# Delineation of Tundra Swan *Cygnus c. columbianus* populations in North America: geographic boundaries and interchange

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**Abstract**

North American Tundra Swans *Cygnus c. columbianus* are composed of two well-recognised populations: an Eastern Population (EP) that breeds across northern Canada and north of the Brooks Range in Alaska, which migrates to the eastern seaboard of the United States, and a Western Population (WP) that breeds in coastal regions of Alaska south of the Brooks Range and migrates to western North America. We present results of a recent major ringing effort from across the breeding range in Alaska to provide a better definition of the geographic extent of the migratory divide in Alaska. We also reassess the staging and winter distributions of these populations based on locations of birds tracked using satellite transmitters, and recent recoveries and sightings of neck-collared birds. Summer sympatry of EP and WP Tundra Swans is very limited, and largely confined to a small area in northwest Alaska. Autumn migration pathways of EP and WP Tundra swans abut in southwest Saskatchewan, a region where migrating WP birds turn west, and EP birds deviate abruptly eastward. Overall, from 1989 to 2013 inclusive, 2.6% of recoveries or resightings reported to the USGS Bird Banding Laboratory were of birds that moved from the domain of the population in which they were initially captured to within the range of the other population; a proportion roughly comparable to the results of Limpert *et al.* (1991) for years before 1990. Of the 70 cross-boundary movements reported since 1989, 39% were of birds marked on breeding areas and 61% were of birds marked on wintering areas. Dispersing swans *(i.e.* those that made cross-boundary movements) did not differ with respect to age or sex from those that did not move between populations. The Brooks Range in northern Alaska effectively separates the two populations within Alaska, but climate-induced changes in tundra breeding habitats and losses of wetlands on staging areas may alter the distribution for both of these populations.

**Key words:** *Cygnus columbianus*, distribution, North America, population, Tundra Swan.

Tundra Swans *Cygnus columbianus* breed in arctic tundra habitat across the Holarctic. The nesting distribution of the North American subspecies *C. c. columbianus* is nearly continuous from the tip of the Alaska Peninsula in southwest Alaska to the east side of Hudson Bay, Canada, and the swans also occur in far eastern Chukotka (Limpert & Earnst 1994; Kear 2005). Tundra Swans in North America have two distinct wintering distributions: swans breeding in northern Alaska and across northern Canada winter in the Atlantic Flyway along the east coast of North America, whereas swans breeding in western and southwest Alaska winter along the Pacific Flyway of western North America (Sladen 1973; Bellrose 1980). Tundra Swans wintering on the east coast are managed as Eastern Population (EP) Tundra Swans (Eastern Population Tundra Swan Committee 2007), and those wintering in western states and provinces as the Western Population (WP; Pacific Flyway Council 2001). There has been considerable interest in the precise distribution of WP and EP swans in northwest Alaska, where the two populations are thought to abut (Sladen 1973; Bellrose 1980; Limpert *et al.* 1991). Early reports showed the distribution of EP swans extending south of Point Hope to the Seward Peninsula (Sladen 1973; Bellrose 1980; Fig. 1), whereas later investigations portrayed the WP occupying breeding habitats as far north as Point Hope, with some possible overlap between the two populations based on recoveries and sightings of northwest Alaska swans in the domain of the EP (Limpert *et al.* 1991). However, the overlap documented by Limpert *et al.* (1991) in northwest Alaska was based on a very small sample of recoveries, and they called for additional marking to verify the wintering affinities of birds breeding and moulting in northwest Alaska. Limpert *et al.* (1991) also summarised the incidence of cross-population recoveries through 1989; a topic which we reassess for recoveries and resightings of Tundra Swans from 1990 through 2013. Our reprise of the work of Limpert *et al.* (1991) is based on nearly 4,000 recent observations of > 1,800 Tundra Swans fitted with neck collars in Alaska from 2006–2010. We interpret our findings in the context of climate change and past vicariance events that likely shaped the extant distribution of the two populations.

## Study area and methods

Flightless Tundra Swans were caught during wing moult in July–August 2006–2010 and fitted with coded plastic neck collars (Sherwood 1966; Sladen 1973) at five major breeding areas throughout the range of the species in Alaska (Fig. 1). The sex of the birds was determined from their cloacal characteristics (Bellrose 1980) and age was classed as either locals (*i.e.* unfledged cygnets), second year birds (SY; birds hatched the previous year) or after second year birds (ASY). Second year birds were distinguished from older birds by the presence of grey feathering on their head and neck and, sometimes, on the back (Bellrose 1980). We generally captured swans without cygnets, to reduce disturbance, except in 2008 when a small number (< 10) of breeding birds with cygnets from each area were implanted with satellite transmitters (see below) to obtain

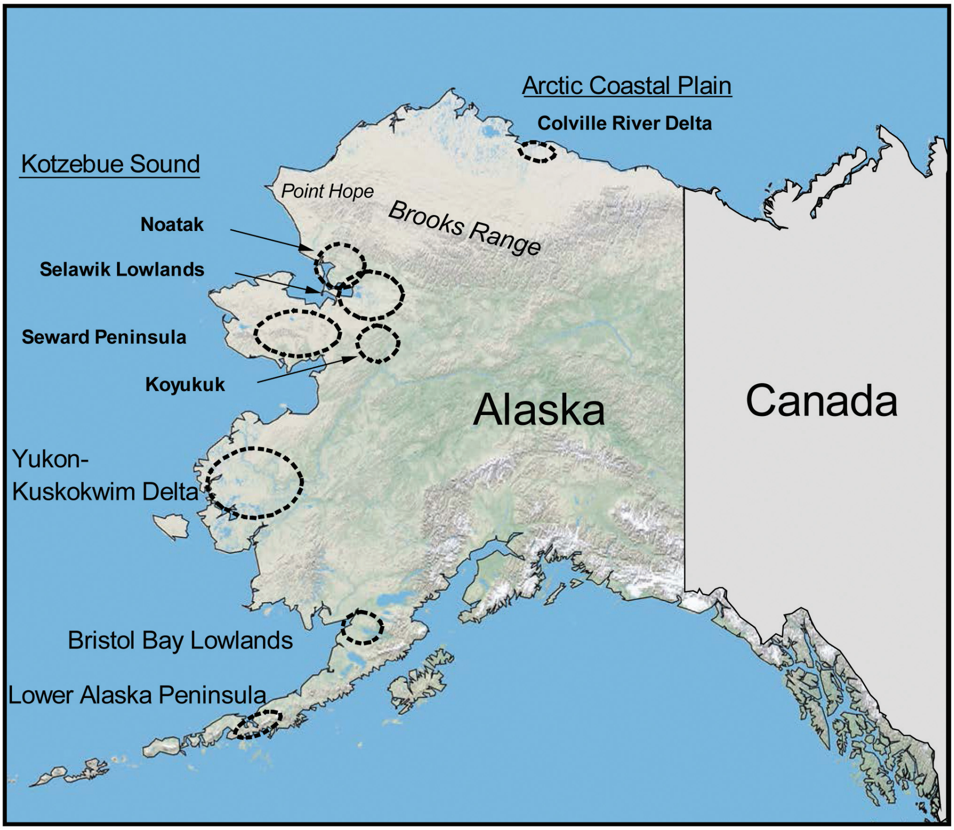


**Figure 1.** Areas where Tundra Swans were captured and marked in Alaska, 2006–2010.

distribution information on breeding individuals. Recovery and observation information reported to the USGS Bird Banding Laboratory (BBL) through to December 2013 were analysed to assess the overall distribution of Tundra Swans in North America. We also obtained observation data from marked swans contributed by participants in our Western Tundra Swan Observation Network, which included sightings by untrained volunteers (public), as well as trained observers who recorded marked birds at main staging and wintering areas used by the swans throughout the western states and provinces of the Pacific Flyway of North America. Sightings made by the public were frequently corroborated by examination of digital photographs sent by observers of the marked swans.

## Satellite-marked swans

Satellite transmitters (platform transmitting terminals (PTTs), supplied by Microwave Telemetry, Maryland, USA) were implanted in the abdomen of 10 birds from each of five breeding locations in Alaska, following the procedure described by Korschgen *et al.* (1996). PTTs were programmed to transmit once every 1–4 days, depending on the season over a two-year period; if the two-year period was exceeded, the duty cycle reverted to data transmissions once every 3 days (Ramey *et al.* 2012). The Argos Data Collection and Location System (CLS America 2007) recorded information on latitude and longitude, date, time and the quality of the location data. We filtered unlikely locations based on rate and angle of movement (Douglas *et al.* 2012) and the highest quality locations were used to represent daily position.

## Population affinities of marked swans

To assess overlap in the range of WP and EP Tundra Swans, we combined determination of their normal breeding and wintering ranges from earlier work (Sladen 1973; Limpert *et al.* 1991; Ely *et al.* 1997; Moermond & Spindler 1997; Petrie & Wilcox 2003) with data from the movements of the PTT-marked swans (see below). Limpert *et al.* (1991) showed that birds nesting north of the Brooks Range and across northern Canada generally wintered on the east coast of the United States and birds that nested south of the Brooks Range in Alaska wintered in coastal states and provinces along the west coast of the United States. Sladen (1973) and Bellrose (1980) considered locations in, or west of, the Rocky Mountain states and provinces to be within the range of the WP and locations east of the Rocky Mountains to be part of the EP. We used location information from our PTT-marked swans to further define the provenance of EP and WP swans, especially in southern Canada where their migratory pathways were in close proximity.

Possible changes in distribution of WP *vs.* EP swans marked in Alaska were assessed by comparing recent (≥ 1990) distribution information with that presented by Limpert *et al.* (1991) for Alaska-marked (< 1990) swans. The analysis by Limpert *et al.* (1991) included BBL recovery data, as well as observations of marked birds made by observers throughout the Atlantic Flyway, many of which were not reported to the BBL. For our overall assessment of population delineation we included recoveries or resightings of birds marked on breeding and wintering areas that were reported to the BBL or observed by our western observation network. In south-central Canada, where the migration corridors of EP and WP Tundra Swans are in close proximity (Sladen 1973), spring and autumn migration tracks from the PTT-marked swans were used to define the areas used by EP and WP swans and thus to assign recoveries and observations of neck-collared birds to the Eastern or Western Population. Recaptures or observations of Tundra Swans in Alaska were not included in analysis of population interchange, as most observations were on southern staging areas which could be used by either population. To compare cross-boundary movements of EP and WP Tundra Swans over two time periods we slightly modified the marking groups used by Limpert *et al.* (1991) by combining all recoveries from across the Arctic Coastal Plain of Alaska (which is represented by the Colville River Delta in our sample), grouping their two Yukon-Kuskokwim Delta samples into one, and adding new sampling locations in the Koyukuk River Valley and on the Lower Alaska Peninsula (Fig. 2).

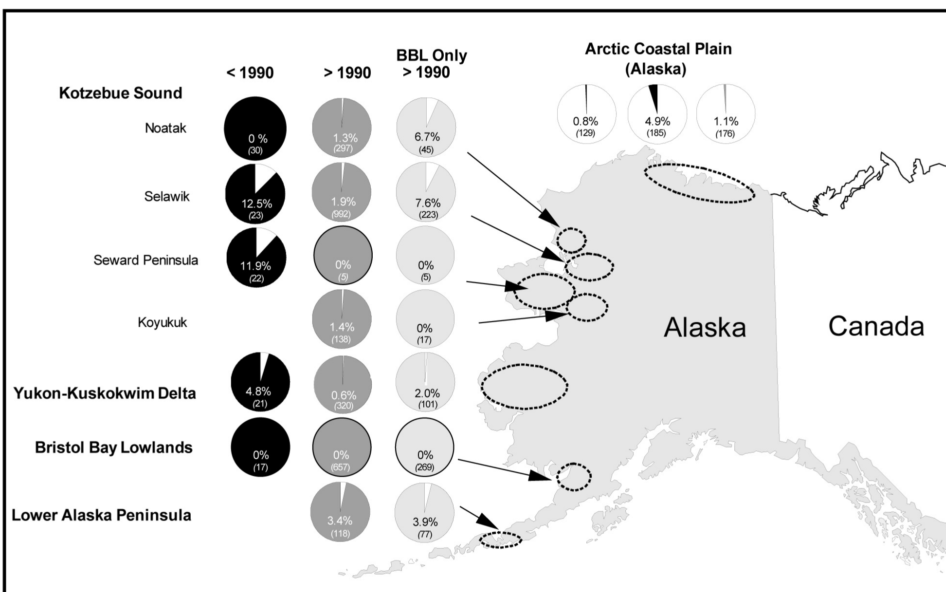


**Figure 2.** Recovery distribution of Tundra Swans in relation to the area where they were ringed in Alaska during two time intervals: before 1990 (Limpert *et al.* 1991; black circles), and from1990–2013 inclusive (this study; dark grey circles). Pie diagrams depict the proportion of birds marked in each area recovered in the range of the Western Population (solid colour), or Eastern Population (white colour). Values in parentheses are the number of recoveries. The light grey circles show the percent recovery of birds reported to the USGS Bird Banding Laboratory.

### Resighting effort

The observation network established by Limpert *et al.* (1991) was in the Atlantic Flyway and some mid-western states along the flyway for EP Tundra Swans. Because of the general lack of observers in western states and provinces during their study, Limpert *et al.* (1991) largely relied on reports to the BBL for determining the distribution of WP Tundra Swans. Our current effort represents the reciprocal approach, with an established network of observers in the western states and provinces, but an absence of trained observers along the eastern seaboard. Hence for the distribution analyses presented here we rely almost exclusively on reports to the BBL for an assessment of the current winter distribution of EP Tundra Swans. To overcome potential geographical biases in observation effort, for analysis of winter distribution relative to marking location in Alaska, we include an analysis of recovery distribution based solely on reports to the BBL.

## Results

Over 1,800 Tundra Swans were caught and fitted with neck collars at five different breeding areas across the range of the species in Alaska during 2006–2010; a further 367 were fitted with metal leg rings only (Table 1, Fig. 1). Nearly half the neck collars were put on birds from the Kotzebue Sound Lowlands (*n* = 850) whereas the fewest number of birds were neck-collared on the Colville River Delta (*n* = 76) because of an expected low resighting rate due to the absence of an established observation network in the eastern United States.

### Recovery distribution of swans marked in Alaska

Our results show that there were few cross-population recoveries of Alaska-ringed Tundra Swans during either of the two time periods, and the recovery distributions were similar across years (Fig. 2). There was, however, evidence that observation effort may have affected the proportion of cross-population recoveries detected. An analysis of all post-1989 encounters (including data from BBL and the western observation network) revealed very little (< 2%) west-to-east population movement. However, when the analysis was restricted to just recoveries reported to the BBL (thereby removing the high observation bias in the west in recent years) the proportion of WP-ringed birds recovered in the east increased substantially and was highest for birds marked in the valleys of the Selawik River (7.6%) and the Noatak River (6.7%) of northwest Alaska (Fig. 2). A similar bias in observation effort was noted for our assessment of the distribution of Tundra Swans ringed in northern Alaska, as the proportion of EP-marked swans detected at WP sites post-1989 was substantially lower when restricting the analysis to BBL reports (1.1% *vs.* 4.9%).

### Overall distribution of marked swans

The majority of recoveries and resightings of Tundra Swans since 1989 occurred within the geographic regions expected (Fig. 3). WP swans were generally found south of the Brooks Range in summer and within and west of the Rocky Mountain states and provinces in winter, whereas EP Tundra Swans were primarily found north of the

 

**Table 1.** Number of Tundra Swans fitted with neck collars and metal leg rings in Alaska, 2006–2010. (Numbers in parentheses refer to birds fitted with only a ring).

| Location | Year | | | | | |
|---|---|---|---|---|---|---|
| | **2006** | **2007** | **2008** | **2009** | **2010** | **Total** |
| Colville River Delta | 58 | 8 (42) | 10 (30) | 0 (100) | 0 (86) | 76 (258) |
| Kotzebue Sound | | | | | | |
| Noatak | 17 (28) | 0 (31) | 65 (1) | 57 | 62 | 201 (60) |
| Selawik | 82 (1) | 90 (7) | 135 (25) | 141 (1) | 134 (1) | 582 (35) |
| Koyukuk | 16 | 10 | 41 | 0 | 0 | 67 |
| Yukon-Kuskokwim Delta | 30 | 99 | 97 | 100 | 0 | 326 |
| Bristol Bay Lowlands | 91 (4) | 47 | 5 (10) | 105 | 104 | 352 (14) |
| Lower Alaska Peninsula | 62 | 59 | 31 | 0 | 101 | 253 |
| **Total** | 356 (33) | 313 (80) | 384 (66) | 403 (101) | 401 (87) | 1,857 (367) |

 

Brooks Range in Alaska and east of the Rocky Mountain states and provinces during the winter months. There were some obvious exceptions however, with cross-boundary movements being particularly evident on wintering areas adjacent to the east and west coasts of North America. Since 1989, 70 of 2,711 (2.6%) unique recoveries of Tundra Swans reported to the BBL have been of birds that moved across population boundaries, with an average of 2.7% ± 0.54 s.e. ($n$ = 24) out-of-range recoveries per year (Table 2, Fig. 3). The proportion of dispersing birds was fairly evenly represented across capture locations, with the possible exception of birds ringed at wintering areas in the west being somewhat more likely to be recovered in the east (4.2%) than other capture-wintering comparisons (Table 2). Overall, of the 70 birds reported to the BBL that crossed flyways since 1989, 39 moved from east to west, and 31 went from west to east.

### Refinement of EP-WP boundary in Saskatchewan

Movements of PTT-marked Tundra Swans from the two populations showed a nearly parallel northwest-to-southeast movement across Alberta and Saskatchewan during autumn, with EP swans being on the northern and WP swans on the southern edge of this movement. The region of closest contact between WP and EP swans was in southwest Saskatchewan (Fig. 4), where EP and WP swans used adjacent areas during autumn. Both populations also migrated through southern Saskatchewan in

**Table 2.** Distribution of recoveries and resightings of Tundra Swans in North America reported to the USGS Bird Banding Laboratory, 1990–2013, in relation to ringing location. Eastern Population Tundra Swans generally breed in northern Alaska and Canada and winter on the east coast, whereas Western Population Tundra Swans usually breed in western Alaska and winter in western North America.

| | Recovery Location | | | |
|---|---|---|---|---|
| **Capture Location** | **Eastern Population** | **Western Population** | **Total** | **Move (%)** |
| **Northern breeding areas** | | | | |
| N. Alaska/Canada | 176 | 2 | 178 | 1.1 |
| Western Alaska | 25 | 642 | 667 | 3.7 |
| **Southern wintering areas** | | | | |
| East coast | 1,700 | 37 | 1,737 | 2.2 |
| West coast | 6 | 123 | 129 | 4.9 |

 

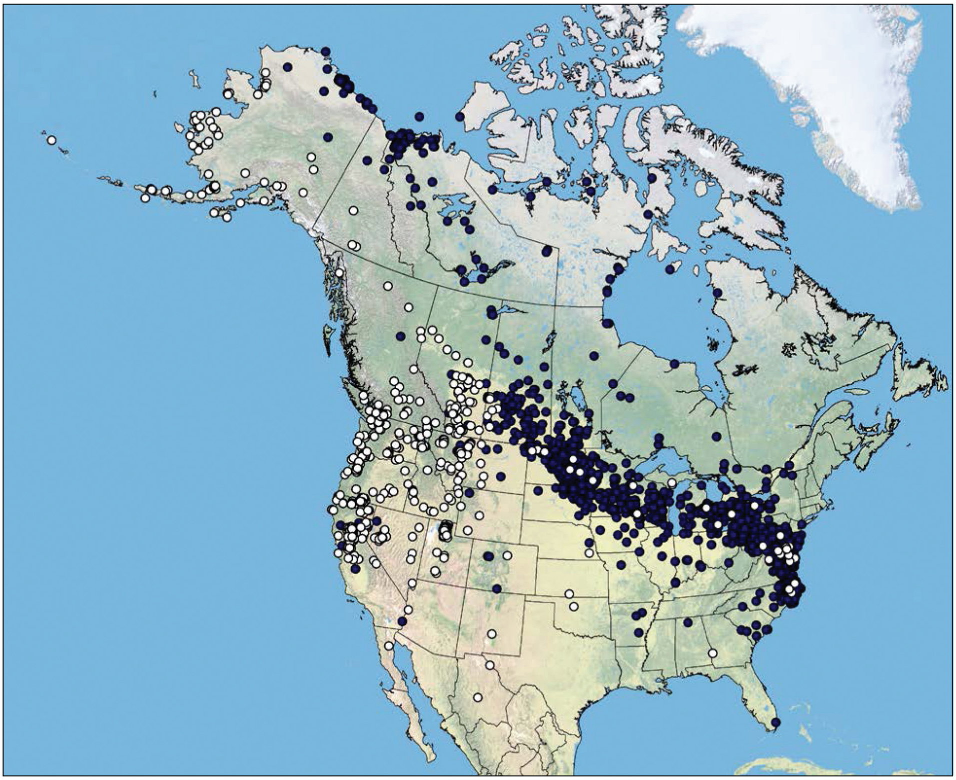

**Figure 3.** Resighting and recovery distribution for Tundra Swans fitted with rings and/or neck collars in North America. Data includes all reports to the USGS Bird Banding Laboratory (BBL) up to and including 2013, and 3,900 observations of neck-collared birds made by the Western Population Tundra Swan Observation Network. White circles represent recovery locations of birds marked in the range of the Western Population; dark circles represent locations of birds marked at sites normally used by Eastern Population Tundra Swans.

spring, but WP swans preceded EP swans by 1–3 weeks.

## Characteristics of dispersing swans

The majority (89.2%) of Tundra Swans that switched flyways in recent years were marked as adults, with the remainder being second year birds or cygnets at the time of marking (Table 3). Females were slightly more likely than males to be recovered in the range of the other population (Table 3). However, the age and sex ratios of Tundra Swans that did not cross the population boundary were nearly identical to the ratios of the dispersing birds (Table 3; $\chi^2_1 = 0.99$, n.s. for age (first and second year age classes combined for analysis), and $\chi^2_1 = 1.22$, n.s. for sex), thereby indicating that there was not a propensity for Tundra Swans of a given age or sex class to disperse. The sex

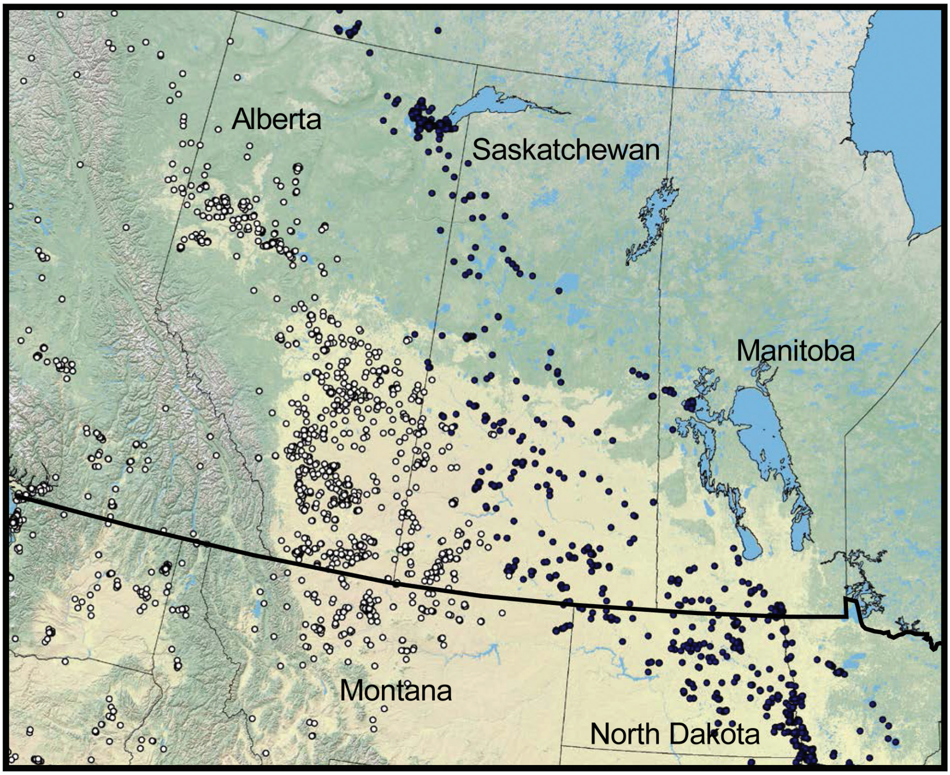


**Figure 4.** Distribution of satellite (PTT)-implanted Tundra Swans during autumn and spring while migrating through southern Canada and the northern United States, 2008–2012. White circles represent locations of birds marked south of the Brooks Range in Alaska (*n* = 28) and dark circles represent locations of birds marked north of the Brooks Range in Alaska (*n* = 10). Not portrayed are locations of two PTT-implanted swans that died on breeding areas in 2008 before migration and 10 birds implanted with PTTs on the lower Alaska Peninsula that either did not migrate or migrated only along the Pacific coast.

and age ratios of dispersing birds initially marked on summering and wintering areas did not substantially differ.

## Discussion

### Distribution of Eastern and Western Population Tundra Swans

The focus of this study was to determine the frequency that Tundra Swans cross-over between the Eastern and Western Populations, and whether there has been a change in cross-boundary movements since a similar summary by Limpert *et al.* (1991). In order to assess movement, the normal geographic range of each population was first established from earlier published studies (Sladen 1973; Bellrose 1980; Petrie & Wilcox 2003) and also from the locations of our PTT-marked birds migrating through

 

**Table 3.** Age and sex of all Tundra Swans recovered or observed in North America and reported to the USGS Bird Banding Laboratory relative to whether or not they crossed population domains, 1990–2013[a].

| | Sex | | | |
|---|---|---|---|---|
| **Age** | **Female** | **Male** | **Total** | **%** |
| **Swans that did not cross flyways** | | | | |
| Adult | 1,112 | 1,082 | 2,194 | 85.4 |
| Second year | 198 | 128 | 326 | 12.8 |
| First year[b] | 27 | 22 | 49 | 1.9 |
| Total | 1,337 (52.0%) | 1,232 (48.0%) | 2,569 | 100.0 |
| **Swans that crossed flyways** | | | | |
| Adult | 35 | 26 | 61 | 89.7 |
| Second year | 5 | 1 | 6 | 8.8 |
| First year | 0 | 1 | 1 | 1.5 |
| Total | 40 (58.8%) | 28 (41.2%) | 68[c] | 100.0 |

[a]Does not include 73 birds of unknown age or sex; [b]includes cygnets ringed as locals (not yet flighted) and hatch-year birds (flighted); [c]age or sex of two birds was not determined.

southern Canada. However, there has not been complete agreement among earlier studies on the geographic extent of each population, particularly in northeast Alberta. Our ringing and telemetry data, combined with encounter data reported to the BBL corroborates earlier work by Sladen (1973) and Petrie & Wilcox (2003) in demonstrating that the Peace-Athabasca Delta region of northeast Alberta is a staging area used solely by EP birds (Fig. 3, Fig. 4), whereas Bellrose (1980) and Paullin & Kridler (1988) reported that the area was also used by WP Tundra Swans during spring. Bellrose (1980) likely presumed the region was a staging area for WP swans based on the timing and magnitude of use by unmarked birds, whereas Paullin & Kridler (1988) reported that several of the Tundra Swans they colour-marked in eastern Oregon were later observed in the Peace-Athabasca Delta region. Paullin & Kridler (1988) also reported that some of their dyed swans were observed during May and June 1962 on the

 

Mackenzie River Delta in the North West Territories, Canada, a breeding area for EP Tundra Swans. If WP Tundra Swans do stage in the Peace-Athabasca Delta and then move on to the Mackenzie River Delta, our data suggest it is likely an uncommonly used route, or the region is used by a subset of swans that has been poorly sampled to date. For our analyses, we considered northeast Alberta and the Mackenzie River Delta to be part of the EP flyway.

## Distributional overlap between populations

The degree of spatial separation we document between EP and WP Tundra Swans in North America since 1989 is quite high, with over 97% of birds being resighted or recovered within the range of the population in which they were initially captured. Limpert *et al.* (1991) reported similarly high fidelity rates for swans encountered before 1990, with 94.5% of WP Alaska-ringed swans and 99.5% of EP Alaska-ringed swans being observed or recovered within their respective flyways, and < 1% of winter-ringed swans switching from one population to the other. Direct comparisons between the two studies should be undertaken with caution, given the extremely small sample sizes in the earlier work when only six Alaska-ringed WP swans were encountered (out of 110 total recoveries) in the range of EP swans, and two EP Alaska-ringed swans were encountered in the west (out of 416 ringed in northern Alaska and Canada; Limpert *et al.* 1991). Also, the analysis by Limpert *et al.* (1991) of Alaska-ringed swans was based primarily on birds captured as cygnets, which remain with their parents their first year of life and hence should initially have complete fidelity to the wintering area of their parents. Only if cygnets survive into their second summer could they possibly be expected to disperse to new wintering or breeding areas.

Our estimates of cross-population movement could be biased high if the swans we initially marked at northern areas were birds that were moult migrants from elsewhere. However PTT-marked swans from each of the five breeding areas in Alaska showed high summer site fidelity, with the exception of a subadult captured on the Colville River Delta that subsequently roamed across northern areas of Alaska and far western Canada within the range of the EP. Our finding that 2.6% of the resightings or recoveries per year were of cross-boundary movements is likely an underestimate of true movement given the relatively low resighting rate of marked birds during this study, particularly along the eastern seaboard. However, even low estimates of cross-population movement may be adequate to facilitate gene flow (Mills & Allendorf 1996), but only if dispersing birds mate with birds in the new population (Rockwell & Barrowclough 1987). A genetic analysis will be necessary to assess definitively the degree of gene flow between these two groups, as undertaken for Trumpeter Swans *Cygnus buccinator* in North America where two populations with overlapping ranges were found to differ genetically due to restricted gene flow (Oyler-McCance *et al.* 2007).

There are several scenarios that could lead to an overlap in staging and wintering distribution of EP and WP Tundra Swans. If EP and WP birds nest sympatrically in northwest Alaska, then nesting pairs and their offspring would naturally migrate back to the wintering area from which they came. However, simple overlap in breeding distribution does not explain the out-of-range occurrences of our Colville River Delta birds (Fig. 2), as these birds nest well within the breeding range of the Eastern Population. Overlap in population distribution could also be affected if pair formation occurs on staging areas or during winter, as reported for some geese (Ganter *et al.* 2005). In such an instance, birds pairing with individuals from another population at a common staging or wintering area might follow them back north to their natal area, as speculated by Limpert *et al.* (1991). However, our data show high fidelity of both males and females to wintering areas, so most males available for a female to pair with would be from the same population. In addition, the only non-summer area shared by EP and WP swans is in southwest Saskatchewan, where they are only sympatric during autumn (Fig. 4).

Movement of individuals across flyways has been reported for other populations of northern swans, but marking programmes and observation networks have generally been too patchy to quantify the degree of actual movement (Rees 1991). Rees (1991) reported the movement of marked Bewick's Swans, *C. c. bewickii*, between wintering areas in NW Europe and the Caspian Sea and also described the sighting of a Bewick's Swan in eastern Europe, that was initially marked in eastern Siberia. Hence it is apparent that although movement between flyways is unusual in Tundra Swans, it is not unprecedented. Such pioneering behaviour is a beneficial attribute for exploiting variable environments, and may prove necessary if the birds are to adjust to climate-induced changes in habitats.

## Stability of WP-EP migratory divide in Alaska

Our analysis of the recovery distribution of Alaska-ringed Tundra Swans shows that there has been little change over time in the population affinities of birds from different breeding areas, with swans breeding on the south side of the Brooks Range distributed nearly exclusively in the Pacific Flyway, and Tundra Swans breeding north and east of the Brooks Range staging and wintering in the Atlantic Flyway, within the realm of the EP. The Brooks Range appears to be an effective barrier separating breeding populations of EP and WP Tundra Swans in Alaska. The proximity of the two populations in southwest Saskatchewan, with little appreciable overlap, is fascinating, especially since the two populations migrate through the area at approximately the same time during autumn (Fig. 3, Fig. 4). The degree of segregation is somewhat surprising, especially in a region without pronounced topographic barriers, given the mobility of migratory waterfowl and their propensity to seek out limited wetlands. Climate-induced changes in wetland dynamics, particularly in south-central Canada could affect population interchange. If wetland drying occurs, and EP and WP swans staging across southwest Saskatchewan are constrained into using the same wetlands, then increased population exchange could result; this would be particularly likely if disturbance events (often associated with over-crowded conditions and human activity) increase. The latter could lead to the break-up of families and pair bonds which might also promote population exchange.

## Characteristics of dispersing swans

We expected that birds moving to a different migration pathway would differ with respect to age and sex relative to swans that did not move. In waterfowl, unlike most other birds, males generally disperse while females are typically more site faithful in the breeding range (Greenwood 1987), whereas the reverse pattern has been reported in winter, with male Bewick's Swans being more likely than females to return to their traditional wintering sites (Rees 1987). We therefore surmised that females would predominate in our sample of dispersing birds. We also suspected that young (second year) swans might be disproportionately represented in our sample of dispersing swans, as young birds have been reported to be more likely to disperse than older birds (Greenwood & Harvey 1982). However, the age and sex composition of dispersing birds was nearly identical to that of the birds that remained in the flyway where they were originally marked. Hence the tendency to emigrate in swans may be somewhat haphazard, although Rees (1991) did find that two of the three Bewick's Swans that moved among flyways in her study were subadults.

## Origin of the migratory divide

Many parts of Alaska were unglaciated during much of the Pleistocene, but most of northern and central Canada was covered by ice up to 3500 m thick (Marshall *et al.* 2002; Dyke *et al.* 2002; Clark *et al.* 2009). There have been numerous expansions and contractions of Nearctic ice fields during the last 450,000 years, and during glacial retreats an ice-free corridor extended from eastern Alaska across Alberta and Saskatchewan to the Great Lakes (Marshall *et al.* 2002). The location of this corridor aligns very closely with the migration route of Tundra Swans from northern Alaska (Figs. 3, 4). It seems plausible that Tundra Swans nesting in tundra regions of eastern Canada during glacial minimums were restricted to nesting in far western Canada and northern Alaska when northern Canada became glaciated during glacial maximums, but maintained their wintering areas on the East Coast of North America. Previous authors have also speculated that Pleistocene glaciations may have dictated the nesting range of Tundra Swans (Ploeger 1968; Limpert *et al.* 1991).

It is apparent that Tundra Swans in North America have changed their migratory paths many times over millennia. Hence it is feasible that in a changing hydrological landscape driven by climate change they will once again be able to adapt. However, while adapting to changing climate cycles in the past Tundra Swans have not had to compete for wetlands with humans; their future fate will likely depend on the extent to which anthropogenic factors influence the landscape and the degree to which humans are able to mitigate such factors.

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