

Range expansion and migration of Trumpeter Swans *Cygnus buccinator* re-introduced in southwest and central Ontario

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Abstract

Trumpeter Swans *Cygnus buccinator* were extirpated from Ontario in 1886 as a result of unregulated subsistence and market hunting. Between 1982–2006 inclusive, 584 captive reared Trumpeter Swans were released in southern Ontario, to re-introduce the species to the region. However, no empirical analysis of the size of the breeding range has occurred since the reintroduction programme commenced. Observational data recorded from 1,394 captive-released and wild-hatched swans marked with uniquely identifiable patagial tags therefore were analysed, using a kernel density spatial framework, to infer changes in breeding distribution. The breeding range increased 16 fold between 1991 (301,938 ha) and 2010 (4,817,904 ha). A linear effect of year best explained breeding range expansion from 1991–2010. However, visual inspection of the relationship suggests that the breeding range did not increase after 2004, which coincided closely with the end of the reintroduction programme in 2006. Migration distances calculated for adult male and female, captive-released and wild-hatched swans from 1982–2010 showed that most swan breeding and wintering locations were close to release sites (median migration distance = 4.6 km, range = 0–1,299 km) and 40% of swans were non-migratory (wintering and breeding locations were the same). The model that best explained migration distance included a quadratic fit of year, sex, and status (captive-released *vs.* wild-hatched birds). Migration distance declined until about year 2000 and then increased thereafter.

Migration distance was shorter for females than for males and shorter for captive-released than wild-hatched swans (26.4 *vs.* 47.9 km for females; 34.3 *vs.* 60.7 km for males). However, migration distances of captive-released and wild-hatched swans were similar by the year 2010. It is suggested that re-introduction of swans into new areas, density-dependence and observer bias in re-sighting rates are the mechanisms leading to the patterns of breeding range expansion and increase in migration distances we detected for Trumpeter Swans in southwest and central Ontario.

Key words: captive rearing, kernel-density estimates, migration distance, population trends.

At the time of European settlement of North America, the breeding range of the Trumpeter Swan *Cygnus buccinator* extended from Nova Scotia in Canada to the coast of Alaska in the United States (Lumsden & Drever 2002). Unregulated subsistence and market hunting associated with early European settlers resulted in Trumpeter Swans being extirpated from Ontario in 1886 (Lumsden 1984), and exploitation of the swans throughout the rest of their range resulted in near extinction of the species by the early 20th century (Banko 1960). Before the Migratory Bird Convention Act was introduced in 1916, the Interior Population of Trumpeter Swans was thought to no longer exist and numbers in the Rocky Mountain Population were estimated at just 69 birds, although some unrecorded flocks remained in the Pacific Population (Mitchell & Eichholz 2010). By 1968, there were 2,847 Trumpeter Swans in the Pacific Population and still < 1,000 swans in the Rocky Mountain Population (Mitchell 1994). The Interior Population of Trumpeter Swans, which historically included birds distributed along the Central, Mississippi and Atlantic flyways (Groves 2012), had disappeared by the mid 20th century, but in 1960, the U.S.

Fish and Wildlife Service initiated the first of several reintroduction programmes to restore the swans to their former range. This, together with protection of the species throughout North America, resulted in a marked increase in the Pacific, Rocky Mountain and Interior (which includes Ontario) Populations, and in 2010 the total number of Trumpeter Swans was put at 46,225 birds (Groves 2012).

Between 1982 and 2006 inclusive, the Ontario Trumpeter Swan Restoration Group (OTSRG), a non-government organisation (NGO), released a total of 584 Trumpeter Swans at 52 locations in southern Ontario (Fig. 1; Lumsden 2007a). Most (566) of the released swans were bred from pinioned breeding pairs of Trumpeter Swans originating from the Rocky Mountain Population which had been obtained from aviculturists (Lumsden 2007a; Lumsden & Drever 2002). The breeding pairs remained in captivity for breeding stock and were never released. In 1993, 50 eggs were also obtained from the nests of Pacific Population pairs breeding in Alaska; these were incubated and hatched in captivity in Ontario (described in Lumsden & Drever 2002). Thirty-eight of the Pacific Population

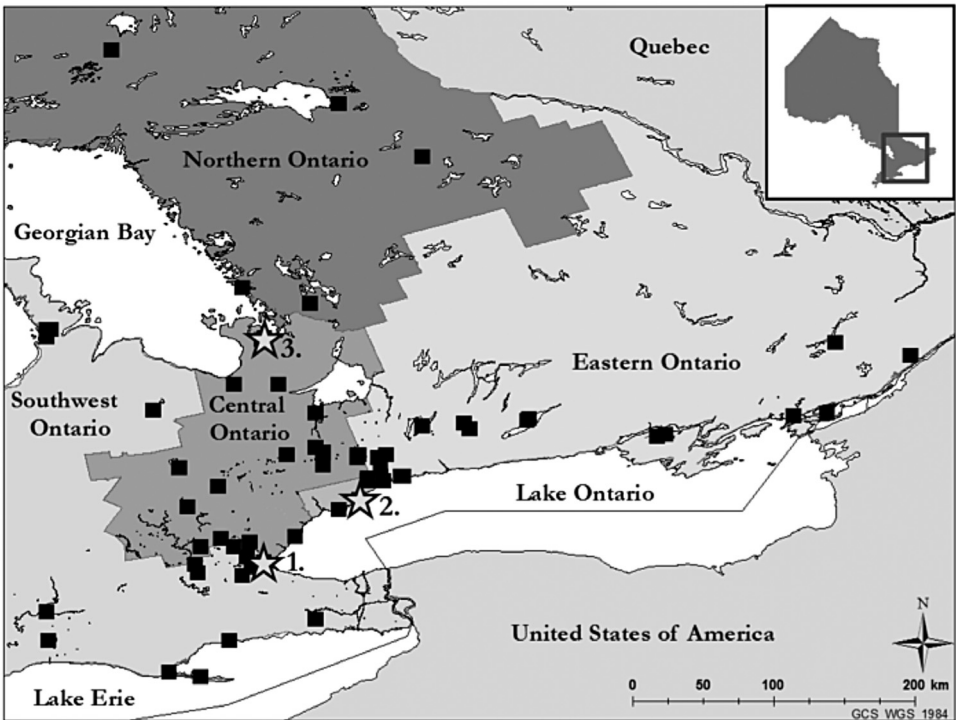


Figure 1. Map of the area covered by the southern Ontario Trumpeter Swan reintroduction programme, 1982–2006. Squares represent release sites; stars represent locations mentioned in text: 1. La Salle Park Marina, 2. Bluffers Park Marina 3. Wye Marsh Wildlife Centre.

eggs were successfully raised to flight stage, 20 hatched swans remained in captivity as breeding stock and the remaining 18 were released in southern Ontario (Lumsden 2008). By 2006, there were an estimated 776 Trumpeter Swans in south-central Ontario, of which 280 (36%) were marked with uniquely-numbered leg-rings as well as yellow patagial-tags with black lettering (Ogilvie 1972; Lumsden 2008). From 2006 onwards, the release of captive-reared Trumpeter Swans by OTSRG was discontinued, because it was thought that the Trumpeter Swans were self-sustaining in Ontario (Intini 2009). Trumpeter Swans

also occur elsewhere in Ontario (in the northwest and southeast) and there is no evidence from banding programmes for an exchange of individuals between the northwest, southeast and south-central regions (Lumsden *et al.* 2012). The northwest birds originated from reintroductions in Minnesota and other adjacent states and are not known to be part of the southern Ontario reintroduction programme (Lumsden 2008; Lumsden *et al.* 2012; Badzinski & Earsom 2015). Those in the southeast likely originated from dispersal of offspring from feral Trumpeter Swans in New York and from captive swans released

there by the OTSRG in 1999, 2000 and 2003 (Lumsden 2008; Lumsden *et al.* 2012; Badzinski & Earsom 2015). During an Ontario-wide aerial survey in 2015, a total of 2,000 Trumpeter Swans were observed, of which 924 were in southern Ontario (Badzinski & Earsom 2015). The remaining 1,076 Trumpeter Swans were observed during the summer in northwest Ontario and are considered part of the northwest flock (Lumsden *et al.* 2012; Badzinski & Earsom 2015).

Complete restoration of Trumpeter Swans should include migration to their ancestral wintering grounds (ADCIPTS 1998; Lumsden 2008), and for the Interior Population there is concern that birds re-introduced to southern Ontario will not migrate to historic wintering areas at latitudes extending further south to 40°N (Slater 2006; but see Lawson 1709, 1714). It has been suggested that unregulated market hunting of Trumpeter Swans in the Pacific and Rocky Mountain Populations (*i.e.* the source of those released in Ontario) resulted in a behavioural bottleneck, with surviving swans exhibiting reduced migration distances and low dispersal rates (James 2000; Oyler-McCance *et al.* 2007). Low rates of seasonal migrations of Trumpeter Swans to ancestral wintering areas have been hypothesised as being one of the main threats to the long-term sustainability of the Interior Population, because of the potential for decreased survival during harsh winters and other density-dependent effects related to disease and depletion of food resources (Slater 2006). Quantifying range expansion and migration metrics of swans reintroduced by

the OTSRG therefore is important for assessing the results of this management programme and for recommending future conservation measures.

Trumpeter Swans begin forming monogamous pair bonds at two years old, typically disperse 4–128 km from natal areas to breed, and are highly philopatric to their breeding territories (Banko 1960; Hansen 1984; Mitchell 1994). Despite the lack of empirical studies of range expansion in Ontario or investigations about their annual migration distances between wintering and breeding areas, observations suggest that Trumpeter Swans have expanded their range in Ontario (Badzinski & Earsom 2015). We therefore examined whether the range of Trumpeter Swans breeding in the region has changed over time, and estimated distances between wintering areas and breeding territories for individually marked swans over the 1982–2010 study period. We also investigated whether the sex and status (*i.e.* wild-hatched or captive-released) of the swans influenced their dispersal from natal or release sites. The overall goal of the study was to determine patterns of colonisation by re-introduced Trumpeter Swans within southwest and central Ontario. The results of this study should help to evaluate the progress of the reintroduction programme and the current and proposed conservation and management strategies for the Ontario flock.

Methods

Field methods

Wild-hatched Trumpeter Swans (*i.e.* birds that were hatched in the wild) were baited

with corn and caught by hand for marking by the OTSRG throughout southwest and central Ontario (Banko 1960; Slater 2006; Lumsden *et al.* 2012). Captive-released swans (*i.e.* birds hatched in captivity as part of the reintroduction programme) were also marked prior to release (Lumsden *et al.* 2012). Swans were captured during winter Oct–Mar, 1995–2010, primarily at three locations: La Salle Park, Burlington Ontario; Bluffers Park Marina, Scarborough, Ontario; and Wye Marsh Wildlife Centre, Midland, Ontario (Fig. 1). The remainder were caught opportunistically throughout southern Ontario. Sex was determined by cloacal examination. Age was designated as hatch year for birds with predominantly grey plumage; second year for predominantly white swans with grey under-wing coverts and a small amount of grey on their primary, tail, and head feathers; and adult for birds with completely white feathering (Baldassarre 2014). When age was not recorded, or observers could not designate birds conclusively as second year or adults, the age was classed as unknown. Data for swans in their hatch year or second year were omitted from the study because Trumpeter Swans do not form monogamous pair bonds or defend breeding territories until they are ≥ 2 years old (Banko 1960), and sightings of sub-adults would more likely reflect exploratory dispersal (Baker 1978) rather than breeding distribution or established migration patterns. For swans with unknown age classification, the first two years of sightings following release were excluded from the study and thereafter these swans were designated as adults. Each captured swan was marked with a uniquely numbered

aluminium leg-ring and patagial-tag and released at the site of capture (Lumsden & Drever 2002).

Sightings data were collected opportunistically by members of OTSRG and additional collaborators. The greatest numbers of Trumpeter Swan sightings were reported by naturalists and the public. Sightings in December–January were categorised as wintering locations and those in May–August (*i.e.* at a time when swans could breed) as breeding locations. All other sightings were categorised as migration locations and were excluded from the current study (Baldassarre 2014).

Estimation of breeding range

Because of the limited number of observations made prior to 1991 ($n = 51$ patagial sightings), only sightings of birds during the breeding season from 1991–2010 were used in the analyses. Breeding ranges for the marked swans were calculated from sightings made over two-year periods because this produced sample sizes large enough to use kernel density analysis ($n > 40$ individuals; *sensu* Lindberg & Walker 2007). If a swan had multiple sightings within a two-year period, one breeding season sighting was selected at random to remove bias caused by unequal abundances of sightings among birds. Also, Trumpeter Swans are philopatric to breeding areas (Baldassarre 2014) and those with multiple, within-seasons sightings were often in the same location. Locations of sightings were imported into ArcGIS 10.0 and Geospatial Modelling Environment was used to conduct kernel density estimates per two-year period using the bandwidth

“PLUGIN”, and a cell size of 1000. The band-width affects the type of kernel used in the estimate, and PLUGIN is appropriate for spatial analysis of animal movements (Silverman 1986). The cell size used in the kernel density estimate affects the output raster data by dictating the size of each kernel. Cell sizes are automatically determined based on input data variability. The raster data from the kernel density estimates was used to create isopleth polygons with a 90% confidence interval. For each two-year period, the area of the isopleth polygons was determined in hectares.

Migration distance calculations

Sightings from 1982–2010 were used to determine migration distance between winter and summer locations. If a swan had multiple sightings within a season, one sighting during the breeding season and one during the winter were selected at random for each year. As for the breeding season, winter sightings were selected at random to reduce bias in our analysis. Breeding season sightings without a subsequent winter sighting or winter sightings without a subsequent breeding season sighting were excluded because migration distances could not be calculated. All other instances of paired breeding season sightings and wintering sightings were used in analysis. For swans using one UTM (Universal Transverse Mercator) zone, Euclidean distances were calculated, whereas ArcGIS 10.0 was used if migration crossed between UTM zones. Calculated distances were taken as being the migration distance per swan per migration season (*i.e.* spring or autumn).

Swans with the same summer and winter location were considered to be non-migratory.

Statistical analysis

An information-theoretic approach was used for model selection, to calculate a second order Akaike's Information Criterion (AIC_c) and to calculate AIC_c weights (w_i). Changes in the size (area) of the breeding range (1991–2010) and migration distance (1982–2010) of swans were examined (PROC MIXED, SAS Institute 2014; Burnham & Anderson 2002). For changes in the breeding range, relative support for the linear, sigmoid, exponential and null models was assessed throughout the study period. We selected the variance components structure because it is appropriate for our data and candidate models used in this study (Kincaid 2005). Models for a change in migration distance included, as explanatory variables, each bird's sex and status (*i.e.* wild-hatched or captive-release), and each two-year period from the 1982–1983 period onwards as linear, quadratic or sigmoid growth functions. We also included interactions between sex, status and two-year period. Swans that had summer and winter sightings at the same location were removed from models of migration because we were interested only in testing for changes in distances travelled by birds that had migrated. Compound symmetry and variance components were selected from a suite of tested covariance structures for the breeding range and migration distance analyses, respectively (Littell *et al.* 2007). Residuals from models of breeding range

were normally distributed whereas \log_{10} transformed migration distance conformed to assumptions of normality. Models with $\leq 2.0 \Delta AIC_c$ were considered, and a 90% confidence interval was used to interpret results. Descriptive statistics on the percentage of swans that migrated, the median migration distance, mean migration distance and associated variance were also calculated.

Results

Greatest weight of evidence was detected for a linear increase between 1991–2010 in the estimated breeding range of Trumpeter Swans in southwest and central Ontario (w_i = 0.88; two examples of breeding range estimates (1991 and 2010) are shown in

Fig. 2; the trend over 1991–2010 is shown in Fig. 3). The sigmoid and quadratic models performed better than the null model ($\Delta AIC_c = 15.20$), but were $> 2.0 AIC_c$ from the top model ($\Delta AIC_c = 5.50$ and 5.80 , respectively).

A total of 1,530 migration distances were calculated for 529 different captive-released ($n = 321$) and wild-hatched ($n = 208$) swans. Of these swans, 47% migrated at least once ($n = 251$) resulting in 914 migrations (41% of the possible migrations; Fig. 4) and 66% of the migration distances calculated had either a breeding or wintering location at their OTSRG release site ($n = 1,009$). Median migration distance for all individuals with both summer and winter sightings was 4.6 km (mean \pm s.e. = $60.9 \text{ km} \pm 3.1 \text{ km}$,

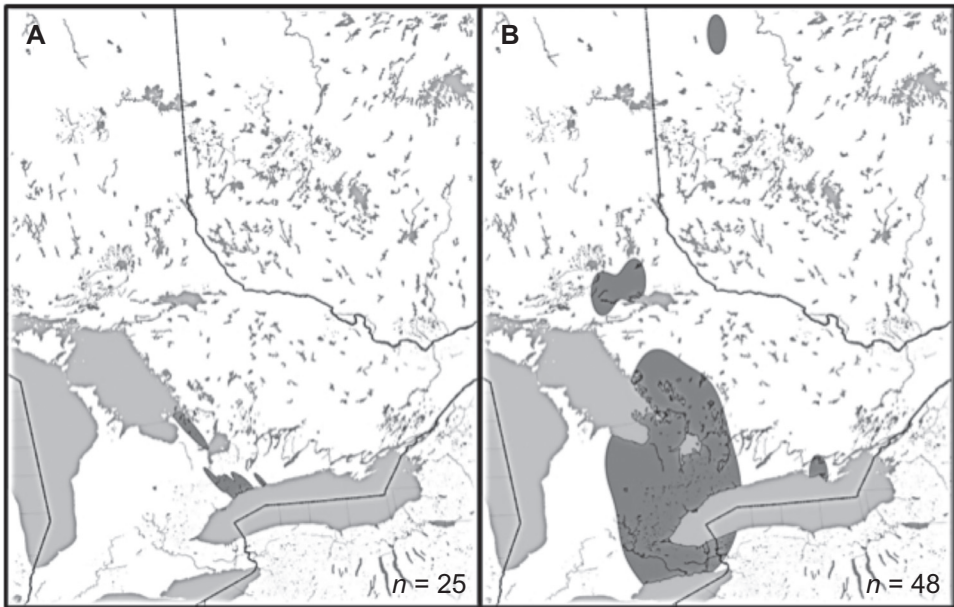


Figure 2. Estimated breeding season range (dark shading) of the southwest and central Ontario Trumpeter Swans: (A) 1991–1992, and (B) 2009–2010; n = number of individual swans included in analysis.

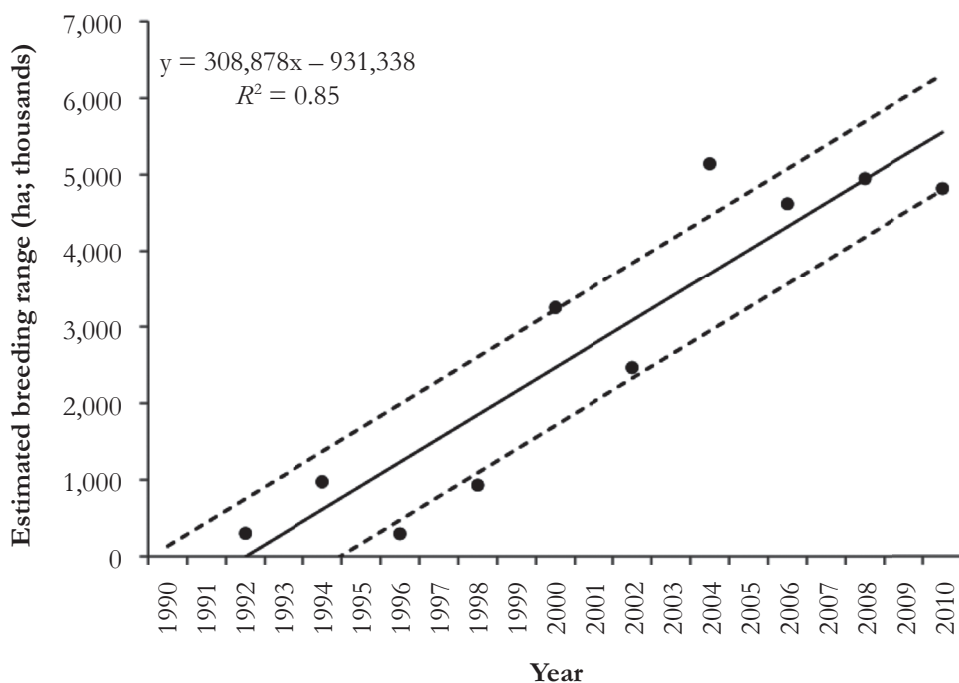


Figure 3. Linear change in estimated breeding range (ha) of southwest and central Ontario Trumpeter Swans from 1991–2010. Samples sizes were: 1991–1992 ($n = 25$), 1993–1994 ($n = 34$), 1995–1996 ($n = 91$), 1997–1998 ($n = 135$), 1999–2000 ($n = 138$), 2001–2002 ($n = 154$), 2003–2004 ($n = 171$), 2005–2006 ($n = 125$), 2007–2008 ($n = 121$), 2009–2010 ($n = 48$). Dashed lines represent the upper and lower 90% confidence limits.

range = 0.0–1,298.8 km) and, when non-migrants were excluded, median migration distance was 56.9 km (mean = 101.9 km \pm 47.5 km, range = 0.3–1,298.8 km). Median migration distance for captive-released swans was 30.9 km (mean \pm s.e. = 91.5 km \pm 6.8 km, range = 0.9–1,298.8 km), whereas, this distance was 108.2 km (mean \pm s.e. = 115.2 km \pm 6.4 km, range = 0.3–980.1 km) for wild-hatched swans. The model explaining migration distance with the greatest weight of evidence included the main effects of sex and status, and year as a quadratic term with an interaction with

status ($w_i = 0.54$; Table 1, Fig. 5). The next best model was the same except it included the sigmoid term for year ($w_i = 0.31$, $\Delta AIC_c = 1.10$). However, rather than fit the typical logistic growth model of the hypothesis, the 3rd order model fit was relatively similar to the quadratic term. After the sigmoid model was removed from analysis, weight for the quadratic model increased to 0.79 and performed substantially better than the next best model ($\Delta AIC_c = 3.50$). The null model was 68.5 AIC_c units from the top model. On average, from 1982–2010, the quadratic models predicted that migration distance

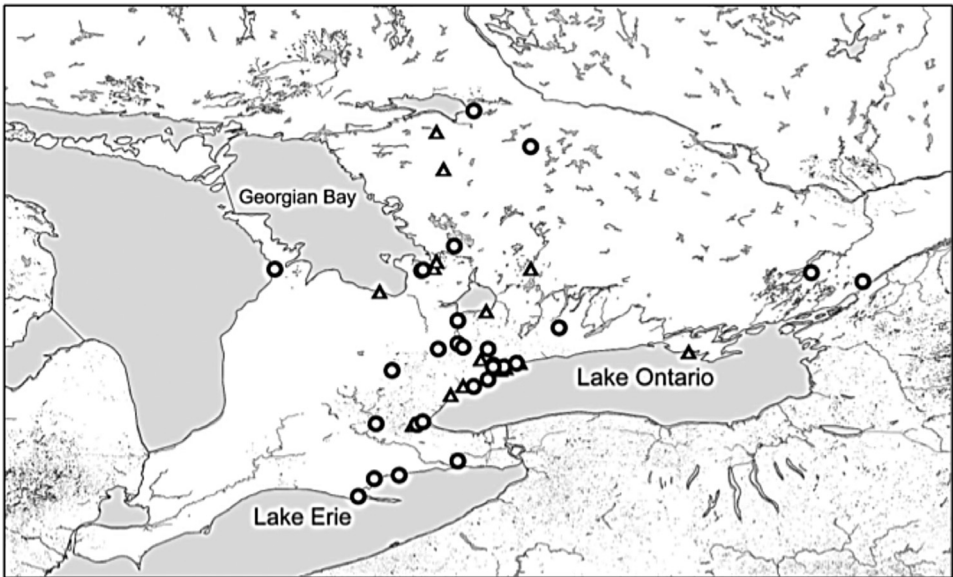


Figure 4. Sightings of tagged non-migrating Trumpeter Swans in Ontario 1982–2010. Circles represent sightings at release sites ($n = 572$) and triangles are sightings that differ geographically from release sites ($n = 44$).

was shorter for captive-released than for wild-hatched females (26.4 *vs.* 47.9 km) and also for male swans (34.3 *vs.* 60.7). However, by the end of the study period in 2010, the model predicted migration distances to be nearly identical for males and females, and confidence intervals for female captive-released and wild-hatched swans overlapped (Table 1, Fig. 5).

Discussion

Our study found evidence for a linear increase in the breeding range of Trumpeter Swans in southwest and central Ontario from 1991–2010. The breeding range of the flock in 2010 was 4,817,904 ha, or approximately 16 \times larger than in 1991 (Fig. 2). The linear growth is atypical from the logistic and geometric growth that is

commonly detected for re-introduced or colonising populations (Mills 2007). Although not detected in our statistical analysis, breeding range expansion appeared to slow or stop by 2004, after which the OTSRG reintroduction programme ceased. Thus, the linear trend we detected could be the result of a relatively short time-series. Hereon, we discuss several hypotheses for this pattern of range expansion by Trumpeter Swans in Ontario.

During the re-introductions in 1982–2006, captive-reared swans were released throughout Ontario in an opportunistic manner, in and outside of their expanding range (H. Lumsden, pers. comm.). When the released swans successfully fledged offspring, these release locations would have served as new starting points for range

Table 1. Parameter estimates (θ), standard errors (s.e.) and 90% confidence intervals (CI) derived from the quadratic model for change in migration distance of Trumpeter Swans between wintering and estimated breeding areas in Ontario, 1982–2010.

Parameter	θ	s.e.	90% CI
Intercept	13.49	0.65	12.43 to 14.55
Sex (Female)	-0.28	0.11	-0.46 to -0.10
Status (Released)	-1.68	0.36	-2.27 to -1.08
Year	-0.28	0.06	-0.37 to -0.18
Year ² × Status (Released)	0.0100	0.0017	0.0070 to 0.0127
Year ² × Status (Wild)	0.0072	0.0014	0.0049 to 0.0094

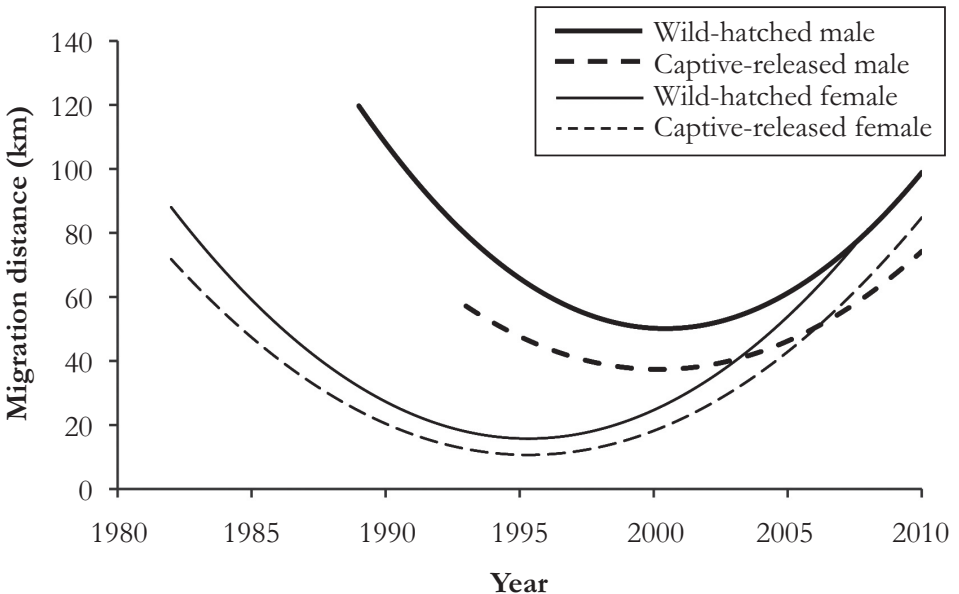


Figure 5. Model predicted change in migration distance by male and female Trumpeter Swans in southwest and central Ontario that were captive-released and wild-hatched, 1982–2010. Mean difference between the lower confidence and upper confidence limits were: wild hatched male = 0.48 km, captive released male = 0.50 km, wild hatched female = 0.52 km, captive released female = 0.50 km.

expansion and for increasing breeding territory density within their current range. Filling of breeding territories through the wild-hatched swans establishing new territories could have played a density-dependent role, whereby Trumpeter Swans needed to colonise new areas on the periphery of their range as territories in the interior of their range became colonised. Thus, the linear pattern of range expansion we detected could have resulted from a combination of releases of captive-reared swans beyond their previous range and the need by wild-hatched swans to settle in unoccupied territories when seeking breeding territories for the first time. The apparent lack of range expansion following 2004 may also be an artefact of Trumpeter Swans tending to establish breeding territories north of release or nesting sites (H. Lumsden, pers. comm.), an area where human population density and thus the potential for re-sightings decreases substantially. We therefore consider that a combination of density-dependence and observer-bias effects are plausible mechanisms for the range expansion pattern detected, with further study required to determine the influence of each in influencing changes to the swans' breeding distribution.

In 2015 the Canadian Wildlife Service and US Fish and Wildlife Service conducted aerial surveys over areas of lower human population density in northwest Ontario. These breeding area surveys detected a substantially greater number of Trumpeter Swans during late summer ($n = 1,076$) compared to a ground-based count in 2010 ($n = 279$; Badzinski & Earson 2015). While the difference could result primarily from

changes in methodology, standardised aerial winter surveys also corroborate these findings with 1.6 times more swans counted in 2015 ($n = 924$) than 2010 ($n = 594$) in southern Ontario (Badzinski & Earson 2015). Lakes and ponds are abundant in the boreal forest region of Ontario and many could serve as potential breeding territories for an increasing Trumpeter Swan population (Ducks Unlimited Canada 2010). Given the abundance of nesting habitats, it seems that the lack of a change detected in estimated range size from 2004 through to 2010 represents a spatial bias because observers are not available to report marked Trumpeter Swans using northern areas. The increase in abundance detected by aerial surveys is consistent with our results and we therefore propose that a linear expansion best explains the Trumpeter Swans' estimated breeding range.

Results suggest that 47% of the Trumpeter Swans in southwest and central Ontario did not migrate between wintering and breeding areas, but rather remained year-round at single localities. The patterns of survival imposed upon the Rocky Mountain Population could have resulted in a reduction in migratory distance that was inherited among the re-introduced Trumpeter Swans in southern Ontario (James 2000). A lack of migration is a characteristic of several re-introduced Trumpeter Swan flocks and although supplementary feeding has been suggested as a causal factor, there is no consensus on the impact of supplemental feeding on migration behaviour (Gillette 2005; Slater 2006). However, there is agreement that supplemental feeding reduces within-winter

movements and increases survival rates of Trumpeter Swans (Gillette 2005; Slater 2006; Lumsden 2007b). Our models predicted an initial decrease in migration up until 1995 (females) and 2000 (males). Thereafter, migration distances of Trumpeter Swans increased through to 2010. We are uncertain why migration distances would have declined initially, but think that subsequent increases in migration distances could have been caused by the need to migrate farther north to find available breeding territories. Also, wild-hatched Trumpeter Swans had greater migration distances than captive-reared swans. An increasing proportion of wild-hatched Trumpeter Swans in the population could have further increased the need to migrate farther as these birds filled breeding territories in areas farther north than captive-released birds. More recently, the need for all swans to migrate increasingly farther north to breed may have resulted in the similar migration distances of wild-hatched and captive-released swans we observed by 2010. Supplemental feeding could influence propensity to migrate, but additional understanding of individual Trumpeter Swan foraging behaviour and migration is necessary to understand the role of this common practice for Trumpeter Swan reintroductions across North America (Slater 2006).

Throughout North America, supplemental feeding has been recommended to increase Trumpeter Swan survival until migratory routes are established, and provision of food resources are recommended for swans exploring habitats at southern latitudes (Gillette 2005). It is hypothesised that reducing supplemental feeding in a timely

manner could result in the development of a population that learns to migrate and exploit waste agricultural grain during winter at southern latitudes in the United States (Gillette 2005). However, continued supplemental feeding may also encourage residency of Trumpeter Swan flocks, decrease migratory behaviours and contribute to overcrowding and increased risk of mortality events (Slater 2006). During severe winters, swans are at greater risk of mortality (Esselink & Beekman 1991). Without supplemental feeding severe winters could serve as a survival bottle-neck when swans in relatively poor body condition, or swans that do not leave for the winter, are more likely to starve. Severe winter survival bottle-necks may thus reinforce migratory behaviour, but this might not occur when supplement feeding is used, hindering the establishment of migration in the re-introduced birds. We suggest that marking Trumpeter Swans with Global Positioning System (GPS) tracking devices, as well as comparing the movements of individual birds when supplemental feeding is occurring and after it has been discontinued, would provide valuable insight into the influence of supplemental feeding on the swans' migratory behaviour.

Additional modelling of southwest and central Ontario Trumpeter Swan abundance growth rates since the start of the reintroduction programme, using the wing-tag data and mark-recapture methods, would help to refine the assessment of Trumpeter Swan range expansion in Ontario and more widely. Including weather data in the analyses would further help to understand Trumpeter Swan migration during the non-

breeding period. During severe winter weather events, Trumpeter Swans are observed in the Finger Lakes region of central New York and most of these swans do not have yellow wing tags representative of the birds marked in southwest and central Ontario (M. Schummer, pers. obs.). Because central New York does not have a well-established breeding flock of Trumpeter Swans ($n \leq 5$ breeding pairs), and those that do breed there are marked with green patagial tags (J. Eckler, New York Department of Environmental Conservation, pers. comm.), at least some of the wintering swans are suspected to be wild unmarked Trumpeter Swans from southern Ontario that are not using supplemental feeding sites but follow traditional migration routes southward when weather severity thresholds are met (*sensu* Schummer *et al.* 2014). Determining the annual movement patterns of breeding Trumpeter Swans marked with GPS telemetry devices would again provide more precise movement patterns of swans for analysis, and would help track swans in areas with lower human population densities during the breeding period. These GPS data would be beneficial to conservationists concerned with their population dynamics and migratory behaviour. Further, lack of movement from release sites suggests that supplemental feeding programmes should be quantified and evaluated empirically, so that feeding may be managed properly to maximise the benefit to the Trumpeter Swans in southwest and central Ontario.

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Photograph: Trumpeter Swan trio in flight, by Tim Fitzharris/Minden Pictures/FLPA.