Migration routes and Bird Conservation Regions used by Eastern Population Tundra Swans *Cygnus columbianus columbianus* in North America

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Abstract

The Eastern Population (EP) of Tundra Swans *Cygnus columbianus columbianus* breeds from the Alaskan North Slope to eastern Hudson Bay in Canada and winters in the eastern United States. Breeding and migration habitats have been difficult to identify because of the species' vast and remote breeding range and its long-distance migration. A total of 43 female EP Tundra Swans were caught in Maryland, North Carolina, Pennsylvania and Virginia and marked with satellite transmitters to follow annual movements, delineate migration routes and determine Bird Conservation Region (BCR) use for EP Tundra Swans from November 2000–March 2002. Marked EP Tundra Swans spent approximately 3.5 months on breeding areas, 3.5 months on wintering areas and 5 months on staging areas, highlighting the importance of migratory habitats to these birds. Marked birds used 15 different ecologically distinct BCRs throughout the year: 10 during the spring, 11 during the autumn, four during the summer and six during the winter. The most important of these were the Prairie

Potholes, Boreal Taiga Plains and Prairie Hardwood Transition during both spring and autumn; the Arctic Plains and Mountains during the summer; and the Mid-Atlantic coast during the winter. Fifty-five spring migration routes and 28 autumn routes used by marked birds were mapped. Seven sites were identified as being key migration staging areas that should be enhanced through habitat protection and management planning.

Key words: Bird Conservation Regions, *Cygnus columbianus columbianus*, Eastern Population, migration, satellite telemetry, stop-over sites, Tundra Swan.

Tundra Swans *Cygnus columbianus columbianus* wintering in the eastern United States from southeast Ontario to South Carolina comprise about 80,000–100,000 birds, collectively referred to as the Eastern Population (EP). Over 90% of the EP winters in three states: Maryland, North Carolina and Virginia; the remainder are distributed from Ontario to South Carolina. A similar number of Tundra Swans that winter from southern British Columbia to central California comprise the Western Population. EP Tundra Swans migrate 5,000 km each year, travelling through the Great Lakes, prairies and boreal forests to reach the breeding grounds that extend from the North Slope of Alaska to the eastern side of the Hudson Bay in Canada (Bellrose 1980; Petrie & Wilcox 2003).

Knowledge of the swans' seasonal movement patterns and habitat use is critical for conservation planning, and may help direct avenues of research should the population decline (Nichols & Kendall 1995). Previous marking studies using passive markers such as leg bands and neck collars have provided useful information about the movements and habitat use of EP Tundra Swans (Sladen 1973), but a more complete understanding has been limited by the large scale of their annual movements and the remote areas utilised during most of the year. Recently, detailed information about annual movements of individual EP Tundra Swans has become available through satellite telemetry studies (Petrie & Wilcox 2003), but sample sizes were small (n = 12).

The objective of the present study therefore was to identify ecoregions and specific sites that are important to breeding, migrating and wintering EP Tundra Swans by marking a larger sample of birds with satellite transmitters, to obtain detailed information on their annual movements and the sites used during the annual cycle. In particular we aimed to describe the swans' migration routes, important concentration areas and the amount of time that individuals spent at particular sites or ecoregions. This type of information can be used by conservation planners and habitat managers seeking guidance on when and where to manage sites for the EP Tundra Swans.

Methods

Marking

Forty-three female swans were marked with U.S. Fish and Wildlife Service (USFWS) aluminium leg bands and 39-gram batterypowered PTT-100 satellite-tracked radio transmitters made by Microwave Telemetry, Inc., Columbia, Maryland. Platform Transmitter Terminals (PTTs) were attached to cryptic white neck collars fitted to the swans; white collars were used to minimise the possibility of hunters selecting marked birds (either intentionally or unintentionally) for harvest. The neck collars were 7.5 cm tall with an inside diameter of 5.7 cm and plastic 3 cm thick; the entire unit weighed 110 g, including 40 g for the radio. All but one swan were >1 year old (after-hatch year; AHY). Swans were captured and marked in Maryland (six birds), North Carolina (20 birds), Pennsylvania (10 birds) and Virginia (seven birds) during winter months (November–March), from November 2000–March 2002. Marking effort was spread throughout the winter range and transmitters were distributed among 20 different locations that included shorelines adjacent to roosting ponds (20 birds marked at six sites), fields adjacent to wetlands (17 birds marked at 10 sites), tidal estuarine rivers (five birds marked at three sites) and a tidal estuarine bay (one bird marked at one site). Several capture methods were used to minimise the effect of catching technique on sample composition (Grand & Fondell 1994; Guyn & Clark 1999). Most birds were caught by rocket-netting over bait (27 birds) or decoys (10 birds) because this method proved to be most reliable and efficient. We also used baited corral traps (five birds) and baited funnel traps (one bird).

Satellite data

PTTs transmitted for 8 hours every 4th day during September–May and 8 hours every 8th day during June–August. Expected PTT battery life was 1.5 years, and transmitters collectively provided data from January 2001–April 2003. Location data were received from the Argos satellite (Service Argos, Landover, Maryland) every 4–21 days from November 2000–December 2003 inclusive. The Argos locations were calculated by computing the Doppler shift on the frequency of the transmitter signals. This method provides two possible locations (latitude and longitude), each with an accuracy code to designate the quality of each pair of data points. We used transmitter signals with location accuracy of < 1,000 m or better (location classes 3, 2 and 1), which was felt to be sufficient for the large areas under consideration here. In order to ensure that we were using the more likely of the two signals, the data were sorted for consistency using a routine developed by Malecki *et al.* (2001). Pairs of consecutive locations in time were compared and the most likely pair of latitude and longitude coordinates was selected. Biologically implausible locations were deleted.

One swan was found dead under a power line in Maryland about one year after it was caught and marked. Of the remaining 42 PTTs, 17 functioned until their batteries died, five failed earlier than expected based on expected battery life and 20 repeatedly transmitted signals from fixed positions. Signals from these fixed positions could be caused by death of the bird, a broken collar becoming detached from the bird, or the radio falling off the collar; we could not confirm the reason for signals from fixed positions unless the bird was found dead. Most transmitters provided information on bird movements for a complete season (spring, summer, autumn or winter) before ceasing to function. Data for three swans were eliminated from the analyses because their transmitters failed before spring migration was completed.

Of the 43 birds marked, 39 were tracked for 141 complete seasons: 56 in spring (22 transmitters providing data for one spring and 17 transmitters providing data for two consecutive springs), 39 in summer (five for one summer; 17 for two consecutive summers), 28 in autumn (18 for one autumn; five for two consecutive autumns) and 18 in winter (18 transmitters functioning over a single winter). Thus, a single bird often provided location data for >1 season for all seasons except the winter period. Because the same individual likely exhibited similar movements, seasonal data from the same bird were not independent. However, we retained data for individuals across multiple migration seasons to provide the maximum information on swan migration routes and migration phenology for this descriptive study.

PTTs only transmitted every 4–8 days, so there were gaps of several days when the swans' locations were not known. The mid-point dates between locations separating seasons therefore were to estimate the number of days a bird spent in each part of the annual cycle. If the gap between locations was an odd number of days, the time spent in the first part of the annual cycle was assigned one less day than the subsequent part. The number of days that each bird spent in each phase of the annual cycle was then summed, and the mean duration (± s.e.) was calculated.

Data from complete seasons were used for all analyses. Use of data from incomplete seasons can bias estimates of time spent in different regions or parts of the annual cycle if: 1) transmitter attrition causes overestimation of time spent in regions or phases of the annual cycle that occurred earlier in the transmitter's life, 2) transmitter failure is related to geographic location or time of year, 3) the number of active transmitters varies non-randomly (*e.g.* the number of active transmitters is greatest during the spring and drops off as the seasons progress), and 4) seasonal duty cycles varied. Seasons and BCRs were assigned using ArcView GIS software (version 3.1) and migration routes were mapped using ArcTools available in ArcGIS software (version 9.0; ESRI Inc., Redlands, California, USA).

The timing of swan migration is strongly driven by photoperiod and internal physiological rhythms but can fluctuate in response to annual weather conditions (Bellrose 1980; Rees 1982, 1989; Gill 1990; Limpert & Earnst 1994). The data recorded during the present study showed a similar pattern, with the timing and chronology of annual movements being highly variable among individual birds and years. We therefore attempted to analyse Tundra Swan movements separately for each year, to remove the confounding influence of annual weather conditions, but found that sample sizes were too small to allow separation of individual variation from annual variation due to weather. The data therefore were pooled across years.

Annual cycle

Satellite locations were assigned to one of the four parts of the annual cycle: spring migration, breeding, autumn migration, or winter. Locations could not be strictly classified based on geography or date, because patterns of movement varied among individuals. In particular, swan locations in Pennsylvania and southeast Ontario (which are north of historic wintering grounds) were problematic to classify because these traditional migration stop-over locations are increasingly functioning as wintering grounds for some swans, with some swans spending the entire winter in these places (Ad Hoc EP Tundra Swan Committee 2007). It was also difficult to know whether to classify some of the remote northern locations as breeding or autumn migration sites, because it was not certain how the resources and habitats were being used. The following rules therefore were developed, based on the swan's location, time of year, and distance moved, to assign each satellite location to a part of the annual cycle:

(1) *Spring migration (February–June)*. In general, northerly movements outside of traditional wintering grounds were considered the start of spring migration. For example, a movement from North Carolina to southeast Ontario in March was considered the beginning of spring migration for that bird. A northerly movement to Pennsylvania or southeast Ontario that occurred in February–March was considered as either spring migration or wintering-ground movement based on the length of stay. If the bird stayed for seven or more days, it was considered a wintering ground movement. If the stop-over was for a shorter period followed by another northerly movement, it was considered the start of spring migration. In one case, however, the movement of a bird from Virginia to southeast Ontario in March was considered as part of the winter period because this bird subsequently returned to the south. Swans marked in Pennsylvania in February were not assigned to an activity (spring migration or wintering ground) for the first year, because it was not certain whether these swans had been resident in Pennsylvania all winter or if they had begun their spring migration.

(2) *Breeding (May–October)*. Satellite locations in the late spring-early autumn that did not vary by > 150 km were all considered to be breeding ground locations.

(3) *Autumn migration (September–December)*. The first southerly movement in the late summer or early autumn that was > 150 km was considered the beginning of autumn migration.

(4) *Winter (October–March)*. Arrival in North Carolina, Virginia, or Maryland in the late autumn or early winter was considered the start of the wintering period. Arrival in Pennsylvania or Ontario was classified as wintering if the bird stayed there for more than seven days. However, if the bird continued south after seven days, the Pennsylvania or southeast Ontario locations were considered part of autumn migration. In three cases, arrival in southeast Ontario was considered the beginning of wintering, because two swans spent the entire winter in

southeast Ontario, and one bird stayed in southeast Ontario for almost two months before moving to North Carolina in early January.

Patterns of site use

Two types of sites were considered: 1) historically used sites, and 2) sites visited by multiple swans in this study. Historically used sites were those that were known *a priori* to be important based on the scientific literature. Sites visited by multiple swans in this study were identified *a posteriori*, based on patterns in satellite data. These latter sites were assigned a name based on the nearest water body (lake, river, delta, bay) or wildlife refuge, as these were assumed to be the attractant for those birds. These sites varied in size from 10 km^2 (*e.g.* breeding locations) to 1,500 km^2 (*e.g.* the Tri-Refuge area of North Carolina).

Site use was characterised as the proportion of swans located in these sites at different times of the year. The number of swans observed at a site was scaled by the number of active transmitters across all years: 56 during spring migrations, 39 during breeding seasons, 28 during autumn migrations and 19 total during the winters. The proportional scaling adjusts for transmitter attrition during time of year (*e.g.* nine marked individuals using a site during autumn represented a larger portion of the population than nine marked individuals using a site during spring, because there were fewer active transmitters during autumn). When the same swan visited the same site in successive years, this swan contributed >1 to the total count for that site. This pseudo-replication rendered calculations of variance inappropriate (Hurlbert 1984). The number of days that each swan spent at each site was also calculated. Important sites were classified as those used by the majority of the marked swans during that time of year, or those where swans spent a long portion of the migration period. This classification of the relative importance of sites does not take into account the relative size of the sites or the location error in the satellite data.

Patterns of use of Bird Conservation Regions

To quantify large-scale habitat use, satellite locations were assigned to ecologically distinct regions known as Bird Conservation Regions (BCRs; North American Bird Conservation Initiative Committee 2000). Fifteen of the 66 BCRs in North America were used by swans in this study. The average number of days that individual birds spent in each BCR during spring migration, breeding, autumn migration and the winter was calculated. Total bird-use days was equal to the average number of days spent in the BCR times the number of birds that visited that BCR. BCR use was then characterised as the proportion of time that the swans spent in each BCR. Calculations were based on days of use by each bird (bird-days) summed across the number of birds for each part of the annual cycle. Time spent in each BCR was calculated in this manner, so that BCRs that were used by more birds would contribute more to the overall calculation of use. The BCRs that were used by most birds for a long portion of each season were deemed to be important areas for the swans.

Results

Annual cycle

Satellite locations were used to determine migration chronology and the geographic distribution of birds throughout the annual cycle. PTT-marked swans spent the largest proportion of time on breeding and wintering grounds and the remainder of the year on staging areas; they spent about 4.7 months each year migrating in the spring and autumn, and about 7.3 months of each year on the breeding and wintering grounds (Table 1). The durations of the spring and autumn migrations were similar, as was the average time spent on the breeding and wintering grounds.

Spring migration. Most birds left the wintering areas during the first half of March, but departure date ranged from 22 February to 10 April (median departure date = 14 March). Swans moved northwest to the Great Lakes region of Ontario and Michigan, where they stayed for 15–30 days and then continued west to the prairies in western Minnesota, North Dakota, and the prairie provinces of Canada (Fig. 1). They stayed on the prairies for 30–40 days, usually until mid-April, but some as late as early May. Migration routes then diverged; some birds migrated northwest toward the Mackenzie River Valley, the western Arctic Islands, or the North Slope of Alaska; others migrated north or northeast to eastern Nunavut or the Hudson Bay. Swans that went northwest first moved into the boreal forests of Saskatchewan and Manitoba and usually stayed in the Athabasca Delta region for 2–3 weeks, where migration routes again diverged. Some birds continued northwest to the North Slope of Alaska or the Mackenzie River Valley, while others moved northeast to the western Arctic Islands. Birds settled onto breeding ground locations from 4 May to 18 June (median arrival date = 29 May).

Table 1. Seasonal time budgets for 39 satellite-tracked Eastern Population Tundra Swans in North America, February 2001–December 2003. [a]Sample size is the number of complete seasons of satellite data, and includes multiple observations from the same bird when a transmitter lasted >1 year.

Season	**Proportion of year**	**Average no. days/year**	**Minimum no. of days**	**Maximum no. of days**	***n*[a]**
Spring migration	0.21	75	39	98	56
Breeding	0.32	115	80	149	39
Autumn migration	0.18	67	32	107	28
Wintering	0.29	108	61	151	19

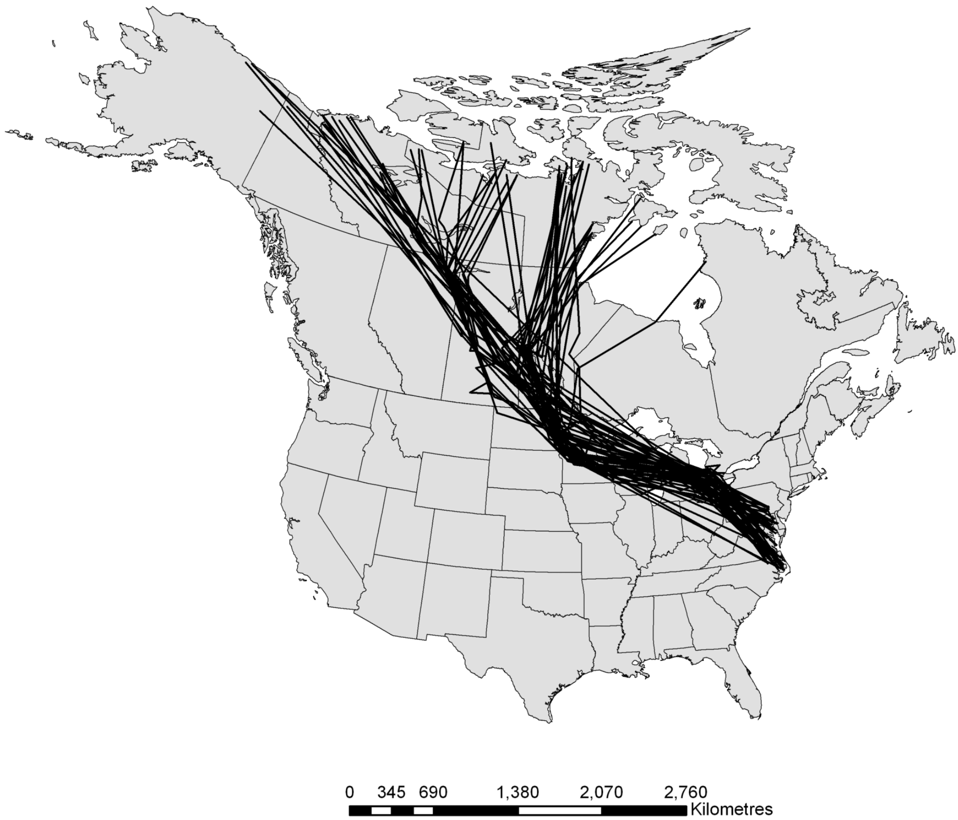

Figure 1. Spring migration routes of North American Eastern Population Tundra Swans marked with satellite-tracked radio transmitters, spring 2001–2003.

Breeding grounds. Breeding locations of EP Tundra Swans were unrelated to the state in which the swan was marked during the winter (Wilkins 2007). Swans spent 3–3.5 months on the breeding grounds and moved little, likely due to nesting and brood-rearing activities. Movements on the breeding grounds followed 2 general patterns: 1) a relatively large southerly movement (80–160 km in length) 2–4 weeks after arriving on the breeding grounds, followed by a movement back north to the earlier breeding location, and 2) a small southern movement (15–160 km) from tundra to river delta habitat shortly before autumn migration. This pre-migration movement usually occurred in the Mackenzie River/ Anderson River Delta area, and was followed by a major journey of 800 km or more to the south at the end of the summer, which marked the beginning of autumn migration.

Of the 17 female Tundra Swans tracked for two consecutive years, all but one used the same summer location in both years. Home ranges during the breeding season ranged from about 5–25 km². The exception was a bird that spent the first summer on the southern tip of Southampton Island, a large island at the mouth of the Hudson Bay in Canada, and the next summer on Coats Island, a small island just south of Southampton Island.

Autumn Migration. Marked swans left their breeding grounds from 6 September–7 October (median departure date = 20 September), and migrated south through the boreal forests of the Northwest Territories and Nunavut, to northern Saskatchewan and Manitoba (Fig. 2), where they again spent about 2–3 weeks. Those birds then continued south into southern Saskatchewan and Manitoba, where they typically stayed for several more weeks. Birds subsequently relocated to the prairies of Montana, the Dakotas and western Minnesota, where they stayed for 20–30 days, then headed east to the Upper Mississippi River region and then to the

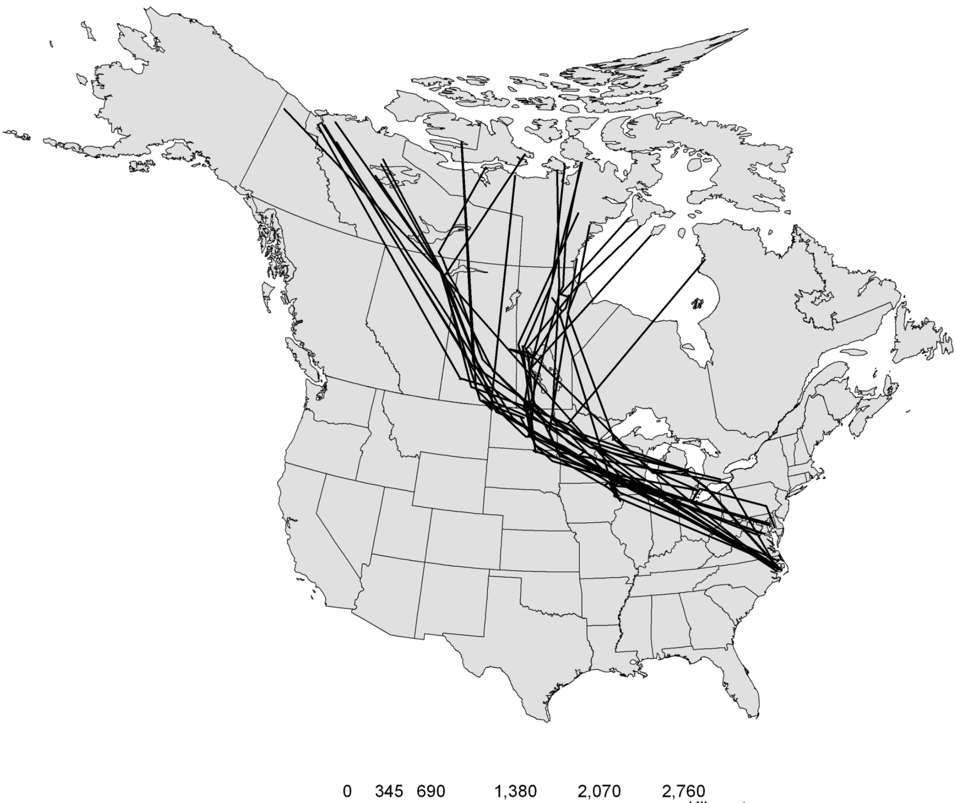

Figure 2. Autumn migration routes of North American Eastern Population Tundra Swans marked with satellite-tracked radio transmitters, autumn 2001–2003.

Great Lakes region. Although most birds migrated a final leg southeast to the wintering grounds of the mid-Atlantic coast and arrived from 27 October–29 December (median arrival date = 29 November), two birds spent most or all of the winter on the Great Lakes in Ontario.

Individual birds took the same general routes south that they took north during spring migration. Furthermore, in all cases in which satellite location data from the same bird were available for two consecutive spring (n = 17) or autumn (n = 5) migration routes, the general route was the same each year, although gaps in satellite location data precluded exact comparison of routes between years. Timing of movements varied between years and was likely dependent upon season phenology.

Patterns of site use

Thirteen sites were identified as being used by a large proportion of the satellite-tracked swans, or were used for long periods during migration (Table 2). Important sites in the spring were: the Red River Valley of Minnesota and the Dakotas (84% of tracked swans spent an average of 20.5 days in this location), southeast Ontario (78% of swans, 16.8 days), Saginaw Bay (49% of swans, 13.7 days), Athabasca Delta (38% of swans, 28 days) and Cedar Lake (33% of swans, 22 days). Important sites in the spring were: the Souris River (54% of swans, 21.8 days), the Upper Mississippi River (43% of swans, 33.6 days) and the Athabasca Delta (32% of swans, 32.3 days). Important wintering sites were the Tri-Refuge area of northeast North Carolina (containing Pocosin Lakes, Mattamuskeet and Alligator River National Wildlife Refuges), where 58% of the swans were located and spent approximately 88.8 days, and the Chesapeake Bay where 63% of swans spent 46.3 days. The most important breeding sites were the Mackenzie and Anderson River Deltas (23% of swans, 75.3 days) and Great Bear Lake (15% of swans, 64.2 days). All of the key migration areas were used during both the spring and autumn, but use often varied by season. Southeast Ontario, Saginaw Bay and the Red River Valley were used by more birds in the spring, whereas the Upper Mississippi River and Souris River received more use by EP Tundra Swans during the autumn. The north and south Saskatchewan Rivers and Athabasca Delta were equally important during spring and autumn migration. Some areas (*e.g.* the North Slope of Alaska), reported to be important to Tundra Swans (Bellrose 1980), were not used by many birds in this study (Table 2). Based on the number of visiting birds, southeast Ontario and Pennsylvania functioned more as spring migration stop-over sites than wintering sites.

Patterns of BCR use

Marked swans used 15 BCRs during the year, and several were important for > 1 season: 10 BCRs were used in the spring, 11 BCRs in the autumn, four BCRs in the summer and six BCRs in the winter. The most important were the Prairie Potholes and Boreal Taiga Plains in the spring, the Prairie Potholes and Prairie Hardwood Transition in the autumn, Arctic Plains and Mountains (including tundra) in the summer and the Southeastern Coastal Plain and Mid-Atlantic Coast in the winter (Table 3).

Table 2. Seasonal use of areas by 39 satellite-tracked Eastern Population Tundra Swans in North America, February 2001–March 2003. [a]Sample size is the number of complete seasons of satellite data, and includes multiple observations from the same bird when a transmitter lasted >1 year; [b]includes Lake St. Clair, Aylmer, Long Point and surrounding area; [c]includes Alligator River, Mattamuskeet and Pocosin Lakes National Wildlife Refuges and surrounding areas.

Site name	Mean days	n^a	Proportion of birds at the site	Minimum number of days	Maximum number of days
Spring migration					
Red River Valley (North Dakota, South Dakota, Minnesota)	20.5	46	0.84	2	40
Southeast Ontario [b]	16.8	43	0.78	2	36
Lake St. Clair/Aylmer Wildlife Management Area	13.4	20	0.36	2	32
Long Point	4.0	6	0.11	2	9
Saginaw Bay (Michigan)	13.7	27	0.49	4	43
Athabasca Delta (Alberta, Northwest Territories, Saskatchewan)	27.6	21	0.38	9	89
Cedar Lake (central Saskatchewan and Manitoba)	21.8	18	0.33	4	39
Souris River (Manitoba, Saskatchewan, North Dakota)	15.3	17	0.31	7	27
Churchill and Hayes Rivers (Manitoba, Nunavut)	14.0	15	0.27	3	28
North and Southern Saskatchewan Rivers (Alberta, Saskatchewan)	15.3	12	0.22	6	28
Upper Mississippi River, Pools 4–8 (Iowa, Minnesota, Wisconsin)	10.1	7	0.13	6	19
Lake Winnebago/Horicon Marsh (Ontario, Wisconsin)	10.3	4	0.07	4	18
Upper Red Lake (Minnesota)	17.8	4	0.07	9	31
Middle Creek WMA/Susquehanna River (Pennsylvania)	5.0	1	0.02	5	5
Breeding					
Mackenzie and Anderson River Deltas (Northwest and Yukon Territories)	75.3	9	0.23	15	159
Great Bear Lake (Northwest Territories)	64.2	6	0.15	5	145
Adelaide Peninsula (Nunavut)	58.3	4	0.10	4	114
Victoria Island (Northwest Territories, Nunavut)	112.0	4	0.10	103	121
Boothia Peninsula (Nunavut)	97.3	3	0.08	55	119
Chesterfield Inlet (Nunavut)	46.7	3	0.08	4	118

King William Island (Nunavut, Saskatchewan)	82.3	3	0.08	55	102
Churchill and Hayes Rivers (Manitoba, Nunavut)	54.0	3	0.08	3	130
Southampton Island (Nunavut)	98.0	3	0.08	83	116
North Slope (Alaska)	105.5	2	0.05	104	107
Old Crow Flats (Alaska,Yukon Territories)	99.0	2	0.05	83	115
Isle Below Southampton (Nunavut)	41.0	1	0.03	41	41
Ungava Peninsula (Quebec)	135.0	1	0.03	135	135
Yukon Flats (Alaska)	31.0	1	0.03	31	31
Autumn migration					
Souris River (Manitoba, Saskatchewan, North Dakota)	21.8	15	0.54	4	80
Upper Mississippi River, Pools 4–8 (Iowa, Minnesota, Wisconsin)	33.6	12	0.43	8	72
Athabasca Delta (Alberta, Northwest Territories, Saskatchewan)	32.3	9	0.32	9	76
Churchill and Hayes Rivers (Manitoba, Nunavut)	20.4	8	0.29	4	37
North and Southern Saskatchewan Rivers (Alberta, Saskatchewan)	15.0	7	0.25	3	40
Red River Valley (North Dakota, South Dakota, Minnesota)	13.8	6	0.21	4	34
Cedar Lake (central Saskatchewan and Manitoba)	19.0	5	0.18	13	35
Saginaw Bay (Michigan)	23.4	5	0.18	4	59
Lake Winnebago/Horicon Marsh (Ontario, Wisconsin)	20.7	3	0.11	6	47
South-east Ontario	19.6	5	0.18	5	40
Lake St. Clair/Aylmer Wildlife Management Area	22.3	3	0.11	5	35
North of Long Point	9.0	1	0.04	9	9
Upper Red Lake (Minnesota)	29.5	2	0.07	14	45
Middle Creek WMA/Susquehanna River (Pennsylvania)	7.0	1	0.04	7	7
Winter					
Chesapeake Bay (Maryland, Virginia)	46.3	12	0.63	4	95
Tri-Refuge Area (North Carolina)[c]	88.8	11	0.58	9	153
Potomac River (Maryland, Virginia)	38.8	6	0.32	4	115
South-east Ontario	95.0	2	0.11	74	117
Lake St. Clair/Aylmer Wildlife Management Area	112.0	1	0.05	112	112
Long Point	7.0	1	0.05	7	7
North of Long Point	66.0	1	0.05	66	66

Table 3. Bird Conservation Regions (BCRs) in North America used by 39 Eastern Population Tundra Swans marked with satellite-tracked radio transmitters during breeding, migration and wintering periods, and approximate proportion of time spent in each BCR during each season, February 2001–March 2003. [a]Individual birds could provide data for >1 season if the transmitter lasted for >1 year.

BCR name	Mean days	*n*[a]	Proportion of bird days in BCR	Minimum number of days	Maximum number of days
Spring Migration					
Prairie Potholes	23.0	52	0.30	4	43
Boreal Taiga Plains	20.8	45	0.23	4	41
Lower Great Lakes/St. Lawrence Plain	15.0	43	0.16	2	31
Boreal Hardwood Transition	12.1	34	0.10	4	40
Prairie Hardwood Transition	9.1	35	0.08	3	31
Boreal Softwood Shield	10.3	21	0.05	3	23
Taiga Shield and Hudson Plains	9.4	21	0.05	4	23
Arctic Plains and Mountains	7.3	6	0.01	4	15
Appalachian Mountains	4.0	2	<0.01	4	4
Eastern Tallgrass Prairie	7.0	1	<0.01	7	7
Piedmont	5.0	1	<0.01	5	5
Breeding					
Arctic Plains and Mountains	93.0	37	0.88	5	131
Boreal Taiga Plains	23.2	11	0.06	4	133
Northwestern Interior Forest	108.0	2	0.05	72	144
Taiga Shield and Hudson Plains	19.0	1	<0.01	19	19
Autumn Migration					
Prairie Potholes	22.0	25	0.31	4	39
Prairie Hardwood Transition	22.9	20	0.25	4	63
Boreal Taiga Plains	14.4	17	0.14	7	25
Boreal Hardwood Transition	19.0	9	0.09	4	57
Taiga Shield and Hudson Plains	12.2	13	0.09	4	31
Lower Great Lakes/St. Lawrence Plain	14.7	7	0.06	4	35
Arctic Plains and Mountains	10.4	5	0.03	4	29
Boreal Softwood Shield	8.0	4	0.02	4	12
Eastern Tallgrass Prairie	5.8	4	0.01	3	9
Piedmont	5.0	1	<0.01	5	5
Badlands and Prairies	4.0	1	<0.01	4	4
Winter					
Southeastern Coastal Plain	89.6	14	0.64	32	150
New England/Mid-Atlantic Coast	36.0	14	0.26	4	97
Lower Great Lakes/St. Lawrence Plain	91.0	2	0.09	70	112
Piedmont	6.5	2	0.01	4	9
Prairie Hardwood Transition	5.0	1	<0.01	5	5
Appalachian Mountains	4.0	1	<0.01	4	4

Within each season, individual birds had different patterns of BCR use. Individual swans used 2–8 BCRs during the spring, 2–6 BCRs during the autumn, 1–2 BCRs during the summer and 1–3 BCRs during the winter.

The BCRs used in the spring and autumn were similar, but importance of BCR types varied by season. The Boreal Taiga Plain was used more in spring than in autumn. In contrast, the Prairie Hardwood Transition in the southern Great Lakes region (Minnesota, Michigan and Wisconsin) was used more in autumn than spring. Four BCRs were used exclusively in either spring (Appalachian Mountains) or autumn (Badlands, New England/Mid-Atlantic Coast and Eastern Tallgrass Prairie), but this was likely due to the limited number of marked birds and short amount of time spent in these regions (4–13 days/year).

Discussion

While leg bands and neck collars yield insights into EP Tundra Swan movements, only satellite-tracked radio transmitters can provide detailed information on migration chronology, important stop-over sites and continental-scale habitat use. As found in other studies (Petrie & Wilcox 2003), satellite-tracked EP Tundra Swans spent over seven months each year on the breeding and wintering grounds. The birds spent most of the remaining five months each year on staging areas, illustrating the key role that Bird Conservation Regions on the migration routes play in their life-cycle. This time is spent refuelling and acquiring nutrient and energy stores needed to fuel the next stage of the migration or the nesting period (Nolet 2006). The study did not find a large difference between the length of time spent on spring and autumn migrations, unlike Petrie & Wilcox (2003), who reported that autumn migration was one month shorter than spring migration. These differing results may perhaps be due to annual variation in migration chronology related to weather, but could also simply be due to differences in duty cycles or analytical techniques between the two studies. Timing of annual spring and autumn migration varied between individuals. However, migration routes were consistent with those described elsewhere (Bellrose 1980; Sladen 1973; Petrie & Wilcox 2003) and were also consistent between years.

While the movement patterns of most swans were typical (*i.e.* short stays at traditional stop-over sites during migration; long stays at traditional breeding and wintering sites), some movement patterns were difficult to classify based on location or time of year. For example, one swan spent two months of the late autumn and early winter in southeast Ontario, a traditional stop-over site, before moving to traditional wintering sites. This swan switched between Ontario and traditional wintering ground sites two more times during January–March. Tundra Swans are increasingly wintering in more northern locations that were traditionally classed as stop-over locations (Ad Hoc EP Tundra Swan Committee 2007). Patterns of shortened autumn migration have been observed in other migratory waterfowl in North America (*e.g.* American Black Duck *Anas rubripes*), and are hypothesized to be primarily related to warmer winter temperatures in the north (Brook *et al.* 2007). If winter temperatures remain steady or increase, it is likely that these types of movement will become more common, making classification of swan sites in southeast Ontario and Pennsylvania as either wintering or autumn/spring migration sites difficult and perhaps of limited value for management. Furthermore, locations traditionally used for brief periods may in future be used for longer periods of time each year.

Traditional stop-over sites presumably provide suitable feeding and roosting habitat at appropriate locations along the migration route. Petrie *et al.* (2002) found that EP Tundra Swans in Ontario spent more time foraging for submerged aquatic vegetation (SAV) in autumn, whereas in spring they spent more time foraging in fields for waste grain. Seasonal use of particular sites may reflect both food availability and the type of food required by the birds. For instance, seasonal feeding patterns may be dictated by changes in the swans' nutritional needs at different stages of the annual cycle (migration, completion of feather moult, preparation for nesting) and also by the nutritional quality of the food being taken (SAVs having a high protein content whereas grain has high carbohydrate levels; Bortner 1985). Food preferences deduced from foraging time may be biased due to seasonal fluctuations in availability, however, and thus must be interpreted with caution (Petrie *et al.* 2002).

Although Tundra Swans were thought to be fairly sedentary during the summer and winter, substantial movement occurred within these seasons. Several marked swans used two different BCRs during either summer or winter. Use of multiple BCRs may help EP Tundra Swans meet different nutritional and habitat needs during the critical nesting, fledging and moulting periods (Baldassarre & Bolen 1994; Grant *et al.* 1994). Movement by satellite-tracked birds on the breeding grounds may be used to infer breeding outcomes (Petrie & Wilcox 2003; Reed *et al.* 2003). A relatively large southern summer movement early in the summer, often followed by a movement back to the north, suggested either a failed nesting attempt because an adult could not travel far with young so early in the season (Monda *et al.* 1994), or a bird that did not breed, because non-breeding females tend to moult earlier and thus can undertake long-distance moves earlier in the summer (Earnst 1994). On the other hand, a short, early autumn movement suggested a successful breeding female with fledged young (Monda *et al.* 1994). Most of these movements were to large river deltas, which suggested that those Bird Conservation Regions were important to recently fledged young preparing for autumn migration. Only one female did not use the same summer location each year; not surprisingly, this was the only female that was a young-of-the-year bird when it was marked, because Tundra Swans do not generally breed until they are 4–5 years old (Bart *et al.* 1991).

Five issues should be borne in mind regarding the satellite tracking data presented in this study. First, the presence of neck collars with transmitters may have altered the behaviour of the swans. For example, if neck collars interfered with tipping feeding behaviour, the swans may have needed more time to feed, particularly at the staging sites (Nolet *et al.* 2001). Second, some sites or BCRs used could have been missed, because there were time gaps of up to 2 weeks between satellite locations. Third, the proportion (not number) of the marked population that travelled through each location was approximate, because the size of the marked sample (number of swans with active transmitters) varied within seasons. Autumn and winter sites were more likely to be missed than spring and summer sites because of transmitter attrition over time. Fourth, because this study was focused on large-scale movements, the 'sites' identified in this study varied in size from 10–1,500 km^2. Finally, because analyses were from only 39 marked females, data from successive years were treated as independent for characterising BCR use and describing important sites. The data were analysed this way to provide the maximum amount of information from each bird but may overestimate the importance of BCRs and sites visited by the same bird in successive years. However, because Tundra Swans mate for life, movements of AHY females should be similar to movements of their male AHY mates (Hawkins 1986). Furthermore, EP Tundra Swans travel as family groups for at least the first spring migration, so movements of AHY females should also be similar to those of hatch-year (HY) birds (Limpert & Earnst 1994). These analyses of satellite data did not provide information about non-breeding AHY Tundra Swans, except for data from the one swan that was banded as a HY bird and did not spend consecutive summers in the same location.

The vast range covered by the EP Tundra Swans means that they do not all rely on one area or habitat type. This may help buffer the population from being negatively affected by changes in any one area. However, many places were identified that were utilised by a large proportion of the marked population. Key concentration points used by the species during migration, breeding and on the wintering grounds should continue to be enhanced through waterfowl management plans (Ad Hoc EP Tundra Swan Committee 2007) and habitat planning. Moreover, joint ventures such as the North American Waterfowl Management Plan (North American Waterfowl Management Plan 2004) are required to coordinate habitat management and conservation efforts.

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