# Variation in Body Composition and Digestive Organs of Tundra Swans during Migration at Long Point, Lake Erie, Ontario

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**Abstract.—**Tundra Swans (*Cygnus columbianus*) spend a substantial portion of their annual cycle at migratory staging areas. Despite the potential importance of staging areas to conservation of Eastern Population (EP) Tundra Swans, few data are available to assess life-history strategies of the species during migration. During 1999 and 2000, 48 adult Tundra Swans were collected during peak periods of spring and autumn migration at Long Point, Ontario, Canada, to establish baselines on nutrient reserve levels and morphology of digestive organs. Results were compared to nutrient reserve data for EP Tundra Swans collected at a major wintering area in North Carolina, USA. Lipid reserve levels did not differ between sexes nor varied with body size, but lipid reserves were approximately two times greater in autumn than spring. Males had greater protein reserves than females, and protein reserves were similar during autumn and spring. Although digestive organs were predicted to be longer and heavier during autumn, no seasonal variation in digestive organs was detected. Lipid reserve levels of Tundra Swans at Long Point during spring were similar to those recorded for wintering birds in North Carolina, suggesting that lipid reserves catabolized from autumn through winter were not replenished prior to arriving at this initial spring staging area. The results highlight the importance of managing quality aquatic and terrestrial foraging habitats at staging areas for conservation EP Tundra Swans. *Received 24 June 2011, accepted 14 September 2011.*

**Key words.—***Cygnus columbianus*, digestive organs, Great Lakes, migration, nutrient reserves, staging area, Tundra Swan.

Knowledge of nutrient reserve and gut morphology dynamics of large-bodied, long distance migrating waterfowl are derived primarily from studies of geese because data are limited for swans (Ankney *et al.* 1991; Limpert and Earnst 1994). Changes in body mass and composition, in addition to digestive organs of arctic-breeding geese throughout the annual cycle result from variations in quality and quantity of diet items, as well as energetic demands associated with thermoregulation, migration, egg production, parental care, and molt (Ankney and MacInnes 1978; Wypkema and Ankney 1979; McLandress and Raveling 1981; Gauthier *et al.* 1984; Craigie and Petrie 2003). Arctic-breeding geese may accumulate and store lipid and protein reserves during winter, migration, or breeding periods that can be mobilized to provision eggs or catabolized to provide energy for survival, migration, or reproductive activities (Ankney *et al.* 1991). Also, because females and males experience different energetic demands,

particularly during the breeding season, endogenous lipid and protein reserves can differ greatly between sexes (and age classes) during major periods of the annual cycle (Ankney and MacInnes 1978; Wypkema and Ankney 1979; Ankney *et al.* 1991).

Seasonal variations, and sex-related differences, in nutrient reserves and gut morphology are well documented in arctic-breeding geese, but similar studies in swans are few (Bortner 1985; Earnst 1992; Powell and Engelhardt 2000; Nolet *et al.* 2001; Nolet and Mooij 2002). Tundra Swans (*Cygnus columbianus*) are the most abundant native swan species in North America (Bart *et al.* 1991); however, nutrient reserve data are generally unavailable for breeding or migrating individuals (Limpert and Earnst 1994). Within-season variation in protein and lipid reserve levels, and digestive organs have only been determined for Eastern Population (EP) Tundra Swans at one major wintering site at Lake Mattamuskeet, North Carolina (Bortner 1985), which determined that swans arrived at wintering areas during

late-autumn with substantial lipid reserves. Lipid reserves were catabolized throughout winter, and swans initiated spring migration with much reduced lipid reserve levels (Bortner 1985). Protein reserves and digestive organ masses did not change throughout winter, but gizzard mass and small intestine and caecal lengths increased presumably from a seasonal increase in dietary fiber (Bortner 1985). Understanding spatial and temporal variation in body condition and digestive organ characteristics of EP Tundra Swans during the annual cycle provides insight into life-history strategies of these large-bodied migrant waterfowl as well as guidance to conservation planners charged with ensuring availability of quality habitat.

Migration is energy demanding for large-bodied animals, such as Tundra Swans, that travel long distances (Pennycuick *et al.* 1996). Further, if Tundra Swans have breeding strategies similar to other large-bodied, arctic-breeding waterfowl that primarily use endogenous reserves for egg development (i.e., capital breeding; Klaassen *et al.* 2001), then lipid stored during spring migration may influence reproductive output and growth of these populations (Bromley and Jarvis 1993; Alisauskas 2002; Glahder *et al.* 2006). Because of substantial energy and nutrient needs of migrating and breeding Tundra Swans, stopover sites may be vital for migration, survival, and possibly reproduction (Wypkema and Ankney 1979). During migration between wintering areas along the US Atlantic coast and breeding areas in northern Canada and Alaska, EP Tundra Swans use three major staging areas which are the lower Great Lakes (LGL) Region, Prairie Pothole Region (PPR), and western boreal forest (Limpert and Earnst 1994; Petrie and Wilcox 2003). Of the 52% of time that Tundra Swans spend each year at staging areas a substantial portion spent within the LGL region (Petrie and Wilcox 2003). The LGL region contains the final and initial stopover sites used by many Tundra Swans during autumn and spring migration, respectively. Also, the location of the LGL along the EP Tundra Swan migration route highlights the importance of this region for energy and nutrient acquisition and a need to establish baseline data on season- and sex-specific lipid and protein reserves at stopover sites, such as at Long Point, Lake Erie. Comparing spring and autumn body condition and digestive organ data for EP Tundra Swans collected at Long Point (first and last stopover sites, respectively) to those collected at a major wintering area provides a unique opportunity to hypothesize migration, survival, and reproductive strategies of this species.

The primary purpose of this study was to provide baseline data on nutrient reserves and digestive organ characteristics for migrant Tundra Swans staging at Long Point, Lake Erie, but comparisons were also made to similar data collected at areas where EP Tundra Swans winter. Objectives were to determine if there were season- or sex-related differences in lipid reserves, protein reserves, and size of digestive organs for adult swans staging at Long Point, Lake Erie during spring and autumn migration. After accounting for body size, detectable differences in lipid or protein reserves between females and males during spring or autumn were not expected because birds were collected in the autumn well after the breeding and brood rearing periods (i.e, females and males had ample time for recovery from earlier incurred nutrient reserve losses associated with the breeding season) and swans collected in spring likely were subject to similar energetic demands throughout winter and during migration to Long Point. At Long Point, Tundra Swans forage primarily in emergent marshes during autumn but reduced availability of aquatic vegetation in marshes during spring necessitates daily foraging flights to nearby agricultural areas where they eat waste corn (Petrie *et al.* 2002; Badzinski *et al.* 2006; Barney 2008). Because of suspected greater intake of dietary fiber in autumn, it was expected that caeca and intestine lengths might be longer and gizzard, intestine and caeca heavier in autumn-migrants (Buchsbaum *et al.* 1986).

METHODS

Field Methods

The study was conducted during the spring and autumn migration at Long Point, Lake Erie, Ontario, Canada (42°38'N 80°24'W). Long Point is a sand-spit extending 32 km east from the southern shore of Ontario and was created by shoreline erosion from the prevailing wind and water currents of Lake Erie. Open lacustrine bays and associated coastal wetlands of Long Point and nearby agricultural lands are among the most important staging areas for waterfowl in eastern North America, particularly for Tundra Swans in the LGL region (Petrie 1998). Concentrations of up to 30,000 Tundra Swans have been observed at this stopover site during migration (Petrie 1998). For a more detailed description of Long Point Bay and the associated marsh complexes see Petrie (1998).

Under the authority of a Canadian Wildlife Service Scientific-Capture Permit (No. CA 0048), 48 adult Tundra Swans were collected during spring 1999 (24-28 March: male [M] = 9, female [F] = 4), spring 2000 (6-11 March: M = 2, F = 6), autumn 1999 (15-30 November: M = 8, F = 6) and autumn 2000 (15-30 November: M = 8, F = 5) at Long Point. Tundra Swan abundance was monitored at Long Point and swans were collected during peak periods of migration in autumn and spring. Shotguns with non-toxic ammunition were used to collect swans from agricultural fields and coastal marsh habitats by jump and pass shooting. After collection, swans were transported to and frozen at Bird Studies Canada in Port Rowan, Ontario. At the end of each collection season, frozen swans were transported to the Avian Energetics Laboratory at the University of Western Ontario, London, Ontario.

Laboratory Methods

At the laboratory, each swan was thawed and four structural measurements were taken including: 1) culmen (±0.1 mm; length of the upper mandible from the tip of the bill to the base of the first central feathers on the head); 2) tarsus (±0.1 mm; length from the external notch of the right tibiotarsus bone to the outermost part of the tarso-metatarsal joint when the joint is fully bent); 3) upper tomia (±0.1 mm; length of the right cutting edge of the upper mandible); and 4) flattened wing (±1 mm; length of the right wing from the shoulder joint to the tip of the longest primary feather). After measurement, electric shears were used to remove contour and flight feathers. Plucked body mass was determined using a digital balance (±0.1 g).

Sex was determined by internal inspection of reproductive organs. The gizzard, small intestine, large intestine, in addition to left and right caecum were removed, while any associated lipids or connective tissues were returned to the body cavity. Lengths of the gizzard, large intestine, small intestine, right and left caecum were measured using digital calipers (± 0.1 mm; gizzard

only) or a meter stick (± 1 mm; all other organs). Wet masses of each organ were measured using a digital balance (± 0.1 g). Food, digesta, and feces were removed from the upper and lower digestive tract and each organ was reweighed to determine ingesta mass. Ingesta mass was subtracted from plucked body carcass mass to determine ingesta-free plucked carcass mass.

Body composition (total mass of water, protein, lipid, and ash) was determined as described by Afton and Ankney (1991). Ingesta-free plucked carcasses were chopped into small pieces with a hatchet and carcasses were ground three times in an industrial meat grinder to homogenize each swan. A 400-g sub-sample of the carcass homogenate was dried at 90°C to a constant mass (±1 g). Proportion of water in sub-samples was used to determine water content of ingesta-free plucked carcasses. Dry carcass mass was used for calculations of lipid, protein, and mineral content (g). Sub-samples of dried carcass homogenate were additionally ground in a coffee grinder to ensure homogenization. A sub-sample of approximately 10 g of dried carcass homogenate from each swan was used in lipid extraction. Sub-samples were placed into cellulose thimbles and immersed for 24 hours in petroleum ether contained within a modified Soxhlet apparatus. Following lipid extraction, thimbles were re-weighed to determine lean (lipid free) dry mass of each sample; the proportion of lipid in the sample was used to calculate total mass of carcass lipid from total dry carcass mass of each swan. Lean, dry sub-samples of homogenate was then placed into a porcelain crucible, weighed, and placed in a muffle furnace at 550°C for 12 hours, and reweighed following combustion. Mass of the remaining ash for each sub-sample was considered mineral content, whereas mass lost from combustion was considered protein. Proportions of protein and mineral in the sub-sample were then multiplied by total dry mass of each carcass to calculate the total protein and mineral mass for each swan.

Statistical Methods

Principal components analysis was performed on the correlation matrix for lengths of culmen, tarsus, upper tomia and flattened wing of females and males combined to derive principal component 1 scores used to index overall structural size of individual swans (Program R-prcomp; R Development Core Team 2005). First principal component scores were used in statistical models to account for variation in nutrient reserves and digestive organs attributable to body size.

General linear models were used to evaluate sources of variation in lipid and protein reserve levels, as well as in length and mass of digestive organs (Program R-lm). The initial model specified included body size (PC1: -3.4 to 3.2) as a covariate and categorical fixed main effects for Year (1999, 2000), Season (spring, autumn), Sex (female, male), plus Year × Season and Season × Sex interactions. F-statistics and Type III sums of square values were examined and used in backward-stepwise model reduction ($P \leq 0.05$) to determine final models. Residuals vs. fitted values, standardized residuals vs. the-

oretical quantiles, square-root of standardized residuals vs. fitted values, and standardized residuals vs. leverage were evaluated to verify that model assumptions were not violated and identify influential outliers. Inspection of residual plots suggested linear models were appropriate, and that there were no influential outliers within each response variable. Model parameter estimates ($\beta_i$) and mean values ± 1 SE are reported.

## Results

### Body Size Index

The first principal component (PC1; i.e., Body Size) accounted for 64% of the variation in structural measurements. The coefficients of variables in PC1 ranged from 0.46-0.56, indicating positive correlation among structural measurements.
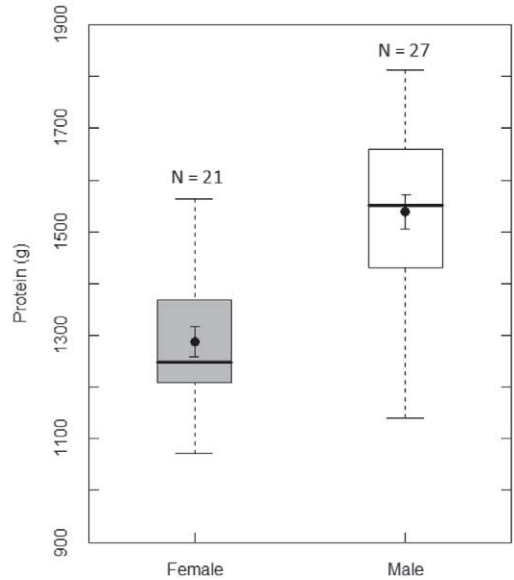
### Lipid and Protein Reserves

The final model explaining variation in protein reserves of adult Tundra Swans included a main effect for Sex and Body Size as a covariate ($R^2 = 0.61$, $F_{2, 45} = 37.18$, $P < 0.001$). Protein reserves ($\beta_0$ [intercept] = 1356.8 ± 30.5 g) varied positively with Body Size ($\beta_1 = 71.5 ± 13.7$ g; $F_{1, 45} = 27.17$, $P < 0.001$). On average, males had 128.7 ± 43.6 g more protein than females ($F_{1, 45} = 8.72$, $P = 0.005$; Fig. 1).

Variation in lipid reserves was best explained by the main effect for Season ($R^2 = 0.61$, $F_{1, 46} = 29.81$, $P < 0.001$). Autumn-staging Tundra Swans had lipid reserves that were, on average, slightly more than twice as great as those of spring-staging swans (autumn = 1304.7 ± 89.9 g; spring = 639.7 ± 75.5 g; Fig. 2).

### Digestive Organs

The final model that best accounted for variation in gizzard mass included the interaction between Year and Season, as well as the covariate Body Size ($R^2 = 0.17$, $F_{4, 43} = 3.42$, $P = 0.016$). Gizzard mass ($\beta_0 = 142.50 ± 6.49$ g) increased with increasing Body Size in adult Tundra Swans ($\beta_1 = 5.2 ± 2.3$ g; $F_{1, 43} = 5.1$, $P < 0.029$). Gizzard masses of adult Tundra Swans were least in autumn 1999 (141.7 ± 5.3 g) and spring 2000 (144.6 ± 10.0 g), intermedi-



Figure 1. Sex-specific protein reserves of adult Tundra Swans collected during autumn and spring at Long Point, Lake Erie, Ontario 1999 and 2000. Black points with solid error bars = mean values ± 1 SE, black horizontal lines = median values, boxes = first and third sample quantiles, dashed whiskers = sample range.

ate in spring 2000 (159.6 ± 8.6 g) and greatest in autumn 2000 (165.9 ± 6.3 g; Fig. 3).

The reduced models that best accounted for variation in total intestine (small + large) length ($R^2 = 0.15$, $F_{1, 46} = 9.50$, $P = 0.0034$), total intestine mass ($R^2 = 0.15$, $F_{1, 46} = 9.37$, $P = 0.004$) and mean caeca length ($R^2 = 0.13$, $F_{1, 46} = 8.30$, $P = 0.006$) only included the Body Size effect. Total intestine length ($\beta_0 = 2907.4 ± 40.2$ mm), total intestine mass ($\beta_0 = 67.0 ± 2.5$ g) and mean caeca length ($\beta_0 = 274.8 ± 5.9$ mm) varied positively with Body Size (intestine length: $\beta_1 = 78.6 ± 25.5$ mm; intestine mass: $\beta_1 = 4.9 ± 1.6$ g; caeca length: $\beta_1 = 10.8 ± 3.7$ mm). Mean caeca mass ($\beta_0 = 3.0 ± 0.1$ g) was not influenced by Body Size and did not differ between sexes or seasons (all $P > 0.05$).

## Discussion

Long Point, Lake Erie, is an important stopover site for EP Tundra Swans in eastern North America. The locale is one of the last stopover sites prior to their arrival at wintering areas and one of the first stopover sites used
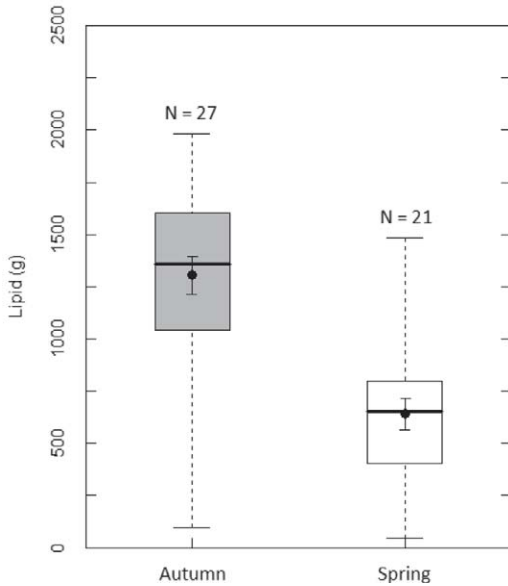
Figure 2. Lipid reserves of adult Tundra Swans collected during autumn and spring at Long Point, Lake Erie, Ontario 1999 and 2000. Black points with solid error bars = mean values ± 1 SE, black horizontal lines = median values, boxes = first and third sample quantiles, dashed whiskers = sample range.
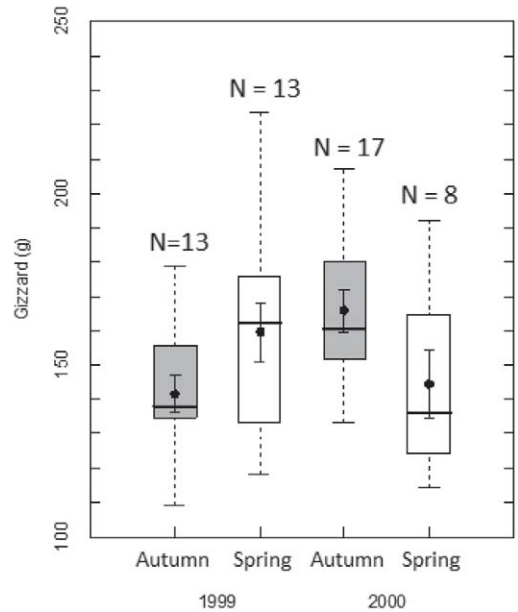


Figure 3. Gizzard masses of adult Tundra Swans collected during autumn and spring at Long Point, Lake Erie, Ontario 1999 and 2000. Black points with solid error bars = mean values ± 1 SE, black horizontal lines = median values, boxes = first and third sample quantiles, dashed whiskers = sample range.

during their spring migration. Adult Tundra Swans collected at Long Point during peak periods of migration had approximately two times greater lipid reserves during autumn as compared to spring. Average autumn lipid reserves of both females and males constituted 22% of their body mass (plucked, ingesta-free), whereas spring reserves were 12% of body mass. Autumn lipid reserve values at Long Point were only slightly greater than early winter values for adult male (1282 ± 83 g, 17% body mass) and adult female (969 ± 313 g, 15%) EP Tundra Swans at Lake Mattamuskeet, North Carolina, during 1983/84. Tundra Swans arrived at Lake Mattamuskeet with substantial lipid reserves, catabolized lipid throughout winter, and departed on spring migration with relatively less lipid compared to arrival (Bortner 1985). Notably, spring lipid values at Long Point were similar to late winter values for adult male (603 ± 313g, 11% body mass) and adult female (683 ± 25g, 13%) Tundra Swans wintering in North Carolina (Bortner 1985). Tundra Swans seem to have evolved

a life history strategy of arriving at southerly staging areas with greater lipid reserves in autumn, catabolizing lipid throughout winter for homeostasis and survival, and initiating spring migration with reduced lipid reserves.

Seasonal differences in lipid reserves of Tundra Swans at Long Point suggests that birds have greater stored energy available for use during autumn as compared to spring at this stopover site. Differences in food availability might partly explain this trend because submerged aquatic plants, especially carbohydrate-rich tubers and rhizomes, are more abundant in autumn than spring (Badzinski *et al.* 2006). However, during spring migration, energy-dense agricultural waste grains (primarily corn) are readily available in agricultural fields adjacent to emergent marshes at Long Point and are utilized during daylight hours by foraging swans (Petrie *et al.* 2002; Barney 2008). Despite readily available waste grains at Long Point, swans spend substantially less time staging at the LGL (27%) than the PPR (40%) during spring (Petrie and Wilcox 2003). Tundra Swans are

Arctic breeders that have a limited number of days to nest and fledge young (Bellrose 1980) and, thus, may migrate as close to breeding areas as soon as possible in spring, while also storing lipid reserves for breeding. Long Point and other spring staging areas likely represent an important network of stopovers where fuel for migration and nutrient reserves for breeding are acquired.

In Tundra Swans, accumulation of lipid throughout migration is influenced by flight costs associated with body size, distance between staging areas, and location of their Arctic breeding grounds (Klaassen *et al.* 2006). In addition, Arctic breeding waterfowl, like the Tundra Swan, primarily use endogenous reserves for egg development (capital breeding) versus nutrients from recently ingested sources (income breeding) (Klaassen *et al.* 2001). Arctic-breeding geese typically store lipids during spring migration, which influences reproductive output and growth of these populations (Bromley and Jarvis 1993; Alisauskas 2002; Glahder *et al.* 2006). In North America, lipid is accumulated by Arctic-breeding geese, and presumably Tundra Swans, by foraging at agricultural areas of the PPR (Alisauskas 2002; Petrie and Wilcox 2003). If Tundra Swans follow a reproductive strategy similar to geese then acquisition of additional endogenous lipid reserves likely come from staging areas north and west of the LGL. Thus, it is important to conserve and manage for quality staging areas where Tundra Swans are able to accumulate nutrients for migration and breeding.

Differences in lipid reserves were detected between seasons, but protein reserves did not differ between autumn and spring. Adult male Tundra Swans maintained protein reserves throughout winter whereas adult females experienced a slight increase from autumn (Bortner 1985). Less protein in females during autumn may be attributable to protein demands of ovulation (Lumsden 2002) and cost of parental care (Earnst and Bart 1991). Therefore, winter might be an important period for acquisition of protein by female Tundra Swans. Perhaps for Tundra Swans, maintaining muscles during winter is more important than maintaining

lipid reserves as they need flight muscles to fly long distances at optimal speed (Lindstrom and Piersma 1998). Either way, maintenance of protein reserves enables migratory flight and is necessary for egg formation in waterfowl (Baldassarre and Bolen 2006).

Tundra Swans staging at Long Point feed primarily on aquatic vegetation during autumn, but swans spend substantial time feeding on waste grains in nearby agricultural fields in spring because foods within emergent marshes is greatly reduced (Petrie *et al.* 2002; Petrie and Wilcox 2003; Badzinski *et al.* 2006). It was anticipated that an autumn diet of aquatic vegetation would result in greater mass and length of digestive organs because of greater dietary fiber (Buchsbaum *et al.* 1986). However, consistent seasonal patterns in masses or lengths of digestive organs were not detected even though adjustment in digestive organ morphology can be relatively rapid in birds (Starck 1999; Dekinga *et al.* 2001). Lengths of staging times of Tundra Swans collected at Long Point were unknown and, thus, timing of seasonal change to eating waste grain at Long Point from a combination of waste grain and vegetation consumed by Tundra Swans on wintering areas (Bellrose 1980; Froelich and Lodge 2001) may have confounded ability to detect seasonal change in gut morphology. Overall, relatively similar diets and dietary fiber from autumn (LGL) throughout winter (Atlantic coast) or slight differences in diets annually may have caused the patterns in masses and lengths of digestive organ that were recorded at Long Point.

Limited data on nutrient reserves in Tundra Swans throughout the annual cycle makes it difficult to determine accurately how changes in foraging habitat may influence these birds (Limpert and Earnst 1994). Further, this lack of information makes development of effective and efficient conservation strategies equally challenging (Serie *et al.* 2002). Additional research categorizing nutrient reserves, habitat use, and diets of Tundra Swans at staging areas in the PPR and western boreal forest is needed. Currently, results from this and other studies suggest that EP Tundra Swans gain the ma-

jority of their annual lipid reserves while on spring and autumn staging areas. Because EP Tundra Swans spend up to 52% of their life roosting and foraging at staging areas (Petrie and Wilcox 2003), conservation of these habitats is likely essential for reproduction and population growth by these birds.

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