Population Structure of Tundra Swans Wintering in Eastern North America

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ABSTRACT Our objective was to determine whether there were subpopulations within the eastern population of tundra swans (Cygnus columbianus columbianus) wintering along the mid-Atlantic coast. Movement rates between regions were substantial enough to result in continual mixing of wintering birds. Thus, we were unable to identify distinct subpopulations based on exclusive use of specific wintering areas. These birds should therefore be monitored, and their harvest managed, as if they were one population.

KEY WORDS Cygnus columbianus columbianus, eastern population, mid-Atlantic United States, movement, satellite transmitter, subpopulation, tundra swan, wintering ground.

Tundra swans (Cygnus columbianus columbianus) in North America are divided into 2 populations for management purposes, based on where swans breed and where they winter. Western population birds nest along the west coast of Alaska, USA, and winter from southern British Columbia, Canada, to central California, USA, whereas eastern population (EP) tundra swans nest from the north slope of Alaska to the eastern side of Hudson Bay and winter primarily in the eastern United States (Bellrose 1980). More than 90% of the EP winters in the mid-Atlantic region in Maryland, North Carolina, Virginia, and Pennsylvania, with the remainder distributed in the Atlantic and Mississippi flyways from Ontario, Canada, to South Carolina. Eastern population tundra swans are hunted in 3 states (MT, ND, and SD) during fall migration and in 2 states (NC and VA) during winter (D. Caswell, Canadian Wildlife Service, unpublished report).

Although EP tundra swans are managed as one population, biologists have speculated that there may be geographically and demographically distinct subpopulations of EP tundra swans within the EP (e.g., in southeastern VA; Sladen 1991; D. Caswell, unpublished report). If subpopulations do exist within the larger population, managers would probably want to establish separate population goals for each subpopulation and monitor the harvest of each (Hilborn 1990). However, information that could support or refute hypotheses about EP tundra swan population structure has been sparse. Our objectives were to identify areas where birds concentrated during winter and to determine whether any of those concentration areas represented spatially isolated groups of birds that could be biologically distinct subpopulations. Although neck-collar resightings, leg-band recoveries, and satellite telemetry have provided some information on wintering swan movements both within and between years, movement rates have never been formally estimated for the EP as a whole (Sladen 1973, Limpert et al. 1991, Petrie and Wilcox 2003). Therefore, we sought to calculate rates of movement among wintering concentration areas to evaluate evidence for subpopulations. High rates of movement among wintering areas would suggest no subpopulation structure, whereas low rates of movement would provide evidence of geographically distinct subpopulations (Hilborn 1990, Hanski 1998).

STUDY AREA Our study area included areas of high swan concentration within =25,000 km² of the mid-Atlantic coast of the United States. Swans were in 3 Bird Conservation Regions: Piedmont, New England-Mid-Atlantic Coasts, and Southeastern Coastal Plain (North American Bird Conservation Initiative Committee 2000). Important concentration sites in the mid-Atlantic Coast included Chesapeake Bay; Mattamuskeet, Pocosin Lakes, and Alligator River National Wildlife Refuges (NWRs); Potomac River; and Middle Creek Management Area-Susquehanna River (Wilkins 2007). Swans used fresh and brackish water wetlands of various sizes and outlying fields.

METHODS We used 39-g battery-powered platform terminal transmitter (PTT) satellite-tracked radiotransmitters (Microwave
Telemetry, Inc., Columbia, MD) to track movements of marked EP tundra swans. We attached PTTs to white neck-collars on 43 birds captured on their mid-Atlantic wintering grounds from November 2000 to March 2002. All but one bird were >1 year old (after-hatch yr). We captured and marked 6 swans in Maryland, 20 in North Carolina, 10 in Pennsylvania, and 7 in Virginia. Swans from Pennsylvania were over-represented in this sample in relation to the proportion of birds that winter there (23% of the PTTs vs. 1% of the average Mid-Winter Inventory [MWI] count in 2001 and 2002; J. Serie and B. Raftovich, United States Fish and Wildlife Service [USFWS], unpublished report), whereas swans from North Carolina were under-represented (47% of PTTs vs. 72% of MWI). We marked swans in Maryland (14% of PTTs vs. 18% of MWI) and Virginia (16% of PTTs vs. 8% of MWI) in closer proportion to the number of birds wintering there.

We distributed PTTs among birds captured in different locations (inland and coastal) and habitat types (fields and wetlands) to ensure a representative sample. We captured most birds by rocket-netting over bait adjacent to wetlands because this method proved to be the most reliable and efficient. We also used rocket-netting over plastic decoys and bait in fields, night-lighting in wetlands, and baited funnel traps in wetlands to sample birds in different habitat types and to minimize the effect of capture method on sample composition (Grand and Fondell 1994, Guyn and Clark 1999). We scheduled PTT duty cycles so that PTTs transmitted for 8 hours every 4th day throughout winter (Oct–Mar). We obtained satellite location data from Argos satellite data location and collection system (<http://www.argos-system.org/manual/>, accessed Oct 2009) in Landover, Maryland. We screened location data with an algorithm that compared pairs of consecutive locations from each satellite pass and selected the most likely pair of latitude and longitude coordinates for each 8-hour period, giving us one location every 4 days for each marked bird. We deleted biologically impossible locations (Malecki et al. 2001).

We also used data collected during an unrelated study of movement patterns and habitat use of EP tundra swans (Petrie et al. 2002, Petrie and Wilcox 2003). In that study, 12 EP tundra swans were equipped with PTTs during spring and fall 1998 and fall 1999 at Long Point, Ontario, Canada (Petrie and Wilcox 2003). Those PTTs collectively provided location information every 1–3 days from December 1998 to September 2000.

Timing of bird migration is strongly driven by photoperiod and internal physiological rhythms but can fluctuate in response to annual weather conditions (Bellrose 1980, Gill 1990, Limpert and Earnst 1994). Although we attempted to analyze movements separately for each year to remove the confounding influence of annual weather conditions, pooling data over years was necessary due to small sample sizes. We grouped location data into 2 15-day periods each month for October–March. Each swan’s movement history consisted of the bird’s location during each time period.

We calculated movement probabilities for individual swans, where \( \Psi_{ji} \) was the probability of moving from state \( i \) to state \( j \), and \( \Psi_{ii} \) was the probability of not leaving state \( i \). For example, \( \Psi_{PA} \) was the probability of a swan moving from Pennsylvania to Maryland, and \( \Psi_{NN} \) was the

![Figure 1. Satellite locations of wintering eastern population tundra swans classified into 4 regions in eastern United States, 1998–2003.](Image 316x500 to 556x740)
probability of staying in North Carolina. Movement among states (i.e., $\Psi_{ij} = 0.25$) would support the hypothesis of one homogenous winter population. Conversely, no movement among states (i.e., $\Psi_{ij} = 0$ and $\Psi_{ii} = 1$ for all $i,j$) would support the alternative hypothesis of discrete subpopulations on the wintering grounds (Hilborn 1990).

We calculated movement rates as the number of transitions from state $i$ to state $j$ divided by total number of movements from state $i$:

$$\Psi_{ij} = \frac{Y_{ij}}{N_i}$$

with a standard error of $\Psi_{ij}$

$$SE(\Psi_{ij}) = \sqrt{\frac{p_{ij}(1-p_{ij})}{N_i}}$$

where $i$ is state of origin and $j$ is state at time $t + 1$.

RESULTS

Of the 55 PPT-marked EP tundra swans, we tracked 21 from their return to the wintering grounds in late fall–early winter until their departure the following spring: 2 birds in 1998–1999, one in 1999–2000, 4 in 2001–2002, and 14 in 2002–2003. Of the 21 swans for which we had complete winter data, we marked 2 in Pennsylvania (10% of the sample), 5 in Maryland (24%), 3 in Virginia (14%), and 8 in North Carolina (38%). This distribution of markers across wintering states was closer to the spatial distribution of the wintering population, although North Carolina was still under-represented in this sample. We marked the remaining 3 swans in Ontario.

Eastern population tundra swans arrived on wintering areas staggered in time, but departures were more correlated in time. Of the 18 birds marked in the United States, we first detected 11 in the same state in which we marked them the previous winter. Of the remaining 7 birds, 4 eventually returned to the state in which we marked them, but 3 did not. Arrival dates of individual swans on wintering areas ranged from 29 October to 7 January (median arrival date 3 Dec), and departure dates ranged from 30 January to 28 March (median departure date 12 Mar). No birds arrived before mid-October, but they gradually filtered down from the Great Lakes area from mid-October through late December. January was the only month when all birds were present on wintering areas. Some swans began moving back to the Great Lakes region as soon as early February, but others remained in wintering areas until late March.

After tracked swans reached the wintering grounds, most of them moved among the 4 states. We detected 6 birds in only one state during the entire winter, but we detected 12 birds in 2 states, 2 birds in 3 states, and 1 individual in all 4 wintering states during one winter (Fig. 2). However, movement rates could be underestimated because satellite transmitters were not programmed to provide daily locations.

In general, swans tended to move south soon after their arrival on the wintering grounds (unless they first arrived in NC) and to move north later in winter. One swan made a northerly movement in the middle of the winter before returning south the next period (Fig. 2). Although 15 of 21 birds used $>1$ state, most birds spent most of the winter in one state, and only 2 swans spent substantial time in $>1$ state.

Tracked swans made all possible transitions among the 4 states except for a direct movement from Pennsylvania to North Carolina (Fig. 3). Within each state, the highest movement probability was that of remaining in the same state ($\Psi_{ii}$). However, probability of moving to another state was $>0.5$ for all states except Pennsylvania. Only in Pennsylvania was a swan more likely to remain in the state than to move to one of the other 3 states ($\Psi_{PA-PA} = 0.71$). Six movement rates from states were approximately $\Psi = 0.25$: North Carolina to Maryland, North Carolina to Virginia, Maryland to North Carolina, Maryland to Pennsylvania, Virginia to North Carolina, and Virginia to Maryland. Movement rates among states ($\Psi_{ij}$) were rarely different from 0.25, and only one confidence interval for the probability of remaining in the same state ($\Psi_{ii}$) included 1.0. However, almost all of the 16 movement rates had overlapping confidence intervals because of large standard errors associated with point estimates, caused by small sample size, especially in Pennsylvania.

DISCUSSION

As the wintering area for $>90\%$ of the population, the mid-Atlantic region of the United States is vital to EP tundra swans. We identified 4 regions in the winter range of particular importance to the EP, as evidenced by the extensive use of those regions by marked birds: southeastern Pennsylvania, northern Chesapeake Bay, the Potomac River and southern Chesapeake Bay, and northeastern North Carolina. Most marked birds used $\geq 2$ of those concentration areas.

Ricklefs and Miller (1999) defined a subpopulation as a group of individuals that live within a homogeneous patch of habitat that provides all of the resources those individuals need. For migratory species, this definition implies that a subpopulation would exclusively occupy a particular habitat patch either during summer or winter, or both, each year. Wilkins (2007) found that although female EP tundra swans exhibited nesting area fidelity by returning to the same location in consecutive summers, birds marked in a specific winter concentration area did not nest near each other, that is, in the same patch. Similarly, marked birds that nested in the same general area did not necessarily winter in the same concentration area. Thus, Wilkins (2007) found no evidence of a subpopulation of EP tundra swans that used both summer and winter habitat patches exclusively.

Likewise, our results lend no empirical support to the hypothesis that EP tundra swans are organized into discrete subpopulations during winter. Detailed examination of movements of individual birds showed no evidence that Virginia tundra swans are a distinct subpopulation, because
those birds seemed to occupy areas that overlapped with North Carolina in the south or Maryland in the north. In fact, most of our marked birds moved from one of the concentration regions to another at least once during winter, indicating mixture of birds among wintering regions. Furthermore, all estimates of movement were minimum estimates, because time gaps of up to 2 weeks between satellite locations meant that we could miss bird movements. The mixture that we observed on the wintering ground, where pair bonds are formed, suggests that formulation of subpopulations is unlikely in EP tundra swans (Limpert and Earnst 1994).

**Management Implications**

Movement patterns we observed show that EP tundra swans intermingle throughout the winter rather than isolate themselves in geographically distinct groups that could be considered subpopulations. Thus, these birds should be...
monitored, and their harvest managed, as if they were one population.

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LITERATURE CITED


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Figure 3. Movement rates (Ψij) of 21 satellite-tracked eastern population tundra swans between Pennsylvania, Maryland, Virginia, and North Carolina, December 1998–March 2003. Vertical lines show 95% confidence intervals. A horizontal reference line is at Ψ = 0.25.