Moult intensity and chronology of Tundra Swans during spring and fall migration at Long Point, Lake Erie, Ontario

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Abstract: Moult intensity and chronology in staging Eastern-Population (EP) Tundra Swans (*Cygnus columbianus columbianus*) were studied during spring in 1999 and 2000 ($n = 35$) and during fall in 1999, 2000, and 2001 ($n = 47$) at Long Point, Lake Erie, Ontario. To test for age, sex, and seasonal differences in moult intensity, 20 feather regions were scored according to the proportion of growing feathers. Adult, subadult, and juvenile Tundra Swans moulted contour feathers at low intensities during spring and fall. Males and females of all three age classes had similar patterns and intensities of moult during spring and fall. Shared costs of incubation and brood rearing, perennial monogamy, and lack of a breeding plumage could be some of the pressures selecting for intersexual similarities in feather replacement during migration. Adult, subadult, and juvenile Tundra Swans moulted more intensively during fall than spring. Larger lipid reserves and seasonal dietary differences may allow fall-staging Tundra Swans to moult more intensively than spring-staging birds at Long Point. Overlap of nutritionally costly events (moult and migration) may be necessary as Tundra Swans spend half of their annual cycle on spring and fall staging areas. However, reduced daily nutritional costs associated with moulting at low intensities and migrating slowly apparently permits the overlap of these two life-cycle events.

Résumé : Nous avons étudié l'intensité de la mue et la chronologie des regroupements de la population orientale (EP) du cygne siffleur (*Cygnus columbianus columbianus*) aux printemps 1999 et 2000 ($n = 35$) et aux automnes 1999, 2000 et 2001 ($n = 47$) à Long Point, lac Érié, Ontario. Pour vérifier les différences d'intensité de la mue selon l'âge, le sexe et la saison, nous avons attribué des points à 20 régions du plumage selon la proportion de plumes en croissance. Les cygnes siffleurs adultes, subadultes et jeunes subissent une mue de faible intensité de leur plumage de contour à l'automne et au printemps. Chez les mâles et les femelles des trois classes d'âge, les patterns et l'intensité de la mue sont semblables au printemps et à l'automne. Les coûts partagés de l'incubation et de l'élevage des oisillons, la monogamie permanente et l'absence de plumage de reproduction pourraient être des facteurs de pression sélective qui favorisent une similarité dans le remplacement des plumes durant la migration chez les deux sexes. Les adultes, les subadultes et les jeunes ont une mue plus importante à l'automne qu'au printemps. Des réserves lipidiques plus grandes et des différences saisonnières du régime alimentaire permettent peut-être aux cygnes d'avoir une mue plus importante sur leurs aires de regroupement l'automne que le printemps à Long Point. Le chevauchement de deux événements qui comportent des coûts alimentaires élevés (mue et migration) peut être inévitable, puisque les cygnes siffleurs passent plus de la moitié de leur cycle annuel sur les lieux de regroupement de printemps et d'automne. Cependant, les coûts alimentaires journaliers réduits, associés à une mue de faible intensité et à une migration lente, permettent, semble-t-il, le chevauchement de ces deux phases du cycle biologique.

[Traduit par la Rédaction]

Introduction

The pattern and process of moult has been described for several species of waterfowl, particularly certain species of the subfamily Anatinae, which replace body plumage twice per annual cycle (Billiard and Humphrey 1972; Young and Boag 1981; Lovvorn and Barzen 1988; Smith and Sheeley 1993). In contrast, little is known about the single annual feather replacement (prebasic moult) of species of the

subfamily Anserinae (geese, swans, whistling ducks) (but see Earnst 1992; Gates et al. 1993; Petrie 1998a, 1998b).

Annual cycles of many waterfowl have evolved to minimize overlap between events that increase nutrient metabolism. For instance, female White-faced Whistling Ducks (*Dendrocygna viduata*) and their mates virtually suspend moult during ovulation and incubation (Petrie 1998a). Also, Lesser Scaup (*Aythya affinis*) (Austin and Fredrickson 1986), Greater Scaup (*Aythya marila*) (Billiard and Humphrey 1972), and Northern Pintails (*Anas acuta*) (Smith and Sheeley 1993) moult body plumage at low intensities or suspend molt altogether during migration. Because Tundra Swans (*Cygnus columbianus columbianus*) moult contour feathers only once during the annual cycle, timing of feather replacement is less temporally constrained than for dichromatic species. However, Eastern-Population (EP) Tundra Swans spend 29% of the annual cycle on breeding areas and 52% on migratory areas (Petrie and Wilcox 2003). Therefore, owing primarily to temporal con-

Fig. 1. Geographic location of Long Point Bay, Lake Erie, Ontario.
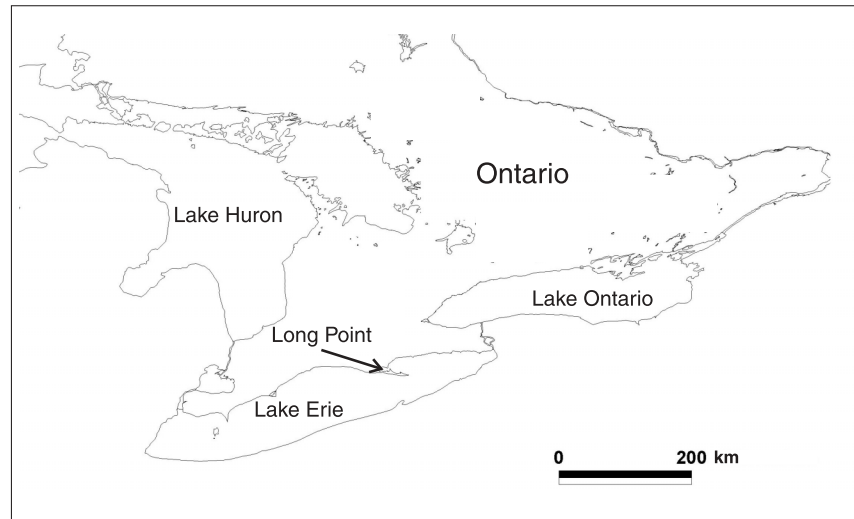
straints, we predicted that Tundra Swans would be incapable of completing feather replacement only during times that do not overlap with nutrient costly events, and as such, would overlap migration and prebasic moult.

Seasonally monogamous waterfowl species are sexually and seasonally dichromatic and display considerable sexual disparity in nutrient and temporal commitment to reproduction. These life-history strategies place temporal constraints on feather replacement (e.g., the need to moult into and out of breeding plumage) and have resulted in distinct sexual differences in moult intensity and chronology throughout the annual cycle (Billiard and Humphrey 1972; Miller 1986; Hohman and Crawford 1995). In contrast, Tundra Swans are perennially monogamous, sexually and seasonally monochromatic, and share incubation and brood-rearing costs (Limpert and Earnst 1994). Therefore, because Tundra Swans are monochromatic and also have less disparity in reproductive commitment than seasonally monogamous species, we predicted that migrating adult male and female EP Tundra Swans would have similar moult patterns and intensities.

Because moult increases nutrient metabolism and nutritional demands (Murphy and King 1984; Heitmeyer 1988), body condition can be an important factor in determining the intensity and chronology of moult for some species (Pehrsson 1987). For example, Mallards (*Anas platyrhynchos*) store nutrients prior to moult for supplementary energy and protein use during moult (Pehrsson 1987). Further, variation in moult intensity in Canada Geese (*Branta canadensis*) is associated with differences in carcass lipid (Gates et al. 1993). Tundra Swans are at their lowest annual body mass when they begin spring migration (Bortner 1985) and still have limited fat reserves upon arrival at Long Point (S.A. Petrie, unpublished data). In contrast, Tundra Swans are in much better condition when arriving at Long Point in fall (S.A. Petrie, unpublished data). Therefore, we further predicted that Tundra Swans would moult more intensively during fall migration through Long Point.

Study area

EP Tundra Swans were collected in aquatic and terrestrial habitats in the vicinity of Long Point, Ontario (80°30′E, 42°35′N to 80°03′E, 42°33′N) (Fig. 1). For a more detailed description of Long Point's habitats see Petrie (1998)[2] or Knapton and Petrie (1999). Long Point Bay and associated wetlands are an important spring and autumn staging area for Tundra Swans (Petrie et al. 2002). Long Point is the first major spring staging area for large numbers of Tundra Swans, many of which have just made a 1000-km migration from Chesapeake Bay (Petrie et al. 2002; Petrie and Wilcox 2003). Long Point is also the last major staging area for large numbers of Tundra Swans in fall (Petrie et al. 2002; Petrie and Wilcox 2003).

Methods

As part of a nutrient reserve dynamic and dietary intake study, 35 spring-staging Tundra Swans were collected throughout March 1999 and March 2000 and 47 fall-staging birds were collected from mid-October to mid-December in 1999, 2000, and 2002. Swans were collected by shotgun over decoys in agricultural fields, by jump and pass shooting in aquatic habitats, or were captured using rocket nets (Canadian Wildlife Service permit No. CA 0048). Each Tundra Swan was tagged with a unique identification code, and collection method, date, and site were recorded.

In the laboratory, all Tundra Swans were sexed and aged using plumage, bursa of fabricus, and internal reproductive organs. Intensity of feather replacement was determined by counting the number of blood quills in 20 feather regions: crown, face, chin-throat, neck, upper back, scapulars, lower back, rump, upper tail coverts, retrices, under tail coverts, belly, centre chest, side chest, side flank, primaries, secondaries, tertials, and wing coverts (Petrie 1998*a*). Each feather region was subject to three grab samples, and moult intensity was determined by comparing the number of blood

Table 1. Combined mean (±SE) feather mass (g) for each of 20 feather regions from three Tundra Swans, *Cygnus columbianus columbianus*, collected during spring (adult male, adult female) and fall (subadult male) migration in 2000 at Long Point, Lake Erie, Ontario.

Feather tract	Total feather mass (g)
Crown	1.7 (0.2)
Face	1.9 (0.2)
Chin/throat	1.0 (0.1)
Neck	56.1 (11.3)
Upper back	15.8 (6.7)
Scapulars	40.4 (10.6)
Lower back	10.6 (2.0)
Rump	7.9 (1.7)
Upper tail coverts	6.9 (1.0)
Retrices	8.4 (1.8)
Lower tail coverts	9.6 (1.6)
Belly	37.2 (5.1)
Centre chest	26.0 (2.2)
Side chest	31.8 (5.7)
Side	26.3 (6.7)
Flank	7.0 (1.9)
Primaries	38.9 (7.2)
Secondaries	13.3 (2.8)
Tertial	18.3 (6.6)
Wing coverts	78.7 (15.1)

Fig. 2. Adjusted mean moult intensity (percent mean ± SE of three grab samples and range) of 20 feather regions from adult male, adult female, subadult, and juvenile Tundra Swans, *Cygnus columbianus columbianus*, collected during spring in 1999 and 2000 (shaded rectangles) and during fall in 1999, 2000, and 2001 (open rectangles) at Long Point, Lake Erie, Ontario.

quills to the number of completely molted feathers in each of the three samples and then converting each to a percentage. Mean (±SE) percentage of moult intensity for the three grab samples were calculated for each feather region. Mean moult intensity (MMI) for each bird was the mean of all 20 feather-region intensities (maximum value = 100%).

Because of the differential size of feather regions, MMI was weighted by the proportional mass of the contributing feather regions. For example, a moult intensity of 10% in the belly region (higher total feather mass) constitutes considerably more moulting feathers than did a similar intensity in the crown region (lower total feather mass). Therefore, to determine the proportion that each region contributed to total feather mass, all feathers from each feather region were plucked and weighed (±0.01 g) for three swans (adult male, adult female, subadult male) (Table 1). Proportional feather mass for each region was obtained by summing the feather mass of all 20 feather regions, calculating the proportional weight of each feather region, and determining the mean proportional feather mass for all regions from the three swans. Region-specific moult intensity scores for each bird were then multiplied by that region's proportional feather mass and summed to provide the adjusted mean moult intensity (AMMI).

Kruskal–Wallis rank-sum tests were used to test for differences in sex, season, and age classes for AMMI, and moult intensity score within each of the 20 feather regions within and between collection periods (Conover 1980; Petrie 1998*a*); Mann–Whitney *U* tests were subsequently used for post-hoc
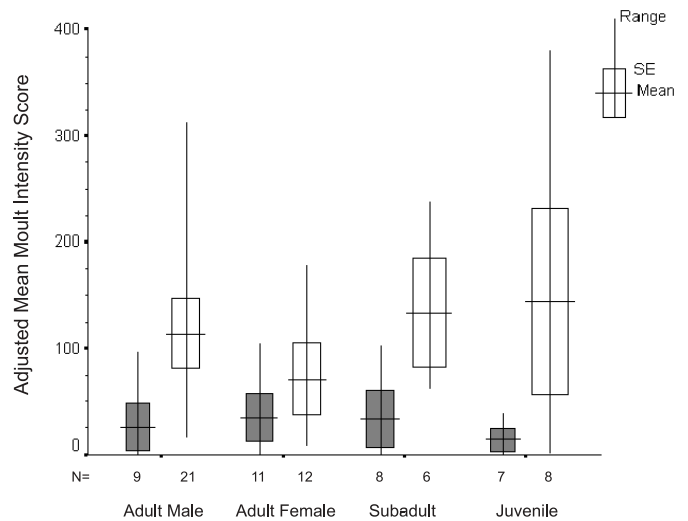
comparisons of mean scores. Significance levels for all tests and comparisons were $P < 0.05$.

Because preliminary analyses showed no sexual differences for subadults (spring: $n = 3$ females, 5 males; fall: $n = 4$ females, 2 males) and juveniles (spring: $n = 3$ females, 4 males; fall: $n = 4$ females, 4 males) during spring or fall, sexes were pooled for further analysis. One-way ANOVA and Tukey's HSD multiple comparisons tests were used to test for seasonal, sexual, and age-related differences in total number of actively moulting feather regions (Wilkinson 1988).

Results

Spring moult

Adult male and female Tundra Swans had similar AMMI during spring migration ($P = 0.31$) (Fig. 2). Females had higher moult intensity scores than did males in most feather regions, but results did not differ significantly for any region ($P > 0.05$ for all comparisons) (Table 2). Males moulted most intensively in the scapular and upper tail regions, but females moulted most intensively in the scapulars and retrices. Whereas males ($n = 9$) showed signs of moult in only 7 of 20 (mean = 1.13, SE = 0.7) feather regions, females ($n = 11$) showed signs of moult in 15 of 20 (mean = 3.91, SE = 1.3) regions ($P = 0.03$).

Subadult and juvenile Tundra Swans had similar AMMI ($P = 0.57$) during spring migration (Fig. 2). AMMI of subadults and juveniles also did not differ from adult males or females ($P > 0.05$). Subadults moulted more intensively than juveniles in most feather regions, but results did not differ significantly for any region ($P > 0.05$) (Table 2). Subadults moulted most intensively in the scapular region, whereas juveniles showed little signs of moult in any of the feather regions. Whereas subadults ($n = 8$) showed signs of

Table 2. Mean (±SE) percentage of moult intensity of 20 feather regions from Tundra Swans collected during spring migration in 1999 and 2000 at Long Point, Lake Erie, Ontario.

Feather tract	Adult male (*n* = 9)	Adult female (*n* = 11)	Subadult* (*n* = 8)	Juvenile* (*n* = 7)
Crown	0.0	2.6 (1.5)	0.0	0.0
Face	0.0	2.0 (1.0)	1.2 (1.2)	0.0
Chin/throat	0.0	4.4 (1.6)	2.8 (2.8)	0.0
Neck	0.0	1.8 (1.4)	0.0	0.0
Upper back	1.7 (1.7)	4.5 (2.7)	1.2 (0.8)	2.7 (1.7)
Scapulars	6.1 (4.1)	5.2 (2.3)	8.7 (4.3)	0.0
Lower back	0.0	1.0 (0.8)	0.0	0.0
Rump	0.7 (0.7)	1.4 (0.8)	0.0	0.0
Upper tail coverts	4.2 (3.1)	0.6 (0.6)	1.6 (1.6)	2.8 (2.8)
Retrices	1.4 (1.4)	2.4 (1.5)	4.2 (4.2)	0.0
Lower tail coverts	0.8 (0.8)	0.0	2.9 (2.1)	2.8 (2.8)
Belly	0.0	1.2 (1.2)	0.0	0.0
Centre chest	0.0	0.6 (0.6)	1.2 (1.2)	0.0
Side chest	0.0	0.0	2.6 (1.5)	0.0
Side	0.7 (0.7)	5.2 (2.2)	4.5 (4.5)	0.7 (0.7)
Flank	0.0	0.4 (0.4)	2.8 (1.9)	0.8 (0.8)
Primaries	0.0	0.0	0.0	0.0
Secondaries	0.0	0.0	0.0	0.0
Tertial	0.0	1.5 (1.5)	0.0	0.0
Wing coverts	0.0	0.0	0.0	0.0
Combined percentage (*n* = 20)	0.78 (0.4)	1.74 (0.6)	1.69 (0.7)	0.49 (0.2)

*Both sexes combined.

moult in 11 of 20 (mean = 2.38, SE = 1.0) feather regions, juveniles (*n* = 7) showed signs of moult in 5 of 20 (mean = 1.0, SE = 0.4) regions (*P* > 0.05). With exception of light tertial moult in one adult female, no adult, subadult or juvenile birds were moulting in any wing-feather regions (primaries, secondaries, tertial, wing coverts) during spring (Table 2).

Fall moult

Adult male Tundra Swans had slightly higher AMMI (*P* = 0.05) than females during fall (Fig. 2). Males moulted more intensively than females in 14 of 17 actively moulting feather regions, although differences were significant only for the chin–throat region (*P* = 0.02) (Table 3). Males moulted most intensively in the retrices, upper and lower tail coverts, side, and neck regions, whereas females moulted most intensively in the lower tail coverts, side, and crown regions. Adult males (*n* = 21) showed signs of moult in 17 of 20 (mean = 7.77, SE = 0.7) feather regions and adult females (*n* = 12) showed signs of moult in 16 of 20 (mean = 5.42, SE = 1.0) regions (*P* = 0.07).

Subadult and juvenile Tundra Swans had similar AMMI (*P* = 0.53) during fall (Fig. 2). AMMI of subadults and juveniles also did not differ from that of adult males or females (*P* > 0.05). Subadults moulted more intensively than juveniles in the crown (*P* = 0.04) and lower tail coverts (*P* = 0.01). Although moult was most intense for subadults in the upper and lower tail coverts, juveniles showed no sign of lower tail covert-feather replacement (Table 3). Juveniles moulted most intensively in the neck and side regions during fall (Table 3). Subadults (*n* = 6) showed signs of moult in 16 of 20 (mean = 9.5, SE = 1.3) feather regions and juveniles (*n* = 8) showed signs of moult in 15 of 20 (mean = 6.9, SE =

1.0) regions (*P* = 0.23). Number of actively moulting feather regions also did not differ from adult males or females during fall (*P* > 0.05). With the exception of light tertial moult in one adult male and one adult female, birds did not moult in any wing-feather regions during fall.

Seasonal comparisons

Adult male Tundra Swans had higher AMMI (*P* = 0.002) and moulted more intensively in 16 of 17 actively moulting feather regions during fall than they did during spring (Fig. 2, Tables 2 and 3); results were significant for 7 of 17 feather regions (*P* < 0.05). Adult females had similar AMMI (*P* = 0.10) during spring and fall (Fig. 2). Moult intensity in adult females appeared higher in 12 of 17 feather regions in spring; however, seasonal differences were significant only for crown and lower tail coverts (*P* < 0.05).

Although subadult AMMI did not differ significantly between seasons (*P* = 0.07) (Fig. 2), subadults moulted more intensively in 15 of 16 actively moulting feather regions during fall; results were significant for 7 of 16 regions (*P* < 0.05). Juveniles had higher AMMI (*P* = 0.03) during fall than during spring (Fig. 2) and moulted more intensively in 15 of 16 actively moulting feather regions; results were significant for 5 of 16 feather regions (*P* < 0.05).

Discussion

Moult intensity and duration

Generally, contour-feather moult and long-distance avian migration are mutually exclusive events (Palmer 1972). Despite the fact that Tundra Swans replace contour feathers only once per annual cycle, we found that adults, subadults,

Table 3. Mean (±SE) percentage of moult intensity of 20 feather regions from Tundra Swans collected during fall migration in 1999, 2000, and 2001 at Long Point, Lake Erie, Ontario.

Feather tract	Adult male (n = 21)	Adult female (n = 12)	Subadult* (n = 6)	Juvenile* (n = 8)
Crown	6.3 (1.2)	8.5 (2.0)	12.9 (2.6)	6.1 (1.2)
Face	5.2 (1.1)	3.7 (1.3)	7.4 (2.4)	5.4 (2.5)
Chin/throat	5.2 (1.7)	1.1 (0.7)	7.3 (2.9)	5.6 (2.0)
Neck	9.1 (2.4)	4.4 (1.3)	7.6 (5.1)	20.2 (5.2)
Upper back	3.6 (1.5)	8.0 (4.8)	3.5 (2.9)	5.7 (3.6)
Scapulars	5.4 (1.7)	5.0 (2.2)	3.7 (3.7)	6.2 (3.8)
Lower back	1.4 (0.7)	1.2 (0.8)	6.9 (4.0)	1.6 (1.6)
Rump	8.3 (2.5)	3.9 (2.6)	9.3 (3.7)	3.7 (3.7)
Upper tail coverts	13.0 (3.4)	4.8 (2.7)	19.1 (8.4)	12.7 (4.9)
Retrices	20.8 (5.2)	7.9 (3.6)	4.6 (3.0)	7.0 (5.6)
Lower tail coverts	13.2 (3.4)	10.7 (4.1)	23.1 (9.4)	0.0
Belly	1.4 (1.0)	0.3 (0.3)	0.7 (0.7)	4.8 (4.8)
Centre chest	0.8 (0.5)	0	2.1 (2.1)	15.1 (9.0)
Side chest	5.4 (2.2)	1.0 (0.7)	6.2 (6.1)	7.2 (5.7)
Side	10.0 (2.3)	8.4 (3.2)	15.9 (8.2)	16.6 (5.8)
Flank	3.7(1.7)	3.1 (2.0)	3.9 (2.8)	14.2 (9.7)
Primaries	0.0	0.0	0.0	0.0
Secondaries	0.0	0.0	0.0	0.0
Tertial	0.6 (0.6)	1.0 (1.0)	0.0	0.0
Wing coverts	0.0	0.0	0.0	0.0
Combined percentage (n = 20)	5.67 (0.8)	3.65 (0.9)	6.71 (1.3)	6.61 (2.0)

*Both sexes combined.

and juveniles moulted contour feathers during spring and fall migration through Long Point, albeit at very low intensities during spring. Intense feather replacement can impose high protein demands, necessitating an omnivorous or carnivorous diet in some species (Heitmeyer 1988). For instance, female Mallards can complete prebasic moult in 6–7 weeks, but daily and total protein costs can be substantial (Heitmeyer 1987). Tundra Swans may be incapable of rapid (intense) feather replacement due to the low protein content of their diet; their diet is either completely herbivorous or consists of small quantities of animal matter (Limpert and Earnst 1994). Therefore, because Tundra Swans spend 52% of their annual cycle on staging areas and 29% on breeding areas (Petrie and Wilcox 2003), there is likely insufficient time to complete contour-feather moult apart from times that are nutritionally costly, such as migration. However, we suggest that Tundra Swans are able to overlap moult and migration, owing to reduced daily nutritional requirements associated with the temporal extension of both these processes. Similarly, Canada Geese extend moult over 5–6 months and moult at low intensities during migration (Gates et al. 1993).

Limpert and Earnst (1994) suggested that adult Tundra Swans complete contour-feather moult between July and December and that juveniles complete moult between October and March, after juvenile moult is complete. Although adult, subadult, and juvenile Tundra Swans migrating through Long Point during fall were replacing contour feathers, they also showed signs of low-intensity feather replacement during spring. This low-intensity spring moult may be the continuation of the prebasic moult (see Petrie 1998b) or simply the replacement of lost feathers.

Sexual and seasonal differences

Adult male and female Tundra Swans had similar moult patterns and intensities during both spring and fall migration. Life-history strategies of adult Tundra Swans differ from Aythini and Anatini in that they have reduced sexual disparity in reproductive commitment and are sexually and seasonally monochromatic. These strategies impose relatively similar nutrient and temporal constraints on male and female Tundra Swans, which have possibly selected for similar moult patterns, at least during migration. Sexual differences in moult intensity could occur on breeding grounds (see Petrie 1998a), but because Tundra Swans were collected well before (early spring) and well after (late fall) breeding periods, we could not test this.

Adult, subadult, and juvenile Tundra Swans moulted more intensively when staging at Long Point during fall than they did during spring. Tundra Swans depart the Atlantic coast wintering areas at their lowest annual body mass (Bortner 1985) and have limited lipid reserves when staging at Long Point during early-spring migration (S.A. Petrie, unpublished data). In contrast, Tundra Swans arriving at Long Point during fall migration have large lipid reserves (S.A. Petrie, unpublished data), and therefore may be nutritionally capable of moulting more intensively during that time. This is consistent with the conclusion that the rate and intensity of moult in Canada Geese are determined primarily by the amount of energy the birds are able to allocate to feather synthesis (Gates et al. 1993).

Protein synthesis during avian moult is met, in part, through dietary intake (Hohman et al. 1992). Tundra Swans spent increased time foraging for submerged aquatic vegetation during fall relative to spring (Petrie et al. 2002; S.S.

Badzinski, unpublished data). Petrie at al. (2002) suggested that fall foraging, winter senescence, and ice cover can limit the availability of submerged aquatic vegetation for Tundra Swans during spring relative to fall. Also, spring-staging Tundra Swans at Long Point have between 2400 km (western shores of Hudson Bay) and 3500 km (Mackenzie River Delta) left to migrate to breeding grounds, whereas fall-staging birds are only 1000 km (Chesapeake Bay) from wintering areas (Petrie and Wilcox 2003). We suggest that increased time spent foraging for submerged aquatic vegetation and reduced demands for nutrient storage during fall enable Tundra Swans to moult contour feathers more intensively during that time.

Acknowledgments

References

Austin, J.E., and Fredrickson, L.H. 1986. Moult of female Lesser Scaup immediately following breeding. Auk, **103**: 293–298.

Billiard, R.S., and Humphrey, P.S. 1972. Molts and plumages in Greater Scaup. J. Wildl. Manag. **36**: 765–774.

Bortner, J.B. 1985. Bioenergetics of wintering Tundra Swans in the Mattamuskeet region of North Carolina. M.Sc. thesis, University of Maryland, College Park.

Conover, W.J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley and Sons, New York.

Earnst, S.L. 1992. The timing of wing molt in Tundra Swans: energetic and non-energetic constraints. Condor, **94**: 847–856.

Gates, R.J., Caithamer, D.F., Tacha, T.C., and Paine, C.R. 1993. The annual molt cycle of *Branta canadensis interior* in relation to nutrient reserve dynamics. Condor, **95**: 680–693.

Heitmeyer, M.E. 1987. The prebasic moult and basic plumage of female mallards (*Anas platyrhynchos*). Can. J. Zool. **65**: 2248–2261.

Heitmeyer, M.E. 1988. Protein costs of the prebasic moult of female mallards. Condor, **90**: 263–266.

Hohman, W.L., and Crawford, R.D. 1995. Molt in the annual cycle of ring-necked ducks. Condor, **97**: 473–483.

Hohman, W.L., Ankney, C.D., and Gordon, D.H. 1992. Ecology and management of postbreeding waterfowl. *In* The ecology and management of breeding waterfowl. *Edited by* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu. University of Minnesota Press, Minneapolis. pp. 128–189.

Knapton, R.W., and Petrie, S.A. 1999. Changes in distribution and abundance of submerged macrophytes in Long Point's Inner Bay, Lake Erie: implications for foraging waterfowl. J. Gt. Lakes Res. **25**: 783–798.

Limpert, R.J., and Earnst, S.L. 1994. Tundra Swan (*Cygnus columbianus*). *In* The birds of North America, No. 89. *Edited by* A. Poole and F. Gills. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Lovvorn, J.R., and Barzen, J.A. 1988. Moult in the annual cycle of Canvasbacks. Auk, **105**: 543–552.

Miller, M.R. 1986. Moult chronology of Northern Pintails in California. J. Wildl. Manag. **50**: 57–64.

Murphy, M.E., and King, J.R. 1984. Sulphur amino acid nutrition during moult in the White-crowned Sparrow. 1. Does dietary sulphur amino acid concentration affect the energetics of moult as assayed by metabolizable energy? Condor, **86**: 314–323.

Palmer, R.S. 1972. Patterns of moulting. *In* Avian biology. Vol. 2. *Edited by* D.S. Farner, J.R. King, and K.C. Parkes. Academic Press, New York. pp. 65–102.

Pehrsson, O. 1987. Effects of body condition on molting in mallards. Condor, **89**: 329–339.

Petrie, S.A. 1998*a*. Intensity and chronology of breeding and post-breeding moult in White-faced Whistling-Ducks (*Dendrocygna viduata*). Wildfowl, **49**: 207–218.

Petrie, S.A. 1998*b*. Moult patterns of non-breeding White-faced Whistling-Ducks in South Africa. Auk, **115**: 774–780.

Petrie, S.A., and Wilcox, K.L. 2003. Migration chronology of Eastern Population Tundra Swans. Can. J. Zool. **81**: 861–870.

Petrie, S.A., Badzinski, S.S., and Wilcox, K.L. 2002. Population trends and habitat use of Tundra Swans staging at Long Point, Lake Erie. Waterbirds, **25**: 143–149.

Smith, L.M., and Sheeley, D.G. 1993. Molt patterns of wintering Northern Pintails in southern high plains. J. Wildl. Manag. **57**: 229–238.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill.

Young, D.A., and Boag, D.A. 1981. A description of moult in male mallards. Can. J. Zool. **59**: 252–259.