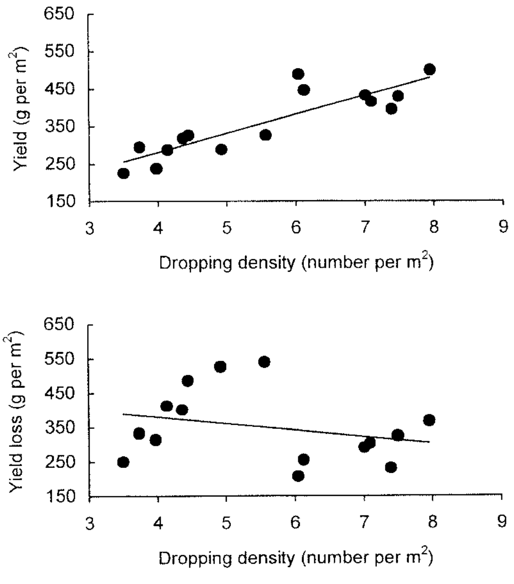

Figure 5. Relationship between grazing intensity and (a) aboveground biomass (g·m^{-2}) and (b) yield loss (difference in aboveground biomass between adjacent grazed/ungrazed areas) (g·m^{-2}) in May 1996 at Inch Levels. The linear regression lines are plotted (yield = 50.1 × dropping density + 80.7, r = 0.87, P < 0.001; and yield loss = -18.9 × dropping density + 455.2, r = -0.28, n.s., respectively).

While grazing resulted in significant reductions in aboveground biomass during the midwinter, early spring and late spring periods, the greatest reduction was evident in early spring. At this time, losses at Inch Levels averaged at about 60% in both fields studied, but some recovery was evident by the mid-May silage cut. Moreover, there was considerable between-field variability in the degree of loss in late spring, probably as a consequence of a change in the usage of fields by the swans during March and April. The later grazing of Field 3 (median date: 15 March), and a substantial decline in the usage of Field 49 at the same time may explain why yield loss in Field 3 remained at a similar level in May (59%) to that in March (62%), whereas in Field 49 yield loss was reduced from 65% to only 41% by May. Grasses are known to be particularly tolerant to grazing, possessing the ability for compensatory growth (McNaughton 1983). Compensatory grazing is likely to be highest at intermediate intensities of defoliation, however, because very intense defoliation inhibits production (Robson *et al.* 1989) and the degree of impact is dependent on the timing of attack relative to plant development (Crawley 1983). Late defoliation especially inhibits regrowth due to meristem removal. Since there were no differences in management of these fields (e.g., fertilization) at this time, it appears likely that the timing of grazing was the primary factor which accounted for the variation in recovery rates between fields.

The intensity of grazing by swans was positively correlated with yield losses in early but not in late spring. Plots that were grazed most heavily, therefore, tended to show the highest reductions in yield, but grazing intensity was also positively correlated with yield in grazed plots. It is likely that grazing was most intensive in areas of highest grass productivity (e.g., Rees 1990) and that in these areas growth rates exceeded rates of consumption. Close grazing of many pasture species increases tillering which, in turn, partially offsets the reduced production per tiller (Grant *et al.* 1981). Grazing, therefore, had the effect of enhancing growth though this positive effect was greatly outweighed by the net losses in yield attributable to grazing.

These results are similar to those of previous studies in the Netherlands (Groot Bruinderink 1989) and Islay (Percival and Houston 1992) that, in addition, highlighted the complexity of the interaction of various factors, leading to variability in the between-year response of swards to grazing. The authors attributed these to variation in weather conditions (primarily temperatures) during the spring growing period. On Islay, for example, early spring aboveground biomass was positively correlated with goose grazing intensity in the warmer of the two study seasons, but was negatively correlated with grazing in the cooler year, when grass growth would have been delayed. The fact that it was not possible to carry out the present study over a number of years means that the results must be interpreted with a degree of caution, because the interaction of factors such as grazing intensity, and the timing of grazing relative to plant growth stage, make the response of the sward unpredictable. Further work would be necessary to examine the response of grasslands to varying Whooper Swan grazing intensities under varying growth conditions.

The potential impact of defoliation by grazing swans on grassland yields has not previously been considered in detail, perhaps due to a perception that the effects of goose-grazing have been a more serious issue for farmers. Given the similarity in grazing ecology between the two families, it is not unexpected that swans could have a similar impact to geese. Indeed, there is increasing evidence that grazing by all three species of swan which occur in the Western Palearctic are causing conflict with farming interests, particularly in situations where large concentrations occur in winter (Madsen 1991; Laubek 1995).

While this study has not examined the effects of grazing or regrazing on plant growth or diet selection, it is likely that the intensity of grazing in this area represents the upper limits to grazing intensity experienced within this country. In a local context, these fields were much more heavily exploited than any others (Colhoun 1998), and within an Irish context it is unlikely that such large yield reductions could occur over a wide area. Concentrations exceeding 127 birds (nationally important levels) occur at a relatively limited number of sites, with only around 20 holding flocks of this size in the most recent mid-January census in Ireland (Colhoun *et al.* 2001). Nevertheless, in areas where intensive grazing occurs, availability of early season vegetation could be reduced as most birds remain on more southerly wintering sites until the end of February or early March. Yield losses are likely to be most significant in cold, wet springs when migration may be delayed, grass growth retarded and defoliation exacerbated by puddling damage. Collectively, this combination of highly variable factors, makes the effects of swan grazing on reseeded grasslands extremely difficult to predict.

ACKNOWLEDGMENTS

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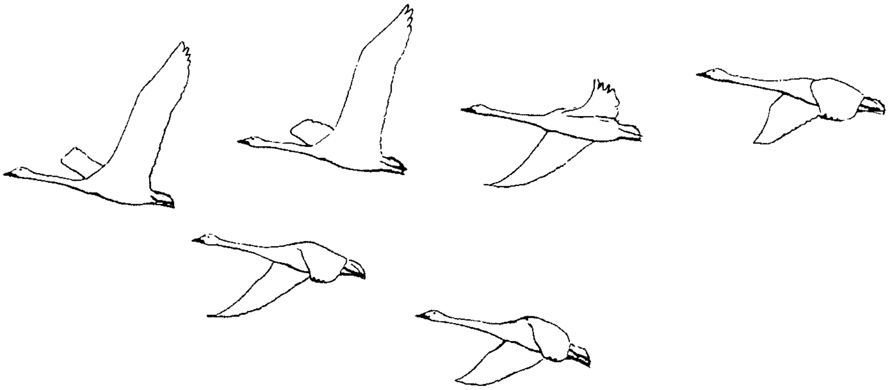
Appendix 1. **Estimated consumption by swans and geese of aboveground biomass in Field 49 at Inch Levels, from December to March inclusive. Estimates of biomass consumption by each species were derived from daily dropping output (as measured by densities), dropping mass and retention rates. Swan and goose dropping mass is based on average weights from the study area (K. Colhoun unpub. data). Retention rate is assumed at 0.4 (P. Clausen, pers. comm.), with the grass in the droppings therefore representing 60% of grasses ingested. Similar calculations for Field 3 give total consumption estimates of 35.1 g·m^{-2} (swans), 5.2 g·m^{-2} (geese) and 40.3 g·m^{-2} (both species).**

		Swans			Geese		
Month	Days	Droppings per day	Dropping mass (g)	Cumulative dropping mass ejected (g per month)	Droppings per day	Dropping mass (g)	Cumulative dropping mass ejected (g per month)
Dec	31	0.02	5.3	3.29	0.000	0.9	0.01
Jan	31	0.02	5.3	3.29	0.001	0.9	0.03
Feb	28	0.07	5.3	10.39	0.008	0.09	0.19
Mar	31	0.17	5.3	27.93	0.054	0.09	1.51
		Total dropping mass (Dec–Mar)		44.9	Total dropping mass (Dec–Mar)		1.74
			Retention rate	0.4		Retention rate	0.4
		Estimated consumption g·m^{-2}		74.8	Estimated consumption g·m^{-2}		2.9
				Total estimated consumption (swans and geese) g·m^{-2}			77.7



Habitat Usage and Field Choice by Mute and Whooper Swans in the Tweed Valley, Scotland

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Abstract.—Habitat availability and usage by Mute Swans (*Cygnus olor*) and Whooper Swans (*Cygnus cygnus*) was studied in the valley of the River Tweed in Scotland from 1996–1999. Monthly surveys were undertaken to describe the seasonal variation in numbers of swans and their choice of habitat, with particular reference to potential factors affecting choice of individual agricultural fields. Mute Swans were present throughout the year, with highest numbers in winter, and lowest numbers during April–August. Whooper Swans were present from October–April. Both species fed on agricultural crops during winter, with Oilseed Rape (*Brassica napus*) fields the favored habitat from December–March. Whooper Swans also showed some preference for winter cereals when in single species flocks, while river vegetation was also important for Mute Swans. Analysis of field choice showed that, although crop type (Oilseed Rape) was the dominant factor, swans also chose larger fields and those closer to water. Neither boundary features nor potential sources of disturbance were significant in influencing field selection. Implications for the management of conflict between swans and farmers include the potential to reduce the likelihood of damage by swans through planting Oilseed Rape in smaller fields away from water. An alternative approach would be to set aside sacrificial fields, the location and size of which could be chosen to be the most attractive combination for grazing swans.

Key words.—Agricultural damage, crop protection, *Cygnus cygnus*, *Cygnus olor*, field choice, habitat usage, Mute Swan, oilseed rape, Whooper Swan.

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Following decreases in numbers during the 1960s, the British Mute Swan (*Cygnus olor*) population increased substantially in the late 1980s, to around 26,000 birds (Delany *et al.* 1992). This rise has been accompanied by increasing concern about potential damage caused by swans to certain agricultural crops and fishery interests in the UK (Trump *et al.* 1994; Maudsley 1996; Sayers and Walsha 1996) and elsewhere (Laubeck 1995).

The aims of this study were to describe habitat availability and usage by Mute Swans and Whooper Swans (*Cygnus cygnus*) in the valley of the River Tweed, and to investigate factors affecting field choice by grazing swans. No attempt has been made so far to assess damage caused to agricultural crops by swans grazing in the Tweed Valley but, by analyzing habitat and field choice, it is hoped to be able to suggest possible management options to reduce potential conflict between swans and farmers.

STUDY AREA AND METHODS

The Tweed Valley study area was a 60 km section of the central valley of the River Tweed, from St. Boswells to Coldstream, including the area around the River Teviot from Denholm to Kelso. This is a lowland, farmed landscape with many field boundaries delineated by hedges. Fields were largely comprised of arable crops (winter wheat and barley ~40%, spring sown barley with associated stubble and plough ~25%, Oilseed Rape ~10%), with some 20% being pasture grazed by sheep, and 5% other, e.g., potatoes and turnips.

Mute Swans are resident in the valley, but many move out of the immediate study area in May, with leg-banded individuals being resighted down the valley on the Tweed estuary in Berwick (J. Coleman, pers. obs.) before returning to the study area in September. The Whooper Swans are from the Icelandic-breeding population, which migrates to winter in Britain and Ireland (Delany *et al.* 1999). Several leg-banded or neck-collared individuals marked in Iceland have been re-sighted in successive winters in the study area.

A standard route of 170 km was driven every month from October 1996 to September 1999. A sample of 768 fields was visible from this route, as well as most of the length of the river and four lochs regularly used by swans for roosting or feeding. Valley topography enabled fields at long distances from the road to be covered, but only fields entirely visible were used in the study. On each occasion data were collected on the number and species of swan present for each field or other habitats.

Field crop type was recorded throughout the first year for each of the 768 fields. In subsequent years, all fields were checked but only the location of Oilseed Rape fields recorded. For each field, five variables were measured: (1) percentage field boundary with high hedge, which was defined as a continuous boundary feature 2 m or more in height which would hide the approach of a person; (2) percentage field boundary with high trees, which was defined as individual trees over 10 m in height which were potential obstacles to a swan's flight path; (3) disturbance, which was defined as the presence of a potential source of disturbance, e.g., roads, farm tracks or buildings along the field boundary; (4) field size, measured from 1:25000 maps of the study area, and (5) distance to nearest water (river or loch), the distance (in meters) being measured from the center of the field to the center of the water feature on a map.

Chi-squared tests (with Yates' Correction Factor where appropriate) were used on the frequency with which flocks were seen on different habitats to compare (1) the number rape and winter cereal fields used by swan flocks in 1996–97, in relation to the total number of fields with these crops present in the study area; and (2) for each year of the study, the distribution of different types of flocks (Mute Swans only, Whooper Swans only and mixed species flocks) across fields with different crops, for the fields used by swans in that winter. Binary logistic regression was used to identify factors influencing field choice during the winter.

RESULTS

The total number of Mute Swans varied between 33 and 294 birds, with a distinct seasonal pattern each year (Fig. 1a). Lowest numbers occurred from April to August, when only territorial pairs were present. Numbers increased in late autumn following the molt period, after which numbers were maintained throughout the winter until the start of the following breeding season. Whooper Swans were present from October to April, with a maximum total of 188 birds counted on a single day (Fig. 1b). Both species occurred as singles, pairs, family groups and flocks; the flocks being single species or mixed, with a maximum flock size of 187 swans composed of both species.

Analysis of the habitats used showed that both species occurred mainly on oilseed rape from December to March inclusive, with Whooper Swans also showing preference for winter wheat and winter barley early in the winter (Figs. 1a,b). For Mute Swans, river vegetation was also important, particularly in autumn and to a lesser extent in early summer.

Of the 768 fields observed each year, swan flocks utilized a total of 26 fields in 1996–97, 23 fields in 1997–98 and 24 fields in 1998–99. The percentage of total rape fields used by swan flocks varied between 22.6% and 31.9% in the three year period; 19 of 55 rape fields were used by swans in 1996–97, 16 of 75 in 1997–98 and 15 of 64 in 1998–99. In 1996–97 the total number of winter cereal fields was also recorded (307), of which a total of seven fields were used by swan flocks. The proportion of rape fields that were used by swans in 1996-97 was significantly higher than the proportion of winter cereal fields used by swans in the same winter ($\chi^2_1 = 72.8$, $P < 0.001$), indicating that the birds were selecting for Oilseed Rape. The different field types used by swans throughout the study, together with the number of single species flocks and mixed species flocks recorded on each crop, is shown in Table 1. There was no significant difference between Mute Swan flocks and mixed flocks in the frequency with which they were recorded on the different crops ($\chi^2_1 = 0.05$, for 1996-97, $\chi^2_1 = 0.002$, for 1997-98 and $\chi^2_1 = 0.26$ for 1998–99, n.s. in each case); both flock types showed the same clear preference for Oilseed Rape. Whooper Swan flocks were more variable in their field choice during the three year study period when compared to Mute Swan flocks ($\chi^2_1 = 4.9$ for 1996–97, $P < 0.05$; $\chi^2_1 = 11.4$, $P < 0.001$ for 1997–98; and $\chi^2_1 = 6.8$, $P < 0.01$ for 1998-99), and when compared to mixed swan flocks in 1997–98 ($\chi^2_1 = 3.6$, n.s. for 1996–97; $\chi^2_1 = 14.9$, $P < 0.001$ for 1997-98; $\chi^2_1 = 2.03$, n.s. for 1998–99).

While crop type (Oilseed Rape) was the dominant factor influencing field selection, swans also chose larger fields and those closer to water (Table 2). Neither the type of field boundary, nor the presence of potential sources of disturbance (farm tracks and buildings), was statistically different over the three years of the study. However, the mean proportion of the boundary composed of trees or high hedges was approximately half of that for fields where swans were present compared to fields not utilized by swans and, in one of the three years studied (1997–98), the fields chosen by swans were significantly less likely to have a farm track, road or building along one boundary than those fields not chosen by swans (n.s. in Table 2). However, approximately 70% of all fields studied had an adjacent feature of this type. There was no significant inter-correlation between the

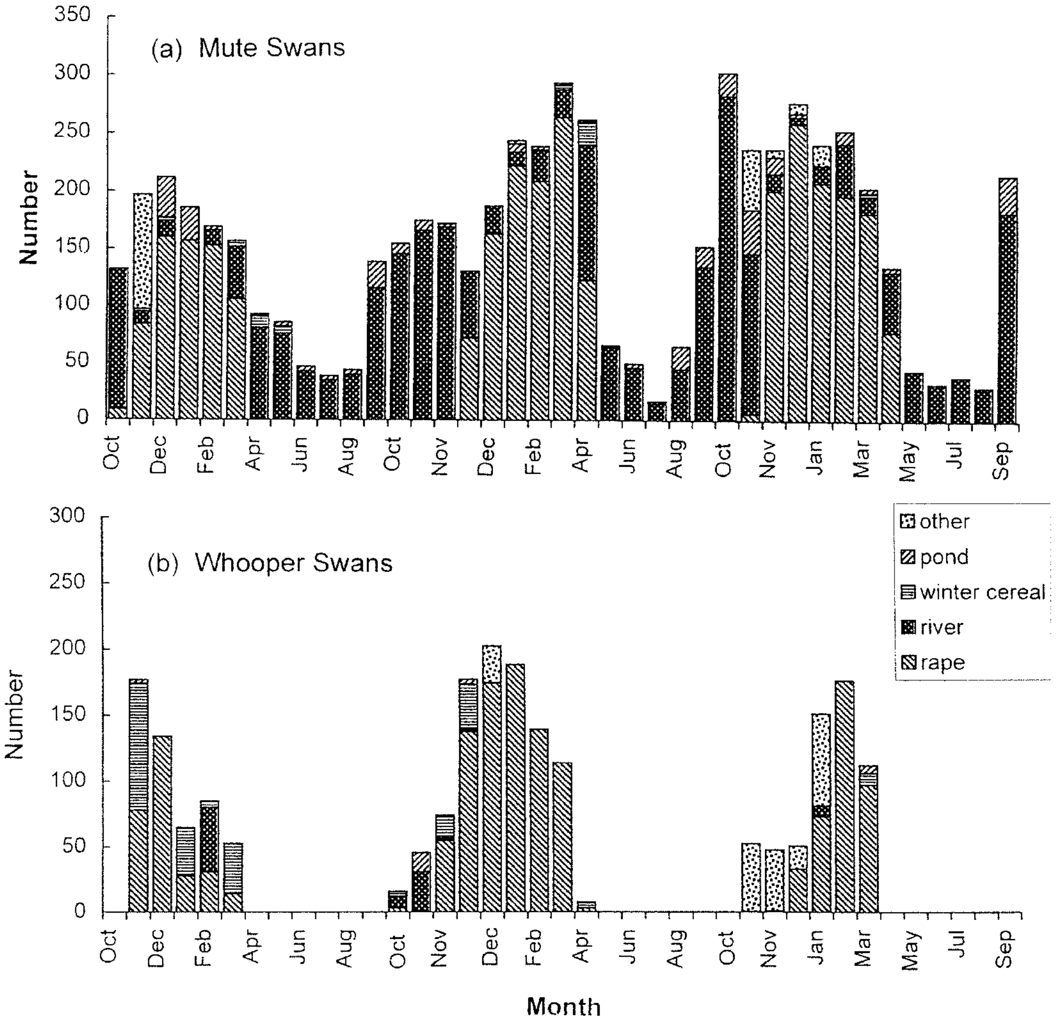

Figure 1. Habitat use by (a) Mute Swans (October 1996–September 1999) and (b) Whooper Swans (winters 1996–97, 1997–98 and 1998–99).

variables included in the binary regression. The analyses excluded those breeding pairs that remained on territory during the winter period.

DISCUSSION

The national increase in Mute Swans numbers (Delany *et al.* 1992) is reflected in the Tweed Valley in the increase in numbers of birds recorded in the molting flock at Berwick upon Tweed (Spray *et al.* 1996).

Seasonal switching between habitats by both Mute Swans and Whooper Swans is well known (Kirby *et al.* 1994) and fields are now used extensively in some areas (Rees *et al.* 1997). In the current study, the switch from aquatic habitats to field feeding usually occurred in December. This is similar to the timing of the switch from the river to improved pastures reported in the Wylye valley, Wiltshire (Harrison 1985). There birds exhibited a clear preference for improved grassland (83% of observations), compared to other crops (Trump *et al.* 1994). However, Oilseed Rape was not grown in their study area and therefore was not available as a food choice.

Table 1. Field selection by Mute Swans only, Whooper Swans only and mixed Mute/Whooper Swan flocks, from monthly surveys during three winters, 1996–97 to 1998–99.

		Mute only flocks			Whooper only flocks			Mixed Flocks					Percentage available fields used by all flock types (%)
Year	Crop utilized	No. fields used	No. of flocks	Total no. of birds	No. fields used	No. of flocks	Total no. of birds	No. fields used	No. of flocks	Total no. of birds	Total Mute Swans seen	Total Whooper Swans seen	
1996/7	Rape	15	24	588	7	8	119	9	16	721	379	342	31.9
	Winter cereal	1	3	12	5	7	170	2	2	44	6	38	0.03
1997/8	Rape	12	19	284	1	1	55	10	21	1582	738	744	22.7
	Winter cereal	2	2	48	5	6	117	1	1	18	9	9	0.02*
1998/9	Rape	15	36	916	2	2	48	5	10	534	201	333	22.6
	Winter cereal	2	2	3	2	2	13	—	—	—	—	—	0.03*
	Others	2	3	18	2	2	82	3	3	162	60	102	<1.0*

*Estimate from survey in first year of study.

Table 2. Factors affecting field selection by Mute Swans and Whooper Swans during October to March (1996–99). Analysis using Binary Logistic Regression (d.f. = 6).

	1996–97			1997–98			1998–99		
Factor	Fields with swans	Fields with no swans	Z, P value	Fields with swans	Fields with no swans	Z, P value	Fields with swans	Fields with no swans	Z, P value
Rape crop (%)	73.1	4.9	7.8 <0.001	69.7	7.9	6.6 <0.001	62.5	6.3	6.5 <0.001
Area (ha) (mean ± SD)	11.7 ± 3.9	8.2 ± 4.8	3.2 <0.001	11.8 ± 5.3	8.2 ± 4.8	2.7 <0.01	12.1 ± 5.2	8.2 ± 4.8	4.2 <0.001
Distance to water (m) (mean ± SD)	635 ± 461	688 ± 578	-1.9 <0.05	518 ± 517	692 ± 576	-2.6 <0.01	420 ± 286	695 ± 579	-4.0 <0.001
Disturbance (%)	57.7	69.5	-1.3 n.s.	43.5	69.9	-1.9 <0.05	62.5	69.4	-0.7 n.s.
High boundary (%)	12.8	21.6	0.27 n.s.	10.0	21.7	-0.85 n.s.	6.3	21.8	-1.83 n.s.
Tree (%)	16.6	27.0	0.22 n.s.	13.7	27.1	-0.43 n.s.	9.2	27.3	0.07 n.s.
Number of fields	26	742		23	745		24	744	

In the Tweed Valley, there was a difference between the behavior of Mute Swans, which grazed mainly on Oilseed Rape fields in winter and early spring, and the behavior of Whooper Swans. When feeding in single species flocks, Whooper Swans favored winter cereals, whereas when in mixed species flocks, Oilseed Rape was the preferred choice. Studies of protein assimilation by swans from oilseed rape and winter wheat have been initiated (S. Percival, pers. comm.), which may help to determine why the two species differ in crop selection. Rees *et al.* (1997) showed that, in the UK as a whole, Mute Swans were observed much more frequently in Oilseed Rape than Whooper Swans, which favored stubbles, root crops and spring cereals.

Field choice itself was dominated by Oilseed Rape as the preferred crop type; however field size and proximity to water were also important. The swans used the river and lochs as roost sites, as bathing areas and as a refuge when disturbed. Disturbance, as measured by the presence of an adjacent road, track or building, only affected field choice in one out of the three years. This may reflect the mainly rural nature of the study area, where there is little foot traffic, and disturbance would tend to be from traffic or agricultural machinery. This contrasts with the situation for Woodpigeons (*Columba palumbus*) feeding on Oilseed Rape where the presence of farm tracks adjacent to a field decreased intensity of use (Inglis *et al.* 1989).

Elsewhere in the UK, Harrison (1985) has shown that grazing by Mute Swans on improved pastures in the Wylye valley led to an 11.4% loss of yield. A study of Whooper Swans wintering on grasslands in Ireland indicated that swan grazing led to significant (up to 59%) reductions in standing crop in May, and could account for 84% of the variation in late spring yield (Colhoun and Day 2002). Locally there have been increasing numbers of complaints about damage by swans to agricultural crops and farmers have attempted to scare them or dissuade them from landing on potentially vulnerable fields. Methods used include gas guns, star shells, scaring with people and dogs and white tapes as physical barriers (pers. obs).

Damage to Oilseed Rape is a relatively recent occurrence and follows the major increase in the acreage of autumn-sown rape in the UK. Significant yield losses have been reported due to Woodpigeons and Brent Geese (*Branta bernicla*) (Inglis *et al.* 1989; McKay *et al.* 1993). As in the present study, feeding on arable land was mainly by flocks of non-territorial birds outside the breeding season.

The implications for management of potential conflict between swans and farmers are twofold. On the one hand, it is apparent that to reduce potential damage farmers would be advised to grow Oilseed Rape in smaller fields away from water. However, since rape is not grown in the same field in successive years, but on a four-year rotation, this will not always be possible. Another approach would be to set up sacrificial areas or alternative feeding sites where swans are tolerated. Such an approach has been attempted in northwest Germany for geese and swans (Sudbeck *et al.* 1996) and more recently for Mute Swans feeding on Oilseed Rape in northwest Scotland (Spray *et al.* 2002). If a number of farmers in one area can be persuaded to cooperate, in this manner, to allow for rotation of the sacrificial area between years, this approach, combined with a program to scare birds away from other potential target Oilseed Rape fields could be considered as a means of potentially mitigating problems associated with damage.

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Habitat Use and Activity Patterns of Mute Swans at a Molting and a Wintering Site in Denmark

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Abstract.—Seasonal variation in the numbers, distribution and behavior of Mute Swans (*Cygnus olor*) between two Danish brackish lagoons, Agger Fjord (a molting site) and Harboør Fjord (a wintering site), was investigated each year from 1994–1999 to determine factors influencing feeding activity and site selection. Water depth, water level fluctuations and biomass of aquatic macrophytes differed between sites, with macrophyte composition and food quality, measured as the proportion of carbohydrate and protein in the vegetation, also differing widely between sites. Rising water levels and declining food availability during autumn affected feeding intensity and foraging methods. Feeding depth on Harboør Fjord influenced spatial distribution of swans, whereas the distribution was influenced by distance to the shore on the shallower Agger Fjord. Distance to areas open to hunting had no influence on distribution. Several factors appeared to affect the swans' selection of Agger Fjord as a molting site. The macrophyte community was dominated by highly nutritious Stoneworts (*Chara* spp.) and average water depth was very low, making more food available within reach of the birds. Furthermore, human disturbance was low and undisturbed islands provided escape routes for flightless birds and refuges suitable for preening and roosting. During autumn, swans left the molting ground as the food stock was depleted, and moved to Harboør Fjord, which offered the best foraging opportunities in winter. Here the macrophyte community consisted of Spiral Tasselweed (*Ruppia cirrhosa*) and, although of low food quality, the food stock was abundant. It is suggested that water levels at Harboør Fjord be managed so that submerged macrophytes are more readily available for Mute Swans.

Key words.—*Chara, Cygnus olor*, disturbance, feeding ecology, habitat selection, macrophyte community, molt, Mute Swan, *Ruppia*, spatial distribution, time budget, water level.

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Denmark supports between 33% (60,000) in summer and 41% (73,000) in winter of the northwest European population of Mute Swans (*Cygnus olor*), estimated at approximately 180,000 birds (Joensen 1974; Andersen-Harild 1981; Rose and Scott 1994; Laursen *et al.* 1997). Because more than 20% of the total population occurs in Denmark, the protected Mute Swan fulfils the national Red List criterion, under which Denmark has a special responsibility for the species' conservation and ecological needs (Madsen *et al.* 1998). From a conservation and management perspective it is important to understand the mechanisms of feeding behavior and habitat selection, in order to ensure that swans do not abandon sites or reserves with high carrying capacities, where food resources are abundant. Possible influencing factors include human disturbance (e.g., hunting), water depth, shelter, preferences concerning the quality and use of resources (e.g., macrophytes) and how the suitability of the habitat is assessed by the swans (Kaminski *et al.* 1988).

The importance of submerged macrophytes in the Mute Swan diet is well documented (Gillham 1956; Mathiasson 1973; Owen and Cadbury 1975; Sears 1989; Madsen *et al.* 1994; Rees *et al.* 1997). In contrast, there is relatively little information published on activity patterns and site selection. Owen and Cadbury (1975) found that Mute Swans increased their feeding activity through the morning, from 20% of birds feeding at dawn to a plateau of 80% feeding three hours after sunrise. Mathiasson (1981) showed that non-breeding Mute Swans move between the same molting grounds and winter quarters year after year, but did not investigate the criteria used by the swans to choose their molting sites. In another study, Gillham (1956) suggested that feeding preferences changed with the growth phases of the food plants, and that this led to seasonal migrations from one area to another. Furthermore, seasonal movements between sites and habitat have been recorded (Mathiasson 1973; Owen and Cadbury 1975; Mathiasson 1981; Scott 1982; Sears 1989; Rees *et al.* 1997) and in some cases these have been attributed to a decline in food supply.

This study compares the number and distribution of Mute Swans using two brackish lagoons from August to December over a six-year period (1994 to 1999), and describes seasonal variation in feeding activity from September 1999 to January 2000. The areas had differing water level management regimes, which affected water depth, macrophyte composition, biomass of the standing crop and proximity of the birds to hunting. These factors made the lagoons suitable for investigating feeding behavior and assessing the abiotic and biotic factors influencing site selection by the swans.

STUDY AREA

The study was carried out on two brackish lagoons, Harboør Fjord (1.95 km^2) and Agger Fjord (3.17 km^2), lying on the peninsulas of Harboør Tange and Agger Tange, respectively, at the Limfjord, northwest Jutland, Denmark (56°43'N, 8°14'E) (Fig. 1). The lagoons were made by the Danish Hydraulic Institute, while building embankments between 1949 and 1957 (Tortzen 1966). Both peninsulas have traffic on the eastern embankment, and additionally at Harboør Tange, where the human population is greatest, a cycle track lies close to the western side of Harboør Fjord. Both lagoons are designated as Ramsar sites under the Convention of Wetlands of International Importance. Furthermore, they are Special Protection Areas under the EU Directive for the Conservation of Wild Birds. Since 1996, they have been part of the newly established reserve network in Denmark, which lies along the main waterfowl migration routes through the country, covering the important wintering and staging sites (Madsen *et al.* 1998). In addition to the preserved embankment, the areas surrounding the lagoons are mainly reed beds and salt marshes, where hunting is allowed from September to December. To investigate the effect of hunting disturbance on the distribution of the protected Mute Swan, as well as on quarry species like Wigeon (*Anas penelope*) and Teal (*Anas crecca*), the start of the hunting season in the Knopper Enge area of Harboør Fjord (Fig. 1) was delayed for two months in 1999, with the closed season ending on 1 November.

Both lagoons provide habitat for waterfowl that roost in shallow water and feed on submerged vegetation. Numbers of most waterfowl peak during autumn migration, with 1,100 Mute Swans, 7,000 Coot (*Fulica atra*), 5,000 Wigeon and 1,200 Teal constituting the most important herbivorous species (counts in 1999).

METHODS

Definitions of Water Depths, Water Levels and Feeding Depths

Throughout this paper the term "water depth" refers to the depth at a vegetation sample site or swan feeding site at DNN = zero ("Danish Ordnance Datum", a fixed point). The shallowest parts of the lagoon therefore may have water depths that are expressed as negative values (i.e., dry if DNN = zero, but potentially covered by water if water levels are high).

The water levels in the two lagoons were managed differently during the study. In Harboør Fjord there was a constantly open passage to the sea because the floodgate between Thyborøn Fjord and Limfjorden was open all year. Consequently, water levels in Harboør Fjord are determined by fluctuating water levels in Limfjorden, which in turn are determined primarily by wind-driven processes, because the tidal fluctuations are relatively small in this part of the North Sea (Clausen 1994). In Agger Fjord the floodgate was permanently closed, and the water level was therefore determined by precipitation and evaporation. Throughout this paper the term "water level" refers to the height of the water table relative to DNN = zero.

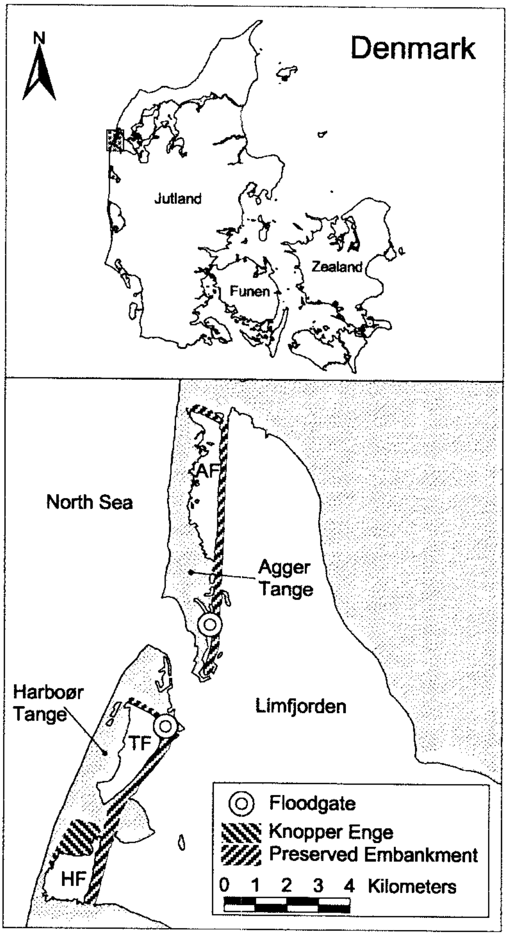

Figure 1. The study area showing the two peninsulas, Harboør Tange and Agger Tange. The brackish lagoons investigated were Harboør Fjord (HF) and Agger Fjord (AF). Due to the absence of macrophytes, very few swans were observed in Thyborøn Fjord (TF), and this lagoon therefore was not included in the study.

The term "feeding depth" is used to express the conditions met by the feeding swans. Thus, if a swan feeds at a patch where the water depth is +30 cm and the water level is +25 cm, both relative to DNN = zero, then the feeding depth will be 55 cm.

Macrophyte Sampling

To quantify the available macrophyte biomass, and to determine macrophyte distribution, depth and salinity, samples were taken along transect lines three times between 13 September 1999 and 12 January 2000. Four transect lines were laid out across Harboør Fjord and two across Agger Fjord, with the lines running in parallel and 500 m apart. Water depth was measured to the nearest cm with a dipstick at 100 m intervals along the transect lines, giving a total of 44 measures at Harboør fjord and 60 measures at Agger Fjord. Furthermore, water levels relative to DNN were recorded at least once a week between August and January. The SAS/GRAPH G3GRID procedure with spline smoothing, using the default parameter of $\lambda = 0.05$ (SAS Institute, Inc. 1990), was used on water depth and water level data recorded concurrently to estimate the depth at DNN = zero for the remaining areas of the two lagoons. Salinity was measured at fixed points at 500 m intervals along the transect lines, and six samples taken to determine biomass. Samples were obtained using a 15 cm diameter circular core-sampler, which cut 20 cm into the sediment, and the core was transferred to a sieve (1 mm mesh) where the sediment was washed and the resulting material stored in plastic bags. The macrophyte samples were then sorted into species and into live and dead material, dried to constant weight at 70°C in an oven and weighed. Standing biomass/m^2 was estimated by multiplying the dried weight (dwt) by the area of the core-sampler for each core. The biomass data were normalized by logarithmic transformation (Zar 1984), and one-way analysis of variance (ANOVA) was used to test for variation in biomass between sites.

Forage Quality

To assess the relative quality of the macrophytes, all plant material exceeding a dry weight of 10 g dry weight from each sample date, were analyzed for nitrogen, ash, sand, fat, neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin (methods follow Robbins 1993). The food composition, expressed as amounts of protein, fat, carbohydrates, hemicellulose, cellulose and lignin were calculated (methods follow Prop and Vulink 1992). The sample size (N = 2 food composition analyses for each sample date) was too small for statistical analysis.

Monitoring Mute Swans

The number of Mute Swans at the two study sites was recorded regularly between August and December each year from 1994 to 1999. Counts were made from the embankments one to five times per month using telescopes. The mean number of bird-days for each month was used to describe changes in the swans' use of the two areas. To calculate bird-days, the number of birds counted each month was summed, then divided by the number of counts per month and multiplied by the number of days in a month. Peak counts were used to express the highest number of birds observed each year. In 1999, the Mute Swan's distribution was recorded in detail by plotting the area of the flocks on maps (1:25,000). For analysis, a 250 × 250 m grid was superimposed on the maps and, assuming that there was an even distribution of birds within the flocks, numbers were apportioned between grid cells. For months in which at least two counts were made, the number of bird-days per grid unit was calculated. Stepwise multiple regression analysis was used to determine the parameters contributing to the swans' spatial distribution in the lagoons. Variables included in the analysis, measured from the center of each grid square, were distance to shore, distance to the nearest part of the salt marsh open to hunting, and water depth. Additionally, the available macrophyte biomass in each square was used as a parameter (i.e., modeled amounts of food available to the swans, corrected for feeding depth, and based on the methods given by Clausen 2000; Clausen and Holm, unpubl. data).

Time budgets were recorded at both study sites from early October to mid November 1999. Additionally, time budgets were recorded at Harboør Tange in late January 2000, where the swans were foraging in an opening in the ice. Observations were made by telescope (20–60× magnification) from sunrise to sunset when light and weather conditions permitted. Every 15–30 minutes, the number of swans engaged in various activities was recorded by scanning the flock (Altmann 1974). Recorded activities were feeding, sleeping, swimming, flying, preening, interacting and walking. Feeding techniques were also recorded as (1) *Pecking*—feeding by picking from the surface, (2) *Head-down*—feeding by submerging the head, (3) *Neck-down*—feeding with head and neck submerged, (4) *Up-ending*, and (5) *Trampling*—trampling the sediment with legs and feet to bring vegetation to the surface, thus facilitating feeding. Activity budgets were expressed as the percentage of birds engaged in each activity for each flock scan. A nested general linear model used to analyze variation in feeding activity. Bird-days and time budget data were normalized using logarithmic and arcsine transformation, respectively (Zar 1984), prior to statistical analysis using SAS/STAT (SAS Institute, Inc. 1989).

RESULTS

Water Depth, Water Levels and Macrophyte Biomass

The depth of Harboør Fjord ranged from 3–65 cm at DNN = zero, with an average depth of 36.0 ± 14.2 cm (Table 1, Fig. 2). Due to the open passage to the sea, the water level fluctuated between 0 and +58 cm (Fig. 3). Consequently, feeding depths experienced by the swans ranged from 3–65 cm at the shallowest water level, and from 53–123 cm at the highest water level. During September 1999 to January 2000, the salinity fluctuated between 7.4‰ and 33.7‰, with 98% of the lagoon covered by Spiral Tasselweed (*Ruppia cirrhosa*) and the remaining

Table 1. Maximum, minimum and mean values for depth, water level and salinity, respectively, measured during September 1999 to January 2000 in Harboør and Agger Fjord, Denmark. Water level (i.e., height of water in the fjords) and water depth (i.e., depth of vegetation at a swan feeding site) are measured in relation DNN (Danish Ordnance Datum) = zero.

	Harboør Fjord			Agger Fjord		
	Max	Min	Mean (±SE)	Max	Min	Mean (±SE)
Water depth (cm)	65	3	36.0 ± 14.2	50	-10	13.5 ± 15.1
Water level (cm)	58	0	32.0 ± 15.5	63	15	43 ± 13.9
Salinity (‰)	33.7	7.4	16.7 ± 9.3	7.27	2.2	4.5 ± 2.5

2% with Sago Pondweed (*Potamogeton pectinatus*). Between September 1999 and January 2000, the average biomass declined from 124 g to 8 g dwt m^{-2} ($F_{2,159}$ = 273, $P < 0.001$) (Fig. 3).

In Agger Fjord, the water depth ranged from -10 cm to +50 cm at DNN = zero with an average of 13.5 ± 15.1 cm (Table 1, Fig. 2). The lagoon floodgate was constantly closed and water level gradually increased from +15 to +63 cm during September 1999–January 2000, which was highly correlated with the cumulated precipitation (r_s = 0.995, N = 13, $P < 0.001$) (source: Danish Meteorological Institute), indicating little or no exchange with the sea (Fig. 3). In the same period, the salinity declined from 7.2‰ to 2.2‰. The two dominant macrophyte species were the stoneworts *Chara vulgaris* and *C. canescens* (95%), but Beaked Tasselweed (*Ruppia maritima*), Sago Pondweed and Horned Pondweed (*Zannichellia palustris*) were also present. The average biomass density in Agger Fjord declined from 38 g to 0.5 g dwt m^{-2} ($F_{2,158}$ = 53.8, $P < 0.001$) during September 1999 to January 2000 (Fig. 3).

Food Quality

The two *Ruppia* species had a high content of NDF (neutral detergent fiber) and therefore were high in structural carbohydrates such as hemicellulose and cellulose (Table 2). For *R. cirrhosa*, over 60% of the food composites were structural carbohydrates, and the nonstructural carbohydrate content declined from 17% to 7% during September to January, when the proportion of protein increased from 12% to 21%. The *Chara* species in Agger Fjord contained half the amount of structural carbohydrates found in *R. cirrhosa*, and 51% and 60% nonstructural carbohydrates in September and October, respectively.

Mute Swan Numbers and Distribution

During 1994–99, the Mute Swans used Harboør Fjord as wintering habitat, where the majority of bird-days occurred between October and December (Fig. 4). Maximum counts and bird-days decreased between 1995 and 1997 then increased to a peak in 1999. In the same six-year period the swans used Agger Fjord as a molting site, and thus most bird-days where recorded there in early autumn, between August and October. After reaching a low point in 1996, peak numbers and bird-days have increased, and a peak was reached in 1999. These seasonal changes in site selection have been very similar since the first counts were made in 1994. The distribution of the Mute Swans during the period of increasing water level from August to November 1999 is shown in Fig. 5. Stepwise multiple regression analysis showed that only feeding depth (partial R^2_{56} = 0.14, $P < 0.01$; $y = 0.356x + 0.042$, SE of slope ± 0.014,) had significant effects on the number of bird days at Harboør Fjord. In Agger Fjord, only distance to the shore (partial R^2_{94} = 0.16, $P < 0.001$; $y = 3.774x + 0.003$, SE of slope ± 0.001) had significant effects on the number of bird days. Distance to hunting (n.s.) and available food (n.s.) had no effect on distribution.

Time Budgets

Feeding (0.41 ± 0.22), sleeping (0.35 ± 0.24) and preening (0.16 ± 0.12) were the three most common behavior patterns for

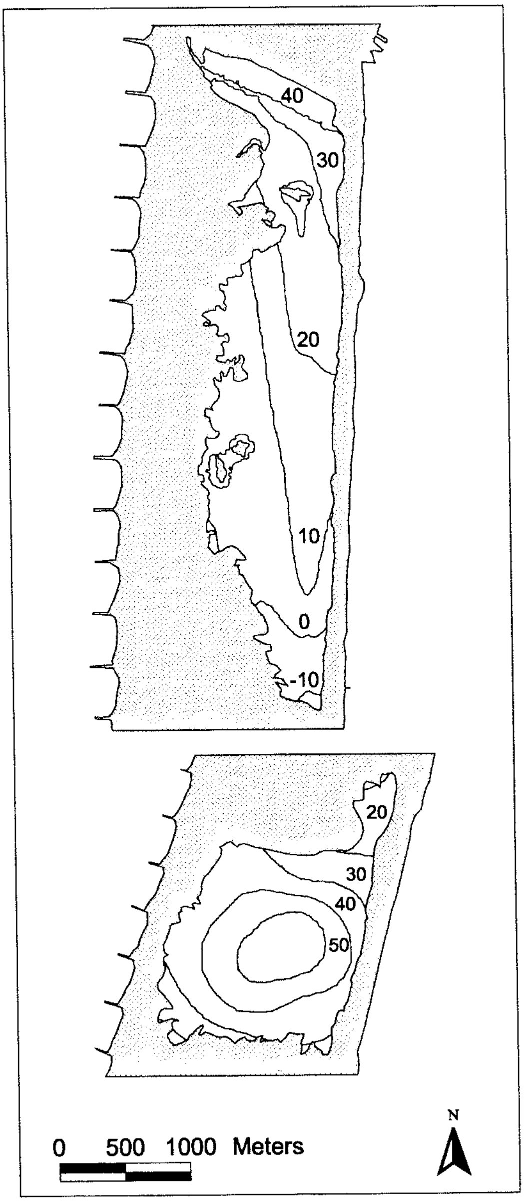

Figure 2. Water depth at zero cm DNN (Danish Ordnance Datum) in Agger Fjord (upper) and Harboør Fjord (lower).

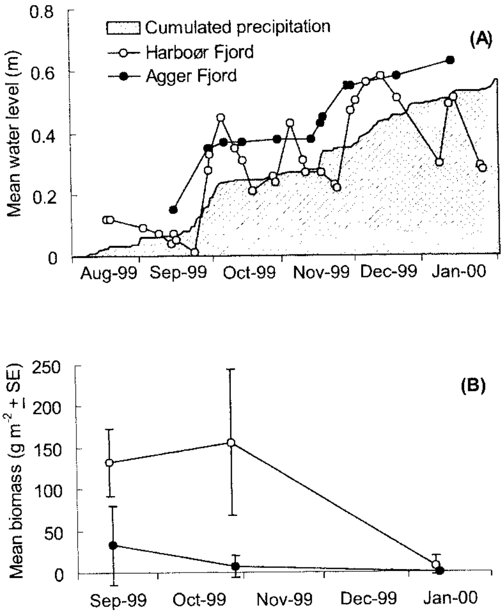

Figure 3. (A) Daily variation in precipitation (source: Danish Meteorological Institute) compared with water levels in Harboør Fjord and Agger Fjord, respectively, during August 1999 to January 2000 (source: Ringkøbing County and personal readings). (B) Variation in macrophytes biomass in autumn and winter.

Mute Swan in Harboør Fjord between September 1999 and January 2000 (Fig. 6). There was a significant difference in the percentage of time feeding between October, November and January ($F_{2,183} = 42.6$, $P < 0.001$) due to feeding activity being significantly higher in November than the other months (Tukey, $P < 0.001$). There was no difference between the October and January observations (Tukey, n.s.). Due to limited areas of open water in January, the birds could not all feed at the same time, lowering foraging time and intake rate to the October level. The predominant foraging method was neck-down (Fig. 6), and the extent to which the birds fed in this way varied between months ($F_{2,211} = 40.0$, $P < 0.001$). Neck-down foraging increased between October and November (Tukey, $P < 0.05$) when the water level rose and the biomass of the macrophytes decreased. In January, there was a substantial decrease in neck-down foraging (Tukey, $P < 0.001$) and an increase in up-ending (Tukey, $P < 0.001$). The feeding activity in Agger Fjord (Fig. 6) was significantly higher in mid November than in early October ($F_{1,113} = 8.27$, $P < 0.01$). The neck-down foraging method ($F_{1,118} = 9.31$, $P < 0.01$) and the trampling method ($F_{1,118} = 4.48$, $P < 0.05$) were significantly increased over the same period.

There was no difference between Agger Fjord and Harboør Fjord in the percentage of time spent foraging in early October

Table 2. Composition of *Ruppia cirrhosa*, *R. maritima* and *Chara* spp. in Harboør Fjord and Agger Fjord, respectively. All analyses were done twice and the mean values calculated. Data are missing where biomass was too low for analysis. The percentages in organic (ash free) dry matter do not add up to 100% because acid detergent fiber (ADF) and lignin are composites of neutral detergent fiber (NDF).

		Macrophyte species		
		Ruppia cirrhosa	*Ruppia cirrhosa*	*Ruppia cirrhosa*
Harboør Fjord	Date	13 Sep 1999	28 Oct 1999	11 Jan 2000
Measured % in organic (ash free) dry matter				
Nitrogen		1.9	2.4	3.3
Fat		1.6	1.7	1.0
Neutral Detergent Fiber (NDF)		70.0	70.9	71.4
Acid Detergent Fiber (ADF)		54.8	54.8	
Lignin		8.4	8.2	9.4
Calculated food composition (%)				
Protein		11.6	15.1	20.8
Fat		1.6	1.7	1.0
Non-structural carbohydrates		16.8	12.3	6.8
Hemicellulose		15.2	16.1	
Cellulose		46.4	46.6	
Lignin		8.4	8.2	9.4

		Macrophyte species			
		Chara spp.	*Chara* spp.	*Ruppia maritima*	*Ruppia maritima*
Agger Fjord	Date	14 Sep 1999	29 Oct 1999	14 Sep 1999	29 Oct 1999
Measured % in organic (ash free) dry matter					
Nitrogen		2.0	1.9	2.8	3.3
Fat		0.9	0.9	0.8	1.5
Neutral Detergent Fiber (NDF)		36.0	27.1	62.5	61.2
Acid Detergent Fiber (ADF)		30.4	26.7		
Lignin		3.2	2.4		12.1
Calculated food composition (%)					
Protein		12.6	11.8	17.2	20.5
Fat		0.9	0.9	0.8	1.5
Non-structural carbohydrate		50.6	60.2	19.4	16.7
Hemicellulose		5.6	0.4		
Cellulose		27.1	24.3		
Lignin		3.2	2.4		12.1

($F_{1,119}$ = 2.93, n.s.), but in mid-November, the swans foraged at a higher rate at Agger Fjord ($F_{1,162}$ = 27.2, $P < 0.001$).

DISCUSSION

Mute Swans used Agger Fjord primary as a molt site and Harboør Fjord as a wintering site during the study. One of the main differences between the two areas investigated, are the water level management. The open floodgate at Harboør Tange (Fig. 1) resulted in fluctuating water levels and a more saline environment (Table 1) compared to Agger Tange, where the connection between the lagoon and the highly saline seawater (35%) was closed. The low salinity makes the plant community more diverse (Santamaria *et al.* 1996) with freshwater species such as the *Zannichellia* and the *Chara* spp. The difference in plant communities between the two lagoons is reflected in large difference in the nutrient content of the dominant plants (Table 2). The large proportion of hemicellulose and

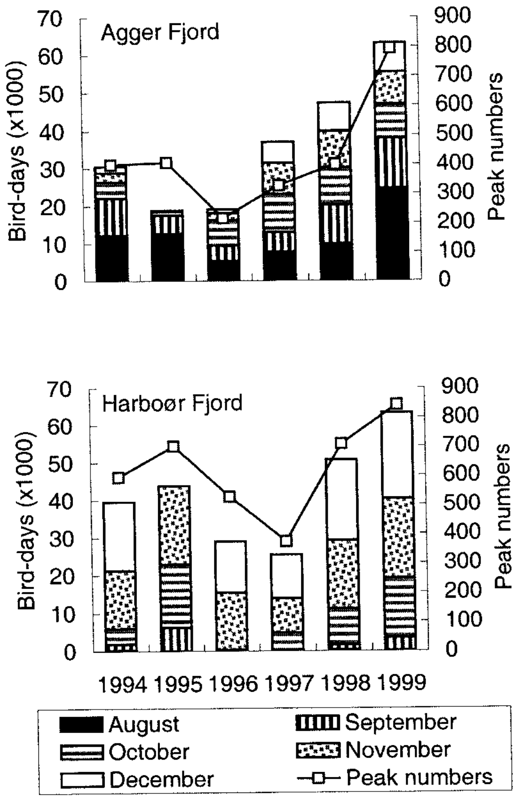

Figure 4. Seasonal variation in numbers of Mute Swans 1994–99 in Agger Fjord (upper) and Harboør Fjord (lower), expressed by the number of bird-days (August–December), and the peak number recorded in the lagoons within an autumn season.

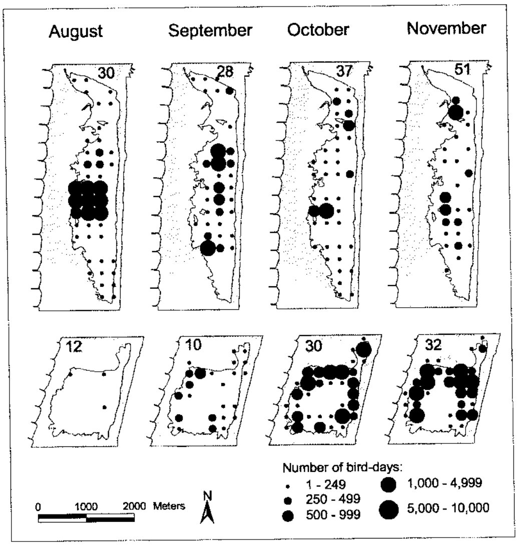

Figure 5. Distribution of Mute Swans at Agger Fjord (above) and Harboør Fjord (below) during August–November 1999, expressed by the number of bird-days in 250 × 250 grid squares. The average water level (cm relative to Danish Ordnance Datum) when counting the swans is shown above the lagoons.

cellulose, the main structural carbohydrates of the plant cell walls (Robbins 1993), in *R. cirrhosa* at Harboør Fjord, are hard to digest in waterfowl and likewise hampers the digestion of the plant cell contents (Prop and Vulink 1992). This and the low content of nonstructural carbohydrates make *R. cirrhosa* low quality food, which is utilized most efficiently by birds with a long retention time. For the *Chara* species in Agger Fjord, the low structural carbohydrate content and high proportion of easily metabolizable components such as protein and nonstructural carbohydrates, make these plants high quality food (see Fox *et al.* 1994). Swans therefore, can derive more energy from the *Chara* spp. in Agger Fjord than from the same amount of *Ruppia cirrhosa* in Harboør Fjord.

Another main difference between the lagoons is their depth profiles. Agger Fjord was shallower on average and had a greater range of water depth than Harboør Fjord, which together with the small and undisturbed islands, provided higher habitat diversity. Molting and autumn staging swans used the islands to preen and for shelter (pers. obs.). The low average water depth and resulting feeding depths met by the swans probably makes foraging less energy demanding (Nolet *et al.* 2001). This is supported by the spatial distribution of birds in Harboør Fjord, where the swans avoid the center of the lagoon (Figs. 2 and 5). Even though they are able to reach approximately one meter depth when up-ending (Madsen *et al.* 1994; Owen and Cadbury 1975) and thus are able to reach the macrophytes in most of the lagoon, they exclusively forage by submerging their necks on the shallowest water near the coast.

A difference in disturbance level is also likely. Madsen *et al.* (1994) investigated Mute Swans around Saltholm Island and argued that swans use shallow waters as molting habitat, because they provide both low disturbance rates and abundant food resources. Both Harboør Fjord and Agger Fjord have a high biomass of aquatic vegetation during the molting

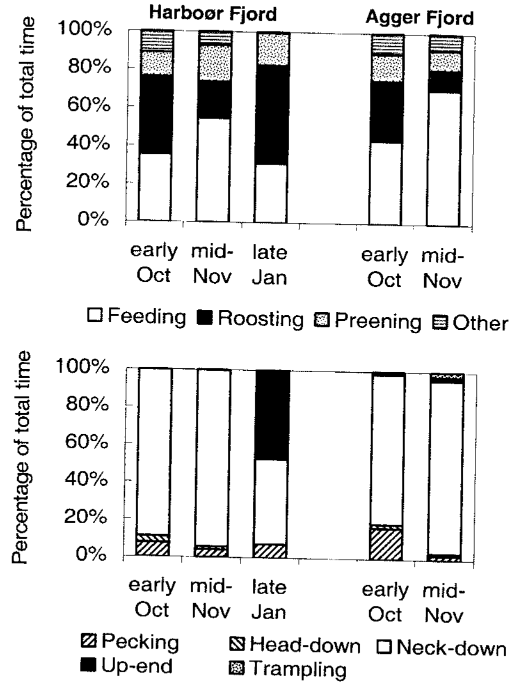

Figure 6. Mute Swan activity during October 1999 to January 2000 (above) and the percentage of total feeding time spent in five foraging modes (below). The three left and two right columns are data from Harboør Fjord and Agger Fjord, respectively.

period (August), but there may be more disturbances at Harboør Fjord. The higher human population and the possibility for more traffic indicate that this site may have a higher disturbance level than Agger Fjord. Furthermore, the topography (i.e., escape routes) may make Agger Fjord more attractive to swans during molt. It is reasonable to assume that birds in a flightless state choose sites that facilitate disturbance avoidance. However, this study showed no effect of hunting on Mute Swan distribution. Furthermore, Tuite *et al.* (1984) found that Mute Swans are extremely tolerant of human activity, and Madsen *et al.* (1994) observed that swans showed low level avoidance behavior, and quickly resumed their activities when disturbed by fishing boats.

Water level and declining food availability affected feeding intensity and foraging methods. Compared to October, birds started to forage earlier relative to sunrise in mid November and fed for a greater proportion of the day during the shorter, colder days. In Agger Fjord, the rise in water level, together with the decreased vegetation biomass, made feeding more time-consuming. Here the reduced macrophyte availability forced the Mute Swans to use more time consuming foraging techniques, such as trampling, to seek their food deeper in the water column. In January, there was no change in feeding activity during the day, probably because of limited available space in the ice holes. Only approximately half of the swans could forage at one time here, reducing the overall foraging to the October level.

Food availability possibly triggers the seasonal move between Agger (molt) and Harboør (wintering) Fjords. As biomass of submerged macrophytes decreased, swans in Agger Fjord spent more time foraging than at Harboør Fjord, and also began using foraging methods that may be more energy demanding. According to optimal foraging theories, swans probably try to maximize intake while minimize foraging costs. Therefore, Mute Swans consume the high quality food in Agger Fjord during molt, but when the food stocks are depleted, they move to Harboør Fjord where food is of lower quality but more readily available. I conclude that Mute Swans molt on Agger Fjord because of its: (1) diverse high quality macrophyte community; (2) low water depth which facilitates foraging; (3) relatively low human disturbance level and the availability of escape habitats; and (4) undisturbed islands which provide refuges for preening and roosting.

Management Implications

Agger Fjord is in a low saline state, where water level, due to the closed floodgate, is controlled by factors such as precipitation and evaporation. Limiting factors for autumn staging swans are decreasing food availability, probably because of grazing by waterfowl and decay. The six years of investigation shows that this most likely is a steady state, giving molting swans good feeding and roosting opportunities. Hence, there should not be any changes in floodgate management.

At Harboør Fjord, the open floodgate results in a more fluctuating saline environment. In autumn, managers should consider closing the floodgate when water level rises in the sea, in order to keep water level at a lower point in the lagoon. This could make more of the abundant food stock readily available in autumn and winter and make foraging less energy demanding. A lower water level could be an advantage, not only to Mute Swans, but also for other herbivorous species like dabbling ducks.

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Population Structure, Survival Rates and Productivity of Mute Swans Breeding in a Colony at Abbotsbury, Dorset, England

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Abstract.—This paper describes factors affecting the size of the Mute Swan (*Cygnus olor*) colony breeding at Abbotsbury, Dorset, a site free from most of the common causes of mortality encountered by swans occurring elsewhere in the UK. The greatest effect on breeding numbers is the survival rate of the breeding adults, which varies with year and has increased with time. The proportion of birds known to have bred, but which fail to breed in any year, varies from 2% to 28%. The number of new breeders in any year is dependent on cygnet survival in their first year, together with the age at which they start to breed. New breeders tend to start breeding at a younger age in years when conditions for breeding seem good (as judged by an increase in the breeding population over the previous year); the reasons for the differences between good and poor years are not known. Despite the site being apparently ideal for the swans, the overall survival and longevity does not differ greatly from Mute Swans studied elsewhere in the UK.

Key words.—Adult survival, age of first breeding, cygnet survival, *Cygnus olor*, Mute Swan, non-breeding adults, population change.

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The Mute Swans (*Cygnus olor*) breeding colonially at Abbotsbury, Dorset, England are unusual in that they do not encounter many of the hazards experienced by most wild Mute Swans in Europe. These include risks of flying into overhead cables (O'Halloran *et al.* 1989; Perrins and Sears 1991), collisions with other objects including boats and bridges, oiling, becoming entangled with fishing tackle and swallowing hooks (Perrins *et al.* 2002) and lead poisoning. Most colony-hatched birds remain in the vicinity of the colony all their lives and hence never encounter any of these hazards. They have abundant stocks of natural foods for much of the year, especially eelgrass (*Zostera* spp.) and tassleweed (*Ruppia* spp.), and are fed supplementary grain, especially in hard weather.

Despite this apparent safety, colonial birds live at high densities, males fight frequently and spend a significant proportion of their day in milder aggressive interactions with their neighbors. In bad weather, especially during southwesterly gales, they can be exposed to very windy conditions and in some years much of their natural food may be uprooted, blown ashore and destroyed. Red Foxes (*Vulpes vulpes*) and European Badgers (*Meles meles*) are present and, although they seldom take fully-grown swans, they may raid the nests. American Mink (*Mustela vison*) and possibly some other mustelids take a number of small cygnets, but pose no threat to the adults.

The aim of this paper is to examine the age structure of the population, to measure survival rates for breeding adults and for cygnets from banding to first breeding, and to use these data to determine factors affecting the number of birds breeding in the colony each year.

STUDY AREA AND METHODS

Study Area

The study site at the Abbotsbury Swannery and adjacent Chesil Fleet (50°35'N, 2°30'W), on the coast of southern England, is described in detail elsewhere (Perrins and Ogilvie 1981; Perrins and McCleery 1996). The Fleet is a tidal lagoon that runs parallel to the sea for 14 km, and is separated from the sea by a high pebble ridge. The Mute Swan colony at Abbotsbury has existed at least since the 1300s, but little is known of the numbers of birds present throughout this time. In 1591, a dispute between Queen Elizabeth I and the owners concerned "Five Hundred Swans of which Four Hundred and ten were white and Ninety the residue etc. are Cygnets." These numbers, recorded at a time when almost all Mute Swans in England were owned and pinioned (Birkhead and Perrins 1986), are similar to current ones, with 330-949 birds (breeders and non-breeders) at Chesil Fleet and Radipole Lake in the 1970s, and up to 1,238 present in 1980 (Perrins and Ogilvie 1981). The site is not completely natural in that some supplementary food is provided for both adults and cygnets. Moreover, cygnets from different broods tend to mix after hatching, and some are put into pens where traditionally they were fattened for food. These have higher survival than cygnets left outside the pens. Hence it has not been possible to follow in detail the survival of the young in the first few months after hatching. In late September or October, when the cygnets are more or less fully grown, the penned cygnets are released and rejoin the others on the Fleet. All cygnets were marked with large, plastic leg bands, each engraved with a three-number or three-letter code, and weighed immediately before release. In this study, cygnet survival therefore is defined as the percentage of each year's cohort that has survived from banding to breeding. This slightly underestimates the total number of cygnets that have survived, since some of the marked birds are known to have emigrated. Also, for the most recent years, some birds present have not yet started breeding.

Survival Analysis

Data on individual swans breeding at Abbotsbury have been recorded since 1976; almost all pairs that had a nest in which at least one egg was laid, have been included in the database. In a very few cases, where a nest failed early, one or both parents may not have been identified. Pairs occasionally nest on the Chesil Bank, opposite the Swannery, or elsewhere along the Fleet; almost without exception these fail, and the identities of the breeding birds are not known.

By 1990, almost all birds present when the study started, and therefore not of known age or origin, had died. From 1990 onwards, about 95% of 327 breeding females and 84% of 365 breeding males were born in the colony, the remainder being immigrants from elsewhere. Release-recapture models were used to estimate the adult swans' survival rates, by sex, year and age. Recapture histories were generated for all Abbotsbury-born birds that bred at least once. These were treated as adult recapture histories, with the first breeding attempt being the release occasion. Goodness of Fit testing for the Cormack-Jolly-Seber (CJS) model, treating the sexes as two groups for both resighting and survival probability, was carried out using the program RELEASE (Burham *et al.* 1987), as recommended by White and Burnham (1999). This was implemented as a part of the MARK program system. RELEASE tests the CJS model assumptions that (1) every marked animal in the population at time i has the same probability of recapture at time $i + 1$, and (2) every marked animal in the population immediately after time i has the same probability of surviving to time i+1. There are two further assumptions not tested by RELEASE, namely that (3) marks are not lost or missed on captured animals, and (4) sampling is instantaneous, relative to the time between sampling occasions. These last two are true in our data. The tests are contingency analyses, using the χ^2 statistic to test for a lack of association between marked status or previous capture status and subsequent recaptures. Thus significant χ^2 values indicate departures from the assumptions of the models.

RELEASE provides TEST1 for group differences in survival and/or capture rates when there is more than one group, but its use is strongly deprecated by Cooch *et al.* (1996) on the grounds that the model tested is much more restricted than the MARK model, which provides different recapture and survival estimates for each group at each time. It therefore was not used in this case. TEST2 measures the uniformity of recapture. The assumption may fail, for example, due to trap-shyness or trap-happiness. In the adult dataset, there was some heterogeneity in TEST2 for the two sexes, but no clear pattern could be detected. The combined goodness of fit score for TEST2 was significant (χ^2_{40} = 169, P < 0.001). TEST3 measures uniformity of survival probabilities. For example, it may fail when there is age structure in the data, which is not permitted in the basic CJS model. In our data, TEST3 was not significant in either sex (females χ^2_{39} = 23.2, n.s.; males χ^2_{40} = 31.0, n.s.). The sexes therefore were combined in subsequent analyses. The combined goodness of fit score for TEST2 and TEST3 was significant (χ^2_{119} = 224, P < 0.001). A correction factor of 1.88 (calculated as 223.83/119), which is within satisfactory limits (Cooch *et al.* 1996), therefore was applied to the hypothesis tests carried out within MARK. The use of a correction factor does not affect the parameter estimates, but does affect their standard errors and the goodness of fit criterion, which becomes the "corrected Quasi-Aikike Information Criterion" (QAICc).

A second data set included all Abbotsbury-born cygnets, including those never detected breeding. Since Mute Swans do not breed at age one, we advanced the "release" observation by one year, so that all cygnets were deemed to be released during their second year, to test for age-dependent survival for all birds of breeding age. In fact very few birds breed at age two, which generated a very strong age structure in this dataset. Inspection of RELEASE TEST2 and TEST3 revealed a poor fit (TEST2 + TEST3, χ^2_{121} = 4,028, P < 0.001). Inspection of the survival contingency tables for TEST3R showed that at every observation time (i), birds seen prior to time (i) were more likely to be seen again than those not previously seen (i.e., those being released on this occasion). This reflects the lower return rate of first-year and second-year swans compared with birds that had started to breed. In the resighting contingency tables for TEST3Sm, most of the birds not seen before were also not seen in the next year, but many were seen subsequently, reflecting the "temporary emigration" of pre-breeders from the dataset. To confirm this interpretation, we constructed a third dataset by deleting the release observation from each recapture history, and repeating the RELEASE analysis. TEST3 of this analysis was not significant (χ^2_{38} = 40.4, n.s.), indicating that using an age-structured model as the global model in the survival analysis would be satisfactory.

The test for uniformity of recapture (TEST2) also showed a lack of fit when the dataset included the Abbotsbury-born cygnets (χ^2_{80} = 547, P < 0.001). The contingency tables indicated that, in 13 out of 23 years, the departure from the binomial is consistent with a bird seen in year (i) being more likely to be seen in year (i + 1) than a bird not seen in year (i). This could be partly due to the "temporary emigration" of pre-breeders from the dataset, with a bird not recorded on the first occasion after release being less likely to be recorded in the following year than one that has already started to breed. Checking this interpretation by using the dataset without cygnet release observations reduced the TEST2 statistic to χ^2_{21} = 167 (P < 0.001). The overall goodness of fit for the model without cygnet releases (TEST2 +

TEST3, $\chi^2_{59} = 208$, $P < 0.001$), suggested a correction factor ($\hat{c}$) of 3.5. We concluded that the age structure generated by young birds returning to breed is responsible for most of the extra-binomial variation in the cygnet dataset. In our analysis of age-related survival we therefore used a model with full age dependence as the global model. A bootstrap goodness of fit simulation for the fully age-dependent model gave a mean $\hat{c} = 5.81 \pm 0.04$ SE, for N = 30 simulations), and a mean deviance of 2721, with mean d.f. = 469. This compares with a deviance of 3132 with d.f. = 359 ($\hat{c} = 8.73$) for the actual data. The more conservative calculation of $\hat{c}$ for the data is:

$$\hat{c}(\text{model})/\hat{c}(\text{simulations}) = 8.73/5.81 = 1.50$$

This value therefore was used in testing hypotheses for age-dependent models, as indicated in the documentation for the MARK program.

RESULTS

Population Size and Annual Adult Survival

The number of breeding pairs has increased during the course of the study (Fig. 1). In all years, birds that have bred previously are the major component of the breeding population, and hence adult survival has an important influence on the number of breeding pairs. Table 1 shows the summary statistics for all models involving sex and time, ranked by corrected Quasi-Akaike's Information Criterion values (QAICc; the lowest value indicating the model that best fits the data), down to the CJS model $\text{Phi}_{(g^*t)}.p_{(g^*t)}$. These include two models that treat time as a continuous variable (numbers 3 and 4). The most satisfactory model is $\text{Phi}_{(t)}.p_{(t)}$, that is with common survival for males and females, but with a separate survival estimate for each year (Fig. 2). The survival rate for the year 1979 has a value of 1.0 because all the birds known to be alive in 1979 survived at least until 1980.

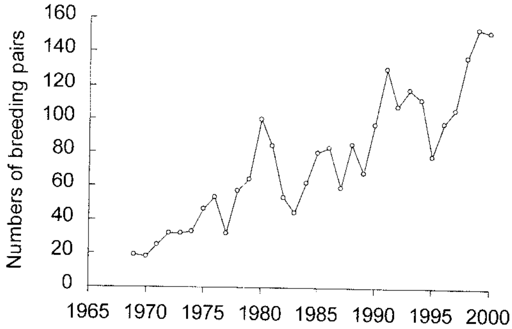

Figure 1. The number of breeding pairs of Mute Swans recorded at Abbotsbury, 1969–2000.

Table 1. Summary statistics for all models ranked by Quasi Aikike Information Criterion (QAICc; see Methods). Phi represents the survival estimate and p is the resighting probability. Subscripts are t for time dependence, and g for group dependence. Phi(seniority) is a model with a pseudo age structure based on time since the animal was marked and released. Phi(covariable) fits a model with time as a continuous variable. The modified model Phi(covariable 80 on) $p_{(t)}$ fits a separate parameters for the first four years of the study, which are poorly estimated and one of which has a very low survival estimate (Fig. 2). The most satisfactory model is $\text{Phi}_{(t)}.p_{(t)}$, indicating time-dependent survival rates and resighting rates, with no difference between the two groups (i.e., between males and females). This is a significantly better fit than the model for a time trend in survival (Likelihood Ratio test, $\chi^2_{18} = 71.1$, $P < 0.001$), indicating that while the time trend is significant, there is also significant between year variation over and above the trend. The equation for the fitted line is logit(Phi) = 1.01 + 0.06(year). The slope differs significantly from zero, ($b = 0.06 \pm 0.02$, $z = 3.67$, $P < 0.001$).

Model	QAICc	Delta QAICc	Parameters	Deviance
$\{\text{Phi}_{(t)}.p_{(t)}\}$	2349.2	0	45	1611.9
$\{\text{Phi(covariable 80 on}.p_{(t)}\}$	2350.1	0.9	27	1683.0
$\{\text{Phi(covariable)}.p_{(t)}\}$	2355.7	6.5	25	1701.2
$\{\text{Phi}_{(.)}.p_{(t)}\}$	2365.4	16.1	24	1723.1
$\{\text{Phi}_{(g)}.p_{(t)}\}$	2366.0	16.8	25	1720.6
$\{\text{Phi}_{(t)}.p_{(g^*t)}\}$	2372.4	23.2	64	1581.1
$\{\text{Phi(seniority)}.p_{(t)}\}$	2372.7	23.4	37	1686.9
$\{\text{Phi}_{(g^*t)}.p_{(t)}\}$	2384.4	35.2	65	1669.6
$\{\text{Phi}_{(.)}.p_{(g^*t)}\}$	2388.5	39.2	43	1665.7
$\{\text{Phi}_{(g)}.p_{(g^*t)}\}$	2389.8	40.5	44	1668.1
$\{\text{Phi}_{(t)}.p_{(.)}\}$	2392.2	43.0	24	1599.7
$\{\text{Phi}_{(t)}.p_{(g)}\}$	2392.7	43.4	25	1693.4
$\{\text{Phi}_{(g^*t)}.p_{(g^*t)}\}$	2410.5	61.3	85	1691.9

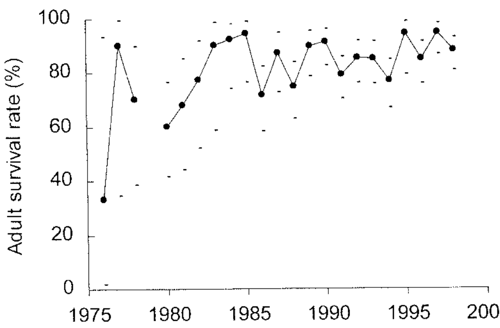

Figure 2. Annual adult survival rates for Mute Swans at Abbotsbury (circles), and the 95% confidence intervals (bars), 1976–1998. The survival rate for 1979 could not be estimated.

There appeared to be a lower survival rate in the early part of the study, but the errors on these early estimates are large (Fig. 2). The average annual survival rate was 81.2% (±1.8) for 1980-89, compared with 86.7% (±1.1) for 1990-98, and 85.0% (±0.9) for the duration of the study. The upward trend in survival was tested by treating time as a continuous variable and testing for a slope on the logit scale (model fitted: logit(p) = intercept + slope*time), with separate estimates for the early years and a linear trend from 1980 onwards. The slope of 0.05 (± 0.01), intercept = 1.03, for the years 1980-98 was significantly greater than zero (z = 3.3, P < 0.01).

Age-Related Survival

Obtaining a measure of age-related survival is more difficult in long-lived birds, such as the Mute Swan, because of small sample sizes in the older age categories. However, because the previous models found no differences between the sexes in survival rates, it was possible to combine data for the sexes in subsequent analyses. The model {Phi(age) .p{age)} was used as the global model for this analysis, which included release data for cygnets, with ĉ = 1.50 as the correction factor (as explained in the Methods). Few swans survive beyond 14 years of age, and parameters for ages 15–23 years were poorly estimated, so the model was refined to {Phi(age to 14).p(age to 14)}.

Recapture probability increased steadily from age one, but leveled off between age five and seven. Survival appeared to increase for the first three years after "release" (with "release" classified as the year after birth) before stabilizing, with indication of a decline in the later age groups (Fig. 3). Refining the recapture structure, by incorporating a constant recapture rate from age five, improved the fit (i.e., lowered the QAICc) and adding time dependence for birds aged six years or more improved the fit still further (recorded as p(age to 5 + t) in Table 2), so this recapture structure was used for the rest of the analysis.

In view of the survival estimates obtained, a reduced age class model {Phi(age reduced). p(age to 5 + t)} was fitted to the data, with age classes 0–2, 2–3, 3–12, 12–13, 13–14, 14–15+. This provided a better fit than the {Phi(age to 14).p(age to 14)} model (Table 2). The parameters of {Phi(age reduced).p(age to 5 + t)} still showed a decline in survival in the older age classes. A composite model with a linear trend for the last three age groups {Phi(age 1, 2, 3–12, covar 12–13, 13–14 and 14–15+).p(age to 5) + t} was used to test this trend. The model fitted, log(phi/(1-phi)) = intercept + slope*age, was marginally preferred to the one with 4 age classes, and the

Figure 3. Adult survival rate and age. Survival estimates are from the preferred model (see text). Estimates for the first three age groupings (i.e., age class 0–2, 2–3, 3–12) are separate. The last 3 points (i.e., age classes 12–13, 13–14, 14–15+ years), are fitted by the model: logit (Phi) = 3.24–0.55*age. Fitted values of the logit model have been back transformed to the linear scale of probability (Crawley 1993, page 170). Note that the curvature results from the transformation. The slope (*b* ± SE) of the logit regression is significantly different from zero (*b* = -0.55 ± 0.19, z = 2.89, P < 0.01).

Table 2. Summary statistics for survival and age. The models are ordered by their corrected Quasi Aikike Information Criterion. The model notation is intended to be self-explanatory; the model definitions are given in full in the Results section. All QAICc calculations are based on a correction factor of ĉ = 1.50, which is derived from a bootstrap Goodness of Fit simulation for the model {Phi(age).p(age)}. The recapture part of the model has age dependent recapture up to age five and time dependent recapture thereafter. The preferred model has separate parameters for survival fledging to age two, survival from age two to age three, constant survival from age four to age 11, and a declining survival rate (linear on the logit scale) for age 12 and above. The slope of the line differs significantly from zero (*b* = -0.56 ± 0.1, z = 5.6, P < 0.001).

Model	QAICc	Delta QAICc	Parameters	Deviance
{Phi(age 1, 2, 3–12, covar 13+).p(age to 5) + t}	6443.0	0.0	28	2994.6
{Phi(age reduced).p(age to 5 + t)}	6343.7	0.75	29	2992.7
{Phi(age 1 & 2, 3–12, covar 13+).p(age to 5) + t}	6343.9	0.88	27	2998.9
{Phi(age to 14).p(age to 5 + t)}	6344.4	1.06	37	2969.3
{Phi(age).p(age)}	6440.8	97.9	31	3132.3
{Phi(age to 14).p(age to 14)}	6441.2	98.2	28	3149.3

slope differed significantly from zero (*b* = -0.56 ± 0.10, z = 5.60, p < 0.001) on the logit scale. This model is preferred by the QAICc criterion (Table 2), but does not differ from {Phi(age reduced).p(age to 5 + t)} on a likelihood ratio test (χ^2_1 = 1.91, n.s.), indicating that most of the variation in survival rate of the older age classes could be described by a linear trend. The magnitude of this decrease is considerable, from a mean annual survival of 89% (±0.7) at ages 3–11 years, to 60% (±7) at ages 14 or more.

Non-breeding

Each year, some swans that have bred in earlier years do not do so, but do breed again in a subsequent season. These are here defined as skippers, because they skip breeding in one or more years. In this study, exactly 400 bird-years of potential breeding were lost, an average of 9% per year, varying from 2% to 28%. As the birds get older, they may skip breeding more frequently. In both sexes, the proportion of non-breeding birds is significantly higher for swans aged 11 years or more (χ^2_1 = 9.1, P < 0.005, Fig. 4). The proportion of males and females that were skippers did not differ significantly (92/729 males versus 103/658 females; χ^2_1 = 2.6, n.s.).

Skipping was also associated with population change during the 1990s. The effects seem to have become greater following the increase in the number of breeding pairs in the second half of the decade (Fig. 1), with a significant (negative) correlation between the numbers of skippers and the numbers of nests (r_7 = -0.81, P < 0.01; Fig. 5).

Cygnet Survival

The survival to breeding of cohorts of cygnets hatched in different years has varied almost seven-fold, ranging from 9% to 62% (Fig. 6). Survival was not related to the mean fledging weight of the cohorts (r_{19} = 0.05, n.s.). Within cohorts however, the heavier young of both sexes are more likely to survive than the lighter ones (Perrins and Ogilvie 1981).

It is likely that the largest and most variable part of this mortality occurs in the first year after hatching, when the swans are least experienced (Perrins and Ogilvie 1981). Cygnet survival from fledging to breeding correlated with the adult survival rate in the

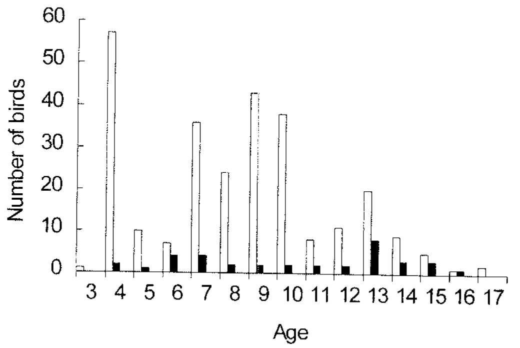

Figure 4. The age of Mute Swans that bred in 1999, and were still present in the colony in 2000, in relation to whether they bred (open columns) or did not breed (filled columns).

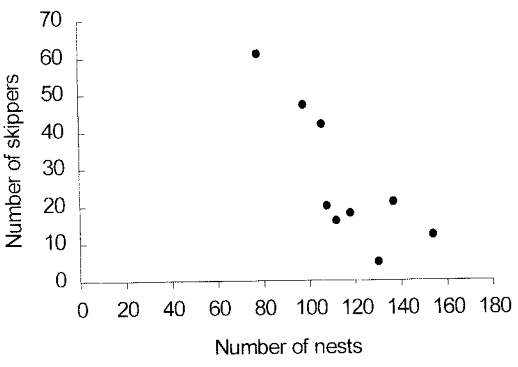

Figure 5. The number of swans that skipped nesting in relation to the numbers of nests, 1991–1999.

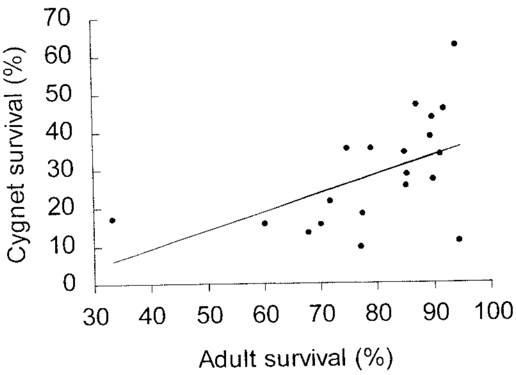

Figure 7. The relationship between the survival of cygnets from fledging to breeding and adult survival in the cygnets' first year of life.

cygnets' first year of life, though more strongly for the years 1976-1989 ($r_{12} = 0.65$, $P < 0.05$), than throughout the study ($r_{18} = 0.47$, $P < 0.05$; Fig. 7).

Age of First Breeding

Ages of first breeding for 357 females and 332 males that hatched in the Abbotsbury colony are shown in Fig. 8. The mean age at first breeding was slightly higher in males than in females (4.61 years, compared with 4.31), but the distributions do not differ statistically (Kolmogorov-Smirnov two sample test, K = 1.26, n.s.) and a small number of birds of both sexes (six males, three females) did not appear to breed until they were aged ten or older.

Mean age of first breeding varied between cohorts, from about 3.4 years for swans hatched in 1986 to 5.4 years for the 1990 cohort, but was strongly correlated between the sexes ($r_{18} = 0.58$, $P < 0.01$). There was no change in the age of first breeding with time (linear regression, $F_{1,18} = 0.01$, n.s.) The cohorts were divided into two groups; those with mean dates of first breeding of around four years and those of around five years. Since the birds commonly start breeding at age three or four, those cohorts that had a mean age of first breeding of five years were assumed to have encountered unfavorable conditions in the year when they were four, which caused them to delay breeding. Springs therefore were divided into "good" (those where the cohort from four years earlier started to breed) or "poor" (those when the four-years old cohort mostly deferred breeding to the next year). The two cohort groups were considered in relation to the residuals of the number of nests against year

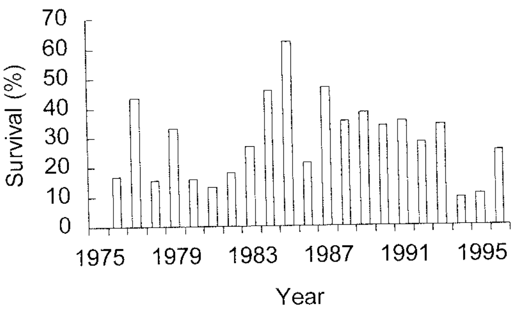

Figure 6. The percentage of cygnets from each year known to have survived until breeding. Since a few birds do not breed until aged 10 or more, the right-hand columns will probably increase slightly with time.

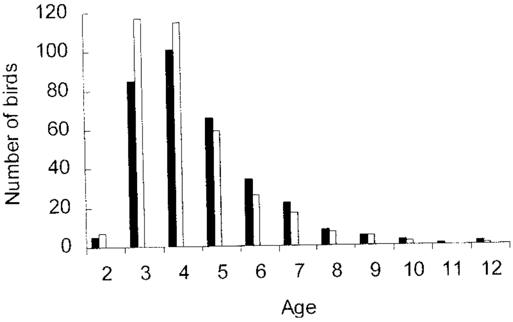

Figure 8. Age of first breeding for Mute Swans at Abbotsbury. Solid columns = males, open columns = females.

(rather than the actual number of nests, because of the rise in numbers nesting over time). There was a significant tendency for "poor" years to occur in years with lower residuals than those classed as "good" years, (pooled $t_{18} = 3.65$, $P < 0.01$; Fig. 9), indicating that young birds are more likely to defer breeding in seasons when fewer birds bred. Because the young birds themselves contribute to the breeding numbers, this finding needs to be treated with caution.

Further evidence that there are traits associated with "poor" years, which cause young swans to defer breeding, is provided in Figure 10. This considers the birds from each cohort that survived to breed, and compares the proportion of these that had bred by age four with the proportion of the adults that skipped a year for each year of the study. Years in which only a low proportion of the young birds are breeding at age four are also years in which a higher proportion of the breeding birds skip breeding ($r_{17} = -0.67$, $P < 0.001$).

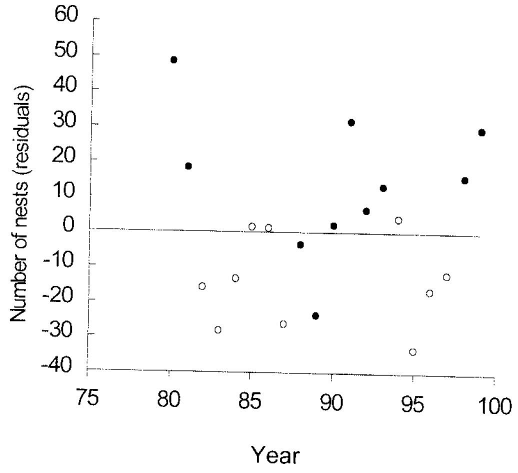

Figure 9. Numbers of breeding pairs (nests) and the age of first breeding. The vertical axis shows the change in numbers of breeding pairs (plotted as the residuals of the general increase in Fig. 1). Each cohort of young birds is plotted along the horizontal axis against the year in which it was four years old. Cohorts whose mean age of first breeding is four years (filled circles) are compared with those with a mean age of first breeding of five years (open circles). The cohort is significantly more likely to defer breeding until five years old if the season was one in which the total number of breeding pairs was lower than in the previous year.

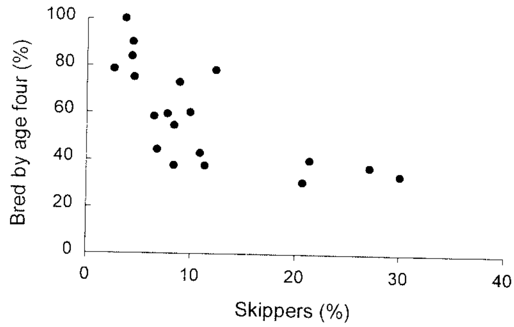

Figure 10. The proportion of the swans from each cohort which survive to breed which breed by age four compared with the proportion of breeding birds from previous year which were alive, but not breeding.

Age Structure of Swans Breeding at Abbotsbury

With a mean survival rate of 85% (±0.9) recorded for adult swans over the study period, a Mute Swan starting to breed at Abbotsbury is likely to breed for a number of years (Fig. 11). On average, each female makes 4.3 breeding attempts compared with 3.9 for males. The difference between the distributions is not statistically significant (Kolmogorov-Smirnov two sample test, K = 0.69, n.s.), which supports the earlier findings of no differences between the sexes in survival, age of first breeding and skipping frequency. These average breeding attempts are underestimates, however, because many of the birds are still alive and may continue breeding. When only birds fledged up to and including 1985 are considered, because very few birds survive beyond 15 years, the mean number of breeding attempts is 5.3 for females and 4.4

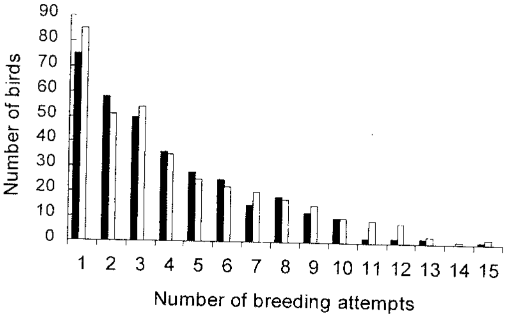

Figure 11. The number of breeding attempts made during their life-times by male (filled columns) and female (open columns) Mute Swans at Abbotsbury.

for males. Females seem more likely to breed at an older age than males; of the 30 birds which bred in more than ten years, 23 were females and only seven were males. Since there were no differences between the sexes in age-related survival, it is unclear whether later breeding by females is due to poor survival estimates for the older age classes, or to males ceasing breeding at an earlier age.

Because individuals breed for a number of years, the size of a single cohort influences the number of breeding pairs for several years. For example, one of the most successful breeding years was 1987; in 1991 no fewer than 47 of the 130 breeders came from this cohort, and there were still 35 birds breeding from this cohort in 1999. Moreover, annual variation in the survival of adult swans has a significant effect on changes in the proportion of adults breeding at Abbotsbury from year to year ($r_{19} = 0.79$, $P < 0.001$, Fig. 12).

DISCUSSION

There are more pairs of Mute Swans currently breeding at Abbotsbury than at any time on record, although almost as many are known to have bred there historically (e.g., 130 pairs in 1885, Abbotsbury Estate, unpubl. data). It is not known why numbers were low in the mid 1960s, although the unusually cold 1962-63 winter and an unexplained die-off in March 1964 probably contributed to this.

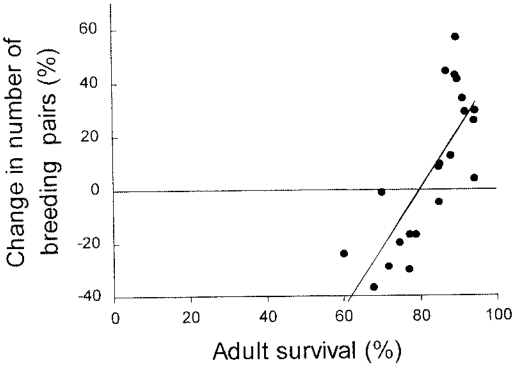

Figure 12. The relationship between adult survival rate and changes in the number of breeding pairs of swans at Abbotsbury. Change in the number of breeding pairs is the difference between breeding numbers in years t and t+1, measured as a percentage of the numbers in year t.

Several studies of Mute Swan demography have been made in the UK and elsewhere (summarized in Bacon and Perrins 1991). All the British studies (excepting Spray 1991) have been made in lowland England, mostly on a mixture of rivers and still waters, and have shown the birds to have similar life-histories in different parts of the country (Bacon and Perrins 1991). Abbotsbury presents a very different habitat; in particular, if the birds choose not to leave the Fleet (and most do not), then they avoid many of the hazards faced by Mute Swans elsewhere in the UK.

Survival

It therefore might be expected that the survival and longevity of Mute Swans at Abbotsbury would differ from those occurring elsewhere. However, during this study the average survival rate of the breeding birds has been similar to those reported from other parts of the UK (which lie in the range of 74–87%, Bacon and Perrins 1991). Similarly, the oldest birds are not older than those monitored elsewhere. However, the Abbotsbury figure needs to be treated with caution, since the survival rates have been more variable than those reported elsewhere, and the exclusion of the early years of the study increases our estimate of the average survival rate.

Given that the majority of the breeding birds have bred before, it is not surprising that the major factor affecting breeding numbers is the survival of the adult birds from the previous year (Fig. 12). When annual adult survival rates exceed about 80%, the breeding numbers tend to increase, whereas with survival rates lower than this figure they tend to decrease.

Other Factors Affecting Breeding Numbers

In any one year, in addition to the effect of variations in adult survival, the number of breeding pairs is affected by other factors, including the recruitment of young birds to the breeding population. The number of swans breeding for the first time is the product of the numbers in each cohort that survived to fledging age and their survival rate from then to breeding. Although, plainly the number fledging (and hence the number of breeding pairs) must be important, in this study the variations in the proportion surviving after fledging swamp the effects of the simple number of fledglings. The proportion surviving to breeding is correlated with the survival rate of the adults in the year in which the cohort survived from fledging to age one, indicating that the most variable part of the survival of the immature birds is that which occurs in their first year of life.

The total number of breeding pairs is also influenced by the age of first breeding, since the number of immature birds entering the breeding population for the first time in any year is influenced by the age at which they start to breed. This pattern is complicated by the fact that the birds from each cohort start to breed over a range of years. However, the mean age of first breeding ranges from about 3.5 to 5.5. In poor years (those when the number of breeding pairs is lower than usual) the immature birds defer starting to breed until a later year. The effect of this variable on the number of breeding pairs is short-lived, because no cohort has deferred breeding for more than two years. In other words if three poor years occurred in a row, presumably the oldest cohort of non-breeders would still start breeding during this period. There are a number of potentially confounding factors in this analysis in that (1) birds from a single cohort do not all start to breed at the same age, but are spread over several years, and (2) there is an element of circularity since, if most swans in the cohort breed at age four, this will increase the total number of breeding pairs in that year. Nevertheless, it seems clear that the age at which each cohort starts to breed is dependent to some extent on the conditions during the run-up to the breeding season when they are aged four.

Apart from a small percentage of immigrants, the cohorts of Abbotsbury cygnets make up the large majority of the swans breeding at the site. The numbers of breeders from each cohort vary markedly. This number is the product of a series of different parameters: the number of breeding pairs, the number of cygnets that they raised to fledging and the subsequent survival of that cohort from fledging to adulthood. Following from that, the number of breeding pairs is greatly influenced by the input of those years that produce many young that go on to breed.

A third factor influencing breeding numbers is the number of breeding birds that skip breeding in one or more years. Birds might miss a year if they lost their mate and take some time to find a new one. However, this is unlikely to be a major factor in this study, since the number of skippers was higher in years of high survival. Moreover, skipping seems to have become slightly more common with the increase in numbers in recent years, suggesting that it is associated more with breeding density rather than with choice of mate.

These variables may not act independently of each other. Years of poor adult survival are accompanied by a lower survival of that year's cohort, which will result in a reduced number of new breeders three to four years later.

Causes of mortality at Abbotsbury are not understood, but possible factors have been identified for some years. In 1976 there was a severe drought that was thought to have reduced the growth of *Zostera* and *Ruppia*; both cygnets and breeding adults had low survival the following winter. However, the hard weather in the late part of the winter of 1978/79, which was thought to have been responsible for a high loss of juveniles in that year, did not have a marked effect on the adults. Similarly, the poor survival of the 1994 cohort was mirrored by a low adult survival rate, but the almost equally low survival of the 1995 cohort is associated with the highest adult survival rate of all. Males may suffer a slightly higher mortality than females from fighting; many males spend a proportion of their time in aggressive encounters with their neighbors. It is difficult to quantify this, but in line with reports by Rees *et al.* (1990) for other species of swans, we have replaced significantly more broken plastic rings on males than on females. This suggests that males are more active in territory, mate or nest defense than their mates. However, it does not follow that this activity is mortality-related and, overall, their survival rates are not very different from those of the females.

The main way in which the life-history pattern for Mute Swans at Abbotsbury differs from those studied elsewhere lies in the productivity of the breeding birds. Colonial-nesting Mute Swans in Denmark seem to be relatively unsuccessful at raising young (Bacon and Andersen-Harild 1989, 1991) and the Abbotsbury population also raises many fewer cygnets per pair to fledging than do territorial Mute Swans elsewhere in the UK (Bacon and Perrins 1991), especially when controlling for the cygnets put into the pens, which have a much higher survival rate. Two points about this low input of new potential breeders merit consideration. First, with a lower reproductive rate one might expect the Abbotsbury swans to behave in a more K-selected way than swans elsewhere (with lower productivity matched by higher survival), yet the survival of the breeding adults is not always higher than recorded in other studies. Second, in most years, a higher proportion of the (reduced number of) fledglings at Abbotsbury survive to breed than is the case elsewhere. This suggests that competition between the adults and the young after fledging is not a serious cause of mortality at Abbotsbury.

Longevity may be important for individual fitness, in terms of maximizing life-time reproductive output, but the old birds make up a relatively small proportion of the breeding population, at least at Abbotsbury; almost half the breeding attempts in the colony were by birds aged six or less, and almost three-quarters by birds aged eight or less. Both figures underestimate breeding age, however, because some of these birds will breed in future years. The large number of breeders of relatively young ages (the cohorts of 1990–1993 and 1996) at Abbotsbury means that, barring severe conditions, epidemics or other unforeseen circumstances, the breeding population is likely to remain high for some years. Even if breeding success and subsequent survival—and hence the input of new young breeders—is low during the next few years, normal survival of those cohorts already alive should ensure that the high breeding numbers are maintained.

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Occupancy and Turnover of Whooper Swans on Territories in Northern Iceland: Results of a Long-term Study

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Abstract.—The occupancy of territories, and the breeding success of pairs on these territories, was recorded for Whooper Swans (*Cygnus cygnus*) nesting at Skagafjordur, northern Iceland, from 1988 to 2000 inclusive. Complete information on occupancy was obtained for 83 (66%) of 125 territories located during the 13-year study. Territories were occupied (by one or more pairs) for an average of 7.4 years; 31% were occupied for three years or less and 31% for most of the study (12 or 13 years). The number of years that Whooper Swans occupied territories was influenced by the area of open water on the territory, but not by the proximity of the nearest nesting pair. There was also a positive correlation between the number of years in which a territory was occupied and annual breeding success (measured as clutch size) for pairs on the territories. Monitoring of individuals showed that only one territory was occupied by the same pair throughout the study, and that 35% of pairs were present for only one season. Territories occupied for most years not only received more pairs, but the average duration of occupancy (in years) by the same pair was also higher for these sites. Further information on habitat quality is needed to determine the reasons underlying variation in frequency of occupancy and breeding success.

Key words.—*Cygnus cygnus*, habitat effects, Iceland, long-term study, occupancy, territories, turnover, Whooper Swan.

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In studies of animal populations, changes in population size are attributable to productivity, survival, emigration and immigration (Lack 1954). Productivity is influenced by extrinsic factors, notably variation in climatic conditions and food availability, and by intrinsic factors such as dominance rank, pair duration and parental care. A combination of these factors affects the proportion of territorial pairs that attempt to breed each year, and the success of these pairs in raising young. For instance, several studies of swans and geese show that weather conditions in the breeding range influence breeding success; fewer adults defend territories in late springs (Owen and Black 1989; Syroechkovskiy *et al.* 1991), and the percentage of juveniles in the population is lower following late springs or early onset of winter (Owen and Norderhaug 1977; Prop *et al.* 1984; Poorter 1991; Monda *et al.* 1994). Other studies have shown that the breeding success of a pair increases with duration of the pair bond (Black *et al.* 1996; Rees *et al.* 1996). In addition, previous breeding experience and occupancy of good quality territories are likely to be relevant factors.

The Whooper Swan (*Cygnus cygnus*) is a migratory species that breeds in sub-arctic and taiga zones across Eurasia, ranging from Iceland and northern Scandinavia to Mongolia, northern China and the Russian Far East (Rees *et al.* 2002). The Icelandic-breeding population, which winters mainly in Britain and Ireland (Gardarsson 1991), nests on a variety of wetland habitats, from low-lying coastal marshes to isolated lakes at altitude of up to 700 m. Variation in breeding success has been described for swans nesting in different parts of Iceland (Rees *et al.* 1991; Einarsson 1996), suggesting that some breeding areas are more important for recruitment to the population than others, due to the timing of the spring thaw, food availability or other environmental conditions. Although variation in breeding success also occurs within study areas (Rees *et al.* 1991; Einarsson 1996), the question of whether some territories are more likely to hold breeding pairs than others, the turnover rate for individuals on different territories, and the characteristics of these territories, has not yet been described.

In this paper we analyze data from a long-term study of Whooper Swans breeding at Skagafjordur, northern Iceland, to investigate annual variation in the occupancy of territories, and consider whether frequency of occupancy is related to the breeding success (measured as clutch size) of pairs on those territories. Frequency of occupancy is also considered in relation to two very broad measures of habitat quality, (1) distance to the nearest nesting pair, indicative of nesting density; and (2) area of open water on the main pool which, since the swans feed mainly on emergent vegetation at Skagafjordur (Einarsson 1996) may reflect food supply on the territory. Return rates for pairs identified by natural or artificial markings are described, with a view to assessing the frequency of turnover of pairs on territories. Whether established pairs switched to another territory on returning to the study area is also addressed. Overall, the study aims to determine whether swans appear to prefer some territories to others (i.e., whether there is a variation in occupancy), whether this is due to continued occupancy by a single pair or to several pairs using well-occupied sites, and whether occupancy of particular sites is associated with improved breeding success.

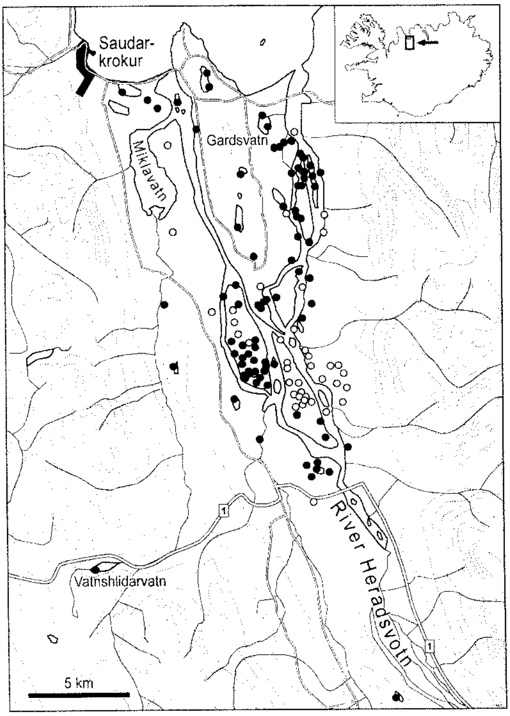

Figure 1. Distribution of Whooper Swan territories at Skagafjordur, indicating those monitored in all years (closed circles; N = 83), and those where occupancy was uncertain in one or more years (open circles; N = 42). Dotted lines = 100 m contours. 1 = Route 1, the main road around Iceland.

STUDY AREA AND METHODS

Whooper Swans breeding at Skagafjordur in northern Iceland (65°40'N 19°30'W) were monitored over a 13-year period, from 1988 to 2000 inclusive. Skagafjordur is a lowland coastal site of some 250 km^2, consisting of grazed pasture and marshes in and around the Heradsvotn river delta (Fig. 1). Several sheep and dairy farms occur within the study area, and the town of Saudarkrokur and its airport are at the northern end.

Ground surveys were made in spring (second half of May) each year, except for 1989, to record the total numbers of birds present, and to map the distribution of swans on territories and in non-breeding flocks. Information on the presence or absence of a nest on the territory was also recorded; pairs with nests were considered to be breeding, those on territories but without nests were recorded as territorial pairs. Accessible territories were visited to record final clutch size and to identify breeding pairs by reading the unique codes engraved on their plastic leg bands (Ogilvie 1972) or, in the case of unmarked birds, by the variation in their black and yellow bill markings (Brazil 1981). Although it is more difficult to differentiate between Whooper Swans than Bewick's Swans (*Cygnus columbianus bewickii*) by their bill markings (Brazil 1981; Scott 1966), variation particularly in the amount of black below the feathering on the forehead was sufficient to determine whether the same pair was using a territory in successive years. Bill markings of swans not recognized therefore were drawn to aid identification later in the study. The swans' legs also were checked carefully for a metal band, to determine whether the plastic band had been lost. Nests were mapped using compass bearings to three fixed points or with GPS location (since 1998). Territories were defined as being the largest waterbody (pool or lake) adjacent to a nest together with its immediate surroundings (including the nest site), except for a small number (less than five) of cases where swans were observed moving between two adjacent pools. For these territories, both pools were included.

Aerial surveys were undertaken in summer (last week of July to first week of August) in 1988 and 1992–2000, and ground surveys also were undertaken during the same period in every year of the study. During both types of survey, breeding pairs again were recorded on their territories, together with the number of cygnets in each brood. Twenty-four families were caught in 1988, and a further 80 families in 1989–2000. Parents and young were fitted with plastic leg bands for identification and an Icelandic Museum metal band was fitted to the other leg. Birds were sexed by cloacal examination. Non-breeding flocks on lakes Miklavatn, Gardsvatn and Vatnshlidarvatn also were caught and banded to allow identification of non-breeders recruited to the breeding population in subsequent years, and to identify any failed breeders that had joined the non-breeding flock. Between 1988–2000, 570 swans were caught in flocks at these sites. Since detailed habitat data were recorded only in one year (1991), variation in habitat was taken as the area of open water of territories for the current analyses, measured from aerial photographs of 29 territories provided by the Icelandic Geodetic Survey. Fecal analysis and field observations have shown that horsetails (*Equisetum* spp.) form 85% of the swans' diet in spring and summer, and horsetails are more abundant in pools than in adjacent marshes (Einarsson 1996). Pool area therefore was taken as an indicator of food supply for the birds.

Analyses of occupancy of territories were restricted to those territories for which presence or absence of a pair was recorded in every year of the study. To assess the effects of breeding density on frequency of occupancy, distance between a territory and its nearest neighboring territory was calculated as the minimum distance between nests built on adjacent territories in the same year. Pairs build only one nest per year, and these disappear by the following season. Trends in occupancy of new territories, frequency of occupancy in relation to the number of different pairs using a territory, factors associated with occupancy (i.e., proximity of nearest nest, pool size, clutch size and the presence of a brood) and the turnover of different pairs identified on the main territories were tested using Pearson correlations, linear regression analyses and one-way ANOVAs in SPSS 10.0. Frequency of occupancy and distances between nests were log transformed to provide a normal distribution for analysis of proximity data, although the results were similar to those using raw data. Sample sizes of broods are higher than for clutches, because not all nests were visited, but the presence or absence of broods was recorded for most (if not all) pairs on territories during the aerial surveys. Means are presented with SD and regression coefficients are given with SEs.

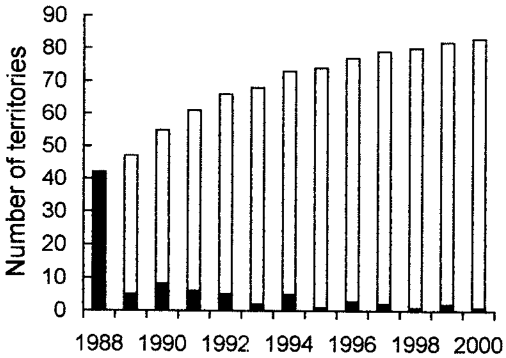

Figure 2. Cumulative number of new territories (black columns) and previously identified territories (open columns) at Skagafjordur, 1988–2000 inclusive. Only the 83 territories monitored for presence or absence of a pair in all years are included. In 1988, the first year of the study, all territories recorded were defined as new.

RESULTS

There was complete (annual) information on the occupation of territories for 83 (66%) of 125 territories recorded at Skagafjordur between 1988 and 2000 (Figs. 1 and 2). Although intensive observations were made in spring and summer 1988, it was the first year of the study, so some breeding pairs may have been missed. Similarly, since observations were made only in summer 1989, not in spring, and since failed breeders sometimes leave their territories to join the non-breeding flock (Rees *et al.* 1991), the number of nesting pairs recorded in 1989 is an underestimate. From 1990 onwards, however, new territories recorded at Skagafjordur are unlikely to have been used previously during the study period. Nineteen new territories were recorded from 1991 to 1995 inclusive, and only nine new territories from 1996 to 2000 (Fig. 2), suggesting that colonization of new territories has diminished in recent years ($\chi^2_1 = 4.95$, $P < 0.05$). Moreover, the number of new territories recorded annually has decreased significantly since 1991 (linear regression, $F_{1,9} = 11.2$, $b = -1.23 \pm 0.37$, $P < 0.01$).

Despite new territories being recorded during the study, the total number of territories occupied by Whooper Swan pairs each year since 1990 was similar, ranging from 44 (in 1997) to 53 (in 1995); there was no trend in the number of territories occupied each year from 1990 ($F_{1,9} = 1.13$, $b = -0.41 \pm 0.38$, n.s., Fig. 3). The number of new territories recorded each year from 1990 (Fig. 2) did not correlate with the number of territories occupied ($r_{10} = 0.30$, n.s., Fig. 3), indicating that occupation of new sites was not due to greater numbers of pairs attempting to breed in that year. There was a significant correlation between the number of territorial pairs and the number of nesting pairs recorded each year ($r_{10} = 0.59$, $P < 0.05$; 1989 excluded), but not between the number of nesting pairs and pairs recorded with broods ($r_{10} = 0.33$, n.s., Fig. 3). Flooding following the snow melt caused several pairs to lose clutches, particularly in springs 1991, 1992 and 1994. Four nests were thought to be flooded in 1991, 17 in 1992 and 19 in 1994. Water levels were highest in1994, with Great Black-backed Gulls (*Larus marinus*) apparently eating flooded and abandoned eggs.

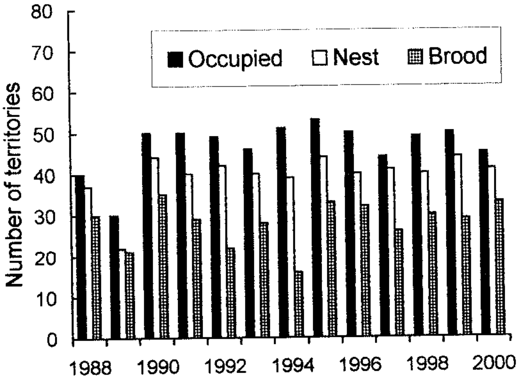

Figure 3. Annual variation in occupancy of territories, nesting attempts and pairs seen with broods for 1988–2000 inclusive.

Cold weather in June 1992 also may have affected breeding success in that year (Einarsson 1996). The effects of flooding and spring weather conditions on occupancy and breeding success will be considered in detail in a future publication.

The number of years that territories were occupied was bimodal in distribution and averaged 7.5 ± 4.6 years, with most territories (51%) either occupied for 1–3 years (31%) or for 11–13 years (36%, Fig. 4). Variation in nesting frequency was more evenly distributed, although 19% (16 of 83) of territories had a nesting pair in only one year, and two more were used only by territorial pairs that did not nest. Pairs (but not necessarily the same individuals) nested on territories for an average of 6.4 ± 4.3 years, and the average number of years per territory in which the nesting pairs hatched young was 5.2 ± 3.8 years. There was no significant association between the proximity of territories (measured as the distance to the nearest nest site, $\log_n$ transformed) and frequency ($\log_n$ transformed) of occupancy ($F_{1,82} = 2.00$, $b = 0.15 \pm 0.11$, n.s.), nesting ($F_{1,80} = 1.39$, $b = 0.12 \pm 0.10$, n.s.) or presence of a brood ($F_{1,69} = 0.40$, $b = 0.08 \pm 0.13$, n.s.). Sample sizes were reduced for nesting pairs and pairs with broods because log values were not obtained for territories without nests or broods, but similar (n.s.) results were obtained when using the raw frequency data for all 83 territories, and also when reducing the sample to 77 territories in "continuous" Whooper Swan habitat (i.e., those without areas of high ground, of >100 m, separating territories). There was a significant association between the number of years in which territories were occupied and the size (in m^2) of the main pool in the territory, for the 29 territories for which pool size data were available ($F_{1,27} = 6.92$, $b = 1.20 \pm 0.46$, $P < 0.02$). Two territories had no discernible pool, although the pairs nested in a marsh. The association between occupancy and pool size remained significant, however, when these two territories were excluded and pool size was log transformed ($F_{1,25}$ =

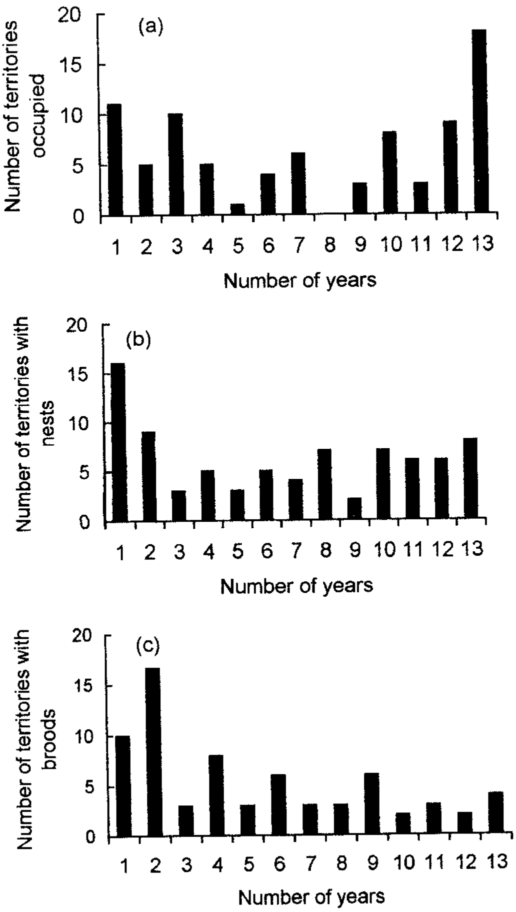

Figure 4. Number of years in which Whooper Swans (a) occupied, (b) nested on, and (c) hatched cygnets on the 83 territories at Skagafjordur for which complete data on presence or absence of a pair were available from 1988–2000. No nests were recorded on two territories, and no young were recorded for 13 territories

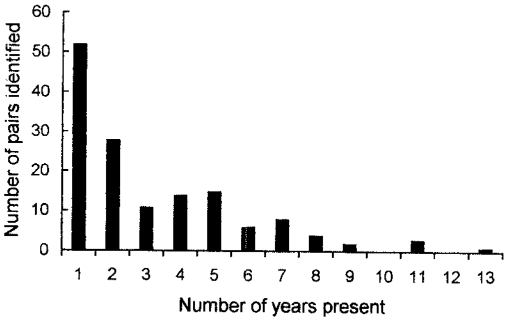

Figure 6. Number of years in which individual pairs were present (identified by leg band or bill markings, N = 144 pairs) for the 52 territories where occupying pairs were identified throughout the study.

8.02, $b = 2.94 \pm 1.04$, $P < 0.01$, Fig. 5). Pool size (log transformed) was similarly associated with the number of years in which pairs nested on the territory ($F_{1,25} = 7.74$, $b = 3.50 \pm 1.26$, $P < 0.01$), and with the number of years in which broods occurred ($F_{1,25} = 4.40$, $b = 2.70 \pm 1.29$, $P < 0.05$). The identity of individuals present in each year was determined for 52 territories, with 144 pairs recorded at these sites between 1988 and 2000. Only one territory was occupied by the same pair (both birds marked) throughout the study. On average, territories were occupied by 2.8 ± 1.3 different pairs during the 13-year period (range 1–7 different pairs). From the 144 different pairs known to use these sites, six were known to be present at Skagafjordur but using a different territory than in other years; all nested on both of their territories. Of the 144 different pairs identified, 36% (52 pairs) were present only for one season and 27% (39) of pairs were seen on territories for five years or more (Fig. 6). Thus, of the 92 pairs seen for at least two years, 93% (86) used the same territory on each occasion, as did 97% (38) of the 39 pairs present for at least five years. Of the 21 pairs that did not build a nest, 18 were present for one year and three for at least two years. Duration of occupancy was a minimum value for the 35 pairs identified on territories in 1988, since this was the first year of the study. Of 109 pairs first identified in 1989 or subsequently, 13 pairs on 11 territories were known to be present for one to three years before nesting. Duration of occupancy was longer for pairs that did not nest in the first year on territory but did so subsequently ($\bar{x} = 4.92 \pm 2.0$ years, N = 13) than for swans that did nest in their first year on territory ($\bar{x} = 3.31 \pm 2.74$, N = 96) (one-way ANOVA, $F_{1,108} = 4.18$, $P < 0.05$; 1988 data excluded). The number of years that the pair nested, however, was the same for both groups ($\bar{x} = 3.69 \pm 1.97$ and $= 3.18 \pm 2.61$ respectively; one-way ANOVA, $F_{1,108} = 0.47$, n.s.).

There was a positive association between the number of years that a territory was occupied and the number of different pairs recorded on that territory (linear regression, $F_{1,51} = 15.24$, $b = 0.14 \pm 0.04$, $P < 0.001$, Fig. 7), with the average occupancy per pair also being higher for sites occupied in most years (linear regression, $F_{1,51} = 21.21$, $b = 0.30 \pm 0.07$, $P < 0.001$, Fig. 8). Thus, although site fidelity contributed to the high occupancy

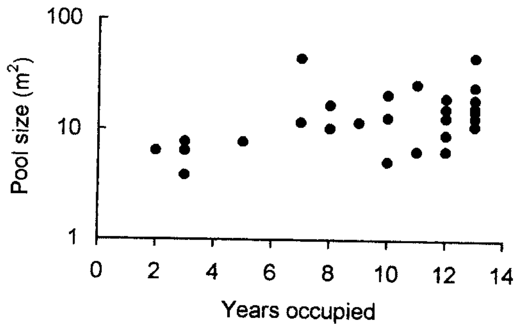

Figure 5. Association between occupancy of territories and pool size within the territory, for territories where pool size was recorded. Pool size plotted on a logarithmic scale.

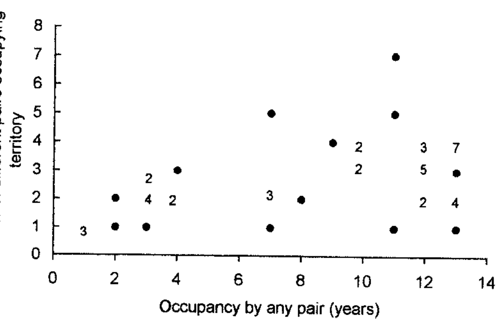

Figure 7. Association between the number of years that a territory was occupied and the number of different pairs recorded on that territory (N = 52 territories where occupying pairs were identified throughout the study).

rates recorded for a territory, several pairs usually were involved, indicating rapid reoccupation rates for these sites. Average clutch size per pair increased with territory occupancy rate (i.e., occupancy by any pair) for 47 territories where pair identity and clutch size was determined in all years (linear regression, $F_{1,46}$ = 136.2, *b* = 0.031 ± 0.31, P < 0.001, Fig. 9), but average brood sizes did not quite reach significance ($F_{1,51}$ = 3.19, *b* = 0.08 ± 0.04, n.s., for the 52 territories where pair identity was determined in all years). A total of six pairs switched territories on seven occasions during the study, including one pair that changed territories twice. On six of these seven occasions, both members of the pair changed territory together; on the seventh, a male returned to an adjacent territory with a new mate. All moved to an adjacent territory within the study area that had previously been occupied by a different pair, and each pair laid a clutch in both territories used. In four cases, average clutch size was higher upon changing territory, but average brood size in August was greater for only two of the pairs (Table 1); further data are required before territory switching can be analyzed in detail.

DISCUSSION

The study of occupancy of territories by Whooper Swans nesting at Skagafjordur showed that although territories were occupied for an average of 7.5 years, most were occupied either for a few years (31% occupied for three years or less) or for most of the study period (36% occupied for 11 to 13 years). Nineteen new territories were recorded in the early part of the study, and only nine between 1996 and 2000, suggesting that the availability of new territories might now be limited. There was no increase in the total number of territory holders or nesting pairs recorded each year during the 1990s, however, and the number of new territories recorded was not associated with annual variation in the total number of pairs seen on territories. Moreover, for the 83 territories monitored throughout the study, only 44 to 52 territorial pairs were recorded each year. It seems, therefore, that the occupation of new sites is not due to greater numbers of pairs attempting to breed, and that some (perhaps suboptimal) territories are vacant each year.

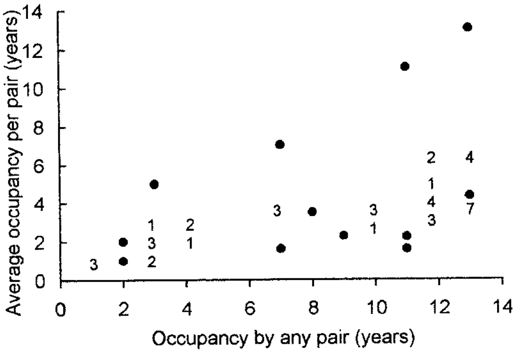

Figure 8. Average number of years that the same pairs were present on territory, for territories occupied for 1 to 13 years (N = 52 territories where occupying pairs were identified throughout the study).

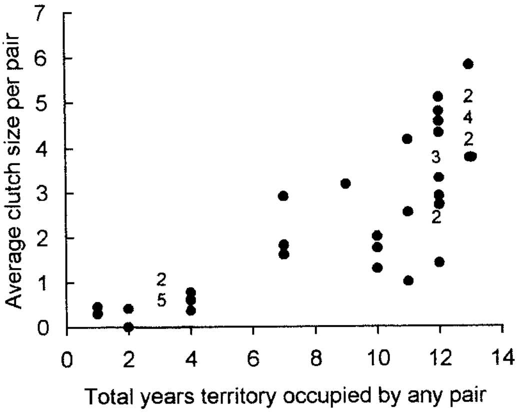

Figure 9. Average clutch size per pair, recorded for territories occupied for 1 to 13 years (N = 47 territories where occupying pairs were identified and clutch size determined throughout the study). For years where pairs were on territory but did not lay a clutch, clutch sizes were included as zero.

The frequency with which a breeding territory was occupied was positively correlated with pool size, but not with proximity of the nearest adjacent nest. Further vegetation measurements are needed to determine whether breeding territories occupied in most years do indeed have better quality habitats, although the higher clutch sizes recorded for these sites suggests that this may be the case, or that such territories may be

Table 1. Mean clutch size and mean brood size recorded on first, second and third territories used by six pairs that switched territories. Clutch size taken as zero for years where a pair occupied a territory but did not build a nest.

Pair code	Territory number	Years on territory (N)	Mean clutch size	Mean brood size
1	1	2	1.0	1.0
1	2	6	4.0	2.5
2	1	1	5.0	3.0
2	2	1	4.0	Not known
3	1	2	5.5	2.5
3	2	4	6.3	2.3
4	1	1	3.0	3.0
4	2	9	5.0	3.7
5	1	4	5.5	3.3
5	2	1	6.0	0
6	1	1	5.0	5.0
6	2	1	5.0	4.0
6	3	1	4.0	0

held by more experienced pairs since breeding success increases with pair duration (Rees *et al.* 1996). Similarly, more detailed analyses are required to determine whether territory density is influencing occupation of territories and breeding success. In particular, the effects of annual variation in nearest neighbor distances and overall breeding density at Skagafjordur on nesting attempts and breeding success each year will be considered. Additionally, behavioral studies are required to determine whether the proximity of a second territorial pair influences the frequency of aggressive encounters and whether this, in turn, influences individual return rates.

Identification of individual birds nesting on the territories indicated that the turnover of territory holders was high. Many (35%) pairs were present for only one season, although 27% (39 of 144) of pairs identified were present for at least five years. The average occupancy rate was 2.8 different pairs per territory over the 13-year study. Some 34 pairs did not build a nest in their first year on territory, of which 18 were seen only for one year, but 13 returned and nested in subsequent years. The duration of occupancy for these individuals was, in fact, higher than for the pairs that nested in their first year, but more detailed analyses of long-term productivity and territory quality, while controlling for the effects of spring weather conditions, are needed to understand delayed nesting. Information on birds banded as cygnets returning to breed also would help to determine whether swans first recorded as territorial pairs, which then nested in subsequent years, were young birds joining the breeding population. At this stage, there is no evidence from the occupancy data to suggest that pairs that do not nest immediately are less able to hold a territory in subsequent years than those that nest in their first season.

Since only one pair was present throughout the study, the question arises of what became of the birds that did not return. Some may have moved to other parts of Iceland, although this is difficult to assess because detailed monitoring occurs only in two other parts of the country. Some may join the non-breeding flocks, and this needs to be addressed more carefully in future studies. Third, the turnover may reflect annual adult mortality rates. Annual Whooper Swan mortality has been estimated at 14% for adults (Rees *et al.* 1996). Thus, for the 104 birds per year (on the 52 territories where pairs were identified throughout), it would be expected that 15.5 birds would die and, if birds that lose their mates do not return, that about 14 territories would become available each year (i.e., number of pairs losing one individual minus the number of pairs losing both individuals = $15.5 - (0.14)^2(52) = 14.48$). This equates with 174 territories becoming available during the twelve years (1988 excluded), compared with 144 different pairs recorded including 1988 or, for the 52 territories 3.3 pairs per territory. It therefore seems that, pending further assessment of variation in survival rates for different groups within the population (particularly comparing breeding birds with non-breeders), the turnover of pairs may be largely due to mortality.

Most pairs (93% of 92) that returned to Skagafjordur used the territory that they had occupied the previous year. Six pairs did switch territories between years but there are insufficient data to determine the reasons for the change. The turnover of territory holders and nesting pairs at Skagafjordur, and the high proportion of territories that were not occupied each year, might suggest that the number of Whooper Swans nesting at Skagafjordur is not currently limited by the availability of territories. However, lower occupancy could be due to a number of these territories being unsuitable for breeding, and the lower average clutch sizes per nesting pair recorded for less frequently used territories supports this view. Thus, availability of territories could be limiting population growth at Skagafjordur and in other parts of Iceland. For instance extensive drainage of wetlands in the southern lowlands and elsewhere in Iceland (Einarsson 2000) may have reduced nesting opportunities in these areas. Analysis of return rates and productivity data are needed to determine whether habitat on the territories is influencing the survival of nesting pairs, and to assess whether breeding density is influencing individual breeding success at Skagafjordur.

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Growth and Survival of Whooper Swan Cygnets Reared in Different Habitats in Finland

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Abstract.—The influence of breeding habitat on the growth and survival of Whooper Swan (*Cygnus cygnus*) cygnets was examined using data collected in central Finland in 1996. Breeding habitats were divided into three categories: peatlands, oligotrophic lakes and eutrophic lakes. Cygnets reared in peatlands and oligotrophic lakes were significantly lighter (35% and 20% respectively) and had shorter skull lengths (12% and 6% respectively) than cygnets from eutrophic lakes, when measurements were adjusted for differences due to age. The estimated age at fledging for cygnets from peatlands and oligotrophic lakes were, on average, 18 days and 10 days later respectively than for cygnets from eutrophic lakes. It is suggested that differences in growth rates and age at fledging can be explained by differences in the availability and nutritional quality of food in the three types of habitat. Survival differed significantly between habitats; 52% of cygnets from peatlands were recorded on the wintering grounds, compared with 77% and 76% from oligotrophic and eutrophic lakes. Cygnets resighted on the wintering grounds were, on average, 640 g heavier when banded in August than cygnets not resighted. This suggests that differences in the survival of cygnets from the three habitat categories were attributable to territory quality influencing the cygnets' growth, which in turn may affect their survival into the first winter.

Key words.—Breeding biology, cygnets, *Cygnus cygnus*, fledging age, Finland, growth rates, habitat types, survival rates, Whooper Swan.

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The short summers at northern latitudes limit the timing of the breeding season in migratory swans and geese (Sedinger and Raveling 1986; Prop and de Vries 1993), because birds have to complete breeding, molt and prepare for migration within the ice-free period. Nutritional demands are very high during the rapid growth of young (Scott 1973; Thomas and Prevett 1982) and in many cases cygnet mortality may be related to food availability, either directly, or indirectly through increased risk of predation or chilling (Owen and Black 1990). Experimental and *in situ* studies of swans, geese and ducks have shown that growth and development of the young are highly sensitive to environmental factors, such as variation in food quality, availability of food and seasonal differences in feeding conditions (Street 1978; Sedinger and Raveling 1986; Coleman and Boag 1987; Cooch *et al.* 1991, 1993; Ubels 1995). Plants show a rapid decline in productivity and nutritional quality after the first flush of spring growth, which may give early hatched young an advantage over those that hatch later (Sedinger and Raveling 1986; Manseau and Gauthier 1993). Early hatched young and those with access to the best food will be sufficiently developed for migration when food quality decreases and autumn freezing sets in (Manseau and Gauthier 1993; Prop and de Vries 1993). Studies on geese show that well developed individuals are more likely to join the breeding population (Owen and Black 1989; Cooch *et al.* 1991, 1993). Furthermore, growth of the young prior to fledging affects their size in adulthood (Boag 1987; Cooch *et al.* 1991, Larsson and Forslund 1991). This is thought to influence adult fitness through the effect of adult body size on fecundity and survival (Cooch *et al.* 1991; Larsson and Forslund 1991).

Two Whooper Swan (*Cygnus cygnus*) populations occur in northwest Europe. The Icelandic-breeding population winters mainly in Britain and Iceland, whereas the continental population breeds in Fenno-Scandia and northwest Russia and winters in mainland Europe (Scott and Rose 1996). Following an international census of Whooper Swans in continental northwest Europe in January 1995, the wintering population was put at *c.* 59,000 individuals, a four-fold increase on the 1960–1970 population estimate (Laubek *et al.* 1999). Most of the population winters in Denmark (40%) and the adjacent regions of Sweden (15%), Norway (11%) and Germany (25%) (Laubek *et al.* 1999).

In order to assess factors that might affect future population trends, a joint Nordic Whooper Swan study was carried out on the Finnish breeding grounds in 1995–96 (Laubek 1998). Whooper Swans use a great variety of wetland habitat types for breeding, which range from highly productive shallow lakes and ponds to low productive peatlands (Haapanen *et al.* 1977; Ohtonen and Huhtala 1991). Breeding biology studies in Finland showed that clutch size and brood size of Whooper Swan pairs nesting in peatlands was significantly lower than that of pairs breeding in lakes with rich vegetation (Haapanen *et al.* 1973; Ohtonen and Huhtala 1991; Knudsen 1999), but little is known about the effect of habitat on cygnet development, fledging success and post-fledging survival. Studies from Iceland in 1988 showed that the development of Whooper Swan cygnets at a lowland site was more advanced by August, and that a higher proportion of these cygnets were recorded in the wintering range, than those from an upland site (Rees *et al.* 1991). The difference in cygnet size was attributed to a combination of factors including age differences, which in turn were due to the late spring thaw in the highlands, and to differences in habitat quality.

In this study we examine in greater detail whether cygnet development is related to habitat, and whether any variation in growth rates affects cygnet survival before and after fledging. Altitudinal variation, which appeared to be an important factor in the Icelandic Whooper Swan study (Rees *et al.* 1991), was not relevant in this study in Finland because all three habitat types were common in all altitudes, and because variation in altitude was less than 270 m. Whooper Swan breeding habitats were grouped into three categories: peatlands, oligotrophic lakes and eutrophic lakes (Knudsen 1999), which were expected to reflect increasing nutrient levels, and a corresponding increase in plant productivity and abundance of important food plants for the birds. Thus the main factors thought to determine the quality of breeding habitat for Whooper Swans in Finland are assessed.

STUDY AREA

The study area, situated in north-central Finland, extends over 300 km from the coast of the Bothnia Bay at Oulu (65°02'N, 25°29'E) in the southwest, to the border of Russia at Kuusamo (65°59'N, 29°13'E) in the northeast (Fig. 1). Breeding habitats used by Whooper Swans were grouped into categories based on data on plant communities. The distribution and abundance of plant species known to be important to Whooper Swans, the size and depth of lakes or ponds used by the birds, and their pH levels, were recorded (Knudsen 1999). The peatlands used by Whooper Swans are typically aapa mires with some ponds (Rüuhijärvi 1979). Apart from *Sphagnum* mosses, the mires characteristically feature low and scattered sedge and cotton-grass communities (*Carex* spp., *Trichophorum* spp., *Eriophorum* spp.) and, in drier areas, dwarf-heath vegetation (*Vaccinum* spp., *Empetrum* spp.). Thus peatlands provided the poorest quality habitat for Whooper Swans in terms of food supply. Oligotrophic lakes have little or no submerged or floating aquatic vegetation, but medium sized sedges (*Carex* spp.) form sparse stands along the shore, and small beds of Water Horsetail (*Equisetum fluviatile*) occasionally occur. Eutrophic lakes are characterized by extensive and dense areas of Water Horsetail and sedges. The well-developed floating and submerged vegetation in these lakes is dominated by pondweeds (*Potamogeton* spp.) and burreeds (*Sparganium* spp.). The three habitat categories were evenly distributed within the study area.

Climate data for the study period were provided by the Finnish Meteorological Institute. Break-up of ice, defined as the date when ice clears from the shore of shallow lakes, was estimated as being the day following the first period of 15 days with average daily air temperatures above 0°C, and the ice-free period as ending when there were at least four days with mean daily air temperatures below zero (Hansen *et al.* 1971).

METHODS

Field Methods

Aerial transects were carried out on 20 May and 23 May 1996 to locate nest sites. In the period 22 May–17 June 1996, a total of 49 nests were visited to determine the number of days that the clutch had been incubated, and thus the age of cygnets when caught during summer survey. Eggs were weighed using an electronic letter balance (±1 g) and egg volume was determined by measuring the amount of water displaced when the egg was immersed in water (±1.25 ml). The device for measuring egg volume was designed following the description by Loftin and Bowman (1978). The specific gravity of the eggs, derived from volume and mass, was used to estimate the number of days into incubation. Specific

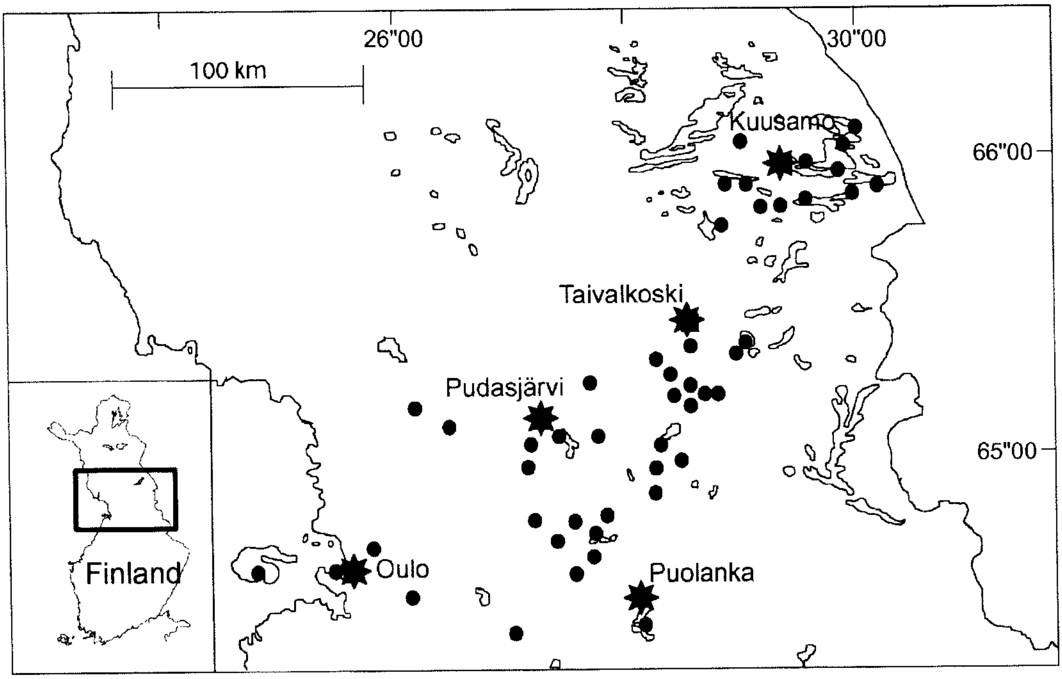

Figure 1. Whooper Swan study area in central-Finland. The positions of 49 nests visited in spring 1996 are indicated by dots, with larger towns shown with name and a star.

gravity of eggs on laying is rather uniform within species, and decreases by a constant rate during incubation (Rahn *et al.* 1976; Dunn *et al.* 1979; O'Malley and Evans 1980). The number of days elapsed since the start of incubation, therefore can be estimated by comparing the eggs' specific gravity against a standard regression of specific gravity against days incubated. The standard regression was derived from a sample of eggs for which both specific gravity and incubation age was known, described by the relationship:

$$SG = 1.098\ (\pm 0.004) - 0.0058\ (\pm 0.0002) \cdot Ai$$

where SG = specific gravity of eggs ($g \cdot ml^{-1}$) and Ai = days incubated (linear regression, $R^2_{adj} = 0.973$, $F_{1,19} = 675$; $P < 0.001$). The mean value of Ai for the twenty eggs used for the standard regression was 12.7 (±2.56) days. Hatching date was derived by adding an incubation period of 31 days to the date of starting incubation (Haapanen *et al.* 1973). The age of cygnets when caught was calculated as the difference between the catching date and hatching date. The characteristic black and yellow bill pattern of individual adults was drawn and used for subsequent identification of family groups (Brazil 1981). However, Whooper Swans are territorial and the breeding pairs studied were geographically isolated, which minimized the risk of misidentifying families.

Aerial transects were repeated from 27 July to 10 August 1996 to locate the breeding pairs recorded in May, and note any new breeding pairs prior, to catching and marking them. Families were caught between mid July and mid September. Each swan was marked with a blue plastic neck collar engraved with a four digit white inscription. Cygnets too small to wear neck collars were fitted with a yellow plastic tarsus band with a three letter black inscription. The birds were sexed by cloacal examination and weighed to nearest 100 g. Wing chord and the 10th primary were measured to nearest mm, while skull and tarsus lengths were measured to nearest 0.1 mm (as in Bowler 1992).

To obtain information on survival of marked cygnets, staging and wintering areas in Denmark were visited and the swans checked for bands or collars, with most sites surveyed 5-50 times per winter. Resightings of swans reported by observers in other parts of northwest Europe also were included in the analysis. Observations of swans originally banded as cygnets in the period 15 December 1996–1 September 2001 were used to estimate survival to the first winter. The two different marking methods used could bias survival estimates, because tarsus bands are more difficult to see and read than neck collars. However, analysis of data for cygnets ringed in1996 found that the proportion of cygnets marked with tarsus bands observed the first time during their second winter (10%; N = 20), was not significantly different from those fitted with neck collars (9%, N = 153) (G-test, $G_1 = 0.049$, n.s.). Moreover, juveniles normally accompany their parents during the first winter, and most tarsus-banded cygnets (83%) were accompanied by at least one sibling or parent wearing a neck collar, which drew the observer's attention to them in the field. It is therefore assumed that the banding methods did not affect survival estimates through variation in resightings rates.

Statistical Methods

Growth and development of cygnets. The effect of breeding habitat on cygnet growth was tested by comparing body mass, skull length and wing chord for cygnets from the three habitat categories. Significant differences in body measurements between habitats were interpreted as reflecting actual differences in growth rates at some stage of cygnet development. Each of the body size measures was investigated, using a General Linear Model (GLM) to determine whether there were any differences in cygnet size between habitats. In each model, habitat and the sex of the birds were included as categorical variables, and the age at catching as a continuous variable; interaction terms between the variables were also included. Age was a covariate, as cygnet age on catching varied between 27–78 days (mean age [±SE] = 51 ± 1.3 days). Only significant interaction effects ($P < 0.05$) are presented in the results. For both body mass and skull length, all interactions between age, habitat and sex were non-significant (n.s.). For wing chord, the interaction between habitat and age was significant, and therefore was included in the final model. Adjusted body size characters refer to the least square means derived for subclasses when size measurements are adjusted for the effects of age (i.e., adjusted in relation to the mean size values calculated for the mean cygnet age of 52 ± 1.3 days, $N = 100$).

Prior to the GLM analyses, each body measurement was fitted to cygnet age for all habitat categories, each sex being treated separately, to determine whether cygnet growth was linear for the ages being studied. In all cases the regression lines were significant ($P < 0.05$), and plots of the residuals were not patterned, indicating no significant departure from linear growth for the range of cygnet ages measured (Knudsen 1999).

Estimating age on fledging. The minimum duration of the Whooper Swan breeding season was calculated, for comparison with the length of the ice-free period in the study area. The minimum duration of the breeding season was calculated as the sum of the rapid follicular growth (RFG) period (calculated at 15 days, on basis of an average egg mass of 341 g, equivalent to 310 ml; formula in Walsberg 1983), the egg laying period, the incubation period (31 days) and cygnets' age at fledging. Studies on geese have shown that rapid follicular growth may start during migration (Ankney and MacInnes 1978), but breeding Whooper Swans may stay on or very close to the nesting grounds two to four weeks before initiating egg-laying (Haapanen and Hautala 1991). To estimate fledging age, it was necessary to make the *a priori* assumption that cygnets fledge at a particular body size, derived from body mass, skull length, wing chord and 10th primary length measurements. Geese generally are able to fly when the primaries reach 85% of full length Owen (1980), and our reanalysis of biometric data recorded for captive Whooper Swan cygnets reared in Slimbridge, UK (data derived from Bowler 1992) indicated that body mass, skull length, wing chord and 10th primary length had reached 75%, 96%, 91% and 85%, respectively, of full size at the time of fledging. To estimate size at fledging for wild Whooper Swans wintering in continental Europe, this information was applied to the body measurements of 34 first-winter male and 23 first-winter female Whooper Swans caught in Denmark. The estimated size at fledging was, for males: body mass 7,120 g, skull 174 mm, wing chord 541 mm, 10th primary 283 mm, and for females: body mass 6,380 g, skull 169 mm, wing chord 530 mm, 10th primary 277 mm. Fledging age of individual cygnets initially was calculated from these estimates on the basis of linear growth to fledging. However, since the actual growth curves are sigmoid (Bowler 1992), fledging age would be underestimated using linear growth. Information on the discrepancy between linear estimates and actual age of fledging in captive cygnets (Bowler 1992) therefore was used to adjust the linear estimates of fledging age in wild cygnets. Applying body mass, skull length, length of wing chord and length of 10th primary as parameters, nine, seven, three and zero days, respectively, were added to the linear estimate of fledging age.

Effect of body mass on cygnet survival. General linear models were used to compare body mass recorded on catching during the summer for cygnets subsequently resighted with those not resighted in the wintering range, to determine whether growth affected survival to the first winter. Resighting status (i.e., resighted or not resighted) and sex were included categorical variables, with catching date or age at catching included as covariates. Interaction terms were tested, and non-significant interaction terms excluded from the models. Means are presented with standard error values.

RESULTS

Timing of Breeding in Different Habitats

Variation in the timing of breeding of pairs from the three habitats was examined, since differences in hatching date might affect cygnet growth rates. Specific gravity of the eggs, which reflects the number of days incubated, therefore was compared between habitats. Habitat was included as a categorical variable in the GLM, and the date of the nest visit as a continuous variable (covariate). The specific gravity of eggs did not differ between habitats ($F_{2,45} = 0.21$, n.s.), and there was no interaction between the date of visiting the nest and habitat ($F_{2,43} = 0.66$, n.s.), suggesting that onset of breeding and the time of hatching did not differ between habitat categories.

Effect of Habitat on Cygnet Growth and Development

The effect of breeding habitat on cygnet body size characters was examined using data from 100 cygnets of known age. Breeding habitat had significant effect on body mass ($F_{2,95} = 67.8$, $P < 0.001$) and skull length ($F_{2,95} = 84.0$, $P < 0.001$), controlling for cygnet age and sex (Table 1). Cygnets from eutrophic lakes were heavier and had longer skulls than those reared in peatlands and oligotrophic lakes (Figs. 2 and 3, Table 2). When body mass was adjusted for age and sex differences (with measurements scaled to those for males and females at age 52 days), cyg-

Table 1. General Linear Models of factors affecting body size measurements (body mass, skull length and wing chord length) in Whooper Swan cygnets. Sources effects are: habitat (peatlands, oligotrophic lakes and eutrophic lakes), sex (male or female) and age when captured (covariate). N = 100 cygnets.

	Body mass			Skull length			Wing chord		
	F	d.f.	P	F	d.f.	P	F	d.f.	P
Model	91.9	4, 95	<0.001	151	4, 95	<0.001	86.3	6, 93	<0.001
Habitat	67.8	2, 95	<0.001	84.0	2, 95	<0.001	1.79	2, 93	n.s.
Sex	12.3	1, 95	<0.001	6.9	1, 95	<0.001	0.09	1, 93	n.s.
Age	287	1, 95	<0.001	526	1, 95	<0.01	338	1, 93	<0.001
Habitat × Age							8.63	2, 93	<0.001

nets reared on peatlands and oligotrophic lakes were on average 1,930 g (35%) and 1,080 g (20%) lighter than those from eutrophic lakes. Similarly, mean skull lengths for cygnets reared on peatlands and oligotrophic lakes were 17.6 mm (12%) and 8.74 mm (6%) shorter, respectively, than of those reared on eutrophic lakes.

For wing chord there was a significant interaction between habitat and age ($F_{2,93}$ = 8.63, P < 0.001; Table 1, Fig. 4). The rate of wing chord growth was lower among cygnets reared on peatlands (5.7 ± 1.02 mm·d^{-1}), compared with cygnets reared on eutrophic lakes (10.0 ± 0.60 mm·d^{-1}) and oligotrophic lakes (9.2 ± 1.05 mm·d^{-1}; Fig 4). The maximum wing chord data suggest that cygnets from peatlands ultimately may have had shorter wing chords than cygnets from oligotrophic and eutrophic lakes (Fig. 4). However, due to the strong interaction between habitat and age, habitat alone did not have a significant effect on the cygnets' wing chord length ($F_{2,93}$ = 1.79, n.s.; Table 1).

The growth of cygnets from eutrophic lakes followed very closely that of cygnets reared in captivity at Slimbridge, UK (data from Bowler [1992] included, for comparison, in Figs. 2-4).

The Effect of Growth Patterns on Fledging of Cygnets

The estimated age at fledging differed significantly between the habitats (one-way ANOVA, $F_{2,97}$ = 96.2, P < 0.001). On average, cygnets took 100 days (±1.1, N = 22) to fledge in peatlands, 92 days (±1.1, N = 25) in oligotrophic lakes and 82 days (±0.8, N = 53) in eutrophic lakes. Bowler (1992) reported that Whooper Swans reared in captivity took 80 days to reach size of fledging, very close to the 82 days needed by cygnets from eutrophic lakes in the present study.

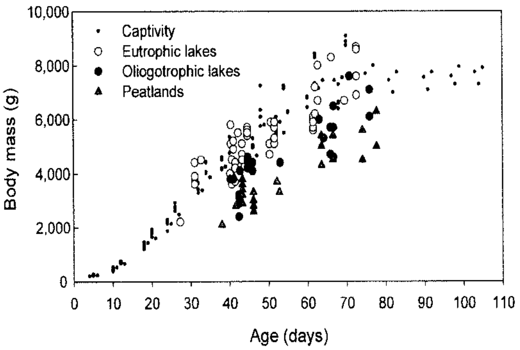

Figure 2. Body mass of Whooper Swan cygnets (N = 100) from peatlands, oligotrophic- and eutrophic lakes plotted against age of cygnets (range 27–77days). Body mass data for cygnets in captivity (Bowler 1992) are presented for comparison.

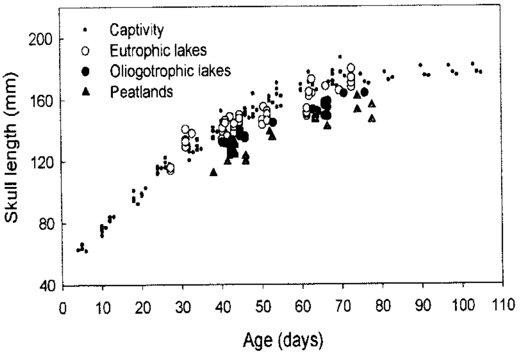

Figure 3. Skull length of Whooper Swan cygnets (N = 100) from peatlands, oligotrophic- and eutrophic lakes plotted against age of cygnets (range 27–77 days). Skull length data for cygnets in captivity (Bowler 1992) are presented for comparison.

Table 2. Effect of habitat (A) and sex (B) on Whooper Swan cygnet body mass, skull length and wing chord length. Data presented are the least-square means for the variables indicated (general linear model: size = age at banding + habitat + sex + interaction terms). Means are adjusted for differences due to age (see text).

	N	Body mass (g) Mean (±SE)	Skull length (mm) Mean (±SE)	Wing chord length (mm) Mean (±SE)
A				
Peatlands	22	3,560 (144)	131.5 (1.2)	110.2 (11.6)
Oligotrophic lakes	25	4,410 (135)	140.4 (1.1)	162.4 (10.7)
Eutrophic lakes	53	5,490 (93)	149.1 (0.7)	247.5 (7.3)
B				
Males	57	4,720 (91)	141.8 (0.7)	175.0 (7.2)
Females	43	4,250 (107)	138.9 (0.9)	171.7 (8.5)

The estimated duration of the breeding period (from initiation of rapid follicular growth until the cygnets fledged) averaged 142 days (±1.6) for the 29 breeding pairs investigated. The length of the breeding period differed significantly between habitats (one-Way ANOVA, $F_{2, 26} = 31.1$, $P < 0.001$). Pairs breeding in peatlands took on average 153 days (±1.5, N = 7) to complete breeding, compared with 143 days (±1.9, N = 8) in oligotrophic lakes and 136 days (±1.3, N = 4) in eutrophic lakes.

Resightings of Cygnets from Different Habitats

In total, 185 cygnets from the study area were fitted with tarsus bands or neck collars during the 1996 summer survey. Twenty-seven were from peatlands, 35 from oligotrophic lakes and 123 from eutrophic lakes. Only cygnets resighted after 15 December 1996 were considered as surviving to their first winter.

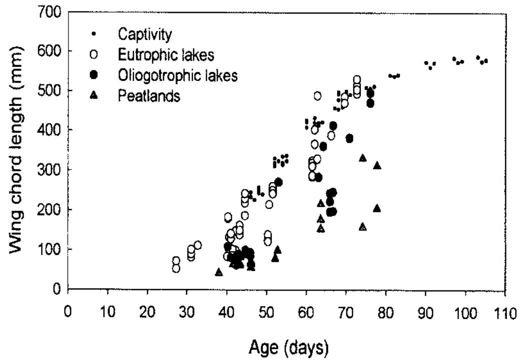

Figure 4. Length of wing chord of Whooper Swan cygnets (N = 100) from peatlands, oligotrophic- and eutrophic lakes plotted against age of cygnets (range 27–77 days). Wing chord data for cygnets in captivity (Bowler 1992) are presented for comparison.

Of the 185 cygnets marked, 135 (73%) were resighted during or after the 1996–97 winter. The proportion of cygnets resighted during or after their first winter differed significantly between habitats; 14 (52%) of the cygnets from peatlands had been resighted by September 2001, compared with 27 (77%) and 94 (76%) from oligotrophic and eutrophic lakes (G-test, $G_2 = 6.53$, $P < 0.05$).

Body Mass and Cygnet Resightings

The body mass of cygnets at the time of the summer survey differed significantly between those subsequently resighted and not resighted in the wintering range, after controlling for the effects of sex and catching date (resighting status in GLM, $F_{1, 181} = 14.9$, $P < 0.001$; Model B in Table 3).

The adjusted mean body mass at the median capture date (18 August) was 640 g higher for resighted cygnets ($\bar{x} = 5{,}140 \pm 86$ g, N = 135) than for non-resighted cygnets ($\bar{x} = 4{,}500 \pm 143$ g, N = 50). Controlling for cygnet age instead of capture date did not change the significant relationship between body mass and resighting status. Among the 100 cygnets of known age, adjusted body mass at the mean age 52 days was, on average, higher for resighted cygnets ($\bar{x} = 4{,}960 \pm 121$ g, N = 71) than for cygnets not resighted ($\bar{x} = 4{,}270 \pm 196$ g, N = 29) (resighting status in GLM, $F_{1; 96} = 8.95$, $P < 0.005$; GLM Model A in Table 3).

Table 3. General Linear Models of factors affecting cygnet body mass. Sources effects are, for Model A: resighting status (resighted, non-resighted), sex (male, female) and age when captured (covariate) (N = 100 cygnets); for Model B: resighting status, sex and date of capture (covariate) (N = 185 cygnets).

	Body mass		
Source	F	d.f.	P
A			
Model	38.0	3, 96	<0.001
Status	8.95	1, 96	<0.005
Sex	6.44	1, 96	<0.02
Age	85.7	1, 96	<0.001
B			
Model	67.8	3, 181	<0.001
Status	14.9	1, 181	<0.001
Sex	7.79	1, 181	<0.01
Capture date	168	1, 181	<0.001

DISCUSSION

Cygnet Growth and Development

Body mass and size of cygnets from the three habitat categories were highly different at given ages, especially cygnets from peatlands, which had slower growth rates. The habitat-related differences in growth could perhaps be associated with a corresponding difference in egg mass; large youngs hatch from large eggs, and size at hatching affects growth rates and size at fledging (Ankney 1980; Cooch *et al.* 1991). However, the volume of Whooper Swan eggs did not differ between habitat categories (peatlands $\bar{x}$ = 304 ml, oligotrophic lakes = $\bar{x}$ 317 ml, eutrophic lakes $\bar{x}$ = 312 ml) (Knudsen 1999). Furthermore, as body size of neither male nor female parents differed between habitats (Knudsen 1999), it is likely that the habitat-related differences in size of cygnets were not heritable. However, we have no record of whether one or both of the parents may have hatched on different habitats. Different growth patterns could be explained as a function of environmental conditions causing differential nutritive intake among cygnets from the three habitat categories. The limiting factor in the diet of fast growing animals normally is the level, and digestibility, of protein (Street 1977). Scott (1973) recommended a diet of 18–22% crude protein for maximum growth in waterfowl. Growth of cygnets from eutrophic lakes in general followed very closely that of captive cygnets fed a high protein pellet diet (Bowler 1992), suggesting that cygnets from eutrophic lakes experienced high levels of protein intake.

Invertebrates as food for cygnets. Studies on Whooper Swans and Trumpeter Swans (*Cygnus buccinator*) indicate that insects and aquatic invertebrates may be important food from the first few days to 30 days (Hansen *et al.* 1971; Haapanen *et al.* 1977; Grant *et al.* 1994). Invertebrates provide a concentrated source of protein, and may contribute significantly to the nutritional intake of young birds after hatching (Krapu and Swanson 1975). Street (1978) showed that the growth rate of newly hatched Mallard (*Anas platyrhynchos*) ducklings, fed with different ratios of plant seed to insect larvae, was proportional to the level of invertebrates in the diet. Abundance and biomass of aquatic invertebrates generally are positively correlated to plant biomass and nutrient levels (total phosphorus) in the waterbody (Schell and Kerekes 1989; Staicer *et al.* 1994). Whooper Swan cygnets from eutrophic lakes therefore may have access to higher quantities of invertebrate food during the critical period after hatching than cygnets from oligotrophic lakes and especially peatlands.

Abundance and nutritional quality of the vegetation. Water Horsetail and submerged or floating aquatic macrophytes (i.e., *Potamogeton* and *Sparganium*) are important food sources for cygnets and adult Whooper Swans (Haapanen *et al.* 1977; Myrberget 1981; Rees *et al.* 1997) and Trumpeter Swans (Grant *et al.* 1994) during the brood rearing period. In our study area, pondweeds and Water Horsetail was exclusively found in eutrophic lakes and oligotrophic lakes. The low abundance of food plants in peatlands may lower the foraging efficiency of cygnets and thereby their rate of food intake. Peatland families have large home ranges and travel many kilometers over land in search of food (Haapanen *et al.* 1977; Ohtonen and Huhtala 1991; own obs.). Such movements may increase the energetic demands on cygnets, which already have limited nutrient intake.

Water Horsetail is an emergent macrophyte normally occurring in large and dense stands, therefore it takes little time to locate and is easy grazed by cygnets (Grant *et al.* 1994). Moreover, the protein levels in fruiting bodies (16.4%), rhizome tips (22.7%) and young aerial stems (17%–23.5%) during spring and summer are relatively high and the fiber content is rather low (Thomas and Prevett 1982; Prop and Vulink 1992; Grant *et al.* 1994). These factors makes Water Horsetail a highly profitable food item to cygnets, and abundance of Water Horsetail on the breeding territories therefore may be a major factor explaining the different growth patterns between Whooper Swan cygnets from the three habitat categories.

Plants growing in oligotrophic lakes, and especially peatlands, may be less digestible than specimens from eutrophic lakes, due to a general increase in fiber content of plants with decreasing nutrient availability. For example plant cells of Common Reed (*Phragmites communis*) are smaller in specimens grown in habitats of low nutrient availability (Anthony 1995). Hence, cygnets in peatland and oligotrophic lakes may experience reduced assimilation efficiency compared with cygnets from eutrophic lakes. Cygnets from eutrophic lakes may also benefit from a higher proportion of floating and submerged macrophytes, as these have low levels of cell wall material (Mathiesen 1980).

Habitat Effects on Cygnet Resightings Rates

Resightings of cygnets were used directly as a measure of survival; this method therefore provides minimum survival estimates. However, there is reason to believe that resighting ratios are close to actual survival ratios in Whooper Swans. This is based on the fact that loss of neck collars was less than 1% per year, and annual resighting probability of banded birds was 80–90% for tarsus bands as well as for neck collars (B. Laubek, unpubl. data). Moreover, resighting data have been collected over a period of five years. Additionally, resightings show that families from peatlands, oligotrophic lakes and eutrophic lakes breeding in the same region also tend to use the same wintering grounds (Laubek 1998). The different banding types used potentially bias survival estimates because tarsus bands, which primarily were fitted to small cygnets from peatlands, are more difficult to spot and read than neck collars. However, as described in the method section, banding method was not found to affect survival estimates in this study.

In the present study, we found a significant relationship between cygnet growth rates and their subsequent survival. Irrespective of habitat category, cygnets sighted on the wintering grounds were heavier, at a given age or date during summer survey, than those not sighted. Cygnets from peatlands were less likely to be recorded during or after their first winter, than cygnets from oligotrophic lakes and eutrophic lakes. On this basis it is suggested that the different survival ratios of Whooper Swan cygnets from the three habitat categories were attributable to different growth rates, and thus cygnet sizes.

Mortality on the breeding grounds. Studies of Mute Swan (*Cygnus olor*) cygnets suggest that the onset of growth of flight feathers requires a certain level of body mass (Leeuw de and Beekman 1991). This implies that the moment of fledging depends strongly on weight gain by the cygnets. The estimated fledging age for Whooper Swan cygnets reared on oligotrophic lakes and peatlands was delayed by an average of 10 days and 18 days respectively, compared to those from eutrophic lakes. Slow growing cygnets may not be capable of flying when lakes freeze and snow covers the feeding areas. An ice-free period of 183-199 days in the Oulu-Pudasjärvi Region was well above the critical number of days needed for cygnets to fledge in any habitat, with the average duration of the breeding season calculated as 153 (±1.5) days for peatlands, 143 (±1.9) days for oligotrophic lakes and 136 (±1.3) days for eutrophic lakes. However an ice-free period of 159–161 days in the Taivalkoski-Kuusamo Region leaves little margin for cygnets fledging in peatlands. According to Haapanen *et al.* (1973), the ice-free period around

Kuusamo was less than 140 days in 25% of years in the period 1931–1970, and cygnets not capable of flying before the lakes freeze have been found in this area.

Cold weather may act on cygnets in peatlands long before the lakes become frozen because plants are more vulnerable to frost on land than in water. In large parts of the study area, night frosts started in mid-September long before peatland cygnets had fledged. Late developed cygnets in peatlands therefore will be tied to a habitat of reduced food availability and deteriorating quality while temperatures continue to fall.

Mortality during migration and in winter. Variation in food supply and the timing of breeding is thought to affect preparedness for autumn migration and the subsequent survival of young (Owen and Black 1989; Rees *et al.* 1991). The 20-day delay in the development of cygnets from peatlands probably means that they leave the summer habitat in poorer body condition than cygnets from the lakes. Owen and Black (1989) found that only 20% of juvenile Barnacle Geese (*Branta leucopsis*) weighing less than 600 g when ringed at Spitsbergen in August 1986 reached the wintering areas in Scotland, compared to 70% of those weighing more than 700 g. Among Whooper Swans banded in Iceland, cygnets from the highlands generally were smaller than cygnets from lowlands. Only 21% of the highland cygnets were sighted on the wintering grounds in UK, compared to 60% of those from the lowland site (Rees *et al.* 1991). However, the autumn migration of continental Whooper Swans is a gradual move southwards along the coast of the Bothnian Bay, with many stopovers and opportunities to replenish energy reserves (Laubek 1998). Mortality during migration therefore may be less important for the Whooper Swans breeding in Finland, than for geese and swans undertaking long non-stop migrations from Spitsbergen and Iceland without the possibility of transit feeding.

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Nesting Ecology of Bewick's Swans on Vaygach Island, Russia

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Abstract.—The nesting ecology of Bewick's Swans (*Cygnus columbianus bewickii*) breeding on Vaygach Island (70°15'N, 58°46'E), Russia was studied in 1986–1988 and 1995–1997. In particular, the effects of spring weather conditions on the use of old nests, breeding density and clutch size were considered. A total of 127 nests were found over the six-year period. All nests were mapped, clutch size was recorded and the eggs were weighed and measured. Bewick's Swan nests occurred across the island in different types of habitat. Nest density varied from 0.12 to 0.36 nests km^{-2}. Mean clutch size, which varied from 2.4 to 3.3 eggs, was significantly smaller than clutch sizes recorded in mainland Russia and negatively correlated with the date of clutch initiation. Calculated fresh egg mass varied depending on the timing of spring and the cold snaps. Nest failure was mostly due to abandonment of nests in cold weather rather then to predation. Climatic conditions in spring are the main determinants of nesting success for swans on Vaygach Island.

Key words.—Arctic, Bewick's Swan, breeding, clutch size, *Cygnus columbianus bewickii*, egg weight, nest density, Vaygach Island, weather conditions.

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The breeding biology of the Bewick's Swan (*Cygnus columbianus bewickii*) and the conspecific Tundra Swan (*Cygnus columbianus columbianus*) has been described extensively (Lensink 1973; Dau 1980; Kondratev 1984; Mineev 1987, 1995; Syroechkovsky *et al.* 1990; Monda 1991; Shchadilov *et al.* 1998; Belousova 1999; Litvin *et al.* 1999). Bewick's and Tundra Swans have a more northerly distribution than other swan species, and are characterized by smaller body size, lower clutch sizes, a shorter period of cygnet growth from hatching to fledging, and stronger pair bonds (Scott and The Wildfowl Trust 1972; Rees *et al.* 1996). In Bewick's Swans, both members of the pair incubate the eggs (Kondratev 1984), and incubation by both sexes has also been recorded in Tundra Swans (Hawkins 1986). This adaptation is thought to shorten the period of incubation, and to ensure that one member of the pair is always present to defend the nest.

The abundance and distribution of Bewick's Swans in the European part of their breeding range has been described (Mineev 1991), but relatively little is known concerning factors affecting breeding success at different latitudes. This study aims to describe the nesting ecology of Bewick's Swans on Vaygach Island, in the northern part of the breeding range, with a view to determining how annual variation in weather conditions influences breeding density, clutch size and hatching success for birds breeding in the high arctic.

STUDY AREA

Investigations of Bewick's Swan nesting ecology were carried in northwest Vaygach Island, near Dolgaya Guba Bay (70°15'N, 58°47'E), about 100 km north of mainland Russia (Fig. 1). The island is hilly, particularly in the center, the highest point being about 150 m above sea level. All the features of a mountainous landscape are present, such as rocks, cliffs, and canyons. The mountain ridges are intersected with numerous rivers and creeks, with narrow valleys in the upper regions widening at the coast to gently sloping plains and marshy lowlands. Where the rivers meet the sea they form lagoons with many small islands, which are covered periodically with tidal water.

The upper slopes of the hills are rocky; in the lowlands, shallow lakes are surrounded by wide marshy plains. Different vegetation cover such as sedges, moss, dwarf willow bushes and lichens change with varying altitude, at 100–200 m intervals. The climate on Vaygach Island is typical of the arctic. In winter, the wind distributes snow unevenly over the territory, so that hill tops und upper slopes may be totally snow free, whereas in the low areas snow can reach 1.5–2 m deep. Persistent winds make the snow very dense, so it melts very slowly in spring, particularly in the lowlands. Here the vegetation is rich, but cannot be used as feeding habitat by geese and swans until relatively late in the breeding season (end of June).

METHODS

Data on nesting ecology were collected each year from the early June to mid August, except in 1995 when data were collected from the end of July to mid August.

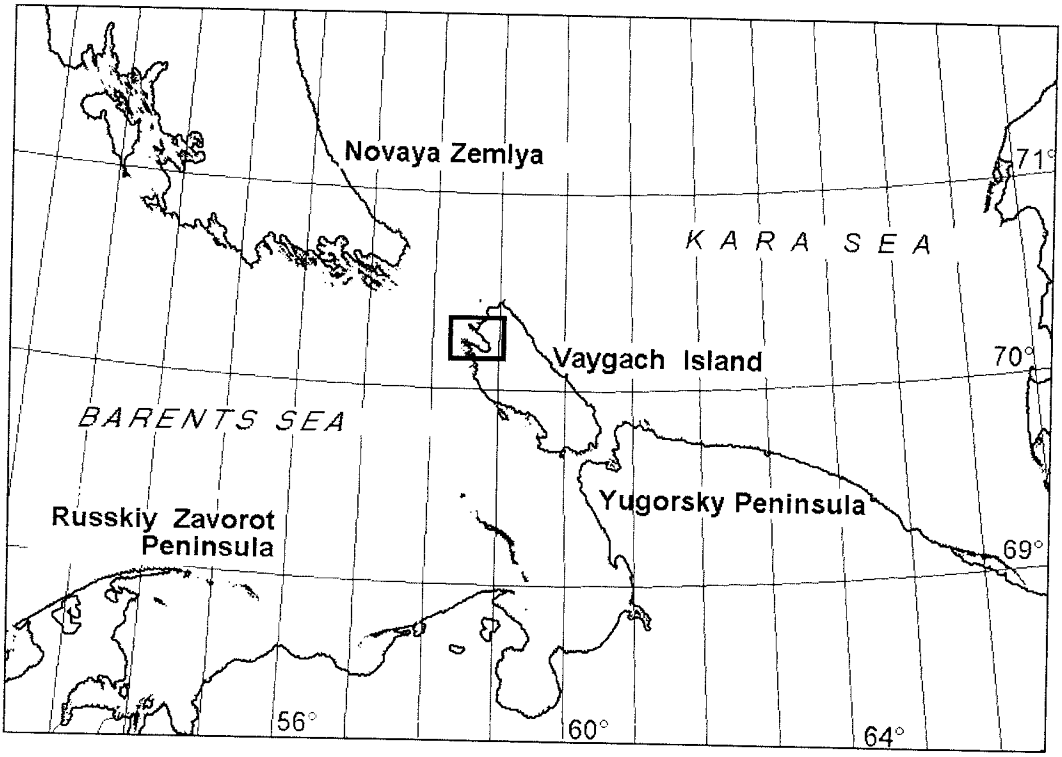

Figure 1. Location of the study area in northwest Vaygach Island.

Weather data were obtained from the Bely Nos weather station, on the Yugorsky Peninsula (69°35'N, 60°11'E) (Fig. 2). Observations usually commenced after the swans had arrived but before the clutches were completed in the majority of nests. Each year we tried to locate all nests of swans within the 80 km^2 study area, and also recorded all territorial pairs without nests seen during the surveys (Litvin *et al.* 1999), with the hilly landscape facilitating the search for swan nests and territorial non-breeders. Three to four observers covered different parts of the study area on skis or on foot, each reaching the top of nearest hill and scanning the surrounding territory over a 1–1.5 km radius with a telescope (45× magnification), recording all nests and swans sighted on a map, then proceeding to the next nearest hill for the next scan. Thus the study area was covered from different angles, which served to verify sightings and reduce the possibility of missing swan nests. Mapping the nests and territorial non-breeders took about five to seven days, depending on the weather, snow conditions and visibility.

All nests recorded during the initial survey were subsequently visited and examined, and areas where swan pairs had been seen regularly in previous years also were visited to determine whether a nest had been missed. Nests were classified as new or old, with compacted vegetation at the base of old nests indicating that they had been used by swans in previous years. The compass orientation of the slope and distance from the nearest water body (in meters) was recorded. Whether egg laying was complete was ascertained by making one or two additional visits to the nest. If a clutch was incomplete, the nest was visited daily until the last egg was laid. The eggs were all measured and weighed using a Pesola 300 g balance. Fresh egg mass was calculated using the formula: $W_0 = K_v LB^2$, where W_0 is the fresh egg weight, L = length (cm), B = width (cm), and K_v is a coefficient (Hoyt 1979). The coefficient was calculated by the method used for geese (Syroechkovsky and Litvin 1985) and appeared to be 0.555 (N = 37 eggs) (Syroechkovsky *et al.* 1990). Most nests were also visited after hatching, to determine whether the nesting was successful (at least one egg hatched), as indicated by the presence of egg shell membranes. Clutch initiation date was determined by deducting 40–45 h for each egg in an incomplete clutch from the date on which the nest was first visited, or the 30-day incubation period plus 40–45 h per egg for complete clutches from the hatching date when hatching date was known.

A total of 127 Bewick's Swans nests were monitored over the 6-year period. Data from six nests found in the Yugorsky Peninsula (69°36'N, 60°13'E) in 1996, and from 34 nests on the Russkiy Zavorot Peninsula (68°40'N, 53°40'E), were used for a comparison of egg dimensions and clutch sizes in different parts of the breeding range. Values presented are means ± SE.

RESULTS AND DISCUSSION

Nests and Nesting Habitats

Bewick's Swans on Vaygach Island showed no obvious preferences for particular nesting habitats, except that they did not use low-

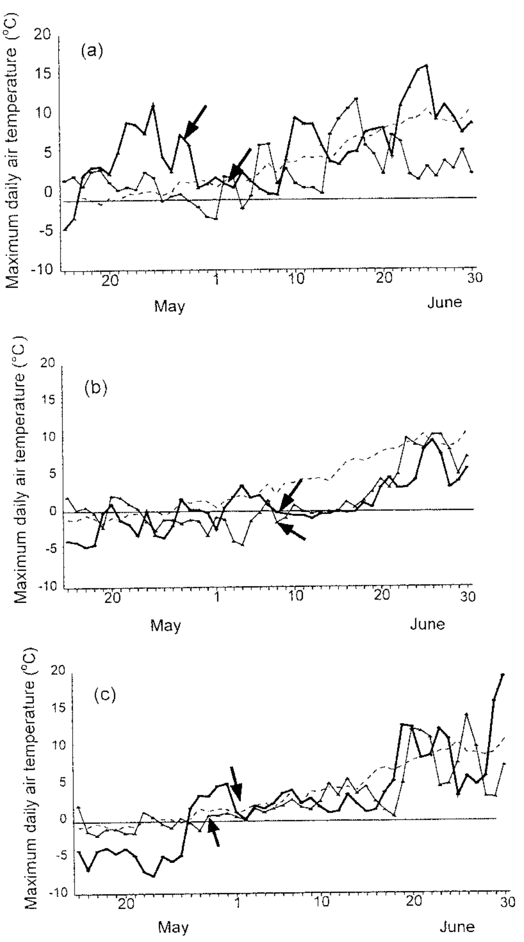

Figure 2. Mean daily temperatures in: (a) early springs (light line = 1986, heavy line = 1995); (b) late springs (light line = 1987, heavy line = 1997); and (c) normal springs (light line = 1988, heavy line = 1996). Dotted lines show the mean daily maximum air temperatures for 1984–1997. Arrows show the date of onset of egg laying in each year. Air temperature data were recorded at the Bely Nos weather station

lands covered with thick snow, and only a few (7%) nests were found on rocky ground, where there was little vegetation for nest building. A relatively high proportion of nests were situated in dry areas characterized by willow bushes (*Salix* spp.) (Fig. 3), whereas in the Bolshezemelskaya Tundra the swans generally use sedge and moss-sedge habitats (Mineev 1995).

The onset of egg laying varied between years, from 28 May in 1995 to 17 June in 1997. Early years were characterized by early mean laying dates, and by the river thawing in late May, whereas late years had later laying dates and the breakup of river ice was not until mid to late June (Tables 1 and 2).

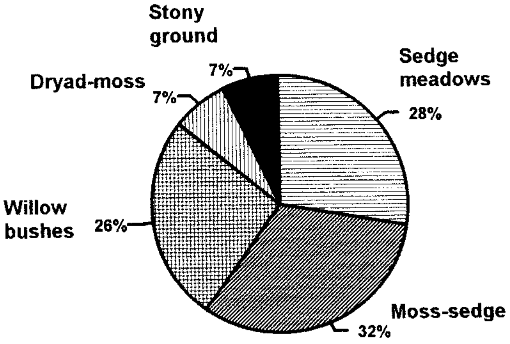

Figure. 3. Proportion of Bewick's Swan nests recorded on different habitats on Vaygach Island (N = 77 nests).

Reports have differed on whether the swans use their nest in only one year. Ptushenko (1952) supposed that Bewick's Swans on Novaya Zemlya used their nests more than once, whereas Mineev (1995) wrote that swans in the Bolshezemelskaya tundra " . . . usually did not use old nests". Of 92 nests examined on Vaygach Island where age was determined, 40 were old and 52 were new. The ratio of old to new nests varied between years (Table 2); the relatively high proportion of old nests in early springs was not significant ($\chi^2_1 = 2.09$, n.s.), but there were significantly more new nests in late springs than in other years ($\chi^2_1 = 4.11$, $P < 0.05$). Moreover, the ratio of old nests correlated with the mean clutch initiation date in that year (Pearson Correlation, $r_4 = -0.82$, $P < 0.05$). This may reflect differences in the availability of old nests for swans in early and late springs. If the spring snow melt is late, old nests that become frozen during winter may not thaw in time, whereas if spring is early some pairs can reuse old nests.

Nest Density

The density of Bewick's Swan nests varied substantially between years, from 0.12 to 0.36 nests km^{-2} over the six-year study (Table 2). Highest nest densities were recorded in medium springs, perhaps because of the combination of a medium arrival date with good

Table 1. Weather conditions on Vaygach Island during the study.

Year	Snow level	Percentage of snow cover on 9 June (%)	River ice breakup (water running)	Spring timing	Cold snaps during egg laying
1986	Low	<50	Late May	Early	+
1987	Medium	100	21 June	Late	–
1988	Medium	70	Early June	Medium	–
1995	Low	?	Late May	Very early	+
1996	High	85	4 June	Medium	–
1997	Medium	75	12 June	Late	+

weather conditions after the swans' arrival. The occurrence of cold weather ("cold snaps") during laying and incubation seems important, which may be why nest density was moderate in 1995 despite an extremely early spring (Fig. 2). Nest density can also be described as mean minimal distances between nests; there was a significant correlation between the mean distances to the nearest nest and the nest density estimated for the study area each year (Pearson correlation, $r_4 = 0.81$, $P < 0.05$; Table 2).

Clutches

Mean clutch size varied between years, ranging from 2.4 in 1997 to 3.3 in 1995, and was correlated with the mean onset of laying date in the same years ($r_4 = 0.90$, $P < 0.02$; Table 2), indicating that clutch size is associated with the timing of the spring thaw, with larger clutches recorded in early springs. Clutches ranged from one to five eggs, although five eggs were recorded in only two of the 127 nests checked (in 1995 and 1996). These probably belonged to the same pair, because both clutches were found in the same nest, and in both years the eggs were similar in size and weight. A preliminary comparison with other parts of the breeding range suggests that Bewick's Swan clutch size on Vaygach Island may differ from that of swans nesting further south in mainland Russia. In 1996, six nests checked on the Yugorsky Peninsula, 100 km south of study area, found clutches of 3, 4, 5, 5, 5 and 6 eggs, whereas five eggs were recorded only twice throughout the study on Vagach Island. The clutch sizes recorded on the Yugorsky Peninsula were significantly greater than for the 27 nests checked on Vaygach Island in 1996 (Mann-Whitney U-test, $U = 18.5$, $P < 0.05$). Moreover, the clutch size of swans nesting in the Russkiy Zavorot Peninsula in the same

Table 2. Breeding parameters for Bewick's Swans nesting on Vaygach Island. Mean values are given ±SE throughout. Sample sizes are given in parentheses.

Year	1986^{+++1}	1987^{+}	1988^{++}	1995^{+++}	1996^{++}	1997^{+}
Mean clutch initiation date (days from 1 June)	8.7 ± 1.0 (13)	11.6 ± 1.3 (5)	9.1 ± 0.9 (25)	1.6 ± 1.5 (10)	9.4 ± 0.8 (24)	12.3 ± 1.2 (6)
Percentage of old nests	47% (15)	17% (12)	46% (24)	63% (8)	50% (26)	33% (6)
Nest density (Nests km^{-2})	0.19 ± 0.05	0.12 ± 0.04	0.31 ± 0.06	0.21 ± 0.05	0.36 ± 0.07	0.13 ± 0.04
Distance (km) to nearest nest	0.97 ± 0.01 (18)	1.73 ± 0.05 (13)	1.08 ± 0.01 (32)	1.29 ± 0.02 (10)	0.86 ± 0.01 (27)	1.98 ± 2.05 (6)
Nesting success (%)	66% (9)	66% (12)	94% (18)	86% (7)	71% (17)	20% (5)
Mean clutch size	3.00 ± 0.18	2.36 ± 0.25	2.79 ± 0.17	3.27 ± 0.36	2.85 ± 0.20	2.40 ± 0.40
Modal clutch size	(18) 3	(14) 3	(29) 3	(11) 4	(27) 3	(5) 3
Calculated fresh egg mass	245.0 ± 2.9 (52)	235.9 ± 3.1 (32)	245.2 ± 2.2 (76)	237.2 ± 3.6 (32)	240.6 ± 2.2 (69)	231.0 ± 5.4 (12)
Range	192.5–291.0	197.3–273.5	196.3–297.2	192.0–281.1	191.2–312.4	196.6–262.4

$^{+++}$Early spring, $^{++}$medium spring, $^{+}$late spring.

year (mean = 3.5, N = 34) was also greater than that on Vaygach Island (mean = 2.85, N = 27) (Student's t-test, $t_{59} = 2.5$, $P < 0.05$).

Egg Mass

A comparison of the average egg mass recorded for each clutch in early springs (1986 and 1995, N = 28), with those in medium springs (1988 and 1996, N = 50) and in late springs (1987 and 1997, N = 19) found a significant difference in egg mass recorded for the three weather categories (Kruskall-Wallis test, $\chi^2_2 = 9.36$, $P < 0.01$). Spring weather conditions therefore appear to affect not only nest density and clutch size, but also fresh egg mass, with egg mass being lower in late springs. Eggs of swans on Vaygach Island appeared to be lighter than those nesting further south; mean egg mass for swans on the Russkiy Zavorot in 1996 was 248.5 ± 1.9 g (N = 129; S. Grigoryan, unpubl. data).

Nesting Success

One of the main reasons for nesting failure appeared to be when the swans stopped incubation before hatching. Four pairs of swans whose territories were situated close to the camp were observed daily from the window of the study cabin, and three of these pairs nested in 1996. At the first nest, one birds was present on the nest on 25 June, both members of the pair were seen at a distance of 100 m from the nest for a long period on 27 June, and on 28 June egg shells were found nearby. A second nest was abandoned at the end of June, but both pairs stayed on their territories until the end of July. The third pair, which was closest to camp, hatched their clutch. Nesting success for 69 clutches monitored through to hatching was lower in years with cold weather during laying (1986 and 1995) or late springs (1987), or both (1997) than in milder seasons (1988 and 1996; Table 1) ($\chi^2_1 = 3.85$, $P < 0.05$; Table 2). We were not able to determine the number of abandoned nests among the unsuccessful ones in the present study, but it was assumed that most clutches were left before being predated because, in some cases, cold eggs remained in the nest for at least two to three days before being destroyed by gulls (*Larus* spp.) or Arctic Foxes (*Alopex lagopus*), perhaps because the continued presence of the pair close to a nest deterred predators from taking the eggs.

In general, predation of swan eggs seemed low on Vaygach Island. The only species of bird likely to threaten swan clutches in the area is the Glaucous Gull (*Larus hyperboreus*), but gulls were not observed successfully stealing swan eggs. Moreover, swans were recorded chasing Arctic Foxes from the nests only once or twice during the six-year study. It seemed that the foxes knew the location of swan nests in their hunting areas and preferred not to go too close; foxes moving in one direction often changed direction to keep a distance of not less than 150–200 m between itself and a swan nest. One nest near the coast was predated by a Polar Bear *(Ursus arctos)* in 1988. Domestic Reindeer (*Rangifer tarandus*), which readily eat goose eggs (Syroechkovsky and Krechmar 1981), did not seem to affect swan nests in this study, although this has been suggested for other parts of the breeding range (Pozdnyakov 2002). Groups of reindeer periodically visited the study area, but there was no evidence of any destroyed swan nests after these visits. Indeed, one pair of nesting swans threatened a group of five to six reindeer to prevent them from coming too close to their nest.

For 45 clutches where the exact number of cygnets that hatched was known, 123 cygnets hatched successfully from a total of 137 eggs (89.8%, data for all years of the study included). Of the 14 eggs that were lost, two (1.5%) remained in the nest after the rest had hatched (cygnets dead in shell, perhaps due to slow embryo growth), five (3.6%) were rotten (perhaps not fertilized), two (3.6%) were predated, presumably by gulls after the nest was checked, and five (3.6%) disappeared from the nests (one from each nest) for reasons not known. The proportion of cygnets that hatched in the study area varied between years (Table 2) and this, together with the variation in nesting density and clutch size, indicates that Bewick's Swan breeding success is influenced by several parameters related to weather conditions, as has been demonstrated for geese nesting in the arctic (Owen 1980, Syroechkovsky *et al.*, 1991). The timing of swan nesting is later in years when the thaw is later, nesting density is lower in these years, and clutch size and egg mass is also lower. Thus spring weather, including the occurrence of cold snaps, appears to be the most important factor affecting Bewick's Swan breeding success on Vaygach Island.

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Spatial Distribution, Habitat Characteristics and Nest-site Selection by Tundra Swans on the Central Arctic Coastal Plain, Northern Alaska

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Abstract.—Annual aerial surveys of nesting Tundra Swans (*Cygnus columbianus columbianus*) were conducted during 1989–2000 on the Kuparuk and Milne Point oilfields and adjacent areas of the central Arctic Coastal Plain of northern Alaska. Spatial analysis indicated that swans selected nest sites close (≤100 m) to large lakes (20–33 ha) and that nests were clumped in distribution each year, although nests on average were greater than 2.5 km apart. The clumped distribution of nests suggests that suitable habitats for nesting swans are not randomly distributed in the study area. Mean distance of nests to the Beaufort Sea coastline ranged annually from 11.1–14.5 km. Waterbodies near nests had significantly higher shoreline complexity each year than the closest waterbodies to random locations. Complex shorelines (i.e., small coves or sheltered areas) provide areas suitable for emergent vegetation such as Pendant Grass (*Arctophila fulva*), a dominant species in preferred foraging habitat in northern Alaska. Photographs of Tundra Swan nests, taken over a seven-year period, were used to characterize nest-site habitats at both macrotype and microtype scales. Nests primarily were located on the driest microtypes and on macrosites associated with lakes, usually within 20 m of the lake shore. Nest sites afforded good visibility and early exposure during spring thaw. Among the 89 swan territories that had at least three years of use, swans used the same mound each year in 36% of territories and used a different mound each year in 12%; swans in remaining territories used the same mound in some years and new mounds in others. Studies such as ours may be useful for evaluating the impacts of oil development, and for planning and permitting future developments in new regions on the Arctic Coastal Plain of Alaska.

Key words.—Alaska, *Cygnus columbianus*, habitat, nearest-neighbor analysis, nest-site selection, spatial distribution, Tundra Swan, waterfowl.

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Most research on Tundra Swans (*Cygnus columbianus columbianus*) in their arctic nesting grounds in North America and Canada has focused on monitoring distribution and abundance on a regional (McLaren and McLaren 1984; Gaston *et al.* 1986; Stewart and Bernier 1989; Mallek and King 2000) or local (Stickney *et al.* 1994; Anderson *et al.* 2000; Ritchie and King 2001) basis. The few studies of swan breeding biology and habitat preferences in arctic Alaska (Hawkins 1986; Earnst 1992; Monda *et al.* 1994; Johnson *et al.* 2000) have been conducted on river deltas, which may have different geomorphologies and wetland types than the rest of the coastal plain.

On the central Arctic Coastal Plain of Alaska, bordered by the Colville River to the west and the Canning River to the east, the nesting distribution of Tundra Swans coincides with oilfield development, including the large fields of Prudhoe Bay and Kuparuk and smaller fields east of Prudhoe Bay (Gilders and Cronin 2000). As many as 2,000 swans are estimated to inhabit this region (Ritchie and King 2000), and populations appear to be increasing (Ritchie *et al.* 2002).

Tundra Swans are considered to be an indicator species of the overall health of waterfowl populations (King 1973) and wetland ecosystems. Tundra Swans have received attention, from both oil industry and regulatory agencies in northern Alaska, during the planning of new oilfield developments. Since 1989, we have used aerial surveys to monitor the distribution and abundance of swans during nesting in the Kuparuk and Milne Point oilfields and adjacent areas. Here we analyze the spatial distribution of swans and assess habitat selection. This information could then be used to mitigate impacts to nesting swans during future oil exploration and development.

STUDY AREA

The study area encompasses 2,247 km^2 of the central Arctic Coastal Plain between the Kuparuk and Colville

Rivers (Fig. 1). The area is a gently rolling plain dominated by thaw lakes that are generally oriented perpendicularly to the prevailing northeast winds (Carson and Hussey 1962; Walker and Acevedo 1987). Surface forms are strongly affected by permafrost, seasonal freezing and thawing of the active layer, and by subsurface thaw degradation. Ice-wedge polygons, which result in patterned (polygonal) ground (Jorgenson *et al.* 1997), are common.

Habitat types range from unvegetated tundra, characteristic of low-lying areas along the coast and shorelines of lakes, to upland tundra with dwarf shrubs in more elevated, better-drained terrain (Walker and Acevedo 1987; Jorgenson *et al.* 1997). The dominant vegetated habitats in the study area include Non-patterned Wet Meadow, Wet Sedge Low Relief Meadow, Basin Wetland Complex, Moist Sedge-Shrub Meadow and Moist Tussock Tundra. Non-patterned Wet Meadow is sedge-dominated and typically occurs within young drained lake basins and as narrow margins of receding waterbodies in areas without extensive ice-wedge polygonization. Water Sedge (*Carex aquatilis*) and Cottongrass (*Eriophorum angustifolium*) usually dominate. Wet Sedge Low Relief Meadow occurs in lowland areas within drained lake basins, and is associated with low-centered polygons and strangmoor (i.e., string bogs comprised of disjunct ridges). Dominant vegetation is *C. aquatilis* and *E. angustifolium* and abundant willows (*Salix* spp.). Basin Wetland Complex (both young and old) occurs in drained lake basins and is a complex mosaic of open water, aquatic sedge and grass marshes (especially Pendant Grass, *Arctophila fulva*), and wet and moist meadows in patches too small to map individually (<0.5 ha). Moist Sedge-Shrub Meadow occurs on better-drained uplands between thaw basins, generally associated with non-patterned ground or high-centered polygons with low relief. Dominant vegetation is *C. aquatilis, E. angustifolium, Salix planifolia pulchra* (Diamond-leaf Willow), and *Dryas integrifolia* (Entire-leaf Mountain Avens) with moss ground cover. Moist Tussock Tundra is similar to Moist Sedge-Shrub Meadow, except the dominant vegetation is the tussock-forming sedge Tussock Cottongrass (*E. vaginatum*).

The study area includes the Kuparuk Oilfield (1,045 km^2) and the Milne Point Unit (220 km^2). The Kuparuk

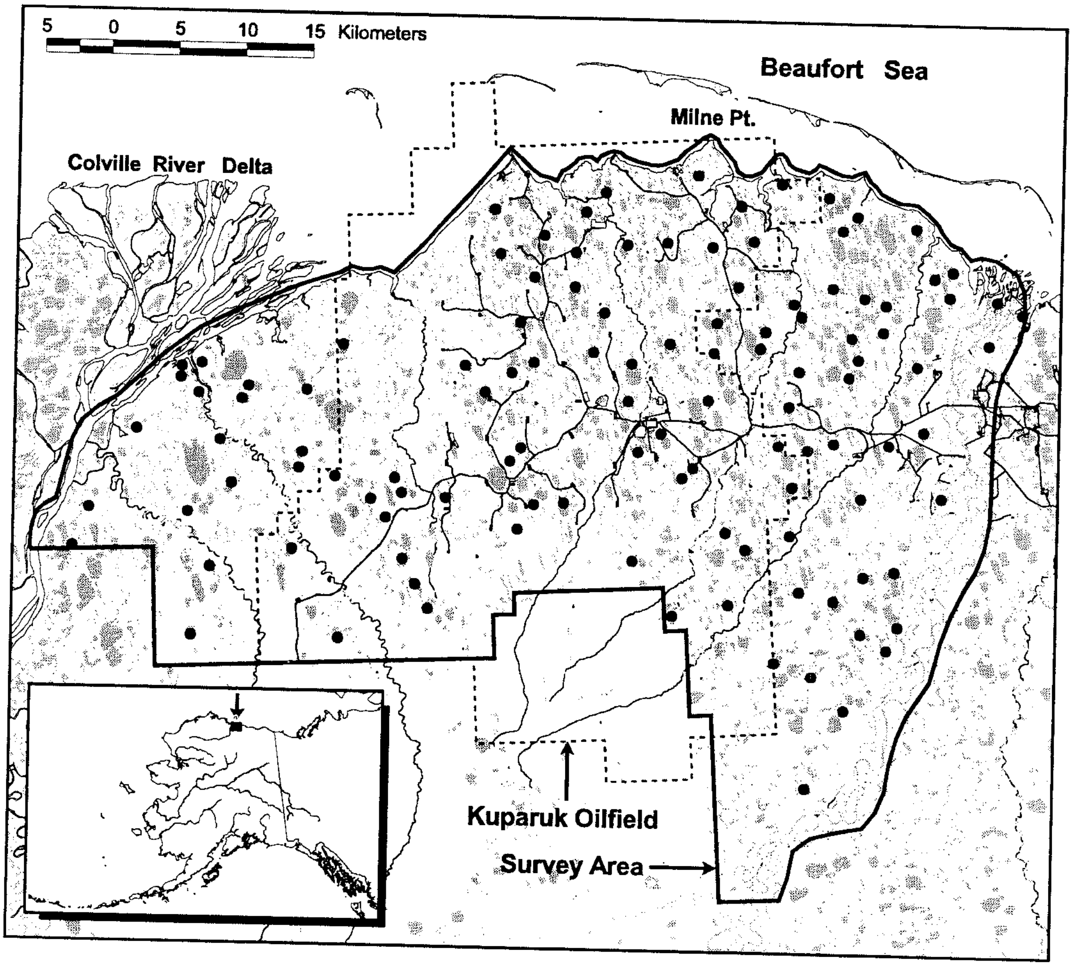

Figure 1. Tundra Swan nest distribution in 1996 (year with highest nest density) in relation to lake distribution (lakes shown in gray), on the central Arctic Coastal Plain, Alaska. Study area boundary, oilfield boundary and roads (solid lines) are indicated.

Oilfield, which started production in 1981, currently has over 50 drilling pads and >10 km^2 disturbed by gravel placement (roads and pads) and mine sites (Gilders and Cronin 2000).

METHODS

Aerial surveys were conducted each year from 1989–2000 using a Cessna 185 with a pilot and two observers and followed U.S. Fish and Wildlife Service protocol (USFWS 1987, 1991). Fixed-width (1.6-km wide), east-west transects were flown at an altitude of 150 m above ground level and at a speed of 145 $km \cdot hr^{-1}$. Each observer scanned a transect 800-m wide on his side of the airplane and recorded observations on 1:63,360 topographic maps. The aircraft circled all nests to aid accurate mapping and allow photography of the nest site using a 35-mm camera with color print film. Surveys were conducted during mid-late incubation, usually 16–22 June.

Nest locations were entered into digital maps (developed from the 1:63,360 maps by AeroMap, USA, Inc., Anchorage, AK) in a geographic information system. Six spatial parameters were measured for each nest: distance to nearest waterbody (e.g., lake), area and perimeter of nearest waterbody, distance to the Beaufort Sea coast, and distance to nearest oilfield road and pad (well pad, storage pad, or processing facility).

Shoreline complexity of the nearest waterbody was defined as the perimeter of that waterbody divided by the perimeter of a circle having identical area. The resulting parameter is unitless and has a minimum value of 1 (i.e., the value of a circular waterbody, which has no shoreline complexity).

To evaluate whether nests were placed at random, we generated a sample of 734 random locations. For each random location, we calculated the same parameters used to characterize nests and used this random set to analyze for differences in spatial characteristics between actual nest sites and random locations.

The distance from each swan nest to its nearest neighbor (i.e., nearest active nest) was calculated and a nearest-neighbor analysis (Clark and Evans 1954; Krebs 1989) was used to determine the relative dispersion of nests in the study area. Pearson's correlation was used to evaluate whether mean nearest-neighbor distances were associated with the number of nests each year. A nearest-neighbor analysis also was conducted on lakes >20 ha in size (minimum mean size used by swans in our study area) to determine whether lake distribution was uniform, random, or clumped.

Because swans are territorial and use of nest sites may not be independent among years, we analyzed spatial characteristics of nest sites only within years. Within years, we tested for significant differences between the spatial characteristics of nests and those of random locations using Mann-Whitney tests. Statistical analyses were performed using SPSS/PC+ software (v.10) and Microsoft Excel data analysis software.

Nest photographs were used in 1994–2000 to determine habitat type at two scales, a macrotype (within 50 m) and a microtype (within 2 m of the nest). Habitat types (see Study Area) were characterized using the ecological land classification system developed for the Colville River Delta region by Jorgenson *et al.* (1997). If more than one habitat type was present, as was often the case at the macrotype scale, the type was classified as the habitat encompassing the most area. Site characteristics (i.e., terrain surface forms) of the nests were evaluated similarly at two scales: the macrosite, defined as the principal landscape feature around the nest, and the microsite, defined as the surface form on which the nest was built. Nests were assigned to one of five macrosites: inland (i.e., nest located >20 m from the shore of a lake or other sizeable waterbody), shore (≤20 m of the water), island, islet (<3 m in diameter), or peninsula. Nests also were assigned to one of five microsites: non-patterned, polygon rim, polygon trough, within a high- or flat-centered polygon and non-polygonal mound. The latter category consisted of all raised surface forms that were not a distinct part of a polygon (such as hummocks or strangmoor).

Nest photographs also were used to identify territories that had at least three years of use by nesting swans. Using a combination of photographs and digital locations of nests, we determined whether adjacent nest sites occupied in different years constituted a likely territory (i.e., they shared the same lake or basin complex), whether nests occupied the same mound in subsequent years, and the distance between nest sites in those territories where more than one nest site was used.

RESULTS

Waterbody Distance, Size and Shoreline Complexity

In 1989–2000, the mean distance from swan nests to the nearest waterbody ranged from 35 to 67 m and the mean size of the waterbody was 20–33 ha (Table 1). In each year, Tundra Swan nests were significantly closer to waterbodies than were random locations, and those waterbodies closest to nests were significantly larger than those closest to random locations (Mann-Whitney tests; all $P < 0.001$) (Table 1). Similarly, of the 22,703 waterbodies within the study area, only 16% (3,736 waterbodies) were large (i.e., >1 ha) and the waterbodies closest to Tundra Swan nests were 2.5–3.5 times larger than the mean large waterbody ($\bar{x}$ = 8.2 ha ± 21.6 [SD]) available in the study area.

Mean shoreline complexity of all waterbodies in the study area was 1.3 ± 1.0 [SD] (N = 22,703), and that of large waterbodies (>1 ha) was 1.6 ± 0.5 [SD] (N = 3,736). Waterbodies closest to Tundra Swan nests had significantly higher shoreline complexity each year ($\bar{x}$ = 1.6–1.8 for 1989–2000; Table 1) than waterbodies closest to random locations ($\bar{x}$ = 1.5) (Mann-Whitney U tests, all $P < 0.001$). Similarly, waterbodies closest to nests had significantly higher shoreline complexity each year than the average waterbody in the study

Table 1. Distance (m) of Tundra Swan nests to the nearest waterbody, and characteristics of that waterbody, on the central Arctic Coastal Plain, Alaska, 1989–2000. Distance to, and characteristics of, the nearest waterbody to 734 random locations also were measured (see last row).

	Distance to waterbody[a] (m)			Waterbody area (ha)			Shoreline complexity[b]			
Year	Mean	SD	Z[c]	Mean	SD	Z[c]	Mean	SD	Z[c]	N
1989	41	86	5.6***	24	31	5.6***	1.8	0.7	4.1***	44
1990	35	44	6.6***	23	27	7.0***	1.7	0.6	4.5***	73
1991	55	83	5.6***	27	44	7.0***	1.7	0.6	3.2**	81
1992	57	97	5.4***	23	33	5.8***	1.6	0.6	3.5***	75
1993	60	104	5.0***	21	23	5.3***	1.7	0.6	4.6***	67
1994	35	82	6.6***	28	38	5.8***	1.7	0.5	4.7***	50
1995	60	64	4.7***	20	26	5.8***	1.6	0.5	3.2**	106
1996	47	73	6.9***	26	31	7.6***	1.7	0.6	5.9***	116
1997	53	71	4.8***	25	37	4.9***	1.6	0.5	3.9***	73
1998	48	64	6.1***	30	35	8.1***	1.8	0.6	6.3***	107
1999	50	75	5.7***	33	49	5.2***	1.6	0.6	3.2**	75
2000	50	96	6.8***	30	46	7.2***	1.6	0.6	4.2***	85
Random	126	150		16	52		1.5	0.5		734

[a] For nests on islands within waterbodies, a distance to the waterbody of 1 m (to account for a minimum island/islet size) was assigned. Random locations falling within waterbodies also were assigned a distance of 1 m.

[b] Shoreline complexity is defined as the ratio of the perimeter of the nearest waterbody and a circular waterbody of equal size (i.e., no complexity). Increasing values greater than 1 indicate increasing complexity.

[c] Z-statistic for yearly data tested against the random set using two-tailed Mann-Whitney tests. Significance levels: * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

area (Mann-Whitney U tests; all P < 0.05) and had significantly higher complexity than the average large waterbody (Mann-Whitney U tests; P < 0.05) in three of twelve years (1994, 1996, 1998). The size of waterbodies closest to nests also was significantly larger than the average size of both all waterbodies and large waterbodies in the study area (Mann Whitney U test; all P < 0.05).

Proximity to the Beaufort Sea Coastline

The mean distance of swan nests to the Beaufort Sea coastline varied from 11.1 km in 1989 to 14.5 km in 1994. In five of twelve years, the mean distance of the coastline to nests was significantly closer than the mean distance of random locations to the coastline (Mann-Whitney U tests, P < 0.05; Table 2).

Distance to Oilfield Infrastructure

Tundra Swan nests ranged from a mean of 4.6–6.8 km to pads and 4.5–7.0 km to roads in 1989–2000 (Table 2). These distances did not differ, however, from those of the random locations in any year (Table 2).

Distance to Nearest Neighbors

The nearest-neighbor analyses of swan nests indicated that nests were clumped in distribution in each year (Fig. 1; Table 3). Mean nearest-neighbor distance ranged from 2.6 km (1995) to 3.8 km (1989) for swan nests (Table 3). Mean nearest-neighbor distances were inversely correlated with the annual number of nests in the study area (r^2_{10} = -0.92, P < 0.01). A nearest-neighbor analysis of large lakes (≥20 ha) in the study area indicated that they also were clumped in distribution (R = 0.00002, Z = -34.6, N = 328).

Habitat Characteristics

In 1994–2000, Tundra Swan nests occurred primarily in five of twelve terrestrial habitats (macrotypes) described for our study area (Table 4). At the microtype level, swans built nests primarily on four of twelve terrestrial habitats, which were the driest habitats in the study area (Table 4). Over 53% of swan nest sites in each year were in two moist tundra types (Moist Sedge-Shrub Meadow and Moist Tussock Tundra), with

Table 2. Distance (km) of Tundra Swan nests to the coastline of the Beaufort Sea and the closest oilfield pad and road, central Arctic Coastal Plain, Alaska, 1989–2000.

	Coastline			Oilfield pad			Oilfield road			
Year	Mean	SD	Z[a]	Mean	SD	Z[a]	Mean	SD	Z[a]	N
1989	11.1	8.4	2.2*	6.1	6.0	0.1	6.1	6.2	0.3	44
1990	11.3	7.9	2.5*	6.0	5.4	0.2	5.9	5.6	0.4	73
1991	11.8	8.7	2.3*	4.6	4.4	1.8	4.5	4.6	1.4	81
1992	12.8	9.0	1.5	6.8	6.5	0.8	6.7	6.8	0.8	75
1993	14.4	10.3	0.3	6.0	5.9	0.0	6.0	6.1	0.5	67
1994	14.5	8.2	0.1	5.5	5.0	0.0	5.3	5.3	0.1	50
1995	12.4	8.5	2.0*	5.7	5.9	0.8	5.5	6.1	0.6	106
1996	12.5	8.8	2.1*	6.0	5.9	0.1	5.9	6.1	0.2	116
1997	12.7	8.7	1.5	5.7	5.7	0.5	5.7	6.0	0.2	73
1998	13.8	9.0	0.7	5.2	5.2	1.2	5.1	5.3	0.3	107
1999	12.4	8.0	1.7	5.5	5.5	0.8	7.0	6.2	1.5	75
2000	13.2	8.7	1.2	4.9	5.0	1.8	4.7	5.2	1.7	85
Random	14.8	10.2		6.2	6.1		6.1	6.3		734

[a] Z-statistic for yearly values tested against the random set using Mann-Whitney tests. Significance levels: * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

33–68% of the sites located in Moist Sedge-Shrub Meadow (Table 4).

Most (>70%) nest sites were on macrosites associated with lakes (e.g., islands, islets, peninsulas, shore), with >50% on a peninsula or on the shore (within 20 m of a lake) (Table 5). Most (>67%) swan nests were constructed on microsites that represented some feature of a polygon, especially polygon rims, that tended to have the highest elevation above the surrounding tundra (Table 5).

We identified 89 swan territories with ≥3 years of photographic coverage. These territories had been occupied a mean of 4.2 years (maximum = 7 years) based on photographic coverage alone and a mean of 5.4 years (maximum = 11 years) based on a combination of photographic coverage and locations

Table 3. Nearest-neighbor analysis of Tundra Swan nests in the central Arctic Coastal Plain, Alaska, 1989–2000.

	Distance to nearest neighbor (m)				Nearest-neighbor analysis[a]		
Year	Mean	SD	Range	N[b]	*R*	*Z*	Distribution
1989	3,812	1,755	44–7,784	44	1.59×10^{-5}	12.7	clumped
1990	3,150	1,453	1,078–7,640	73	1.63×10^{-5}	16.4	clumped
1991	2,770	1,101	1,141–6,388	81	1.68×10^{-5}	17.1	clumped
1992	3,117	1,525	1,177–7,990	75	1.75×10^{-5}	16.6	clumped
1993	3,492	1,788	965–9,494	67	1.91×10^{-5}	15.7	clumped
1994	3,727	1,922	1,345–10,049	50	1.59×10^{-5}	13.5	clumped
1995	2,637	1,179	640–7,158	106	1.70×10^{-5}	19.7	clumped
1996	2,640	1,201	825–7,020	116	1.76×10^{-5}	20.6	clumped
1997	3,093	1,640	367–9,982	73	1.74×10^{-5}	16.1	clumped
1998	2,689	1,236	1,097–7,230	107	1.79×10^{-5}	19.8	clumped
1999	2,878	1,589	665–9,600	75	1.54×10^{-5}	16.2	clumped
2000	3,046	1,657	545–8,503	85	1.69×10^{-5}	17.4	clumped

[a] Nearest-neighbor analysis follows Clark and Evans (1954), as modified by Krebs (1989), for a bounded study area: $R < 1$—clumped distribution; $R = 1$—random distribution; $R > 1$—uniform distribution. The Z test is a test of significance from a random distribution (H_0 is $R = 1$), using the standard error of the expected difference; Z is significant at 1.96.

[b] N = number of nests.

Table 4. Number and percentage (in parentheses) of Tundra Swan nests in different habitats at the macrotype and microtype scales. Nests were photographed during aerial surveys in the central Arctic Coastal Plain, Alaska, June 1994–2000. Data are not combined because swans reuse nest sites between years.

	Number (%) of nest sites						
Scale/habitat[a]	1994	1995	1996	1997	1998	1999	2000
Macrotype (within 50 m)[b]							
Moist Sedge-Shrub Meadow	19 (39)	31 (30)	34 (30)	22 (31)	29 (27)	24 (34)	22 (27)
Wet Sedge Low Relief	7 (15)	25 (24)	23 (20)	23 (32)	26 (25)	32 (45)	33 (40)
Non-patterned Wet Meadow	6 (12)	10 (10)	22 (19)	10 (14)	29 (27)	7 (10)	7 (9)
Basin Wetland Complex	9 (18)	16 (15)	20 (18)	6 (9)	11 (10)	2 (3)	8 (10)
Moist Tussock Tundra	5 (10)	21 (20)	14 (12)	8 (12)	8 (8)	5 (7)	11 (13)
Other	6 (6)	2 (2)	1 (1)	2 (3)	3 (3)	1 (1)	1 (1)
Total Nest Sites	49	105	114	71	106	71	82
Microtype (within 2 m)[b]							
Moist Sedge-Shrub Meadow	34 (68)	64 (60)	69 (59)	38 (53)	59 (55)	24 (34)	45 (54)
Non-patterned Wet Meadow	7 (14)	14 (13)	26 (22)	15 (21)	26 (24)	10 (14)	4 (5)
Moist Tussock Tundra	6 (12)	25 (24)	18 (16)	14 (19)	17 (16)	14 (20)	19 (23)
Wet Sedge Low Relief	2 (4)	2 (2)	3 (3)	5 (7)	5 (5)	22 (31)	14 (17)
Other	1 (2)	1 (1)				1 (1)	1 (1)
Total Nest Sites	50	106	116	72	107	71	83

[a] Habitat types follow the ecological land classification system for the Colville River Delta region (Jorgenson *et al.* 1997). See study area section for descriptions of the major types. Other habitats include Salt Marsh, Aquatic Sedge Marsh, Aquatic Sedge with Deep Polygons, and Aquatic Grass Marsh.

[b] Only photographs of sites at an appropriate scale were evaluated.

mapped during aerial surveys (pre-1994). In 36% of all territories, swans used the same nest mound in each year of use (based on three to seven years of photographs). In only eleven territories (12%) did swans use a different nest site each year (maximum of five

Table 5. Number and percentage (in parentheses) of Tundra Swan nest sites occurring on various macrosite and microsite surface forms. Nests were photographed during the nesting survey, central Arctic Coastal Plain, Alaska, June 1994–2000. Data were not combined because swans reuse nest sites between years.

	Number (%) of nest sites						
Scale/habitat	1994	1995	1996	1997	1998	1999	2000
Macrosite (within 50 m)[a]							
Island	8 (16)	11 (10)	14 (12)	7 (10)	18 (17)	6 (8)	17 (21)
Islet	1 (2)	5 (5)	5 (4)	5 (7)	8 (8)	4 (6)	3 (4)
Peninsula	19 (38)	17 (16)	33 (28)	17 (24)	32 (30)	24 (33)	16 (19)
Shore	15 (30)	43 (41)	45 (39)	27 (38)	29 (27)	23 (32)	26 (31)
Inland	6 (12)	29 (27)	19 (16)	16 (22)	20 (19)	14 (19)	21 (25)
Polygon Complex	1 (2)	1 (1)				1 (1)	
Total Nest Sites	50	106	116	72	107	72	83
Microsite (within 2 m)[a]							
Nonpatterned	10 (20)	20 (19)	33 (28)	14 (19)	31 (29)	17 (24)	12 (15)
High/Flat Polygon	16 (32)	48 (45)	33 (28)	19 (26)	26 (24)	16 (23)	19 (23)
Polygon Rim	20 (40)	33 (31)	45 (39)	33 (46)	39 (36)	34 (48)	46 (55)
Polygon Trough	1 (2)	3 (3)	1 (1)	1 (1)	3 (3)	1 (1)	
Non-polygonal Mounds	3 (6)	2 (2)	4 (3)	5 (7)	8 (8)	3 (4)	6 (7)
Total Nest Sites	50	106	116	72	107	71	83

[a] Only photographs of sites at an appropriate scale were evaluated.

years of occupation). The mean distance between nearest nest sites within a territory was 242 m (range = 16–831 m; N = 142 nest sites within 89 territories).

DISCUSSION

Waterbody Distance, Size and Shoreline Complexity

Tundra Swans clearly selected nest sites near larger lakes and those with higher shoreline complexity. Waterbodies closest to swan nests were larger than those closest to random locations, and were 2.5–3.5 times larger than the mean large (>1 ha) waterbody available in the study area. Similarly, on the Colville River Delta, breeding and nonbreeding swans preferred habitats near larger lakes (Earnst 1992). Monda *et al.* (1994) noted that swans in the Canning River Delta, Alaska, with a thaw-lake terrain similar to our study area, nested near large lakes with emergent vegetation, whereas swans on the Kongakut River Delta, with river floodplain terrain, nested near the coastal lagoon.

King and Hodges (1981) found that not only lake availability and size, but also shoreline complexity (defined as linear miles of shoreline), were correlated with numbers of Tundra Swans in western Alaska. Lakes with higher shoreline complexity tend to have more sheltered areas that are suitable for growth of emergent vegetation, such as *Arctophila fulva* and *C. aquatilis*, species associated with foraging habitats of Tundra Swans on the Arctic Coastal Plain (Derksen *et al.* 1981; Earnst 1992; Limpert and Earnst 1994; Monda *et al.* 1994).

Proximity to the Beaufort Sea Coastline

The lack of a clear trend in the location of Tundra Swan nests relative to the Beaufort Sea coastline may be a function of two conflicting processes. In some years, coastal areas may provide a longer breeding season than inland areas, because the local microclimate is moderated by open ocean waters later in the summer, allowing pairs with broods to remain in nearshore waters or open rivers when sites farther inland have frozen (McLaren and McLaren 1984; Monda *et al.* 1994). Conversely, availability of coastal habitats in spring can be limited in some years because snow melt tends to occur later there than at inland sites (pers. obs.). The largest mean distance (14.5 km) of swan nests to the coastline was recorded in 1994, when cold spring weather delayed nesting and snow persisted later into June than average (Anderson *et al.* 1995).

Distance to Oilfield Infrastructure

Distances of Tundra Swan nests to the closest oilfield road and pad were not significantly different from those for the random locations, suggesting that these oilfield developments (given their relatively small area) play less of a role in the selection of swan nest sites than does the attraction of swans to suitable waterbodies. However, a further analysis comparing swan use of large lakes near infrastructures to use of other lakes would be a more powerful test of the relationship between swan nests and infrastructure. Oilfield planners have located most roads and pads in drier, upland habitats and thus they may have a limited impact on the wetter habitats more often used by nesting swans. The presence of infrastructure alone may not be a source of disturbance to nesting swans, but associated human activities can be a factor. Incubating swans are sensitive to human disturbance and may leave their nests when humans are less than two km away (Monda *et al.* 1994). Murphy and Anderson (1993) found that Tundra Swans were disturbed most commonly by vehicular traffic in the Prudhoe Bay Oilfield, especially during pre-nesting; however, these swans appear to have habituated to other common sources of oilfield disturbance (e.g., facility noise, aircraft, flaring).

Distances to Nearest Neighbors

The mean distance between nests decreased as the number of nests (effectively nest density) increased. Nest distribution was clumped each year, and appears to be related to the clumped distribution of large lakes, which swans were shown to prefer. However, visual inspection of our twelve years of distributional data also suggests that as more swans nest (both new and returning territorial pairs), they placed their nests in areas where swans already were nesting, rather than choosing similar habitats unoccupied by swans.

Although few data are available on territory sizes for Tundra Swans on the Arctic Coastal Plain, territory sizes were estimated at 0.5–1.0 km^2 on the Colville River Delta (Limpert and Earnst 1994). We can estimate a maximum territory size in our study area by comparing the mean distance between nest mounds used during different years within territories (242 m) and between nests of different pairs in a year (i.e., mean nearest-neighbor distance; range = 2,637–3,812 m). These two measures suggest that maximum territory size may be as much as 3–4 km^2 (using the maximum distance between nest mounds within a territory as the minimal diameter of that territory). However, the actual territories likely are smaller with large areas of apparently unsuitable habitat between them.

Habitat Characteristics

Most swan nests were in locations classified as moist (Moist Sedge-Shrub Meadow and Moist Tussock Tundra) or wet (Nonpatterned Wet Meadow and Wet Sedge Low Relief) habitat types; however, most areas surrounding nests contained a complex of terrestrial and aquatic components that provided a diversity of habitats for foraging and other activities. An analysis of nest site selection by Tundra Swans on the Colville River Delta indicated that swans preferred (i.e., use was greater than availability) Wet Sedge-Willow Meadow, Moist Sedge-Shrub Meadow, and Deep Open Lakes with Islands (Johnson *et al.* 2000), all of which also occurred in our study area. Monda *et al.* (1994) found that 63% of the nests on the Canning River Delta occurred in the equivalent of our Wet Sedge-Willow Meadow and Moist-Shrub Meadow habitat types.

Tundra Swans tended to place nests on surface forms that afforded a combination of good visibility and early exposure during spring thaw, such as the centers of high- and flat-centered polygons or on polygon rims. In northeastern Alaska (Monda 1991) and the Colville River Delta (Limpert and Earnst 1994), swans also selected sites with unobstructed views that presumably aided in territorial and nest defense. In this study and elsewhere on the Arctic Coastal Plain, investigators have found swans nesting on mounds constructed in previous years (Hawkins 1986; Monda *et al.* 1994; Limpert and Earnst 1994). Reuse of nest mounds by Tundra Swans may be advantageous because it reduces time spent prospecting for nest sites and constructing nests in regions where the nesting season is short (Monda *et al.* 1994).

Because Tundra Swans are large, conspicuous birds that return to nest in the same area each year, they have been used in monitoring programs to assess the effects of human development across a broad geographic region. Our long-term monitoring study of Tundra Swans on the central Arctic Coastal Plain of Alaska has provided an important data set for investigating how large-scale geographic (lakes, coastlines) and small-scale terrain (habitats and surface forms) features influence the selection of nest sites by swans in this arctic ecosystem. Although agencies and oil companies already include swans as a factor in new site exploration and development planning, the additional insights into habitat requirements for nesting swans (lake size and complexity) provided by our study can refine these planning processes. We hope such planning will minimize disturbance, loss of habitat and possible dislocation of swans in these new areas.

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Nesting Ecology of Tundra Swans on the Coastal Yukon-Kuskokwim Delta, Alaska

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Abstract.—Nesting ecology of Tundra Swans (*Cygnus columbianus columbianus*) was studied along the Kashunuk River near Old Chevak (61°26'N, 165°27'W), on the Yukon-Kuskokwim Delta of western Alaska from 1988–2000. Annual variation in snow-melt chronology, nesting phenology, nesting density, clutch size and nest success was examined. The same area (approximately 23 km^2) was searched each year and nests were found as early as possible in the laying period. Laying initiation dates ranged from 1–27 May and hatch dates from 12 June–4 July among pairs and years of study. The peak arrival of Tundra Swans and the phenology of nest initiation and hatch were highly correlated with the progression of ice and snow melt in spring. Nest density averaged 0.71 km^{-2} and 89% of nesting pairs hatched at least one egg. Incubation period ranged from 26 to 33 days with a median of 30 days. Clutch size varied significantly among years, driven by a low mean value of 3.4 eggs in 1999. Clutch sizes were generally larger than found in previous investigations on the Yukon-Kuskokwim Delta, and nearly one egg larger than reported for clutches from Alaska's North Slope ($\approx$70°N). There was no indication of reduced clutch size in years of late spring snow melt, although nesting density tended to be lower.

Key words.—Tundra Swan, *Cygnus columbianus*, nesting ecology, clutch size, annual variation, Alaska.

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Tundra Swans (*Cygnus columbianus columbianus*) reach their highest breeding densities on the coastal Yukon-Kuskokwim Delta of Alaska (Dau 1981). Previous work on Tundra Swan reproduction on the Yukon-Kuskokwim Delta has focused on the use of aerial survey techniques to examine demographic and breeding productivity parameters (Lensink 1973; Dau 1981), or on description of behavior (Scott 1977; Ely *et al.* 1987). Here data are presented from 13 consecutive years of ground-based breeding studies on the coastal Yukon-Kuskokwim Delta. Annual variation in timing of nesting and snow-melt chronology, clutch size, nesting density, and nesting success is reported. Many of these parameters have been shown in other northern breeding birds to be sensitive to changes in the timing of spring environmental conditions (Crick *et al.* 1997).

STUDY AREA AND METHODS

The study area is located near Old Chevak (61°26'N, 165°27'W) on the central Yukon-Kuskokwim Delta of Alaska (Fig. 1). The physiography and vegetation of the area have been described in detail elsewhere (Babcock and Ely 1994). Briefly, lowland areas are composed of mixed sedge/grass/forb meadows with many lakes and shallow ponds that have maximum depths of <1 m. Upland areas, dominated by dwarf shrub/moss/lichen tundra, are 0.5–1.5 m higher in elevation than lowland meadows, and have numerous larger and deeper lakes.

Date of peak arrival of Tundra Swans was recorded as the day on which daily estimates of numbers on the study area showed the greatest increase. River ice break-up was the date on which river ice first broke and began flowing past our campsite, and date on which uplands were 90% snow-free was determined from daily ocular estimates from 3 m observation towers. Nests were found as early as possible in initiation of laying, so that laying sequence of eggs could be followed. The same area of about 23 km^2 was searched each year using consistent methods and effort. In most years some nests were also monitored outside our plots to increase the sample of nesting data. Nests were visited at least weekly to check status, though somewhat more frequently around initiation and hatch. Nest initiation date was defined as the date that the first egg was observed, or was back-calculated when possible from incomplete clutches assuming a laying interval of 42 hours (Hawkins 1986). Likewise, hatch date was the date that a cygnet was first observed in a nest, or back-dated one day if all eggs were hatched and cygnets were still present in the nest. Incubation period was only calculated from nests for which both initiation and hatch dates were known. Incubation period is defined as the span from the day the last egg was laid to the day of hatching

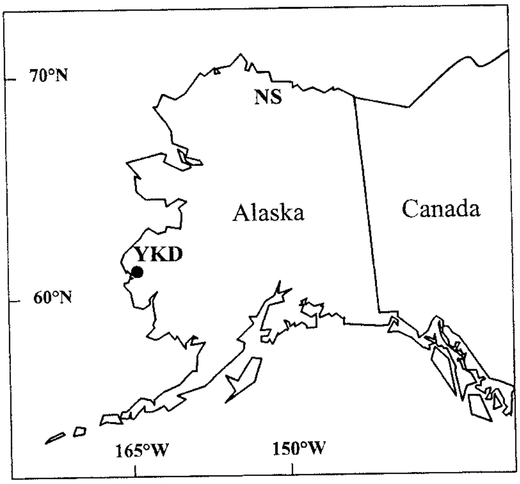

Figure 1. Location of the study area (●) on the Yukon-Kuskokwim Delta (YKD) of Alaska, and location of Alaska's North Slope (NS).

the first egg. Nests were considered successful if we saw at least one pipped egg or a cygnet in the nest, or if visited after hatch, by the presence of at least one characteristic hatched eggshell membrane (Girard 1939).

RESULTS

Tundra Swans were usually present on the study area upon our arrival in late April or early May of each year, when most of the nesting habitat was still snow covered. Measures of spring ice break-up phenology had an interannual range of 15–20 days; peak arrival of swans varied by 17 days among years, and both median nest initiation and hatch date had similar interannual ranges (Table 1). During 1988–1995, with the exception of 1992, median initiation date followed peak arrival by an average of 12 days (range 9–14 days), and in no year did the earliest laid egg precede the date on which uplands were estimated 90% snow-free. Initiation and hatch dates were most highly correlated (Pearson product-moment, here and below) with the date of 90% snow-free uplands ($r_{10} = 0.96$, $P < 0.0003$, and $r_{10} = 0.95$, $P < 0.0004$, respectively), and peak arrival with the date of Kashunuk River ice break-up ($r_6 = 0.89$, $P < 0.003$). Incubation period lengths ranged from 26 to 33 days, with a mean of 29.51 ± 0.17 days (N = 63). Variation among individuals in incubation period was correlated with date of 90% snow free uplands ($r_{61} = 0.29$, $P < 0.02$) and river ice break-up date ($r_{61} = 0.32$, $P < 0.01$), but was not correlated with variation in clutch size ($r_{61} = -0.22$, n.s.). Clutch size varied among years (ANOVA $F_{12, 259} = 2.86$, $P < 0.001$), due mostly to the low value for 1999. There was no significant correlation between average clutch size and river ice break-up date ($r_{11} = -0.48$, n.s.), date of peak arrival ($r_6 = -0.10$, n.s.), or mean nest initiation date ($r_{11} = -0.07$, n.s.). Nest density ranged from 0.48–0.96 km^{-2} and correlated negatively with river ice break-up date ($r_{11} = -0.59$, $P < 0.04$). The proportion of nests that successfully hatched at least one cygnet had a 13-year mean of 0.89 (range 0.73–1.0).

DISCUSSION

Timing of nest initiation and hatch were highly correlated with snow-melt phenology. Median initiation date followed peak arrival by an average of 12 days, suggesting that the estimated 12 day rapid follicle development for Tundra Swans (Alisauskas and Ankney 1992) may begin around the time of arrival on the breeding grounds. Median initiation date from this study (17 May, Table 1) was considerably earlier than the 8-year median of 24 May for the coastal Yukon-Kuskokwim Delta reported by Dau (1981) for the period 1972–1979. This result is consistent with observed trends in northern regional climate inferred from atmospheric CO_2 records (Keeling *et al.* 1996) and satellite imagery (Myneni *et al.* 1997) showing earlier spring plant green-up. Changes in Tundra Swan nesting phenology parallel the advances in laying dates reported for several species of birds in the United Kingdom (Crick *et al.* 1997).

Although incubation period ranged from 26–33 days, the median of 30 days was somewhat shorter than the commonly reported 32 days (Kear 1972; Hawkins 1986). This difference may be due to geographic differences or small sample sizes in the earlier studies. In the present study, incubation periods were shorter and nest initiation earlier in years of earlier snow melt, thus it is possible that better body condition in early years allowed higher incubation constancy

Table 1. Annual variation in spring snow-melt chronology and Tundra Swan nesting variables, 1988–2000, near Old Chevak on the Yukon-Kuskokwim Delta, Alaska. Sample sizes given in parentheses.

Year	Uplands 90% snow-free	Kashunuk River ice break-up	Peak arrival	Median date initiation, range	Median date hatch, range	Mean ±SE clutch size	Nests km^{-2}	Proportion of nests hatching ≥1 egg
1988	12 May	24 May	4 May	17 May (11) 12–25 May	22 June 17–29 June	4.6 ± 0.3 (17)	0.61 (14)	0.92 (12)
1989	22 May	3 June	12 May	25 May (10) 23–27 May	1 July 29 June–3 July	4.6 ± 0.2 (20)	0.61 (14)	0.85 (13)
1990	12 May	26 May	6 May	18 May (20) 11–26 May	23 June 17–30 June	4.7 ± 0.1 (27)	0.91 (21)	0.96 (25)
1991	6 May	24 May	2 May	16 May (19) 12–23 May	21 June 18–28 June	4.8 ± 0.2 (24)	0.96 (22)	0.83 (23)
1992	20 May	5 June	19 May	23 May (12) 20–27 May	28 June 23 June–2 July	4.7 ± 0.1 (23)	0.74 (17)	0.96 (23)
1993	13 May	24 May	7 May	18 May (24) 13–22 May	23 June 19–27 June	4.6 ± 0.2 (28)	0.83 (19)	0.82 (22)
1994	3 May	22 May	4 May	13 May (21) 7–20 May	18 June 13–25 June	4.8 ± 0.1 (23)	0.78 (18)	1.00 (25)
1995	6 May	21 May	6 May	17 May (8) 15–20 May	22 June 18–26 June	4.4 ± 0.2 (17)	0.65 (15)	0.73 (15)
1996	30 April	18 May	—	12 May (13) 6–27 May	20 June 15 June–4 July	4.8 ± 0.2 (21)	0.83 (19)	0.89 (19)
1997	25 April	19 May	—	7 May (8) 1–11 May	15 June 12–19 June	4.2 ± 0.1 (21)	0.78 (18)	0.88 (16)
1998	20 May	31 May	—	20 May (3) 18–22 May	28 June 27–29 June	3.9 ± 0.2 (18)	0.57 (13)	1.00 (7)
1999	14 May	5 June	—	20 May (1)	28 June	3.4 ± 0.1 (10)	0.48 (11)	0.86 (7)
2000	—	4 June	—	16 May (5) 12–19 May	23 June 19–26 June	3.8 ± 0.1 (14)	0.52 (12)	0.89 (9)
Median or mean	10 May	27 May	7 May	17 May	23 June	4.5	0.71	0.89

and therefore shorter incubation length. Nesting density appeared to be stable or even decrease somewhat during our study, and was lower in late break-up years. Apparent nesting success was generally high with a mean of 89%, compared with a range of 25%–85% for Cackling Canada Geese (*Branta canadensis minima*) and Greater White-fronted Geese (*Anser albifrons frontalis*) nesting on the area over the same years (C. R. Ely, unpub.), and there was little apparent variation between years. The large body size of Tundra Swans compared with other waterfowl breeding in the area likely affords them greater protection from the typically small-bodied local egg predators such as Arctic Fox (*Alopex lagopus*), Mink (*Mustela vison*), Glaucous Gull (*Larus hyperboreus*), and Parasitic Jaeger (*Stercorarius parasiticus*).

Clutch size varied little during this study and was slightly greater than earlier estimates for the coastal Yukon-Kuskokwim Delta (4.42 this study; 4.26 in Lensink 1973; and 4.26 in Dau 1981). Our mean clutch size was almost one egg larger than the 3.62 average clutch size recorded for a sample of Tundra Swans nesting on Alaska's North Slope (Monda *et al.* 1994). The geographic difference in reproductive investment could be related to the earlier springs and longer snow-free period of the Yukon-Kuskokwim Delta. Also, Tundra Swans breeding on the Yukon-Kuskokwim Delta are of the Western Flyway population and have a shorter spring migration route (3,500–4,000 km) than do Eastern Flyway swans nesting on the North Slope (5,000–5,500 km), and this may lead to differences in the amount of reserves available for reproduction (Bart *et al.* 1991). Assuming a body mass of 6.3 kg and individual egg mass of 280 g (Alisauskas and Ankney 1992), North Slope swans invest only 16% of their mass in eggs versus 20% for Yukon-Kuskokwim Delta females. We saw no evidence of late spring thaws leading to reduced clutch sizes as found by Lensink (1973) and Dau (1981) for Tundra Swans, and for geese by Barry (1962) and MacInnes and Dunn (1988). Bruggink *et al.* (1994) found no effect of spring conditions on reproductive performance of Canada Geese (*B. canadensis*), while Lindberg *et al.* (1997) found that clutch size actually increased in late spring years for Brant (*B. bernicla*) breeding on the Yukon-Kuskokwim Delta. Our inability to detect effects of spring phenology on Tundra Swan clutch size is possibly due to the lack of very late spring thaws during the years of our study.

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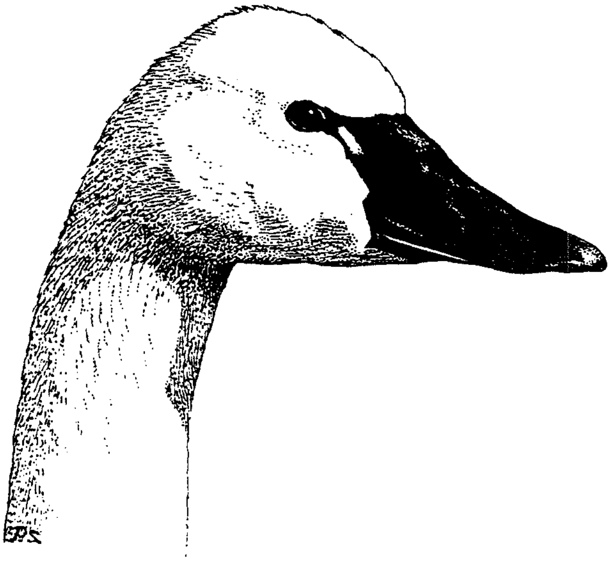

Tundra Swans of the Lower Alaska Peninsula: Differences in Migratory Behavior and Productivity

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Abstract.—Migratory behavior and abundance of Tundra Swans (*Cygnus columbianus columbianus*) were studied from 1977 to 1996 at two adjacent sites on the lower Alaska Peninsula. Winter re-sightings of swans captured and neck banded during molt revealed that swans from one site (Pavlof) were consistently migratory while those from the other (Izembek) were essentially resident during 17 of 20 years when they wintered at nearby Unimak Island. Large emigrations occurred from Izembek in three consecutive years to winter sites in the U.S. Pacific Northwest where swans from Pavlof and elsewhere also wintered. There was no indication of mixing between swans from Izembek and Pavlof on the breeding grounds or Alaskan wintering grounds. The average number of swans on Izembek and Pavlof breeding grounds was 212 ± 34 (0.20 ± 0.03 swans per km^2) and 586 ± 77 (0.31 ± 0.05 swans per km^2), respectively. Breeding habitats appeared similar, however, densities of total swans and breeding pairs were 35% and 48% higher at Pavlof. Emigrations from Izembek resulted in 37% and 94% declines in numbers of swans on the breeding grounds and Alaskan wintering grounds. The number of swans at Izembek recovered at 19% per year following emigrations to near normal numbers. At Pavlof, where swans were consistently migratory, densities did not show the same patterns of variation as those at Izembek.

Key words.—Alaska Peninsula, *Cygnus columbianus columbianus*, dynamics, migratory behavior, productivity, Tundra Swan.

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Tundra Swans (*Cygnus columbianus columbianus*) nest in tundra habitats of Alaska from the Alaska Peninsula to the Arctic Coastal Plain (Gabrielson and Lincoln 1959; King and Lensink 1971; Palmer 1976). Swans from Unimak Island and the lower Alaska Peninsula are the most southerly and westerly breeding Tundra Swans in North America. Tundra Swans there nest in low wetlands along the Bering Sea coast (Sarvis 1982; Wilk 1988). Tundra Swans have long been known to winter on the Alaska Peninsula (Murie 1959; Palmer 1976), but little has been reported on their breeding origin, number or status.

This study was initiated in response to a lack of baseline data on the dynamics of swans breeding on the Alaska Peninsula and to provide data relevant to a proposed autumn hunting season. Swans were neck-banded and aerial surveys were flown to determine distribution, abundance, and proportion of swans in pairs at two study sites, Izembek and Pavlof, on and adjacent to the Izembek National Wildlife Refuge. Swan flocks wintering on nearby Unimak Island were monitored to determine its use by swans from Izembek and Pavlof.

STUDY AREA

Study sites consisted of low elevation wetlands at Izembek (1,072 km^2; 55°10'N, 162°40'W) and Pavlof (1,833 km^2; 55°50'N, 161°20'W) on the Alaska Peninsula (Fig. 1). Small, shallow closed- and open-basin freshwater lakes with adjacent wet marshes and ericaceous uplands (elevation <30 m) were characteristic of both sites. Closed-basin lakes were clear and had little aquatic life, and in contrast, open-basin lakes were turbid and had abundant aquatic vegetation (e.g., pondweeds [*Potamogeton* spp.] and water milfoil [*Myriophyllum* spp.]). Izembek contained distinct wetland complexes, separated by uplands that were unused by swans, whereas Pavlof consisted of a large homogeneous wetland complex. Annual climate was maritime and cool (mean temperature = 3.3°C), windy (mean wind speed 27.0 km·h^{-1}), wet (mean monthly precipitation = 7.3 cm), and cloudy (mean of 27.4 overcast days per month).

Unimak Island provided the only reliable ice-free winter habitat for swans near the study sites. Geothermal activities on the island kept some marine lagoons with Eelgrass (*Zostera* spp.) and streams with freshwater aquatic vegetation available to foraging swans even during severe winters.

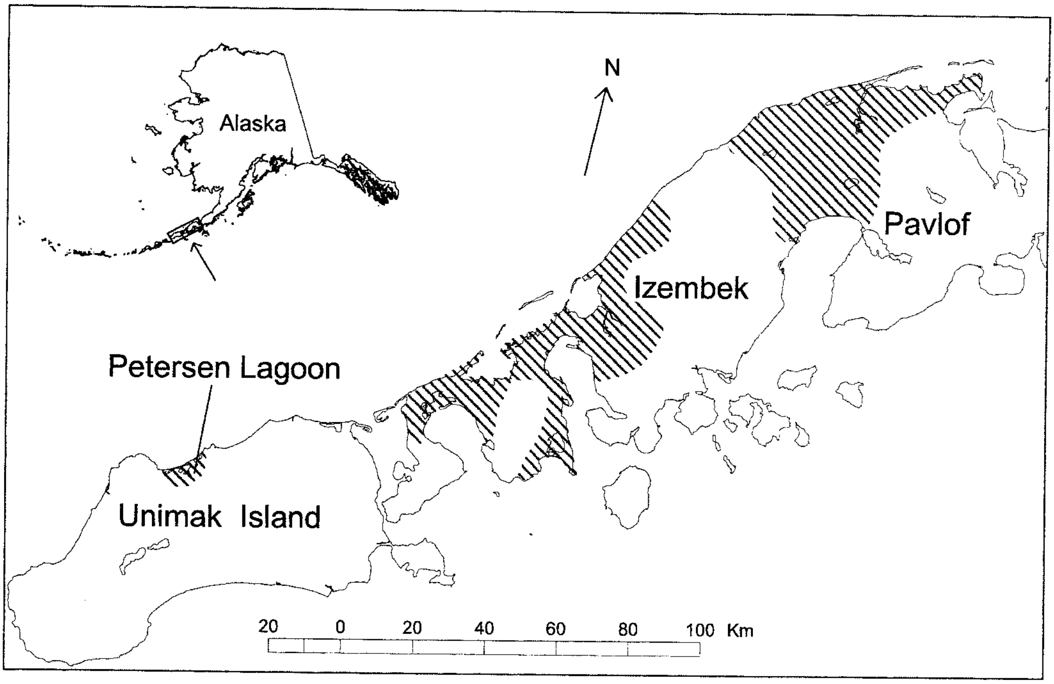

Figure 1. Location of study sites at Izembek, Pavlof, and Unimak Island on the lower Alaska Peninsula.

METHODS

Molting adult and flightless juvenile swans were captured by hand or with dip-nets from small boats or a taxiing floatplane during July and August at Izembek (1977–1988, 1990–1995) and Pavlof (1985–1986). Swans were aged by plumage with second-year birds showing remnant gray feathering on the head, neck, wing coverts or tail. Swans were marked with plastic neck and tarsus bands with engraved alphanumeric characters and U.S. Fish and Wildlife Service metal tarsus bands. Broods were captured beginning in late July when cygnets were large enough to be fitted with neck bands; parents and their offspring were released together after banding. Non-breeders and failed breeders were captured during mid to late July in flocks up to 40.

Aerial and ground re-sightings of banded birds were obtained during summer (April to September) at Izembek (1980–1996) and Pavlof (1984–1996), and during winter (November to March, 1979–1991) at Unimak Island. Unimak Island was not surveyed during breeding seasons, but incidental observations suggest that up to ten pairs nested there each summer. Winter aerial and ground surveys were by small aircraft capable of landing on beaches or frozen lakes. Wintering areas on Unimak Island were small, allowing complete coverage from the air. When landing was possible, swans were approached and viewed with 20–60× scopes to read neck bands and determine age ratios. Re-sightings during migration and winter outside Alaska were obtained annually, including some from the U.S. Bird Banding Laboratory.

Izembek and Pavlof study sites were surveyed annually in late May to early June during 1980–1996 and 1984–1996, respectively. Surveys were conducted in a Piper PA-18 Supercub flown at 100 m above the ground and at 130 km per hour. Swans within 0.8 km of the aircraft were recorded on 1:63,360 topographic maps as singles, pairs with or without nests, and flocks. All breeding habitat at Izembek (1076 km^2) was surveyed within two days using a meandering search pattern. Pavlof was surveyed during four to five days using linear transects 1.6 km apart. The area surveyed at Pavlof was 732 km^2 in 1984; 1307 km^2 in 1985; 1764 km^2 in 1986 and 1988; and 1840 km^2 in 1987 and 1989–1996. The number of breeding swans was estimated as the number of swans observed as singles and pairs (Lensink 1973). Dau (1981) found that paired birds were often separate from their mates at or near nests. Sightings were entered into a statewide electronic geographic information system database (Groves *et al.* 1990; Conant *et al.* 1991).

At Izembek, nests were monitored regularly from aircraft to determine clutch size, hatching dates and success. A successful nest was defined as one in which at least one egg hatched. Hatching success was defined as the proportion of eggs that hatched in relation to the total number laid. Brood size and survival of young were monitored until fledging. Missing cygnets were assumed to have been killed by predators; intact dead cygnets were assumed to have died from exposure. All active nest sites used in previous years and new nests found during aerial surveys were monitored. Because fewer than two unknown broods (i.e., those not from monitored nests) were found each year, we suspect that few nests were missed during aerial surveys.

Winter counts at Unimak Island were attempted several times from November through March, 1979–1993, with zero to eleven counts made each year. Other potential wintering habitats on or near study sites, available during mild winters, were surveyed opportunistically. Throughout the text, the year of the winter survey is given as that of the corresponding January.

Statistical comparisons were made with t-tests, and SDs are presented with means.

RESULTS

Movements and Migration

Swan movements were determined by resightings from 608 swans neck banded at Izembek (1977–1996) and 102 swans neck banded at Pavlof (1985–1986) (Table 1). From 1978 to 1986, only 18 of 383 swans banded at Izembek were observed during winter or migration outside Alaska while up to 290 banded swans wintered at Unimak Island. At capture just prior to migration, these migrants included two successful breeding adults, five failed or non-breeding adults, eight cygnets, and three adults of unknown breeding status. From autumn 1987 to 1989, emigrations from Izembek increased with 45 of 514 banded swans observed outside Alaska during these winters compared with only one banded swan observed among the fewer than 50 known to winter locally at Unimak Island (Fig. 2). At capture just prior to migration, these migrants included 2 (4%) breeding adults, 11 (25%) failed or non-breeding adults, 19 (42%) second-year birds and 13 (29%) cygnets. Swans were again less migratory at Izembek from 1990–1996 with only 27 of 608 marked birds observed outside Alaska.

Four Izembek swans were seen during migration in Alberta and most winter re-sightings were in the Pacific Northwest with stragglers to New York and Baja California, Mexico. Five Izembek swans returned to winter locally after previously wintering outside Alaska and two of these, a mated pair, nested successfully before and after emigrations. Five others were re-sighted during spring or summer elsewhere in Alaska during one or more years after marking. However, the remainder of the 64 swans observed outside Alaska were not known to return to Alaska during subsequent years.

At Pavlof, swans were banded only in 1985–1986 and were completely migratory with all 32 (31% of those banded) re-sightings made during migration and winter outside Alaska. At capture during previous summers, these swans included 25 (78%) failed or non-breeding adults, 5 (16%) second-year birds and 2 (6%) cygnets. Twenty-four of 102 banded Pavlof swans were re-sighted outside of Alaska during the winters of 1985–1986, compared to only one of 383 banded Izembek swans observed outside Alaska in the same winters. All re-sightings of Pavlof swans during winter were made in western Washington and Oregon except for one in California. Although migrants from Izembek and Pavlof shared some staging and wintering sites outside Alaska, there is no indication that these groups mixed during breeding or molt.

Trends in Abundance

At Izembek, total swan density (swans per km^2) during summers that immediately followed an emigration event ($\bar{x} = 0.15 \pm 0.025$,

Table 1. Number of Tundra Swans neck-banded at Izembek and Pavlof study sites, Alaska Peninsula, during 1978–1995, and number resighted during the subsequent winter.

		Number banded							Number[a] resighted during winters at	
		Adult		Second-year		Cygnet				
Area	Years of banding	Male	Female	Male	Female	Male	Female	Total	Unimak Island	Outside Alaska
Izembek	1977–1986	92	102	29	38	55	67	383	290	18
Izembek	1987–1989	29	26	27	19	16	14	131	1	45
Izembek	1990–1996	24	26	14	30	0	0	94	—[b]	27
Pavlof	1985–1986	40	36	6	12	4	4	102	0	24[c]

[a] Number resighted out of all swans banded in all previous summers.

[b] No survey.

[c] Eight Pavlof swans wintered outside Alaska between 1987–1996.

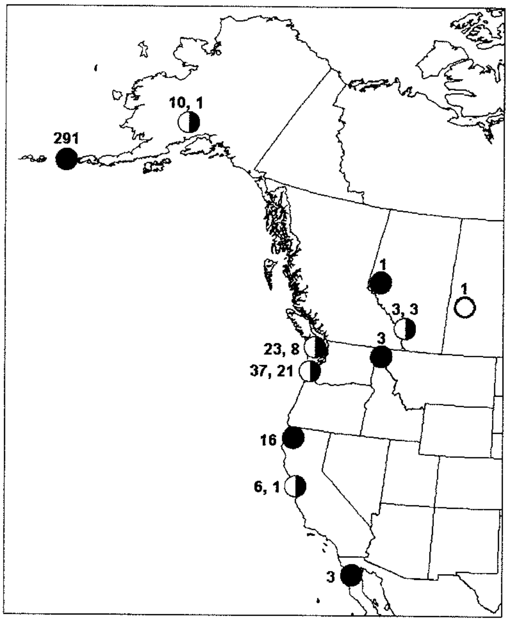

Figure 2. Locations of re-sightings during migration and winter of Tundra Swans banded at Izembek (closed circle) and Pavlof (open circle), lower Alaska Peninsula, 1978–1996. Numbers besides circles indicate the number of re-sightings of swans from Izembek, followed by those from Pavlof. In addition, one swan from Izembek was resighted in New York state.

1988-1990) was significantly lower than previous summers ($\bar{x}$ = 0.21 ± 0.02, 1980–1987, $t_9 = 4.4$, $P < 0.01$) or subsequent summers ($\bar{x}$ = 0.20 ± 0.03, 1991–1996, $t_7 = 2.5$, $P < 0.05$, Table 2). The density of swans in singles and pairs during summers that immediately followed an emigration event ($\bar{x}$ = 0.09 ± 0.01) also was significantly lower than previous summers ($\bar{x}$ = 0.14 ± 0.02, $t_9 = 5.6$, $P < 0.0001$) and did not differ during subsequent summers ($\bar{x}$ = 0.09 ± 0.01, $t_7 = 0.55$, n.s., Table 2). The average number of swans observed at Izembek during these years was 228 ± 20 (1980–1987), 163 ± 27 (1988–1990), and 215 ± 30 (1991–1995).

At Pavlof, average density of all swans and those in singles and pairs was 0.31 ± 0.05 and 0.22 ± 0.03 per km^2, respectively, for the years in which Pavlof was surveyed (1984–1989 and 1991–1996, Table 3), and these densities were 35% and 48% higher than corresponding densities at Izembek during 1980–1996 (0.20 ± 0.03 per km^2 and 0.11 ± 0.03 per km^2, respectively), suggesting higher potential reproductive output. However, second-year swans composed 19.2% of molting flocks at Pavlof, compared to 33.9% at Izembek, suggesting lower reproductive output at Pavlof. The average number of swans at Pavlof from 1989–1996, with a constant study area size, was 586 ± 77 with no apparent trend in either size or composition (Table 3). Site fidelity of cygnets was high with 71% (17 of 24) of recaptures or re-sightings near natal areas during subsequent years. Site fidelity of second-year swans was low with only 35% (8 of 23) of recaptures or re-sightings near natal areas during subsequent years.

Swans wintered at Unimak Island every year. Essentially all (>90%) of approximately 600 swans known to winter in the area were found wintering at Petersen Lagoon on Unimak Island. Mild conditions during some winters allowed some swans to use areas elsewhere on Unimak Island, and also freshwater ice-free areas at Izembek and Pavlof, but swans were not observed at these secondary sites during winters following autumn emigrations. Emigrations from Izembek during autumns of 1987–1989 contributed to a 94% decline in the number of swans wintering at Unimak Island, from an average of 585 ± 94 swans during the winters of 1979–1987 to 38 ± 5 swans during the winters of 1988–1990. Number of swans increased to 367 ± 106 during the subsequent winters of 1991–1993 (Fig. 3). Using the ratio of banded migrant to resident Izembek swans from 1978–1987, we estimated that 95% of Izembek swans were resident and that Izembek swans composed 54% of the resident winter population. Among the eight winters in which age ratios were recorded, cygnets made up 10.9% ± 3.7% of swans at Unimak Island during the winters of 1979–1986 and 18.1% during the winter of 1993.

Reproductive Success at Izembek

At Izembek, the number of nest attempts during summers immediately following each of the three autumn emigrations (15.3 ± 7.0, for summers 1988–1990) was significantly lower than during previous summers (38.8 ± 6.1, 1980–1987, $t_9 = 5.4$, $P < 0.0001$), but did

Table 2. Number of Tundra Swan nests and individuals observed during spring aerial surveys at Izembek study site (1,076 km²), Alaska Peninsula, 1980–1996.

	Number swans observed in				Density (swans per km²)	
Year	Singles + pairs	Flocks	Total	No. nests		
Prior years[a]						
1980	153	80	233	34	0.14	0.22
1981	168	29	197	47	0.16	0.18
1982	171	55	226	44	0.16	0.21
1983	150	77	227	28	0.14	0.21
1984	137	85	222	42	0.13	0.21
1985	126	140	266	35	0.12	0.25
1986	147	90	237	40	0.14	0.22
1987	133	81	214	40	0.12	0.20
Years immediately following emigrations[b]						
1988	92	41	133	14	0.09	0.12
1989	101	69	170	9	0.09	0.16
1990	87	99	186	23	0.08	0.17
Subsequent years						
1991	86	138	224	26	0.08	0.21
1992	86	140	226	18	0.08	0.21
1993	108	134	242	25	0.10	0.22
1994	113	120	233	25	0.11	0.22
1995	94	64	158	20	0.09	0.15
1996	97	112	209	22	0.00	0.19
Average ± SD						
1980–1987[a]	148 ± 16	80 ± 32	229 ± 20	39 ± 6	0.14 ± 0.01	0.21 ± 0.02
1988–1990[b]	93 ± 7	70 ± 29	163 ± 27	15 ± 7	0.09 ± 0.01	0.15 ± 0.02
1991-1996[a]	97 ± 11	118 ± 29	215 ± 30	23 ± 3	0.09 ± 0.01	0.20 ± 0.03

[a] Breeding seasons with no major emigration during the previous autumn.

[b] Breeding seasons immediately following the autumn migrations of 1987–1989 (i.e., breeding seasons of 1988–1990).

not differ significantly from the number of attempts during subsequent summers (22.7 ± 3.2, 1991–1996, $t_7 = 2.2$, n.s.) (Table 2). Average clutch size also was significantly lower during summers immediately following autumn emigrations (3.9 ± 0.4) than during previous (4.9 ± 0.1, 1980–1987, $t_9 = 5.9$, $P < 0.05$) or subsequent summers (5.1 ± 0.1, 1991–1996, $t_6 = 4.6$, $P < 0.05$). Other reproductive parameters did not differ significantly between summers immediately following emigration compared to other years. Neither the percentage of eggs hatching (51% ± 13% compared to 37% ± 12%, $t_{14} = 1.69$, n.s.), percentage of cygnets surviving to fledging (58% ± 34% compared to 54% ± 16%, $t_{14} = 0.35$, n.s.), nor number of cygnets fledging (19.3 ± 14.2 compared to 31.9 ± 21.0, $t_{15} = 0.97$, n.s.) differed for years following an emigration compared to other years (Fig. 4).

The timing and extent of cygnet mortality from 1981–1987 at Izembek was determined by following 148 broods. Of the 236 cygnets that died, 52.6% (N = 124) were lost within ten days after hatching, 32.6% (N = 77) during days 11–30, and 14.8% (N = 35) from day 31 to fledging.

DISCUSSION

Movements and Migration

Swans summering at Izembek are unique among North American Tundra Swans in being resident in most years but exhibiting large emigrations in some years. Izembek

Table 3. Number of Tundra Swan nests and individuals observed during spring aerial surveys at Pavlof study site, Alaska Peninsula, 1984–1996.

	Number of swans observed in				Density[a] (swans per km^2)	
Year	Singles + pairs	Flocks	Total	Nests	Singles + pairs	Total
1984	146	25	171	31	0.20	0.23
1985	320	166	486	21	0.24	0.37
1986	324	182	506	56	0.18	0.29
1987	324	196	520	54	0.18	0.28
1988	347	287	634	52	0.20	0.36
1989	434	245	679	52	0.24	0.37
1990	—[b]	—[b]	—[b]	—[b]	—[b]	—[b]
1991	421	164	585	57	0.23	0.32
1992	399	145	544	77	0.22	0.30
1993	421	150	571	72	0.23	0.31
1994	356	133	489	63	0.19	0.27
1995	363	169	532	53	0.20	0.29
1996	494	205	699	59	0.27	0.38
Average ± SD	413 ± 47[c]	173 ± 39[c]	586 ± 77[c]	62 ± 9[c]	0.22 ± 0.03	0.31 ± 0.05

[a] Surveyed area was 732 km^2 in 1984; 1707 km^2 in 1985; 1764 km^2 in 1986 and 1988; and 1840 km^2 in 1987 and 1989–1996.

[b] No surveys conducted in 1990.

[c] Average for 1989–1996 when surveyed area was constant.

emigrants mixed with large numbers of Western Population and some Eastern Population Tundra Swans at staging and wintering sites. Two re-sightings on the Yukon-Kuskokwim Delta in southwestern Alaska, where up to 100,000 swans occur in summer (Conant *et al.* 1999; Wege 1989), suggest that some Izembek swans joined flocks from that area. Both were second-year females captured in 1987. One had wintered in California during the 1987–1988 winter prior to its May 1990 re-sighting on the Yukon-Kuskokwim Delta, and the other, shot in autumn 1989, had not been seen since capture. Five other re-sightings of Izembek swans in Alaska, each of a single bird, were made in upper Cook Inlet; near King Salmon; at St. Paul Island in the Pribilof Islands; near the village of Tetlin; and on Kodiak Island.

Only five of 63 swans banded at Izembek and observed at wintering sites outside Alaska returned to winter at Unimak Island in subsequent years. There are two likely explanations for the low return rate. Izembek

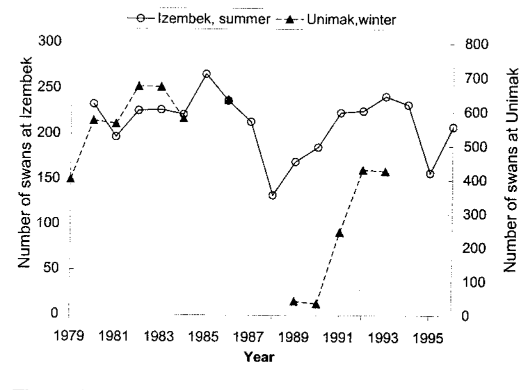

Figure 3. Trends in number of Tundra Swans present in Izembek during the summer breeding season and at Unimak Island during the winter. The winter date is that of the corresponding January. No counts were made during the winters of 1985, 1987, and 1989.

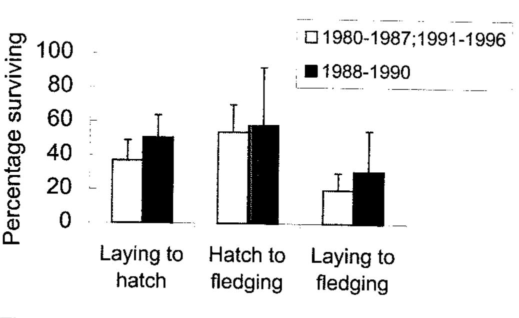

Figure 4. Egg (N = 3,973) and cygnet (N = 895) survival at Izembek during summers immediately following large emigrations (1988–1990) compared to other years (1980–1987; 1991–1996 excluding 1995 when survival was not recorded). Error bars and one SD.

emigrants mixed with swans from other breeding grounds at staging or wintering sites, and may have followed them to new breeding grounds, as suggested by the re-sightings mentioned above. It is also possible that mortality was high among Izembek migrants, especially if they emigrated in early winter. For example, Pacific Black Brant (*Branta bernicla nigricans*) that breed at Izembek and undertake a 60 h trans-oceanic migration to wintering sites near those used by Izembek swans, lose up to 30% of their body weight (Dau 1992). Tundra Swans from Izembek are likely to follow a longer overland route, to migrate more slowly, and could encounter lack of ice-free foraging habitat along much of their route. Earliest winter re-sightings of swans from Izembek in the Pacific Northwest were in late November, and most were in December through February, suggesting that swans left Izembek in early to mid-winter.

Swans banded at Pavlof consistently undertook normal annual migrations and tended to return to Pavlof in subsequent summers, resulting in little annual variation in densities (Table 3). This pattern of migratory behavior is similar to that of other Tundra Swans in Alaska (Paullin and Kridler 1988; Limpert *et al.* 1991; Ely *et al.* 1997; Moermond and Spindler 1997), but contrasts with that of swans in the adjacent Izembek area.

Trends in Abundance

Total numbers of Tundra Swans at Izembek declined during the summers of 1988–1990 which immediately followed the large emigrations during the autumns of 1987–1989 (Table 2, Fig. 3). Numbers of singles and pairs also decreased during those years, suggesting a smaller proportion of potential breeders. Our data suggest that most migrants were sub-adults or failed breeders (94%) and that successful breeders (6%) were reluctant to migrate. When large emigrations ceased, numbers rebounded at 19% per year, perhaps due in part to an increase in productivity to previous levels.

The mild maritime climate of the study area may result in less annual variability in reproduction than is typical of more northerly Tundra Swan breeding areas. It is likely that swans on the adjacent sites of Izembek and Pavlof were affected by similar annual variability in weather and predation, and that the large fluctuations in numbers at Izembek were a direct result of large emigrations that occurred there but not at Pavlof. Densities of up to 0.19 swans per km^2 at Izembek and 0.31 swans per km^2 at Pavlof were comparable to the adjacent northern Alaska Peninsula (0.22 swans per km^2; Wilk 1988), twice that on the Arctic Coastal Plain (0.13 swans per km^2; King and Brackney 1997), and nearly 80% lower than the Yukon-Kuskokwim Delta (1.41 swans per km^2; Conant *et al.* 1999).

Reproductive Success

At Izembek, 52% of singles and pairs were known to nest during 1980–1987 and 1991–1996, compared to only 33% during years immediately following emigrations (1988–1990, Table 2). At Pavlof, 31% of singles and pairs were known to be associated with nests (Table 3). Fewer nests might have been detected at Pavlof because ground searches were not conducted as they were at Izembek. At both sites, some nests probably went undetected, especially those that failed prior to aerial surveys.

At Izembek, there were fewer nests and smaller clutches during 1988–1990, but no significant difference in hatching success or cygnet survival (Fig. 4). Smaller clutch sizes during summers immediately following large emigrations could be the result of fewer birds attempting to breed, which allowed increased participation by young or inexperienced breeders which are thought to have smaller clutches. Our observations suggest that neither differences in weather nor predation were likely explanations of these differences in reproductive parameters for years immediately following emigrations compared to other years. We therefore believe that the differences were due to the emigrations themselves. Egg and cygnet survival to fledging during this study were 22% and 46% below estimates from the Yukon-

Kuskokwim Delta (Lensink 1973; Dau 1981). Brood sizes at fledging observed during this study ($\bar{x}$ = 3.1) were comparable to those on the northern Alaska Peninsula ($\bar{x}$ = 2.8; Wilk 1988) and Yukon-Kuskokwim Delta ($\bar{x}$ = 3.0; Lensink 1973, Dau 1981).

Recovery of Numbers at Izembek after Emigrations

Recovery of numbers of swans at Izembek following emigrations (Fig. 3) could have been due to the return of migrants to Izembek or to immigration. Re-sightings suggest that few of the Izembek migrants returned to Izembek. Only five of 18 marked swans that migrated outside Alaska returned to Izembek during 1980–1986, none of 56 during 1987–1989, and none of 13 during 1990–1996.

Observations of banded birds suggest no mixing of swans from Izembek and Pavlof at breeding sites, molting sites, or wintering sites on Unimak Island. Hence, our data indicate that the increase in swan numbers at Izembek during 1990–1996 cannot be attributed to immigration from Pavlof. Immigration by swans from other more geographically separated breeding locations in Alaska seems more improbable and has not been documented by banding. Thus, the origin of swans that repopulated Izembek during 1990–1996 remains uncertain.

In summary, Tundra Swans at Izembek typically wintered nearby on Unimak Island but exhibited large emigrations in some autumns which resulted in reduced numbers in subsequent summers, whereas swans at Pavlof were consistently migratory and numbers fluctuated little among summers. Mechanisms involved in migratory behavior and the large fluctuations in number at Izembek are unclear. Further monitoring of swans at Izembek and the adjacent Pavlof site is important if causative factors resulting in differences in migratory behavior are to be understood.

ACKNOWLEDGMENTS

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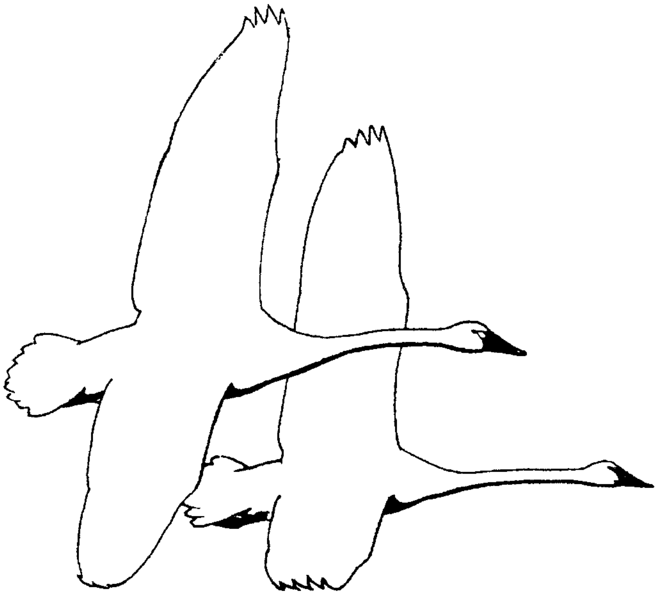

Egg Size Variation in Mute Swans: Its Influence on Egg Hatchability, Cygnet Body Size and Cygnet Survival

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Abstract.—This study describes variation of egg size in Mute Swans (*Cygnus olor*) nesting on fishponds in the Barycz valley, Poland, determines repeatability in mean egg volume of the same females nesting in consecutive breeding seasons, and determines if egg size influences hatchability, chick body size, mass and survival. Within a clutch, the smallest egg was laid first or last in the laying sequence. Differences in volume between eggs within a clutch were significant for all categories of clutch size. Mean egg volume in a clutch did not vary significantly between years for the same females nesting in consecutive breeding seasons, and was not related to female body size. Repeatability of mean egg dimensions in the next breeding seasons was 0.69–0.75. Later onset of laying was correlated with laying smaller eggs. On average, a delay in laying the first egg corresponded with a reduction in mean egg size of 1.8% per each 10 days. Unhatched eggs were not significantly smaller than eggs that produced chicks. Large eggs produced larger and heavier cygnets. Egg volume explained about 70% of the variation in cygnet body mass and 18–38% of the variation in body size measured at one day of age. Mean egg volume in a clutch influenced cygnet survival to age 100 days.

Key words.— Chick body size, *Cygnus olor*, egg size, inter-clutch variation, intra-clutch variation, hatchability, Mute Swan, survival.

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In several bird species, egg size has been shown to be related to chick size, mass or survival (Williams 1994). Birkhead (1984) found that the total amount of yolk and yolk lipid increased with egg mass in Mute Swans (*Cygnus olor*) and suggested that chicks from larger eggs should survive better. The aims of this study were to describe variation of egg size in Mute Swans nesting on fishponds in the Barycz valley, Poland, determine repeatability in mean egg volume of the same females nesting in consecutive breeding seasons, and determine if egg size influences hatchability, chick body size, mass and survival.

STUDY AREA

The study was conducted mainly in the eastern part of the Barycz river valley in Poland where there were several fishpond complexes ranging from a few hundred to nearly 1,700 ha in area. Complexes were surrounded by fields and meadows. Most ponds were 20 to 200 ha in area, but the largest were 300 ha. Average depth was about 1 m, with islets of Common Reeds (*Phragmites australis*) or cattails (*Typha* sp.) occurring on many ponds. Dikes between ponds were usually narrow (>10 m) and covered with trees, mainly oaks (*Quercus* sp.), alder (*Alnus* sp.), and willow (*Salix* sp.). Belts of emergent vegetation also occurred along the dikes and varied in width from a few meters to >100 m. All ponds were used in fish production and were drained once each year.

Some analyses included data from the "Przemków Ponds" reserve, which is located about 60 km west of the Barycz valley. The total area of fishpond complexes in this reserve was about 900 ha. Single ponds were <2 m deep and from a few ha to 130 ha in area. Emergent vegetation occurred mainly along dams, with ground and reed islands in some ponds.

METHODS

Collection of Data

Mute Swans were studied from 1988 to 1995, but field effort was lower in 1994 than in other years. Nests were visited two to eight times during incubation to determine clutch size, and laying and hatching date. The water test, or flotation method, was used to estimate stage of incubation at each visit by floating each egg in water and calculating the angle of the egg's long axis relative to vertical (Nedzinskas 1972; Czapulak in press).

Laying date was determined to within at least ±2 days for 352 of 429 nests and to within ±5 days for 77 nests. Hatch date was determined to within ± 1 day for 138 of 181 clutches, to within ±2 days for 31 clutches and to within ±5 days for the remainder. Laying order was determined by ranking the staining on eggshells. Maximum length and width of the eggs was measured to the nearest 0.1 mm for 1,973 eggs from 369 clutches in the Barycz valley and 503 eggs from 91 clutches in the Przemków ponds. In almost all cases, all eggs in a clutch were measured. In 1995, nests were visited more frequently during hatching to match chicks with eggs. Also in 1995, one-day-old cygnets were measured (skull and tarsus length, and width of web-foot) and weighed. Mass was noted separately for cygnets with wet and dry down. In 1992–1993 and 1995, the study area was surveyed every 7–10 days to determine cygnet survival. Most broods stayed through the season on territories where they had hatched. There was no amalgamation of broods, except in three cases where a single cygnet was adopted. Families with both parents unmarked were distinguished on the basis of known hatch date and number of chicks in this and neighboring families. In many broods, one-day-old chicks were marked with wing tags and identification of families was checked during summer capture of broods.

In some analyses, data from the Przemków ponds collected in 1981–1984 (Czapulak and Wieloch 1991) and in 1997–1998 were included.

Data Analyses

Egg volume was calculated using the following formula (Hoyt 1979):

$$V = K_v \times L \times B^2$$

where L = egg length, B = egg breadth, and K_v = shape constant (= 0.512). The correlation between egg volume and mass of 38 unincubated eggs was very high (r = 0.965, $P < 0.001$). Mean volume of eggs in a clutch was calculated only for clutches in which all eggs were measured. The volume of the smallest egg was excluded from the mean volume because it would have influenced the mean of small clutches more than large clutches.

Relative egg volume was used to analyze the relationship between laying sequence and egg volume. It was calculated as egg volume minus the mean egg volume of the clutch (based on all eggs), divided by the standard deviation in egg volume of the clutch (Arnold 1991). Only clutches with known laying sequence for all eggs were included in the analysis.

Data from 26 females that were identifiable by plastic neck bands, and that were known to breed in at least two years, were used in assessing between-year variation in egg volume for individual females. Repeatability, a measure of the proportion of variance in a character that occurs among individuals rather than within individuals (Falconer 1981), was estimated for mean egg length, width and volume. Repeatability, r, was calculated as:

$$r = s^2_A/(s^2 + s^2_A)$$

where s^2_A is variance among individuals and s^2 is variance within individuals, and each variance component was calculated according to Lessels and Boag (1987).

Differences between means were examined using one-way analysis of variance (ANOVA). Egg volume in relation to laying order was examined using a nested ANOVA with clutch as the nested factor. Influence of independent factors on mean egg volume, hatchability and cygnet survival was examined using General Linear Models. If interaction terms were not significant, they were deleted and models were rerun with only main effects.

RESULTS

The average volume of individual eggs was 321.1 cm³ (±20.4 [SD], N = 439 clutches). Excluding one clutch with very small eggs, the difference in mean individual egg volume between the largest and smallest clutches was about 109 cm³ (Fig. 1). The volume of the smallest egg was only 187 cm³ and the largest egg was 469 cm³ and weighed >0.5 kg.

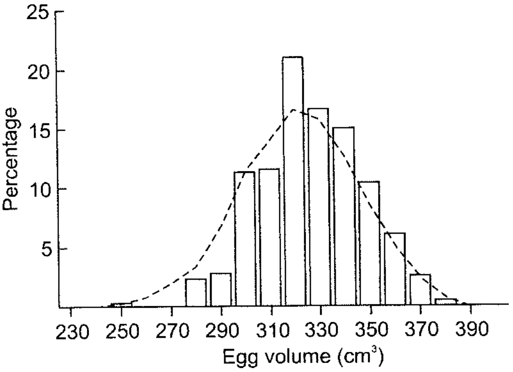

Figure 1. Frequency distribution of mean egg volume averaged per clutch (bars) and volume of individual eggs (line). The smallest (187 cm³) and the largest egg (469 cm³) are not included.

Intra- and Inter-clutch Variation

The maximum within-clutch difference in egg volume between the smallest and the largest egg was 32%. An egg's volume was related to its laying sequence in all clutch sizes (ANOVA, $P < 0.0001$ in all cases, Fig. 2a-f). The first and last egg laid were significantly smaller than all other eggs in all clutch sizes (Tukey's test, $P < 0.05$). The first egg was significantly smaller than the last egg in clutches of four to seven (Tukey's test, $P < 0.01$). The second egg was significantly smaller than the fourth egg in clutches of six, and smaller than the fourth and fifth eggs in clutches of seven (Tukey's test, $P < 0.05$). All other differences within clutches were not significant.

Mean egg volume did not vary significantly between years (range of annual means = 315.4 to 326.5 cm³, ANOVA, $F_{7,344} = 1.52$, n.s.). Results of multiple regression with laying date and clutch size as predictors indicated that mean egg volume was positively related to clutch size and negatively related to the interaction between laying date and clutch size, but was not related to laying date (Table 1).

Egg Volume of Individual Females in Different Seasons

Among the 26 females known to have bred in at least two years, 20 bred in two, four in three and two in four breeding seasons.

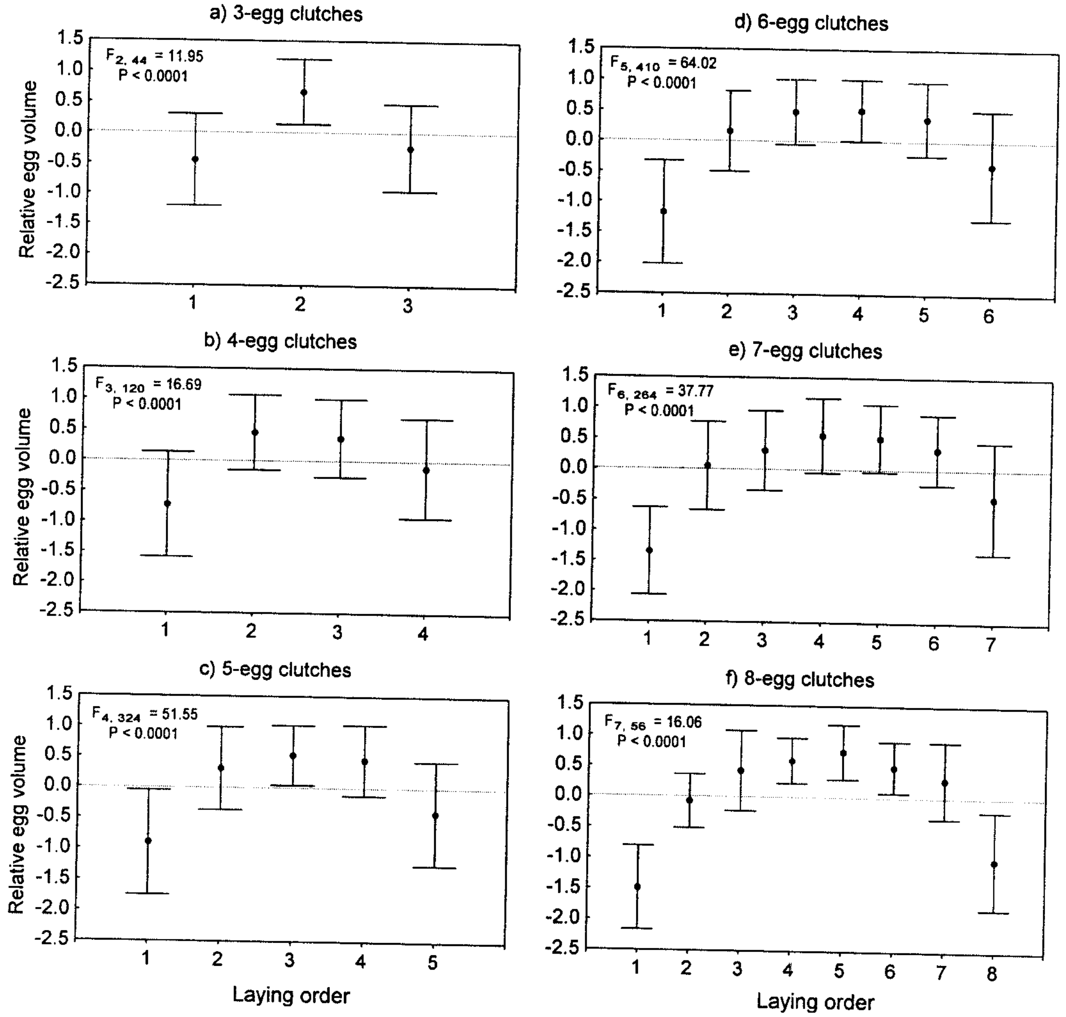

Figure 2. Relationship of egg volume to laying sequence in clutch sizes of (a) three, (b) four, (c) five, (d) six, (e) seven and (f) eight eggs. Bars represent SDs.

Females laid eggs of similar size in consecutive breeding attempts and the largest difference in mean volume was 10.8%. Repeatability of mean egg volume, width and length, calculated by the method described in Lessells and Boag (1987), was 0.75, 0.75, and 0.69, respectively (Table 2).

Most females (18 of 29 comparisons) laid smaller eggs in years when they bred later, although the differences were not always strong (Fig. 3). On average, egg volume decreased by 1.8% for each 10 days delay in laying (slope = -0.18 ± 0.04, r_{27} = -0.71, P < 0.0001, Fig. 4). Changes in mean egg volume with date were due to changes in egg width (slope = -0.08 ± 0.01, r_{27} = -0.79, P < 0.0001), rather than length (r_{27} = 0.21, n.s.). Similarly clutch size decreased by 0.5 eggs for each 10 days delay in laying (slope = -0.05 ± 0.01; r_{27} = -0.59, P < 0.001). Given that clutch size and egg volume decreased with laying date, one might expect females that laid fewer eggs in subsequent years to also lay smaller eggs. Changes in mean egg volume between years were related to changes in laying date (slope = -0.20 ± 0.04, t_{27} = 4.62, P < 0.0001) but not to changes in clutch size (slope = -0.41 ± 0.55, t_{27} = 0.75, n.s.). However, differences in clutch size were small. Among 23 cases in which clutch size differed, the difference was only one or two eggs, except in one case where the difference was three.

Table 1. The effect of laying date and clutch size on mean egg volume in Mute Swans. Y-intercept = 277.2 ± 32.7, R = 0.18, N = 390 clutches.

Independent variable	Regression coefficient ± SE	t	P
Clutch size	11.94 ± 5.58	2.14	<0.05
Laying date	0.39 ± 0.29	1.37	n.s.
Clutch size*Laying date	-0.11 ± 0.05	2.09	<0.05

Egg Volume and Hatchability

Unhatched eggs did not differ in volume ($\bar{x}$ = 314.7 ± 26.3 [SD] cm^3, N = 85) from those that produced chicks ($\bar{x}$ = 318.6 ± 23.7 [SD] cm^3, N = 1008, ANOVA, $F_{1,1091}$ = 2.09, n.s.). The difference between the smallest and largest egg that produced a chick was 128 cm^3.

Laying order did not affect hatchability (χ^2_2 = 2.15, n.s.). Percentage of hatched eggs among the first, middle (one egg was randomly chosen in the clutch) and the last laid eggs was 89% (N = 171), 92% (N = 163) and 93% (N = 163), respectively. Hatchability was not related to mean egg volume in the clutch (r_{171} = 0.01, n.s.). The smallest egg within a clutch appeared to remain unhatched more frequently than other eggs for all clutch sizes (Fig. 5), but the difference was not significant for individual clutch sizes or for all clutches combined (χ^2 tests, all n.s.).

Egg Volume and Chick Size

The body mass of freshly hatched cygnets was highly correlated with egg volume (Table 3). Heavier and larger chicks hatched from larger eggs. When controlling for effect of body mass by using partial regression, body size was still correlated with egg volume (Table 3). Thus, for a given body mass, larger eggs produced larger chicks. Similarly, when the effects of all three measures of body size (skull and tarsus length, web width) were controlled, body mass was significantly related to egg size.

Table 2. Repeatability of mean egg volume, width and length for individual female Mute Swans. Repeatability is a measure of the proportion of variance in egg size due to among-female rather than within-female variance. Based on 26 females that bred in two to four different seasons.

	Repeatability	$F_{25,34}$	P
Volume	0.75	7.86	<0.0001
Width	0.75	7.92	<0.0001
Length	0.69	6.13	<0.0001

Egg Volume and Cygnets Survival

Cygnet survival in the first month of life was not related to clutch size, mean egg volume of the clutch, or date of hatching (Table 4). However, mean egg volume significantly affected cygnet survival up to 100 days of life (slope = 0.003 ± 0.001, t_{154} = 2.43, P < 0.05) in the model with clutch size, mean egg volume and date of hatch as predictors, and the effect of hatch date was nearly significant (slope = -0.004 ± 0.002, t_{154} = 1.90, P = 0.06, Table 4).

DISCUSSION

Intra-clutch Variation

Eggs within clutches varied in volume and the pattern was similar for all clutch sizes. The smallest eggs were laid first and last in

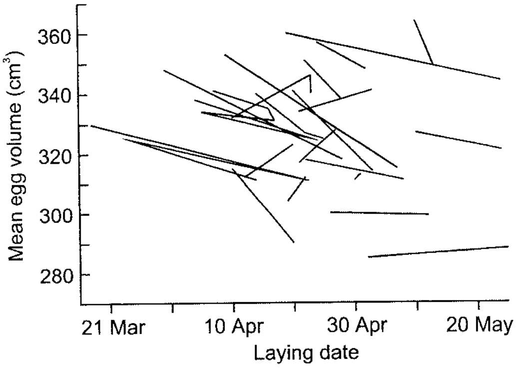

Figure 3. Relationship of mean egg volume and laying date for 29 comparisons of 26 female swans that bred in more than one breeding season.

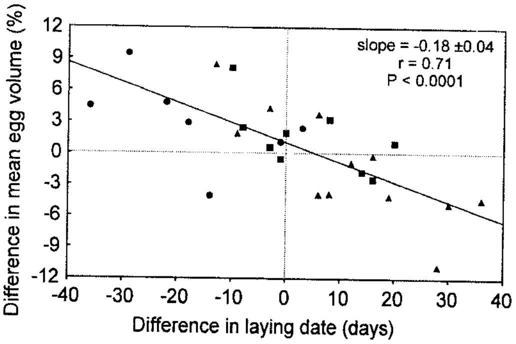

Figure 4. Differences in mean egg volume in relation to differences in laying dates for the same female swans in different seasons. Triangles represent cases in which clutch size was larger in the first season, squares represent cases in which clutch size was the same in both seasons, and circles represent cases in which clutch size was smaller in the first season.

the laying sequence. However, in the Black Swan (*Cygnus atratus*) (Brathwaite 1977) and geese in the genus *Branta* (Cooper 1978; Leblanc 1987; Flint and Sedinger 1992; Williams *et al.* 1996), the largest egg was usually the second and size decreased through the last egg. In American Coot (*Fulica americana*), size increased through the first two to four eggs and then systematically decreased (Arnold 1991).

In the Herring Gull (*Larus argentatus*), the first egg of the first clutch was smaller than the second egg (Parsons 1976), but the relationship was not found in replacement clutches, suggesting that it is the first egg of the season, not of the clutch, that is smaller than others. In the Barnacle Goose (*Branta leucopsis*), the first egg was the largest in some replacement clutches, though in others the pattern was the same as in first clutches (Williams *et al.* 1996). Smaller differences between the first and second egg in replacement clutches than in the first clutches were recorded in American Coot (Arnold 1991). According to Flint and Sedinger (1992) the increase in size of the second egg relative to the first may be related to physiological or morphological constraints on the size of the first egg. Leblanc (1987) suggested that the smaller size of the first and last egg in Canada Goose (*Branta canadensis*) clutches may be physiological responses to changing levels of hormones that are connected to the onset of laying and of incubation, respectively. Similarly, Arnold (1991) found that in American Coot, the decrease of egg size within a clutch is associated with the beginning of incubation. Physiological responses may also explain the pattern of egg volume changes recorded in this study.

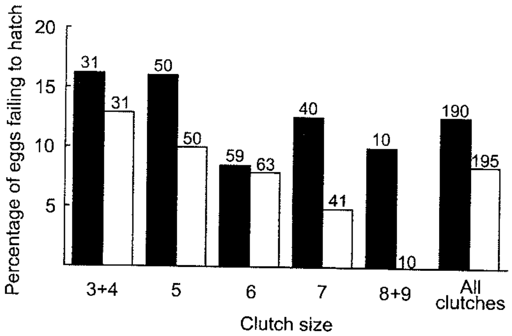

Figure 5. Comparison of smallest eggs (black bars) and other eggs (white bars) within clutches in the percentage that fail to hatch. The other egg category was based on one egg (other than the smallest egg) in every clutch chosen using a table of random numbers.

The smaller size of the last egg in a clutch has also been explained as an adaptation to synchronize hatch (Parsons 1972). This hypothesis is based on the finding that, in the Herring Gull, the incubation period of the last and smallest egg in the clutch was significantly shorter than for the remainder of eggs (Parsons 1972), although others found that the relationship between egg size and length of incubation period was weak (Runde and Barret 1981; Martin and Arnold 1991). Despite this, Flint and Sedinger (1992) proposed that this hypothesis might apply to intra-clutch egg size variation in Black Brant (*Branta bernicla nigricans*). Although not tested here, the smaller size of the last egg also may be related to increased hatch synchronization in Mute Swans, especially since some females initiated incubation prior to laying the last egg (Czapulak, in press).

Changes in Egg Volume within Season

Egg volume in this study decreased with laying date. A similar relationship was found for Mute Swans nesting near Oxford in one year (Scott and Birkhead 1983) but was not

Table 3. Relationships between egg volume and body size and mass of one-day old cygnets. Some cygnets were weighed when newly hatched, thus with wet down, and others were weighed when the down was dry.

	Pearson correlation				Partial correlation			
	N	df	r	P<	N	df	r	P<
Skull length	51	49	0.62	0.001	37	34	0.73[a]	0.001
Web width	51	49	0.52	0.001	37	34	0.55[a]	0.001
Tarsus length	51	49	0.43	0.01	37	34	0.69[a]	0.001
Mass (wet)	27	25	0.83	0.001	26	22	0.77[b]	0.001
Mass (dry)	38	36	0.84	0.001	37	33	0.87[b]	0.001

[a] Effect of body mass (dry) was removed.

[b] Effect of all 3 body size measurements was removed.

present in a larger sample analyzed by Birkhead *et al.* (1983). Decrease of egg volume or mass with laying date has been noted in several species, for example, Black-legged Kittiwake (*Rissa tridactyla*) (Coulson 1963), European Shag (*Phalacrocorax aristotelis*) (Coulson *et al.* 1969), Tufted Duck (*Aythya fuligula*) (Hill 1984), and Black Brant (Flint and Sedinger 1992). This phenomenon has been explained mainly by the tendency for young females to lay smaller eggs and breed later in the season compared to older birds. Flint and Sedinger (1992) found that other factors could be important too. Second-year Black Brant laid significantly smaller eggs, but the relationship between egg size and laying date remained when these birds were excluded from the analysis, and female experience was thought to play some role. The authors suggested that the decrease in egg size was not related to decreasing nutrient reserves, because repeatability of egg size was very high. In this study of Mute Swans in Poland, the age of breeding females was not known, so its importance was impossible to evaluate, but some females laid smaller eggs in subsequent seasons and thus at older ages.

Seasonal decline of mean egg volume in Mute Swans may be related to changes in the proportion of females with different esterase genotypes laying at different times of the season. In another study, homozygous F females laid significantly smaller eggs and bred later in the season compared to homozygous S females (Birkhead *et al.* 1983; Bacon and Mountford 1990).

Lack (1967, 1968) found a negative relationship between egg size and clutch size across species. However, such a relationship within a species has not been reported in the waterfowl literature (Rohwer 1988; Rohwer and Eisenhauer 1989; Flint and Sedinger 1992; Robertson and Cooke 1993; Flint and Grand 1996) nor in this study. On the contrary, larger clutches contained larger eggs in the studies cited above and also in Whooper Swans (*Cygnus cygnus*) (Rees *et al.* 1991), but not in Black Swans (Braithwaite 1977). Flint *et al.* (1996) suggested that a third variable may be masking such a relationship, and they noted a positive relationship between body size, egg size, and amount of nutrient reserves in some species.

Table 4. General linear models to explain variation in cygnet survival in the first month of life and up to 100 days after hatching using clutch size, mean egg volume and date of hatch as predictors. All interactions terms were non-significant and deleted from the models.

	Survival to 30 days (N = 88 broods)			Survival to 100 days (N = 158 broods)		
	Regression coefficient ± SE	t	P	Regression coefficient ± SE	t	P
Clutch size	0.027 ± 0.018	1.54	n.s.	0.022 ± 0.019	1.16	n.s.
Egg volume	0.000 ± 0.001	0.34	n.s.	0.003 ± 0.001	2.43	0.05
Hatch date	0.000 ± 0.002	0.12	n.s.	-0.004 ± 0.002	1.90	0.06

Changes in Egg Volume between Seasons

Bacon and Beekman (1991) suggested that females that breed late in the season, or in poor quality territories, may increase egg volume and quality by laying smaller clutches to promote higher survival of cygnets. This suggestion was not confirmed in this study. Instead later onset of laying resulted in a decrease in egg volume. In only six of 29 within-female, between-year comparisons was later laying associated with larger eggs. Why should females lay larger eggs when they breed earlier? Williams (1994) suggested that larger eggs cool more slowly, because they have a lower surface area to volume ratio. This may be especially important for species such as Mute Swans in which only females incubate and eggs are left unattended during recesses. Early-breeding females are incubating when temperatures are lower. During this study, it was more windy and colder in March and April than in May (mean temperature up to 10°C lower). Thus larger eggs may be especially advantageous to females breeding early in the season.

Egg Volume and Cygnet Size

Body mass and size of one-day-old cygnets was correlated with egg volume. Egg volume explained about 70% of variation in body mass, similar to the mean value of 66% obtained by Williams (1994) for 35 bird species. The higher body mass of chicks hatched from larger eggs is mainly due to their larger nutrient reserves. The relationship between egg volume and body size is usually poorer. In 18 species, egg volume explained only 30% of variation in body size. Similarly, in Mute Swans, egg volume explained 18%–38% of body size variation.

In the Thick-billed Murre (*Uria lomvia*) (Birkhead and Nettleship 1982) and Pied Flycatcher (*Ficedula hypoleuca*) (Jarvinen and Ylimaunu 1984), body size of chicks was not related to egg size when controlling for body mass. Therefore, Williams (1994) suggested that chicks hatched from larger eggs are heavier, rather than being larger in size. However, in Mute Swans, egg volume explained 30%–53% of variation in body size when controlling for body mass and 59%-77% of body mass when controlling for body size. Thus in Mute Swans, larger eggs produced both heavier and structurally larger chicks, although egg volume explained more of the variation in body mass than in body size.

Rhymer (1988) showed that Mallard (*Anas platyrhynchos*) ducklings that hatch from larger eggs were better able to maintain homeothermy in low temperature due to their larger body mass and lower mass-specific cooling rates. Costs of thermoregulation in Mute Swan cygnets hatched in May are probably higher than chicks hatched in June due to distinctly lower temperatures in May, thus suggesting that larger eggs (and chicks) may be especially advantageous to females breeding early in the season.

Egg Volume and Cygnet Survival

Birkhead (1984) found that the total amount of yolk and yolk lipid increased with Mute Swan egg size. This suggests that cygnets that hatch from larger eggs may have larger nutrient reserves of yolk. Given that cygnets hatching from larger eggs were heavier and structurally larger, as described above, it therefore might be expected that egg volume should affect chick survival. Such a relationship was recorded in eight of 17 studies of precocial species (Williams 1994), although Birkhead *et al.* (1983) did not find a relationship between egg size and Mute Swan cygnet survival. In Barycz valley Mute Swans, mean egg volume influenced cygnet survival up to 100 days after hatching, but not survival in the first month of life. This difference in results may be connected to the different number of years included in the analyses and to less variable weather conditions in the spring. The benefits of hatching from a larger egg (larger nutrient reserves of yolk and body size) should be more important in years with less favorable weather. The analysis of survival to fledging was based on data collected in 1992–1995 when yearly differences in mean May-June temperatures were small. It is likely that weather conditions during the first weeks of life and territory quality may affect cygnet survival, but further study is needed to investigate the importance of these factors.

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Timing of Primary Molt in Breeding Mute Swans

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Abstract.—Non-energetic and energetic constraints have been used to explain asynchronous molt in breeding pairs of waterfowl. This study of Mute Swans (*Cygnus olor*) in the Barycz valley of Poland during 1990–1995 describes the timing of female molt in relation to timing of hatch, clutch size, body weight and condition at the end of incubation, and the timing of her mate's molt. Females (N = 89) initiated molt from 20 June to mid-August. Female date of molt initiation was significantly related to hatch date and body condition at the end of incubation. Females started molt on average 46 days after the hatching of her eggs. The hatch-to-molt interval was positively related to body condition at hatch. Males (N = 102) initiated molt from mid-July to the first of September. Males in poorer body condition initiated molt later. There was a positive correlation between female and male molt dates within a pair. Males began molt on average 28 days later than their mates (N = 52). In addition to energetic constraints of reproduction and molt, the delay of molt by breeding females is likely to be influenced by the need to brood cygnets and protect them from predators. The delay of molt by breeding males is likely to be influenced by the need to protect cygnets from predators and the need to protect mates and territories from conspecifics.

Key words.—Brood protection, *Cygnus olor*, energetics, Mute Swan, wing molt.

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Reproduction, molt and migration are annual events in avian life that require energy and typically occur in different parts of the annual cycle. The lack of overlap in reproductive, molting and migration periods in many species, and evidence that molt results in increased energy and nutrient demands or loss of body mass (Hanson 1962; King and Murphy 1985; Hohman *et al.* 1992), have been used to support the importance of energetic constraints on the timing of molt (Payne 1972; King 1980; Walsberg 1983). However, in some species there is overlap between breeding and molting or between molting and migration (Payne 1972; Lovvorn and Barzen 1988). Some studies have found little or no loss of nutrient reserves during molt in waterfowl (reviewed in Hohman *et al.* 1992), and for species in which a decrease in body mass was recorded, other explanations, such as constraints on foraging time, were sometimes given (Austin and Fredrickson 1987; Panek and Majewski 1990).

In breeding waterfowl, molt of primaries occurs during brood-rearing. The timing of molt can depend on energetic or non-energetic constraints. In some species, breeders molt primaries later than non-breeders, females molt later than their mates, or timing of molt is related to hatching date or brood size (Bellrose 1980; Hansen *et al.* 1971; Lessels 1986; Earnst 1992). In addition, in some species, non-energetic constraints such as territory defense, defense of young from predators or a short breeding season appear to be important (Kear 1972; Earnst 1992).

In Mute Swans (*Cygnus olor*), timing of molt is related to sex. Non-breeding males initiate molt earlier than non-breeding females (Mathiasson 1973; Czapulak 1989; van Dijk and van Eerden 1991), whereas among breeders, males molt later than females (Kear 1972; Birkhead and Perrins 1986). Kear (1972) suggested that breeding males postpone primary molt to protect their broods from predators; males have fully feathered wings when cygnets are younger and more vulnerable to predators. Little is known about the influence of energetic and non-energetic constraints on molt initiation by females. Females vary in reproductive effort: clutch initiation varies by eleven weeks; clutches contain two to nine eggs; and egg volume and clutch volume varies significantly between females (Bacon 1980; Collins 1991; Czapulak 1997; Czapulak and Wieloch 1991). In Mute Swans, only females incubate, and female body weight at the end of incubation varies significantly among individuals (Czapulak 1997). One might expect that females need time to replenish nutrient reserves before initiating molt and that the length of time needed might depend on the female's body condition at the end of incubation.

This study describes the relationship between reproduction and the timing of primary molt in Mute Swans. The aims of the study were to determine (1) if laying date, clutch size, clutch volume and female body condition at the end of incubation influence the timing of molt; (2) factors influencing molting asynchrony of mates; and (3) likely energetic and non-energetic constraints on the timing of molt.

STUDY AREA

This study was conducted on 6,000 ha of fishponds in the Barycz river valley (50 km north of Wroclaw, southwest Poland). Ponds were grouped in 15 complexes, which varied in size from 120 to 1,740 ha. Five complexes were part of the Reserve "Milicz ponds". The area of consecutive ponds was usually <100 ha, but the four largest ones were about 300 ha. Most ponds were shallow (≤1.5 m), and many had Common Reeds (*Phragmites australis*) growing as islands or in wide belts along dikes. In some complexes, emergent vegetation was limited, Common Reeds occurred as narrow belts along dikes, and terrestrial islands were covered with different species of grass and herbs.

METHODS

Data Collection

Swans were captured from mid-July to the end of September in 1990–1993 and 1995. Breeders were defined as those pairs accompanied by cygnets at the time of capture. Only one pair of failed breeders was captured. In total, 102 males and 89 females from 140 pairs were captured; most were captured only once. Both parents were captured in 52 pairs, and in 33 cases birds were captured on different days. Swans were captured using a canoe and capture attempts were made only if the family was close to a dike and far from reed beds. Some capture attempts were unsuccessful even though swans were unable to fly. Twenty-two females were netted on nests at the end of incubation (to ≤5 days before hatch). The following measurements were taken on each individual: length of skull (from tip of bill to back of head, length of the forearm (radius and ulna), the width of foot-web (between outermost toe-webs, fully stretched), length of tarsus and length of sixth primary (from tip to distal end of the feather sheath). Swans were weighed to the nearest 0.1 kg. Clutch size, egg size and dates of hatch (defined as the date that the first egg hatched) were known for 90 pairs and were determined during two to eight visits to each nest during the spring. Nests were visited irregularly, but the stage of incubation of each egg in the clutch was determined using the water test, or flotation method, in which the egg was floated in water and the angle of the egg's long axis relative to vertical was calculated (Nedzinskas 1972; Czapulak, in press). The next visit was planned based on results of this test. The exact hatch date was determined for 66 of 90 nests, to within ±1 day for 15 clutches and to within ±2 days for the remainder. Hatch dates were divided into five equal time periods to investigate the distribution of hatch dates among captured and uncaptured birds. The distribution of hatch dates of pairs that were not captured did not differ from the distribution of hatch dates of captured males ($\chi^2_4 = 2.06$, n.s.), females ($\chi^2_4 = 3.70$, n.s.), pairs in which both mates were captured ($\chi^2_4 = 2.16$, n.s.), or pairs in which at least one mate was captured ($\chi^2_4 = 2.21$, n.s.). All pairs in the sample were on their first clutch. Laying a replacement clutch after clutch loss was very rare (Czapulak 1997), occurring in only once during the study.

Data on swans captured in molting flocks on fishponds near Racibórz (180 km south of the Barycz valley) in 1996–2000 were used in comparisons between breeders and non-breeders.

Data Analysis

Body size measurements were used in a principle component analysis to extract a single variable. A body condition index was then defined as a bird's mass minus its expected mass calculated from the regression of mass on the first principal component.

The length of the fully grown sixth primary and its average growth rate (7.1 mm per day, Czapulak 1989) were used to estimate molt initiation and completion date for each individual. Individuals were assumed to be capable of flight on the date of molt completion. The fledging date of cygnets was estimated based on length of the sixth primary at capture, average growth rate (5.8 mm per day, unpubl. data) and average length of the sixth primary in first winter birds (females—326 mm, males—347 mm, unpubl. data).

The relationship between a dependent variable and two or more independent variables was examined using General Linear Models. If the interaction terms were non-significant they were deleted and models were rerun with only main effects. Statistical analyses were performed using Statistica (StatSoft, Inc. 2000).

RESULTS

Timing of Molt

The timing of the onset of primary molt in breeding females and males was variable (Fig. 1). Females initiated molt between 24 June and 17 August with an average initiation date of 18 July (±12 days [SD], N = 89). Breeding females initiated molt significantly later than non-breeding adult females (18 July compared to 1 July, N = 89 and 293, $t_{380} = 11.3$, $P < 0.0001$, Fig. 1).

Breeding males initiated molt from 13 July to 16 September with an average initiation date of 16 August (±13 days [SD], N = 102). On average, breeding males initiated molt one month later than breeding females (16 August compared to 18 July, N = 101 and 89,

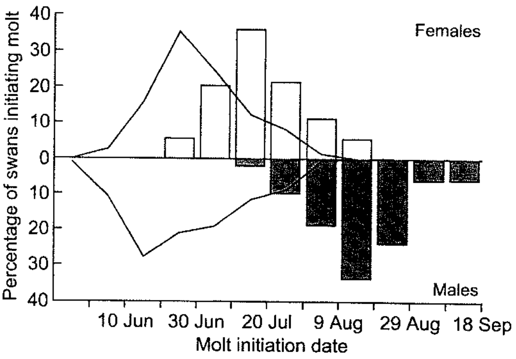

Figure 1. Distribution of female and male molt initiation dates. Bars represent breeding birds (females N = 89, males N = 102), the line represents non-breeding birds (females N = 293, males N = 442).

t_{188} = 15.7, $P < 0.0001$) and >1.5 months later than non-breeding males (16 August compared to 29 June, N = 101 and 442, t_{141} = 30.8, $P < 0.0001$). A male's molt initiation date was significantly related to his mate's date of molt initiation (slope = 0.43 ± 0.11, r_{49} = 0.48, $P < 0.001$, Fig. 2). Male molt initiation was not related to his mate's molt initiation among pairs with broods hatched in May (slope = 0.19 ± 0.19, r_{16} = 0.24, n.s.), but the relationship was significant among pairs with broods hatched in June (slope = 0.74 ± 0.21, r_{14} = 0.69, $P < 0.01$).

All females finished molt before the estimated fledging date of their broods ($\bar{x}$ = -27.5 ± 12.5 [SD], N = 40, range -62 to -3 days), whereas the average male finished molt 6.1 days after this date (±15.9 [SD], N = 68, range -36 to 38 days). Differences between dates on which parents and offspring were able to fly were related to hatch date (female slope = -0.67 ± 0.23, r_{30} = 0.47, $P < 0.01$, male slope = -0.55 ± 0.23, r_{48} = 0.32, $P < 0.05$, Fig. 3).

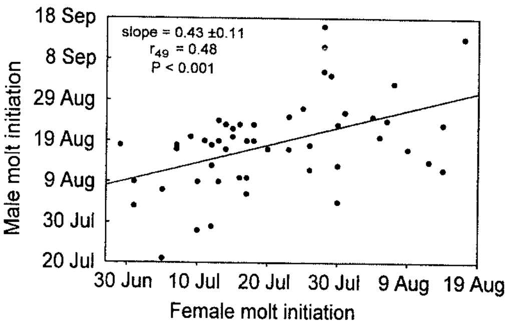

Figure 2. Male's date of molt initiation in relation to his mate's date of molt initiation.

Influence of Reproduction on Timing of Molt

A female started molt, on average, 46 days (±15 days [SD], N = 64, range 25–85 days) after her brood hatched. The only failed female initiated molt at least 27 days after the expected hatch date of her brood. Female date of molt initiation was not related to hatch date in simple regression (slope = 0.23 ± 0.13, t_{63} = 1.76, n.s.), and the lack of a strong relationship between molt and hatch means that birds hatching earlier had a longer hatch-to-molt interval relative to birds hatching later (Fig. 4). Multiple regression showed that the length of the hatch-to-molt interval was significantly related to the body condition index at the end of incuba-

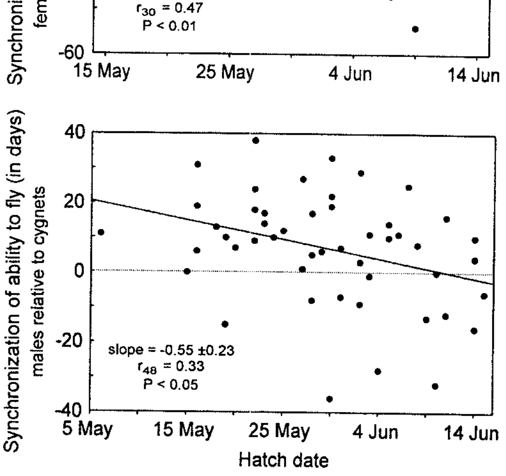

Figure 3. Synchronization of ability to fly within families in relation to the date of hatch. Presented as parent's date of attaining flight minus cygnet's date. Females were capable of flight prior to their cygnets, and males were capable of flight near the time that their cygnet gained flight.

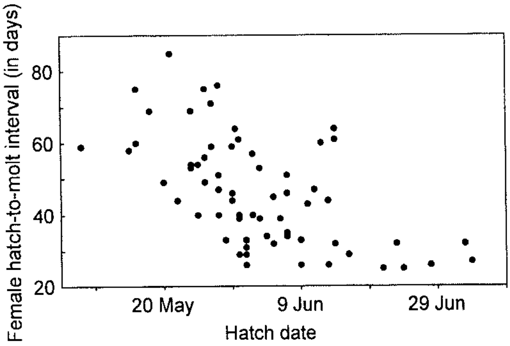

Figure 4. Length of female swan's hatch-to-molt interval in relation to the date of hatch.

tion (coefficient = 23.7 ± 7.6, t_{17} = 3.10, $P < 0.01$) but not to clutch size (coefficient = 3.75 ± 2.16, t_{17} = 1.74, n.s., Table 1). Multiple regression also indicated that female date of molt initiation was related to hatch date (coefficient = 1.01 ± 0.27, t_{16} = 3.79, $P < 0.01$) and body condition index (coefficient = 23.8 ± 8.6, t_{16} = 2.76, $P < 0.05$) but not to clutch size (coefficient = 3.77 ± 2.35, t_{16} = 1.60, n.s., Table 1) when all three variables were included in the equation.

Mean age of cygnets at molt initiation by male parents was 76.6 days (±14.4 days [SD], N = 59) and most males (75%) initiated molt when cygnets were at least 70 days old. Male date of molt initiation was significantly related to date of hatch (slope = 0.31 ± 0.14, r_{57} = 0.28, $P < 0.05$).

Neither the hatch-to-molt interval of male nor female parents was related to the number of cygnets hatched (female slope = 0.71, n.s.; male slope = 2.14, n.s.) or fledged (female slope = 0.64, n.s.; male slope = 1.84, n.s.).

Asynchrony of Molt Within Breeding Pairs

Males began molt on average 28 days later (±12 days, N = 51, range -2 to 50) than their mates (paired t-test, t_{50} = 16.9, $P < 0.0001$). Based on a 337 mm mean length of a fully feathered sixth primary in females and a 7.1 mm per day growth rate (Czapulak 1989), it requires about 47 days for full growth. Thus, in pairs with the largest asynchrony of molt, males initiated molt when females were again able to fly. But on average, males initiated molt when the sixth primary of his mate reached about 60% of its final length. The length of the period when both parents were unable to fly was not related to brood size at hatch (slope = 0.03 ± 0.02, r_{39} = 0.25, n.s.), or to the number of fledged cygnets (slope = 0.03 ± 0.02, r_{39} = 0.24, n.s.). The male of the one failed pair initiated molt on the same date as his mate.

Body Mass and Body Condition Index During Molt

The average body mass of females at the beginning of molt (sixth primary = 0 mm) was 9.38 kg (±0.540 [SD], N = 7). Females were significantly heavier during molt than at hatch (9.30 kg ± 0.69 [SD] compared to 6.62 kg ± 0.58 [SD], paired t-test, t_{21} = 17.8, $P < 0.0001$). The average difference between female body mass at hatch and during the primary molt was 2.7 kg (±0.69 [SD], N = 22, range 1.2 to 4.0).

Female body condition index during molt was quite stable throughout molt (slope = -0.001 ± 0.001, n.s., Fig. 5). It was not relat-

Table 1. The effect of body condition index, hatch date and clutch size on female swan date of molt initiation and length of hatch-to-molt interval. Interaction terms between independent variables were not significant in either analysis. Date of molt intercept = 26.4 ± 46.8, R = 0.72, N = 20. Hatch-to-molt intercept = 27.5 ± 12.9, R = 0.73, N = 20.

Dependent variable	Predictor	Regression coefficient ± SE	t	P
Date of molt	Body condition index	23.8 ± 8.63	2.76	<0.05
	Hatch date	1.01 ± 0.27	3.79	<0.01
	Clutch size	3.77 ± 2.35	1.60	n.s.
Hatch-to-molt interval	Body condition index	23.7 ± 7.64	3.10	<0.01
	Clutch size	3.75 ± 2.16	1.74	n.s.

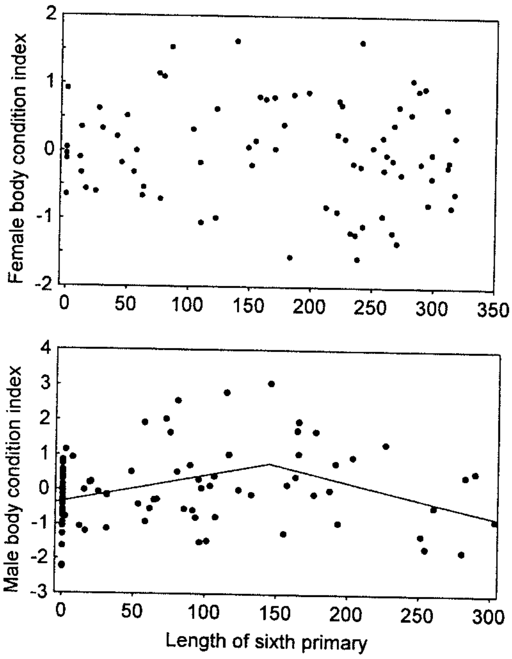

Figure 5. Female swan body condition index (scale -2 to 2) and male body condition index (scale -3 to 4) in relation to length of the sixth primary.

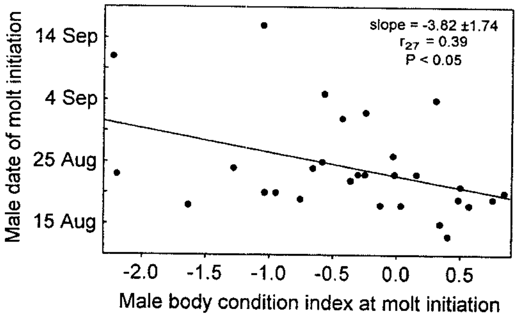

Figure 6. Male swan body condition index at molt initiation in relation to the date of molt initiation.

ed to date of hatch (slope = 0.007 ± 0.010, n.s.), clutch size (slope = 0.044 ± 0.095, n.s.), date of molt initiation (slope = -0.005 ± 0.009, n.s.) or body size (slope = -0.032 ± 0.102, n.s., Table 2).

The average mass of flightless males with old feathers or without all primaries was 12.2 kg (±0.96 [SD], N = 34). Males that molted later were in poorer body condition at molt initiation (slope = -3.82 ± 1.74, r_{27} = -0.39, P < 0.05, Fig. 6). Male body condition index at the beginning of molt increased with asynchrony between mates for males that initiated molt up to 29 days after their mates (slope = 0.13 ± 0.04, t_6 = 3.25, P < 0.01), but decreased with asynchrony for males from pairs with difference in dates of molt initiation larger than 29 days (slope = -0.10 ± 0.03, t_{17} = 2.97, P < 0.01, Fig. 7). Body condition index increased with development of the sixth primary until it reached a length of 150 mm (slope = 0.008 ± 0.003, t_{67} = 2.80, P < 0.01), then decreased thereafter (slope = -0.010 ± 0.004, t_{20} = 2.16, P < 0.05, Fig. 5).

DISCUSSION

The Energetic Constraint of Reproduction

Breeding females initiated primary molt significantly later than non-breeding females. In Tundra Swans (*Cygnus columbianus columbianus*), breeding females also started molt later than non-breeding females (Earnst 1992). This pattern is consistent with the energetic constraints of laying and incubation.

Table 2. The effect of hatch date, clutch size, date of molt initiation and body size on female swan body condition index during molt. Interaction terms between independent variables were non-significant. Y-intercept = -0.51 ± 2.12, R = 0.11, N = 60.

Independent variable	Regression coefficient ± SE	t	P
Hatch date	0.007 ± 0.010	0.72	n.s.
Clutch size	0.044 ± 0.095	0.46	n.s.
Date of molt initiation	-0.005 ± 0.009	0.54	n.s.
Body size	-0.032 ± 0.102	0.31	n.s.

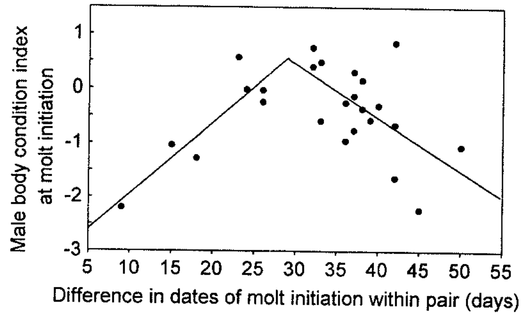

Figure 7. Male swan body condition index at molt initiation in relation to difference in dates of molt initiation within pair (presented as male date minus female date).

However the timing of molt in breeding female Mute Swans was not related to clutch size, date of hatch, body weight or body condition at the end of incubation. Females that bred earlier in the season, and laid larger clutches, delayed molt longer after hatch than late breeders. This could suggest that females with higher reproductive effort need more time to recover energetic reserves before molt. However, the finding that length of the hatch-to-molt interval was positively related to body condition at the end of incubation does not support this interpretation.

It is possible that the energetic constraints of breeding and molt might dictate a threshold mass that must be reached before molt begins, and that once this threshold is reached, one would not expect a relationship between the hatch-to-molt interval and body condition of females. If there is such a threshold in Mute Swans, we can estimate it in the following manner. The average mass of females was 6.79 kg at the end of incubation (Czapulak 1997) and 9.38 kg at the beginning of molt (this study). The difference of 2.79 kg can be replenished within about 34 days after hatch if females gain weight at 80 g per day as reported by Beekman (1991). If breeders could molt at the same weight as non-breeders (8.73 kg; unpubl. data), then the threshold would be only 25 days. Thus, it seems reasonable to assume that 25–34 days after hatch are needed to replenish necessary body reserves for molt. The average hatch-to-molt interval of 46 days for breeders in this study, and of 27 days for the one failed female, is consistent with this threshold.

Lessells (1986) found that pairs of Canada Geese (*Branta canadensis*) with experimentally enlarged broods delayed molt. Brood size did not influence the timing of molt in this study of Mute Swans.

The Constraint of Defending a Territory

Mainly males defend the territory in Mute Swans. Females participate in defense more actively during the pre-incubation period, but rarely after hatch (Demarest 1981). Earnst (1992) suggested that the need for territory defense might influence the timing of molt in breeding Tundra Swans, favoring asynchrony between mates and synchrony between breeding and non-breeding males. In Mute Swans, the last non-breeding adult males initiated molt in August and most breeding males initiate molt at the same time. This indicates that territory defense may be an important constraint on the timing of molt of breeding males in this species also. It seems that this constraint, although it may be important, does not explain all of the variation in the timing of molt in male Mute Swans. Single pairs breed on many ponds, their territories include the whole pond, and there is no contact with others pairs through the season. Non-breeders occur on some ponds, especially in late spring and summer, and they may influence the timing of molt of some breeding males. Demarest (1981) found that territorial defense decreased rapidly after hatch and two of three tested males did not react to the presence of an intruder in the territory. Given the large differences in hatch dates between pairs, it seems that the ability to defend a territory using fully feathered wings should be especially important for early breeders.

The Constraint of Brooding Young

Cygnets are brooded during the first three weeks of life (Kear 1970) and females use primaries to shelter chicks during brooding (males rarely brood). The need for primaries during brooding may be a factor influencing the timing of molt in female Mute Swans, but it is difficult to distinguish this hypothesis, which would predict a delay of at least 21 days after hatch, from the hypothesis of an energetic threshold of approximately 25–34 days after hatch as discussed above. The single case of a failed female who waited 27 days after hatch to begin molt, despite not having any cygnets to brood or protect, suggests that energetic constraints may be more important than constraints of brooding or protecting young, but an analysis based on a larger number of failed females, including their body condition, is needed.

The Constraint of Cygnet Protection from Predators

The estimated time needed to replenish body reserves before molting is 25–34 days (see above), but on average females initiated molt 46 days after hatch. Early breeders delayed molt longer after hatch than did late breeders, and the delay was not connected to poor body condition. In the Barycz study area, chicks from the earliest clutches hatched in the first half of May (Czapulak 1997), about 50 days prior to the average molt initiation of non-breeders who presumably molt near the optimal time (see below), but early breeding females initiated molt on average two to three weeks later than non-breeders. Although energetic constraints are likely to be important, the constraint of brood protection may explain why females, particularly early breeding females, waited nearly three weeks longer after hatch than is necessary to replenish body reserves.

The finding that females in better body condition at the end of incubation delayed molt longer after hatch also seems to suggest that energetic constraints are not the only factors of importance in determining molt initiation. It is possible that superior females are able to maintain their body condition throughout incubation, and that those females are also more able to invest in offspring care by delaying molt past the point at which environmental conditions are most suitable for molt (assuming non-breeders are molting at the optimal time, see below). Females in good body condition delayed molt up to 85 days after hatch; if they had postponed molt much longer, their molt would not have completed before their offspring fledged. Low quality females, which are in worse condition after incubation, may not delay molt as long after hatch because molting in less favorable environmental conditions may be more disadvantageous for them.

It seems that the timing of molt of nonbreeding swans indicates an "optimal" time to undergo molt. Difference between years in the mean date of molt initiation of nonbreeding females near Racibórz, was ±1 day (unpubl. data). Observations from other years and other places in southwest Poland suggest that the initiation of molt by non-breeding females at the beginning of July, on average, is typical for this region. Food resources are probably largest in early summer and decrease through the season. In August, non-breeders feed more frequently on reeds (Szelag 2001), which are lower in calories and less digestible, and it is likely that the abundance of other food is limited during that period. These findings suggest that breeding females that delay molt for a longer period and initiate molt later in the season, molt after the "optimal" time.

Protection of the brood from predators was used as an explanation the delay of primary molt by Mute Swans males (Kear 1972). Although males invest much less energy in breeding than females, the average male initiated molt 28 days after his mate and 1.5 months later than non-breeding males. Males in flocks of non-breeders and in pairs without offspring begin molt earlier than females (Matthiason 1973; Czapulak 1989; van Dijk and van Eerden 1991). In this study, the average male initiated molt when his offspring were around 77 days old. At this age, cygnets are nearly fully grown, and they weigh around eight kg (de Leeuw and Beekman 1991; unpubl. data). Causes of cygnet deaths in the Barycz valley are unknown (Czapulak 1997), but it is possible that some cygnets are taken by Red Fox (*Vulpes vulpes*). In Poland, Red Fox prey mainly on animals that weigh up to five kg (Goszczyński 1974; Goszczynski and Wasilewski 1992), although there is a known case of a Red Fox killing an incubating female (Puchalski 1956). Initiation of molt by males when cygnets are almost fully grown indicates that the constraint of brood protection may be an important reason of delayed molt by males too. In some pairs, asynchrony in molt between mates is so large that males, which do most of the brood defense (Kear 1972), retain primaries for almost the whole pre-fledging period.

The Constraint of Female Protection

The constraint of female protection has not been considered in the existing literature. It seems that it may be at least as important as brood protection. In many cases, males actively defend flightless female during capture. In some situations, when two people captured the female and cygnets simultaneously, the male tried to distract the person capturing the female. This suggests that protection of the female rather than the brood may be more important to the male. If a mate is lost, a male may have difficulty finding a new mate, especially since Mute Swans show a strong tendency to mate with birds of the same age (Perrins *et al.* 1994).

Synchronization of Ability to Fly Within a Family

There are a few sources of potential bias in the estimation of cygnet fledging time. It was assumed that cygnets were able to fly when the sixth primary reached its final length. In fact, it is likely that cygnets were not able to fly until a few days after it reached final length. The calculation also was based on mean growth rate whereas cygnets that hatched later in the season grew more slowly (Czapulak 1997), thus time of fledging for these broods may be overestimated. Nevertheless, these sources of bias do not change the finding that all females had finished molt at the time of cygnet fledging or before. The potential biases are more important in interpreting synchronization between males and cygnets. If cygnets need time to learn to fly after growth of their primaries, and if a specific growth rate for each brood were used to estimate fledging date, males probably finish molt around the time of fledging of their offspring. Thus, the need for male-cygnet synchronization in the ability to fly may influence the timing of molt initiation in males.

Body Condition During Molt

It has been shown that the timing of molt in non-breeders is related to body mass across sex and age classes (van Dijk and van Eerden 1991). The molt of body feathers in first winter swans also depends on body mass (Andersen-Harild 1981). Such a relationship was not found in this study for breeding females, but was found for males. It is interesting that male body condition was negatively related to length of the hatch-to-molt interval. Breeding males weigh about one kg more than non-breeders (Mathiasson 1981; unpubl. data) and body mass of breeding males is quite stable through the season (Beekman 1991). Thus, it would be surprising if the timing of molt in breeding males was limited by body mass or body condition. Instead, it seems that the low body condition index of late molting males was a result of prolonged protection of the family. This supposition is consistent with the finding that male body condition decreased with an increase in the difference in molt initiation dates within the pair. The poorer condition of late molting males may be due to a limited time for feeding and a higher proportion of time spent in vigilant behavior.

Influence of Photoperiod on Molt

Molt is under hormonal control and is related to the level of gonadal hormones. Experimental studies have shown that day length might stimulate changes in hormone balance and molt initiation (Payne 1972). It was suggested that wing molt in male ducks may be under photoperiodic control, due to the highly synchronized and consistent timing of molt between years (Hohman *et al.* 1992). In breeding Mute Swans, the range in dates of molt initiation in both sexes was about two months. Breeding males and breeding females differed significantly in the timing of molt and breeders differed from non-breeders. These findings indicate that photoperiod does little to explain the timing of molt in breeding swans.

Comparisons with Other Swan Species

There is a little known about factors affecting timing of molt in other swan species. In Tundra Swans, females initiated molt three days later than non-breeding females and their mates, and female molt initiation was positively related to date of hatch. Females with larger clutches initiated molt sooner after hatch and had better body condition during molt, similar to findings in this study. On average females initiated molt 21 days after hatch. The timing of molt in Tundra Swans was interpreted as being due to both energetic and non-energetic constraints like territory defense, brooding, and brood defense (Earnst 1992).

In Icelandic Whooper Swans (*Cygnus cygnus*), breeding females had significantly longer primaries than breeding males when caught in early August, indicating that females initiated molt earlier (Rees *et al.* 1991). Data is lacking from other Whooper Swan populations, especially from southern parts of their range.

To understand the strategies of molt in breeding swans, comparative studies are needed, especially for populations of the same species breeding at different latitudes. In addition, data on the timing of molt would be useful for Black Swans (*Cygnus melanocorypha*), in which males participate fully in incubation, and for Trumpeter Swans (*Cygnus buccinator*), in which some males are reported to molt before their mates and some after (reviewed in Earnst 1992). If one purpose of the delay of molt in males is protection of females and territories from conspecifics, as suggested in this paper for Mute Swans, it would be interesting to investigate whether molt asynchrony within a pair changes with length of the pair bond or male experience.

There were some problems with interpretation of findings recorded in this study. Small sample sizes, especially the low number of pairs for which both mates were captured and reproductive parameters were known, made it impossible to control for the effect of year in analyses. Also, the age and experience of swans was unknown in this study. It is likely that swan behavior during brood-rearing is related to age and/or experience and may thus affect the timing of molt. Finally, the low probability of an individual breeding in consecutive seasons in the study population made it impossible to compare the timing of molt in relation to changes in reproductive effort between years.

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Parental Care in Tundra Swans During the Pre-fledging Period

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Abstract.—Among studies that have quantified the care of precocial young, few have investigated forms of parental care other than vigilance. During the pre-fledging period, Tundra Swan (*Cygnus columbianus columbianus*) parents provided simultaneous biparental care by foraging near each other and their cygnets, and cygnets spent more time foraging during bouts in which both parents were foraging nearby than when only one parent was foraging nearby. Parents spent nearly twice as much foraging time on land than did non-parents, a habitat in which cygnets foraged more intensely than parents (i.e., spent more time foraging during foraging bouts) and could graze on protein-rich sedges rather than use more difficult below-water foraging methods. Parents also spent more than twice as much time being vigilant and more than three times as much time defending their territory than non-parents, behaviors that presumably benefited cygnets by decreasing predation risk and indirect foraging competition, respectively. Parents therefore incurred the costs of foraging less intensely during foraging bouts, spending more time interacting, more time in vigilance, and less time sleeping/preening than non-parents.

Key words.—Alaska, breeding grounds, *Cygnus columbianus*, foraging, habitat use, parental care, Tundra Swan.

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Among avian species with self-feeding, precocial young, parental care was traditionally assumed to require little time and energy (e.g., Emlen and Oring 1973; Parmelee and Payne 1977). However, most studies of precocial young that have quantified parental care (i.e., behavior likely to increase the survival and productivity of offspring, Clutton-Brock 1991, p. 8) during the pre-fledging period have found that it substantially constrains the time and energy of parents (Table 1). Despite such studies, the parental care of self-feeding, precocial young remains less understood than that of altricial young.

Care of precocial young is often subtle and thus difficult to investigate; indeed, few studies have investigated forms of care other than vigilance (Table 1). An exemplary exception is the study of lapwings (genus *Vanellus*) in which Walters (1982) documented vigilance, leading and following young, showing food to young, and foraging away from young as care-giving behavior.

Most studies of parental care during pre-fledging have identified behavioral adaptations that benefit offspring by comparing (1) parental behavior to adult behavior in non-breeding years or seasons, or (2) examining parental behavior in relation to brood age or brood size (Table 1). However, comparisons of behavior between breeding and non-breeding seasons are complicated by social and ecological differences among seasons, and there are conflicting interpretations of differences in parental care with brood size and brood age (Clutton-Brock 1991, chapter 9; Sedinger *et al.* 1995). Tundra Swans (*Cygnus columbianus columbianus*) provide an ideal opportunity to compare parent and non-parent behavior under similar ecological and social conditions because, in the northern-breeding swans, many pairs hold territories in years in which they do not raise cygnets (Rees *et al.* 1991; Henson and Cooper 1994).

Among many shorebirds and waterfowl, proximate measures of costs to parents indicate that there is a trade-off between time spent in parental care and time spent resting or foraging (Table 1). The longer-term fitness consequences of parental care in waterfowl have been measured only in relation to differences in current brood size, and most of these studies suggest that there are no meaningful fitness costs of raising larger broods (Rohwer 1985; Lessells 1987; Rohwer and Heusmann 1991; Williams *et al.* 1994; Loonen *et al.* 1999). However, Lessells (1986) found that Canada Geese (*Branta canadensis atlantica*) that raised experimentally enlarged broods had lower body mass at the end of the rearing period, molted later, and laid eggs later the following year. Delayed breeding

Table 1. Studies that have quantified parental care and its proximate costs during the pre-fledging period in shorebirds and waterfowl. Three forms of parental care are considered: vigilance (VG), maintaining proximity (PX), and defending a foraging area or protecting young from foraging competition (DF). "X" = behavior varied as expected (i.e., more effort expended by parents than non-parents, and on larger and younger broods); "—" = behavior did not vary as expected; blank = comparison not quantified.

		Form of care				
Species	Comparison	VG	PX[a]	DF[b]	Cost to parents	Reference
Trumpeter Swan *Cygnus buccinator*	Non-parents	X			↓ foraging time	Henson and Cooper 1992
Pink-footed Goose *Anser brachyrhynchus*	Non-parents	X		X	↓ preen, sleep, forage	Lazarus and Inglis 1978
	Brood age	X			no ↓ preen, sleep, forage	
Greater Snow Goose *A. caerulescens atlantica*	Non-parents	X			↓ preening, no ↓ in foraging	Giroux *et al.* 1986
Lesser Snow Goose *A. caerulescens caerulescens*	Non-parents	X			↓ foraging time	Lessells 1987
	Brood size	—	X		no ↓ in foraging	
Lesser Snow Goose	Non-parents	X			↓ foraging time	Williams *et al.* 1994
	Brood size	X			↓ foraging time	
Light-bellied Brant *Branta bernicla hrota*	Non-parents	X		X	↓ foraging time	Bregnballe and Madsen 1990
Black Brant *B. bernicla nigricans*	Brood size	X			no ↓ foraging time	Sedinger *et al.* 1995
Cackling Canada Goose *B. canadensis minima*	Brood size	X				Sedinger and Raveling 1990
Giant Canada Goose *B. canadensis maxima*	Non-parents	X		—	↓ foraging time	Seddon and Nudds 1994
	Brood size	—	X	—	no ↓ foraging time	
	Brood age	X	X		no ↓ foraging time	
Canada Goose *B. canadensis atlantica*	Brood size				↓ mass, delay molt, laying[c]	Lessells 1986
Barnacle Goose *B. leucopsis*	Non-parents	X			↓ foraging time	Forslund 1993
	Brood size	X	X		↓ foraging time	
	Brood size	X		X	no costs[d]	Loonen *et al.* 1999
Bar-headed Goose *A. indicus*	Brood size	X	X	X	↓ foraging time	Schindler and Lamprecht 1987
Cape Barren Goose *Cereopsis novaehollandiae*	Brood age	X			↓ foraging time	Pellis and Pellis 1982
Northern Pintail *Anas acuta*	Brood age	X	X		↓ foraging time	Rushforth Guinn and Batt 1985
Australian Wood Duck *Chenonetta jubata*	Non-parents	X			↓ foraging time[e]	Kingsford 1990
	Brood size	—				
	Brood age	X				
Killdeer *Charadrius vociferus*	Brood age	X	X		↓ foraging time	Lennington 1980
Semipalmated Sandpiper *Calidris pusilla*	Brood age				↑ energy requirements	Ashkenazie and Safriel 1979
Southern Lapwing *Vanellus chilensis*	Non-breeding season	X			↓ foraging time	Walters 1982
Long-toed Lapwing *V. crassirostris*	Non-breeding season	X			↓ foraging time	Walters 1982
Blacksmith Plover *V. armatus*	Non-breeding season	X			no ↓ in foraging	Walters 1982

[a] Proximity measured as frequency with which parents approached young in Bar-headed Geese, as time spent following brood in Northern Pintails, and as parent-brood distance in Killdeer, Giant Canada Geese, and Barnacle Geese. [b] Defense of foraging area measured as dominance over non-parents in Pink-footed Geese, dominance of families relative to all other social units in Barnacle Geese, and as attacks on conspecifics in Bar-headed Geese and Light-bellied Brant. [c] Females only. Females with experimentally enlarged broods also delayed laying in following years but their fecundity and survival to next year was not affected. [d] Rather than costs to parents, the benefits of increased social dominance and better female body condition during molt were associated with increased brood size. [e] Data appear to show difference, but author does not give direct statistical comparison of time spent foraging by parents and non-parents.

has substantial fitness costs in northern-breeding geese because late-hatching goslings grow more slowly and have lower survival rates (Cooch *et al.* 1991a; Sedinger and Flint 1991; Prop and de Vries 1993; Lindholm *et al.* 1994).

Although other studies have investigated parental care in Tundra Swans during the non-breeding seasons (Earnst and Bart 1991), this is the first field study of parental care in Tundra Swans during the pre-fledging period, a time when they are wary and sparsely distributed. The aims of this study are to document and quantify parental care in Tundra Swans during the pre-fledging period, and to investigate its proximate costs to parents. To achieve these aims, the following forms of parental care were quantified: vigilance, territory defense, foraging intensity (measured as proportion of time spent foraging during a foraging bout), proximity to the brood during foraging bouts, habitat use while foraging, and use of an activity cycle assumed to be beneficial to cygnets (measured as average length of foraging periods).

METHODS

Study Site and Phenology

Tundra Swans were studied during May-August, 1987–1990, on the Colville River Delta, 90 km east of Prudhoe Bay, on the northern coast of Alaska. The 500-km^2 Delta supports an average of 31 breeding pairs, 53 non-breeding pairs, and several non-breeding flocks each year (Bart *et al.* 1991). Territories were approximately 1 km^2 and included a large waterbody and usually numerous polygonal ponds. Swans fed on aquatic and terrestrial vegetation in and around both types of waterbodies (Earnst 1992a). Breeding pairs arrived in late May when most wetlands were ice-covered and began egg-laying soon after. The brief arctic summer places severe time constraints on the development of cygnets which typically hatch around 8 July and fledge 65–75 days later, shortly before wetlands freeze for the winter (Bellrose 1980; Earnst 1992a).

Observations

Behavioral observations of breeding pairs with cygnets were compared to those of non-breeding pairs after 8 July (the average hatching date). Most observations (90%) had been made by the fifth week after hatching (2 August), and the remainder were made before August 28. The behavior of undisturbed swans was recorded from three enclosed blinds located 2–4 km apart in an area known to support numerous breeding territories. Blinds were built on a tower or ridge, providing a viewing platform 2–4 m above the swan habitat, and were accessible with minimal disturbance to swans. Focal swans were usually 0.5 to 1.0 km from the blind and were observed through a 60–90× telescope.

Instantaneous, focal-animal sampling (Altman 1974) was used on pairs and families occupying known territories within viewing distance from the blinds. Observations were made from one blind per day and focal pairs and families were chosen systematically (i.e., from left to right) from those that were visible, while attempting to achieve similar total observation hours per focal unit. Observation period length was determined prior to approaching the blind to avoid bias arising from any unintentional association with swan behavior. Swans usually appeared unaware of movement to the blind but, if they were disturbed, data collection was postponed until they resumed their previous behavior or assumed a relaxed posture, typically after 15–30 minutes. For each focal pair or family, the following parameters were recorded at one-minute intervals: behavior and habitat of each mate, distance between mates, and behavior and distance-to-nearest-parent (in adult body-lengths) for each cygnet. A continuous count-down timer with alarm was used to notify the observer at each one-minute interval. Distance was recorded in adult swan body-lengths. Specific behavior was recorded and later categorized into five behavioral types (in order of precedence): feeding, interacting agonistically with non-family members, preening, traveling (walking, running, swimming, and flying), and resting (sleeping, sitting, standing, floating). If swans were engaged in two behavioral types simultaneously (e.g., feeding and standing), the behavior was categorized into the type having higher precedence. Specific feeding behaviors included up-ending, neck-under, head-under, dabbling, treadling (paddling the feet to scrape vegetation to the surface), and grazing (see Owen and Kear 1972 for definitions). Swan posture was recorded at each one-minute interval as head-up (the plane of the neck being above horizontal), alert (the extreme head-up, as defined by Lazarus and Inglis 1978), or neither. Feeding habitat was categorized as aquatic (surface water present) or terrestrial (no surface water). Continuous sampling was used for observations of territorial interactions and encounters with predators. Swans were out of sight on 5% of the instantaneous samples (range 0 to 9%) and appeared to be approximately equally visible when engaged in each of the five behavior types. Thus, recorded observations are considered a representative sample of each focal animal's behavior.

Bout Definitions

Observations made at consecutive one-minute intervals were pooled into behavioral bouts in order to address questions of foraging intensity and foraging period length. Five bout-types, corresponding to the five behavioral types listed above (feeding, interacting, preening, traveling, and resting), were identified. The following set of rules was used to determine bouts: (1) a new bout-type began on a one-minute interval if it was the first of six consecutive intervals in which at least three of the six were of a single behavioral type; (2) once begun, a bout-type continued if the interval behavior matched the bout-type or if the interval was the first of six consecutive intervals in which at least two of the six intervals matched the bout-type; and (3) if an interval did not meet the criteria for continuing a bout or initiating a new bout-type, it was coded as transitional.

Subsequently, to simplify analysis, preening and resting bouts were combined, traveling bouts that directly preceded or followed an interaction bout were added to the interaction bout (this type of traveling usually resulted from a bird moving towards an intruder and back to its original position), and transition intervals were added to the preceding bout. Thus, four bout-types (feeding, interacting, traveling, and resting) were used in the final analysis. This set of rules was chosen because it avoided production of short resting and traveling bouts, minimized the number of transitional intervals, and produced bouts in which most behaviors were of the bout-type (e.g, foraging comprised 73% of intervals within foraging bouts), and because time spent in each bout-type was similar to time spent in the respective behavior categories over all bout types (e.g., 47% vs. 41% foraging; 42% vs. 46% resting). In addition to the set of rules described here, analyses using four other sets of bout rules (i.e., criteria used to identify a bout) revealed that bout lengths and the estimated time spent in each bout-type were similar among bout rules, indicating that the choice of this set of rules over others likely had little affect on subsequent analyses.

Bouts were assigned only for those periods in which the identity of adults could be kept separate. Foraging intensity was defined as the proportion of intervals during a foraging bout recorded as foraging. Foraging time spent in proximity to the mate was measured as the proportion of an individual's foraging bout in which it was within six adult body-lengths of its mate (Scott 1980). The foraging intensity of cygnets was used to determine whether cygnets gained any advantage of foraging near both, rather than only one, parent. Because the identity of cygnets could not be kept separate, their behavior was not assigned to bouts. Thus, the foraging intensity of each cygnet was defined as the proportion of intervals in the nearest parent's foraging bout in which the cygnet's behavior was also recorded as foraging. The foraging intensities of all cygnets within a brood were averaged to obtain a mean foraging intensity for each brood. Except for an occasional moment immediately before or after a parental foraging bout, cygnets were never seen foraging unless at least one parent was in a foraging bout.

To investigate activity cycles, two types of periods were distinguished: those in which foraging was the predominant activity and those in which resting, and thus food digestion, was predominant. Thus, foraging periods were defined as foraging bouts plus any interacting, traveling, floating, and standing intervals that were of short duration (<5 min) and interrupted an otherwise continuous foraging bout. Defining foraging periods in this way was also appropriate because cygnets continued to forage during brief interruptions in their parents' foraging bouts. The inter-foraging period was the time between foraging periods. Only foraging bouts completed within the observation period were used in calculating foraging period length. The potential for bias in estimating the length of the foraging period is minimal because the average foraging bout was substantially shorter than the average observation period (36 and 204 min, respectively).

Statistical Analysis

In the four years of this study, nine different territories were visible from blinds during the brood-rearing period. One or both members of four focal pairs wore neck collars containing individually identifiable codes in at least one year of study. Studies on northern-breeding swans indicate that breeding pairs typically occupy the same territory in consecutive years (Whooper Swans, *Cygnus cygnus*, Einarsson and Rees 2002; Bewick's Swans, *Cygnus columbianus bewickii*, Rees pers. comm.). Similarly, in this study, five breeding pairs were banded on territory (two in the observed area, three elsewhere on the Delta), both members were known to be alive in subsequent seasons, and their territories were checked thoroughly enough to provide resightings of banded birds. In all five cases, the pair occupied its same territory in subsequent years, irrespective of whether it bred. Thus, as a conservative approach to avoid pseudoreplication, data from pairs present as breeders in more than one year (three pairs) or as non-breeders in more than one year (two pairs) were pooled across years (see also Henson and Cooper 1992; Grant *et al.* 1994). Analyses were based on means per pair or brood. The proportion of time spent on each behavior by a focal pair was calculated for each observation period and then averaged across observation periods. Average proportions for each focal pair were weighted by the total time it was observed (analogous to weighting by sample size; Cochran 1977) then averaged with the weighted means of other focal pairs. Statistical comparisons were made using independent t-tests unless noted otherwise. Standard errors are reported with means throughout the text, tables, and figures.

RESULTS

Of the nine territories visible from blinds, seven were breeding territories in at least one year of the study. Analyses were based on seven breeding pairs observed for a total of 156 h during ten pair-years, and five non-breeding pairs (three of which were also observed as breeders) observed for a total of 76.1 h during six pair-years. However, some parameters could not be quantified for social units with territories far from the blind, thus degrees of freedom differ among tests. Pairs were observed for an average of 3.4 h per observation period, 6.1 observation periods, and 20.7 total hours each.

Maintaining Proximity

Parents spent nearly twice as much of their foraging time in proximity (within six body-lengths) to one another as did non-parents ($P < 0.001$, Table 2). Because cygnets were, on average, only 1.3 (±0.2) adult body-lengths from their nearest parent, parents near one another were also both near their brood.

Cygnets fed significantly more intensely (i.e., spent more time foraging during their parent's foraging bout, see Methods) when

Table 2. Mean proportion of time spent in parental care behaviors, and mean length of foraging and inter-foraging intervals, by parents and non-parents during the brood-rearing period. Standard errors in parentheses. N = 7 parental pairs and 4 non-parental pairs, except where noted otherwise, and statistical significance based on independent t-tests.

Form of parental care	Measure	Parents	Non-parents	t	P <
Proximity	Proportion of foraging time <6 body-lengths	0.58 (0.05)	0.30 (0.01)	5.57	0.001
Foraging habitat	Proportion of foraging time on land[a]	0.41 (0.02)	0.24 (0.05)	3.19	0.02
Vigilance	Proportion of time alert[b]	0.05 (0.007)	0.02 (0.007)	3.43	0.01
	Proportion of time head-up[b]	0.48 (0.04)	0.37 (0.07)	1.39	n.s.
Territory defense	Proportion of time interacting[b]	0.014 (0.004)	0.004 (0.002)	2.24	0.05
Activity cycle	Length of foraging period (min)	41.6 (3.7)	26.1 (2.1)	3.64	0.005
	Interval between foraging periods (min)	40.7 (3.8)	49.1 (8.6)	0.89	n.s.

[a] N = 6 parental pairs, 4 non-parental pairs. Alert posture is defined as the neck being held rigidly vertical.

[b] N = 7 parental pairs, 5 non-parental pairs. Head-up posture includes all behaviors in which the plane of the neck is above horizontal.

both parents were foraging nearby than when only one parent was foraging nearby ($P < 0.01$, Table 3).

Parents did not appear to incur costs, as measured by decreased feeding intensity, when foraging in proximity to one another. In fact, when both parents were foraging and near one another, they fed significantly more intensely than during other feeding bouts ($P < 0.001$, Table 3).

Activity Cycle and Foraging Habitat

Parents engaged in foraging periods about 1.5 times longer than those of non-parents ($P < 0.01$) and did not differ from non-parents in length of intervals between foraging periods (n.s., Table 2). Parents spent nearly twice as much foraging time on land as did non-parents ($P < 0.01$, Table 2) and cygnets always foraged in the same habitat as their parents. The one pair for which sufficient data were available used terrestrial habitat significantly more during a breeding than a non-breeding year ($\bar{x} = 0.45 \pm 0.12$ and 0.10 ± 0.07, respectively, with the observation periods as the sampling units, $t_{11} = 2.53$, $P < 0.05$).

When feeding on land, cygnets fed with nearly twice the intensity as their parents ($t_{10} = 4.31$, $P < 0.01$, Fig. 1). When feeding on water, cygnets did not forage significantly more intensely than parents ($t_{12} = 1.33$, n.s., Fig. 1), and rarely used the below-surface foraging methods (head-under, neck-under, and up-end) that were commonly used by their parents ($\bar{x} = 0.12 \pm 0.02$ and 0.49 ± 0.07, respectively, $t_{12} = 4.96$, $P < 0.001$). Although cygnets foraged 81% of the time during foraging bouts on land and 64% on water, the SE on land was large, and the difference was not significant (Fig. 1). In contrast, the foraging intensity of adults (non-parents and parents combined) was significantly lower, rather than higher, on land than on water ($P < 0.05$, Fig. 1). The pattern was similar when considering parents only, but was not statistically significant.

Table 3. Foraging intensity (i.e., proportion of time spent foraging during a foraging bout) of broods and parents when both parents were foraging and near the brood (<6 body-lengths) compared to foraging intensity when only one parent was foraging near the brood. N = 7 parental pairs and 4 broods; statistical significance based on paired t-tests. SEs given in parentheses.

	Both parents foraging and near brood	One parent foraging near brood	t	P <
Broods	0.76 (0.03)	0.65 (0.03)	5.67	0.01
Parents	0.69 (0.02)	0.44 (0.02)	6.67	0.001

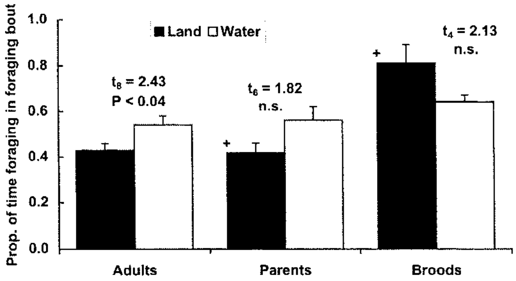

Figure 1. Foraging intensity of all adults (parents and non-parents combined), parental pairs, and broods, when foraging on land and water. Error bars denote one SE and + denotes a significant difference between parents and broods. Total sample sizes were nine pairs, seven parental pairs, and seven broods, but foraging intensity of some broods could not be quantified on land due to poor visibility (thus d.f. varies among tests). Statistical tests of behavior on land compared to water were paired t-tests (shown on graph); tests comparing parents to broods were independent t-tests. Broods foraged more intensely than parents on land ($t_{10} = 4.31$, $P < 0.01$) but not on water ($t_{12} = 1.33$, n.s.)

Vigilance and Territory Defense

Parents spent more than twice as much time alert ($P < 0.01$) and more than three times as much time in agonistic interactions with other adult swans ($P < 0.05$) than did non-parents during the brood-rearing period (Table 2). Interactions included threatening or chasing intruders from the territory either in the air or on the ground (especially during molt). During interactions, one parent engaged the intruder while the other, sometimes in a hiding posture, remained with the brood. As a result, parents were in synchrony during interaction bouts (i.e., both interacting) significantly less often than were non-parents ($\bar{x} = 0.61 \pm 0.08$ and 0.84 ± 0.03, respectively, $t_7 = 2.59$, $P < 0.05$). The division of labor did not appear to be sex-specific: male and female parents were observed in each role and spent similar amounts of time interacting ($\bar{x} = 0.7 \pm 0.5$ and 0.7 ± 0.6, respectively, $t_5 = 0.0$, n.s.).

Parents spent less time sleeping/preening than non-parents ($\bar{x} = 0.18 \pm 0.02$ vs. 0.32 ± 0.05, $t_{10} = 2.50$, $P < 0.05$). Parents also fed less intensely during foraging bouts than did non-parents ($\bar{x} = 0.62 \pm 0.05$ vs. 0.73 ± 0.02, $t_9 = 2.29$, $P < 0.05$), but parents did not spend less time foraging overall ($\bar{x} = 0.34 \pm 0.04$ vs. 0.31 ± 0.02, $t_{10} = 0.77$, n.s.).

DISCUSSION

Comparison of behavior of parents and non-parents revealed several forms of parental care in Tundra Swans during the prefledging period. Tundra Swan parents spent more time being vigilant, defending their territory, foraging in proximity to one another, and foraging on land than non-parents. In addition to the energetic costs of vigilance and territory defense, parents incurred costs related to foraging less intensely during foraging bouts and spending less time sleeping/preening, but did not spend a lower proportion of time foraging overall.

Maintaining Proximity

Parents foraging near one another provide their brood with simultaneous biparental care. Any benefits that cygnets gain from foraging near a parent (such as assistance in finding food and protection from predators) are presumably greater when two parents, rather than one, are nearby. Other studies of waterfowl that have identified maintaining proximity as a form of parental care have found that parents maintain greater proximity when brood size is smaller (Schindler and Lamprecht 1987; Forslund 1993), offspring are younger (Seddon and Nudds 1994), and when foraging in high quality patches (Eberhardt *et al.* 1989; Mulder *et al.* 1995). This study's finding that parents spent more foraging time in proximity with one another than did non-parents, and that cygnets benefited from these behaviors by having increased foraging intensity when both parents, rather than only one, were foraging nearby, suggests that these behaviors are components of parental care in this species. Cygnets have been shown to copy the precise foraging location of their parents and to forage on vegetation paddled to the surface by parents on migratory stopovers and wintering grounds (Earnst and Bart 1991), and although not quantified here, these are likely advantages of foraging near parents in this study also, particularly when foraging on water. An alternate explanation, that parental territories had richer patches of food that allowed closer proximity while foraging, raises the possibility that maintaining high quality territories, rather than maintaining proximity, may be the parental behavior under selection.

Any cost to parents of foraging near one another was not detectable in feeding intensity, and in fact, parents may have benefited from proximity to one another since parents fed more intensely when feeding near their mate than at other times.

Activity Cycle

Data from Trumpeter Swans (*Cygnus buccinator*) and geese indicate that, compared with adults, young have longer foraging bouts (Giroux *et al.* 1986; Grant 1991) and spend more time foraging (Giroux *et al.* 1986; Bregnballe and Madsen 1990; Grant 1991; Sedinger *et al.* 1995). Tundra Swan parents had longer foraging periods than non-parents, which suggests that parents may adjust their activity cycle according to cygnets' needs. The longer foraging bouts of cygnets may result from their lower foraging efficiency and greater nutritional requirements. Nutrient intake of geese and swans is limited by processing rate and gut capacity as well as by time available for foraging (Sedinger and Raveling 1988; Squires 1991; Manseau and Gauthier 1993), so individuals often respond to decreased food availability or foraging efficiency by increasing foraging bout length (Drent and Swierstra 1977; Sedinger and Raveling 1988).

Foraging Habitat

Differences between parents and non-parents in habitat use during foraging bouts suggest that habitat use by parents corresponds to the foraging needs of cygnets. Parents spent nearly twice as much time foraging on land as did non-parents.

Several lines of evidence suggest that grazing on terrestrial vegetation is more beneficial to cygnets than foraging on aquatic vegetation. First, cygnets have poorer access to submerged plants than adults because their necks are shorter and they are inefficient at neck-under and tip-up postures for the first few weeks of life (Owen and Kear 1972, pers. obs.). In this study, cygnets dabbled for floating vegetation or grazed on emergent vegetation, but used below-surface foraging methods only one-fourth as often as parents (12% vs. 49% of foraging time on water). Similarly, Grant *et al.* (1994) found that Trumpeter Swan cygnets foraged on submerged vegetation less than adults, and Monda *et al.* (1994) found that young Tundra Swan cygnets grazed on terrestrial vegetation more than older cygnets. The poor foraging performance of cygnets on water is also illustrated by parents treadling vegetation to the surface where cygnets dabbled for it (Earnst 1992a).

Second, cygnets foraged with about the same intensity as their parents during foraging bouts on water, but foraged substantially more intensely than their parents during foraging bouts on land. Similarly, when foraging in nutrient rich patches, goslings of Canada Geese and Lesser Snow Geese (*Chen caerulescens caerulescens*) spent more time foraging and less time moving than when foraging elsewhere (Eberhardt *et al.* 1989; Mulder *et al.* 1995). A direct comparison of cygnet foraging intensity on land ($\bar{x}$ = 0.81) compared to water ($\bar{x}$ = 0.61) was hampered by the high variation in foraging intensity on land, suggesting that further study of a larger sample of broods and territories is needed to understand the benefits to cygnets of foraging on land.

Third, grazing on terrestrial plants involves less search time (Grant *et al.* 1994, pers. obs.) and less energetic cost (Wooley and Owen 1978; Coleman and Boag 1987) than foraging beneath the water's surface, and the protein content of terrestrial forage is probably high shortly after hatching (Sedinger and Raveling 1986). These advantages are presumably more important to rapidly growing cygnets than adults because cygnets have higher protein demands, and their growth rate and survival may be limited by plant nutrient levels, as is true of arctic-breeding geese (Sedinger and Raveling 1986; Cooch *et al.* 1991a,b; Larsson and Forslund 1991; Sedinger and Flint 1991; Lindholm *et al.* 1994). Although the caloric and protein content of aquatic and terrestrial forage have not been compared at this study site, results from other studies suggest that aquatic plants, although high in caloric content, lack the protein content of newly grown sedges (*Carex* spp.) (Clausen 1994; Prop and Deerenberg 1991).

When feeding on land, parents did not accrue any advantage in foraging intensity relative to foraging on water. In fact, parents fed less intensely and spent more time in head-up behaviors than when foraging on water, probably due in part to (1) the need for greater vigilance on land where cygnets are more vulnerable to predators, and (2) greater forage quality allowing more time for parental care. Similarly, Mulder *et al.* (1995) found that when Lesser Snow Geese foraged in high-biomass patches compared to control plots, parents fed for shorter periods, spent more time vigilant, and moved less rapidly which likely reduced distances between adults and goslings, and that these differences were more pronounced in parents than non-parents.

Vigilance

Parents were in an alert posture more often than non-parents and tended to spend more time in head-up behaviors. Parents are known to be more vigilant than non-parents in several species of waterfowl and shorebirds (Table 1). Vigilance probably functions to detect conspecific territorial intruders and predators. Cygnets were primarily at risk of predation by Snowy Owls (*Nyctea scandiaca*), Arctic Foxes (*Alopex lagopus*), and Parasitic Jaegers (*Stercorarius parasiticus*). Vigilance presumably enabled parents to detect predators earlier, allowed more time to respond appropriately, and thus decreased the risk of predation to cygnets.

In most studies reviewed in Table 1, increased time spent vigilant by parents relative to non-parents was accompanied by decreased time spent feeding or resting, suggesting that there is a trade-off being made by parents. Similarly, when parents encountered higher food availability, they tended to reduce time spent foraging while increasing time in vigilance (Sedinger *et al.* 1995; Mulder *et al.* 1995). In this study, parents spent more time in vigilance and less time sleeping/preening. Parents did not spend less time in feeding behaviors or feeding bouts, but they fed less intensely during foraging bouts than did non-parents.

Territory Defense

Tundra Swan parents, like those of other northern-breeding swans, typically maintain territories throughout brood-rearing. One advantage of territoriality during brood-rearing is thought to be the exclusive use of a foraging area for cygnets. In breeding populations of Black Swans (*Cygnus atratus*) and Black-necked Swans (*Cygnus melancoryphus*) where parents do not defend exclusive foraging areas, young are continually driven from foraging sites by conspecifics, and incur high mortality as a result (e.g., Braithwaite 1981; Schlatter *et al.* 1991).

Parents spent significantly more time interacting with other swans than did non-parents. This larger effort by parents can be interpreted as a form of parental care (given the probable benefit to cygnets). Increased time spent interacting by parents may be influenced, in part, by higher quality territories and therefore greater attractiveness of their territories to intruders, but the need to maintain a high quality territory is also a form of parental investment. In other studies of geese and swans, parents attacked or threatened conspecifics more frequently than did non-parents (Schindler and Lamprecht 1987; Bregnballe and Madsen 1990) and were dominant to non-parents during breeding (Lazarus and Inglis 1978; Mulder *et al.* 1995) and non-breeding seasons (Boyd 1953; Raveling 1970; Scott 1980; Black and Owen 1989a,b; Earnst and Bart 1991).

Although exclusive use of a foraging area is likely beneficial to cygnets, they may also incur costs of territoriality if left alone during interactions. Unattended cygnets are at risk of predation but may also risk being separated from their parents and adopted by the intruding pair as has been reported in Whooper Swans (Rees *et al.* 1990) and Mute

Swans, *Cygnus olor* (Minton 1968; Bacon 1980). Tundra Swan parents minimized these threats by a clear division of labor during interactions: one parent, sometimes in a hiding posture, remained with the brood while the other engaged the intruder. The division of labor did not appear to be sex-specific since male and female parents were observed in each role and spent similar amounts of time interacting. During segments of the brood-rearing period during which one mate was undergoing complete wing molt and the other was not (six days on average), the fully-feathered parent assumed all territory defense (Earnst 1992b). The division of labor was evident in the larger proportion of time that parents spent in asynchrony during interactions compared to that of non-parents.

In conclusion, comparisons with non-parents indicated that parents provided young with substantial parental care during the pre-fledging period. Parents spent more time in vigilance and in territory defense, more foraging time on land where cygnets foraged more efficiently than their parents, and more of their foraging time near one another and thus near their cygnets.

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Parental Care Behavior and Double-brooding in Coscoroba Swan in Central Chile

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Abstract.—The behavior of individuals in twelve Coscoroba Swan (*Coscoroba coscoroba*) families was observed from 24 October to 13 November 2000 and 6–18 January 2001 at four locations in the El Yali wetland, located about 200 km south of Santiago, Chile. In all families, both parents were vigilant and aggressive toward conspecifics and, in one location, territories were defended throughout the season. In most cases, both parents still accompanied their first broods until the end of the study period, when the oldest broods were four to five months old and flying. Males spent less time feeding than cygnets, and spent more time in aggressive activities than females. Two females began incubating a second clutch 40–50 days after hatching broods of eight and seven cygnets, with second broods containing seven and three cygnets, respectively. In both of these families, the male accompanied the first brood while the female incubated the second clutch. In the first case, both parents were aggressive towards the first brood and preferentially accompanied the second brood, whereas in the other case, the first and second broods formed one large family accompanied by both parents. These two families, especially the male parents, differed in the percentage of time spent in a number of activities. The overall activity pattern of one pair differed depending on whether they were attending one or two broods. Further study is needed to document the frequency of double-brooding, the ecological and social factors that favor it, and parental care of first broods.

Key words.—Coscoroba Swan, *Coscoroba coscoroba*, double-brooding, parental care.

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Coscoroba Swans (*Coscoroba coscoroba*) are one of two species of swans found in South America, breeding from Tierra del Fuego north to central Chile, northern Argentina, Uruguay, and southeastern Brazil (Wilmore 1979; Vaz-Ferreira and Rilla 1991; del Hoyo *et al.* 1992). This species differs in a number of ways from other swan species, including a flattened bill, feathering between the eyes and bill, lack of a typical "triumph ceremony," copulation in shallow water, and distinctive patterning of the downy young (Johnsgard 1965). Because of the distinguishing characteristics of Coscoroba Swans, the relationship of this species to other swans has been of interest. Recent morphological (Livezey 1996) and genetic studies (Zimmer *et al.* 1994) suggest that Coscoroba Swans are basal to the true swan group, and are most closely related to the Cape Barren Goose (*Cereopsis cereopsis*) (Harvey 1999).

Behavioral traits have been used successfully to describe waterfowl taxonomy (Lorenz 1971), and can also suggest the importance of environmental influences. One area of Coscoroba Swan behavior that has not been studied, and which may contribute to understanding these influences on the evolution of behavior, is parental care. Parental care in the swans typically includes strong defense of the young, care by both parents and prolonged family bonds (Kear 1972; Wilmore 1979). Little information is available specifically for Coscoroba Swans; limited captive studies suggest that both Coscoroba Swan parents are very defensive of their broods and territories (Kojima 1978). In wild birds, both parents have been noted with the young, and double-brooding has been reported but not well-described (Wilmore 1979). The objective of this study is to begin to document the breeding behavior of this species in the wild. This information is valuable for comparative purposes and for the conservation of this relatively recently-established breeding population of Coscoroba Swan in the central region of Chile.

STUDY AREAS

Behavioral observations were conducted at four study areas within approximately ten km of each other in central Chile. All of these shallow wetlands are included in the El Yali Ramsar site located about 200 km southwest of Santiago, Chile (33°47'S, 71°23'W). The wetland complex is located in the sub-humid Mediterranean region, which has hot, dry summers and cold, rainy winters (further described in Vilina and Cofre 2000). Seven wetlands support breeding waterfowl in the El Yali site, and all were periodically searched for breeding Coscoroba Swans. We estimate that 50 adult Coscoroba Swans were present in El Yali during the 2000–2001 breeding season. This area represents a northern range extension in Chile for breeding Coscoroba Swans, with birds first recorded breeding here in the late 1980s. The next closest breeding pairs are several hundred km to the south (Vilina 1994). All breeding pairs present in the wetland complex were observed during the study, except for one brood found in a wetland that dried early in the study. Behavioral data were collected on six breeding pairs (including two with double broods) at Laguna Cabildo, which has several small islands used for nesting; two breeding pairs at Tranque Los Molles, a large lake formed by a dam; three breeding pairs at Laguna El Rey, a large lake with an extensive flooded marsh present early in the breeding season; and one family at Laguna Matanzas, a large lake close to Laguna Cabildo that is ringed by emergent vegetation (*Scirpus* sp., *Typha* sp.).

METHODS

Families were observed through binoculars and spotting telescopes at distances of 30–500 m during 0.5-h to 2-h observation periods from 24 October to 13 November 2000 and 6–18 January 2001. Of the 146 observation periods, 75% were 1 h in length, 18% were 0.5–1 h, 4% were 2 h, and 3% were less than 0.5 h. Observation periods shorter than 30 min resulted when an entire family or both parents moved out of sight. During observation periods, individuals were out of sight for a total of only 1.6% of the time. Instantaneous focal animal sampling (Altmann 1974) was used to record the behavior of cygnets, juveniles, and male and female parents every 30 s during observation periods. Behavioral categories recorded were alert posture (neck stretched upwards), feeding, moving, preening or bathing, loafing or sleeping, and social behavior (aggression, nest-building, and vocalizing). Definitions of these categories follow those of other waterfowl studies (Lazarus and Inglis 1978; Sedinger and Raveling 1990). Other categories of behavior and any aggressive interactions were recorded whenever they occurred. Aggressive interactions included time spent in the *wings-up* posture (Johnsgard 1965) in addition to chases and fights.

Because all brood members typically engaged in the same behavior at the same time, their behavior was recorded as that of the majority of brood members, with cygnet and juvenile behavior recorded separately. Male and female adults were distinguished by comparing calls, body size, head shape, neck length, and bill length relative to head length (Nascimento *et al.* 2001). Ages of cygnets and juveniles were estimated by comparing plumage features and body size to broods of known ages (first observed soon after hatch), and by referring to descriptions for captive birds (Kojima 1978). Observations were made on all families present on each of four wetland study areas, with families observed simultaneously by different observers or the focal family chosen at random. Observations were carried out from 07.30 to 18.00 h, and an attempt was made to observe each family at all times of day, every 3–4 days.

Data from each observation period were used to calculate the mean percentage of time spent in the activity categories for the male parent, female parent, cygnets, and juveniles in each family. The means for each family were then averaged to obtain overall means and standard errors. For families with a first or single brood, the means for males, females, and cygnets were compared separately for each behavior category (feeding, moving, preening/bathing, sleeping/loafing) using a Friedman's test, with families defined as blocks and family members as the treatments. If the Friedman's test was significant, it was followed by a Tukey-type multiple comparisons test for nonparametric data (Zar 1999) to identify differences between family members. Wilcoxon matched-pairs tests were used to determine differences between males and females of a pair in the time spent in alert posture and aggressive behavior.

For families with two broods present, the means for males, females, juveniles, or cygnets were compared between families using a Spearman's correlation test rather than a Friedman's test, as suggested by Zar (1999) when the number of blocks (families) is two. The lack of a significant correlation (lack of similarity in behavior pattern) was followed by Mann Whitney U-tests, using each observation period as the sampling unit, to identify any significant differences between families for each behavior category and family member. Similarly, Spearman's correlation tests were used to identify differences in overall behavior patterns when males and females were tending one or two broods. The lack of a significant correlation was followed by Mann Whitney U-tests, using each observation period as the sampling unit, to identify any significant differences between first and second broods for each behavior category and parent.

RESULTS

Twelve swan families were observed for a total of 132 h during the 2000–2001 breeding season. Eleven families (first broods) were observed from 3.5 to 18.5 h ($\bar{x}$ = 9.45 ± 5.4 h), and the two pairs with second broods were observed for an additional 14.5 and 12 h. One family at Tranque Los Molles was only observed for 1 h, and was excluded from the analyses. Nine broods were approximately 25–45 days old when first observed in the week of 24 October (N = 8) or 9 January (N = 1); two broods were 1–7 days old when first observed on 30 October and 10 November, respectively. Two pairs produced two broods, and the second broods were approximately 30 days old when first observed on 6 January. Average size of first broods was 5.5 ±

3.6 (range 1–8, N = 11). One second brood had three young and the other seven. Three parents were noted to be flightless (primary feathers molted) during the study period: a male parent with one-week-old cygnets on 30 October, and the male and female parents of four-month-old juveniles on 6 January. Cygnets could fly at about 90 days, and were considered juveniles at that time. Of the original 12 families, four could not be relocated (two disappeared, two suspected to have broken up) and eight were still together at the end of the study period in mid-January when the oldest juveniles were 4–5 months old.

For first or single broods, family members differed in the mean percentage of time spent feeding (Friedman's $\chi^2_{3,\,11} = 7.82$, $P < 0.05$), with males differing significantly from cygnets (Tukey's, $q_{3,\,11} = 3.92$, $P < 0.05$, Table 1). Family members did not differ in the mean percentage of time spent moving, preening/bathing, or loafing/sleeping (Friedman's $\chi^2_{3,\,11} = 0.73$, 3.82, 2.36, all n.s., Table 1). Males spent significantly more time in aggressive activities than females (Wilcoxon $T = 3$, $N = 11$, $P < 0.01$), but there was no significant difference between the sexes in time spent in alert postures ($T = 28$, $N = 11$, n.s., Table 1). Almost all aggression was directed at conspecific adults. Males of three families and females of two of the same families spent time working on old nests, but the sample size was too small to test for differences in nest-building activity between the sexes. One of these pairs later re-nested.

Two pairs produced two broods during the 2000–2001 breeding season. Females began to incubate second clutches around 27 and 30 October, when their first broods were approximately 40 d and 50 d old, respectively. In family 1, the seven cygnets hatched from the second nest were cared for by both parents, who became aggressive towards their first brood of eight juveniles. In family 2, three cygnets hatched from the second nest, and all offspring were accompanied by both parents, with little aggression displayed towards the first brood of seven juveniles. Each clutch was incubated for about 35 days, and both males accompanied and defended the first broods while females incubated the second clutches. Males also stood guard near nests when females were feeding or bathing during incubation recesses.

The two double-brooded families differed considerably from each other in the time that they spent in various activities when two broods were present (Table 2), consequently, there were no significant correlations between the two families in mean time spent in behavior categories for males, females, juveniles, or cygnets (Spearman's correlation, r = 0.07, 0.25, 0.1, and 0.1, respectively, N = 7 behavior categories, all n.s.). Males of the two families differed significantly in proportion of time spent alert, feeding, moving, preening, and loafing (Mann-Whitney U = 150, 143, 160, 143, 167, respectively, $N_1 = 15$ and $N_2 = 12$ observation periods, all $P < 0.01$, Table 2). Females and juveniles of the two families differed in the proportion of time spent moving and loafing (Mann-Whitney U = 139 and 144 for females, and U = 154 and 150 for juveniles, $N_1 = 15$ and $N_2 = 12$, all $P < 0.01$),

Table 1. Mean percentage of time (±SE) spent by male parents, female parents, and cygnets in various activities for all eleven Coscoroba Swan families with single or first broods. A mean was first calculated for each family, then these values were averaged to give the means and SEs presented below.

Family member	Alert	Feed*	Move	Preen/bathe	Loaf/sleep	Aggression**	Nest-building
Male	15.5 ± 2.91	^{a}14.2 ± 2.17	27.6 ± 6.12	21.8 ± 3.34	17.7 ± 5.16	8.2 ± 0.96	0.40 ± 0.37
Female	16.5 ± 3.06	^{ab}18.1 ± 2.93	26.3 ± 6.28	18.8 ± 3.35	15.7 ± 3.11	4.3 ± 1.00	0.25 ± 0.17
Cygnet	0.16 ± 0.07	^{b}32.9 ± 6.48	26.4 ± 5.41	16.9 ± 3.46	23.8 ± 5.23	0	0

*Significant difference ($P < 0.05$) among family members in behavior indicated, based on a Friedman's test. Different letters indicate a significant difference between specific family members based on a Tukey's multiple comparison.

**Significant difference ($P < 0.05$) between males and females in behavior indicated, based on a Wilcoxon test.

Table 2. Mean percentage of time (±SE) spent by male parents, female parents, cygnets, and juveniles (young capable of flight) for two families (denoted as 1 and 2) with double broods. Family 1 had seven cygnets in its second brood and eight juveniles in its first (N = 15 and 7 observation periods, respectively). Family 2 had three cygnets in its second brood and seven juveniles in its first (N = 12 and 8 observation periods, respectively).

Family member	Alert	Feed	Move	Preen/bathe	Loaf/sleep	Aggression	Nest-building
Both broods:	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE
Male 1	*17.7 ± 3.1	*9.8 ± 4.2	*6.0 ± 1.9	*40.0 ± 6.2	*15.1 ± 4.8	9.5 ± 4.5	1.9 ± 1.6
Male 2	*6.9 ± 1.4	*23.3 ± 4.8	*35.4 ± 6.2	*17.4 ± 5.9	*0.37 ± 0.25	16.7 ± 6.1	0
Female 1	15.0 ± 2.5	14.4 ± 3.6	*11.1 ± 3.1	28.2 ± 4.1	*20.6 ± 5.5	10.6 ± 2.7	0
Female 2	9.5 ± 2.0	24.7 ± 4.6	*34.7 ± 7.6	21.5 ± 7.2	*1.0 ± 0.4	8.8 ± 3.7	0
Cygnets 1	0.11 ± 0.08	*16.2 ± 5.6	*14.9 ± 3.7	25.5 ± 5.5	*43.4 ± 8.5	0	0
Cygnets 2	0	*43.3 ± 6.7	*38.9 ± 7.6	14.9 ± 5.2	*2.9 ± 1.7	0	0
Juveniles 1	0.97 ± 0.48	33.9 ± 9.2	*9.32 ± 5.5	20.1 ± 6.9	*35.8 ± 10.5	0	0
Juveniles 2	0	38.5 ± 7.1	*40.0 ± 8.4	19.4 ± 7.5	*2.1 ± 1.1	0	0
First brood:							
Male 1[a]	24.5 ± 4.7	10.0 ± 6.0	10.4 ± 2.5	35.4 ± 4.6	11.8 ± 3.9	7.7 ± 2.5	0.24 ± 0.24
Female 1[a]	15.7 ± 3.5	11.3 ± 6.5	3.5 ± 2.6	22.0 ± 4.4	41.7 ± 11.8	4.4 ± 2.6	1.4 ± 0.99
Male 2[b]	7.2 ± 1.6	**4.9 ± 2.5	54.2 ± 8.0	15.0 ± 6.9	**5.3 ± 2.8	13.3 ± 4.8	0
Female 2[b]	27.8 ± 10.0	22.1 ± 10.9	31.4 ± 9.6	5.5 ± 2.0	**12.2 ± 6.0	0.83 ± 0.83	0

*Significant difference ($P < 0.01$) between members of family 1 and 2 in behavior indicated.

[a] Male 1 and Female 1 each showed a significant correlation between mean time spent in activities when they were tending their first and second broods, indicating that their behavior was similar in these two situations.

[b] Neither Male 2 nor Female 2 showed a significant correlation between mean time spent in activities when they were tending their first and second broods, thus differences in individual behavioral categories were tested using Mann-Whitney U tests, as indicated in next footnote.

**Significant difference ($P < 0.05$) in parent's behavior when tending first as compared to second broods in behavior category indicated, based on Mann-Whitney U tests.

and cygnets differed in mean time spent feeding, moving and loafing (Mann-Whitney U = 148, 152, and 158, respectively, $N_1 = 15$ and $N_2 = 12$, all $P < 0.01$, Table 2). When the behavior of each parent with its first brood was compared to its behavior with its second brood, the male and female of family 1 each showed a significant correlation between mean time spent in activities when they were tending their first and second broods (Spearman's correlation, $r = 0.89$ and 0.93, respectively, N = 7 behavior categories, both $P < 0.01$) but male 2 and female 2 did not ($r = 0.43$, n.s., and 0.6, n.s., respectively, N = 7, Table 2). Male 2 spent more time feeding (Mann-Whitney U = 84, $P < 0.005$) and less time loafing (Mann-Whitney U = 79, $P < 0.05$) when accompanying the second brood compared to the first brood (N = 12 and 8 observation periods, respectively, Table 2). Female 2 spent less time loafing (Mann-Whitney U = 81.5, $P < 0.01$) when accompanying the second brood compared to the first brood (N = 12 and 8, respectively, Table 2).

DISCUSSION

Double-brooding is a rare phenomenon in general for waterfowl (Johnsgard 1978; Afton and Paulus 1992). For many species, including the northern swans, double-brooding and even regular re-nesting are precluded by the limited time that resources on the breeding grounds are available, and the need for young birds to be ready for migration (Kear 1972). Double-brooding is more likely to occur in waterfowl species with extended breeding seasons, such as those inhabiting tropical regions or areas where opportunistic breeding occurs when conditions are favorable (Sorenson 1991; Rohwer 1992). For swans, these conditions are most likely to occur in the more temperate ranges of the three southern hemisphere species, the Black Swan (*Cygnus atratus*), Black-necked Swan (*Cygnus melancoryphus*) and Coscoroba Swan. Although data are limited for these three species, nests have been initiated while tending cygnets in captivity (Black Swan and Black-necked Swan, Kear 1972), and more than one brood has been produced in the wild (Black Swan, Bowler in press; Coscoroba Swan, Wilmore 1979; possibly Black-necked Swan, Humphrey *et al.* 1970). Captive Mute Swans (*Cygnus olor*), however, have also been noted to initiate second nests while tending cygnets (Kear 1972), and one case of double-brooding in a wild pair is known (C. M. Perrins, pers. comm.).

The production of as many as four broods in succession for Black Swans appears to be influenced by flexible social relations and male incubation, in addition to an extended breeding season (summarized in Bowler in press). Limited information on the frequency and characteristics of double-brooding in Black-necked Swans, Coscoroba Swans, and Mute Swans make it difficult to identify ecological or social factors that might favor double-brooding in these species. For example, Coscoroba Swans are said to breed twice in succession on small islands in shallow water in an area that borders Brazil and Uruguay (Wilmore 1979). Although the sample size was small in this study, double broods were only produced by pairs nesting on small islands. These pairs also apparently defend their territories year-round (pers. observ.), unlike breeding pairs on the more ephemeral wetlands where no pairs re-nested during this study. The study population represents the northernmost breeders in Chile, and double-brooding has not been noted to date in more southern parts of the Coscoroba Swan range. Cygnets could fly at three months rather than the reported four months for wild birds (Wilmore 1979; Todd 1996), and some family groups started to break up soon after. Only three parents became flightless through molt during brood-rearing, unlike the typical pattern for many swans (Kear 1972). As more examples of double-brooding are documented in Coscoroba Swans (and other species), we will be better able to determine the influence of factors such as the length of the breeding season (as affected by latitude, rainfall, etc.), nesting habitat, territoriality and duration of family bonds on this interesting phenomenon.

The limited results from this study show that, although the two double-brooded pairs initiated second nests around the same date and age of their first broods, they did not show the same behavior once the second brood had hatched. These two families, especially the males, differed in time spent in several activity categories, and most notably, in their cohesion as family groups. It may be that the large size of the new brood of seven cygnets influenced the parents' intolerance of their first eight cygnets, now juveniles, due to limited resources within the territory. These parents did not change their overall activity pattern from their first to second brood, and essentially only attended one brood (the youngest). In contrast, the male parent of three new cygnets, which mixed freely with their seven juvenile siblings, spent less time in alert postures and more time feeding than the other male, possibly due to a decreased risk to the young offspring as they were accompanied by their older siblings (and part of a larger group). The male parent of this brood was particularly aggressive, which may have been influenced by the large number of offspring he was tending. In addition, the behavior pattern of this pair differed when they were tending their first brood and the amalgamated first and second broods.

Although sample sizes were small, this study also provides the first data on parental care and breeding behavior of individual wild Coscoroba Swans. Coscoroba Swan parents were found to be attentive to their broods and remained with them for at least four months. The brood size of eight cygnets, recorded in three of the twelve families, is larger than that usually reported for Coscoroba Swans (Wilmore 1979; del Hoyo *et al.* 1992). Similar to studies on Trumpeter Swans (*Cygnus buccinator*) (Henson and Cooper 1992; Grant *et al.* 1997; Bollinger and King 2002) and Tundra Swans (*Cygnus columbianus columbianus*) (Earnst 2002), cygnets spent a greater proportion of time feeding than parents. However, in contrast to these studies and that of Scott (1977) on Tundra Swans, male and female Coscoroba Swan did not spend as much time in alert postures, but considerably more time in defense of territories and broods. This was especially notable for pairs with two broods. A contributing factor to more frequent aggressive encounters in this study may be the use of Laguna Cabildo by six families, where they nested at fairly high densities on adjacent islands that they continued to defend throughout the study period.

In summary, preliminary data on double-brooding and parental care behavior of Coscoroba Swan indicate that parents provide fairly typical care to their first broods, but can differ with respect to their second. Further study is needed to determine factors favoring double-brooding and to explain variation in parental behavior between first and second broods and among pairs with second broods. Future field work will also examine male and female roles, the influence of brood size and age on activity budgets, territorial behavior, and family cohesion.

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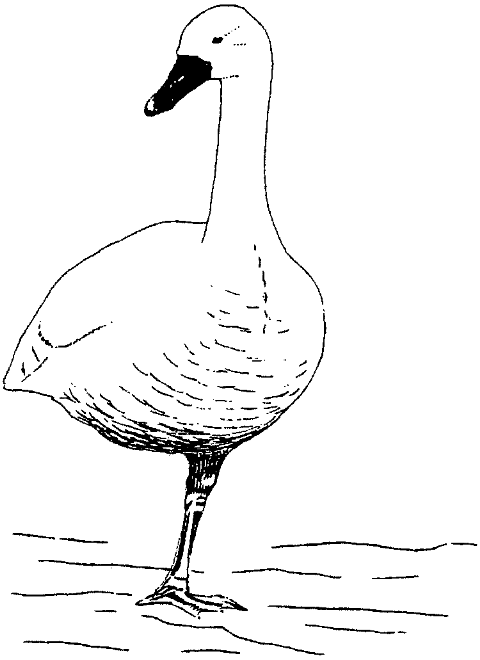

Activity Budgets of Nesting Trumpeter Swans in Interior Alaska

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Abstract.—Activity budgets of wild Trumpeter Swans (*Cygnus buccinator*) nesting in interior Alaska were recorded in 1982 and 1983. Analysis of these time budgets were used to quantify and compare the behavior of females, males and broods during incubation, hatching and brood-rearing. Male behavior changed little during the breeding season; however, they fed less and were alert more during hatching than during either incubation or brood-rearing. Females interrupted incubation sessions only to feed and occasionally to assist males in chasing intruding swans. Females initiated recesses during incubation usually when males were near the nest. Males attended nests during their mates' absence, but were never observed to sit on the eggs. During brood-rearing, behavior of females and males was similar, but cygnets spent more time feeding and resting, and less time preening and being alert, than did parents. Activity budgets are compared to those from other studies of wild Trumpeter Swans and Tundra Swans (*Cygnus columbianus columbianus*) in Alaska.

Key words.—Activity budgets, Alaska, *Cygnus buccinator*, nesting behavior, Trumpeter Swan.

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The first aerial survey of Trumpeter Swans (*Cygnus buccinator*) in Alaska in 1959 documented 1,124 swans (King and Conant 1981). Since then, the number of Trumpeter Swans in Alaska has increased dramatically from 2,847 in 1968, when the first complete survey was flown, to 7,696 in 1980 and 17,155 in 2000 (Conant *et al.* 2002). Birds in Alaska accounted for 76%, 87% and 72% of the continent-wide Trumpeter Swan population during these three surveys, respectively (Caithamer 2001).

In the early 1980s, when this study was initiated, only the general breeding behavior of wild Trumpeter Swans (Banko 1960; Hansen *et al.* 1971), and the detailed breeding behavior of captive birds (Cooper 1979), had been described; no detailed activity budgets for nesting wild Trumpeter Swans existed. This study therefore was undertaken to quantify Trumpeter Swan nesting behavior in a natural setting in interior Alaska (also see Henson and Cooper 1992).

STUDY AREA

The study was conducted on the Minto Flats area (64°54'N, 148°49'W), approximately 65 km west of Fairbanks, Alaska. This area was one of the first known breeding areas in the state, with nesting pairs recorded in 1960 (Hansen *et al.* 1971), and swan densities here have traditionally been one of the highest in Alaska (King and Conant 1981; Conant *et al.* 2002). Classified as boreal forest, the habitat is primarily marsh-wetland <150 m in elevation and is characterized by a myriad of lakes and marshes, including two large lakes (810 ha and 650 ha). Goldstream Creek and Chatanika River flow into Minto Lakes and, along with numerous sloughs and channels, provide boat access to much of the area. Human disturbance of nesting swans in the study area was minimal.

METHODS

Field Methods

Aerial surveys were done (18 May in 1982, 29 April in 1983) after break-up of ice on lakes and rivers to assess nest initiation and select nest sites for observation. The break-up of ice in spring 1982 was very late, whereas in 1983 it was normal or slightly early. After ground investigation to confirm nesting, four territories were selected for observation in 1982 and 1983. Three of the four territories were the same both years. Territories were selected non-randomly to ensure that the pairs were nesting and the sites accessible; all were situated a short distance (0.5–1.0 km) from a navigable slough or channel. Observation sites were reached by sport canoe with outboard motor and by walking the remaining distance. Nesting ponds selected measured 18 ha, 30 ha, 36 ha, 64 ha, and 79 ha in size.

Because ice limited access prior to initiation of incubation, observations began in early incubation and continued through brood-rearing. Earliest observations were made on the seventh day of incubation. Incubation onset was based on back-dating from known hatching dates and assuming a 35-day incubation period (Banko 1960). Observations were made from 3 June to 23 September in 1982 and from 25 May to 29 August 1983. Observations were made using a 15-60× spotting scope at a distance of 75–650 m at ground sites hidden by vegetation from the swans' view. Attempts were made to distribute the 4-h observation periods evenly among nesting pairs, the 24-h daylight period and each reproductive phase (i.e., incubation, hatching and brood-rearing).

Since direct observation into the nest bowl was not possible, hatching stage was estimated from the parents' behavior, seeing females toss egg shells over the side of the nest, glimpses of newly hatched cygnets in the nest, and subsequent observations (i.e., within 1–3 days) showing families behaving as one unit.

Behavioral data were collected for each member of the pair and the brood using continuous observation (Altmann 1974). Time in-view, out-of-view (which included both time on and off the nest pond), behavior, and habitat medium (i.e., nest, land, water and air) were recorded by noting beginning and ending times whenever a change occurred. During incubation and hatching, a swan's location relative to the nest was also recorded. In addition to the quantitative data, descriptive narratives were recorded when relevant (e.g., for interactions), and daily observation summaries were kept. The behavior of the majority of cygnets in a brood was recorded as the brood's behavior when the cygnets were small because they primarily acted as a group. When cygnets were older and behavior differed among them, individual behavior was averaged to obtain behavior for the brood (N = 9 broods).

Age and breeding experience of focal pairs were unknown, since none had previously been marked. Individuals of each pair could be recognized within years, however, by unique feather stain patterns on the head and neck (Cooper 1979). Sex was assigned to each individual of a pair based on behavior (i.e., only females are known to incubate; Banko 1960), and assigned sex was consistent with observations of the timing of molt. In all pairs observed, the individual assigned as the male, based on behavior during incubation, initiated molt of primaries at or shortly before hatching. There was little overlap in flightlessness between pair members, and individuals assigned as females, based on behavior during incubation, were flightless during mid to late brood-rearing. Similarly, three other nesting adults captured when flightless during mid to late brood-rearing were confirmed to be female. Earnst (1992) found this same molt sequence for Tundra Swans (*Cygnus columbianus columbianus*) in northern Alaska, but some studies have also found female Trumpeter Swans to molt first (Hansen *et al.* 1971; and see citations in Earnst 1992).

For the purpose of this study, individuals of pairs occupying the same territory in both years were assumed to be the same even though they were not marked, although our method of data analysis does not require this assumption (see below). Other studies on swans in Alaska indicate that breeding pairs typically occupy the same territory in consecutive years (Trumpeter Swans, Henson and Cooper 1992; Grant *et al.* 1997; Tundra Swans, Earnst 2002). The fact that the same nest bowl was used between years at all territories in this study also supports this assumption.

Behavioral Categories

Incubation terminology follows that of Cooper (1979). He defined incubation constancy as the percentage of time that the female spent on the nest, and termed each period of incubation, a session. Thus, incubation included time spent sitting on eggs (i.e., sitting spells) and time spent standing over the eggs (i.e., breaks or position shifts). Recesses were periods that the female spent off the nest. For the purpose of this paper, female behavior is not presented separately for recesses. Time spent on the nest by the male indicated only sitting or standing on the edge of the nest mound; males were never observed sitting in the nest bowl on the eggs.

Feeding included grazing on emergent vegetation, surface feeding, head dipping, up-ending, and "digging" with the feet (Owen and Kear 1972). All feeding was done in the water except for incidental jabbing at insects by females when incubating. No grazing on land was observed.

Swimming was defined as actively moving in the water, but did not include floating or movement associated with feeding.

Preening was defined as all maintenance activities including preening, bathing, stretching, wing-flapping, head or body shake, scratching, yawning, drinking and defecating.

Alert status usually denoted head up and eyes open, but also included the hiding posture in which the neck was held prone. The hiding posture was assumed by incubating females and molting adults in response to unknown disturbances or other swans.

Resting status usually indicated head prone on the back with eyes open or closed, but also included head relaxed and tip of bill resting on the breast or ground.

Nest maintenance was defined as arranging or adding material to the nest mound; it also included moving material to locations where the female brooded cygnets. The female often added material to the nest site after incubation recesses, and usually arranged nest material around her after she shifted position.

Position shifts occurred when the female stood between sitting spells and invariably resulted in a change of position on the nest and a settling sequence (Cooper 1979). Females often turned eggs during these shifts. During hatching, when the female often stood for extended periods, she draped her wings over the nest, apparently to provide shading. Time spent in nest maintenance and position shifts were combined for analysis in this paper.

Interactions were both interspecific and intraspecific and included displays between members of a pair (see Banko 1960 and Cooper 1979 for descriptions).

Statistical Analysis

Comparisons were made of the proportion of time spent in different habitat media (i.e, nest, land, water and air), different behavior (i.e., feeding, swimming, preening, being alert, resting and other) and during the different stages of the breeding season (i.e., incubation, hatching and brood-rearing) by females, males and cygnets. Weighted multivariate analysis of the ranked proportions were made as a general alternative to the Freidman's and Wilcoxon Signed Rank tests (Iman *et al.* 1984). The proportion of time spent in each medium or activity in each session (N = 188 total sessions of females, males, and broods) was ranked from 1 to the number of categories times N; ties were averaged. Planned comparisons were made using Hotelling's T^2 test (a multivariate F-statistic; Littell *et al.* 1991). This analysis does not take into account the lack of independence between behavioral sessions resulting from the repeated sampling of swan pairs and individuals within family groups (see Hurlbert 1984). Thus, statistical inferences can be made for pairs observed in this study, but not extrapolated to a larger statistical population. Since any inferences to a larger population would be limited by the small number of pairs observed anyway, it seems reasonable to use the multivariate analysis described above and emphasize that results should not be extrapolated to other pairs without further field work and analysis.

Since the SEs from these analyses are based on the ranked transformed data, no SEs are available for the original proportional weighted data presented in the figures and text of this paper.

RESULTS

During two years of study, eight nesting attempts made by five Trumpeter Swan pairs were observed. The 343 h of observations were made during 1982 (47%) and 1983 (53%). Observation bout length (N = 78 sessions on nesting territories) varied from 0.8 to 10 h and averaged 4.4 h ± 1.6 [SD]. Observations during incubation were distributed evenly throughout the 24-h daylight; those during hatching were opportunistic; and those during brood-rearing had fewer samples from 00.00 h–06.00 h due to decreasing day length (Table 1). Total hours of observations per pair varied from 19 to 156 h. Territories 11 and 23 were each occupied for only one of the two years. In 1982, the pair in territory 38 made a renesting attempt and incubated until 8 July, but the eggs failed to hatch. At the beginning of brood-rearing, focal broods varied in size from five to eight cygnets.

Females were in-view 94%, 100%, and 89% of the time during incubation, hatching and brood-rearing, respectively, and males were in-view 71%, 86% and 88% of the time. Cygnets were only slightly less visible (84% of time in-view) than their parents during brood-rearing. The risk of bias due to time out-of-view is low because birds were rarely out-of-view and there was no indication that swans tended to perform some categories of behavior more when out-of-view than in-view, except perhaps for females during incubation. Almost all out-of-view time recorded for females during incubation occurred when birds were on water; but during most of the in-view time on water during incubation, females were either feeding or swimming. Thus, time spent in these categories of behavior might be underestimated during the incubation phase.

Incubation

During incubation, the male usually returned to near the nest before the female left on recess and remained near the nest during her absence. The female covered the eggs with nest material before departing for a recess, except on one occasion when she

Table 1. Distribution of Trumpeter Swan observations throughout the 24-h time period and among nesting pairs during the breeding season at Minto Flats, Alaska, 1982-1983. Values corresponding to time period and nesting pair are percentages of the total hours of observation.

		Reproductive stage			
		Incubation	Hatching	Brood-rearing	Total
Number of observation bouts		38	7	33	78
Total h of observation		178.7	37.6	127.3	343.6
Time period					
00.00–06.00		21.5	13.7	6.3	15.1
06.00–12.00		25.3	11.9	31.1	26.2
12.00–18.00		29.0	51.4	35.1	33.4
18.00–24.00		24.2	23.0	27.5	25.3
Nesting pair	Brood size (1982, 1983)				
11	(6, –)	18.6	31.6	16.5	19.0
13	(7, 7)	44.5	13.3	55.1	45.5
23	(–, 5)	2.2	28.5	4.7	5.5
30	(6, 8)	24.4	26.6	23.7	24.5
38	(0, 6)	10.3	0.0	0.0	5.5

left to help the male chase intruders. On this occasion, the female began a feeding recess after the chase and the male returned to the nest and covered the eggs. None of the males was observed sitting on eggs. During recesses, females spent most time either feeding or swimming and were not observed to rest when off the nest. During incubation, position shifts by females were of short duration and accounted for little of their time (3%). This behavior represented 16% of the female's time during hatching, when they stood over pipped eggs and newly hatched cygnets for longer intervals.

Hatching

Average date of hatching was ten days later in 1982 compared to 1983. Hatching extended from 24–30 June in 1982 (N = 3; $\bar{x}$ = 27 June) and from 14–21 June in 1983 (N = 4; $\bar{x}$ = 17 June).

Seven observation bouts were made during hatching at five nests (i.e., two consecutive observations, within 12–16 h of each other, were made during hatching at two nests). Females were not observed to leave the nest during hatching, except for one, who left to chase an intruding swan swimming near the nest. Direct evidence of hatching (i.e., newly hatched cygnets and/or the female tossing eggshell fragments over the side of the nest) was observed during five of the seven observations. During both observations made on the second day of hatching, some of the cygnets (presumably the first to have hatched) were observed feeding with the male in the water near the nest, while the female remained on the nest with other cygnets. Time spent off the nest and in the water during the second day of hatching varied between 27.6% and 37.6% for individual cygnets that did leave the nest (N = 6 from two broods); this represents a maximum percentage, however, since cygnets spent two separate intervals in the water at both nests and it was not possible to determine if the same cygnet(s) were in the water both times. At least one cygnet was viewed on the nest with the female when others were in the water, and it is assumed that some of the cygnets remained on the nest throughout the observation.

Use of Habitat Medium

Use of the nest, land and water by nesting swans was compared among the three stages of reproduction. Time spent in the air was not included in the analysis since it accounted for <0.5% of all habitat medium use. Both female ($F_{6,356}$ = 36.0, P < 0.0001) and male ($F_{6,356}$ = 2.84, P < 0.01) use differed among the three stages of reproduction (Fig. 1). Time spent on the nest by females was similar during incubation and hatching ($F_{1,180}$ = 0.43, n.s.), but females spent more time on the nest during these stages (>90%) than during brood-rearing ($\bar{x}$ = 12%, $F_{1,180}$ = 168.7, P < 0.0001; $F_{1,180}$ = 81.4, P < 0.0001, respectively). Females spent <9% of their time in the water during incubation and hatching compared to 70% during brood-rearing ($F_{2,180}$ = 84.0, P < 0.0001). Males spent more time on the nest during hatching than during either incubation ($F_{1,180}$ = 11.0, P < 0.001) or brood-rearing ($F_{1,180}$ = 13.9, P < 0.001).

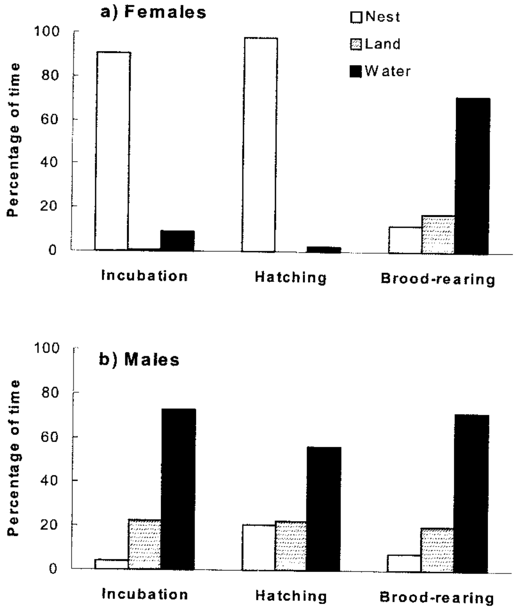

Figure 1. Percentage of time Trumpeter Swan females (a) and males (b) spent on the nest, land and water during the breeding season at Minto Flats, Alaska, 1982 and 1983. Males and females spent <0.5% of time in the air in each stage.

Males spent similar amounts of time in the water during the three stages ($F_{2,180}$ = 0.86, n.s.). Females spent more time than males at the nest during both incubation ($F_{1,180}$ = 186.3, $P < 0.0001$) and hatching ($F_{1,180}$ = 20.7, $P < 0.0001$), but nest use by females and males did not differ during brood-rearing ($F_{1,180}$ = 0.86, n.s.). During incubation, females were usually absent from the nest when their mate was present at the nest. However, during both hatching and brood-rearing, the male was rarely, if ever, on the nest without the female also being present.

Females were rarely observed on land during either incubation or hatching, while males were observed on land one-fifth of the time throughout the breeding season (Fig. 1). Major activities performed on land were preening and resting. No feeding on land was observed.

During brood-rearing, cygnet use of habitat mediums did not differ from that of their parents ($F_{3,178}$ = 1.66, n.s.). The family essentially acted as one unit, especially during early brood-rearing (i.e., 1–4 days after hatching). During observations in early brood-rearing (N = 7), the nest and other land sites were used for resting and brooding the young on ten occasions. The male accompanied the female and cygnets to these sites on nine occasions and stayed with them on eight (on the ninth, the male spent 90 min on the nest compared to 148 by the female). On the one occasion that the male did not leave the water with the rest of the family, he stayed mostly within 25 m of the nest where the female was brooding the cygnets. During all observation bouts, only the female was observed brooding the cygnets.

Behavior

Activity budgets for females and males during each nesting stage are shown in Fig. 2. Only the five major categories of behavior (i.e., feed, swim, preen, alert and rest) are illustrated. Behavioral types not shown include nest maintenance, position shifts, interactions, flying and walking. These categories each accounted for <1% of time-budgets, except for (1) nest maintenance and position shifts by the female during incubation (12%) and hatching (16%) and by the male during incubation (2%), and (2) interactions by the male during hatching (2%).

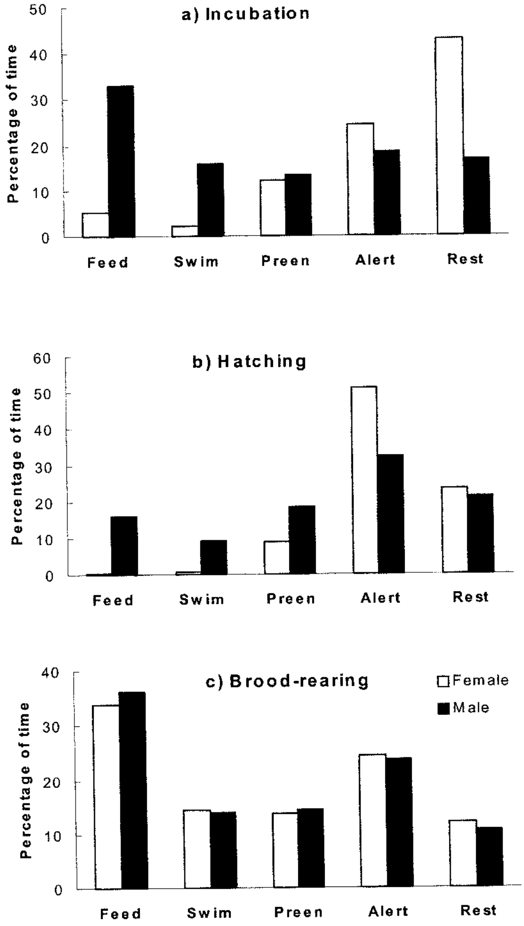

Figure 2. Mean time-activity budgets of male and female Trumpeter Swans during incubation (a), hatching (b) and brood-rearing (c) at Minto Flats, Alaska, 1982 and 1983.

Females fed very little during both incubation and hatching (< 5.3%) and fed slightly more during incubation than hatching ($F_{1,180}$ = 6.08, $P < 0.05$). Females spent significantly more time feeding during brood-rearing (33.9%) than during incubation or hatching ($F_{1,180}$ = 119.9, $P < 0.0001$; $F_{1,180}$ = 89.0, $P < 0.0001$, respectively). Females spent more time alert during hatching ($\bar{x}$ = 51.1%) than during incubation ($\bar{x}$ = 24.3%, $F_{1,180}$ = 8.70, $P < 0.005$) or brood-rearing ($\bar{x}$ = 24.3%, $F_{1,180}$ = 6.38, $P < 0.05$).

Males spent similar amounts of time feeding during incubation (33.1%) and brood-rearing (36.1%, $F_{1,180} = 0.10$, n.s.), but less time feeding during hatching (16.1%, $F_{1,180} = 7.55$, $P < 0.01$; $F_{1,180} = 8.58$, $P < 0.005$, respectively). Males spent more time alert during hatching (32.3%) than during incubation (18.4%, $F_{1,180} = 4.47$, $P < 0.05$). Time spent alert during brood-rearing was intermediate (23.7%) and did not differ from the other stages ($F_{1,180} = 1.34$, n.s.; $F_{1,180} = 1.76$, n.s., respectively).

Female behavior differed significantly from male behavior during both incubation and hatching ($F_{5,176} = 40.0$, $P < 0.0001$; $F_{5,176} = 11.6$, $P < 0.0001$, respectively), but not during brood-rearing ($F_{5,176} = 0.15$, n.s., Fig. 2). Females fed significantly less than males during incubation and hatching ($F_{1,180} = 112.8$, $P < 0.0001$; $F_{1,180} = 23.9$, $P < 0.0001$, respectively). Females rested significantly more than males during incubation ($F_{1,180} = 25.5$, $P < 0.0001$), but not during hatching ($F_{1,180} = 1.52$, n.s.). Time spent being alert did not differ between females and males during incubation, hatching, or brood-rearing ($F_{1,180} = 2.19$, n.s.; $F_{1,180} = 1.52$, n.s.; $F_{1,180} = 0.37$, n.s., respectively).

Cygnet time-budgets differed significantly from that of parents during brood-rearing ($F_{5,176} = 32.7$, $P < 0.0001$, Fig. 3). Cygnets fed and rested more ($F_{1,180} = 4.02$, $P < 0.05$; $F_{1,180} = 8.14$, $P < 0.005$, respectively), and spent less time alert ($F_{1,180} = 77.6$, $P < 0.0001$).

DISCUSSION

Successful reproduction requires that parents balance the needs of embryos and young with their own needs of survival and future fitness (Afton and Paulus 1992). Trumpeter Swans are territorial throughout the breeding season and are highly attentive to eggs during incubation and cygnets during brood-rearing (Cooper 1979; Mitchell 1994). As in most waterfowl species with long-term monogamy, there is the opportunity for division of labor between the sexes in Trumpeter Swans (Henson and Cooper 1992). Female waterfowl tend to expend energy on egg production and incubation (Alisauskas and Ankney 1992; Sedinger and Raveling 1990), while males expend energy on vigilance and defense of the female, eggs, nesting territory and their young (Oring and Sayler 1992).

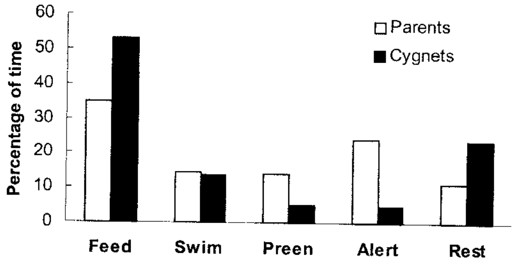

Figure 3. Mean time-activity budgets of Trumpeter Swan parents and cygnets during brood-rearing at Minto Flats, Alaska, 1982 and 1983.

High incubation constancy may serve to maintain adequate egg temperature, shorten the incubation period and minimize egg predation (Owen and Black 1990; Afton and Paulus 1992). Incubation constancy (i.e., time spent on the nest during incubation) in this study (91%) was similar to constancy rates for female Trumpeter Swans in southern Alaska (88%, Henson and Cooper 1993); both are higher than for female Tundra Swans in western Alaska (81%, Scott 1977) and northern Alaska (60–79%, Hawkins 1986). All Tundra Swan males in both studies, and at least some Trumpeter Swan males in southern Alaska, sat on eggs. Resulting pair constancy rates (i.e., males plus females) for Tundra Swans (97–99%, Scott 1977; Hawkins 1986) exceeded the time Trumpeter Swan females spent on the nest at both Minto Flats and in southern Alaska. The more moderate climate of Minto Flats in comparison to the cool maritime climate of southern Alaska and the arctic climate of northern Alaska might help to explain why males participated in incubation at other areas but not at Minto Flats.

Efforts to maximize embryo development rates during incubation are compromised by the need for females to feed in order to maintain energy reserves (Afton and Paulus 1992). Female feeding rates (5%) during incubation at Minto Flats were similar to those in other studies of Trumpeter Swans (8%) (Henson and Cooper 1992; Grant *et al.* 1997) but lower than those for Tundra Swans (15–

29%) (Hawkins 1986) in which males share in incubation. Similarly, male feeding rates during incubation at Minto Flats (33%) were similar to those in other studies of Trumpeter Swans (36%, Henson and Cooper 1992), and only slightly lower than those of Tundra Swan males (38–43%, Hawkins 1986).

Because females at Minto Flats fed almost entirely in their nest ponds, they usually swam (84%, N = 75 recesses), and only occasionally flew, to and from feeding sites during incubation recesses. In contrast, Tundra Swan females on the North Slope flew to and from feeding sites on their territory during 90% of recesses (Hawkins 1986), suggesting that food resources may have been further from nests there than at Minto Flats or that male incubation allows females to move further from nest sites. As a result, females at Minto Flats may have needed to expend less time and energy to meet nutritional requirements.

Females at Minto Flats increased their feeding rates from incubation (5%) to brood-rearing (33%), as did females at the Copper River Delta (8% to 30%, respectively; Henson and Cooper 1992). Male feeding rates did not differ significantly between incubation (34%) and brood-rearing (36%) in this study or at the Copper River Delta (36% and 31%, Henson and Cooper 1992). Although one would expect females to spend more time feeding than males during brood-rearing in order to replenish reserves lost during egg-laying and incubation, Trumpeter Swan females did not feed significantly more than males during brood-rearing in this study or at the Copper River Delta (67.6 versus 62.3%) (Grant *et al.* 1997).

If the male's major role is territory defense and protection from predators, one would expect the male to spend more time alert and in interactions than the female. Consistent with this idea, other studies of Trumpeter Swans (Henson and Cooper 1992) and Tundra Swans (Hawkins 1986) found that males spent significantly more time alert than females during incubation. However, in this study at Minto Flats, females spent as much or more time in alert posture as males throughout the nesting season. It is possible that our interpretation of alert posture (defined as head-up) may have differed from that of Henson and Cooper (1992) (defined as head-up and extreme head-up).

Time spent feeding by cygnets in this study (52.9%) is almost identical to that reported by Grant *et al.* (1997) for Trumpeter Swan cygnets in southern Alaskan (52.7%). Cygnets in this study spent over 80% of the their time in self-maintenance activities (feeding, resting and preening), compared to 60% by parents. In contrast, parents were alert more than five times as much as were cygnets.

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Laying and Incubation Behavior of Captive Trumpeter Swans

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Abstract.—Trumpeter Swans (*Cygnus buccinator*) do not develop a brood patch as do most other species of waterfowl. Observations of three pairs of captive breeding Trumpeter Swans, which were uncharacteristically non-aggressive, showed that they incubated with their feet on top of the eggs. In addition, two instances of egg-laying were witnessed at close range and are described here. First view of the egg in the cloaca to final emergence took just over two minutes. Trumpeter Swans lay very small eggs in proportion to their body size, and their large feet can theoretically cover 5.7 eggs. It is suggested that Trumpeter Swans are able to regulate blood flow to their feet and provide effective incubation.

Key words.—*Cygnus buccinator*, incubation with feet, egg-laying, Trumpeter Swan.

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The females of most species of Anatidae lose their belly feathers and molt their down into the nest just before incubation begins. Hanson (1959) described this process in detail for geese. The down provides a well insulated layer beneath and around the eggs during incubation and particularly during recesses from the nest when the departing female covers the eggs. The majority of birds develop thickened epidermis, edema leading to general flabbiness, and an increase in vascularization of the belly area. These brood patches facilitate heat transfer to the eggs (Drent 1975; Afton and Paulus 1992). There are exceptions to this generalized behavior. Trumpeter Swans (*Cygnus buccinator)* retain the feathers and down on the belly throughout incubation (Mitchell 1994). Scott (1964) reports that tree ducks (*Dendrocygna* spp.) do not have down in their nests, and one can infer that they also do not develop a brood patch. Similarly, Pelecaniform birds lack a brood patch and must modify their incubation behavior. For example, the Northern Gannet (*Morus bassanus*) lays a single egg which it clasps between its feet which become highly vascularized (Nelson 1966). The Red-footed Booby (*Sula sula*) on tropical Midway Island covers its eggs with the webbing between the first and second toes of each foot (Howell and Bartholomew 1962). Here it is suggested that Trumpeter Swans are able to regulate blood flow to their feet and provide effective incubation.

METHODS

During 1999 and 2000, three captive Trumpeter Swan nests in Ontario were checked regularly and the position of the feet relative to the eggs was noted. Detailed observations of egg-laying were made from close range (35 m with binoculars) at a nest built in 2000 by captive Trumpeter Swans. The area of the feet of four female swans was measured by spreading them on paper backed with plywood and tracing the outline. The longitudinal cross-section of an egg was measured by tracing the outline of the egg on a sheet of paper.

RESULTS

Observations of Egg-laying

In 2000, a female Trumpeter Swan nested on a raft 35 m from the window of my study. She laid her first egg on 16 May and her second on 18 May in light rain and 14°C. After standing on the nest for a while rearranging material, she settled on the nest facing three-quarters away so that the whole posterior part of her body was visible. She rested her upper breast on the edge of the nest, moved her feet to the center, spread her tarsal joints and raised the posterior part of her body. She appeared to push with her legs as the posterior part of her body was slowly raised and lowered. The cloaca opened slightly and the egg was visible; it took 138 seconds for the egg to drop into the nest. The blunt end of the egg emerged first and the white color of the shell over the air cell clearly demarcated it from the very pale pinkish opaque color of the remainder of the moist egg. After the egg emergence she stood up, turned and poked at the nest material at the bottom of the nest bowl. She did not touch the egg, which remained in full view. The egg was laid at 09.18 h and at 09.25 h she started to move material over the nest bowl. At 09.39 h, the egg was no longer visible, and she preened particularly on the lower belly and around the cloaca. At 10.40 h, she was asleep, standing on the nest. The male stood on the raft beside the nest throughout.

On 20 May at 05.14 h, the female was sitting on the nest. At 05.43 h, she reversed her position on the nest, facing so that the posterior part of her body was not visible. At 06.42 h, she began reaching down to the bottom of the nest to pull up nest material to the rim. Ten minutes later a nest check revealed three eggs. At 19.27 h, on 21 May, the female rearranged nest material very vigorously for eight minutes, sat down for two minutes and then stood and began rearranging nest material again. She then settled on the nest facing three-quarters away. The cloaca opened at 19.39 h and the egg became visible. In 130 seconds, the egg dropped into the nest. She rearranged nest material for some time and was asleep on the nest at 20.30 h. By 19.21 h on 23 May, the nest contained five eggs.

Observations of Incubation

In 1999, a captive pair of Trumpeter Swans at Aurora, Ontario, was observed during incubation. The pair proved to be uncharacteristically docile in defense of their nest during nest checks and did not threaten or attack. On 4 June, the female had to be lifted to count the eggs. During subsequent nest checks, one foot was spread on top of the eggs once and both feet were spread on top of the eggs during two checks. The eggs were preyed upon approximately 2 weeks after completion of laying.

In 2000, a second female nested near the window of my study and laid her first and second egg on 16 and 18 May, as described in the previous section. When checked at 19.21 h on 23 May the nest had 5 eggs; the female stood and hissed, revealing that her feet were on top of the eggs. Six additional nest checks (25 May–18 June) each revealed that she was incubating with her feet on top of the eggs. Meanwhile the male remained passive either on or beside the raft. In the last few days of incubation, the female spent much time standing on the eggs and presumably incubating them. She hatched one cygnet on 29 June.

In addition, at a nest on the MacJohnston Wildlife Management Area in Ontario, during each of six nest checks between 26 May and 9 July, the female had her feet on top of the eggs.

The average area of the foot of the four adult females measured in this study was 184.8 cm^2 (±7.8 [SD], N = 4), and the average longitudinal cross section of the thirteen eggs measured was 64.7 cm^2 (±8.5 [SD], N = 13).

DISCUSSION

Birds have some ability to increase their body temperature by adjusting their metabolic rate (Kilgor and Schmidt-Nielson 1975) and by regulating blood flow to the brood patch (Haftorn and Reinertsen 1982). It seems likely that Trumpeter Swans are making similar adjustments to their feet during incubation. Several known mechanisms may improve the efficiency of incubation by Trumpeter Swan feet. First, Trumpeter Swans lay very small eggs in proportion to their body size; a clutch of six eggs weighs only 19–20% of the female's weight. A single egg averages about 3.3% of the female's body mass (Mitchell 1994), compared to 4.7% for the Hudson Bay Lowland Canada Goose (*Branta canadensis interior*), 6.7% for the Brant (*B. bernicla*) (Raveling and Lumsden 1977), 8.4% for the Common Goldeneye (*Bucephala clangula*), and 11.1% for the Hooded Merganser (*Mergus cucullatus*) (H. G. Lumsden, unpubl. data). This trend is consistent with the tendency of larger avian species to lay smaller eggs relative to other species in the same taxa (Lack 1968). Given the longitudinal cross-section of a Trumpeter Swan egg (64.7 cm^2) and the area of a female's foot (184.8 cm^2), both feet could theoretically cover 5.7 eggs at one time if there is little space between the eggs. Second, Drent (1975) noted that the growing embryo in a Herring Gull (*Larus argentatus*) egg was located on the upper surface of the yolk close beneath the shell. The rotation of the yolk under the influence of the chalazae in Mute Swan (*C. olor*) eggs opened to examine the state of incubation, was so fast that the embryo was almost continuously at the top and therefore closest to the source of incubation heat (Afton and Paulus 1992; H. G. Lumsden, unpubl). Third, Howey *et al.* (1984) showed that there was a temperature gradient in the vertical plane in the nest bowl of the Black Swan (*C. atrata*) and Whooper Swan (*C. cygnus*). Heat for the embryos, therefore, was concentrated where it was needed.

Observations from several species indicate that male swans sometimes incubate, and since males do not possess brood patches, it is likely that males incubate with their feet. Cramp *et al.* (1977) cited a report that a male Mute Swan incubated successfully after the death of the female. Black Swan males undertake more than half the incubation duties (Brugger and Taborsky 1994). Hawkins (1986) and Scott (1977) reported that a male Tundra Swan (*C. columbianus columbianus*) sat on the nest consistently during the incubation period when the female left on recess. Hawkins, however, reported that an artificial egg cooled while the male incubated but much more slowly than when he did not sit. Finally, Trumpeter Swan males incubate approximately 1–1.75% of the time (Mitchell 1994).

These observations of Trumpeter Swans incubating with their feet is based on a small number of females. Thus, it would be useful, where circumstances permit, if observers recorded the position of the feet relative to eggs on nest checks.

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Restoration of Trumpeter Swans in North America: A Century of Progress and Challenges

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Abstract.—By the beginning of the 20th Century, North America's once widespread and abundant populations of Trumpeter Swans (*Cygnus buccinator*) had been devastated by overharvest and were nearing extinction. By the close of the century, due to growth of remnant populations and restoration efforts, over 23,000 Trumpeter Swans existed in the wild. Large portions of vacant historic breeding habitats in Canada and the United States remain suitable for future reoccupation, however, traditional migration patterns to southerly wintering areas have been disrupted, winter habitat has been reduced in quantity and quality, and some populations that depend upon marginal winter habitat are vulnerable to high winter mortality. To maintain current populations and allow for growth, we recommend protecting and improving current winter habitat, creating new wintering sites, and developing methods to establish use of these areas. Particular emphasis should be placed on using the National Wildlife Refuge System to provide secure focus areas for expansion of migration and winter distribution and exploring ways to create additional wintering habitat in partnership with agricultural interests.

Key words.—Migratory traditions, remnant populations, restoration, Trumpeter Swans, winter habitat, *Cygnus buccinator*.

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Although Trumpeter Swans (*Cygnus buccinator*) were widespread and abundant in North America prior to European settlement, they were rapidly eliminated by commercial and subsistence harvest. Commercial harvest for swan skins across the heart of their Canadian breeding range, from about 1772–1903, caused much of the decline (Banko 1960; Houston *et al.* 1997). Habitat loss may have also contributed to extirpation in some localities; however, in most areas Trumpeter Swans were eliminated long before substantial habitat alteration occurred (Banko 1960; Lumsden 1984; Whittam and Lumsden 1995; Rogers and Hammer 1998). By 1900, the species had been reduced to three remnant breeding populations, totaling only 1,000–2,000 birds, with most surviving in Alaska (Pacific Coast Population) and perhaps no more than 200 in Canada (Western Canada Population) and the contiguous United States (Greater Yellowstone Population) (Banko 1960; Hansen *et al.* 1971; Gale *et al.* 1987; Oakleaf *et al.* 1996).

By 1932, only about 70 Trumpeter Swans survived in the Greater Yellowstone Population (formerly known as the Tri-state Population). These nested and wintered in remote portions of Idaho, Montana, and Wyoming including Yellowstone National Park. In 1946, aerial surveys confirmed that a second remnant of about 100 Trumpeter Swans had persisted in the Western Canada Population, nesting in the Grande Prairie Region along the Alberta-British Columbia border (Mackay 1978). Marking studies later showed that these Canadian swans wintered primarily in Greater Yellowstone with the resident nesting population (Mackay 1957; Gale *et al.* 1987; Mitchell and Shandruk 1992). The extreme isolation of this high elevation Greater Yellowstone Region, where geothermal influence kept small areas of water ice-free regardless of winter severity, protected these few Trumpeter Swans from the harvest that eliminated the species from the remainder of Canada and the contiguous USA (Banko 1960; Gale *et al.* 1987). For management purposes, these two disjunct breeding populations as well as two small disjunct restoration flocks in Oregon and Nevada, collectively are often referred to as the Rocky Mountain Population (Pacific Flyway 1998; Shea 2000; Trost *et al.* 2000).

The status of the Pacific Coast Population was poorly known until 1959, when aerial surveys found 1,124 birds. Additional surveys in Alaska found 2,848 Trumpeter Swans in 1968, revealing that this population was increasing and pioneering into habitat that had recently emerged from glaciation (Hansen *et al.* 1971). Pacific Coast Population swans winter primarily in Oregon, Washington, and British Columbia.

EARLY CONSERVATION EFFORTS

Two landmark conservation measures laid the foundation for Trumpeter Swan restoration. The Migratory Bird Treaty Act (1918) ended unregulated harvest of swans in the USA and Canada, and the Migratory Bird Conservation Act (1929) authorized establishment of national wildlife refuges in the USA. Red Rock Lakes National Wildlife Refuge, 80 km west of Yellowstone National Park, was established in 1935 to protect key nesting habitat and marked the beginning of efforts by the U.S. Fish and Wildlife Service to restore the species (Banko 1960).

In the USA, the initial conservation goal was to prevent the elimination of the Greater Yellowstone Population, which was widely thought to be the only surviving breeding population in the 1920s–1930s. In addition to protecting nesting habitat at Red Rock Lakes National Wildlife Refuge, conservation measures included winter feeding, predator control, eliminating human disturbance at nest territories, and reducing illegal shooting through increased law enforcement and public education. The population increased in response to these measures and in 1938 managers began translocating Trumpeter Swans from Red Rock Lakes National Wildlife Refuge to other national wildlife refuges in Wyoming, Oregon, and Nevada to broaden distribution and reduce the possibility of species extinction (Banko 1960; Gale *et al.* 1987). In Canada, early efforts focused on monitoring population status in Alberta, protecting nest-site lakes from human disturbance, and reducing illegal harvest (Mackay 1978). In Alaska, effort focused on reducing harvest through increased enforcement of the Migratory Bird Treaty Act.

By 1959, when Alaskan nesting areas were first surveyed, the total number of wild Trumpeter Swans had increased to at least 1,914, including 1,124 in Alaska, 127 in western Canada, 631 in Greater Yellowstone, and 32 on national wildlife refuges elsewhere in the western USA (Table 1). Although the Western Canada Population was still precariously small, direct intervention had halted the decline of the three remnant groups, achieved a 9-fold increase in the Greater Yellowstone Population, and the potential for increase appeared good in the Alaska-breeding Pacific Coast Population. With the threat of extinction fading, a new phase of Trumpeter Swan restoration was launched.

RECENT RESTORATION AND CONSERVATION EFFORTS

Beginning in 1959, substantially larger numbers of swans from Red Rock Lakes National Wildlife Refuge were provided to zoos and private propagators, translocated to other National Wildlife Refuges, and used in various restoration programs (Gale *et al.* 1987). This increased availability of Trumpeter Swans prompted efforts to re-introduce them into historic habitat in the Midwestern USA, and subsequently into the Canadian province of Ontario (Whittam and Lumsden 1995; Johnson 2000); the combined restoration flocks are known as the Interior Population. The midwestern restoration effort began in 1960 at Lacreek National Wildlife Refuge, South Dakota, and in 1966 was followed by the first non-federal program to re-introduce Trumpeter Swans, at the Hennepin County Park Reserve District, Minnesota. The Trumpeter Swan Society, a private non-profit organization based in the latter location, was formed in 1968 to help restore Trumpeter Swans, improve their management, and protect essential habitat.

Table 1. Abundance of Trumpeter Swans in North America during the 20th Century. All data represent direct counts except for the Yukon-northern British Columbia portion of the Western Canada Population, which was estimated from stratified samples in 1995 and 2000 (Banko 1960; Hansen *et al.* 1971; Gale *et al.* 1987; Mackay 1988; U.S. Fish and Wildlife Service *et al.* 1994; Caithamer 2001).

		Rocky Mountains			N. America
	Pacific Coast	Western Canada	United States[a]	Interior	Total
Initial surveys					
1932	not surveyed	not surveyed	69	0	69+
1946	not surveyed	100	361	0	461+
1959	1,124	127	663	0	1,914
Range-wide surveys					
1968	2,847	106	705	64	3,722
1974-75	4,170	131	668	116	5,085
1980	7,696	379	596	176	8,847
1985	9,504	614	581	209	10,908
1990	13,456	1,117	630	422	15,625
1995	16,312	2,076	441	927	19,756
2000	17,551	3,184	482	2,430	23,647

[a] Includes Greater Yellowstone Population and disjunct restoration flocks in Oregon and Nevada.

By 1999, seven midwestern states (South Dakota, Minnesota, Missouri, Michigan, Wisconsin, Iowa, and Ohio) and Ontario had launched restoration programs and 1,629 Trumpeter Swans had been captive-reared and released into the wild (Johnson 2000). Private propagators helped refine captive breeding techniques and became important partners with states and universities in restoration programs. Swans of Alaskan, as well as Red Rock Lakes National Wildlife Refuge origin, were used to increase the numbers and genetic diversity of these re-introduced flocks (Johnson 2000; Lumsden 2000). By summer 2000, the combined restoration flocks in the midwest and Ontario contained 2,430 free-flying Trumpeter Swans, with most wintering near their breeding areas and a substantial portion sustained by supplemental winter feeding (Johnson 2000; Caithamer 2001).

During the past 30 years, the Western Canada Population expanded its breeding distribution and grew to approximately 3,184 birds by summer 2000 (Caithamer 2001). Concerns for its security and that of the Greater Yellowstone Population continue, however, because their winter distributions remain greatly reduced. As Trumpeter Swans that migrated to other wintering areas were eliminated, both groups became dependent upon habitats in Greater Yellowstone where mortality risk is high in severe winters, when foraging areas become ice-covered (Pacific Flyway 1998; Shea 2000). Currently, 482 Trumpeter Swans summer in the contiguous western USA, with only nine nesting pairs found outside the Greater Yellowstone Region (Reed 2000; Caithamer 2001).

Since the mid-1980s, efforts to reduce the vulnerability of Western Canada and Greater Yellowstone swans, which winter in the Greater Yellowstone Region, have focused on expanding winter distribution and reducing concentrations of swans at sites in Greater Yellowstone where risk of starvation during periods of extensive ice formation is high. Major actions included termination of winter feeding at Red Rock Lakes National Wildlife Refuge (Niethammer *et al.* 1993), winter and summer translocations of over 1,400 swans to alternate potential wintering habitat in Idaho, Wyoming, Oregon, and Utah, and fall hazing of swans from high-risk wintering sites in eastern Idaho (Pacific Flyway 1998; Shea and Drewien 1999; Bouffard 2000; Shea 2000; Drewien *et al.* 2002).

These combined actions have increased Trumpeter Swan use at three target wintering sites south of Greater Yellowstone, where about 300 Trumpeter Swans wintered in February 2001 (Olson 2001). At several other winter translocation sites, Trumpeter Swan use was hindered by lack of adequate ice-free feeding habitat and human disturbance, primarily from hunting and boating. In addition, key potential migration and wintering habitat in northern Utah could not be used effectively as release sites in range expansion efforts due to Tundra Swan *(C. columbianus columbianus)* hunting (Shea and Drewien 1999; Drewien *et al.* 2002). Despite some limited success in encouraging southward expansion, about 90% of the Rocky Mountain Population continue to winter at sites in Greater Yellowstone where risk of mortality during severe winters is high (Shea and Drewien 1999; Shea 2000).

By summer 2000, the Alaska-breeding Pacific Coast Population had grown to over 17,500 and accounted for about 75% of the total increase of Trumpeter Swans in North America (Table 1). In contrast to other remnant populations, the Pacific Coast Population retained substantial southerly migrations to southern British Columbia, Washington, and Oregon and in recent decades learned to use a wide variety of agricultural crop residues and pastures on its southerly wintering grounds. Much of the Pacific Coast Population winter habitat is unprotected, however, and will likely be lost to future industrial and residential development, or conversion to non-edible crops (King 2000). Lead poisoning, due to ingestion of accumulated lead shot, also remains a threat to some wintering segments, as evidenced by the lead-induced deaths of about 200 Trumpeter Swans along the Washington-British Columbia border in January–February 2001 (M. Jordan, pers. comm.).

RECOMMENDATIONS FOR FUTURE CONSERVATION

Most past conservation efforts have focused on halting the harvest of remnant populations, protecting their nesting habitat, and re-establishing nesting Trumpeter Swans in long-vacant habitat. Today's foremost challenge is to ensure that all populations regain use of winter habitat sufficient to sustain them during severe winters. In the Rocky Mountains, this will require re-establishing southward migrations and providing additional wintering sites with adequate food and security from human disturbance, including Tundra Swan hunts (Shea and Drewien 1999; Shea 2000). National Wildlife Refuges provide high quality wetlands along key migration routes and should be used to help provide the essential habitat foundation for rebuilding secure winter distributions (U.S. Fish and Wildlife Service 1999; Shea 2000).

Although much of their natural wintering habitat has been destroyed or degraded, Trumpeter Swans have proven their ability to winter in proximity to humans and to use a variety of agricultural foods. In addition to using national wildlife refuges as secure focus areas for Trumpeter Swan range expansion, we recommend working with the agricultural industry to develop additional habitat. Swans can be encouraged to feed on crop residues with minimal exposure to lead and other toxicants, while they are decoyed away from situations where crop depredations are problematic.

Management plans to conserve and restore Trumpeter Swans have been implemented in three of North America's four Flyways and a draft plan has been created for the Atlantic Flyway. Full implementation of these four plans will help ensure the long-term security of all populations. The Trumpeter Swan was the first avian species to return from the brink of extinction in North America and has become a symbol of hope in the struggle to restore wildlife. Rebuilding secure winter distributions and ensuring long-term protection of habitat will allow this magnificent bird to continue to increase and successfully reoccupy large portions of its historic range.

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Overview of the Trumpeter Swan Reintroduction Program in Ontario, 1982-2000

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Abstract.—Restoration of Trumpeter Swans (*Cygnus buccinator*) to their former range in Ontario has involved many techniques, some more successful than others. Rearing methods included cross-fostering on wild Mute Swans (*Cygnus olor*), artificial incubation, and incubation and rearing by their own Trumpeter Swan parents. Egg hatchability was low ($\bar{x}$ = 56%) for eggs laid by captive pairs and was suspected to be due to inbreeding. Few toxic contaminants were found in unhatched eggs, but 15–17% of unhatched eggs that had been artificially incubated were infertile. Eggs cross-fostered under wild Mute Swans had lower hatchability than those incubated by Trumpeter Swans, and cygnets raised by Mute Swans survived less well to fledging. Time budgets revealed that rearing methods significantly influenced behavior but differences disappeared by 26 weeks of age. However, wild-hatched swans, when adults, bred somewhat but not significantly more frequently than those hatched by their own, captive parents. Translocating adult wild-caught Trumpeter Swans did not prove to be an effective reintroduction technique; none of the six translocated adults were resighted after the first year. Annual survival rate of wild-hatched males and females more than 2 years old was 0.831; survival rates did not differ between captive- and wild-hatched swans in any age or sex category. The most common cause of death was lead poisoning. Released Trumpeter Swans bred for the first time at two to eight years of age. Four adults were taught to follow an ultralight aircraft to a predetermined wintering site. They returned on their own in the spring but did not migrate back to the wintering site during the next autumn.

Key words.—Cross-fostering, *Cygnus buccinator*, *Cygnus olor*, genetic diversity, hatchability, lead poisoning, mortality, Mute Swan, Ontario, restoration, survival rates, Trumpeter Swan.

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Trumpeter Swans (*Cygnus buccinator*) were extirpated from the eastern part of North America early in European settlement but previously had bred from the Bay of Fundy on the Atlantic Coast to the Pacific Coast in Alaska (Webster 1933; Lumsden and Whittam 1993). The last Ontario record was an autumn migrant from the west, shot on Long Point, Lake Erie, in 1886 (Lumsden 1984a). One objective of The Trumpeter Swan Society is the restoration of this species to as much of its former range as possible, and many states in the mid-western United States have undertaken restoration projects.

By 1982, Ontario had lost 68% of its wetlands in agricultural areas. There remained over 900,000 ha (Snell 1987) including marshes which supported large numbers of Trumpeter Swans in the 1600s (Lumsden 1984b). A thriving population of the exotic Mute Swan (*C. olor*) occupies parts of southern Ontario as elsewhere in North America (Nelson 1997). The Canadian Wildlife Service and Ontario Ministry of Natural Resources deemed it desirable to try to replace Mute Swans with native Trumpeter Swans (Lumsden 1998). The purpose of this paper is to review the effectiveness of the various methods used in the Ontario reintroduction program during 1982-2000.

RESTORATION METHODS

Three techniques were used for hatching and raising cygnets: (1) eggs were placed in nests of feral Mute Swans on the northwest shore of Lake Ontario for foster-raising; (2) eggs were hatched in incubators and cygnets raised by humans; (3) eggs were left with captive breeding pairs for incubation and raising of cygnets. Egg production by captive Trumpeter Swans was increased by taking the first clutch, causing some females to lay a second, or by leaving a dummy egg in the nest and removing eggs as they were laid (Lumsden 1986a). In addition, 32 eggs in an advanced stage of incubation were acquired from Grande Prairie, Alberta from 1982–1984, and 50 in 1993 from Alaska. Captive pairs, acquired from aviculturists, were placed in suitable fenced ponds that could be kept ice-free in winter. Each cooperator agreed to feed and care for a breeding pair and provide the program with eggs and cygnets for eventual release to the wild.

Cygnets raised in the program were either held in covered pens at Fair Lake and Metro Toronto Zoo or at the Wye Marsh Wildlife Center. They were released as cygnets or held for one to two years and then released at Metro Toronto Zoo, Wye Marsh and a variety of areas with suitable habitat. Released swans were generally wing-clipped, marked with yellow patagial tags with a black three-digit number and leg bands. Wild-hatched swans were trapped, tagged and banded.

ANNUAL INVENTORIES

Annual inventories were conducted on 1 September when the fate of most of the wild-hatched broods was known. A continuous record was kept of the patagial tag numbers reported by the public, and volunteers searched for swans in areas not generally covered by the public. At winter concentration areas, ratios of tagged to untagged birds were recorded. An annual estimate of total numbers was compiled from all the marked swans recorded during the year starting 2 September, plus the number of cygnets hatched in the wild still alive on 1 September, plus the number released from the propagation program.

Trumpeter Swans at liberty have increased steadily from 12 birds in 1990 to over 300 in 2000, largely because of annual releases of captives (Table 1). Ninety-eight swans have disappeared since the program began, either due to loss of tags, emigration outside the study area, or death. In 1999, about 75% of Ontario Trumpeter Swans had patagial tags.

METHODS USED TO ESTIMATE SURVIVAL

We used resightings of patagial tag numbers and the program MARK (White and Burnham 1999) to provide preliminary estimates of annual survival (ϕ) and recapture (p) probabilities and to test effect of rearing experience (captive vs. wild) on these parameters. Annual survival was defined as the probability that a swan alive in year i survives until year $i + 1$ and remains in the study area. Swans began hatching in the wild in 1993, and thus, we only used data on birds released in 1993 and afterwards to enable comparisons between captive-hatched and wild-hatched swans. All captive-hatched swans were grouped into one category that included swans hatched and raised by captive parents and those hatched in incubators and raised artificially. Because male swans typically disperse further than females in waterfowl (Anderson *et al.* 1992), and since this would affect the survival estimate, we analyzed males and females separately.

We began with the Cormack-Jolly Seber model ($\phi_{group*time}, p_{group*time}$), which considers survival and recapture separately for each group and year. The mark-recapture program RELEASE (TEST 2 and TEST 3; Burnham *et al.* 1987) was used to evaluate goodness of fit of this model to the data. We used Akaike's Information Criterion corrected for sample size and overdispersion ($QAIC_c$; Anderson *et al.* 1994) to select the most parsimonious model from a series of candidate models, first reducing variation in recapture probabilities, and then testing for year and group effects (Lebreton *et al.* 1992). The

Table 1. Estimated size of Ontario's wild flock of Trumpeter Swans on 1 September, including those fledged by wild parents during the year in question, those raised in captivity and released to the wild, and those adults surviving from previous years and whose tag numbers were tallied during the year.

	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Wild-reared	0	0	0	6	3	9	14	25	41	36	42
Captive-reared	0	10	13	1	19	52	44	23	59	47	51
Wild adults	10	8	5	22	13	21	65	95	91	169	210
Total	12	18	18	29	35	82	123	143	191	252	303

bootstrapping procedure in MARK was used to calculate the variance inflation factor ($\hat{c}$), a measure of overdispersion in the data (Anderson *et al.* 1994), as the observed deviance of this general model divided by the average deviance of 1,000 simulated deviances. Overdispersion occurs when observed variance of survival estimates exceeds theoretical variance, reflecting lack of independence among individuals (Anderson *et al.* 1994). For example, banding brood mates typically results in overdispersion because fates of these birds are linked, thus violating the assumption of independence. In the case of complete independence and homogeneity (no overdispersion), $\hat{c}$ will equal one. $QAIC_c$ will adequately select parsimonious models for c-hat values ranging between one and three (Anderson *et al.* 1994). Model plausibility was gauged using $\Delta QAIC_c$, the difference between the $QAIC_c$ of each model and the smallest $QAIC_c$ of all the models considered. Models with $\Delta QAIC_c < 7$ can be considered plausible, and models with $\Delta QAIC_c \leq 2$ have the greatest support. We also compared support for models using Akaike weights, which are proportional to the normalized relative likelihoods of each model and can be used to gauge the extent to which each model is more likely than another (Buckland *et al.* 1997). In order to incorporate uncertainty about model selection into the parameters, we used model averaging (Buckland *et al.* 1997) using only plausible models to derive estimates of survival and recapture probabilities.

SURVIVAL

Between 1993 and 2000, 161 male cygnets (36 wild-hatched and 125 captive-hatched) and 145 female cygnets (30 wild-hatched and 115 captive-hatched) were marked in the wild at 2–3 months of age or released from captivity at 3–6 months of age. Males were re-encountered 420 times and females 500 times.

The Cormack-Jolly Seber model for male swans, considered separately for each group (i.e., captive-hatched vs. wild-hatched), had no detectable lack of fit (TEST 2 + TEST 3: $\chi^2_9 = 8.86$, n.s. for wild swans; and $\chi^2_9 = 8.86$, n.s. for captive swans). Conversely, the Cormack-Jolly Seber model for female swans, considered separately for each group, showed no detectable lack of fit for captive swans (TEST 2 + TEST 3: $\chi^2_5 = 0.98$, n.s.), but the model fitted the data poorly for wild swans (TEST 2 + TEST 3: $\chi^2_6 = 12.4$, $P = 0.053$). However, the greater part of this latter χ^2 statistic can be explained by an effect of age class (ac) on survival (TEST 3:SR: $\chi^2_5 = 12.0$, $P < 0.05$). Under these conditions, the sum of TEST 3.3m + the components of TEST 2 represents a goodness-of-fit for a two age class model ($\phi_{2ac*group*year}, p_{group*year}$; Lebreton *et al.* 1992), and this test shows no detectable lack of fit ($\chi^2_1 = 0.42$, n.s.). In addition, incorporating age structure into the general model results in a significant drop in deviance (Likelihood ratio test: $\chi^2_{13} = 29.9$, $P < 0.005$). Therefore, this became our general model for female swans. The general model for males ($\phi_{group*year}, p_{group*year}$) and females ($\phi_{2ac*group*year}, p_{group*year}$) had $\hat{c} = 2.17$ and 1.51, respectively, suggesting moderate overdispersion. Model selection was based on models adjusted for these values. We examined models for male and female swans that included age class and group (captive-hatched vs. wild-hatched) effects (Appendix). Resighting probabilities (p) for both male and female swans were best modeled as a constant throughout the study period. Weighted average annual resighting probability was 0.976 (SE = 0.013) for males and 0.984 (SE = 0.011) for females.

For male swans, the most parsimonious model included three age classes (first-year, second-year, and after-second-year) and no group effect (Model VI, Appendix). Based on Akaike weights, this model had ~5 (0.81/0.16) times more support than the next best model (Model IV), which has three age classes and a group effect, suggesting survival does not differ between wild-hatched and captive-hatched swans. For female swans, the most parsimonious model also included two age classes (first-year and after first-year) and a group effect (Model V, Appendix). However, this model had only 1.26 (0.48/0.38), or nearly equal, support as the model that does not include the group effect (Model VII) and the model with three age classes (Model VI), suggesting that both the third age class and group effect, if present, may be fairly weak. The weakness of these effects may be seen in the similarity among survival estimates (Table 2).

In summary, we conclude that mean annual survival of males and females did not differ between captive-hatched and wild-hatched swans for any age class (independent t-tests, all P-values >0.27, Table 2). Mean annual survival for wild-hatched birds >2 years of age was 0.83 (± 0.05) for both males and females (Table 2). We note that because we have not incorporated band loss or emigration from the study area, these estimates likely underestimate actual survival and should be viewed as minimum estimates. Band loss will be examined in more detail in a later publication.

CAUSES OF MORTALITY

Of 84 carcasses submitted for necropsy to the Metro Toronto Zoo or the Canadian Cooperative Wildlife Health Unit (Table 3), the most common cause of death was lead poisoning, caused by eating shotgun pellets or fishing sinkers, which accounted for 32 deaths (38%). Lead poisoning also was a contributing factor for some of the 11% that flew into power lines, and the 12% caught with broken limbs that subsequently died (H. G. Lumsden, unpub. data). Predators such as Coyotes (*Canis latrans*) and Red Foxes (*Vulpes vulpes*) accounted for 11% of deaths, but foxes may also have scavenged. Only four swans are known to have been killed by people.

The percentage of deaths due to lead poisoning in this study was higher than the 30% recorded for Minnesota and Wisconsin and substantially higher than the 23% loss for the Mississippi Flyway, where it was the second most common cause of death (Johnson 2000). In six states in the Mississippi Flyway, illegal hunting was the most common cause of death and accounted for 26% of known mortalities (range 17%–42%) from 1976–1999 (Johnson 2000). Thus, 49% of all losses in the Mississippi Flyway can be attributed directly or indirectly to hunters and anglers.

In Ontario from 1982 to 1997, 78% of deaths (N = 25) due to lead poisoning occurred within two years of release while relatively few occurred after three years. Among those released at two years of age, 90% of the loss (N = 10) occurred within the first year. Thus, lead poisoning appears to be a phenomenon largely confined to the young and newly released in Ontario. Of 36 swans treated for lead poisoning during this study, 16 (44%) survived and were released, and six (38%) of these subsequently bred. Because Trumpeter Swans spend much time foraging deep in the mud and die at a lower lead-blood level than most other waterfowl (Blus *et al.* 1989), they may be useful as sentinel species for lead available in marshes. Calle *et al.* (1982) concluded that conversion from lead to steel shot in parts of Pennsylvania reduced the prevalence of lead shot in the gizzards of

Table 2. Estimates of annual survival rate (ϕ) of male and female Trumpeter Swans in southern Ontario, 1993–2000, that were captive-hatched and released as cygnets or wild-hatched. Estimates obtained by model averaging of models IV and VI for males and V and VII for females (see Appendix). Sample size, i.e., number of individuals entering each age class, given in column heading. No significant differences in survival, based on independent t-tests, between captive- and wild-hatched males (all P-values >0.68) or females (all P-values >0.27) for any age class.

	Males				Females			
	Captive-hatched (N = 125, 122, 109)		Wild-hatched (N = 36, 35, 31)		Captive-hatched (N = 125, 122, 109)		Wild-hatched (N = 36, 35, 31)	
Age class	ϕ	SE	ϕ	SE	ϕ	SE	ϕ	SE
<1 yr	0.979	0.019	0.978	0.023	0.950	0.025	0.873	0.065
1 to 2 yrs	0.893	0.019	0.879	0.028	0.780	0.034	0.831	0.055
2+ yr	0.855	0.047	0.831	0.056	0.765	0.035	0.831	0.052

Table 3. Causes of mortality of reintroduced Trumpeter Swans in Ontario, based on 84 necropsies, 1982–2000.

Cause of death	Number of deaths	Percentage of known causes
Lead poisoning	32	38
Power lines	9	11
Broken wing (one with broken leg)	10	12
Accidents and highway deaths	9	11
Diseases (aspergillosis, gout, amyloidosis)	11	13
Predators (coyote, fox)	9	11
Shot illegally	2	2
Vandals (decapitation)	2	2

Black Ducks (*Anas rubripes*) and Mallards (*Anas platyrhynchos*) from 11.2% to 5.6%. In 1999, Canada imposed a nation-wide ban on the use of lead shot for waterfowl hunting for the first time. Since 1990, local hot spots for lead poisoning in Ontario have had non-toxic shot regulation. Compliance with non-toxic shot regulations will be important in improving survival of all waterfowl species.

HATCHABILITY

It was recognized early in the Trumpeter Swan restoration program that hatchability of eggs laid by the captive breeding Trumpeter Swans was low, whether hatched by their parents (56%), Mute Swan foster parents (39%) or in incubators (26%, Table 4). Trumpeter Swan parents performed better than Mute Swans (χ^2_1 = 13.2, P < 0.001), and incubators performed more poorly than either Trumpeter Swans (χ^2_1 = 78.2, P < 0.001), or Mute Swans (χ^2_1 = 7.52, P < 0.01, Table 4). One reason for the low success of incubators was that they often malfunctioned, particularly in the later years of the study.

Hamilton (1996) found that among 75 eggs artificially incubated in two seasons, 15% and 17% were infertile. Of the embryos that died in the shell, 59% died during the first 14 days of incubation and 41% died in the last ten days. Hatchability was reduced among eggs that were kept in damp peat moss for more than seven days before incubation. Transport to and from storage may also have damaged delicate tissues. Toxicological analysis of selected embryos failed to reveal significant levels of DDT, DDE, organophosphates, PCBs, captan, mercury, lead or pyrethroids, suggesting that contaminants were not the cause of low hatchability.

In 1991 and 1992, a further 88 eggs incubated by Trumpeter Swan pairs were examined (H. G. Lumsden and R. J. Hampson, unpub. data). These eggs had endured at least 33 days of incubation and were decomposing. Of these, 37% were infertile or showed no sign of development. The cause of failure could not be determined in 15%; 32% died early in incubation and 14% in late incubation. In addition, two cygnets hatched with deformed feet and died within one to two days.

Table 4. Rates of hatching and fledging success of Trumpeter Swans in Ontario (1982–2000) under three rearing techniques: hatched in incubators and raised by humans; hatched and raised by wild Mute Swans; hatched and raised by captive Trumpeter Swans. Percentages within columns that do not share letters (A,B,C) were significantly different (χ^2 with Yates correction).

Rearing method	Percentage of eggs hatched successfully (no. successful/total eggs)[a]	Percentage of cygnets fledged successfully (no. successful/total cygnets)[b]
Incubator	26 (79/303)^{A}	69 (55/79)^{A}
Mute Swan parents	39 (57/145)^{B}	29 (16/57)^{B}
Trumpeter Swan parents	56 (454/810)^{C}	70 (318/454)^{AC}

[a] Hatching success of incubator compared to Mute Swan parents, χ^2=7.52, P < 0.01; Trumpeter Swan compared to Mute Swan parents, χ^2= 13.2, P < 0.001; and Trumpeter Swan parents compared to incubator, χ^2= 78.2, P < 0.0001.

[b] Fledging success of incubator compared to Mute Swan parents, χ^2= 21.3, P < 0.0001; Trumpeter Swan compared to Mute Swan parents, χ^2= 37.6, P < 0.0001; and Trumpeter Swan parents compared to incubator, χ^2= 0.01, n.s.

Dead cygnets with deformed feet also were noted in nests of wild swans nesting at the Red Rock Lakes National Wildlife Refuge in Montana (E. Stroops, pers. comm.). Improper incubation temperatures (Romanoff 1972) can cause deformed feet, but that is unlikely to be the cause here, as the eggs were naturally incubated by the swans that laid them.

Over an 18 year period, our captive breeding pairs incubating 810 of their own eggs had a hatching failure rate averaging 44%. This failure rate is similar to the 40% hatching failure recorded among the Greater Yellowstone Population by Banko (1960) and Page (1976, in Gale *et al.* 1987). However, Maj (1983, in Gale *et al.* 1987) recorded a six-year mean egg failure rate of 25% in the portion of the Greater Yellowstone Population that breeds in the lower elevation Targhee National Forest. These hatching failure rates are higher than the 24% reported from the Pacific Coast Population breeding in Alaska (Hansen *et al.* 1971). All are substantially higher than the rates recorded for Mute Swans in England of one in ten (Birkhead and Perrins 1986) and 6% (Reynolds 1965).

GENETIC DIVERSITY

The Greater Yellowstone breeding population, from which most of the Ontario stock is descended, is known to have been reduced to only about 50 adults and their cygnets in the 1930s (Gale *et al.* 1987) and is thought to have experienced a genetic bottleneck (Marsolais 1994). The high failure rate of Trumpeter Swan eggs in the Ontario restoration program prompted a genetic study. Marsolais and White (1997) isolated DNA from the blood of 259 Trumpeter Swans from three wild populations and the Ontario captive and released population. Two mini-satellite probes, Jeffrey's 33.15 and 33.6, were used to produce DNA fingerprints and to calculate Band Sharing Coefficients which can be used as a general indication of a population's genetic variation. Among the four Trumpeter Swan and one Mute Swan populations (Meng *et al.* 1990) for which data were available, hatch failure was correlated with Band Sharing Coefficients using Jeffrey's 33.6 probe (Spearman rank correlation, $r_3 = 1.00$, $P < 0.0001$, Table 5). The Greater Yellowstone Population, from which most of Ontario's flock originated, had higher Band Sharing Coefficients than either the Pacific Coast or Western Canada Populations (Mantel test, $P < 0.001$ and $P < 0.025$, respectively; Marsolais, unpub. data). We suspect that lack of genetic variation is the cause of low hatchability in the Ontario captive and released population. To reduce as far as possible further inbreeding, eggs were collected from the Pacific Coast Population in 1993 (Lumsden 1993) and some of the resulting adults have been integrated into the Ontario breeding population.

Table 5. Hatching failures and mean Band Sharing Coefficients for four populations of Trumpeter Swans and for Mute Swans, Whooper Swans (*Cygnus cygnus*), and Tundra Swans. Hatch failure was correlated with Band Sharing Coefficients based on Jeffrey's 33.6 probe (Spearman rank correlation, $r_3 = 1.00$, $P < 0.0001$).

Population	Proportion eggs not hatched	Band Sharing Coefficient using Jeffrey's probe: 33.15	33.6	No. DNA samples
Ontario	0.45[c]	0.41	0.53[a]	132
Greater Yellowstone	0.40[d]	0.36	0.42[a]	41
Western Canada	—	0.32	0.40[a]	9
Pacific Coast	0.24[e]	0.28	0.33[a]	27
Mute Swan	0.06[f]	—	0.28[b]	15
Whooper Swan	—	—	0.28[b]	15
Tundra Swan	—	—	0.20[b]	5

[a]Marsolais and White (1995); [b]Meng *et al.* (1990); [c]this study; [d]Banko (1960) and Page (1976), but see Maj (1983); [e]Hansen *et al.* (1971); [f]Reynolds (1965).

Pelizza and Britten (2002) examined genetic differences among the Greater Yellowstone Population (i.e., their Tristate subpopulation), the High Plains flock, and the Pacific Coast Population. Since the High Plains flock is descended from a translocation of Greater Yellowstone individuals, it is not surprising that the authors found them genetically indistinguishable. The study did not include the Western Canada Population. Swan banding and color marking programs of the Greater Yellowstone Population (1,050 birds) and the Western Canada Population (300 birds) showed that while these populations intermingle in winter, there is no evidence of pair formation and genetic exchange between them. They appear to be reproductively isolated (Gale *et al.* 1987). To enlarge the Ontario gene pool further, it would be an advantage to introduce more birds from the Western Canada Population.

EFFECTS OF REARING TECHNIQUES

Eadie *et al.* (1995) studied time-activity budgets of incubator-hatched, hand-reared Trumpeter Swan cygnets imprinted on their keepers, hand-reared cygnets not imprinted on their caretakers, and on a brood incubated and raised by their own parents. In both years of study (1992 and 1993), cygnets imprinted on keepers fed significantly more, were less vigilant and clustered less than cygnets not imprinted on keepers. In 1993, a brood being raised by its own parents on a natural pond spent significantly less time feeding, preening and resting, and exhibited higher levels of vigilance than the other two groups. The captive groups did not differ in mass. These differences in behavior disappeared by 26 weeks of age. Eadie *et al.* (1995) concluded that the rearing environment can significantly influence time budgets but may be transitory and without long-term consequences. Similarly, Pichner *et al.* (1992) found no significant difference in rates of survival between hand-reared and parent-reared Trumpeter Swans. However, they found that hand-reared birds bred at a slightly but not significantly higher rate than those parent-reared in captivity.

We also looked for long-term effects of rearing method. When over three years of age, 38% (8 of 21) of wild-hatched swans bred compared to only 17% (19 of 111) of those raised in captivity by their own parents and released, but the difference was not significant ($\chi^2_1 = 3.57$, n.s.). In addition, the sex ratio of 3-year-old wild-hatched swans was 10 females:4 males compared to the 6 females:11 males sex ratio of captive released cygnets raised by their own parents, but the difference was not significant ($\chi^2_1 = 2.70$, n.s.).

Cygnets hatched in incubators and those hatched by their parents survived equally well to fledging (69% vs. 70%, $\chi^2_1 = 0.01$, n.s., Table 4). Similarly, for those swans released at 2 years of age (1982–2000), there was no significant difference between those hatched by their own parents (N = 68) and those incubator-hatched (N = 51) in survival to age 3 years (65% vs. 67%, $\chi^2_1 = 0.01$, n.s.), to age 6 years (12% vs. 21%, $\chi^2_1 = 1.42$, n.s.), or to age 9 years (3% vs. 6%, $\chi^2_1 = 0.11$, n.s., Table 6), suggesting that rearing method made no difference to survival. For those released as cygnets, wild-hatched swans (N = 29) tended to survive better than captive-hatched (N = 69) to age 3 (48% vs. 25%, $\chi^2_1 = 4.24$, $P < 0.05$), but the difference disappeared by age 6 (14% vs. 12%, $\chi^2_1 = 0.01$, n.s., Table 6). Similarly, the mark-recapture analysis (see previous sections), which was performed on a subset of the data (swans released as cygnets or wild-hatched, 1993–2000), also indicated that survival did not differ between wild- and captive-hatched birds for males or females of any age class.

MUTE SWAN FOSTER PARENTS

Cross-fostering under Mute Swans was not entirely successful. Hatchability (39% of 145 eggs) was lower than that of eggs hatched under Trumpeter Swan parents (56% of 810 eggs, $\chi^2_1 = 13.2$, $P < 0.0001$, Table 4), possibly because many eggs were initially stored for up to ten days and later transported to Mute Swan nests. Mute Swans were also less successful in rearing cygnets to fledging (29% vs. 70% survived, $\chi^2_1 = 13.2$, $P < 0.001$, Table 4). Male Mute Swans frequently attacked the pearl-colored Trumpeter Swan

Table 6. Number of Trumpeter Swans surviving to age 3, 6, and 9 years under different rearing and release protocols in Ontario from 1982 to 1997. Percentage surviving given in parentheses; χ^2 with 1 df calculated with Yates' correction; none of the χ^2 values significant at $P < 0.05$.

	Free or released as cygnets, reared by:				Released at 1 yr, reared by	Released at 2 yrs, reared by:		
Age (yrs)	Wild Mute Swans (N = 16)	Wild Trumpeter Swans (N = 29)	Captive Trumpeter Swans (N = 69)	χ^2_2	Captive Trumpeter Swans (N = 62)	Captive Trumpeter Swans (N = 68)	Incubator-hatched (N = 51)	χ^2_1
3	6 (37)	14 (48)	17 (25)	5.42	31 (50)	44 (65)	34 (67)	0.01
6	3 (19)	4 (14)	8 (12)	0.59	10 (16)	8 (12)	11 (21)	1.42
9	2 (12)	0 (–)	2 (3)	4.95	6 (10)	2 (3)	3 (6)	0.11

cygnets. These attacks stopped when the cygnets were appropriately dyed before they left the nest (Lumsden 1985). Poor family bonds resulted if the eggs were kept in an incubator until the embryo started to call or pip the shell (Lumsden 1984). In addition, many cygnets were probably taken by Snapping Turtles (*Chelydra serpentina)* (D. Foxall, pers. comm.; Abel 1992). The Mute Swan foster parents did not seem to have an effective defense strategy against turtles (Lumsden 1986b). Wild Trumpeter Swan parents were more than twice as successful (71% vs. 28%) as Mute Swans in raising their cygnets in waters occupied by turtles (133 of 188 vs. 15 of 62 hatched cygnets, $\chi^2_1 = 39.9$, $P < 0.0001$). We do not know if the Trumpeter Swans' apparent success is accomplished by antipredator behavior or by avoidance. After fledging, these cross-fostered cygnets survived as well as those raised by Trumpeter Swan parents. About five Trumpeter Swans raised by Mute Swans have reached four or more years of age. Although they flew free among a large population of feral Mute Swans, none formed a pair bond with a Mute Swan. One was injured, taken into captivity, kept in the company of Trumpeter Swans and bred successfully in 1999 and 2000.

USE OF WILD-CAUGHT SWANS FOR RESTORATION

Reintroduction of Canada Geese (*Branta canadensis*) by translocating wild-caught adults has achieved considerable success (Aldrich *et al.* 1998). There was a possibility that the same approach might work for Trumpeter Swans. In 1988, nine Trumpeter Swans were trapped near Comox on Vancouver Island. These wild-caught birds were held a few days and then flown 16–18 hours to Toronto. Three birds not treated with electrolytes before shipment suffered from extreme dehydration and stress. One died nine days after shipment and was diagnosed with aspergillosis and pneumonia. The five birds treated with electrolytes before shipment fared better. Six of these wild caught swans were released to the wild in April, about four months after capture, and at least three were known to have survived the winter. However, none were resighted after one year. The conclusion is that moving wild-caught Trumpeter Swans in this way is not a practical technique for establishing a breeding population in new habitat. However, moving wild-caught cygnets before they move on their first migration might be an effective technique for restoration.

BREEDING OF WILD PAIRS

Age-specific breeding among released Trumpeter Swans in Ontario conformed closely to that noted by Mitchell (1994). About 29% of pairs over two years of age nested (Table 7) and successful pairs had a mean brood size of 3.03 at fledging. Forty-three marked swans, some of which are mated to one another, have nested since 1993. Of these 43 individuals, 5% first nested at 2 years old, 34% at 3, 33% at 4, 19% at 5, 5%

at 6, 2% at 7 and 2% at 8. At present the number of mortalities exceeds survival of wild-hatched cygnets to three years of age, and Turner (1982) estimated that a pair of the Western Canada Population must breed for 4.3 years to replace the pair unit. Thus, we conclude that Ontario's population is not yet self-sustaining.

MIGRATION

Trumpeter Swans, like geese and cranes, lead their young to and from wintering grounds (Hochbaum 1955; Scott and the Wildfowl Trust 1972) which appears to facilitate offspring in learning the route and wintering area and thus in returning in subsequent years. In a restoration program, young swans have no migratory parents to lead them. When frozen out of their release site, Ontario swans generally moved in a southeasterly direction until they encountered suitable open water with adequate food. Since 1992, a small regular migration has developed between Wye Marsh near Georgian Bay and the northwest shore of Lake Ontario, about 120 km to the south, where algae are available and the swans are fed by the public. In some years, some swans moved as far as New York (11), Pennsylvania and Ohio (6), Virginia (1), West Virginia (3), Connecticut and New Jersey (1), and Maryland (2). Gillette (1997) suggested that the failure of swans to leave their original home range in fall is because they are artificially fed. In restoration programs where populations are relatively low and struggling, the failure to move far may be an advantage if swans that move considerable distance have a higher mortality rate than those that stay (Gillette 1988).

Table 7. Age distribution of individual Trumpeter Swans breeding in the wild for the first time in Ontario from 1993 to 1997.

Age (yrs)	Number alive	Number first breeding	Percentage first breeding
2	43	2	5
3	40	2	5
4	12	2	17
5	12	5	42
6	9	3	33
7	6	3	50
8	8	7	88
9	6	3	50
10	3	3	100

However, it is a widely-held desire among waterfowl managers that restored flocks of Trumpeter Swans should be migratory. There is also a desire to exclude Trumpeter Swans from areas where Tundra Swan (*Cygnus columbianus columbianus*) hunting seasons are established. Any management technique that allows us to induce Trumpeter Swans to avoid areas where they are not wanted and persuade them to winter in areas of our own choosing would be an advantage. In 1965, W. Carrick thought that ultralight aircraft might be used to induce traditional migrations to suitable wintering grounds (Lumsden *et al.* 1990). In 1996, as a precursor to training swans to follow an ultralight, Carrick trained Trumpeter Swans to fly beside a boat (Lumsden 2000).

In 1997 and again in 1998, the Ontario Restoration Program provided W. Bezner-Kerr with four groups of five Trumpeter Swan cygnets. Two groups were hatched naturally and imprinted on their parents and two groups were hatched in incubators and imprinted on their keepers. The objectives were to test (1) whether swans could be led to a wintering ground with an ultralight and if they would return and; (2) the effect of filial imprinting on the following response that appears with the development of flight. The only consistent followers of the ultralight aircraft were cygnets hatched by and imprinted on their own parents and removed at 10 days of age for captive rearing. In 1998, four out of five of these birds flew 1,085 km (direct line) beside an ultralight aircraft from Ramsey Lake, Ontario, to the Muscatatuck National Wildlife Refuge in Indiana (Bezner-Kerr 2001) At least two returned in May 1999 to Ramsey Lake. None returned to Muscatatuck the next autumn. In conclusion, swans taught to follow an ultralight to a wintering site have some tendency to return to near their site of origin, and filial imprinting on humans did not help and may even have impeded the process of learning to follow an ultralight aircraft.

CONCLUSIONS

Placing breeding pairs with private pond owners for propagation worked very well with minimum cost to the program. Artificially incubated eggs had low hatchability, thus unless incubators are thoroughly reliable, eggs should be incubated under Trumpeter Swan parents. However, once hatched, incubator-hatched Trumpeter Swans survived as well as those raised by their own parents in captivity. Breeding stock should include birds from the Pacific Coast, the Western Canada, and the Greater Yellowstone Populations to provide as broad a gene pool as possible. Numbered patagial tags identified wild swans well and incurred less public opposition than neck collars.

Use of wild-caught swans for restoration should not include birds that have migrated, however, it would be useful to test the effectiveness of translocating wild-caught cygnets. Released Trumpeter Swans may establish their own migration patterns but are more likely to wander in a southerly direction without tradition. The use of ultralight aircraft to lead cygnets to a good wintering area is effective but expensive.

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Appendix. Akaike's Information Criterion corrected for sample size and overdispersion (QAIC$_c$), differences in QAIC$_c$ (ΔQAIC$_c$), Akaike's weights, number of estimable parameters (*np*), and deviance corrected for overdispersion (QDeviance) for models describing annual survival and recapture probabilities for male and female Trumpeter Swans in Ontario, 1993–2000. The two groups considered were those wild-hatched and those hatched in captivity and released as 3–5 month-old cygnets. Models were adjusted by $\hat{c} = 2.17$ for male swans, and $\hat{c} = 1.51$ for female swans. The most parsimonious models (VI for males, V and VII for females) are those with ΔQAIC$_c$ < 2.

Survival (ϕ)	Recapture (p)	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ wt	*np*	QDeviance
Males						
Base Model						
I. Group*year	Group*year	239.4	34.3		26	47.2
Modeling recapture						
II. Group*year	Group*constant	221.0	19.6		16	50.6
III. Group*year	Constant	219.3	17.9		15	50.1
Modeling survival						
IV. Group*3 age classes	Constant	204.7	3.3	0.16	7	53.2
V. Group*2 age classes	Constant	208.0	6.7	0.03	5	60.7
VI. 3 age classes	Constant	201.4	0.0	0.81	5	75.5
Females						
Base Model						
I. Group*year	Group*year	312.2	31.5		26	48.1
II. Group*2 age classes*year	Group*year	323.2	42.4		38	30.9
Modeling recapture						
III. Group*2 age classes*year	Group*constant	303.6	22.8		27	37.1
IV. Group*2 age classes*year	Constant	301.5	20.7		26	37.3
Modeling survival						
V. Group*2 age classes	Constant	280.8	0.00	0.48	5	61.9
VI. Group*3 age classes	Constant	283.2	2.42	0.14	7	60.2
VII. 2 age classes	Constant	281.3	0.44	0.38	3	66.5

Development of an Expert System for Assessing Trumpeter Swan Breeding Habitat in the Northern Rocky Mountains

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Abstract.—A decision support system for the management of the Rocky Mountain Population of Trumpeter Swans (*Cygnus buccinator*) is being developed. As part of this, three expert systems are also in development: one for assessing the quality of Trumpeter Swan breeding habitat; one for making water level recommendations in montane, palustrine wetlands; and one for assessing the contribution a particular site can make towards meeting objectives from a flyway perspective. The focus of this paper is the development of the breeding habitat expert system, which currently consists of 157 rules. Our purpose is to provide decision support for issues that appear to be beyond the capability of single persons to conceptualize and solve. We propose that by involving multiple experts in the development and use of the system, management will be significantly improved. The knowledge base for the expert system has been developed using standard knowledge engineering techniques with a small team of ecological experts. Knowledge was then coded using production rules organized in decision trees using a commercial expert system development shell. The final system has been deployed on the world wide web.

Key words.—Artificial intelligence, breeding habitat, *Cygnus buccinator*, decision support system, expert systems, knowledge engineering, Rocky Mountains, Trumpeter Swan.

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During many years of interaction with Trumpeter Swan (*Cygnus buccinator*) managers, including the Rocky Mountain Population of Trumpeter Swans Subcommittee of the Pacific Flyway Council, it became apparent that it would be useful to integrate what is known about Trumpeter Swan ecology into a model that could be used to simulate and test different management scenarios. The lack of an objective mechanism for exploration of management options and identification of critical information gaps seemed to be contributing to inadequate population recovery. Swan managers make decisions in a cyclic fashion; they plan, implement, evaluate, and improve their management strategies iteratively. Optimizing management of migratory birds throughout a flyway with cyclic planning is so complex that it is difficult to implement without computerized decision support (Sojda *et al.* 1994). In addition, past conditions and future needs are ecological constraints to current decisions. Distributed decision making approaches are appropriate for problems where the complexity prevents an individual decision maker from conceptualizing, or otherwise dealing with the entire problem (Boland *et al.* 1992; Brehmer 1991). A decision support system to assist in realistic and ecologically-based management of Trumpeter Swans is being developed. A key component is an expert system that provides an assessment of an area's quality as breeding habitat for Trumpeter Swans, focusing primarily on the northern Rocky Mountains of the United States. Other similar components include an expert system for management of montane, palustrine, semipermanent wetlands, and one for assessing the contribution a particular site can make towards meeting flyway objectives. These are being linked using multiagent systems development software, and involve other problem solving methods from the field of artificial intelligence. The focus of this paper is on the expert system that assesses Trumpeter Swan breeding habitat.

METHODS

The approach used here followed the evolutionary prototyping method of software development recommended by Sprague and Carlson (1982) and Carter *et al.*

(1992). This required developing a prototype system and conducting verification and validation as part of the development process, thereby continually refining the system. The process for building the prototype consisted of five steps: 1) completing a requirements analysis to determine the question to be addressed, 2) conducting a knowledge engineering workshop to assemble the pieces of pertinent knowledge, 3) constructing a flowchart of the underlying ecological logic in the system, 4) encoding that knowledge into digital format, and 5) making the system available on the World Wide Web.

At the onset of this project, we met with field and regional biologists of the U.S. Fish and Wildlife Service, state waterfowl biologists, the Rocky Mountain Population of Trumpeter Swans Subcommittee of the Pacific Flyway Council, and various university scientists. Information and tools for assessing the quality of Trumpeter Swan breeding habitat was one of their foremost requirements for inclusion in a decision support system.

The knowledge engineering workshop relating to breeding habitat encompassed three days and was led by two knowledge engineers using standard techniques (Scott *et al.* 1991). The expertise of the following three scientists was utilized: Mr. Todd Grant, wildlife biologist at J. Clark Salyer National Wildlife Refuge, who had conducted research on breeding swans on the Copper River Delta in Alaska; Dr. Leigh Fredrickson, Director of the Gaylord Laboratory of the University of Missouri, who has over 30 years experience investigating inter-relationships among wetland structure, functions, and waterbird use; and Mr. Murray Laubhan, ecologist with the Mid-continent Ecological Science Center of the U.S. Geological Survey, who is conducting research on migratory bird use of montane wetland complexes. Published literature was relied upon extensively during the workshop.

The workshop included discussions of 1) the general life history of Trumpeter Swans, including anatomy, mortality, behavior, and food habits; 2) nesting habitat descriptions, including work by Banko (1960), Holton (1982), Lockman *et al.* (1982), Maj (1983), and Shea (1979); and 3) annual life cycle events, especially from an energetics perspective.

Discussion of specific ecological relationships was often generated by using detailed slide shows of actual wetland conditions and management options. The experts were asked to delineate their level of confidence in pieces of knowledge so that uncertainties could be represented in the knowledge base and associated with recommendations from the system. At the conclusion of the knowledge acquisition workshop, a flow chart of the most pertinent ecological knowledge and relationships was developed and provided to the experts for critique.

Subsequently, knowledge was encoded with a commercial expert system shell (Multilogic Exsys Developer, version 8.0(32)), using typical production rules organized into decision trees (Russell and Norvig 1995). An expert system shell is software that facilitates the development of expert systems by providing for the representation of knowledge. The evaluation, selection, and use of expert system shells has been described by Scott *et al.* (1991), Stylianou *et al.* (1995), and Vedder (1989). At run time, our system only uses the backward chaining capabilities of the shell's inference engine. Production rules are generally of the form:

IF
  the wetland is generally ice-free
  during the prelaying period
    AND
      30% of the wetland has Sago Pondweed
      (*Potamogeton pectinatus*) present
THEN
  the wetland should be considered
  good prelaying habitat.

Initially, a consultation can pertain to any wetland of interest by the user, but wetlands of inappropriate size and depth are eliminated from consideration during the first stages of each consultation. Thereafter, the spatial scope of individual rules is simple and straightforward. Correct interpretation by the user of questions posed by the system is dependent on our use of judicious wording of those questions, providing specific definitions to the user where necessary, and allowing user input only from lists of specific responses.

After conclusion of the workshop, knowledge was encoded and experts were contacted for further clarification of ecological information. Finally, the prototype system was demonstrated to swan managers and biologists and their input was used to further refine the knowledge base. The expert system was made available for evaluation via the World Wide Web (http://swan.msu.montana.edu/cygnet).

RESULTS

Knowledge engineering allowed us to categorize pertinent facts into six decision trees and 20 stand-alone rules, for a total of 157 total rules. The six trees are depth and size of the wetland, length of the annual ice free period, prelaying food resources, nest site availability, propensity for nest flooding, and brood habitat. The interaction of these decision trees and production rules is shown in the flowchart in Figure 1. Table 1 provides an example of the criteria used to determine the confidence values underlying one of the six trees, the brood habitat tree. The top row in the table is interpreted as:

IF
  some water remains available until
  typical fledging time
    AND
      emergents are growing at the
      water's surface during brood rearing
    AND
      dry sites for brooding exist the
      first few weeks after hatch
THEN
  we are 100 percent confident that
  brood habitat is sufficient.

The experts encouraged us to provide a quantitative assessment of the value of an area

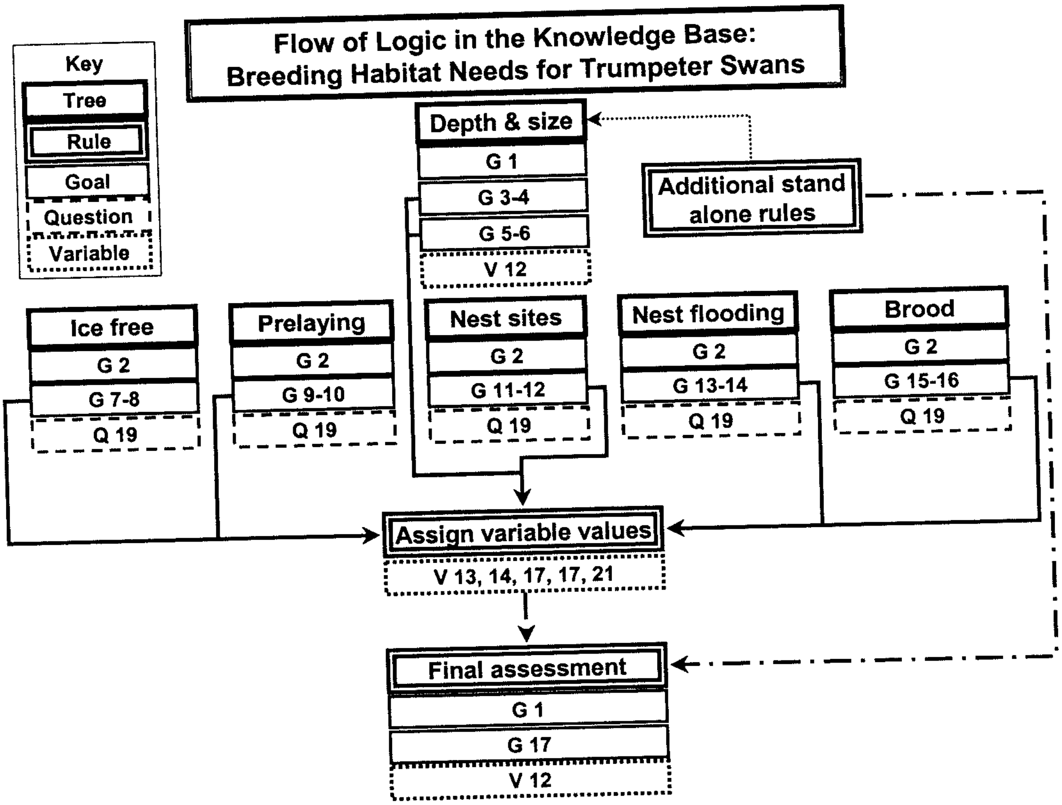


Figure 1. A flowchart of ecological logic in the knowledge base for assessing breeding habitat for Trumpeter Swans in the Northern Rocky Mountains. The consequents of rules, that are not internal to individual trees, are shown as antecedents to other rules external to those trees. The direction of flow is indicated by arrows.

as Trumpeter Swan breeding habitat. During each run of the system, an intermediate qualitative assessment is developed and subsequently converted to a quantitative final assessment. To do this, each of five intermediate output parameters from the knowledge base (*Depth, Size, Prelay, Nest,* and *Brood*) is associated with a pair of variables. One is used as a base variable and one as a multiplier, the latter providing emphasis to certain ecological parameters. Two additional intermediate output parameters (*Ice* and *Flood*) are assigned a multiplier variable only. Potential values of these variables are found in Table 2. Eighteen production rules are used to assign values to the intermediate variables and to provide a final assessment value using the following algorithm:

```
IF
    >= 1 parameter fails
THEN
    final assessment = 0
ELSE
    final assessment = (Depth + Size + Prelay + Nest + Brood)
    * Depth Multiplier * Size Multiplier
    * Prelay Multiplier * Nest Multiplier
    * Brood Multiplier * Ice Multiplier
    * Flood Multiplier.
```

The algorithm, along with the additive and multiplicative values listed in Table 2, provide a mathematical representation of the experts' description of how the ecological knowledge should combine to form an assessment. A key aspect of this algorithm is that whenever one parameter does not meet certain minimum conditions (*fails*), the area is not considered to be adequate breeding habitat and receives a final assessment value of zero. The importance of the ice-fee period and the frequency with which nests are flooded is also emphasized algebraically. The final assessment value is described to the user as an . . .

Table 1. Criteria used to determine confidence values in the brood habitat tree. The brood habitat tree is one of three trees in the expert system used to assess Trumpeter Swan breeding habitat quality. An "X" indicates the presence of that characteristic.

Confidence value	Brood water available	Primary food: emergents	Primary food: submergents	Food provided primarily by treadling	Dry sites for brooding
100	X	X			X
100	X		X		X
90	X			X	X
85	X	X			
85	X		X		
75	X			X	
0	X				X
0					

". . . assessment of the degree to which this wetland represents ideal habitat for breeding Trumpeter Swans, based on a synthesis of all information. On a scale of 0-100, the higher the number, the more confident one can be that satisfactory habitat exists. A zero indicates that at least one habitat component is severely compromised."

Input from the user is gathered by using questions with responses chosen from lists of potential answers (Fig. 2). Actual questions posed to the user are determined at run time through the backward chaining nature of the inference engine. An example of output from the expert system as provided to the user is found in Figure 3.

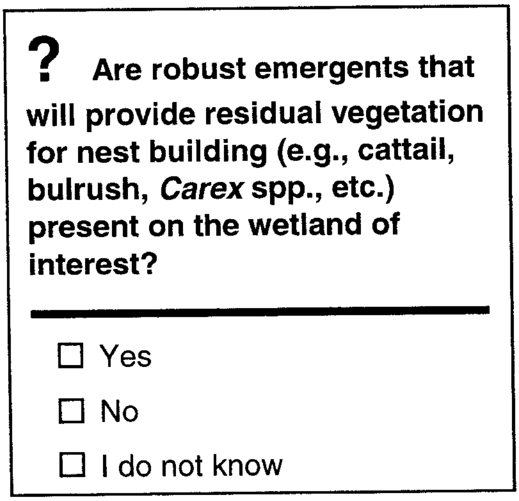
Table 2. Potential values of variables assigned for each ecological parameter used to calculate a final assessment of Trumpeter Swan breeding habitat quality.

Parameter	Parameter's value	Additive variable	Multiplier variable
Depth	Fails	0	0
	Passes[a]	25	1
Size	Fails	0	0
	Passes[a]	25	1
Ice free [no. yrs out of 10]	10-6[a]	0	1
	5-3	0	0.4
	0-2	0	0
Prelaying[b]	100[a]	15	1
	80	10	1
	Fails	0	0
Nest sites[b]	95[a]	20	1
	90	15	1
	Fails	0	0
Brood habitat[b]	90-100[a]	15	1
	75-85	10	1
	Fails	0	0
Nest flooding[b]	10-6[a]	0	0
	5-3	0	0.6
	0-2	0	1

---

[a] This combination of variable values would result in a final assessment value of 100.

[b] The value of the parameter is equal to the confidence value from the decision tree.



? **Are robust emergents that will provide residual vegetation for nest building (e.g., cattail, bulrush, *Carex* spp., etc.) present on the wetland of interest?**

☐ Yes

☐ No

☐ I do not know

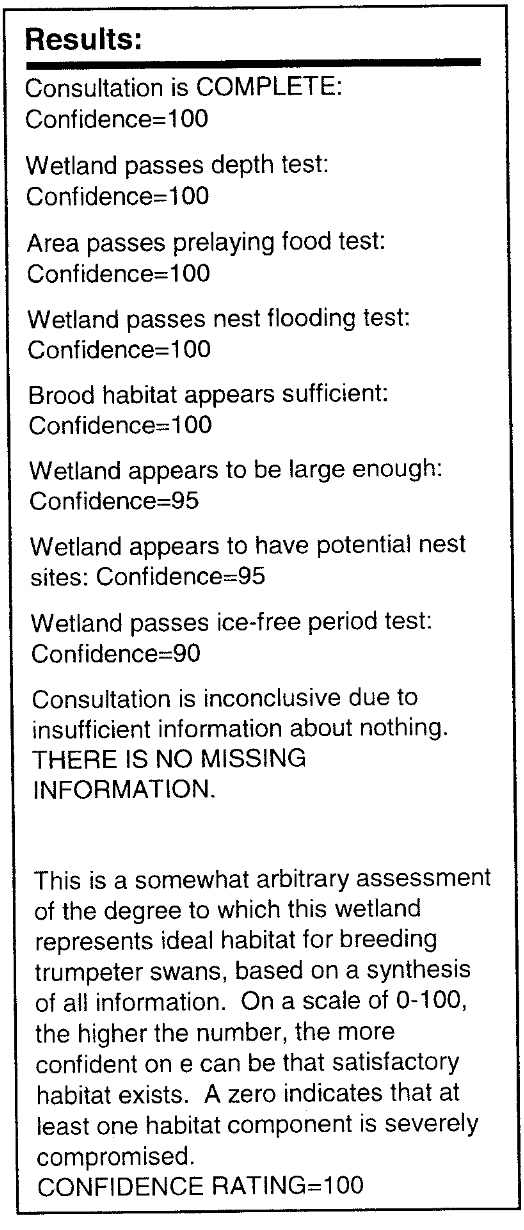
Figure 2. Example of an input screen from the expert system.

Verification of the expert system relied on utilities within the expert system development shell that identify variables, rules, and goals that were not used or where attempts were made to establish multiple values for them. The verification involved both a static logic check and completing 500,000 runs with random data. Additionally, hundreds of runs were made using scenarios based on known northern Rocky Mountain wetlands and hypothetical wetlands. We know of no logical inconsistencies in the current version.

DISCUSSION

The verification and validation efforts described above demonstrate the feasibility of representing complex ecological knowledge as symbolic computer code. The expert system encapsulates the knowledge necessary to describe breeding Trumpeter Swan habitat in the northern Rocky Mountains as subjectively and empirically described by the ecological experts. In addition, this knowledge was used to provide a quantitative assessment of the degree to which a particular wetland represents ideal Trumpeter Swan habitat. The knowledge base has been well-accepted by swan managers to whom it has been demonstrated.

This expert system is part of a project to examine the feasibility of applying cooperative distributed problem solving methods to flyway management of swans (Sojda and Howe 1999). Future validation efforts will be targeted towards those algorithms and how the different modules interact as intelligent entities. Although detailed, empirical, field evaluation of this particular expert system is necessary, it was beyond the scope of the current project. One of the values of expert sys-



Results:

Consultation is COMPLETE:
Confidence=100

Wetland passes depth test:
Confidence=100

Area passes prelaying food test:
Confidence=100

Wetland passes nest flooding test:
Confidence=100

Brood habitat appears sufficient:
Confidence=100

Wetland appears to be large enough:
Confidence=95

Wetland appears to have potential nest
sites: Confidence=95

Wetland passes ice-free period test:
Confidence=90

Consultation is inconclusive due to
insufficient information about nothing.
THERE IS NO MISSING
INFORMATION.

This is a somewhat arbitrary assessment
of the degree to which this wetland
represents ideal habitat for breeding
trumpeter swans, based on a synthesis
of all information. On a scale of 0-100,
the higher the number, the more
confident on e can be that satisfactory
habitat exists. A zero indicates that at
least one habitat component is severely
compromised.
CONFIDENCE RATING=100

Figure 3. Example of an output screen from the expert system.

tem technology is that it allows knowledge engineers to make existing expertise available to others. Often such an approach is most valuable in situations where it is not currently feasible to procedurally model causal relationships because 1) empirical data from scientific experiments are lacking, or 2) the complexity of the system of interest prevents mathematical descriptions of those causal relationships. It is our opinion that both of these conditions exist for Trumpeter Swans in the northern Rocky Mountains. Once a detailed understanding of the breeding ecology of these birds is more complete, we can design field experiments to validate this expert system.

ACKNOWLEDGMENTS

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Bayesian Time Series Analysis of Segments of the Rocky Mountain Trumpeter Swan Population

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Abstract.—A Bayesian time series analysis technique, the dynamic linear model, was used to analyze counts of Trumpeter Swans (*Cygnus buccinator*) summering in Idaho, Montana, and Wyoming from 1931 to 2000. For the Yellowstone National Park segment of white birds (sub-adults and adults combined) the estimated probability of a positive growth rate is 0.01. The estimated probability of achieving the Subcommittee on Rocky Mountain Trumpeter Swans 2002 population goal of 40 white birds for the Yellowstone segment is less than 0.01. Outside of Yellowstone National Park, Wyoming white birds are estimated to have a 0.79 probability of a positive growth rate with a 0.05 probability of achieving the 2002 objective of 120 white birds. In the Centennial Valley in southwest Montana, results indicate a probability of 0.87 that the white bird population is growing at a positive rate with considerable uncertainty. The estimated probability of achieving the 2002 Centennial Valley objective of 160 white birds is 0.14 but under an alternative model falls to 0.04. The estimated probability that the Targhee National Forest segment of white birds has a positive growth rate is 0.03. In Idaho outside of the Targhee National Forest, white birds are estimated to have a 0.97 probability of a positive growth rate with a 0.18 probability of attaining the 2002 goal of 150 white birds.

Key words.—Bayesian analysis, *Cygnus buccinator*, dynamic linear model, Rocky Mountain Population, Trumpeter Swans.

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The Greater Yellowstone and Western Canada Populations of Trumpeter Swans (*Cygnus buccinator*) summer along the Rocky Mountains in the Tri-state area of the United States and in Canada, respectively, and share wintering grounds in the Tri-state area (i.e., southwest Montana, eastern Idaho, and western Wyoming) (Gale *et al.* 1987). Following European settlement, these populations were pushed nearly to extinction. In 1932, the Greater Yellowstone Population was comprised of 58 white birds (sub-adults and adults combined) and 12 cygnets (Subcommittee on Rocky Mountain Trumpeter Swans 1998), while the Western Canada Population was comprised of approximately 77 white birds and their cygnets which summered near Grande Prairie, Alberta (Gale *et al.* 1987). In 1935, the Red Rock Lakes National Wildlife Refuge was established in the Centennial Valley of southwest Montana. Supplemental winter feeding at Red Rock Lakes from 1935 to 1993 allowed the Centennial Valley segment of the Greater Yellowstone Population to increase to a maximum of 401 white birds in 1954 while contributing over 530 swans to restoration efforts at other sites from 1938–1983 (Subcommittee on Rocky Mountain Trumpeter Swans 1998). Over the entire region, the Greater Yellowstone Population increased to a maximum of 554 white birds in 1964, but has generally decreased since, with 324 white birds present in the autumn of 2000 (U.S. Fish and Wildlife Service 2000). By contrast, the Western Canada Population increased through the 1980s and 1990s, with an estimated 2,397 Canadian white birds wintering in the USA in February, 2000 (U.S. Fish and Wildlife Service 2000).

In this paper, time series of numbers of white birds in the Greater Yellowstone Population are analyzed. Greater Yellowstone swans are the focus for two reasons: (1) since 1931, relatively continuous records of autumn Trumpeter Swan counts have been recorded from Idaho, Montana, and Wyoming (Subcommittee on Rocky Mountain Trumpeter Swans 1998); and (2) the apparent decline of the Greater Yellowstone Population in the face of a rapidly growing Western Canada Population seems to merit examination.

For the purpose of these analyses, the Greater Yellowstone Population was divided into the five segments specified in the Pacific Flyway Management Plan (Subcommittee on Rocky Mountain Trumpeter Swans 1998): Yellowstone National Park (NP), the state of Wyoming outside of Yellowstone NP, the Centennial Valley (including Red Rock Lakes National Wildlife Refuge), the greater Targhee National Forest area including Harriman State Park, and the state of Idaho outside of Targhee National Forest (Fig. 1). For each segment, we estimated the growth rate and quantitatively assessed the likelihood of achieving 2002 population goals specified in the Pacific Flyway Management Plan.

The dynamic linear model, a Bayesian method of time series analysis widely employed in economic forecasting (Pole *et al.* 1994; West and Harrison 1997), was used to analyze Trumpeter Swan time series. While this methodology has seen limited use in environmental toxicology (Lamon *et al.* 1998, 1999), to the best of our knowledge, we present its first use as a tool for analyzing time series of animal abundance. The method is not presented as a critique of more traditional techniques of trend analysis, like linear regression, but rather as a demonstration of a new approach on its own merits.

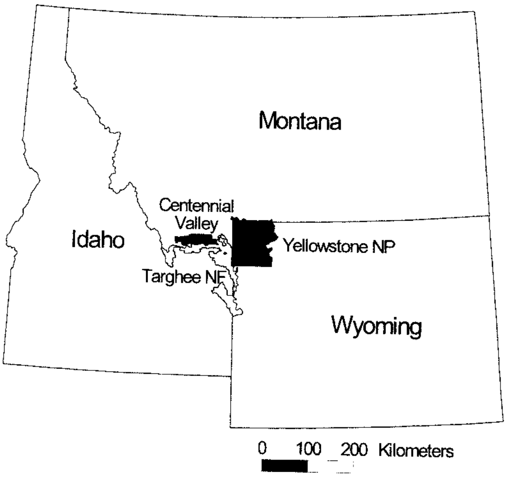

Figure 1. Map of the Tri-state area of Montana, Idaho, and Wyoming where the following five segments of the Greater Yellowstone Population of Trumpeter Swans breed: Yellowstone National Park (NP), the state of Wyoming outside of Yellowstone NP, the Centennial Valley, the greater Targhee National Forest (NF), and the state of Idaho outside of Targhee NF.

METHODS

Within the dynamic linear model, swan counts at each autumn census are modeled by an "observation equation", equation [1], where the number of swans counted at year t, Y_t, is treated as a random variable drawn from some probability distribution, for example a normal distribution.

$$\text{Observation equation: } Y_t = \mu_t + v_t \quad v_t \sim N(0, V) \quad [1]$$

The mean of this distribution, μ_t, can be thought of as a "true" number of swans that cannot be determined exactly, thus we add v_t, a normally distributed measurement error with a mean of zero and a variance of V. Assuming that a time series of Trumpeter Swan counts is a manifestation of both systematic and random influences, time-evolution of the μ_t term is represented in the dynamic linear model by the first component of the "system equation", equation [2a], where μ_t equals μ_{t-1} plus a growth rate or trend, β_t, plus a zero-mean, stochastic term, $\omega_{1,t}$. In other words, the change in the number of swans over one year is represented as a combination of a positive or negative trend, β_t, with random variation about that trend, $\omega_{1,t}$. The trend can be thought of as the result of some systematic influence or influences acting on a population segment, for instance the supplemental winter feeding program at Red Rock Lakes. Additionally, the trend might reflect some systematic attribute of a Trumpeter Swan population, say range expansion into suitable habitat. By contrast, the stochastic error term, $\omega_{1,t}$, reflects the result of chance events acting on a population segment, for example mortality caused by unusually cold winter weather. Intuitively, it would not seem reasonable to assume that the growth term would remain constant over time, for example it might slow as a swan population approaches an environmental carrying capacity. Thus, β_t is modeled as a random walk over time in equation [2b] where β_t equals β_{t-1} plus another zero-mean, stochastic term, $\omega_{2,t}$.

$$\text{System equation: } \mu_t = \mu_{t-1} + \beta_t + \omega_{1,t} \quad \omega_{1,t} \sim N(0,W_1) \quad [2a]$$

$$\beta_t = \beta_{t-1} + \omega_{2,t} \quad \omega_{2,t} \sim N(0,W_2) \quad [2b]$$

The observation and system equations are used in tandem to make forecasts. Given estimates of the parameters μ_t and β_t, and estimates of the variances W_1, W_2, and V, substitution of the system equation into the observation equation yields a forecast distribution of swans one year into the future,

$$Y_{t+1} = \mu_t + \beta_t + \omega_{1,t+1} + \omega_{2,t+1} + v_{t+1} \quad [3]$$

Conversely, in making a forecast further into the future, say t + k years, the system equation would be applied k years into the future, substituting into the observation equation so that,

$$Y_{t+k} = \mu_t + k*\beta_t + \omega_{1,t+1} + \omega_{1,t+2} + \ldots + \omega_{1,t+k} + \omega_{2,t+1} + \omega_{2,t+2} + \ldots + \omega_{2,t+k} + v_{t+k} \quad [4]$$

Note that as forecasts extend further into the future, more ω_1 and ω_2 error terms are added, thus increasing forecast uncertainty over longer time-horizons.

The next step in application of the dynamic linear model is to evaluate the accuracy of the forecast when actual data becomes available. Central to the model is the sequential nature of this analysis. Starting with some prior belief about the μ_t and β_t parameters at time t, the model forecasts swan abundance at time t + 1. Then the actual number of swans at time t + 1 is observed and used to modify estimates of μ_t and β_t. This updated estimate is known as a posterior belief. Now, suppose that a time series of Trumpeter Swan abundances is in hand. In this case, our sequential analysis begins at the first observation in the time series. Given a prior belief, we forecast the first observation, use the first actual observation to determine a posterior belief, and move on to the next value in the time series, transforming our posterior belief at time t into a prior belief at time t + 1. Repeating this sequence of analysis, the model proceeds through the time series.

Bayes' theorem is the tool by which a prior belief is combined with an observation to generate a posterior belief. Given a prior probability distribution of μ and β, $p(\mu_t, \beta_t)$, and observed Trumpeter Swan counts at time t, the posterior distribution of μ and β, $p(\mu_t, \beta_t \mid Y_t = y_t)$ is calculated by Bayes' theorem as,

$$p(\mu_t, \beta_t \mid Y_t = y_t) \propto p(\mu_t, \beta_t) L(Y_t = y_t \mid \mu_t, \beta_t) \quad [5]$$

where the likelihood function, $L(Y_t = y_t \mid \mu_t, \beta_t)$, is the forecast distribution of Y_t (equation [3]) evaluated at the observed value, y_t, over all possible values of μ_t and β_t so that,

$$L(Y_t = y_t \mid \mu_t, \beta_t) \propto p(Y_t = y_t \mid \mu_t, \beta_t) \quad [6]$$

Thus the posterior distribution of μ_t and β_t is proportional to the prior probability distribution of μ_t and β_t times the probability of observing y_t over the range of all possible values of μ_t and β_t. In other words, the likelihood function more heavily weights those values of μ_t and β_t that are consistent with the observed number of swans. The posterior distribution at time t is then used as a prior distribution at time t + 1 following the addition of system evolution variance via equation [2]. A complete development of the dynamic linear model, including the method used to estimate the three variances (V, W_1, and W_2), is presented in Pole *et al.* (1994) West and Harrison (1997).

Systematic efforts to conduct censuses of the Greater Yellowstone Population have been ongoing since 1929. While the census was limited to known nesting areas before 1936, coordinated ground surveys were made by the U.S. Fish and Wildlife Service and U.S. Park Service from 1936 to 1945. From 1946 to the present, the U.S. Fish and Wildlife Service has conducted aerial surveys of the Tri-state area, allowing thorough coverage of potential habitat (Gale *et al.* 1987). All time series used in this study were assembled from autumn (typically September) counts of white birds (sub-adults and adults combined) and include counts from 1931 to 1968 (archived in Subcommittee on Rocky Mountain Trumpeter Swans 1998)and counts from 1971 to 2000 (archived in U.S. Fish and Wildlife Service 1971–2000).

All time series were analyzed using BATS (Bayesian Analysis of Time Series) software distributed with Pole *et al.* (1994) or available as freeware from the Institute of Statistics and Decision Sciences at Duke University (www.stat.duke.edu). All time series were transformed by the natural log operation. Given this transformation, the trend, β_t, has units of $\log_e$(white birds) year^{-1}. This additive trend in log-space (equation [2]) corresponds to a multiplicative trend in the original measurement space (white birds) so that β_t is equivalent to a percent change in white birds year^{-1}. For each analysis, the initial marginal prior distribution of μ was specified as a Student-t distribution with a mean equal to the first available $\log_e$(white birds) data point and a standard deviation of 0.50. This specification combines the information inherent in the first observation with a high degree of uncertainty. Similarly, the marginal prior distribution of the growth parameter was specified as Student-t with a mean of 0.0 and a standard deviation of 0.10. Given only one data point at time t = 0, a prudent choice is to assume zero growth with large uncertainty. Given these priors, the first round of forecast-based inference was begun using the second value of each time series.

RESULTS

Log-transformed white bird counts for five segments of the Greater Yellowstone Population are plotted in Figure 2. Forecast distributions of autumn counts were computed annually regardless of whether an autumn census was conducted in a particular year. Each forecast probability distribution is Student-t distributed with solid lines marking forecast means over time. The spread of each forecast distribution is summarized by 90% credible intervals (Fig. 2) where these intervals delineate equal-tailed, upper and lower bounds such that the estimated probability of the true number of $\log_e$(white birds) falling within the interval is equal to 0.90. Credible intervals of 90% also correspond to values such that the true number of $\log_e$(white birds) is estimated to be less than the upper bound, or greater than the lower bound, with probability equal to 0.95.

The 2002 forecast distributions (Table 1) were used to estimate the probability that true 2002 $\log_e$(white bird) counts would be greater than or equal to $\log_e$(white bird goals). The probabilities of achieving individual population goals, as specified in the 1998 Pacific Flyway Management Plan (Subcommittee on Rocky Mountain Trumpeter Swans 1998), are reported in Table 1. For comparison to 2002 population goals, Table 1 also reports the 2002 forecast mean in $\log_e$(white birds) back-transformed to white bird units, which is equivalent to a 2002 forecast median in white bird units (Lamon *et al.* 1998).

Posterior distributions of the trend parameter, β_t, are Student-t random variables and, as above, are described by time plots of their means and 90% credible intervals (Fig. 3). Year 2000 posterior distributions of β_t for each Trumpeter Swan population segment,

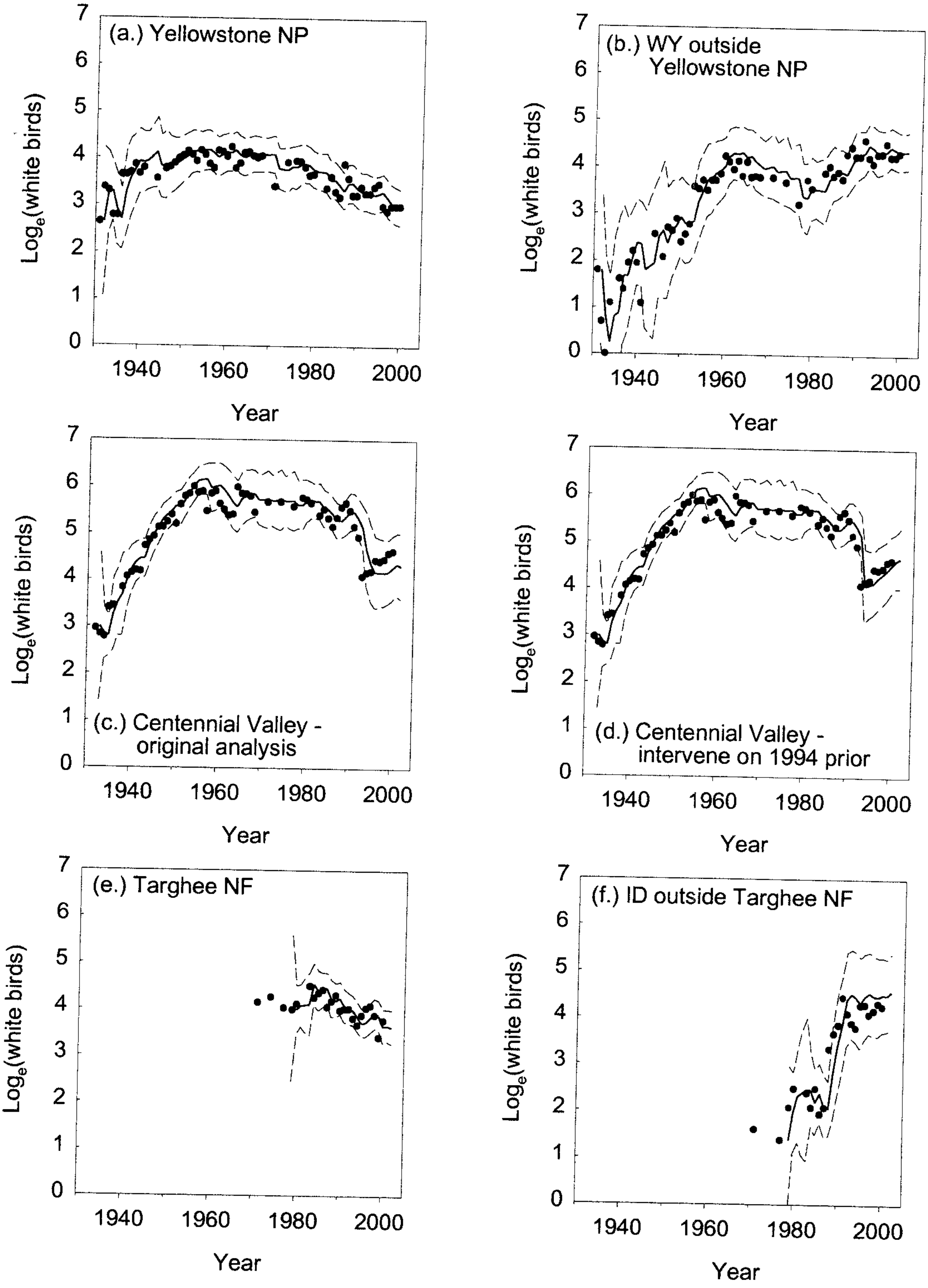

Figure 2. Forecast distributions of log$_e$(white birds) for five segments of the Greater Yellowstone Population of Trumpeter Swans. Filled circles are actual autumn counts. Solid lines represent the mean of forecast distributions while dashed lines delineate 90% credible intervals about the mean.

and the probability that the trend is positive, i.e. the probability that $\beta_t > 0$, are summarized in Table 1.

Within Yellowstone National Park, increasing white bird numbers were observed from 1931 to the mid-1950s, but from 1969 to the present, the Yellowstone segment has gradually declined (Fig. 2a). This decline is reflected in a plot of Yellowstone National Park trend parameters over time where posterior distributions exhibit strictly negative means from 1971 to 2000 (Fig. 3a). Given the 2002 forecast distribution, the estimated probability of achieving the 2002 goal is less than 0.01 (Table 1). Another way to express the likelihood of achieving the 2002 goal is as an odds-ratio computed as the ratio of the probability mass less than the goal to the probability of meeting the goal (Lamon *et al.* 1998). In this case, the odds are approximately 1,406:1 against achieving the 2002 goal. Similarly, there is only a 0.01 probability that the current Yellowstone growth rate is greater than zero (Table 1), and 189:1 odds against positive growth.

In the state of Wyoming outside of Yellowstone National Park, a more encouraging population trajectory is observed. In this segment, white bird counts have generally increased over the past 70 years (Fig. 2b). Given the 2002 forecast distribution, there is a 0.05 probability of achieving the 2002 goal of 120 white birds (Table 1) and 21:1 odds against achieving the stated goal. While the posterior mean of this segment's trend was slightly negative through the late 1970s and early 1980s, a positive mean trend is estimated up to the present (Fig. 3b). Although the year 2000 posterior trend has a modest mean of 1.5% year^{-1}, there is a 0.79 probability that the current growth rate is greater than zero (Table 1) and 4:1 odds in support of a positive growth rate.

In the Centennial Valley, a dramatic decline from 289 white birds in 1989 to 60 white birds in 1993 is observed following a gradual decline from the early 1960s to the mid-1980s (Fig. 2c). This decline coincides with two significant management interventions at Red Rock Lakes National Wildlife Refuge. From 1990 to 1992, a total of 100

Table 1. Summary of 2002 forecast distributions, 2002 population goals, and 2000 posterior distributions of the trend parameter, β_t, for five segments of the Greater Yellowstone Population of Trumpeter Swans.

	2002 forecast				2000 posterior trend	
Population segment	Mean $\log_e$(white birds) ±90% credible interval	Median white birds	2002 white bird population goal[a]	Probability achieving goal	Mean trend (% yr^{-1}) ±90% credible interval	Probability trend > 0
Yellowstone National Park	2.91 ± 0.38	18	40	<0.01	-3.5 ± 2.2	0.01
Wyoming outside Yellowstone	4.37 ± 0.41	79	120	0.05	1.5 ± 3.3	0.79
Centennial Valley—original analysis	4.32 ± 0.70	75	160	0.04	-4.9 ± 5.8	0.08
Centennial Valley—intervene on 1994 prior	4.68 ± 0.64	108	160	0.14	5.2 ± 7.9	0.87
Targhee National Forest	3.61 ± 0.36	37	—[b]	—[b]	-3.8 ± 3.2	0.03
Idaho outside Targhee	4.58 ± 0.81	97	150	0.18	8.7 ± 7.1	0.97

[a] Subcommittee on Rocky Mountain Trumpeter Swans (1998).

[b] No goal specified.

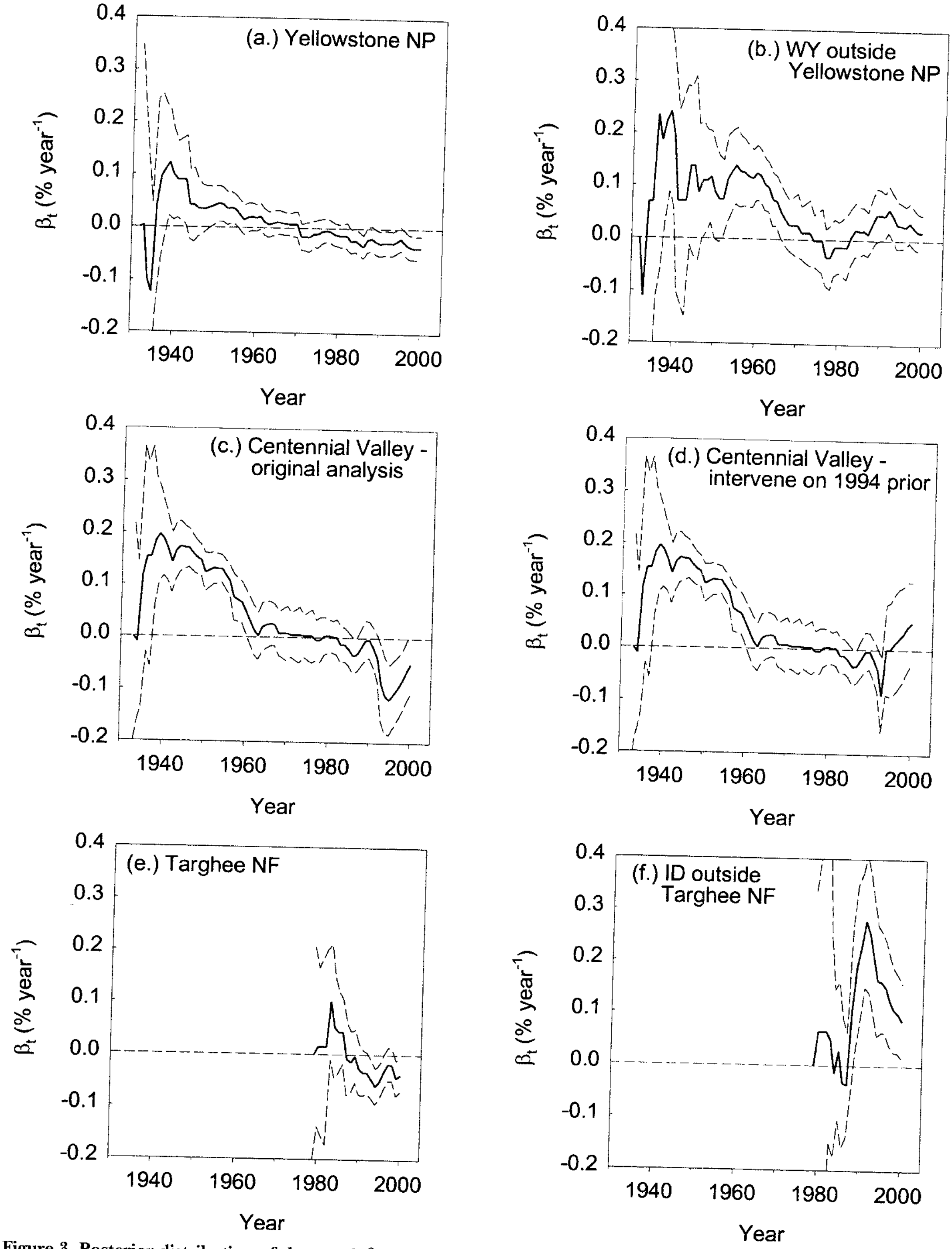

Figure 3. Posterior distribution of the trend, β_t, for five segments of the Greater Yellowstone Population of Trumpeter Swans. Solid lines represent the mean of posterior distributions while dashed lines delineate 90% credible intervals about the mean.

white birds and 54 cygnets were translocated from Red Rock Lakes to sites in southern Idaho, the Green River basin in Wyoming, and Summer Lake, Oregon. And over the winter of 1992-1993, supplemental feeding at Red Rock Lakes was terminated (Subcommittee on Rocky Mountain Trumpeter Swans 1998). Post-1993, however, the Centennial Valley segment appears to be increasing (Fig. 2c).

Given the gradual decline up to the mid-1980s, and the rapid decline from 1989 to 1993, our original analysis of the Centennial Valley segment tends to discount the apparent increase in white birds post-1993 (Fig. 2c). Qualitatively, our iterative method retains a "memory" of past system behavior. The posterior trend parameter is driven negative by the 1989 to 1993 decline and the slight increases observed in 1994 and 1995 are not sufficiently inconsistent with the existing model to force a reversal of the trend (Fig. 3c). Post-1995, the trend parameter becomes increasingly less negative (Fig. 3c), although the 2000 posterior mean is -4.9% year^{-1} with only a 0.08 probability of a positive value (Table 1), or 12:1 odds against a trend greater than zero. However, the dynamic linear model is designed with the principle of "management by exception" in mind (Pole *et al.* 1994). Under "typical" conditions, it assumes that model parameters will vary fairly smoothly over time. However, the model also allows the analyst to subjectively intervene in the analysis when it appears that the time series of interest has changed in some "exceptional" way. Given the history of management at Red Rock Lakes discussed above, we decided there was sufficient evidence to justify intervening on the analysis post-1993.

Intervention was implemented by manually specifying prior distributions for the μ_t and β_t parameters before the 1994 forecast analysis. The 1994 marginal prior distribution of the mean parameter was set at the 1993 count, $\log_e$(60 white birds). The 1994 prior distribution of the trend parameter was set to zero with a standard deviation of 0.05. Qualitatively, locating the trend at zero with an intermediate level of uncertainty forces the data from 1994–2000 to determine the trend, irrespective of the time series' previous history.

The effect of intervening on the 1994 prior distribution of the trend is pronounced. The intervention analysis indicates an increasingly positive mean posterior trend from 1995 to 2000 (Fig. 3d). As a result, the mean of the Centennial Valley forecast distribution trends upward from 1995 to 2002 (Fig. 2d). Given the year 2000 posterior distribution of the trend, there is an estimated 0.87 probability that the Centennial Valley segment has a positive trend (Table 1). Given a 2002 forecast distribution with a median of 108 white birds, there is an estimated 0.14 probability of achieving the 2002 population goal of 160 white birds (Table 1). This prediction contrasts with our original analysis, where we predicted a 2002 forecast median of 75 white birds and found the probability of achieving the 2002 goal to be 0.04 (Table 1).

Prior to 1971, Targhee National Forest white birds were not distinguishable from Idaho counts in general. Given that Targhee counts are sparse through the 1970s, we chose to postpone the starting point of our forecast analysis until 1979 (Fig 2e). The Targhee segment of white birds has generally declined over the past 20 years. Given this decline, there is a 2002 forecast median of 37 white birds (Table 1). No 2002 population goals have been specified for this segment. Based on the 2000 posterior distribution of the trend, there is a 0.03 probability that the trend is greater than zero (Table 1), or equivalently, 36:1 odds against a positive value.

The Idaho outside of Targhee National Forest segment of white birds has generally increased over the last 20 years (Fig. 2f). While the trend appears to have slowed over the 1990s (Fig. 3f), the estimated 2000 mean growth is 8.7% year^{-1} (Table 1). This value may be slightly high given that the mean forecast is greater than all measured log(white bird) values from 1992 to 2000 (Fig. 2f). The transition from the high-growth interval of 1987 to 1991 to slower growth is abrupt, and the model appears to lag slightly. Nonetheless, the current estimate is a 0.97 probability of a positive trend (Table 1), or 38:1 odds supporting a value greater than zero. Given a 2002 median forecast of 97 white birds, there is a 0.18 probability of achieving the 2002 objective of 150 white birds (Table 1) (Subcommittee on Rocky Mountain Trumpeter Swans 1998).

DISCUSSION

While the contrast between the two analyses of the Centennial Valley time series over the last ten years might raise concern that the dynamic linear model can be parameterized in ways that provide whatever answer is desired, we think that these contrasting results nicely bracket the question of whether removing a number of Trumpeter Swans from Red Rock Lakes National Wildlife Refuge and terminating winter feeding have sufficiently reset the Centennial Valley segment at a population level where it is now increasing, or whether a long-term population decline is occurring in addition to the reductions brought about by management. The iterative fashion in which the dynamic linear model is applied should make it well suited to addressing this question as more census data becomes available.

The ability to intervene on the Centennial Valley analysis discussed above is implicit in the definition of μ_t and β_t as varying over time in equation [2]. This definition of a trend that varies over time contrasts with a more traditional technique, like linear regression, where a static slope parameter is estimated for an entire time series (Pole *et al.* 1994). However, the dynamic linear model is a much more complicated model than linear regression. In most management scenarios, a less complex statistical model might be perfectly appropriate. The dynamic linear model is presented here not as a criticism of other methods, but rather as a relatively new technique that Trumpeter Swan managers might find useful.

In summary, white bird population trends in the state of Wyoming outside of Yellowstone National Park, and in the state of Idaho outside of Targhee National Forest, are encouraging. However, higher elevation segments in the core Tristate area, especially white birds in Yellowstone National Park and the Targhee National Forest, may merit concern. The status of the Centennial Valley segment appears to be uncertain and most likely will require additional monitoring to resolve. Across the five segments of the Greater Yellowstone Population considered, our analysis indicates low to very low probabilities of meeting 2002 white bird goals. Finally, we suggest that the Bayesian approach described in this paper is readily applicable to future monitoring of the Greater Yellowstone Population of Trumpeter Swans.

ACKNOWLEDGMENTS

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Potential Wind Park Impacts on Whooper Swans in Winter: the Risk of Collision

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Abstract.—Morning and evening flights of Whooper Swans (*Cygnus cygnus*) wintering near Overgaard, in eastern Jutland, Denmark, were studied to assess the potential risk of collisions with medium sized or with large turbines, should a proposed wind park be developed in the area. The birds could be particularly prone to collisions during evening flights, as these took place in rather poor light conditions. Recorded heights of swan flights indicated that a park consisting of medium sized wind turbines would be more critical in terms of collision risk than one with large turbines, with 38% of observed individuals flying within height range of the rotors in the former, only 13% in the latter.

Key words.—Altitude of flight, collision risk, *Cygnus cygnus*, light conditions, wind parks, wind turbines, Whooper Swan.

Waterbirds 25 (Special Publication 1):327–330, 2002

Of the potential impacts of wind turbines on birds, the risk of collision is perhaps the most severe, since it has an immediate effect on the survival of individuals and perhaps longer-term consequences if mortality levels for the population are raised. Existing knowledge of the extent to which birds collide with wind turbines suggests that, in general, the risk is low (Clausager and Nøhr 1995). For waterfowl, however, data on this issue are very limited (Winkelman 1992; Dirksen *et al.* 1998) and, in the case of swans, rest solely on anecdotal evidence. Because of their low maneuverability in flight, swans may be particularly prone to collisions with wind turbines. Furthermore, populations of long-lived species such as swans could be susceptible to even small increases in adult mortality levels (Saether *et al.* 1996).

This note considers the risk of wintering Whooper Swans (*Cygnus cygnus*) colliding with wind turbines, based on observations recorded during an environmental impact assessment study for a proposed wind park. The daily movements of swans between nocturnal roosts and daytime feeding areas were monitored and analyzed with respect to timing relative to sunrise and sunset, light conditions and altitude of flights. Apart from constituting the most intense periods of flight activity during the day, these flights take place at a time of day (dawn and dusk) when light conditions are poor, and the swans' ability to see the turbines is likely to be diminished. The point at which the swans' eyes are no longer able to compensate for decreased light is not known, but birds flying at night are considered unlikely to have more visual information available to them than humans under the same circumstances (Martin 1990).

STUDY AREA AND WIND PARK

The study was conducted near Overgaard (56°67' N, 10°30' E), south of Mariager Fiord in eastern Jutland, Denmark, within an internationally important Whooper Swan wintering area. Two scenarios were considered for a proposed 41.25 Megawatt (MW) wind park. Both had the same location, and covered the same area, but differed in the size and numbers of turbines involved. The first scenario consisted of 55 medium sized turbines, each producing 0.75 MW, with towers 45 m high and rotors 48 m in diameter. The second scenario consisted of 25 large turbines, each producing 1.65 MW, with towers 68 m high and rotors 66 m in diameter. The rotors, which are thought to present the main risk of collision, sweep the heights of 21–69 m and 35–101 m, respectively. The sum of the turbine rotor areas was comparable for the two park scenarios (16% larger rotor area for the park with medium sized turbines).

METHODS

The daily movements of Whooper Swans between coastal roost sites and daytime inland feeding sites were investigated on four occasions each for the morning and evening flights. Morning flights were monitored on

21 January, 10 February, 15 and 23 March 1998; evening flights on 21 January, 10 and 16 February and 15 March 1998. Observations were carried out by one or two observers who, for the morning flights, positioned themselves either in the vicinity of swans roosting on the coast, or at the inland feeding sites, half an hour before sunrise. Evening observations were conducted from a position overlooking one or more large flocks of swans, starting one hour before sunset. For each flock flying in or out, the time, flock size and altitude of flight were determined. Altitude was estimated in 5 m intervals, using landscape features of known height as visual reference. The height of landscape features, such as hedgerows, single trees, woodland and wind turbines, was determined from existing sources or measured using a laser binocular (Zeiss Halem II). As landscape features of differing heights were present at all observation sites, it is thought that errors in estimating altitude did not usually exceed 5 m for each flight. Flight altitudes were estimated for the center of flocks at the maximum height reached within the site. In addition, light conditions were recorded at 5 min intervals using a light intensity-measuring device (Mavolux digital). Morning observations were terminated when the frequency of flights had reached levels attributable to local changes in feeding distribution, and evening observations when the last birds had left the feeding site.

RESULTS

Birds leaving coastal roosts and flying inland were observed from 15 min before sunrise until about 2 h after sunrise. Light intensity during morning flights ranged between 100 lux and10,000 lux, corresponding to a change from dim but clear light to full daylight conditions. On one occasion, the arrival of 230 individuals at an inland feeding site was followed. Birds arrived gradually, the great majority (91%) within the first half hour after sunrise, at light intensities ranging from 500 to >2,000 lux.

Evening flights mainly occurred 20-50 min after sunset in the very last light of the day, with light intensities in this period ranging between 1 and 15 lux (Fig. 1). Flights on 21 January took place about 20 min later than during observations in February and March, a difference that could not be attributed to differing light conditions during observation days. Evening flights were very concentrated in time; on all four occasions 75% or more of the individuals present left within a 10 min period. The last swans were observed to leave at a light intensity of 0.3 lux. At light intensities of about 1 lux it was barely possible for observers to discern the contours of landscape features by eye.

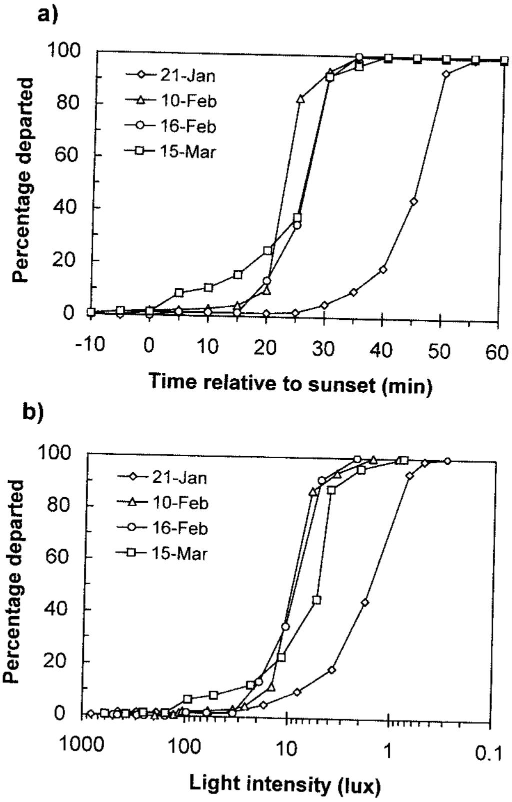

Figure 1. Timing of Whooper Swan evening flights, from feeding sites to nocturnal roosting sites, relative to: a) sunset and b) light intensity (note logarithmic scale). The number of individuals involved during the four observation days was 635 (21 January), 747 (10 February), 218 (16 February) and 470 (15 March).

The altitude of Whooper Swan flight was estimated for a total of 93 flocks, comprising 1,338 individuals, with morning and evening data combined. Altitude varied between 5 and 45 m, and the great majority of flocks flew 5-30 m above ground (Fig. 2). Relating the observed flight altitudes to the two models of turbines considered, 32% of all flocks and 38% of all individuals flew within the vertical height range swept by the rotors of the medium sized turbines, corresponding values being 9% and 13%, respectively, for the large turbines.

DISCUSSION

It seems likely that Whooper Swans will be fully capable of avoiding wind turbines during daylight and good visibility, as has

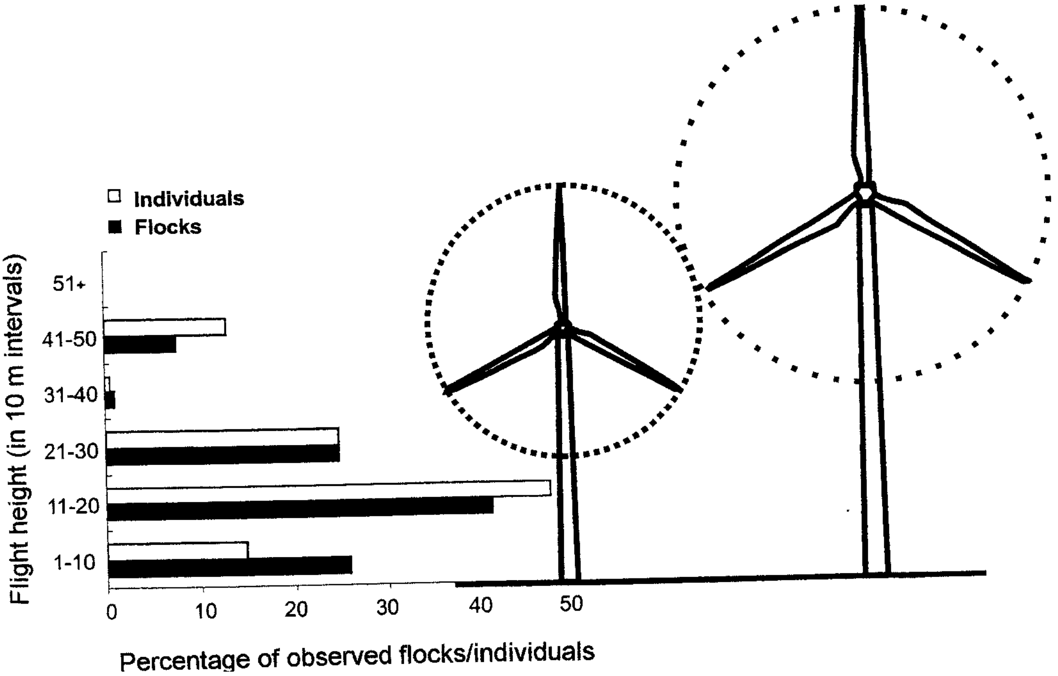

Figure 2. Heights reached by Whooper Swans flying between roosts and feeding sites, with the relative size of the two potential turbine types indicated. The figure is based on a total of 93 flocks and 1,338 individuals, and presents the combined data for morning and evening flights.

been found for other bird species (Winkelman 1992). The risk of collision for Whooper Swans in winter therefore is mainly during morning and evening flights to and from the roost and, since radar observations and satellite tracking have shown that swans may fly at night (Pennycuick *et al.* 1999; S. Dirksen pers. comm.), during any movements after dark.

The results of the present study suggest that, for the daily flights between roosts and feeding sites, the collision risk is greatest during the evening flight. Whooper Swans left their inland feeding sites when it was nearly dark, whereas they arrived at the same sites in the morning in full daylight conditions. The results also suggest that the risk of collision during evening flights may vary with season; flights mainly took place 40–50 min after sunset in January, compared to 20–30 min after sunset during observations in February-March. However, in addition to the shorter daylength, temperatures were below freezing during the January observation date. One or both factors therefore may have influenced the time of departure from the feeding grounds.

With respect to the two park scenarios considered, the results indicate that a risk of collision is present for both. It seems that the risk would be higher if medium sized turbines were used, rather than large turbines, as about a third of swan flocks (and individuals) flew within the height range of the medium sized turbine rotors, compared to a tenth for the large turbines. These proportions express the relative collision risk for the two park scenarios, assuming that swans—irrespective of turbine type—will continue passing through the park area, and that no adjustment in flight altitude will occur. The actual collision risk for Whooper Swan is likely to be substantially less than indicated by these figures due to avoidance behavior, with swans adjusting their flight paths (either vertically or horizontally) in response to the presence of the turbines, although it is also possible that some low-flying birds passing under the rotors may be disturbed and veer upwards in response to the rotor noise. It should be noted that the present study addressed flight altitude for local movements of swans only, which constituted the main risk of collisions for the proposed wind park. The pattern of flight altitudes may differ for other locations, especially if longer distance movements or actual migration is involved (Pennycuick *et al.* 1999).

If the two wind park scenarios have different disturbance effects on feeding Whooper Swans (i.e., avoidance distances differing between parks), this might influence the relative risk of collision. Disturbance effects of wind parks have been demonstrated for other large waterbird species, such as Pink-footed Geese (*Anser brachyrhynchus*), where habitat use was suppressed within 100–200 m of wind turbines (Larsen and Madsen 2000). However, studies have not yet addressed the relationship between the size of turbines in a wind park, and the extent to which these disturb the birds. It might be speculated that a large turbine wind park would be less disturbing to Whooper Swans than a medium sized turbine wind park, due to the greater distances between turbines. If this is the case, and swans were to continue feeding within the area of a large turbine wind park, but not in a medium turbine wind park, this could increase the risk of collision for the former.

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Threats to Whooper Swans in Xinjiang, China

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Abstract.—This paper presents the most recent information on threats to Whooper Swans (*Cygnus cygnus*) in Xinjiang, northwest China. Xinjiang holds the largest breeding and wintering numbers of Whooper Swans in the country. There are many illegal activities which affect the wildlife in the area, including hunting, fishing with explosives, poisoning, trapping, collecting eggs, and destroying nests. Moreover, over-population of domesticated animals causes serious degradation of the grassland.

Key words.—Breeding numbers, *Cygnus cygnus*, threats, Whooper Swan, Xinjiang.

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Swans have been hunted in China over many years, mainly for food and medicinal purposes (Pang 1974; Pang 1976). More recently, additional threats have become apparent, such as pollution of the environment (Ma and Cai 2000) and loss of habitat (Yuan and Zhang 1991; Yuan and Guo 1992). These developments have prompted people to express their concern over the future of swans in China (Xian 1982; Xu 1986); however, no population estimates have been published that show the effects directly.

Xinjiang harbors both the main breeding and wintering grounds for Whooper Swans (*Cygnus cygnus*) in China. The main breeding areas are at Ebinur Lake, Sailim Lake, and Ulungur Lake, along the Ili River Valley, and at Bayinbuluke Swan Lake. During migration and winter, swans are seen around the Ertix River, Ulungur Lake, Mushroom Lake at Shihetze, the Manas River Valley, wetlands outside of Urumqi, Bosten Lake, Tarim River Valley (from Aksu and Xayar to Yuli), Hotien River, Kashgar River, Yarkant River (from Zepu to Bachu), the lower regions of the Qarqan River, and Lop Nur.

The marsh at Bayinbuluke holds the largest breeding concentration of Whooper Swans in China. It was officially established as a nature-protection area, under local government legislation, in 1980. On 9 July 1986, the Forestry Department of the Chinese Government designated Bayinbuluke as a National Nature Conservation Area for wild animals, with a total area of 136,894 ha. It was also added to the list of important wetlands in Asia (Scott 1989). Two to three people were appointed to manage the area from 1980, increasing to five from 1986, with the aim of preventing fishing, trapping and egg collection, but it is a large area to protect.

Here we report on the numbers and potential threats to Whooper Swans breeding at Bayinbuluke.

STUDY AREA AND METHODS

Bayinbuluke is situated in a basin amid the central Tienshan Mountain range, at 42°18'–43°35'N, 83°00'–86°17'E, about 2,300–2,800 m above sea level (Fig. 1), and is surrounded by snow-capped mountains. It is 270 km long and 136 km wide, with a total area of 23,835 km^2, including 20,518 km^2 of grassland. Bayinbuluke therefore is one of the largest grassland areas in China, second only to Erduosi in Inner Mongolia. The grassland habitat includes freshwater marshes, flooded areas, streams and rivers. The main sources of water are precipitation and run-off from glaciers.

Observations were made from a tower (42°50'N, 84°15'E) at 2,433 m above sea level near Bayansumukol in Bayan-Ulu Village. To the south and east of the tower is the central area of Swan Lake, surrounded by large areas of wetlands and marshes. The lakes and wetlands are about 10 km from the Kaidu River, and the diameter of the area is about 30 km. Every year, large numbers of swans breed at the site. In the east, around the Big and Small Zakesitai Rivers, there is a large area of marshy grassland. The observation tower, which is >20 m high, is situated on a hillock at the edge of this marsh. Observations of the distribution of swan flocks within a 1–5 km radius of the tower were made using a single lens, high power telescopic camera DWY-2 (900 mm), and an OPTICRON (18×) telescope, with the tower also providing a good vantage point for counts and behavioral studies when the birds were in range. Other observations of

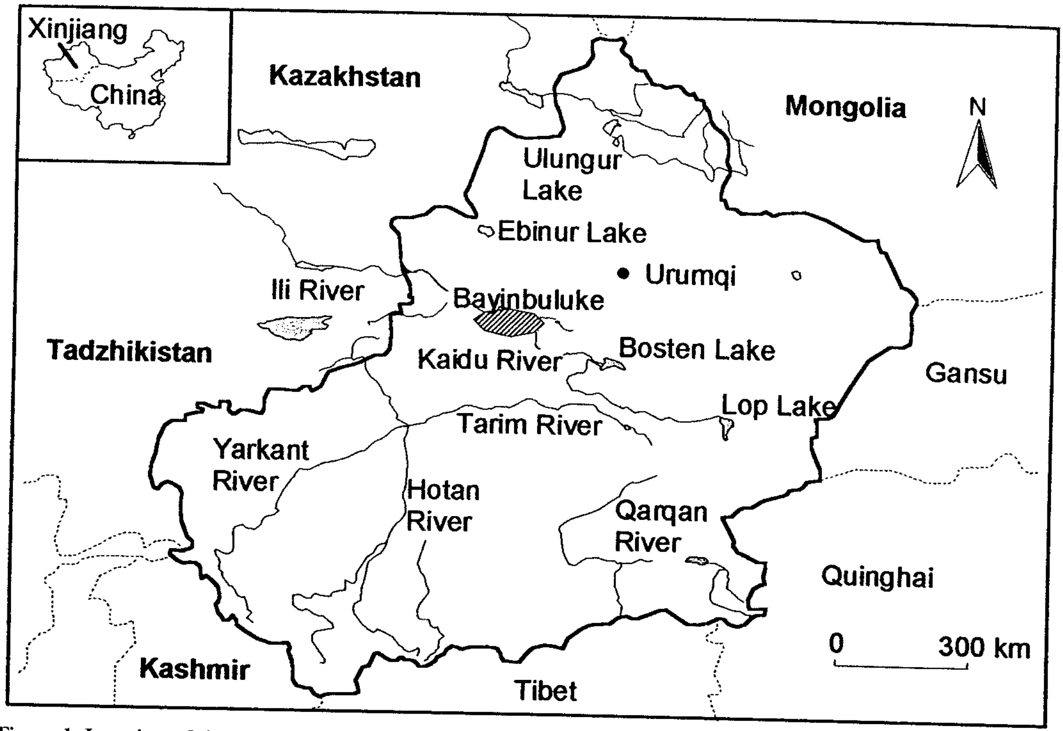

Figure 1. Location of the study area, the Bayinbuluk National Nature Conservation Area, in Xianjiang, China.

wintering, migrating and breeding swans were made from temporary observation points at Baxilike Mountain, Arxan Village, Bayan-Guolen Village and the Academia Sinica Grassland Ecology Station. We interviewed local people to assess the pressure from hunting, fishing, egg collecting, nest destruction and other human activities.

RESULTS AND DISCUSSION

In China, the largest breeding concentration of Whooper Swans is found in the Bayinbuluk National Reserve, Tianshan Mountains, Xinjiang. The number of swans breeding on the reserve has declined from 10,000 in the 1970s (Liang 1982) to 2,000-3,000 in the 1980s (Cai and Ma 1997; Ma and Cai 2000) and only 1,000 were present in the year 2000 (this study; Fig. 2). Numbers present in winter vary from 100–400 swans, with fewer birds recorded in very cold years (Jing *et al.* 1992). The three main wintering habitats are unfrozen streams near springs in Arxan and Bayinbuluke, lakes (0.3–1.5 ha, with a depth of 0.5–1.5 m) formed by the springs, and sections of the Kaidu River not totally frozen but a mixture of ice and water (Ma and Cai 2000).

Several factors may have contributed to the decline in the number of swans present during the breeding season. First, the number of grazing livestock (0.8–1.0 million sheep, horses and yaks) is three to four times as large as in the 1970s and this has seriously altered the height of the vegetation. For instance, Feathergrass (*Stipa* spp., previously 40–80 cm at Bayinbuluke), Wheatgrass (*Agropyron* spp., 30–75 cm) and Fescues *(Festuca*

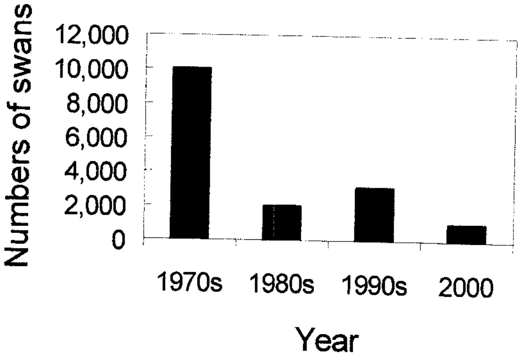

Figure 2. Numbers of Whooper Swans at Bayinbuluk, Xianjiang, China. Estimates for the 1970s are from Liang (1982) and for the 1980s from Cai and Ma (1997).

spp., 20–40 cm) are now only 5–15 cm in height (Zhang and Slabek 1998). Second, wetland vegetation is cut to provide food for over-wintering sheep, horses and yaks. Third, many lakes and rivers in the plains at lower elevations have dried up due to irrigation, which has had a direct effect on the availability of stopover and over-wintering sites for swans. In particular, Manas Lake and River (45°50'N, 86°00'E), held water until the 1970s; Lop Nur (40°–41°N, 90°–91°E), the largest lake in Xinjiang from 1950–1970 is now diminished and dried and is now a salt desert; and Kuytun River, Tarim River and Hotan River have all dried and shortened in length and no longer reach their lakes. Fourth, adult swans are hunted, eggs are taken for food, and nests are destroyed (Ma 2000). Fifth, increasing numbers of tourists visit Swan-lake in the breeding season. Sixth, several development projects affect the area, for example, highways, mining, a hydroelectric dam and the exploitation of an oil field. As a result, herdsmen that used to have a nomadic life-style are settling down. And seventh, natural disasters, such as drought and the 1997 snowstorm that killed about 400 swans, also affects the numbers of breeding pairs.

The decrease of swan numbers in China is evident. As an indication of environmental changes, swans have sounded an early alarm. If we do not adopt effective measures quickly, many rare species, including the swans, will become extinct. In Xinjiang, the basic problem in protecting swans and other wild animals is how to protect their habitats and control expansion of human populations into important breeding and wintering areas of swans.

ACKNOWLEDGMENTS

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Age and Sex Differences in Biometrics Data Recorded for Whooper Swans Wintering in Japan

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Abstract.—Between 1986 and 2000, biometrics data were recorded for 108 Whooper Swans (*Cygnus cygnus*) caught and banded while wintering at Hokkaido, Japan. Sex was determined by cloacal examination and also, in later years, by molecular analysis. A comparison of the two methods found a discrepancy in classification for 20% of the sexed individuals. Adult males were heavier than adult females, and had longer wing lengths, but there were no significant sex differences between the adult swans for the other body size measurements. Juvenile swans showed greater size dimorphism, with males proving larger than females for four of the six measurements tested.

Key words.—Age differences, biometry, cloacal examination, *Cygnus cygnus*, molecular sexing, sex differences, Whooper Swan.

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Swans, despite being generally monomorphic, show some interesting age and sexual differences in body traits. For instance, male and female Bewick's Swans (*Cygnus columbianus bewickii*) differ in several structural measurements, and also in body mass (Evans and Kear 1978). Similar differences have been described in the two other Palearctic swan species. In the Mute Swan (*Cygnus olor*), the frontal knob varies with age and sex classes (Mathiasson 1981), with other body measurements also varying with age and sex (Andersen-Harild 1981; Mathiasson 1981; Van Dijk and van Eerden 1991). Likewise, biometrics data recorded for Whooper Swans (Cygnus cygnus) in Europe indicate that males are larger than females (Preuss 1981; Rees *et al.* 1997a), and that sex differences in body mass in August and the timing of molt may be associated with site and breeding status (Rees *et al.* 1991).

Although many waterfowl species are monomorphic, making it difficult to determine their sex ratios without trapping and examining the birds, sex differences in body size can help gender classification in the field. Several swan studies compare body sizes within pairs, to determine which is the male and which is the female (Scott 1978, 1980, 1988). Behavioral traits, such as noting which member of the pair leads in aggressive encounters, are also used to determine sex (Scott 1978; Rees *et al.* 1997b). None of these methods are totally accurate, but provide useful tools for field-based studies. The most reliable ways of determining sex for monomorphic waterfowl outside the breeding season are cloacal examination and molecular analysis, which both involve handling the birds. Waterfowl tend to congregate during molt, and also in winter, so more birds can be caught at one time at these sites than on breeding territories. Biometrics data recorded during these catches therefore can provide valuable information on sexual and age dimorphism, or on differences between populations and sub-species (Rasmussen *et al.* 2001).

Whooper Swans breed in diverse wetland habitats, near lakes and pools in arctic, subarctic and taiga zones, and also in steppe regions, across the Palearctic from Iceland to the Pacific (Cramp and Simmons 1977). Autumn migration usually commences when the breeding grounds start to freeze, from mid-late September to mid-October (Rees *et al.* 1997a). National banding programs have described the movement of waterfowl through eastern Asia and, although many gaps remain in information on the migration routes and distribution of different populations, two major flyways are recognized, the central-south Asian flyway and the east Asian flyway (Miyabayashi and Mundkur 1999). Whooper Swans in the east Asian flyway are thought to breed from central Siberia to the Bering Sea, Mongolia and northern China, with birds flying some 3,000 km to winter areas in China, Korea, Japan and Kamchatka (Miyabayashi and Mundkur 1999). Whooper Swans caught in Japan have been satellite-tracked to breeding grounds in northeast Russia (Kanai *et al.* 1997). Approximately half of the Whooper Swans estimated to occur in the east Asian Flyway, winter in Japan (Miyabayashi and Mundkur 1999) and, during the 1990s, up to 30,000 birds have arrived annually in October to November (Environment Agency of Japan 1999).

Fifteen years ago, the Nakashibetsu Bird Banding Group began catching and banding Whooper Swans in east Hokkaido, Japan, on behalf of the Yamashina Institute for Ornithology. Neck bands engraved with unique alphanumeric codes were fitted to the birds in order to obtain resighting records, and thus describe the within-winter movements, migration routes and perhaps the breeding areas for Whooper Swans wintering in Japan. Biometrics data also were recorded, to determine variation in body size measurements within the East Asian Whooper Swan population, with a view to comparing these with other populations in due course. This paper presents the biometry data for Whooper Swans wintering in Japan, and investigates if there are any sexual differences or age-related differences in body size for swans caught during the study.

STUDY AREA

Since the banding program commenced in 1986, the main Whooper Swan catching site has been at Notsuke Bay (60 ha; 43°35'N, 145°18'E), east Hokkaido, Japan (Fig. 1). This area is one of the most important migratory sites for the species in Japan. The bay is vegetated by large Eelgrass (*Zostera marina*) beds that provide the migrants with food. Swans arrive from late October onwards and, while some quickly move south, most stay until the bay starts to freeze over during December. The Eelgrass beds are mostly covered by ice during winter; nevertheless about 400 Whooper Swans remain in mid-January (Environment Agency of Japan 1999).

From 1997 to 2000, an additional site was used; the Akkeshi Estuary (30 ha; 43°02'N, 144°42'E), about 80 km south of Notsuke Bay (Fig. 1). This estuary can hold up to 8,000 Whooper Swans at the peak of migration season in autumn but, as with Notsuke Bay, freezing induces southerly movement. Tidal movements and salinity do, however, keep some parts of the estuary open through the winter, and about 2,500 swans find sufficient Eelgrass to eat even in midwinter (Environment Agency of Japan 1999), making the Akkeshi Estuary the most important wintering site for Whooper Swans in Hokkaido.

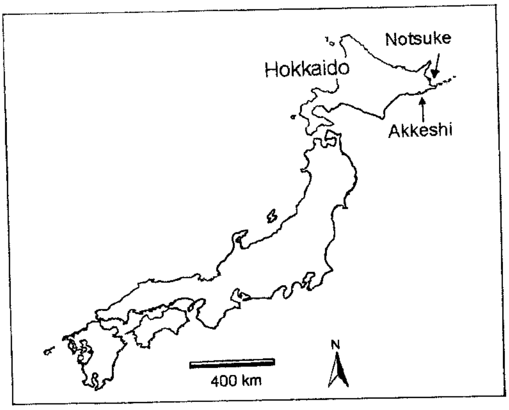

Figure 1. Map of Japan, showing catching sites in eastern Hokkaido.

METHODS

Swans were caught annually from 1986 to 2000 between mid-January and early March. Most Whooper Swans were caught using a clap net (3.5 m × 1.7 m) baited with bread. Although ten swans were caught on one occasion, most catches comprised fewer than three birds. Attempts were limited to one or two per day, due to the potential for regular catches (including those that failed) deterring birds from entering the catching area. A small number of more approachable birds were caught by hand.

Body mass was measured to the nearest 0.1 kg using a Pesola spring balance. Wing (maximum length; wing flattened and feathers straightened) and tail (distance from backbone to tip of longest feather) measurements were recorded with a tape measure (both rounded to the nearest millimetre). Four other structural measurements were taken using a caliper (to 0.1 mm): (1) culmen (distance from bill tip to feathering on top of bill); (2) gape–tip (distance from bill tip to gape); (3) nostril–tip (distance from bill tip to nostril); and (4) tarsus (distance from notch on outside of knee joint to outside of ankle joint, when the foot was held at 90 degrees to the tarsus bone). Four ringers, with more than ten years of experience in collecting biometrics data and fitting bands to birds, collected all measurements.

Two methods were used to determine the sex of the swans. In all cases, a visual assessment was made by cloacal examination, by four ringers with more than five years of experience in this technique. Additionally, since 1997, blood samples collected for a feeding ecology study were used for DNA extraction and molecular sexing, following the methods described in Griffiths *et al.* (1996, 1998) and Fridolfsson and Ellegren (1999). If there was a difference between cloacal sex determination and molecular sexing, the latter was taken as the sex of the swan in subsequent analyses.

Birds were aged according to differences in plumage and bare body parts (Cramp and Simmons 1977). First-winter birds (juveniles) retain much of their gray feathering, easily distinguishable from the white adult plumage. In late winter, juveniles have dark gray feet and the base of the bill is light yellow, whereas adults have black feet and a sharp contrast between the bill's black tip and yellow base. Individuals with a few remaining gray feathers and pink spotting on their feet were recorded as yearlings (second-winter birds; Rees *et al.* 1997a).

Each individual was fitted with one metal tarsus band, one plastic tarsus band and a plastic neck band before its release. Three neck-banded individuals (two adult females and one juvenile of unknown sex) were found dead shortly after catching. The body mass of these birds was excluded from the analysis, due to the possibility that they were sick when caught.

Student's t-tests (two-tailed) were used to determine whether any sex differences in the biometry data were statistically significant.

RESULTS

Since 1986, 108 Whooper Swans have been caught: 74 adults, 3 yearlings, and 31 juveniles. Blood samples from 27 swans: 19 adults, 2 yearlings and 6 juveniles, were used to determine sex by molecular analysis. Two of these samples, both from adults, helped to determine the sex of birds that were classified as unknown after cloacal examination. Of the other 25 samples, five (20%) were not consistent with the results of the visual assessment. Two juveniles and two adults believed to be females after the visual check were identified as males after molecular sexing and, likewise, one juvenile male was re-sexed by DNA as female. The sex ratio appeared to differ between cloacal sexing (10 males, 15 females) and genetic sexing (13 males, 12 females) but this was not significant ($\chi^2_1 = 0.81$, n.s.), and the sex difference in the proportion of birds re-sexed by DNA also was not significant ($\chi^2_1 = 1.67$, n.s.). The age and sex ratios for all individuals were: 74 adults (31 males, 42 females, 1 unknown), 3 yearlings (1 male, 2 females) and 31 juveniles (8 males, 18 females, 5 unknown). Although more females were recorded, the ratio of males to females did not differ significantly from 1:1 (binomial test, z = -0.41, n.s., data for all age categories combined).

Age and sex differences in the biometrics data for adults and juveniles are shown in Table 1. In addition, one adult and five juveniles of unknown sex were measured, but the data are not presented here. Adult males differed significantly from adult females in two of the seven measured biometrics traits; they were heavier and had longer wings lengths. There were no sex differences detected in adult swans for the size measurements of tail, tarsus, culmen, nostril–tip, or gape–tip. Juvenile males were significantly larger than juvenile females in culmen, gape–tip, wing and tail measurements. Although the juvenile males were heavier than the juvenile females, and had larger nostril–tip size, these differences were not significant. Three yearlings were measured: one male (culmen = 103 mm, nostril–tip = 48 mm, gape–tip = 101 mm, wing = 625 mm, tail = 200 mm, body mass = 8.9 kg) and two females (culmen = 94–102 mm, nostril–tip = 46–47 mm, gape - tip = 95–102 mm, wing = 530–575 mm, tail = 170–230 mm, body mass = 6.8–7.5 kg).

Adult males were significantly heavier ($t_{37} = 4.18$, $P < 0.001$) than juvenile males, and had longer culmens ($t_{37} = 2.52$, $P < 0.05$) and wings ($t_{37} = 3.54$, $P < 0.01$). There were no age differences for males in the measurements of gape - tip ($t_{37} = -1.68$, n.s.), nostril - tip ($t_{37} = 0.44$, n.s.), or tail length ($t_{37} = 1.36$, n.s.). Adult females were significantly heavier than juvenile females ($t_{56} = 5.14$, $P < 0.001$), and they had longer culmens ($t_{57} = 7.10$, $P < 0.001$) and wings ($t_{57} = 4.80$, $P < 0.001$). In addition, adult females had longer tails ($t_{57} = 3.93$, $P < 0.001$) and measured 2 mm more between nostril and bill tip ($t_{58} = 2.82$, $P < 0.01$) than juvenile females, but no difference was found in gape - tip ($t_{58} = 1.80$, n.s.) size.

DISCUSSION

Molecular sexing, using blood samples, verifies the accuracy of field identification by cloacal examination. Testing CHD (chromo-helicase-DNA-binding) genes for sex identification is highly robust and reliable as demonstrated by Griffiths *et al.* (1998) and Fridolsson and Ellegren (1999); more than

Table 1. Biometry data for Whooper Swans wintering in eastern Hokkaido, Japan in 1986–2000 (mean ± SD and number of individuals). P values are for sex differences for each of the body size measurements (Student's t-tests).

	Adult male		Adult female			
	Mean ± SD	N	Mean ± SD	N	t value	P value
Culmen (mm)	108 ± 13	31	108 ± 10	42	0.04	n.s.
Gape-Tip (mm)	99 ± 4	31	99 ± 4	42	0.24	n.s.
Nostril-Tip (mm)	47 ± 3	31	46 ± 4	42	0.44	n.s.
Wing (mm)	604 ± 23	31	583 ± 21	41	4.02	<0.001
Tail (mm)	205 ± 12	31	202 ± 23	41	0.65	n.s.
Tarsus (mm)	120 ± 6	8	124 ± 11	12	0.77	n.s.
Body mass (kg)	9.8 ± 1.1	31	9.0 ± 1.3	40	2.78	<0.01
	Juvenile male		**Juvenile female**			
	Mean ± SD	N	Mean ± SD	N	t value	P value
Culmen (mm)	95 ± 10	8	89 ± 5	17	2.16	<0.05
Gape-Tip (mm)	103 ± 8	8	97 ± 5	18	2.29	<0.05
Nostril-Tip (mm)	46 ± 4	8	44 ± 2	18	2.06	n.s.
Wing (mm)	573 ± 18	8	553 ± 24	18	2.08	<0.05
Tail (mm)	197 ± 24	8	176 ± 22	18	2.09	<0.05
Tarsus (mm)	136	2	No data			
Body mass (kg)	8.0 ± 0.9	8	7.1 ± 1.4	18	1.63	n.s.

160 known-sex individuals from 27 species, and 77 verified males and 89 verified females from 47 species, respectively, were all sexed correctly with PCR (polymerase chain reaction). The financial cost of sexing by molecular techniques can deter its application, but recent, less expensive PCR methods can balance costs with the benefit of increased accuracy. The observed difference of 20% in sex ratios between cloacal sexing and molecular sexing indicates a discrepancy between the two methods, and molecular sexing was chosen as the most accurate way of deciding sex in the subsequent analysis. Data from the earlier catches also suggest that the sex ratio could be biased, since rather more females were reported than males, although the difference was not significant. One reason for the few discrepancies in sexing could be that, under cold and icy conditions, viewing the sexual organs may be difficult. The genitals might also be partly atrophied, as are other muscles, due to poor feeding conditions in winter (Jehl 1997). Moreover, ringers are aware of the stress that catching may cause to the birds, and might tend to decide in the favor of females if they have difficulties in finding the penis. Behavioral differences between the sexes could also lead to a bias in the ratio of males to females caught. Females might require more food during winter if they are to attempt to breed the following year, and therefore be more readily attracted to provisions. This behavior could increase the number of females recorded, but the higher proportion of females was not significant in this study, and would not necessarily occur amongst species such as the Mute Swan in a temperate environment. Another study of misclassification during cloacal sex checking indicated that 11% of Mute Swan cygnets were wrongly sexed (Brown and Brown 2002), and suggested that any bias in accuracy was against females, which was the opposite of the trend in this study. In both studies, the number of misclassified birds was small, making it difficult to determine whether there was a consistent bias towards males or females, and in both cases the biases in accuracy of sexing were not significant. Evans and Kear (1978) also mention that some juvenile Bewick's Swans, sexed as female by cloacal examination, were re-sexed as males on monitoring their behavior in subsequent years. This was attributed to the penis not always being well developed in

juveniles, but the percentage of wrongly classified birds was not given.

Biometrics data revealed that adult males and adult females shared similar morphometric traits, as shown by the lack of significant differences between their bill, tail and tarsus measurements. There were, however, highly significant differences between adult males and adult females in both wing length and body mass. Adult male wings were on average 4% longer than the wings of adult females, and the adult males were 9% heavier than adult females. Cramp and Simmons (1977) similarly reported sex differences in wing length, measured from the skins of 17 adult male and 14 adult female Whooper Swans, preserved in museums in the Netherlands but of "eastern origin". While the wing lengths in this study are very similar to those for the Dutch skins, Preuss (1981) reported that 65 adult males and 45 adult females caught in Denmark had 21 mm and 10 mm longer wings, respectively, than the conspecific adults in Japan. Cramp and Simmons (1977) also reported significant sex differences in bill length and tarsus length, but no difference in tail length between the two sexes. We were unable to find any sex differences in these particular structures; for adult males, mean culmen length and mean tarsus length were close to those reported by Cramp and Simmons (1977), but our measurements for females tended to be higher. The tail lengths measured in this study were approximately 35 mm longer than those of the skins in the Netherlands, which may be due to different measuring techniques. Adult males wintering in East Hokkaido had comparable body mass with adult males caught in the Netherlands (8.7 kg in January and 10.4 kg in March; Cramp and Simmons 1977). Both adult males and adult females in Japan were slightly lighter than adult males and adult females in Great Britain (10.2 kg and 9.2 kg, respectively; Rees *et al.* 1997a). They were heavier than adult males and adult females in Denmark in the late 1970s (9.2 kg and 7.8 kg, respectively; Preuss 1981), but these swans were caught during unusually long spells of low temperatures, and more recent data from Denmark indicates a higher body mass for Whooper Swans on mainland Europe (11.0 and 9.0 for males and females; Rees *et al.* 1997a).

The results show a high degree of dimorphism between juvenile males and juvenile females. Cramp and Simmons (1977) reported significant sex differences in both wing and tail lengths for juveniles, based on measurements made of 13 skins (6 males and 7 females) of "eastern origin" held in Dutch museums. The mean wing length of juvenile females is the same as those reported by Cramp and Simmons (1977), but the juvenile male values are 48 mm shorter than the skins in the Netherlands. They found juvenile males and adult males to have same wing lengths, but mention that the difference between adult males and juvenile males is more pronounced in live birds in England. Eight juvenile females trapped in Denmark had, on average, 22 mm longer wings than juvenile females in this study (Preuss 1981). As for adults, there was a difference of about 40 mm in tail lengths between juveniles in this study and the skins in the Netherlands (Cramp and Simmons 1977), which supports the view that different methods were used to record tail lengths. Juveniles in this study are approximately one kilogram lighter than juvenile males and juvenile females in Britain and Denmark (9.0 kg and 8.4 kg, respectively, for Britain, 9.5 kg and 8.5 kg for Denmark; Rees *et al.* 1997a), but similar to juvenile females in an earlier study in Denmark (7.4 kg; Preuss 1981). Whooper Swans in Britain were caught at a site where their diet is supplemented by grain (Rees *et al.* 1997a), but it is uncertain if this is the cause of the differences in winter mass observed between juveniles in Britain and Japan.

Age and sex differences in body mass and linear measurements have been reported for other swan species. For instance, during winter in Britain, Bewick's Swan males were heavier than females by 13% in adults and 10%-11% in yearlings and juveniles (Evans and Kear 1978). This is similar to the sex differences in body mass of 9% and 12% in adults and juveniles, respectively, found in this study. Van Dijk and van Eerden (1991) found slightly larger differences between

Mute Swans caught while molting in the Netherlands; males were 18%–19% heavier than females for both adults and yearlings. Male Bewick's Swan males were significantly larger than females at every age in their wing, skull, bill, and tarsus measurements (Evans and Kear 1978). Similarly, Mute Swan males were significantly larger than females in five measures of wing, foot and bill (Van Dijk and van Eerden 1991). Although, in this study, both adult males and juvenile males were larger than the respective females for many of the body size measurements, there was significant sexual dimorphism only in juveniles. Evans and Kear (1978) found significant differences between adult, yearling and juvenile Bewick's Swans in their body mass, wing length and bill length, and the same differences are found between adults and juveniles, both males and females, in Whooper Swans in eastern Hokkaido.

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A Preliminary Analysis of Mute Swan Biometrics in Relation to Sex, Region and Breeding Status

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Abstract.—Biometrics data for Mute Swans (*Cygnus olor*) taken during the months of July, August and September, are presented for two discrete study areas in England, separated by approximately 320 km. Males in northeast England were significantly larger than those in central England, whereas females were of similar size. Birds in central England were in better condition than those in northeast England. Sexual dimorphism was demonstrated in both areas, males being significantly larger and in better body condition than females, but there was an overlap of 87.6% in the radius measurements of males and females within the two areas. In both sexes, breeding birds were in better condition than non-breeding birds. While breeding males were larger than their non-breeding counterparts, breeding females were smaller than non-breeding females in both areas.

Keywords.—Body condition, *Cygnus olor,* geographic location, mass, Mute Swan, size, status.

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Sexual dimorphism is well documented in many animal species. In birds it can manifest itself through plumage differences and through variation in body size (Welty and Baptista 1988). Where size is the dimorphic feature the larger sex is often the male, but the reverse is shown in raptors, owls and jaegers (Newton 1979). Size can vary substantially between individuals of the same species, with significant overlaps in size recorded between the sexes (Van Dijk *et al.* 1991) and between different age categories (Evans and Kear 1978).

Variability in size within a population is known to increase in larger species, and the degree of variability increases as body size increases (Halgrimsson and Moriana 2000). Mute Swans (*Cygnus olor*) are among the largest and heaviest flying birds, and individual size variation within the population therefore could be expected to be high. Such variation may confer advantages or disadvantages on individuals in different parts of the size range.

This paper explores, through a comparative analysis of biometric measures from two discrete study areas, (1) size variation within and between the sexes in the two regions; and (2) how size, mass and condition differs between birds of different sex and status.

STUDY AREA AND METHODS

Two study areas, separated by approximately 320 km, were included in the analysis. Birds from central England were from the inland counties of Staffordshire, Warwickshire, Derbyshire and the West Midlands, where Mute Swans have been studied since 1961, and 9,370 individuals had been marked with tarsus bands by early 2001. The study area extended to 40 km north and 36 km east of 52°30'N and 2°8'W. Much of the area was rural, but there were many large towns and industrialized zones, and swans nested in a variety of habitats including rivers, pools, canals, reservoirs and gravel pits.

Birds from northeast England were from the counties of Northumberland, Tyne and Wear, Durham, Cleveland and parts of North Yorkshire, where Mute Swans have been studied since 1988, and 3,957 individuals had been marked by early 2001. The area extended 100 km east and 140 km north of 54°30'N and 2°20'W. Again swans bred in a variety of habitats, including rivers, pools, gravel pits and estuaries.

Catching and monitoring techniques were similar in both areas and have been described in previous publications (Minton 1968; Coleman and Minton 1979, 1980). All birds considered in the analysis were marked with large, colored, individually coded, plastic leg bands that enabled their movements, breeding status and breeding success to be monitored. Most birds were banded as prefledged cygnets or by the end of their first year, so their ages were known precisely. To date, no bird marked in either study area has been recorded in the other, suggesting that there is little or no interchange between the two regions.

In fledged birds, age was determined from plumage characters, and all birds were sexed by cloacal examination. Size was determined by measuring the length of the radius bone in the wing to the nearest mm using a retractable metal rule. Radius length was the only measure recorded consistently in both study areas. In the northeast study, total head length and tarsus were also measured at a site during 1994. A factor analysis of the three size measures indicated that radius length accounted for 81% and 67% of size variation in females and males respectively, indicating that it was a reasonable measure of variation in Mute Swan body size. In adults, if measures of recaptured birds differed by more than 5 mm from the original measure both records were discarded, otherwise the average recorded value was used for analysis. Measurements were made by a small number of experienced banders, who regularly participate in molt catches and cygnet banding programs in both study areas. Measuring therefore is assumed to be consistent between individual banders, and regular crosschecks confirm the accuracy of measurements made by the group.

Body mass was measured to the nearest 0.1 kg using a Salter balance and weighing cradle. The mean average body mass was calculated for every bird, using all the masses taken for each individual. This value was cube root transformed and divided by radius length, to give an estimate of body condition corrected for body size for each bird. The cube root of mass was used to provide a linear relationship between mass (a volume) and radius length.

All birds were sexed cloacally. Each year a sample of recaptured swans, from the molting herds in Central England, was again sexed cloacally to verify the accuracy of the previous sexing. On average, accuracy was 96% for birds sexed as adults on both occasions (N = 420 swans), and 90% for birds initially sexed as cygnets (N = 1,420 swans). In addition, all birds were sexed cloacally when caught on first being recorded as breeding. Sex was checked against any previous records as non-breeders, and breeding birds marked for the first time were sexed again the following year if present on the territory.

Birds were divided into two status categories, breeding and non-breeding. A breeding bird was a member of a pair that held territory, built a nest and laid eggs during any year, whereas non-breeding birds were those recorded in the non-breeding flocks during the breeding season, and were never recorded holding a territory and nesting. Biometrics data for breeding birds were recorded when family parties were caught to mark cygnets during the months of July, August and September. Failed breeders were captured in molting herds during July and August. At this time a high percentage of the adults were in molt. Measurements for non-breeding adults in molting herds were recorded over the same time period and included some paired birds that had never been recorded as breeding.

General Linear Model Multivariate analysis (SPSS v9.0) was used to investigate effects of sex and region on body size and body condition, and to assess the effects of region and breeding status on body size and condition for each sex separately. All interactions between variables were also tested.

RESULTS

Body Size Variation Between Regions and Sexes

Analysis of adult radius length measurements from all adults showed that, in both study areas, males had significantly larger radii than females ($F_{1,2110} = 1136$, $P < 0.001$), although there was much overlap in the ranges recorded (Table 1). The average radius length differed between sexes by 17.4 mm in central England, and by 17.3 mm in northeast England.

Birds in northeast England had longer radii than birds in central England ($F_{1,2110} = 9.9$, $P < 0.02$, Fig. 1a,b). For males, mean radius length was 1.7 mm longer in northeast England than in central England ($F_{1,1142} = 6.8$, $P < 0.01$, Fig. 1b), and for females it was 1.6 mm longer in the northeast, but the latter difference was not significant ($F_{1,963} = 0.9$, n.s., Fig. 1a).

In both study areas, the radius length of breeding females was significantly smaller than that of non-breeding females, by an average of 3.3 mm in central England and 2.0 mm in the northeast ($F_{1,963} = 12.3$, $P < 0.001$, Table 2). However, breeding males were significantly larger than non-breeding males, by 4.7 mm in central England and 0.9 mm in northeast England ($F_{1,1142} = 4.6$, $P < 0.03$) (Table 2). The region × breeding status interaction was not significant in relation to radius length for either sex (males $F_{1,1142} = 0.9$, n.s., females $F_{1,963} = 0.5$, n.s.), indicating that the association between breeding status and radius length was not influenced by region.

Variation in Body Size, Mass and Condition between Sexes and Breeding Status Categories

Average body mass recorded for breeding and non-breeding swans in central England (Fig. 2) and northeast England (Fig. 3) were considered for each sex separately. Body mass increased with size in both sexes

Table 1. Radius length (mm) for all adult (3 years of age or older) male and female Mute Swans measured in the two study areas (mean values ± SD, with range and sample size in parentheses).

Location	Males	Females
Central England	292.8 ± 11.7 (225-320; 608)	275.6 ± 12.4 (233-317; 465)
Northeast England	294.5 ± 11.6 (230-326; 535)	277.2 ± 11.1 (245-310; 503)

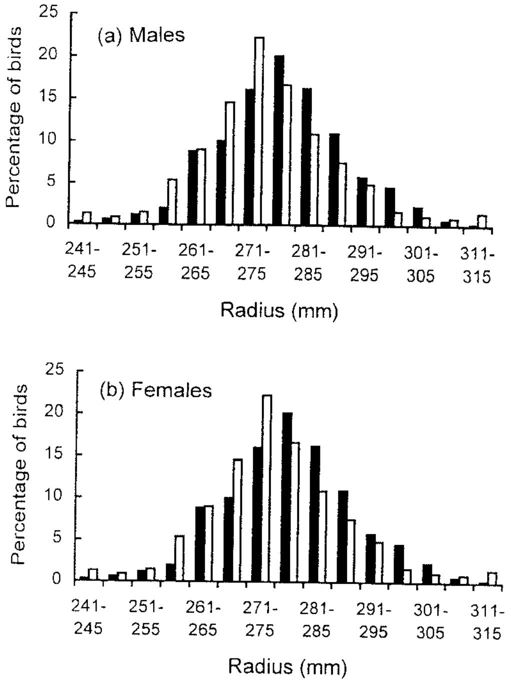

Figure 1. Distribution of radius lengths for (a) female, and (b) male swans in northeast England (black columns) and central England (open columns).

(Pearson correlation, $r_{1141} = 0.18$, $P < 0.01$ for males; $r_{963} = 0.19$, $P = 0.01$ for females), irrespective of breeding status (Figs. 2 and 3). Moreover, mass data recorded for breeding and non-breeding males and females showed that, when considering the two study areas together, breeding birds tended to be heavier than non-breeding birds in the same size category; the differences were significant for medium and large males, but for only one of the female groups (Table 3).

The average body condition for breeding and non-breeding swans of each sex, in both study areas, is summarized in Table 4. Males were in better condition than females ($F_{1,2110} = 178.1$, $P < 0.001$), and birds in central England were in better condition than those in the northeast of England ($F_{1,2110} = 40.1$, $P < 0.001$, Table 4). The interaction of sex and region on body condition was also significant ($F_{1,2110} = 85.5$, $P < 0.001$). Differences in body condition between the two regions existed for males ($F_{1,1142} = 171.9$, $P < 0.001$), and also for females ($F_{1,963} = 8.0$, $P < 0.05$), indicating that birds in central England were in better condition than those in the northeast for both sexes. Breeding birds of both sexes were in better condition than their non-breeding counterparts (males $F_{1,1142} = 13.1$, $P < 0.001$; females $F_{1,963} = 16.9$, $P < 0.001$).

DISCUSSION

Mute Swans are large, generally monogamous, territorial birds (Scott 1977) with potentially high adult longevity and life-time productivity (Coleman *et al.* 2001). Mass has often been used as an index of condition in male and female Mute Swans (Anderson-Harild 1981; Reynolds 1972; Bacon and Coleman 1986), but the combination of radius length and mass allows a measure of body condition because it provides a control for body size.

Biometric measures in adult Mute Swans indicate that males are, on average, larger and heavier than females. This dimorphism has been identified in other studies (Mathiasson 1981) and may be related to the differing roles of the two sexes. Female swans are smaller and lighter than males and require about 25% less food for body maintenance (Kendeigh 1970). Smaller breeding females may therefore have the advantage of being

Table 2. Variation in radius length (mm) between adult birds of different breeding status measured in central and northeast England (mean values ± SD, with range and sample size in parentheses).

	Males		Females	
Region	Breeding	Non-breeding	Breeding	Non-breeding
Central England	293.9 ± 11.4 (215–319; 325)	291.6 ± 11.7 (225–320; 283)	275.6 ± 12.4 (233–317; 465)	277.7 ± 14.4 (233–317; 160)
Northeast England	295.1 ± 11.1 (255–325; 166)	294.2 ± 11.8 (230–326; 369)	275.8 ± 10.3 (246–304; 184)	278.0 ± 11.5 (211–310; 319)

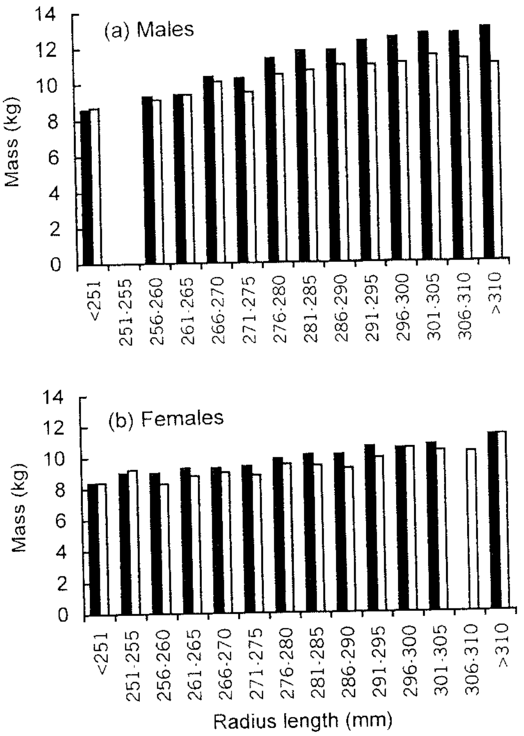

Figure 2. Relationship between body mass and radius length for (a) males and (b) females in central England. Black columns denote breeding birds; open columns denote non-breeding birds.

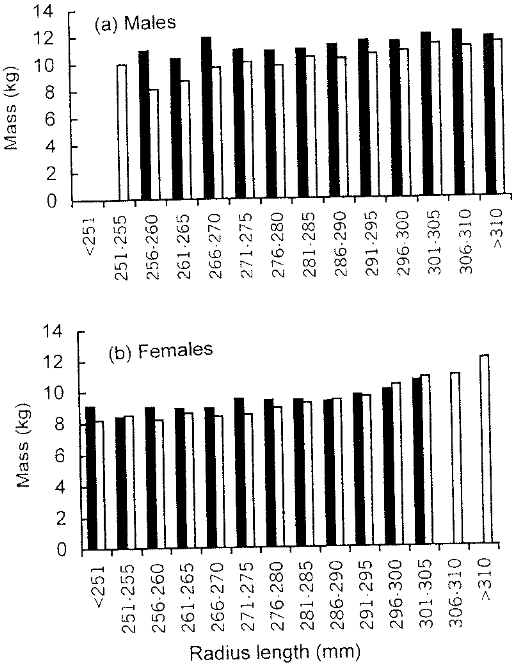

Figure 3. Relationship between body mass and radius length for (a) males and (b) females in northeast England. Black columns denote breeding birds; open columns denote non-breeding birds.

able to devote a higher percentage of ingested food for egg production.

Rees *et al.* (1996) proposed that, in both migratory swans and Mute Swans, size is only one factor involved in achieving breeding status. Our data is supportive, showing substantial overlap in radius lengths among breeding and non-breeding adults of both sexes. Also, in northeast England 68% of adult males with relatively long radii (i.e., over 300 mm) were non-breeders, as opposed to 42% in central England, but the region × status interaction indicated that the association between breeding status and radius length was not significantly greater in one region than the other.

In migratory swans and Mute Swans, male size is associated with reproductive success (Rees *et al.* 1996), with males benefiting from larger size in competing for potential mates, defense of a territory and acquisition of food in non-breeding flocks. However, the range in size of breeding birds and the improved condition of breeding birds, when compared to non-breeding birds of similar size, suggests that other factors may also impact on reproductive ability. Our data do not elucidate whether the higher masses and better condition of breeding swans of both sexes in both study areas was due to a better body condition when they arrived on their territories, or to better food quality on the territories compared to non-breeding sites. However, adult Mute Swans have been shown to accumulate body reserves during winter to enhance over-winter survival and facilitate early breeding (Reynolds 1972; Anderson-Harild 1981; Beekman 1991), and the data presented here indicate that breeding birds are at least able to maintain this differential through the breeding season.

The negative effect of incubation on female condition is significant (Beekman 1991), and the better condition of breeding males relative to breeding females may be the result of females still recovering the mass lost during incubation. The disadvantage of

Table 3. Differences in body mass (kg) between breeding and non-breeding males and females for different size (radius length) categories. Mass data (mean values ± SD, with sample size in parentheses) are for both study areas combined. F values are for one-way ANOVAs, comparing mass recorded between breeding and non-breeding birds in each size category; *P < 0.02, ***P < 0.001, n.s. = not significant.

Radius length (mm)	Males		Females	
	Breeding	Non-breeding	Breeding	Non-breeding
261–270	9.9 ± 0.04 (12)	9.8 ± 0.06 (21)	9.1 ± 0.03 (30)	9.3 ± 0.06 (21)
	$F_{1,31} = 0.05$, n.s.		$F_{1,49} = 0.40$, n.s.	
271–280	10.6 ± 0.04 (29)	10.0 ± 0.02 (57)	9.7 ± 0.01 (120)	9.7 ± 0.01 (100)
	$F_{1,84} = 2.3$, n.s.		$F_{1,218} = 0.06$, n.s.	
281–290	11.3 ± 0.01 (111)	10.4 ± 0.01 (151)	9.8 ± 0.01 (197)	9.7 ± 0.01 (45)
	$F_{1,260} = 20.4^{***}$		$F_{1,340} = 1.0$, n.s.	
291–300	11.7 ± 0.01 (208)	10.4 ± 0.01 (253)	10.1 ± 0.01 (94)	10.0 ± 0.01 (129)
	$F_{1,459} = 77.6^{***}$		$F_{1,221} = 0.01$, n.s.	
301–310	11.9 ± 0.01 (103)	10.5 ± 0.01 (136)	10.7 ± 0.03 (30)	10.0 ± 0.02 (46)
	$F_{1,237} = 42.0^{***}$		$F_{1,76} = 5.4^{*}$	
310+	12.1 ± 0.07 (20)	9.9 ± 0.05 (24)	10.8 ± 0.2 (5)	10.5 ± 0.1 (23)
	$F_{1,42} = 17.2^{***}$		$F_{1,26} = 0.10$, n.s.	

smaller size while competing for food in the flocks (Scott 1988) is likely to be the cause of lower condition in non-breeding females relative to non-breeding males. However, requiring less food may explain why smaller females appear to have an advantage over larger females in achieving breeding status, in that they attain better condition on acquiring the same amount of body mass.

In non-breeding flocks, larger size in both sexes may confer dominance in relation to the acquisition of food, enabling birds to achieve or maintain good condition (Scott 1980). The large number of non-breeding birds with similar radius length to breeding birds, but with lower mass, may indicate that although large size is important in achieving dominance (Scott 1988), it may be less important in achieving breeding status. The consistently higher mass and better condition of breeding birds of both sexes in central England may reflect of higher territory quality there than in northeast England (Bacon and Coleman 1986).

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Table 4. Differences in body condition (i.e., cube root of mass divided by radius length) between breeding and non-breeding males and females in central England and northeast England (mean values ± SD, with range and sample size in parentheses).

Region	Males		Females	
	Breeding	Non-breeding	Breeding	Non-breeding
Central England	0.64 ± 0.003 (0.56–0.85; 325)	0.62 ± 0.002 (0.57–0.79; 283)	0.64 ± 0.002 (0.55–0.73; 303)	0.62 ± 0.002 (0.56–0.72; 160)
Northeast England	0.61 ± 0.002 (0.53–0.7; 166)	0.6 ± 0.004 (0.53–0.87; 368)	0.65 ± 0.003 (0.57–0.78; 184)	0.64 ± 0.003 (0.53–0.74; 317)

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The Dynamics of a Flock of Mute Swans at Berwick-upon-Tweed with Particular Reference to the Effects of Age, Sex, Social Status and Body Condition on Molt

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Abstract.—The Mute Swan (*Cygnus olor*) flock at Berwick-upon-Tweed, northeast England, was studied intensively for a twelve-month period in 1994. An influx of birds occurred during May and June as birds came to the site from the surrounding area to molt. The origin of molting birds was restricted by local geography; ground higher than 200 m above sea level appeared to reduce movement to the site. The sex ratio and age ratio of the flock did not vary significantly throughout the year. Primary feathers grew at a rate of 6.1 mm per day, and age, sex and body condition did not influence the rate of feather growth. Status had an impact on the timing of molt, with resident birds molting earlier than migrants. Body condition varied throughout the year. Age, sex and month were all significant factors in explaining variation in body condition.

Key words.—Body condition, *Cygnus olor*, flock dynamics, molt, molt migration, Mute Swan, phenology.

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As part of a long-term study of Mute Swans (*Cygnus olor*) in northeast England and southeast Scotland, a detailed study was undertaken throughout 1994 on the non-breeding flock at Berwick-upon-Tweed, Northumberland. This site on the Tweed estuary holds a resident flock of Mute Swans, with an influx of molting birds in summer. Most data collected on molting Mute Swans have originated from single capture events, that provide a snapshot of a molting flock. These captures have described the origins of molting birds in various flocks (Minton 1971; Anderson Harild 1981; Mathiasson 1981), and provided information on the effects of molt on survival, with lighter birds having lower survival rates after molt (Perrins and McCleery 1995). Due to the difficulties of catching and handling large numbers of swans, little is known concerning their physiological changes during molt. Anderson Harild (1981) indicated that the heaviest birds molt first, and that they can lose up to 20% of their body weight during molt. These results were confirmed by a more recent study (Van Dijk and Van Eerden 1991), which further demonstrated that males molt before females and that the molt at Lake IJsselmeer, The Netherlands, started mainly during the first ten days of July. Anderson Harild (1981) found that habitat was important, with birds molting on habitats rich in Sea Lettuce (*Ulva lactuca*) faring better than those on habitats predominated by wracks (*Fucus* spp.) or eelgrass (*Zostera* spp.).

Primary feather growth rates have been investigated, with Mathiasson (1973) and Van Dijk and Van Eerden (1991) recording rates of 6.5 mm and 6.3 mm per day, respectively, and Czapulak (1989) recording 7.1 mm per day.

This paper builds on earlier studies by providing larger sample sizes for studying the timing of molt, and also includes many repeat captures of the same individuals during the molt period. Understanding the functioning of Berwick-upon-Tweed as a molt site is important for the Mute Swan in Britain because it is the only major molting area in the region, and holds up to 4% of the

British Mute Swan population during the summer (Cranswick *et al.* 1997). The specific aims of the study therefore were to describe the annual dynamics of the swans at Berwick and to investigate the factors affecting molt phenology at the site.

STUDY AREA AND METHODS

The Tweed estuary in Northumberland (55°46'N, 2°00'W) holds the largest flock of molting Mute Swans in northern England, with smaller numbers present throughout the year (Fig. 1). The lower estuary is within the town of Berwick-upon-Tweed and the study site extends some 4 km upstream to more rural surroundings, encompassing all the areas normally used by swans in the vicinity. The estuary is tidal and at low tide extensive mud and shingle beds are exposed. Heavy vegetation growth in the estuarine river channel during summer, mainly brown algae (*Fucus* spp.) and green marine algae (*Ulva* spp. and *Enteromorpha* spp.), provides the main food for the swans during their molt. Small amounts of grain were provided for the birds during the winter months by a local charity, and the swans also feed on bread from the public.

Birds have been caught for marking at Berwick since 1986, using bread as a bait to lure the birds into an enclosure, where they could be surrounded and penned. In July, when most birds were flightless, canoes were also used to help herd the birds into the pen. Each bird was fitted with a plastic leg band engraved with a numerical code, and with a metal band fitted to the opposite leg. Although band codes were recorded for any recaptured swans, observers also report bands read in the field. Thus, sightings of swans not caught accounted for an additional 0% to 58% of the birds identified at Berwick each month in 1994 (Fig. 1). For birds marked at Berwick but identified away from the area, band resightings (as opposed to recaptures) accounted for over 90% of all records. Most birds were already marked by 1994; 2,549 individuals were banded at Berwick and in the surrounding area between 1986 and the end of 1994. Mute Swans were also banded extensively elsewhere in northern England, to the west of the Pennine Mountains and to the south of the North Yorkshire Moors.

During 1994, a sample of birds was caught for weighing and measuring every month. The Mute Swan flock was also counted monthly, with individual swans identified by reading their band codes during both the counts and the captures. Upon first capture of each individual, data were collected on age, sex, mass, and length of skull, radius, tarsus and third primary. Molt score (Table 1) was also recorded. All body measurements were made to the nearest mm, using calipers to measure skull and tarsus length, and a retractable ruler to measure radius and primary length. The third outermost primary was identified as the longest primary and measured from the point at which the feather emerged from the skin to the tip. During 1994, measures of mass, molt score and length of the third primary were also recorded each time that a bird was recaptured. Breeders and non-breeders were caught in most months even though no birds actually bred on the study site. Mass was measured to the nearest 0.1 kg, using a balance, by placing the swans in a weighing cradle. Principal component analysis was used to assess the three skeletal measurements (radius, tarsus and skull length), and to derive a single size variable using the first principal component (PC1) axis. The percentage variation in the body size data explained by PC1 was 67% for males (PC1 factor loading: radius = 0.67, skull = 0.60, tarsus = 0.74) and 81% for females (PC1 factor loading: radius = 0.83, skull = 0.78, tarsus = 0.83). Mass was cube root transformed and divided by the PC1 score to give a measure of body condition. Average body condition throughout the year was used as a baseline value against which monthly condition was plotted. Analyses were made separately for males and females.

Birds caught for the first time in 1994 were aged as adult or juvenile (i.e., less than one year old), depending on their plumage characteristics. Recaptured swans were aged according to the original banding data. All birds were sexed cloacally on their initial capture.

In 1994, it was possible to classify individual birds molting at Berwick as being resident or immigrant and, from additional observations outside the study area, to determine whether the latter were failed breeders, or non-breeders during 1994. Resident birds were those recorded at Berwick in every month during 1994, whereas immigrant birds were those recorded away from the

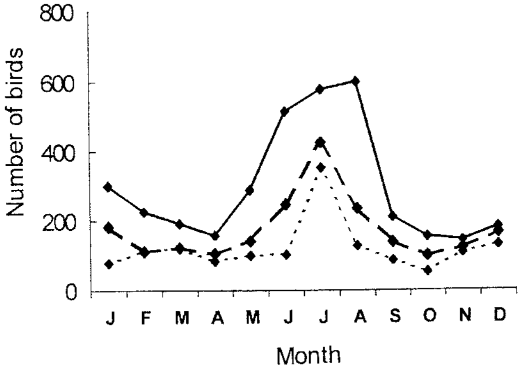

Figure 1. Monthly counts of Mute Swans recorded at Berwick upon Tweed during 1994. Solid line = total number of birds counted; dotted line = number of birds caught; dashed line = total number of birds individually identified, either as recaptures or resightings.

Table 1. Molt stage categories used during the study.

Stage	Description
0	No primary feathers present at all
1	Primaries present as quills only, or at most with a tiny brush of feather present
2	Actual feather growth between stage 1 and approximately one third grown
3	Actual feather growth between one third grown and two thirds grown
4	Actual feather growth between two thirds grown and fully grown
5	New feathers, with no trace of feather sheath at base of quill
9	Old feathers. A score of 5 becomes a 9, by default, on 1 January

Berwick flock during non-molt periods. The resident birds were all non-breeding birds. For immigrant birds, failed breeders were defined as birds that had held a territory and nested but subsequently failed to hatch cygnets during 1994, whereas non-breeders were those that did not nest in 1994 and were recorded in non-breeding flocks during the breeding season. A third immigrant category, "unknown breeding status", included swans that were recorded away from Berwick in 1994, but whose breeding activity in that year was not known. Finally, a small number of immigrant birds were successful breeders arriving on the estuary with their cygnets from further upstream. Birds not recorded for one or more months in 1994 were not classified as resident or immigrant, but as a separate group of "origin not known". This category may have included birds from all of the breeding status classes and birds that may have died after being seen in the Berwick flock.

A binomial test was used to assess any deviation from the expected 50:50 sex ratio, with chi-square tests used to assess monthly variation in the sex and age ratios throughout the year. General Linear Model Multivariate analysis (SPSS v9.0) was used to investigate factors affecting body condition, timing of the onset of molt and feather growth rates. For body condition, the effects of age, sex and month were assessed, with the effects of age on condition first being considered for males and females separately, and the effects of sex on condition also being considered for juveniles and adults separately using General Linear Model Multivariate analysis (SPSS v9.0). For primary growth rate, the variables tested were age, sex, condition and molt stage (used as an estimate of primary size). For molt initiation date, the effects of status, condition, age and sex were analyzed. All interaction terms between the variables being tested were also included in the models. To avoid pseudoreplication, only one randomly selected instance per individual was used in analyses of body condition variation. The timing of molt initiation between birds of differing status was compared using one-way ANOVAs.

RESULTS

Monthly counts in 1994 found marked seasonal variation in the number of Mute Swans in the study area, with peak counts of 500-600 birds in June, July and August, but fewer (144–300) at other times of year (Fig. 1). A total of 724 different banded birds were recorded during the year, of which 594 were caught on at least one occasion, and 74 were recaptured and measured at least twice while in active wing molt. On average, over 50% of individuals in the flock were identified each month, with up to 90% in some months and less than 50% only in August. Usually between 100 and 300 swans were caught on each occasion (Fig. 1). Molt scores indicated that wing molt occurred from May to October, though the peak period was early July when 93.5% (N = 353) of the birds caught were in active wing molt (Fig. 2), coinciding with the peak counts for swans at the site (Fig. 1).

The banding origins of the 367 birds caught in the July molt catch are illustrated in Figure 3. The 184 birds banded at sites away from Berwick upon Tweed came mainly from low-lying coastal areas to the south (30.8%), and from inland along the Tweed valley (57.9%). The initial banding site for most birds was less than 50 km from Berwick (71.6%), a further 22.8% were marked 51-100 km away, and the remainder at over 100 km from the study site. The maximum distance between a banding site and the Berwick molt site was 167 km.

The adult sex ratio tended to favor males (54% males), while for juvenile birds the sex ratio favored females (54% females, Table 2). These ratios did not differ significantly from 50:50 for the two age classes (z = 0.14, n.s., for adults; z = 0.14, n.s., for juveniles), and sex ratios of birds caught also did not vary significantly between months (χ^2_{11} = 9.59, n.s. for adults; χ^2_{11} = 12.5, n.s., for juveniles; Table 2). The proportion of juveniles recorded in the flock did not differ significantly among months from an overall annual average of 20% (SE ± 0.3) (χ^2_{11} = 5.53, n.s.). The oldest bird in the flock was at least 14 years old, and non-breeding birds of eight years and older were present in all months of the year. Although some of these older individuals were resident others were only present at certain times of the year.

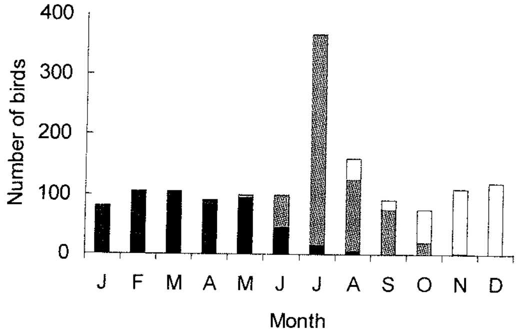

Figure 2. Number of birds recorded in molt in each month during 1994. Black bars are birds that have not yet initiated molt (i.e., with molt score = 9, Table 1), gray bars are birds in molt (molt scores 0–4), and open bars are birds that have completed molt (molt score = 5).

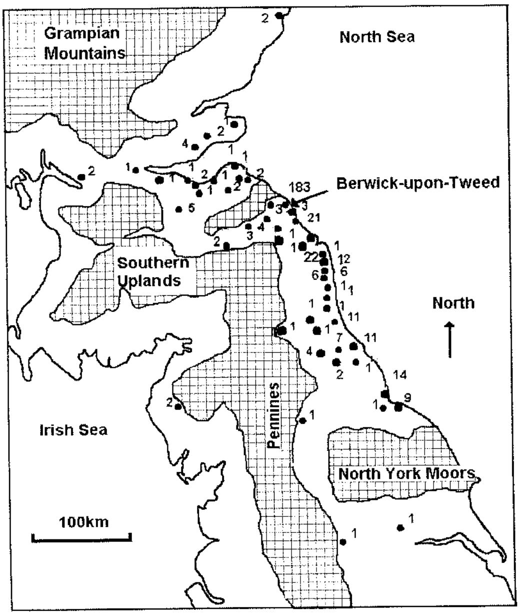

Figure 3. First banding sites for birds recorded molting at Berwick-upon-Tweed. Tiled area is land at least 200 m above sea level (numbers represent number of birds originating from that location).

The swans showed considerable variation in body condition through the year, the pattern appearing consistent between sexes and age classes, peaking in spring (March–April) and lowest in July to October (Fig. 4a and Fig. 4b). Sex had a significant effect on condition, with adult males being in better condition than adult females ($F_{1,426}$ = 23.7, $P < 0.001$) but this difference was not apparent for juveniles ($F_{1,101}$ = 0.8, n.s). Age also had a significant effect on condition in males, with adults being in better condition than juveniles ($F_{1,267}$ = 10.1, $P < 0.02$), but the same was not true for females ($F_{1,260}$ = 3.5, n.s.).

Body condition varied with month ($F_{12,528}$ = 3.1, $P < 0.001$). This variation was not influenced by sex ($F_{10,504}$ = 0.2, n.s., for the month × sex interaction), but was by age ($F_{11,504}$ = 3.3, $P < 0.001$, for the month × age interaction), indicating that age had a greater influence on body condition in some months than in others (Fig. 4a,b). No significant interactions between the other variables were identified.

Seventy-three individuals were caught on two or more occasions while in molt, and their primary feathers were calculated to grow at an average rate of 6.1 mm per day (SE ± 0.2). The growth rate was not influenced by age, sex, body condition or molt stage ($F_{1,70}$ = 0.2, n.s.; $F_{1,70}$ = 0.3, n.s.; $F_{7,70}$ = 0.2, n.s.; and $F_{2,70}$ = 0.5, n.s., respectively), nor by any interactions between these variables. The mean length of the third primary, for birds not in molt, was 365 mm (SE ± 0.9, N = 434). Using the calculated growth rate, molt was estimated to last for 60 days. However, this estimate did not include the time lag between losing flight feathers and the re-emergence of primaries through the skin.

The date of the onset of molt (measured in days after 1 January) was calculated for all birds using the growth rate calculated from the primary feather measurements. The timing of the onset of molt was not associated with body condition ($F_{40,199}$ = 1.1, n.s.), nor with the age of the bird ($F_{1,199}$ = 3.0, n.s.). Status alone was important in the timing of molt ($F_{6,199}$ = 5.6, $P < 0.001$ when comparing all status categories). The timing of molt for resident birds seen at Berwick each month (N = 33) did not differ significantly from that of non-breeding immigrants (N = 127) (one-way ANOVA, $F_{1,158}$ = 1.0, n.s.), but non-breeding immigrants molted significantly earlier than immigrant failed breeders (N = 32) (one-way ANOVA, $F_{1,157}$ = 30.2, $P < 0.001$). The few immigrant breeders (N = 9) molted last of all (Table 3). Sex did not have a significant effect on the timing of onset of

Table 2. Sexes of Mute Swans caught in the flock at Berwick-upon-Tweed in each month during 1994.

Category	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
No. juvenile males	2	4	7	6	8	7	41	8	2	4	4	5	46
No. juvenile females	1	10	22	8	19	9	39	14	3	3	8	17	54
No. non-juvenile males	45	65	50	37	43	55	155	58	23	23	49	56	320
No. non-juvenile females	30	36	37	33	30	32	118	48	16	16	39	51	278

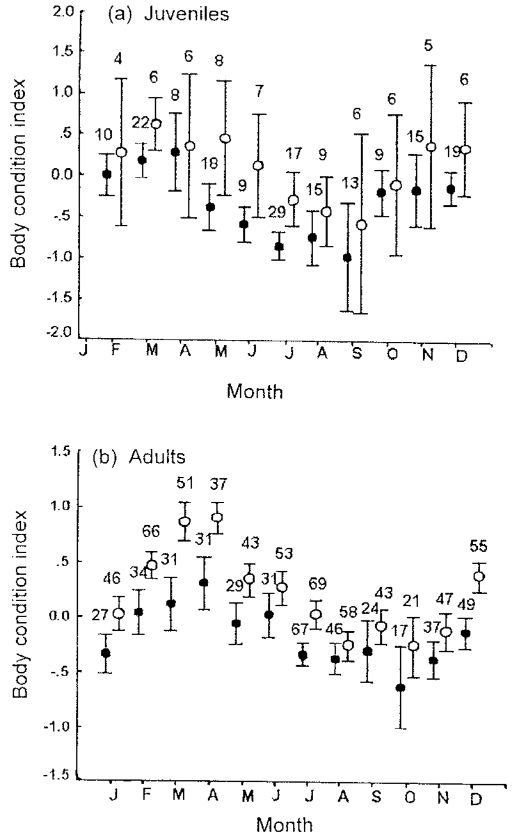

Figure 4. Annual variation in the mean body condition index (±SE) for (a) juvenile (less than one year old) and (b) adult Mute Swans (open circles = males; closed circles = females). N values are given above the SE bars.

molt ($F_{1,299}$ = 0.9, n.s.) when all birds were analyzed together. Further analysis of sex differences in the timing of molt initiation was undertaken for adults to identify any differences within each known status category (Table 4). This showed that, while the difference between sexes in the timing of molt in non-breeding immigrant birds was only one day, successful breeding immigrant females molted an average of nine days earlier than males, that in immigrant failed breeders females molted an average of five days later than males, and that resident females molted, on average, six days earlier than resident males, but again there were no significant sex differences when each category was considered separately ($F_{1,78}$ = 0.1, $F_{1,10}$ = 0.3 and $F_{1,31}$ = 0.5, $F_{1,27}$ = 0.5, for sex differences for non-breeding immigrants, breeding immigrants, immigrant failed breeders and resident birds, respectively, n.s. in each case).

DISCUSSION

The movement of swans to the Berwick flock to molt is similar to that recorded at other sites (Van Dijk and Van Eerden 1991; Perrins and McCleery 1995), with resident birds being augmented in summer by an influx of birds from the surrounding area. The large beds of algae present in the River Tweed, including *Ulva* and *Enteromorpha*, provide one of the best food supplies for molting swans in the area (Anderson-Harild 1981), which would explain the large numbers present during the summer. Body condition peaked in spring, presumably reflecting the availability of natural food resources at this time.

The age and sex structure throughout the molt period was not different to that present at other times of the year, so it is likely that Berwick is not used by any particular age or sex class for molting. These swans appeared to travel to a favored or geographically suitable site, rather than to a site determined by the age or sex of the bird.

The average primary feather growth rate of 6.1 mm per day was similar to that recorded for Mute Swans in Sweden (6.5 mm per day;

Table 3. Timing of the onset of molt for birds of different origins and breeding status.

Status	N	Mean date of molt onset (in days from 1 January)	Standard deviation
Resident	33	24 June (174)	17.9
Immigrant non-breeders	127	27 June (177)	19.7
Immigrant failed breeders	32	19 July (199)	20.4
Immigrant successful breeders	9	15 August (226)	19.1
Immigrant - status unknown	62	30 June (180)	19.1
Unknown	175	1 July (181)	21.4

Table 4. Timing of the onset of molt for birds of different sexes.

	Male			Female		
Status	Timing of onset (in days from 1 January)	N	Standard deviation	Timing of onset (in days from 1 January)	N	Standard deviation
Resident	175	23	18.8	169	6	16.3
Immigrant non-breeder	180	40	16.6	181	40	23.5
Immigrant failed breeder	197	18	19.5	202	14	21.8
Immigrant successful breeder	228	7	21.1	219	2	10.6
Immigrant—status unknown	180	30	16.1	182	22	24.3
Unknown	178	77	18.4	185	157	234

Mathiasson 1981), and The Netherlands (6.1 mm per day; Van Dijk and Van Eerden 1991), but somewhat lower than recorded for breeding Mute Swans in Poland (Czapulak 1989).

Breeding status, and whether non-breeders were resident, affected the timing of onset of molt, and it is likely that this reflects arrival time on the molt site. The resident non-breeders are already present at Berwick and molt first, whereas failed breeders generally are the last to arrive in the molting flock and hence the last to molt. This supports data from elsewhere, where sex differences in the onset of molt were linked to arrival time at the molt site (Mathiasson 1973).

Czapulak (2002) highlighted the differences between breeding male and female Mute Swans in the timing of molt, with females molting earlier than their mates. A tendency for females to molt earlier than males was shown in the Berwick data but the results were not significant, perhaps because the male-female difference was calculated as an average across birds rather than as the difference between mates. Non-breeding birds coming into Berwick for molting appeared to be more synchronous in their molt than breeding pairs.

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The Accuracy of Sexing Mute Swan Cygnets by Cloacal Examination

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Abstract.—Cloacal examination is a long-established method of sexing Mute Swans (*Cygnus olor*) yet its accuracy has not been considered in detail. This technique was used for 708 cygnets fledged and banded in the Lothians, UK between 1982 and 1995. Of the 681 where sex was determined, the numbers of males and females differed significantly (57% were male). Behavioral observations of 113 of the banded cygnets subsequently recorded while breeding indicated that 89% had been sexed correctly. Although a higher proportion of females than males were sexed correctly, the bias in accuracy was not significant.

Key words.—Cloacal examination, cygnet, *Cygnus olor*, Mute Swan, United Kingdom.

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Adult and juvenile Mute Swans (*Cygnus olor*) are sexually monomorphic throughout the year. Males are generally larger than females but a substantial overlap in the range of measurements has been recorded (Birkhead and Perrins 1986). Behavioral differences within breeding pairs, including incubation of the full clutch of eggs and the timing of commencement of primary wing feather molt, enable the sex of paired individuals to be determined (Perrins and Reynolds 1967; Birkhead and Perrins 1986). However, such an approach is applicable to only a proportion of the population.

Cloacal examination was developed as a means of determining the sex of waterfowl in North America during the first half of the 20th century (Hochbaum 1942), refined more recently by Hanson (1967) for Canada Geese and by Reynolds (1972) for Mute Swans. A range of methods have been described for sex determination in other avian species, such as laproscapy, cloacascope and DNA analysis of blood samples (Griffiths *et al.* 1996; Martin *et al.* 2000; Sladen *et al.* 1978), however, cloacal examination continues to be the preferred method for sexing swans (Redfern and Clark 2001). Swennen *et al.* (1979) demonstrated cloacal examination to be 100% accurate for sexing Common Eider (*Somateria mollissima*) ducklings in the Netherlands and Owen (1982) found "no age bias in its accuracy" amongst Barnacle Geese (*Branta leucopsis*). Although cloacal examination has been used for many years, and is currently the most common method of sexing Mute Swans (Bacon and Coleman 1986; Sears 1989; Bacon and Andersen-Harild 1989; Van Dijk and Van Eerden 1991), the reliability of the technique has not been quantified. Bacon and Andersen-Harild (1989) found it "reliable for adults, but less so for cygnets" in Denmark. Data collected from a long-term study of Mute Swans in the UK are analyzed here to enable the accuracy of cloacal examination in determining sex in Mute Swan cygnets to be quantified.

STUDY AREA AND METHODS

The study area covers an area of 3,245 km^2, comprising the regions of East Lothian, Midlothian, West Lothian, The City of Edinburgh and Fife in southeast Scotland, UK, and is bisected by the Firth of Forth (56°N, 3°W). The swans nest on freshwater ponds, lochs and reservoirs, canals and rivers and occasionally at coastal sites, which is similar to breeding habitats used elsewhere in the UK and Ireland (Coleman *et al.* 1991; Smiddy and O'Halloran 1991). Long-term population monitoring commenced in 1978 and color banding was instigated in 1982 (Brown and Brown 1984, 1999).

Cygnets, which were the subject of this analysis, were caught just prior to fledging during the period 1982 to 1995 and fitted with a metal band on one leg, and a plastic band engraved with a unique alphanumeric code on the other (Ogilvie 1972). Two observers determined the sex of these cygnets by cloacal examination (Hanson 1967; Redfern and Clark 2001) but no assessment was made of inter-observer variability in the use of this technique. Although intra-observer variability was not quantified, the cygnets were relatively large birds and were docile and easy to handle during capture, so it was considered that repeatability in individual assessments should have been high in this study (Harper 1994). As swans which had been banded as cygnets in the study area, and were thus of known age, entered the breeding population, their sex was re-assessed by observation of at least four factors throughout the breeding season. In general, the head and the bill knob size were larger in males (Birkhead and Perrins 1986), females normally incubated the full clutch of eggs although some males tended the nest closely during the egg laying period (Reynolds 1972), and breeding females tended to commence primary wing feather moult earlier than their mate (Birkhead and Perrins 1986). When a banded individual re-paired following divorce or loss of mate, it was also possible to verify the initial behavioral classification through continued observations. Bands subsequently lost or broken were replaced when it was possible to recapture the individuals involved. The analysis was confined to those broods where all surviving cygnets in each brood were banded just prior to fledging in order to avoid any possible bias as a consequence of catching only partial broods.

RESULTS AND DISCUSSION

The sex of 708 cygnets was determined by cloacal examination from 158 complete broods, ranging in size from one to eleven cygnets. In 27 (4%) cases, sex could not be determined. Of the 681 sexed cygnets fewer were classified as female than male, 291 (43%) and 390 (57%) respectively ($\chi_1^2 = 14.10, P < 0.01$). Reassessment of the sex was possible in later years for 113 of these 681 birds, when they bred, and 12 (11%) were found to have been misclassified. Of 60 originally classed as males, nine (15%) were found to be females, and of 53 originally classified as females, three (6%) were in fact male. This apparent bias, towards females being sexed more accurately than males, was not statistically significant ($\chi_1^2 = 2.91$, n.s.), but warrants further study. Meanwhile, application of these findings as a proportional correction factor to the 681 originally inspected suggested that there was no significant difference in the sex ratio on sexing ($\chi_1^2 = 0.29$, n.s.), with 333 (49%) estimated as female and 348 (51%) as male. Amongst 16 single sex broods recorded, which ranged in size from two to eight cygnets, twelve broods consisted entirely of males and four broods entirely of females (Fig. 1).

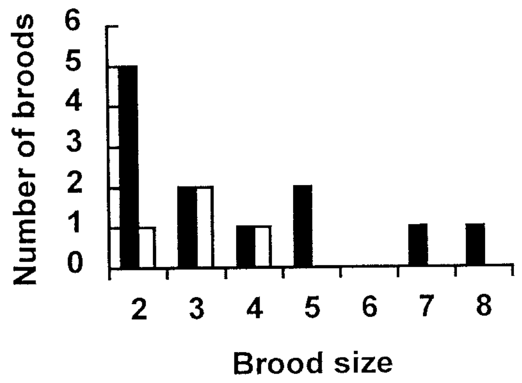

Figure 1. The numbers and sizes of complete, single-sex broods (>1 cygnet) of Mute Swans fledged between 1982 and 1995. Closed columns indicate all male broods, open columns all female broods. The total number of broods (both single-sex and mixed-sex) caught and marked over the same period were: 16 of 2 cygnets, 23 of 3 cygnets, 31 of 4 cygnets, 20 of 5 cygnets, 16 of 6 cygnets, 13 of 7 cygnets, 13 of 8 cygnets, 7 of 9 cygnets, 0 of 10 cygnets and 1 of 11 cygnets. Additionally, 18 families with just 1 cygnet were caught and the cygnets banded (14 males and 4 females) during the study.

It has been argued that the sex ratio in bird populations should be equal on hatching (Clutton-Brock 1986). Cygnet survival prior to fledging in this study was high at 69% and the pattern of survival was similar to that in other areas of Britain (Brown and Brown 2002). There was less scope, therefore, for differential mortality between the sexes due to disease (Swennen *et al.* 1979) and food scarcity (Clutton-Brock 1986), suggesting that the sex ratio at fledging should have been equal. Although this study found a higher proportion of males (57%), sexual parity at fledging was indicated after correction for errors in the initial sex determination.

The results demonstrate that sexing by cloacal examination was not totally reliable for fledglings, although the procedure did assign correctly 89% of cygnets. Any bias against females differs from observations of colonially bred cygnets at Abbotsbury, UK where higher proportions of females were recorded at fledging (C. Perrins, pers. comm.). This demonstrates the need for a cautious approach in the application of cloacal examination for sexing Mute Swans.

Determination of the sex of individuals in a population allows greater depth in the investigation of parameters such as survival rate, dispersal, life-time reproduction, philopatry, flock structure and population dynamics. Many biological techniques used to determine sex are less than 100% accurate (e.g., discriminant analysis, Hamer and Furness 1991) and cloacal examination would seem to be no exception. In this study using cloacal examination, 4% of cygnets could not be classified and an additional 11% were incorrectly classified. Analysis of data from elsewhere would help to substantiate or refute the results of this study.

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Isozyme Analysis Reveals Genetic Differences Between Three Trumpeter Swan Populations

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Abstract.—Reintroduction efforts have established small, scattered flocks of Trumpeter Swans (*Cygnus buccinator*) in the Midwestern United States. Management of these flocks as distinct population units is debated among wildlife managers. The purpose of this study was to quantify genetic differences among three recognized populations of Trumpeter Swans. Blood and tissue samples were collected during 1999 and 2000 and analyzed using horizontal starch-gel electrophoresis. Trumpeter Swans from the High Plains Flock and the Greater Yellowstone Population, from which the High Plains Flock was derived, were genetically indistinguishable. However, both flocks differed from the Pacific Coast Population in allele frequencies at the adenosine deaminase (ADA) locus. Founder effects may have influenced both the High Plains Flock and the Greater Yellowstone Population. Results also suggest unidirectional gene flow from the Pacific Coast Population into the other populations. The High Plains Flock may be a suitable source of individuals to increase the size of the Greater Yellowstone Population while maintaining similar allele frequencies. Additional higher resolution genetic surveys are warranted.

Key words.—Bottleneck, *Cygnus buccinator*, founder effect, gene flow, isozymes, Trumpeter Swan.

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The Trumpeter Swan (*Cygnus buccinator*) was once relatively common throughout much of the conterminous United States, Canada, and Alaska, but was nearly extirpated from the conterminous United States, with only 69 individuals remaining in 1935 (Mitchell 1994). Most of these breed and winter within a 97 km radius in the Tri-state area of southwestern Montana, eastern Idaho, and northwestern Wyoming (Banko 1960). This remnant flock is now known as the Greater Yellowstone Population (formerly known as the Tri-state Flock of the Rocky Mountain Population). It also winters in the Tri-state area and shares this wintering ground with the Western Canada Population, which breeds in the Rocky Mountains of Canada east of the Continental Divide. Two additional Trumpeter Swan populations are recognized for management purposes (Mississippi and Central Flyway Councils 1998). The Pacific Coast Population breeds in Alaska and winters from Oregon to British Columbia. The Interior Population is composed of reintroduced flocks that breed in the northern Midwestern United States (Nebraska, South Dakota, Minnesota, Wisconsin, Michigan and Ohio) and southern Canada (Ontario) and winter from these states to as far south as Texas. Restoration of the Interior Population was accomplished initially with individuals from Greater Yellowstone, but more recently, with captive flocks of mixed lineage and eggs from the Pacific Coast Population (Mississippi and Central Flyway Councils 1998).

This study investigates genetic variation among the Pacific Coast Population, the Greater Yellowstone Population, and the High Plains Flock of the Interior Population. The High Plains Flock was established from 56 Greater Yellowstone swans that were released in western South Dakota during 1960–1962. The High Plains Flock currently breeds and winters primarily in western South Dakota and the Sandhills of Nebraska. Local recruitment, as well as natural recruitment from the migratory Western Canada Population, increased its winter population to 455 individuals in 1998 (C. Pelizza, pers. obs.).

The genetic composition of Trumpeter Swan flocks has been investigated previously. Barrett and Vyse (1982), using horizontal starch gel electrophoresis, found high genetic similarity among the Greater Yellowstone, Western Canada and Pacific Coast Populations. Barrett and Vyse (1982) concluded that there was no genetic reason for selecting one population as a source for restoration efforts over another. Meng *et al.* (1990), using a minisatellite probe, reported mean Band Sharing Coefficients for three species of swans: Mute Swans (*C. olor*), Whooper Swans (*C. cygnus*) and Bewick's Swans (*C. columbianus bewickii*). Marsolais and White (1997) used the same minisatelite probes to estimate Band Sharing Coefficients for Trumpeter Swan population units, and found that Trumpeter Swans had higher Band Sharing Coefficients, i.e., were less variable, than the species studied by Meng *et al.* (1990). Among Trumpeter Swan population units, the reintroduced Ontario Flock and the Greater Yellowstone Population had higher Band Sharing Coefficients than the Pacific Coast or Western Canada Populations. Marsolais and White (1997) suggested founder effects were the probable cause of this reduced variability. They concluded that the Ontario reintroduction program could increase genetic diversity by using birds from other populations, such as the Pacific Coast Population.

Whether to maintain the genetic integrity of reintroduced flocks or to maximize genetic variation within flocks has been the subject of debate among wildlife managers. For example, the Trumpeter Swan reintroduction protocol for the Greater Yellowstone Population in Wyoming (Long 1996) is in direct conflict with the perspectives of Marsolais and White (1997). The Wyoming protocol recognized the possibility that the remnant Greater Yellowstone Population may be genetically unique and established protection of its genetic integrity as a goal for all new releases in Wyoming.

In a precursor to the study described here, Pelizza (2001) analyzed genetic variability in the High Plains Flock and Pacific Coast Population using isozyme markers similar to those used by Barrett and Vyse (1982). Only one of 25 loci examined, the adenosine deaminase (ADA) locus, showed consistently scorable variability among the 37 swans sampled (Appendix). Of the two alleles detected, only the C allele was found in the High Plains Flock and only the D allele was found in the Pacific Coast Population; however, the small sample size from the latter (N = 4) precluded strong support for this finding. The present study was designed to expand upon the use of ADA as an easily obtainable genetic marker for Trumpeter Swan populations and to further inform managers of the population genetic consequences of reintroduction efforts.

METHODS

Samples from a total of 98 birds from three population units were analyzed. Blood samples from the High Plains Flock (N = 37) and Greater Yellowstone Population (N = 37) were collected from Lacreek National Wildlife Refuge and the Nebraska Sandhills, and Red Rock Lakes National Wildlife Refuge, respectively, during summers of 1999 and 2000. Muscle samples from the Pacific Coast Population (N = 24) were obtained from birds that died from lead poisoning near Bellingham, Washington, during the winter of 1999. Collection techniques did not allow identification of individual family groups in any of the three population units sampled.

Blood and muscle sample preparation and storage followed standard methods (May 1992; Utter *et al.* 1987). Blood samples (5 ml) were collected using Becton Dickinson & Co. 5 ml Luer-lok® syringes and 21 gauge 1.5 inch sterile disposable needles. Each 5 ml sample was divided into two equal parts and dispensed into two 2.5 ml K3 EDTA Vacutainer® blood collection tubes, and stored at -80°C until analyzed. A sample of approximately 5 g of muscle tissue was obtained from each carcass and approximately 1 g was minced in a Tris-HCL buffer for 5 minutes. Minced samples were kept at 4°C for 20 min, centrifuged at 12,000 rpm, and the supernatant was stored at -80°C until analyzed.

Standard starch gel electrophoresis (May 1992; Utter, *et al.* 1987) was conducted on muscle and blood samples. An earlier study had shown that muscle and blood proteins yield identical results (Pelizza 2001). Because the initial study revealed consistently scorable variability at only one locus, adenosine deaminase (ADA, EC 3.5.4.4) (see Appendix), this study reports results for the ADA locus only.

Statistical analyses were carried out with Tools for Population Genetic Analysis (Miller 1997). Differences in allele frequencies among populations and conformance to Hardy-Weinberg expectations were analyzed with Fisher's Exact test (Raymond and Rousset 1995).

RESULTS

The Greater Yellowstone Population and the High Plains Flock did not differ in allele frequency at the ADA locus (46% and 58% frequency of C allele, respectively, $P > 0.05$), but both differed significantly from the Pacific Coast Population (9% frequency of C allele, $P < 0.01$). The Pacific Coast Population demonstrated agreement with the Hardy-

Weinberg equilibrium (29% heterozygosity vs. 25% expected, P > 0.99; Table 1). However, both the Greater Yellowstone Population (30% observed and 49% expected, P < 0.05) and High Plains Flock (3% observed and 49% expected, P < 0.01) showed a significant deficiency of heterozygotes (Table 1).

DISCUSSION

While results are preliminary and involve only one locus, they indicate the potential for genetic differentiation between the Pacific Coast Population on the one hand, and the High Plains Flock and Greater Yellowstone Population on the other. This is similar to the finding by Marsolais and White (1997) that the Greater Yellowstone Population was less variable than the Pacific Coast or Western Canada Populations. Additionally, the results of this study indicate no difference in allele frequency at the ADA locus between the High Plains Flock and Greater Yellowstone Populations, which is not surprising given that the High Plains Flock was formed from the Greater Yellowstone Population in 1960. The distribution of the C and D alleles at the ADA locus in the three study populations suggests a mix of population bottlenecks and/or founder effects for the High Plains and Greater Yellowstone Populations, possibly influenced by unidirectional gene flow from the Pacific Coast Population.

Two processes, population bottlenecks and genetic drift, probably decreased genetic variability in the Greater Yellowstone and High Plains population units, and have been shown to be important in the conservation biology of other species (O'Brien *et al.* 1987; Britten and Rust 1996; Bouzat *et al.* 1998; Petit *et al.* 1998). The Greater Yellowstone Population consisted of only 69 individuals when it was discovered in 1935 and it may have been even smaller prior to its discovery. In addition, several demographic and behavioral factors likely decreased the genetically effective size of the population. For example, Trumpeter Swans form life-long pair bonds suggesting that a maximum of 34 pairs was present in 1935 and that subsequent mating was not random. Furthermore, not all adults breed every year, and immature birds may have accounted for a sizeable proportion of the population, further reducing the genetically effective population size. Genetic drift acting on these small effective population sizes may have driven the ADA C allele to a higher frequency in the remnant Greater Yellowstone Population than in the Pacific Coast Population. The High Plains Flock originated from the Greater Yellowstone Population in 1960 and thus was affected by the same bottleneck and genetic drift processes.

Deficiencies in the frequency of heterozygous individuals were observed in both the Greater Yellowstone Population and High Plains Flocks, although birds from the larger and more widespread Pacific Coast Population were in Hardy-Weinberg equilibrium. There are three possible explanations for this result. First, inbreeding in the two smaller flocks could have accounted for the low frequency of heterozygotes, although we have no evidence as to why this should be so. Second, low levels of heterozygosity could have been an artifact of including family

Table 1. Observed genotype frequencies at the ADA locus and those expected under Hardy-Weinberg equilibrium in three Trumpeter Swan population units. Significance values (P in last row) based on Fisher's Exact tests used to test for conformance to Hardy-Weinberg expectations.

	Greater Yellowstone Population (N = 37)		High Plains Flock (N = 37)		Pacific Coast Population (N = 24)	
Genotype	Observed	Expected	Observed	Expected	Observed	Expected
CC	11	7.36	21	12.49	0	0.51
CD	11	18.28	1	18.01	7	5.89
DD	15	11.36	15	6.49	17	17.51
P	<0.05		<0.01		>0.99	

groups, rather than randomly selected individuals (the Wahland Effect), in our Greater Yellowstone and High Plains samples which were collected during late summer on the breeding grounds. The Pacific Coast sample, which consisted of swans killed by lead poisoning at one wintering site, was more likely to have been a random sample of the population. However, family groups typically winter and feed together in swans (Lockman *et al.* 1987), so some sampling of related individuals probably occurred there also. Third, low levels of heterozygosity could have been due to assortative mating. Pacific Coast swans that were translocated, or were migrants, into the High Plains Flock may have preferentially bred with other Pacific Coast birds while High Plains swans continued to mate among themselves. Assortative mating may also have served to segregate the non-migratory Greater Yellowstone Population from the migratory Western Canada Population with which it shares wintering grounds. There is evidence, from the timing of pairing, that assortative mating may occur (Gale *et al.* 1987; Lockman *et al.* 1987), although another study suggested that this is unlikely (Turner 1988). Any combination of inbreeding, artifacts in our sampling, or assortative mating could account for the heterozygote deficiencies.

Any natural recruitment or human-mediated introductions into the non-migratory Greater Yellowstone Population and High Plains Flocks from the Pacific Coast Population represents a potential unidirectional gene flow that could alter the frequencies of neutral markers (such as ADA allozymes) in the recipient populations. While there is no evidence that either allele at the ADA locus affects fitness in Trumpeter Swans, non-neutral alleles at other loci may also spread from the Pacific Coast Population to those in the south. Thus, the High Plains Flock may represent a suitable source of individuals to increase the size of the Greater Yellowstone Population while maintaining similar allele frequencies. In any case, our data, although limited, suggest that some genetic differentiation has occurred between major Trumpeter Swan population groups. Genetic evaluation of other swan flocks would further illuminate this possibility. Higher resolution methods such as mtDNA analysis, DNA fingerprinting and microsatellite analysis would be appropriate to further investigate the relationship among population units. It is important that decisions related to the conservation of swan populations be based on a careful review of all available biological, ecological and genetic information.

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Appendix. Enzymes and other proteins, number of loci, enzyme commission numbers, and electrophoretic conditions used to assay isozyme variability in 37 samples of individual Trumpeter Swans from the High Plains Flock and Pacific Coast Population (from Pelizza 2001). No variability was found in 22 of the 25 loci; ACP and G6PDH were not consistently scorable; only ADA exhibited consistently scorable variability.

Locus	Enzyme or protein	Number of loci	Enzyme commission number	Buffer[a]
ACP	Acid phosphatase	1	3.1.3.2	TC1
ADA	Adenosine deaminase	1	3.5.4.4	TC1
AAT	Aspartate aminotransferase	2	2.6.1.1	4
EST-F	Esterase	2	—	4, R
G3P	Glycerol-3-phosphate dehydrogenase	2	1.1.1.8	R
G6PDH	Glucose-6-phosphate dehydrogenase	1	1.1.1.49	4
GP	General protein	1	—	R
GPI	Glucosephosphate isomerase	1	5.3.1.9	4
HB	Hemoglobin	1	—	4
IDH	Isocitrate dehydrogenase	1	1.1.1.27	C
LAP	Leucine aminopeptidase	1	3.4.11.1	R
LDH	Lactate dehydrogenase	1	1.1.1.27	C
MDH	Malate dehydrogenase	2	1.1.1.37	4, C
ME	Malic enzyme	1	1.1.1.40	C
MPI	Mannosephosphate isomerase	1	5.3.1.8	4
NP	Nucleoside phosphorylase	1	2.4.2.1	TC1, 4
PEPGL	Peptidase glycyl-leucine	1	3.4.–.–	R
PGD	Phosphogluconate dehydrogenase	1	1.1.1.43	TC1
PGM	Phosphoglucomutase	1	5.4.2.2	C
SDH	Sorbitol dehydrogenase	1	1.1.1.14	R
SOD	Superoxide dismutase	1	1.15.1.1	4, R

[a] See May (1992).

Vocal Characteristics of Trumpeter and Tundra Swans and Their Hybrid Offspring

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Abstract.—Trumpeter Swans (*Cygnus buccinator*) and Tundra Swans (*C. columbianus columbianus*) in captivity produce hybrid offspring that are visually similar to their parent species. In this study, call note vocalizations of Trumpeter Swans, Tundra Swans, and their hybrid offspring were analyzed for differences in call duration and initial low frequency. Sixty-five locator vocalizations were digitally recorded from four Trumpeter Swans, four Tundra Swans, and seven known Trumpeter-x-Tundra Swan hybrids. Call duration did not differ significantly among swan types ($\bar{x}$ = 200.5 mS ± 53.3 [SD], N = 65). However, the initial frequency of the locator call was significantly lower in the Trumpeter Swan ($\bar{x}$ = 303 Hz ± 73[SD]) than in the Tundra Swan ($\bar{x}$ = 479 Hz ± 89[SD]). Initial low frequency of hybrid swan locator calls was intermediate ($\bar{x}$ = 398 Hz ± 58[SD]) and did not differ significantly from either parent species. This suggests that the duration of the locator call does not vary among these swan species or their hybrids. However, the initial low frequency of the locator call differs in the two species and their hybrids demonstrate intermediate values.

Key words.—Trumpeter Swan, Tundra Swan, hybrid, *Cygnus buccinator, Cygnus columbianus*, vocalization, bioacoustic.

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Trumpeter Swans (*Cygnus buccinator*) and Tundra Swans (*C. columbianus columbianus*) maintain separate breeding ranges, but have some sympatric breeding areas in Alaska (Wilk 1993). Hybridization in captive swans has been observed (King and King 1978) and therefore may occur in the wild where breeding ranges overlap. Because Trumpeter-x-Tundra Swan hybrids are visually similar to their parent species, it is difficult to determine how much hybridization, if any, takes place within wild populations. Identification of distinguishing vocalizations in swan populations might provide useful information for understanding divergent evolution, and might be useful for distinguishing hybrid animals from their parent species in the wild.

The voices of Trumpeter Swans and Tundra Swans have been described (Banko 1960; Palmer 1976; Mitchell 1994) and are readily distinguishable. To the trained ear, the Trumpeter Swan's voice has a vociferous quality that distinguishes it from the Tundra Swan's. Both species and their hybrid offspring share a common "locator" call note that was selected for analysis in this study. The single syllable Trumpeter Swan locator call, "hoo", is a relatively flat frequency sweep with emphasis remaining nearly the same throughout the call (Fig. 1). The Tundra Swan locator call, a single syllable "hOo" or "wOo", is rounded, creating a crescent frequency sweep. The locator call of a hybrid may sound similar to either parent species, but is duller and somewhat raspy. This hoarseness is also characteristic of other Trumpeter-x-Tundra Swan hybrid calls.

Initial low frequency and call duration has been used in loons to investigate identi-

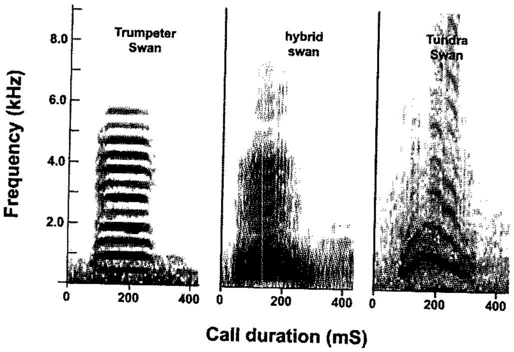

Figure 1. Representative sonograms of the locator call of a Trumpeter Swan, Trumpeter-x-Tundra Swan hybrid, and Tundra Swan.

fication of individual birds (Walcott *et al.* 1999), and we selected these two parameters of the locator call as a means of comparing vocalizations in swans.

METHODS

Locator call vocalizations from 15 adult swans (4 Trumpeter Swans; 4 Tundra Swans; 7 Trumpeter-x-Tundra Swan hybrids) were recorded for this study. Except for one wild adult Tundra Swan, all swans were part of a collection maintained by the Swan Research Program, Environmental Studies at Airlie, near Warrenton, Virginia (Sladen *et al.* 2002). Recordings were acquired at the Airlie reservoir and lower Clifton Lake. Each swan wore a unique alphanumeric neck collar that allowed rapid identification (Sladen 1973). Pedigree and age of each individual was known for all captive birds. Sixty-five (11 Trumpeter Swan, 30 Tundra Swan, and 24 hybrid) distinct vocalizations were isolated from digital recordings of identified birds in similar environments and conditions. Recordings were used from birds that were vocally interacting with one another. Only vocalizations obtained from birds in "standing alert" and "on water" postures were used. Recordings were made at distances of 12–90 m between February and May, 1999 and 2000.

Vocalizations were recorded with a TASCAM DA-P1 digital audio tape (DAT) recorder and a Sennheiser ME66 shotgun microphone with a K6 power module. The microphone was enclosed in a Light Wave zeppelin windscreen. Recordings were analyzed with Canary 1.2.4 Bioacoustics Workstation software. Call duration (mS) and initial frequency (Hz) taken at the base (lowest value) were measured on sonogram displays (Walcott *et al.* 1999). Because multiple vocalizations were recorded from each bird, the individual's mean value was weighted so that each bird was equally represented. Weighted means were calculated by multiplying the reciprocal of the number of vocalizations per bird by the individual's mean value. Analysis of variance, followed by pairwise comparisons of weighted means (Blaisdell 1993), was conducted on mean duration of calls (mS) and mean initial low frequency of calls (Hz) for Trumpeter Swans, Tundra Swans and hybrid swans.

RESULTS

The range of call duration for all Trumpeter Swan locator calls was 63–332 mS, for Tundra Swans 161–299 mS, and for hybrid swans 126–236 mS. Mean call duration did not differ significantly among the three swan types ($F_{2,12}$ = 1.61, n.s.). The overall mean locator call duration was 200.0 mS ± 53.3[SD], N = 65 (Fig. 2).

The mean initial low frequency of the locator call differed significantly among the three swan types ($F_{2,12}$ = 50.76; P < 0.001), and was lower in the Trumpeter Swan ($\bar{x}$ = 303 Hz ± 73[SD]) than in the Tundra Swan ($\bar{x}$ = 479 Hz ± 89[SD], P = 0.04, Fig. 2). The mean initial low frequency of the hybrid call was intermediate ($\bar{x}$ = 398 Hz ± 58[SD]) and did not differ significantly from either parent species. There was no overlap in the range of initial low frequencies exhibited by Trumpeter Swans (200–370 Hz) and Tundra Swans (400–650 Hz), however the range in hybrid swans (310–510 Hz) overlapped that of both parent species.

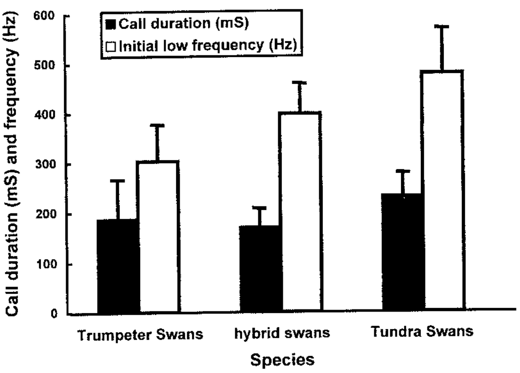

Figure 2. Locator call duration and initial low frequency for Trumpeter Swans, Tundra Swans and hybrid swans. Error bars represent one SD. Trumpeter Swans had significantly lower initial low frequencies than Tundra Swans (*P* = 0.04); no other differences among swan types were significant.

DISCUSSION

Vocalization in birds is a primary means of communication between conspecifics, and a powerful isolating mechanism during divergent evolution. Differences in vocalizations in territorial songbirds have been linked to divergence that may occur either without significant morphological variation, such as in chiffchaffs (*Phylloscopus* spp.) (Martens 1996), or with significant morphological change as in Darwin's finches (Podos 2001). Little is known about the co-evolution of morphological and vocal characteristics in non-songbird species. Basic data on vocal characteristics, morphological traits and behavioral patterns may prove valuable in understanding this issue in swans.

The differences in vocalizations identified in this study may be correlated to differences in morphological traits. Compared to Tundra swans, Trumpeter Swans have a longer trachea, with a second loop extending through the sternum, that provides a higher capacity for holding and moving air (Banko 1960), and is likely associated with their distinct low-frequency, trumpet-like locator call. Given the intermediate value of the initial low frequency of the locator call in hybrid swans, it would be interesting to compare the morphological characteristics of the trachea in both species with their hybrids.

In conclusion, the initial low frequency of the locator call appears to be a distinguishing characteristic of Trumpeter Swans and Tundra Swans. However, hybrid swans produce an intermediate frequency that is not readily distinguishable from either parent species. Therefore, the locator call alone will not be useful for distinguishing hybrid swans in wild populations. Additional analysis of locator and other calls, especially the more complicated calls such as the "triumph", may reveal unique vocal characteristics. We encourage further investigation of swan vocalizations and their relationship to morphological traits.

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Trends in Mute Swan Blood Lead Levels: Evidence of Grit Reducing Lead Poisoning

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Abstract.—Lead from spent gunshot and discarded anglers' weights continues to pose a threat to Mute Swans (*Cygnus olor*) in Europe. In many parts of the world, lead is still widely used in fishing and hunting, and in areas where it is banned previous losses still pose a threat. We collected 590 blood samples from ringed Mute Swans between October and January over six winters: 1983–84 to 1986–87 inclusive, 1994–95 and 1999–2000. Most samples were collected from swans wintering at Cork Lough, Ireland, an urban site where coarse fishing is popular, while a smaller number were collected from swans at rural sites within a 50 km radius of Cork Lough. The median blood lead levels in swans at Cork Lough declined from 36.2 µg/100 ml in 1983-84 to 12.1 µg/100 ml in 1999–2000. There was also a significant decline in the proportion of birds suffering from acute lead poisoning (>40 µg/100 ml of whole blood), from 60% in the winter of 1985-86 to 2% in the winter of 1994-95. A significant decline in the median blood lead level of Mute Swans in rural areas, from 49.7 µg/100 ml in 1984-85 to 7.7 µg/100 ml in 1999-2000, was also noted. The decline in the median blood lead level and in the proportion of birds suffering from acute lead poisoning is most likely explained by a combination of factors, including the provision of grit at Cork Lough.

Key words.—Angling, blood, *Cygnus olor*, grit, lead, Mute Swan, poisoning, remediation.

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Heavy metals continue to affect swan populations worldwide. Lead from spent gunshot and discarded anglers' weights or sinkers, has posed problems for Mute Swans (*Cygnus olor*) for decades in Ireland and elsewhere (O'Halloran *et al.* 1991; Sears 1988). The lead pellets are mistakenly ingested as grit particles and are ground down in the gizzard before being absorbed into the blood, resulting in lead poisoning. Lead pellets can be found in sediments, often in large quantities, and are consumed by waterfowl, including swans (Beyer *et al.* 2000). While much attention has focussed on mortality attributable to lead in Mute Swans (Simpson *et al.* 1979; Birkhead 1982; Sears 1988), few have identified sub-lethal effects (O'Halloran *et al.* 1989). In many countries the use of lead in hunting and fishing has either been banned or controlled (USA, Sweden, UK). In Ireland, lead is still widely used in fishing and hunting and, in the absence of legislation to control its use in these activities, it may become necessary at some sites to undertake management and mitigation measures to minimize lead poisoning in Mute Swans and other waterfowl. Lost lead weights were found to cause elevated blood lead levels and mortality due to lead poisoning in swans at Cork Lough during the 1980s (O'Halloran *et al.* 1991). Here we consider the effect that the provision of grit at Cork Lough has on Mute Swan blood lead levels, and compare these data with those for swans from rural sites. We also examine how the provision of grit might affect the proportion of lead-poisoned swans at Cork Lough.

STUDY AREA

The main study area is an urban lake, Cork Lough, in Cork city (51°52'N, 08°29'W), southwest Ireland. Blood samples were collected from Mute Swans in the winters of 1983–84 to 1986–87 inclusive, 1994–95 and 1999–2000. This freshwater lake (about 6 ha) is a refuge for a range of domestic and wild waterfowl, including about 50 Canada Geese (*Branta canadensis*) and over 200 Mute Swans. The maximum depth is 1.5 m in the northern basin. The area is an internationally known coarse angling site, and lead weights and sinkers continue to be used. There is year-round fishing with little or no controls. The intensity of angling varies from one to ten anglers at any one time. Blood samples were taken from swans at rural sites upon catching the swans opportunistically during the winters of 1984–85, 1994–95 and 1999–2000. These samples were collected at a range of rural sites, mostly within 50 km of Cork Lough, and were either from cygnets (which had never visited Cork Lough) or fully-grown birds (some of which may have visited Cork Lough outside of the winter months, or wintered there in previous years).

METHODS

Collection and Analysis of Blood Samples

Blood samples were collected from the brachial vein and frozen until analyzed. All swans were aged and sexed by cloacal examination as described by Baker (1993). Whole blood samples were digested in 10% Aristar nitric acid and analyzed using a Pye Unicam and Varian Graphite furnace. The digested blood sample was spun in a centrifuge for ten minutes at 2,500 G, the clear supernatant removed and analyzed using atomic absorption spectroscopy. Standards were prepared using a standard addition method with routine inter-calibration and quality control (for details see O'Halloran *et al.* 1988a; O'Halloran *et al.* 1997). Swans with blood lead levels in excess of 40 µg/100 ml of whole blood were deemed to have acute lead poisoning (Simpson *et al.* 1979).

Grit Application

Following publicity gained from earlier studies, 40 tonnes of grit (sandstone <10 mm diameter) was scattered across the bed of Cork Lough in the summer of 1986 (T. O'Connor, pers. comm.). An additional 50 tonnes was added in each of the four years 1997–2000 (L. Casey, pers. comm., Cork Corporation Environment Department). Grit is now visible on the bed of Cork Lough, whereas in the past mud was the most obvious substrate. Mute Swans and other waterfowl can now be seen ingesting grit (O'Halloran, pers. obs.).

Data Presentation

The data are presented as median blood lead levels (µg/100 ml) for comparisons with other published works (such as Sears 1988; Simpson *et al.* 1979). In order to summarize the higher values, which are biologically significant, the percentage of lead poisoned birds (>40 µg/100 ml) is also presented.

RESULTS

Blood from 590 Mute Swans was collected and analyzed in six winters between 1983–84 and 1999–2000 (Tables 1 and 2). There was significant variation in the median blood lead level of birds sampled at Cork Lough between 1983–84 and 1999–2000 (Kruskal-Wallis, H_5 = 291, P < 0.001; Fig. 1). The median level declined from 36.2 µg/100 ml in 1983–84 to 12.1 µg/100 ml in 1999–2000 (Table 1), and blood lead levels recorded before the distribution of grit in summer 1986 were significantly higher than in subsequent years (Mann Whitney U = 20,640, N_1 = 268, N_2 = 285, P < 0.001). The proportion of swans suffering from acute lead poisoning (i.e., blood lead level >40 µg/100 ml) also declined during the study, from 60% in 1985–1986 to 2% in 1994–95 (Fig. 2), and the number of birds with acute lead poisoning was significantly higher before than after the distribution of grit in summer 1986 (χ^2_1 = 55.2, P < 0.001). However, despite the reduction in the median blood lead level, swans continue to suffer from lead poisoning at Cork Lough, with some high lead levels recorded even in 1999–2000 (Table 1). There was no significant difference in the blood lead levels for birds of different sex (one-way ANOVA, $F_{1,385}$ = 0.23, n.s.), or age ($F_{2,385}$ = 0.79, n.s.), nor was the age-sex interaction significant ($F_{2,385}$ = 0.49, n.s.).

Variation in the median blood lead levels of swans at rural sites over the same period were also significant (Kruskal-Wallis, H_2 = 17.2, P < 0.001), declining from 49.7 µg/100 ml in 1984–85 to 7.7 µg/100 ml in 1999–2000 (Table 2). The proportion of swans suffering from acute lead poisoning detected at rural sites ranged from 57% in 1984–85 to 0% in 1999–2000 (Table 2, but note small sample size in 1984–85).

DISCUSSION

This study shows a decline in the median blood lead levels and the proportion of Mute Swans suffering from acute lead poisoning in

Table 1. Summary of winter blood lead levels (µg/100 ml) for Mute Swans at Cork Lough, Ireland. The first (Q1) and third (Q3) quartiles are shown.

Winter	N	Median	Range	Q1	Q3	% >40 µg
1983/1984	116	36.2	4.1–1478	25.9	53.8	42
1984/1985	19	41.4	20.7–149	28.9	72.4	52
1985/1986	133	46.6	9.3–683	35.2	66.7	60
1986/1987	165	33.1	2.5–310	24.8	47.6	19
1994/1995	42	14.0	5.0–44	11.7	18.0	2
1999/2000	78	12.1	2.3–95	8.7	19.9	4

Table 2. Summary of winter blood lead levels (µg/100 ml) for Mute Swans at sites outside Cork Lough, Ireland. The first (Q1) and third (Q3) quartiles are shown.

Winter	N	Median	Range	Q1	Q3	% >40 µg
1984/1985	7	49.7	26.9-68	28.9	62.1	57
1994/1995	15	9.0	3.0-18	8.0	13.0	0
1999/2000	15	7.7	3.0-19	3.3	11.8	0

southwest Ireland since the early 1980s. The decline at one site, Cork Lough, seemed to be associated with the distribution of grit in 1986, and the decrease noted during winter 1986–87 was sustained into the 1990s. In this study, most samples were collected from swans at Cork Lough, where lead poisoning was identified in the early 1980s (O'Halloran and Duggan 1984; O'Halloran *et al.* 1988b). Some seasonal variation in blood lead levels was noted during these studies, with the highest levels of lead and acute lead poisoning occurring in winter (O'Halloran *et al.* 1991). These high levels were probably due to the high density of birds present at this time as the birds sought the limited grit available, and poor diet because of a reliance on bread as food (Keane and O'Halloran 1992). The data reported here is based on swans sampled in winter. This time period was selected as representing the "worst-case scenario" at a time when Mute Swans are less mobile. The swans sampled at the rural sites were a mixture of cygnets that had never visited Cork Lough and sub-adults and adults, which may have visited Cork Lough at some time in the past, but not in the preceding months. Given that blood lead levels in birds are indicative of recent exposure (35–40 days, Sturkie 1965), we believe that the values obtained outside Cork Lough truly represent the level of lead in swans in the wider County Cork countryside.

At Cork Lough there has been a considerable improvement in the blood lead status of Mute Swans during the course of this study. The decline in the median blood lead level (Table 1), and the number of acutely lead poisoned swans (Fig. 2) is considerable, and this is likely to lead to an increase in the condition of birds at Cork Lough, though further analysis of weight and condition are required.

The most likely reason for the decline in lead poisoned birds is the addition of grit to the bed of Cork Lough. The use of grit in digestion is well described and its absence has been shown to cause increased lead poison-

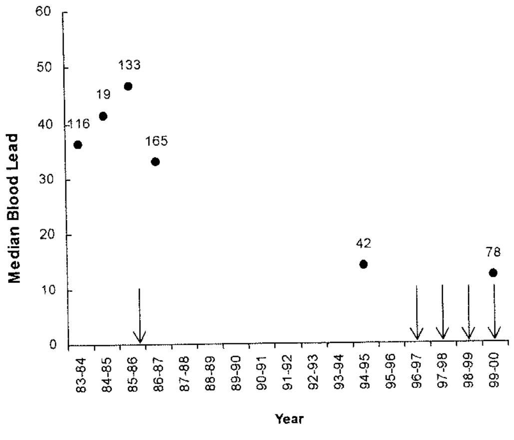

Figure 1. Median blood lead levels (µg/100 ml) for Mute Swans at Cork Lough, Ireland, between 1983–84 and 1999–2000. Arrows indicate when grit was applied. Sample sizes are presented above each point.

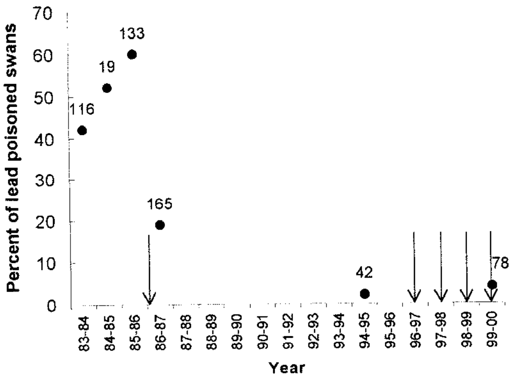

Figure 2. Percentage of lead poisoned (>40 µg/100 ml) Mute Swans at Cork Lough, Ireland, between 1983–84 and 1999–2000. Arrows indicate when grit was applied. Sample sizes are presented above each point.

ing in ducks and swans (Mateo *et al.* 1997). Moreover, that the provision of grit reduces lead poisoning in waterfowl is well known and has been described by Thomas (1980). Because lead persists in the environment, it can pose a risk to swans for a considerable period of time after loss as the birds ingest lead weights or pellets in place of grit. It has been reported elsewhere that lead pellets in mud caused lead poisoning in Whooper Swans (*Cygnus cygnus*) 20 years after shooting ceased at the site (O'Halloran *et al.* 1988b). At Cork Lough, discarded anglers' weights were found at a density of 0.02 m^{-2} while at Lough Neagh in Northern Ireland the pellet density adjacent to a clay-pigeon shooting site was 2,400 m^{-2}. Thomas (1980) described a number of approaches to reduce lead poisoning resulting from pellets in sediments: raising water levels, avoid flooding hunting areas, cultivation, removal of sediment, use of non-toxic sinkers or shot and the addition of grit. Some of these approaches have been used with differing success. For example, the cleaning of a lagoon in France caused high mortality in Mallard (*Anas platyrhynchos*), presumably because it exposed pellets that were previously beyond the reach of birds (Pain 1991). In contrast, in a Spanish study no lead poisoning was recorded following the cleaning of a small part of a lagoon (Mateo *et al.* 1997). It is unclear whether longer-term monitoring of lead poisoning was continued at any of these sites. In our study, the application of grit was made on a number of occasions and the lead levels monitored over a 17-year period. The application of grit seems to have resulted in a reduction in lead levels and acute lead poisoning in swans at Cork Lough, and these benefits may have been accrued by other waterfowl species. However, the role of grit in reducing lead poisoning in this study must be regarded as suggestive as no field data on the availability (or the change in availability) of lead pellets at Cork Lough are available.

The decline in acute lead poisoning and blood lead levels at both the urban and rural sites may also be related to an apparent decline in hunting in Ireland. The number of hunters with unlimited hunting licences was 90,500 in 1987 and this dropped to 80,000 in 1999 (Owen *et al.* 2000). Although the use of lead by hunters has continued in Ireland, there have been few studies on the incidence of lead poisoning in waterfowl other than Mute Swans. Butler (1990) found that the incidence of ingestion of spent gunshot pellets by a range of dabbling and diving ducks was low in Ireland. However, a number of cases of acute lead poisoning due to gunshot have been reported in Mute Swans in Ireland (O'Halloran *et al.* 1988b). Because of the continued use and persistence of lead in the environment, it continues to pose a threat to Mute Swans. The data reported here would suggest that at Cork Lough, this threat is limited, and that the number of Mute Swans with elevated lead has declined. Therefore, management measures such as the addition of grit, at individual sites can reduce blood lead levels and lead poisoning in Mute Swans. However, the success of management measures relies on surveillance and monitoring to identify the problem in the first place. Actions taken should also be monitored to test their impact on bird populations. Because lead poisoned Mute Swans often die unnoticed away from flocks, the best approach to this monitoring might be a routine blood sampling program of important swan flocks over long periods of time (such as reported here). Despite a reduction in some of the uses of lead by society, the use of lead in hunting and fishing still needs to be addressed in Ireland and elsewhere in order to eliminate this unwelcome source of contamination of swans and other waterfowl.

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Survival and Reproductive Success of Trumpeter Swans After Treatment for Lead Poisoning

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Abstract.—During the peak of the Trumpeter Swan (*Cygnus buccinator*) restoration programs in Minnesota and Wisconsin, in 1988–1990, many swans developed lead poisoning. Drought conditions allowed the birds access to spent lead shot in lakes and refuges. At least 94 swans developed lead poisoning, 63 were treated, of which 29 were successfully treated and released. The birds that were successfully treated were normal on physical examination, had blood lead levels in the normal range and no longer had radiographic evidence of lead shot in their gastrointestinal tract. In all, 23% of free-flying birds were successfully treated for lead poisoning compared to 67% of captive (previously pinioned or wing-clipped) birds. Six of 29 swans successfully treated for lead poisoning were confirmed to reproduce two to 10.5 years after treatment. Males and females were equally likely to reproduce after treatment for lead poisoning. Only one of 20 cygnets successfully treated was confirmed to reproduce compared to five of nine birds treated as subadult/adults (1–2 years or ≥2 years of age).

Key words.—*Cygnus buccinator*, lead poisoning, reproductive success, Trumpeter Swan, waterfowl.

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Before the 1991 ban on using lead shot for waterfowl hunting in the United States, it was estimated that millions of waterfowl died of lead poisoning (Bellrose 1959). Despite the ban, thousands of tons of lead shot remain in the environment and are potentially available to waterfowl through ingestion during feeding (Lagerquist *et al.* 1994). During the peak of the Trumpeter Swan (*Cygnus buccinator*) restoration programs in Minnesota and Wisconsin, in 1988–1990, a large number of swans developed lead poisoning. From 1980–1987, only ten cases of lead poisoning were documented in Trumpeter Swans in this region (Gillette 1989; Degernes and Redig 1989) compared to 94 cases from 1988–1990 (Degernes *et al.* 1989; Degernes and Frank 1991), and relative to a total of only 256 birds in this region in 1989 (Compton 1991; Hines 1991; Matteson 1991). Drought conditions during 1988–1990 were thought to allow access to previously unattainable spent lead shot in refuges that had been closed to hunting for decades (Degernes and Frank 1991). During this period, 63 swans were treated for lead poisoning. Although there is little published data on whether lead poisoning has an adverse effect on post-treatment survival (Sears *et al.* 1989) and future reproduction, future management decisions in the United States are likely to be based, in part, on the probability of survival and reproduction of treated swans. The purpose of this paper is to review the treatment outcome and reproductive activity of swans following treatment for lead poisoning.

METHODS

Birds included in this retrospective study were part of Trumpeter Swan restoration programs in Minnesota and Wisconsin, USA. A total of 63 Trumpeter Swans were treated for lead poisoning at The Raptor Center at the University of Minnesota, St. Paul between January 1988 and April 1990. Of the 63 Trumpeter Swans treated, 28 were cygnets (<1 year old), seven were subadults (1–2 years old), and 28 were adults (≥2 years old) at the time of treatment. Subadults and adults were combined for data analysis. Another 31 Trumpeter Swans died of lead poisoning prior to treatment and were not included in these analyses.

Diagnosis and Treatment

The diagnosis of lead poisoning has been previously described and blood lead levels $>0.4\ \mu g \cdot ml^{-1}$ were considered diagnostic (Degernes *et al.* 1989; Sears *et al.* 1989). Treatment followed established protocols, using a combination of supportive care (fluid and nutritional support, and antibiotics or antifungals, as indicated), chelation therapy (calcium EDTA and/or dimercaptosuccinic acid) and lead shot removal from the ventriculus (gastric lavage, with or without endoscopic retrieval of shot) (Degernes *et al.* 1989; Degernes 1991). Treatment duration ranged from two to six weeks. Length of treatment was determined by the severity of clinical signs (including weight loss and neurologic signs), hematological derangements (anemia, blood lead elevation, hypoproteinemia, etc.) and response to therapy. A swan was considered successfully treated when it was normal on physical examination and the hematological parameters were within normal reference ranges, including blood lead level $<0.4\ \mu g \cdot ml^{-1}$ (Degernes *et al.* 1989). After treatment, all birds were wing-clipped (if not pinioned or previously wing-clipped) and placed in a fenced refuge for further monitoring for approximately two to 16 months. Throughout the text, the mean ±SD blood lead level is given.

Resighting Effort

The survival and reproductive history of birds successfully treated for lead poisoning was based on resightings of neck collars, leg bands and/or wing tags. Cause and date of mortality or disappearance after treatment was reported when known.

The 27 swans released to the wild after treatment were marked with one of three combinations of permanent markers: alphanumeric neck collar and aluminum leg band (N = 20 cygnets; Wisconsin Department of Natural Resources), alphanumeric patagial tag and aluminum leg band (N = 6 adults; Minnesota Department of Natural Resources), or alphanumeric neck collar and identical coded leg band and aluminum leg band on the opposite leg (N = 1 adult; Hennepin Parks). In addition, two pinioned swans were banded with aluminum leg bands (one with neck collar also) and monitored in captivity daily from 1989-2000 (Table 2, Swans 2 and 6).

Six of the seven treated subadult and adult birds were released on remote wetlands in Minnesota during the spring, two to five months after treatment. They were monitored approximately twice weekly via ground checks or aerial surveys during the nesting seasons from 1989–1994. Monitoring was not continued after 1994 except opportunistically. One treated adult was allowed to fly from its captive refuge at Hennepin Parks in Maple Plain, Minnesota, after the summer molt, five months after treatment. It was monitored three to five times per week during the nesting season and weekly during the winter from 1989–1996.

The treated cygnets (N = 20) were released from captivity with a mate at two years of age at various wetlands in Wisconsin. After release, they were monitored approximately weekly by field biologists during each nesting season. The public also reported sightings opportunistically throughout the year. When possible, adult Wisconsin birds with missing markers were recaptured for band replacement.

Failure to resight birds released to the wild could have been due to death, marker loss, movement outside the study area, or failure to resight individuals in remote areas. Resighting efforts varied with the agency and location of the released swan. The monitored areas included the wetland or lake where the birds were originally released and, if not observed, nearby likely areas. Most swans seen by aerial survey were not individually identified, but ground checks were done whenever possible to identify swans. If these birds were in locations inaccessible by land, individual swan identification was impossible. One free-flying bird (released by Hennepin Parks) was easily resighted because it nested in a large regional park in close proximity to a large metropolitan area in Minnesota. Swans released in northern Minnesota and Wisconsin were initially released as wing-clipped birds at wetlands that were accessible by ground; however, once these birds molted, many frequently moved to different lakes and wetlands and were more difficult to relocate (pers. obs.).

Independent t-tests, paired t-tests and chi-squared tests were used to analyze the data. All chi-squared tests with 1 df were calculated with Yates correction for continuity.

RESULTS

Treatment Results

In all, 29 of 63 (46%) Trumpeter Swans were successfully treated for lead poisoning (Table 1). Most (54%) of those treated died before release. Of the cygnets treated, 71% (20 of 28) were successfully treated compared to 26% of subadults or adults (nine of 35; $\chi^2_1 = 13.1$, $P < 0.001$). Approximately half of the swans presented for treatment were free-flying (N = 30) and half were captive (N = 33; Table 1). Of the free-flying birds, 23% were successfully treated compared to 67% of captive birds ($\chi^2_1 = 11.8$, $P < 0.001$, Table 1). Most cygnets (25 of 28) had become lead poisoned while being raised in captive refuges for eventual release as part of Trumpeter Swan restoration programs. Nine cygnets were treated a second time 10–12 months after the first treatment (two died) and one was unsuccessfully treated a third time five months later. Cygnets were moved to a different captive refuge after each incident in an effort to prevent further lead exposure. Seven of nine successfully treated subadults and adults had been previously released to the wild or were offspring of birds previously released. Two successfully treated adults were pinioned, captive birds and were not released to the wild.

Mean (±SD) blood lead level at time of admission of all swans, including those that

Table 1. Percentage of swans successfully treated for lead poisoning and percentage known to breed after treatment.

	Age at treatment (yrs)		
	Cygnet (<1)	Adult (>1)	Total
Successfully treated	71% (20[a]/28)[b]	26% (9/35)[b]	46% (29/63)
Successfully treated and known to breed[c]	5% (1/20)[d]	56% (5/9)[d]	21% (6/29)
Free-flying successfully treated	0% (0/3)	26% (7/27)	23% (7/30)[e]
Captive successfully treated	80% (20/25)	25% (2/8)	67% (22/33)[e]

[a] Included 9 swans that were treated twice (N = 8) or three times (N = 1), of which six survived multiple treatments.

[b] Difference between cygnets and adults was significant, $\chi^2_1 = 13.1$; $P < 0.001$.

[c] Number of swans successfully treated for lead poisoning that had confirmed offspring after treatment, defined as one or more cygnets that fledged.

[d] Difference between cygnets and adults was significant, $\chi^2_1 = 9.55$; $P < 0.01$.

[e] A significantly higher percentage of captive than free-flying swans were successfully treated, $\chi^2_1 = 11.8$; $P < 0.001$.

died during treatment, was 2.04 $\mu g \cdot ml^{-1}$ ± 1.29 (N = 63). At the time of admission, mean blood lead levels ($\mu g \cdot ml^{-1}$) did not differ significantly in captive from free-flying swans (2.01 ± 1.47 and 2.28 ± 0.99, N = 33 and 30, $t_{61} = 1.68$, P = 0.09), in cygnets compared to subadults or adults (2.21 ± 1.62 and 2.09 ± 0.89, N = 28 and 35, $t_{61} = 0.36$, n.s.), and in swans that survived treatment compared to those that died during treatment (1.79 ± 1.13 and 2.44 ± 1.36, N = 29 and 34, $t_{61} = 1.69$, P = 0.09). In all birds successfully treated, mean blood lead levels decreased significantly from pre- to post-treatment (1.79 ± 1.13 and 0.27 ± 0.16, N = 29, paired t-test, $t_{27} = 6.89$, $P < 0.0001$). After successful treatment, there were no statistical differences in final mean blood lead levels between captive and free-flying swans (0.26 ± 0.17 and 0.28 ± 0.14, N = 22 and 7, $t_{27} = 0.28$, n.s.), or between cygnets and adults (0.27 ± 0.18 and 0.26 ± 0.11, N = 20 and 9, $t_{27} = 0.27$, n.s.), or between those that subsequently reproduced compared to those that did not (0.26 ± 0.10 and 0.27 ± 0.17, N = 23 and 6, $t_{27} = 0.21$, n.s.).

Reproduction After Treatment

Of the Trumpeter Swans successfully treated for lead poisoning, 56% (five of nine) of those treated as subadults or adults and 5% (one of 20) treated as cygnets were recorded as having reproduced (Tables 1 and 2) ($\chi^2_1 = 9.56$; $P < 0.01$). Of 63 lead poisoned swans presented for treatment, 14% treated as adults and 3.5% treated as cygnets were known to have reproduced after treatment ($\chi^2_1 = 2.00$, n.s.). Excluding two captive adult swans and three cygnets never released as two-year-olds, adults released to the wild were more likely to reproduce than cygnets released to the wild as two-year-olds ($\chi^2_1 = 4.77$, $P < 0.05$). The six swans (three males and three females) known to have reproduced were treated at a median age of 2.3 years (range 0.7 to 10.5) and they produced cygnets at a median age of 8.5 years (range five to 19), which corresponds to a median of 6.2 years after treatment (range 2.5 to 10.5). In total, 10% of swans treated for lead poisoning, and 21% of those successfully treated, subsequently bred. The actual number of breeding swans may be higher if some that were not accounted for had lost their markers or were breeding in locations where they were not resighted.

Of the six successfully treated swans that bred, two adults bred in captivity and the others were free-flying. Of the five subadults or adults that later bred, only one had produced cygnets prior to treatment; three others had mates prior to becoming lead poisoned but had not reproduced. Of the four successfully treated non-breeding adults, only one female had reproduced prior to becoming lead poisoned; all were paired when originally released as part of the reintroduction program. The median age of four non-breeding adults was 2.5 years (range 2 to 3.5)

Table 2. Characteristics of Trumpeter Swans that reproduced successfully after treatment for lead poisoning.

	Swan 1	Swan 2	Swan 3	Swan 4	Swan 5	Swan 6
Sex	female	female	female	male	male	male
Age (years) at treatment	2	10.5	2	2.5	0.7	8.5
Age at 1st production of cygnets	8	13	5	7	9	19
Status at time of treatment	Free-flying[a]	Pinioned[b]	Free-flying[a]	Free-flying[a]	Wing-clipped[a,c]	Pinioned[b]
Blood lead pre-treatment ($\mu g \cdot ml^{-1}$)	2.78	0.70	0.54	1.80	1.23	1.60
Blood lead post-treatment ($\mu g \cdot ml^{-1}$)	0.29	0.28	0.39	0.12	0.16	0.30
Years post-treatment to 1st cygnets	6	2.5	3	4.5	8	10.5
Years when cygnets produced	1995, 1996	1991, 1993, 2000	1991	1992, 1993, 1994, 1995	1997, 1998, 1999, 2000	2000
Number of cygnets in each year	5, 6	2, 2, 1	6	5, 6, 2, 7	3, 4, 5, 2	1
Current status	Missing 1997	Alive 2001	Missing 1991	Died 1996	Alive 2001	Alive 2001

[a] Free-flying at time of breeding.

[b] Captive at time of breeding.

[c] Captive, wing-clipped cygnet when treated, but released to wild at 2 years of age.

at the time of treatment for lead poisoning, comparable to the median age of breeding swans when treated (2.3 years).

Survival After Treatment

The median length of survival after treatment for lead poisoning was two years, with adult swans surviving a median of four years (range six months to twelve years) compared to 1.5 years (range three months to twelve years) for cygnets. Of the nine successfully treated subadult or adult swans, three died within two years of treatment, two disappeared 3–4 years after treatment, one died and one disappeared eight years after treatment, and two are known to be alive 12 years after treatment (2001). Of the four known deaths, two were due to unknown causes, one was shot, and one death was unrelated to lead poisoning. Thus, 67%, 56%, 44%, and 22% were known to be alive 2, 4, 8 and 12 years after treatment, respectively. The failure to resight the three swans that 'disappeared' could have been due to their death, marker loss, movement outside the study area, or failure to resight all individuals in remote sections of the study area. One breeding adult (Table 2, Swan 1) was re-collared three years after treatment, and last resighted 4.5 years later prior to severe winter conditions when many swans were observed with iced collars (Lawrence 1999). Another adult that bred (Table 2, Swan 4) was neck-collared five years after release after it lost its patagial tag (metal leg band present, as well as the patagial tag "button").

Of the 20 successfully treated cygnets, three died of causes unrelated to lead poisoning before release, and 17 were released to the wild at two years of age. Of these 17 released cygnets, nine died or disappeared within two years of treatment, five died or disappeared within 2–4 years, two disappeared within 4–5 years, and one is known to be alive 12 years after treatment (2001). Four of 17 released swans later died of lead poisoning and two died of unknown causes. The failure to resight the ten swans that "disappeared" could have been due to their death, movement outside the study area, marker loss, or failure to resight all individuals in remote sections of the study area. Thus, only 40%, 15%, and 5% of the treated cygnets were known to be alive 2, 4, and 12 years after treatment, respectively.

DISCUSSION

Three times as many pinioned and wing-clipped swans were treated successfully than free-flying birds. Captive birds were managed in settings that allowed relatively rapid capture and testing for lead poisoning after a problem was identified within a flock, so it is possible that these birds were in better physical condition at admission. In contrast, free-flying birds were often debilitated by the time that they were captured.

The disproportionately high number of captive cygnets in the treatment group was due to the high number of wing-clipped cygnets in captive refuges in Minnesota and Wisconsin where drought conditions apparently exposed lead shot. All captive facilities used to house pinioned and wing-clipped swans were natural lakes or ponds that had been closed to waterfowl hunting for 20–60 years. Lead poisoning in Minnesota and Wisconsin swans was uncommon prior to the drought years of 1988–90 (Gillette 1989; Degernes and Redig 1989). Similarly, sediment in Wisconsin refuges had been checked for lead shot prior to placement of swans in these facilities, and the conditions were thought to be safe prior to the drought.

One difficulty in interpreting the rates of survival and reproduction reported here is that rates of band loss and resighting probabilities of banded birds were unknown. Three different marking systems were used, and the quality of neck collars and patagial tags varied among years as designs were improved. Once a collar or patagial tag was lost, it was unlikely that the bird would be resighted on the basis of its aluminum leg band which is probably rarely lost but difficult to read. The number of treated and released birds was too low to use a mark-recapture model, and the longevity of patagial tags and neck collars used in this study is unknown. However, it is clear that rates of marker loss can be much higher than mortality rates, and thus can overwhelm and distort apparent mortality rates. For example, Nichols *et al.* (1992) reported >90% collar retention rate after one year in Tundra Swans collared and banded on their wintering grounds, decreasing to 59%, 37%, 24%, and 0% by the fifth year after marking. Thus, the comparison of our data to similar data from other studies (see below) is probably the best way to understand potential effects of lead poisoning and its treatment on subsequent survival and reproduction.

Few studies have monitored survival and reproductive success after treatment for lead poisoning, especially for ten years after treatment. In our study, 14% of swans died within one year after treatment for lead poisoning, compared to 23% of Mute Swans in a study in England (Sears *et al.* 1989). Most swans in our study were kept in captivity for more than one year after treatment (20 cygnets and two pinioned adults), which increased their chances for survival during this period (Pichner *et al.* 1992). Once the treated cygnets (N = 17) were released to the wild as two-year-olds, 47% (N = 8) were resighted in one year. This result is comparable to the 43% first year resighting of 65 non-lead poisoned Trumpeter Swans released as two-year-olds in Minnesota (Hines 1991). Our estimates of 40% known alive at two years after release (out of 20 cygnets successfully treated), 15% at four years, and 5% at 12 years is similar to the rates reported for non-lead poisoned cygnets reared by their parents and released to the wild in Ontario (65% at one year after release, 12% at six years and 3% at nine years (Lumsden and Drever 2002).

Two of five adult swans that reproduced were permanently maintained in captivity after treatment. Their resighting rate and survival was expected to be very high compared to swans released to the wild. One of these captive birds did not reproduce for 10.5 years after treatment. It is unlikely that this breeding would have been documented had he been a free-flying swan considering potential marker loss and mortality in the wild. A third adult swan nested and wintered near a large metropolitan area in Minnesota, and was more easily and frequently monitored than other swans released in remote areas of northern Minnesota. This bird was re-collared three years after treatment, and bred for the first time three years later (six years after treatment). Resighting this bird to document breeding would have been unlikely if the collar had not been replaced (Nichols *et al.* 1992). Six treated adults, including two that later reproduced, were released in less accessible areas of northern Minnesota. Only one of these birds (Table 2; Swan 4) was remarked five years after release, and his death was documented seven years after treatment (he produced 20 cygnets). It is possible that some reproductive activity was not documented due to loss of markers or inability to find marked breeders in remote areas.

A much higher percentage of treated adults later bred compared to cygnets. If the two captive adult birds are excluded from comparison, the adult swans released to the wild were still more likely to reproduce than the cygnets released as two-year-olds. The higher survival and breeding success with the older birds is consistent with survival and breeding studies of non-lead poisoned swan populations (Nichols *et al.* 1992; Lumsden and Drever 2002).

The 21% breeding success of the treated birds within 12 years of treatment in our study was higher than the 7% breeding success within three years of treatment reported for Mute Swans (Sears *et al.* 1989). If we consider breeding success to only three years post-treatment, then our result of 7% (two of 29) is similar to that of Sears *et al.* (1989). Three swans in our study did not breed until 6, 8, and 10.5 years after treatment, a finding that emphasizes the importance of longer term studies of reproduction following treatment for lead poisoning.

Treating lead poisoned swans is labor intensive and expensive. Adult lead-poisoned swans have a much higher reproductive potential after treatment compared to lead poisoned cygnets. Future decisions of whether treatment of lead poisoned birds is consistent with goals of a reintroduction program might include, among other factors, the age and future reproductive potential of the lead poisoned swans.

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Baseline Hematology and Clinical Chemistry Results from Captive-raised Trumpeter Swans

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Abstract.—Results from hematology and clinical chemistry tests are presented for healthy captive-raised Trumpeter Swans (*Cygnus buccinator*) to help establish baseline data. Blood samples were obtained from 14 cygnets between the ages of three to four and seven to eight months that were the subjects of a study to teach migration routes to swans. Males and females differed significantly in asparatate aminotransferase, alanine aminotransferase and total protein. Age categories differed significantly in hematocrit, white blood cell counts, alkaline phosphatase, aspartate aminotransferase, glucose, cholesterol and uric acid. There were no significant differences among age categories in values of alanine aminotransferase, calcium, triglycerides and total protein.

Key words.—Biochemistry, complete blood counts, *Cygnus buccinator*, hematology, migration, Trumpeter Swan, ultralight aircraft.

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Complete blood counts are useful measures of the health of birds if the normal reference values are known. Previous work in avian species has centered around poultry, raptors, and pet psittacines (Campbell 1994), or waterfowl, especially ducks (Balasch *et al.* 1974; Mulley 1980), seabirds (Work 1996) and cranes (Abelenda *et al.* 1993; Olsen *et al.* 1996). We investigated whether hematology and biochemistry values differed by age and sex for Trumpeter Swans (*Cygnus buccinator*), as has been shown in other birds (cranes, Olsen *et al.*1996; psittacines, Clubb *et al.*1992).

Values for complete blood counts can prove valuable, not only in detecting problems in individual sick birds, but for diagnosis and treatment of birds involved in catastrophes such as oil spills. Normal reference ranges for most wild avian species are not available, and this information can be important in such situations. Here we present reference clinical values obtained from 14 three to eight month-old Trumpeter Swans that were being raised as part of a migration study (Sladen *et al.* 2002).

METHODS

Fourteen Trumpeter Swans were captured at ages of 10–30 days on the breeding grounds near Cordova, Alaska. They were transported to Warrenton, Virginia to be raised as part of an experiment to teach swans to migrate behind an ultralight aircraft (Sladen *et al.* 2002). Cygnets were initially housed in a hatchery (a fenced facility with small concrete pools), then when six to nine weeks old, moved to chain link enclosures (9.2 × 18.4 m) covered with nylon netting, and placed on grass. Electric fencing was used around pens to discourage predators. All swans were led for walks four times daily. Starting in August, all swans were trained behind the ultralight aircraft twice daily, weather permitting. Initially this training consisted of walking or running behind the ultralight as it taxied, but by mid-September the swans were flying behind the aircraft. Blood samples were collected in the afternoon, after the second of the four daily walks and after one ultralight flight for the day. As part of the migration experiment, swans were moved by truck to Basom, New York on 5 October and to the Chesapeake Bay near Grasonville, Maryland on 18 January. For the move to the Chesapeake, five of the swans flew behind the ultralights, while the remainder rode in a truck.

Swans were fed Mazuri Waterfowl Starter (a pelleted diet with 20.4% crude protein, Purina Mills/Mazuri, PMI Nutrition International Inc., Brentwood, MO) from 1–10 July, 2000; a 1:1 mix of Mazuri Waterfowl Starter and Mazuri Waterfowl Maintenance (crude protein 14.0%) from 10–20 July; exclusively Mazuri Waterfowl Maintenance from 21 July to 7 October, and a 1:1 mix of Mazuri Waterfowl Maintenance and whole corn after 7 October. Swans had free access to grass in the pens, and fresh water was available for drinking and bathing at all times.

The 14 Trumpeter Swans (six males and eight females) were given physical examinations (Orosz 2000) at one month intervals until age five months, then at two month intervals until age eight months. Blood samples were taken from all swans at three to four months of age (in Virginia in September) and five to six months of age (in New York in November). A third sample was taken at seven to eight months of age from six of the 14 swans selected at random (three males and three females) just prior to their release on the Chesapeake Bay in January. Blood samples were taken either from the jugular vein or the medial metatarsal vein using standard veterinary techniques (Dein 1984; Campbell 1994). Blood was collected into heparinized tubes (1 cc per bird), EDTA tubes (1 cc), and serum separator tubes without anticoagulant (4–5 cc), except on the last sampling when only the heparinized tubes were used. Slides were made when the blood was collected using the two coverslip method (Dein 1984). Standard avian hematological techniques were used (Dein 1984) including Eosinophil Unopette (Becton Dickinson and Company, Franklin Lakes, NJ) count of heterophils and eosinophils and differential staining with a commercial stain (Dip Quick Stain, Jorgensen Laboratories, Inc., Loveland, CO). Hematological values obtained included hematocrit, total solids, heterophil/eosinophil count, differential white blood cell count and a total white blood cell count. All blood chemistries were performed on a Du Pont Analyst benchtop chemistry system (Du Pont Company, Wilmington, DE). Blood chemistry values include alkaline phosphatase, aspartate aminotransferase, alanine aminotransferase, glucose, calcium, cholesterol, triglycerides, uric acid and total protein. Glucose and calcium levels could not be performed on the seven to eight month samples because the anticoagulant used in the blood collection interfered with the process used in the bench top chemistry system.

Statistical comparisons were made using two-way (age × sex) analysis of variance (ANOVA) and Tukey-Kramer tests with the mixed-models procedure in SAS (version 6.12, PROC MIXED; Littell *et al.* 1996). Bird identity was the subject factor nested within sex. The mixed-models procedure is robust to missing data, therefore data from all swans were used (six tested at 3–4, 5–6, and 7–8 months, and an additional eight tested at only 3–4 and 5–6 months).

RESULTS

Physical examinations of all Trumpeter Swans showed healthy, growing birds with only minor medical problems including small abrasions, one case of tapeworms treated successfully with praziquantel (Droncit, Bayer Corporation, Shawnee Mission, KS), and occasional coccidia oocysts seen on fecal flotations. Because the coccidia numbers were low, and birds develop immunity, no treatment was initiated. Although samples were small, results suggest age-related differences in some blood parameters (Table 1). Males and females did not differ in hematocrit values (Table 1). However, males had higher aspartate aminotransferase ($F_{1,14} = 8.38$, $P < 0.05$), higher alanine aminotransferase ($F_{1,14} = 8.24$, $P < 0.05$), and higher total protein ($F_{1,14} = 5.39$, $P < 0.05$) (Tables 1 and 2). There were significant differences among age classes in hematocrits ($F_{2,14} = 35.3$, $P < 0.001$), cholesterol ($F_{2,13} = 18.4$, $P < 0.001$), white blood cell counts ($F_{2,14} = 29.3$, $P < 0.001$), uric acid ($F_{2,13} = 10.1$, $P < 0.01$), aspartate aminotransferase ($F_{2,13} = 8.22$, $P < 0.01$) and alkaline phosphatase ($F_{2,13} = 29.8$, $P < 0.001$). Both males and females at 5–6 and 7–8 months of age had significantly higher hematocrits and cholesterol and lower white blood cell counts than at 3–4 months of age (Tukey-Kramer, $P < 0.05$, Table 2). Values of uric acid were higher at 3–4 and 5–6 months of age than at 7–8 months, and values of aspartate aminotransferase were higher at 3–4 and 7–8 months of age than at 5-6 months of age for both males

Table 1. Analysis of variance (PROC MIXED, SAS) table for two-way (age × sex) repeated measures analysis comparing Trumpeter Swan hematology results among sex and age categories. Significance of F-value given as *P < 0.05, **P < 0.01, and ***P < 0.001.

	Source					
	Age		Sex		Sex*Age	
Parameter	df	F	df	F	df	F
Hematocrit	2,14	35.28***	1,14	0.04	2,14	3.49
White blood cell count	2,14	29.32***	1,14	0.04	2,14	0.01
Alkaline phosphatase	2,13	29.83***	1,14	0.06	2,13	0.16
Aspartate aminotransferase	2,13	8.22**	1,14	8.38*	2,13	2.70
Alanine aminotransferase	2,14	1.39	1,14	8.24*	2,14	1.52
Glucose	2,13	28.81***	1,14	1.07	2,13	1.62
Calcium	1,11	3.14	1,12	0.0	1,11	0.07
Cholesterol	2,13	18.42***	1,14	0.19	2,13	1.44
Triglycerides	2,13	2.97	1,14	0.06	2,13	0.04
Uric acid	2,13	10.13**	1,14	0.99	2,13	0.03
Total protein	2,13	2.63	1,14	5.39*	2,13	5.18*

Table 2. Least square mean ±SD of hematology and clinical chemistry parameters by age and sex for young Trumpeter Swans (*Cygnus buccinator*) involved in a migration experiment. Sample sizes in parenthesis. Means with the same superscript are not significantly different when comparing between age classes using a Tukey-Kramer test (SAS, PROC MIXED, Littell *et al.* 1996). IU/l = International units per liter.

	Age											
	3–4 months				5–6 months				7–8 months			
	Male (6)		Female (8)		Male (6)		Female (8)		Male (3)		Female (3)	
Parameter	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Hematocrit (%)	37.3^{a}	±2.0	33.7^{a}	±6.9	4.49^{b}	±2.0	45.7^{b}	±1.7	41.3^{b}	±2.7	47.7^{b}	±2.6
White blood cell count (10^3/mm^3)	18.1^{a}	±1.4	18.3^{a}	±1.2	10.9^{b}	±1.4	11.4^{b}	±1.2	12.5^{b}	±1.9	12.8^{b}	±1.8
Alkaline phosphatase (IU/l)	262^{a}	±30	272^{a}	±25	127^{b}	±30	109^{b}	±26	27^{c}	±51	11^{c}	±41
Aspartate aminotransferase (IU/l)	43.6^{a}	±2.5	39.6^{a}	±2.2	34.9^{b}	±2.8	32.9^{b}	±2.2	52.1^{a}	±3.6	36.4^{a}	±3.6
Alanine aminotransferase (IU/l)	18.5^{a}	±1.6	13.1^{a}	±1.4	14.5^{a}	±1.6	13.5^{a}	±1.4	20.1^{a}	±2.3	13.7^{a}	±2.3
Glucose (mg/dl)	228^{a}	±12	223^{a}	±11	210^{a}	±12	215^{a}	±10	115^{b}	±16	154^{b}	±16
Calcium (mg/dl)	10.4^{a}	±0.2	10.5^{a}	±0.2	10.2^{a}	±0.2	10.2^{a}	±0.2	—	—	—	—
Cholesterol (mg/dl)	174^{a}	±18	152^{a}	±17	253^{b}	±18	252^{b}	±16	202^{b}	±25	250^{b}	±25
Triglycerides (mg/dl)	228^{a}	±21	228^{a}	±20	237^{a}	±21	244^{a}	±19	185^{a}	±28	196^{a}	±27
Uric acid (mg/dl)	9.1^{a}	±1.0	7.9^{a}	±1.0	6.8^{a}	±1.0	6.0^{a}	±0.9	3.8^{b}	±1.5	2.6^{b}	±0.2
Total protein (g/dl)	3.0^{a}	±0.2	2.9^{a}	±0.2	3.2^{a}	±0.2	3.3^{a}	±0.1	2.6^{a}	±0.2	3.7^{a}	±0.2

and females (Tukey-Kramer, $P < 0.05$, Table 2). Alkaline phosphatase was highest at 3–4 months and decreased through 7–8 months of age for both males and females, with all differences among age classes being significant (Tukey-Kramer, $P < 0.05$, Table 2).

DISCUSSION

Establishing normal, baseline hematological values for Trumpeter Swans of different ages may be useful for future treatment of swans in zoological collections or in rehabilitation situations, but also for the evaluation of flocks affected by such man-made disasters as oil spills. Although based on a small sample, our results showed some differences between stages of development. Hematocrits have been shown to increase with age in young birds of other species such as cranes (Olsen *et al.* 1996) and psittacines (Clubb *et al.* 1992). Hematocrits in this study increased from age 3–4 months through age 5–6 months, but not through age 7–8 months. White blood cell counts decreased from 3–4 months to 5–6 months, but not through 7–8 months. Alkaline phosphatase declined significantly from 3–4 to 5–6 to 7–8 months of age. Alkaline phosphatase is related to bone cell changes in birds and its decline with age reflects the tremendous shift from cartilagenous bone in very young swans to calcified bone in more mature birds. Elevations in alkaline phosphatase have been associated with increased osteoblastic activity associated with skeletal growth (Lumeij 1987; Lewandowski *et al.* 1986). Other causes of elevation include nutritional secondary hyperparathyroidism, rickets, fracture repair, osteomyelitis, and impending ovulation (Lumeij 1987). Swans in this study were clinically healthy throughout and showed none of the above medical conditions, leading us to believe that the significant declines in alkaline phosphatase values were a function of normal bone growth and development. The increase in cholesterol with age may be related to increased liver synthesis of this lipid (Lewandowski *et al.* 1987).

Results from this study provide baseline data on normal blood parameters for young Trumpeter Swans, but more information, especially larger sample sizes, would be helpful. Only alkaline phosphatase showed a significant change consistently related to age. As the migration studies continue, we will accumulate more hematological data and will continue to ensure that our migration experiments are using healthy swans.

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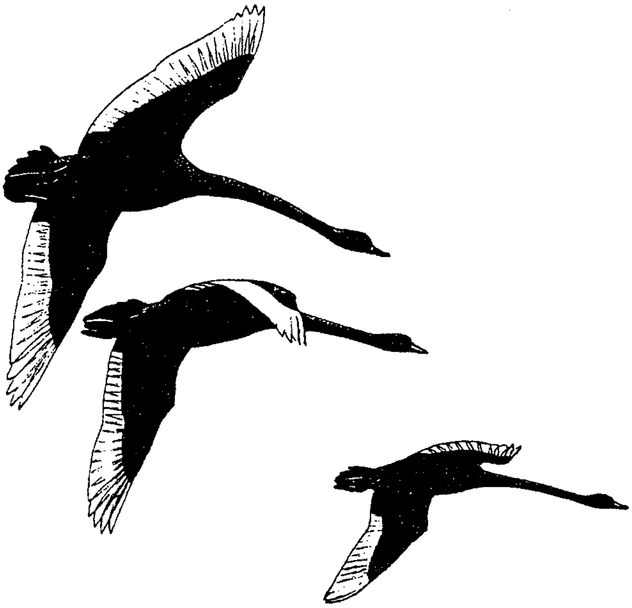


Recommendations

EILEEN REES, ROBERTO SCHLATTER, CARL MITCHELL, JAN BEEKMAN, BERT COLEMAN, SUSAN EARNST, OLAFUR EINARSSON, BJARKE LAUBEK, MA MING, DONIELLE RININGER, MARIA WIELOCH AND GERARD BOERE

Scientific Committee of the Fourth International Swan Symposium

The Fourth International Swan Symposium of the Wetlands International Swan Specialist Group took place from 13–18 February 2001 at Airlie, Virginia, USA, in conjunction with the 18th Conference of the Trumpeter Swan Society. The Symposium was attended by 143 swan biologists from 16 countries: Canada, Chile, China, Denmark, Estonia, Hungary, Iceland, Ireland, Japan, Netherlands, Norway, Poland, Russia, Sweden, United Kingdom, and United States. The Symposium is grateful for the hospitality of Environmental Studies at Airlie, who hosted the meeting.

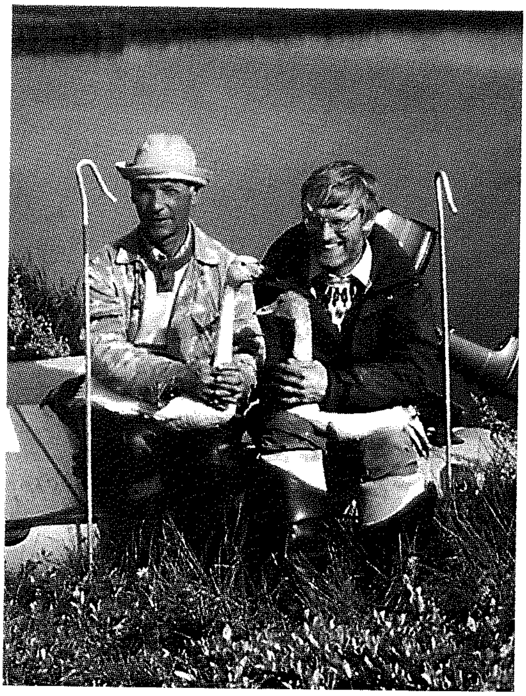
Recommendations arising from the meeting

- Noting the value of long-term monitoring for determining population trends and changes in distribution, as illustrated by several of the presentations, the Symposium urges the continuation of such efforts to support the global overviews on waterfowl populations, conducted by the International Waterfowl Censuses (IWC) and the Waterbird Population Estimates (WPE), which in turn supports the work of international conventions.
- Recognizing the value of satellite-tracking, stable isotope ratios and other technologies, the Symposium recommends greater use of these methods to describe swan populations and sub-populations where the migration routes remain uncertain, notably in the Siberian and Central Asian flyways and South America, and to identify key sites for future protection.
- Noting the substantial lack of data on the unpredictable movements of the South American swans, the Symposium advocates the development of a region-wide coordinated banding program.
- Noting that productivity, survival and dispersal varies within and between populations, for instance in relation to different habitats, the Symposium recognizes the importance of understanding the biological processes that underlie population change.
- Noting the key role of weather conditions in influencing nesting phenology and breeding success, and recognizing that global climate change (identified as an important issue in the 3rd International Swan Symposium in 1989) is increasingly likely to influence swan populations, the implications of global climate change for swan populations should be addressed. These implications should be considered both for arctic habitats, and for unpredictable Neotropical and Australian habitats where the frequency of El Niño events may increase.
- Noting that complete counts of some swan populations on breeding and wintering grounds is not possible, the Symposium recommends reviewing appropriate sampling methods, with a view to ensuring that estimates of population size and trends are comparable between years and populations, and that they are as precise and unbiased as possible. The potential standardization of biometric methods should also be reviewed.
- Recognizing the importance of dynamic wetlands in maintaining Black-necked Swans (*Cygnus melancoryphus*) and Coscoroba Swans (*Coscoroba coscoroba*), the

Symposium urges a broad survey of the species in relation to habitat with a view to protecting the appropriate network of wetlands for these species. The Symposium would welcome the rapid publication of the South American Wetlands Assessment to help design an appropriate banding and conservation program.

- Bearing in mind the increasing overlap of species in both the breeding and wintering ranges, the Symposium identifies the need for further research into competition/coexistence, and to quantify the effect of increasing swan numbers on aquatic and terrestrial ecosystem function.
- Noting that the potential for crop damage remains a concern in many areas, the Symposium recommends that investigations be undertaken to determine the extent to which swans cause agricultural damage, and that methods be developed for reducing swan-human conflicts in those cases where scientific evidence for damage is convincing. Potential benefits of grazing (such as fertilization of the sward) also should be addressed.
- Noting the increasing industrial development in circumpolar regions, especially for oil and mineral extraction, the Symposium urges further studies of the effects of development on swan numbers, distribution, and reproductive success.
- Noting that a small and isolated Whooper Swan (*Cygnus cygnus*) population/sub-population in northwestern China is threatened with extinction, immediate action is urged to preserve the unique grazed grassland and alpine-wetland habitat in which this vulnerable population/sub-population has co-existed with nomadic herdsman, through habitat management and environmental education in the region.
- The Symposium commends governments and local authorities for banning the use of lead for shooting and angling, but notes that spent lead remains an important health hazard for swans. Further efforts therefore need to be made to reduce lead levels, and research undertaken on how best to deal with lead in the environment.
- Noting the increased dependency of swans on artificial feeding in some areas, the Symposium recommends reviewing the costs and benefits of different methods for managing swans, including assessing the health risks for large concentrations of birds.
- Noting the value of a scientifically sound basis for management and conservation decisions, the Symposium recommends re-emphasizing the need for dissemination of research to the public and to policy-makers.
- The Symposium urges that Wetlands International, as the parent organization for the Swan Specialist Group, circulate these recommendations to the appropriate bodies of the international conventions, such as the Bonn Convention Scientific Council, the International Panel for Climate Change (IPCC), the Ramsar Convention Scientific Technical Review Panel (STRP), and the Conservation of Arctic Flora and Fauna (CAFF) working group.
- The Symposium recommends that the 5th International Swan Symposium be held in the Southern Hemisphere to stimulate participation of researchers in that area, and Chile has tentatively been recommended as the host country.

Dr. Yuri Mikhailovich Shchadilov
1937–2001



Dr. Yuri Shchadilov (left), with Dr. Chris Spray and Bewick's Swans caught for banding at Khabuicka, Nenetskiy National Nature Reserve, August 1993.

Swan researchers in Russia and western Europe are saddened by the untimely death of Dr. Yuri Shchadilov, following a short illness, in August 2001. Yuri had a long and illustrious career as Chief Scientist at the All-Russia Research Institute for Nature Protection, where he was involved in a wide variety of research and conservation programs ranging from studies of Red-breasted Geese and Goitred Gazelle to, most recently, working on the Russian biodiversity strategy. His involvement in swan research commenced in the early 1980s, when he first visited the Russkiy Zavorot peninsula to study Bewick's Swan numbers and distribution in the Nenetskiy National Region of the Russian arctic, and published the results of this work in the proceedings of the First All-Union Conference on Swans in the USSR in 1987 (Shchadilov and Orlov 1987; Syroechkovski 1987). It was renewed during the Third International Swan Symposium, held at Oxford in 1989, when Yuri invited scientists from the Wildfowl and Wetlands Trust, UK, to make a joint expedition to study Bewick's Swans at Khabuicka on the Russkiy Zavorot peninsula, an area known to have a high nesting density of Bewick's Swans (Mineev 1991) but previously closed to western scientists.

The first joint expedition by Russian and British scientists to Khabuicka on the Russkiy Zavorot peninsula was made in 1991, in what was to become a long-term study of Bewick's Swan breeding biology at the site. With several other ecological studies ongoing in the area during the 1990s, notably those made jointly by Dutch scientists with the Ural Division of the Russian Academy of Sciences, Yuri's presence each year was invaluable for maintaining communication between collaborative and parallel studies. A highlight for all ecologists working in the area was the designation of the Russkiy Zavorot peninsula and Pechora Delta region as a National Nature Reserve ('Zapovednik') by the Russian Government in 1997 because of its importance for Bewick's Swans and other waterbirds nesting in the high arctic.

Yuri fully appreciated the importance of disseminating the results of his swan research, which he undertook both by publishing and through education programs. He supervised a post-graduate study of factors affecting productivity, based on the Bewick's Swan research program (Belousova 1999) and, with Russian and Wildfowl and Wetlands Trust colleagues, prepared a paper presented at the Fourth International Swan Symposium, published in this volume (Shchadilov *et al.* 2002). He was a member of the Russian delegation attending the Fourth International Swan Symposium in February 2001, when he appeared in good health, and was planning future joint studies with Wildfowl and Wetlands Trust scientists during a visit to the UK the following month.

Yuri's skill and enthusiasm for birdwatching, which went well beyond his scientific life, was an inspiration to those who worked with him. His kindness, integrity and sense of humor were invaluable and cannot be replaced. Nevertheless, British and Russian colleagues aim to continue working jointly on the long-term study of Bewick's Swans in the Russian arctic, in hope that this will provide a fitting memorial to Yuri.

Eileen C. Rees

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The following oral and poster presentations, given at the Fourth International Swan Symposium, have been published or accepted for publication elsewhere:

Beekman, J. H., B. A. Nolet and M. Klaassen. In press. Skipping swans: differential use of migratory stopover sites in spring and autumn in relation to fuelling rates. Ardea.

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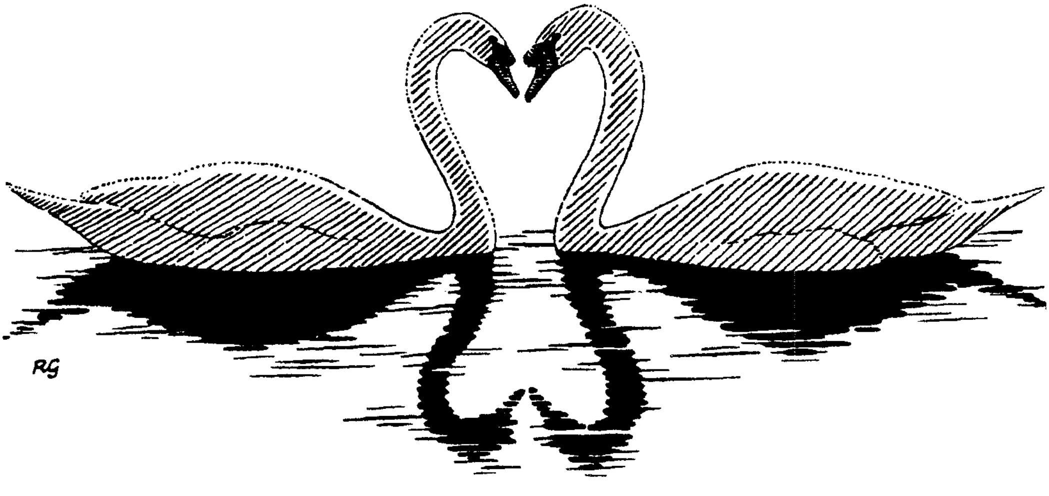

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- To ensure good communication between swan researchers worldwide, promote co-operative research and ringing programs where appropriate, and improve links and information exchange with other research groups.
- To identify gaps in knowledge on swan populations, and stimulate new projects in these areas.
- To advise effectively on swan management and conservation issues, especially at an international level.

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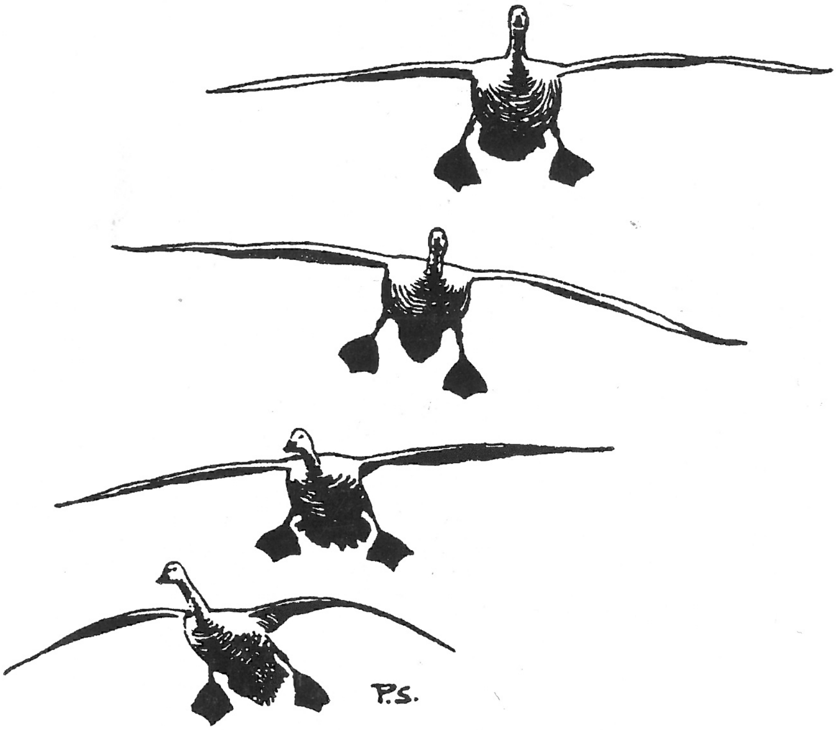

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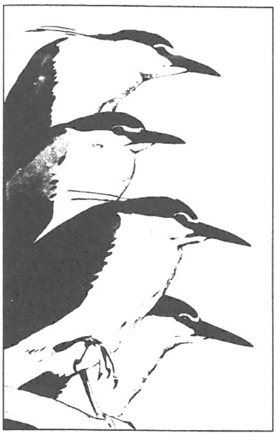

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