

THE TIMING OF WING MOLT IN TUNDRA SWANS: ENERGETIC AND NON-ENERGETIC CONSTRAINTS¹

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Abstract. Date of wing molt initiation, based on the regression of tenth primary length on capture date, was calculated for breeding and nonbreeding Tundra Swans (*Cygnus columbianus columbianus*) on the Colville River Delta, Alaska. Breeding females initiated wing molt significantly later than breeding males and nonbreeding males and females; the molt of breeding females was correlated with the date on which their eggs hatched. Breeding males did not differ significantly from nonbreeding males and females in the date of molt initiation. Timing of molt in breeding males and females was consistent with the views that females delay molt while replenishing energy spent on reproduction, but was also consistent with the breeding pair's need for primaries to defend territories and to defend and brood young. Other results, including an increase in an index of female body condition throughout most of the molt period, and a positive correlation between clutch size and female hatch-to-molt interval, were not predicted by the hypothesis that past energy expenditures constrain the timing of molt. Patterns of wing molt within and among other Northern Hemisphere geese and swans are also difficult to explain on the basis of energetics alone. For example, breeding females initiate molt before breeding males in many species. Also, there is extreme asynchrony between mates in two swan species; one of those species also exhibits variation in which sex initiates wing molt first. Both patterns suggest that asynchrony, per se, is important, probably to facilitate brood protection or territory defense. In Tundra Swans and other northern breeding geese and swans, the non-energetic demands of territory defense, brood defense, and brooding are probably important constraints on the timing of wing molt.

Key words: *Tundra Swans; Cygnus columbianus columbianus; wing molt; energetics; brood protection; territory defense.*

INTRODUCTION

The timing of wing and body molt in the annual cycle of birds is typically discussed in relation to energetic costs of molt and other annual events (e.g., Payne 1972, King 1980, Walsberg 1983, Lovvorn and Barzen 1988). The degree to which non-energetic constraints influence the timing of molt has rarely been addressed, even though the importance of energetic constraints has been questioned. For example, several studies have concluded that the requirements of feather synthesis can be met without depletion of protein reserves (Newton 1968, Murphy and King 1984, Austin and Fredrickson 1987, Heitmeyer 1988), or without mass loss, or depletion of protein and fat reserves (Morton and Welton 1973; Ankey 1979, 1984; but see Austin and Fredrickson 1987; Heitmeyer 1988). In addition, an overlap between molt and other energetically demanding annual events has been observed in many species (e.g., Lovvorn and Barzen 1988 and references

therein). Although neither type of study conclusively precludes energetic constraints as one of several selective forces acting on the timing of molt, they do suggest that non-energetic constraints should be investigated (see also King and Murphy 1985).

The following patterns in the timing of wing molt, which have been well-documented in species that exhibit sequential wing molt (i.e., molt in which only a few feathers are missing at once and individuals typically do not become flightless), have usually been interpreted as evidence that the energetic demands of breeding constrain the timing of molt: (1) Successful breeders suspend molt, initiate molt later, or molt fewer feathers at once than do other individuals (e.g., Newton and Marquiss 1982, Furness 1988), (2) Breeding females initiate molt later than breeding males (e.g., Emslie et al. 1990, Morton and Morton 1990), (3) Parents with later hatching broods initiate molt later (e.g., Bensch et al. 1985), and (4) Parents with larger broods initiate molt later or molt fewer feathers at once (e.g., Pietiäinen et al. 1984).

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Similar patterns, suggesting the importance of energetics in the timing of wing molt, occur in many of the simultaneously molting waterfowl. In many Northern Hemisphere geese and swans, breeders initiate molt later than nonbreeders (geese: Cramp and Simmons 1977, Bellrose 1980; swans: Hansen et al. 1971, Kear 1972, Wood and Gelston 1972, Beekman 1991, this study). Second, breeding females initiate molt later than breeding males in some Trumpeter Swan pairs (*Cygnus buccinator*, see DISCUSSION) and in Tundra Swans (*C. columbianus columbianus*, this study). Third, differences in the timing of molt among breeding pairs appear to be correlated with the timing of hatch in at least four species (Barry 1962, 1966; Hansen et al. 1971; Bellrose 1980; Lessels 1986). Fourth, Canada Goose (*Branta canadensis*) parents with experimentally enlarged broods tend to initiate molt later than other parents (Lessels 1986).

Likewise, in dabbling ducks, breeding males (which do not participate in incubation or brood-rearing) migrate to molting grounds with nonbreeders and initiate molt about a month earlier than their mates. Breeding females postpone molt until broods are near independence (Bellrose 1980).

The inability to fly during simultaneous wing molt has obvious and substantial non-energetic costs. For example, Kear (1972) and Owen and Ogilvie (1979) suggested that the timing of wing molt in breeding Mute Swans (*C. olor*) and Barnacle Geese (*B. leucopsis*) is influenced by the need for primaries when protecting young broods from predators. Non-energetic costs suggest alternative explanations for the patterns discussed in the preceding paragraphs but have received little attention in the literature.

This study describes the timing of wing molt in breeding Tundra Swans in relation to the timing of reproduction and the timing of molt in nonbreeders. The results of this study and comparisons among other Northern Hemisphere geese and swans are used to evaluate the importance of energetic and non-energetic constraints on the timing of molt.

METHODS

STUDY SITE

As part of a five-year study on Tundra Swan behavioral ecology, Tundra Swans were captured and banded during the summers of 1988–1990

on the Colville River Delta, Alaska (70°N, 151°W). The 500-km² Delta supports the highest density of breeding Tundra Swans on the North Slope of Alaska (Welling and Sladen, unpubl. manuscript) and is characterized by numerous large lakes and small polygonal ponds on which the swans feed. The delta is braided by river channels, facilitating boat access to the lakes where swans seek refuge when disturbed.

SWAN CAPTURE AND MEASUREMENTS

Flightless Tundra Swans were captured from an inflatable boat with a long-handled dip net (1 m diameter). Families were captured as a group and released together. Most nonbreeders were captured in flocks of 3 to 23 birds. Breeders were defined as those pairs having cygnets at the time of capture; failed breeders were not distinguishable from nonbreeders. The proportion of “nonbreeders” that were actually breeders that had failed between clutch completion and time of capture was roughly 9% (18% of breeding attempts failed, unpubl. data, and the ratio of attempted breeders to nonbreeders was 0.52, Bart et al. 1991).

Each swan was weighed to the nearest 0.05 kg and sexed by cloacal examination. Dial calipers were used to measure length of the tenth primary, middle toe, tarsus, culmen, gape, and anterior end of the nares to tip of bill. Birds with gray feathers on the neck and head were classified as subadults (i.e., one year old); birds with all white necks and heads were classified as adults (Evans and Kear 1978, Limpert et al. 1987). Only data from adults were used in the following analyses. Each adult and subadult was fitted with individually coded plastic neck and tarsus bands and an aluminum U.S. Fish and Wildlife Service tarsus band.

A body condition index, which removed the effect of structural size from mass, was calculated for breeders and nonbreeders of each sex. Toe length was chosen because, of the five structural measurements recorded, it had the highest correlation with mass in this study ($r = 0.65$) and on the wintering grounds ($r = 0.64$; Limpert, unpubl. data), it had the highest average correlation with the other measurements of structural size ($r = 0.56$), and it was reliably measured. The body condition index for a given bird was defined as its mass minus its expected mass calculated from the regression of mass on toe length. This index provides an intuitive measure of the non-

structural component of body mass (i.e., total mass minus mass due to structural size). Separate regressions were used for breeders and nonbreeders of each sex. I compared results based on the index calculated above to those based on three other indices (mass divided by toe length; mass divided by gape length; and mass). Results based on the four indices were very similar; exceptions are noted in the relevant tables and figures.

DATE OF HATCH AND CLUTCH SIZE

The date of hatch of individual nests was estimated by frequent visits to lookouts near nests. Cygnets may be brooded on the nest during hatching and for several hours thereafter in poor weather; however, brooding shortly after hatch could be distinguished from incubation by the presence of both parents on or near the nest mound. Only those nests for which hatch date was known within ± 4 days were used in analyses concerning hatch date. Clutch size was determined during a single visit to each nest during the last two weeks before hatch.

STATISTICAL ANALYSIS

The slope of the linear regression of tenth primary length on capture date was used to estimate the average growth rate of the tenth primary. The average growth rate (based on all birds) and each bird's primary length at capture were then used to estimate the date on which each individual initiated molt.

The use of linear regression to estimate molt duration is often complicated by nonhomogeneity of variance (Pimm 1976, Underhill and Zucchini 1988). The nonhomogeneity is caused by a lower variance early and late in the molt period when many birds have either not begun, or have finished, molt. By restricting capture effort primarily to that period when all birds were flightless, I minimized the problem of nonhomogeneity. Furthermore, the purpose of my analyses was to detect differences in molt initiation among categories of swans, not to estimate the duration of molt. Because I used a common slope to estimate molt initiation (no differences in slope among categories of swans were detected, see RESULTS), presumably any bias in the slope would equally affect estimates of molt initiation for all categories of swans and thus not affect the differences among molt initiation dates.

Multiple or simple linear regressions, with categorical variables coded as indicator variables,

were used in most analyses. Student's *t*-tests and *F*-tests were used to compare 2 and >2 means, respectively. Standard errors (SE) accompany means and standard deviations (SD) accompany regression coefficients throughout the text and figures. Clutch size and hatch date were not known for all breeding pairs, thus sample size varied among analyses. There was no evidence that year affected date of molt initiation, hatch-to-molt interval, or body condition index within any category of sex and breeding status, therefore data were pooled across years. Of the 10 comparisons necessary to test for a year effect, one was marginally significant ($P = 0.05$); all other *P*-values exceeded 0.3.

RESULTS

EFFECT OF BREEDING STATUS AND SEX

Capture date, sex, and breeding status (nonbreeding vs. breeding) were significant predictors of primary length at capture (Fig. 1, Table 1). The positive coefficients for sex and breeding status indicate that, given a particular capture date, males had significantly longer primaries than females, and nonbreeders had significantly longer primaries than breeders.

The "Breeding Status \times Date" and "Sex \times Date" interactions were not significant (Table 1), indicating that the slopes of the regression of primary length on date were not detectably different for breeders vs. nonbreeders (8.32 vs. 9.43) or for males vs. females (9.37 vs. 8.59). Therefore, it was most parsimonious to use the slope of 8.96 (corresponding to a growth rate of 8.96 mm/day), which was calculated from the combined data, in subsequent analyses. The common growth rate of 8.96 was similar to that exhibited by a small sample of recaptured individuals ($\bar{x} = 8.76$ mm/day, $n = 6$).

Effects of breeding status and sex on the timing of molt were investigated further by calculating mean molt initiation dates, based on a growth rate of 8.96 mm/day, for breeders and nonbreeders of each sex (Table 2). Breeding females initiated molt 3.1 days later than their mates ($P = 0.013$) and 3.1 days later than nonbreeding females ($P = 0.007$). Nonbreeding females did not differ significantly from nonbreeding males, and breeding males did not differ significantly from nonbreeding males, in the timing of wing molt.

The significant differences reported in the preceding paragraph would remain significant even

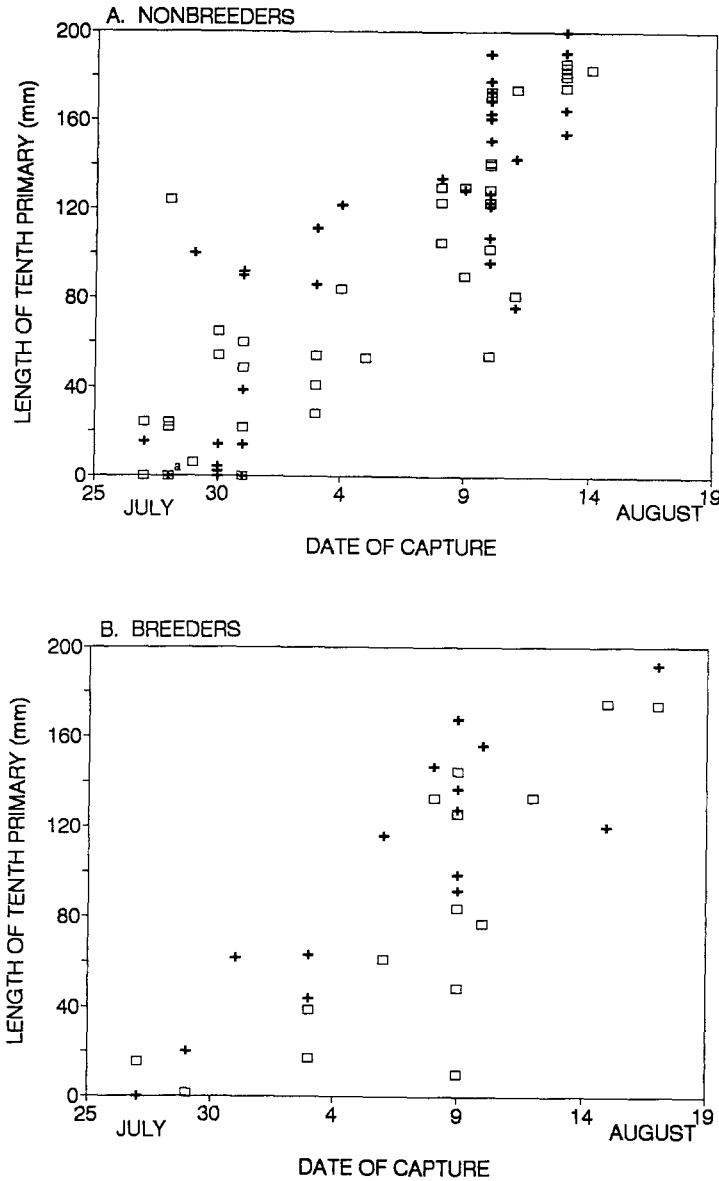


FIGURE 1. Length of the tenth primary in relation to date of capture for nonbreeding (A) and breeding (B) Tundra Swans. Plus symbols = males ($n = 36$ nonbreeders and 15 breeders); open squares = females ($n = 41$ nonbreeders and 15 breeders). * The symbol at coordinates 0,28 represents 2 males and 3 females.

if the primary growth rate of breeding females was up to 6% and 8% lower than that of their mates and nonbreeding females, respectively. Differences among slopes were not detectably different in my sample (thus a common slope was used, see above), although the primary growth rate of breeding females was somewhat (3%) higher than that of their mates (note that this

difference, if significant, would make the difference between male and female initiation dates more significant) and somewhat (5%) lower than that of nonbreeding females.

The date of molt completion, based on a final primary length of 302 mm for males and 292 mm for females (Limpert, unpubl. data), was approximately 29 and 31 August for males and

TABLE 1. The effect of capture date, sex, and breeding status (breeding vs. nonbreeding) on primary length. Sample sizes given in Figure 1. Interaction terms were removed from the equation when found to be nonsignificant. Y-intercept = -262 ; $R^2 = 73\%$; $SD = 32.8$; $n = 107$.

Effect	Independent variable	Regression coefficient (\pm SD)	P	Partial r^2
A. Main effects	Date	9.1 (\pm 0.5)	0.00	73%
	Sex ^a	12.6 (\pm 6.4)	0.05	4%
	Status ^b	18.2 (\pm 7.1)	0.01	6%
B. Interactions	Sex \times Date	0.7 (\pm 1.1)	0.54	0.4%
	Status \times Date	1.0 (\pm 1.2)	0.44	0.6%
	Sex \times Status \times Date	-0.4 (\pm 0.4)	0.30	1%

^a Females coded as 0, males as 1.

^b Breeders coded as 0, nonbreeders as 1.

females, respectively. Swans were capable of flight before the end of their 33–34 day molt period, particularly when pursued by a boat (e.g., no captured swan exhibited more than 22 days of primary growth), however they probably were not capable of prolonged, efficient flight.

BODY CONDITION INDEX

The body condition index of nonbreeders did not change detectably as molt progressed (Fig. 2A, B).

For breeding males and females, the body condition index appeared to reach its highest values

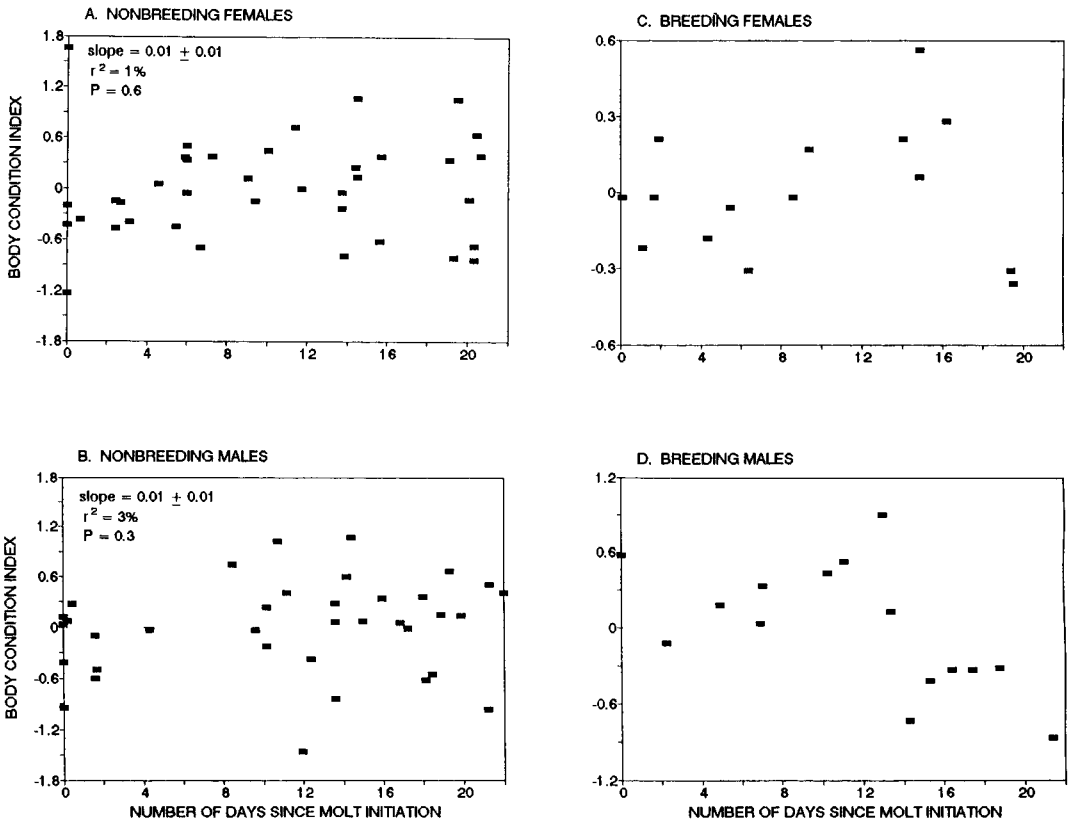


FIGURE 2. Body condition index as a function of the number of days since molt initiation for nonbreeding females (A) and males (B), and for breeding females (C) and males (D). See METHODS for explanation of body condition index. Other body condition indices gave similar results.

TABLE 2. Mean number of days (\pm SE) after 1 July that molt was initiated, based on a growth rate of 8.96 mm/day for breeding and nonbreeding males and females. Breeding males and females are compared with a paired *t*-test. Sample sizes given in Figure 1.

	Nonbreeders	Breeders	<i>t</i>
Males	25.4 (\pm 0.6)	26.2 (\pm 0.8)	0.76 ^{ns}
Females	26.2 (\pm 0.5)	29.3 (\pm 1.1)	2.81**
<i>t</i>	0.91 ^{ns}	2.84*	

* = *P* < 0.05.
 ** = *P* < 0.01.

at half to two-thirds through the flightless period and to be at its lowest values at the end of the period (Fig. 2C, D). Female body condition showed a significant increase through day 18 (slope = 0.025 \pm 0.009, *r*² = 39%, *P* = 0.02). Because only two females were captured after day 18, it is impossible to reach any conclusions about the apparent drop in body condition at the end of the flightless period. Male body condition was higher on days 0 through 13 than thereafter (\bar{x} = 0.33 \pm 0.11 vs. \bar{x} = -0.50 \pm 0.1, *t* = 2.24, *P* = 0.04) and did not change significantly within either period (through day 13: slope = 0.02 \pm 0.02, *r*² = 12%, *P* = 0.37; after day 13: slope = -0.03 \pm 0.04, *r*² = 8%, *P* = 0.58).

For breeding females, there was also a slight, but nonsignificant, tendency for body condition to increase with time since hatch (slope = 0.04 \pm 0.02, *r*² = 36.5%, *P* = 0.085). For breeding males, there was no tendency for body condition index to change with time since hatch (slope = 0.003 \pm 0.06, *r*² = 0.1%, *P* = 0.95).

EFFECT OF HATCH DATE AND CLUTCH SIZE

Breeding females showed a positive relationship between hatch date and molt initiation date, i.e., females that hatched broods later began molt later (*P* = 0.01; Fig. 3). The average breeding female initiated molt 21 (\pm 1) days after her brood hatched. There was no tendency for the interval between hatch and molt to decrease for females that hatched nests later (slope = -0.09 \pm 0.33, *r*² = 1.0%, *P* = 0.79).

For breeding males, there was no tendency for molt initiation date to change with hatch date (slope = -0.19 \pm 0.35, *r*² = 4.2%, *P* = 0.60) or with the molt initiation date of their mates (*P* = 0.99, Fig. 4).

If breeding females experienced an energy deficit during laying and incubation, one possibility is that those females that had expended relatively

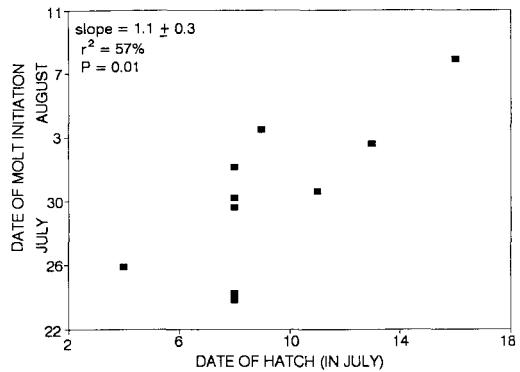


FIGURE 3. The relationship between date of molt initiation and date of hatch for breeding female Tundra Swans.

more energy during laying would delay molt or have lower body condition during molt. In fact, females that produced larger clutches began molt sooner after hatch than did females with smaller clutches (*P* = 0.03; Table 3). Similarly, those females that produced larger clutches tended to be in better body condition at capture (*P* = 0.055) and had cygnets that were relatively heavy for their age (*P* = 0.003).

DISCUSSION

The four principle findings of this study were (1) breeding females began molt later than their mates and later than nonbreeding females, (2) molt initiation in breeding females was directly related to date of hatch, (3) females with larger clutches began molt sooner after hatch, and had better body condition during molt, than did females with smaller clutches, and (4) breeding males did not differ from nonbreeders in the timing of molt.

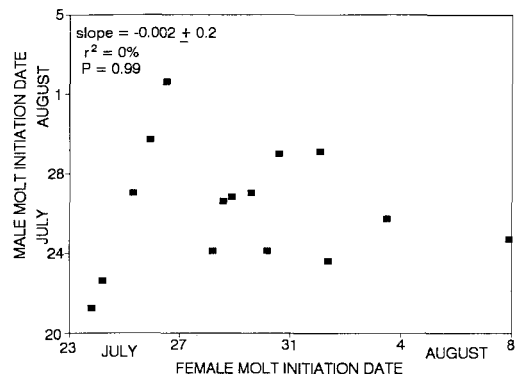


FIGURE 4. The relationship between date of molt initiation in breeding male Tundra Swans and the date of molt initiation of their mates.

TABLE 3. Linear regression of hatch-to-molt interval ($n = 10$), female body condition index ($n = 11$), and cygnet mass after accounting for cygnet age ($n = 10$) on clutch size.

Dependent variable	Independent variable	Regression coefficient (\pm SD)	P	r^2
Hatch-to-molt interval	Clutch size	-2.21 (\pm 0.83)	0.03	47%
Body condition index ^a	Clutch size	0.17 (\pm 0.08)	0.055	35%
Cygnet mass	Cl sz \cdot age	0.54 (\pm 0.12)	0.003	79%

^a See Methods for explanation of body condition index. Other body condition indices give similar results, except results based on mass/gape give $P > 0.10$.

The energetic constraints of laying and incubation. The timing of molt in breeding female Tundra Swans is consistent with the hypothesis that the energetic constraints of laying and incubation affect the timing of molt. Breeding females, which devote energy to egg laying and undertake up to 80% of the incubation duties (Hawkins 1986), begin molt after their mates and nonbreeders. Note that because a small (9%) proportion of nonbreeders were actually failed breeders (see METHODS), and because females whose breeding attempts failed had probably already incurred most of the energetic costs of reproduction, the difference between breeding and nonbreeding females may be somewhat greater than the 3.1 days reported here.

Also, as would be expected if females recovered from energy spent during incubation before initiating molt, the timing of molt in females is significantly related to the date on which their clutch hatches. Molt commenced an average of 21 days after hatch.

However, other findings indicate that constraints other than energetics are important in the timing of molt. First, breeding males, whose energetic costs are probably less than those of breeding females but more than those of nonbreeding males, did not initiate molt later than nonbreeding males. Second, female body condition index increased with time since molt initiation for most of the molt period, suggesting that recovery of energetic reserves can be concurrent with molt and need not delay its onset. Third, females that produced larger clutches, even though they presumably had more energy to recover, began molt sooner after hatch, and were in better body condition at capture, than females with smaller clutches. This implies that some superior females tended to do well in several sequential stages of the breeding season, and that energy spent prior to molt did not necessarily delay molt or produce energetic stress during molt. Note that these findings do not preclude energetic explanations for the timing of molt at

either the proximate or ultimate level, but they do suggest that non-energetic constraints may also be important. Such non-energetic constraints include defending territories from conspecifics, defending young from predators, brooding young, and the time available for breeding and molting. Each is discussed below.

The constraint of defending territories from conspecifics. Although the timing of molt in breeders and the relationship between hatch date and molt are consistent with energetic constraints, they could also be explained by the difficulty of defending territories and providing parental care to young cygnets while lacking primaries.

Territorial defense, during which intruders are chased and beaten with the wings if captured, is probably an important non-energetic constraint on the timing of molt in Tundra Swans. Molting individuals are at a disadvantage in fights because they are flightless and because they risk injury to growing, fragile, primaries. A swan capable of flight will repeatedly attack a retreating flightless swan, using its fully-feathered wings to beat its opponent severely (pers. observ.). During the period when only one member of a pair is capable of flight, that member will engage intruders while its mate maintains a hiding posture. When both members can fly, they often defend the territory in concert. The territorial defense hypothesis, in its simplest form, assumes that defense is equally important before and after molt and predicts that members of a breeding pair will molt asynchronously such that one member can fly during all periods in which nonbreeders can fly (Prediction 1). This suggests that one member should initiate molt in synchrony with (or before) the first nonbreeders to initiate molt, and the other mate should molt in synchrony with (or after) the last nonbreeders to initiate. However, if territory defense is more important in the pre-molt period and if two defenders are substantially better than one, then the first mate to initiate molt should do so in

synchrony with (or after) the last nonbreeders to initiate (Prediction 2).

The finding that breeding males molt asynchronously with their mates is consistent with the constraint of territorial defense. The finding that breeding males initiate molt around the average initiation date of nonbreeders, rather than at about the same time as the first nonbreeders (Prediction 1), suggests that territorial defense is somewhat more important in the pre- than post-molt period, or that constraints other than territorial defense are acting. It is very likely that defense during the pre-molt period is more important than during post-molt because the potential cost of being displaced from a territory, temporarily or permanently, would be much greater for a breeder with a three-week-old, rather than seven-week-old, brood. It is also likely that defense by males and females is substantially better than defense by females alone (females are 14% smaller than males, on average, Limpert et al. 1987).

The constraint of defending young from predators. Male and female swans defend their nests and young broods by threatening with outstretched wings and, if necessary, physically beating predators with their wings. Presumably brood defense, like territory defense, is inhibited by molt because flightless individuals can travel less quickly, and because they risk injury to their growing primaries.

Cygnets may be vulnerable to Snowy Owls (*Nyctea scandiaca*) and arctic foxes (*Alopex lagopus*) for up to one month posthatch (mean cygnet mass at one month was 2.0 kg in this study), although they are probably more vulnerable when younger. The predator defense constraint thus suggests a strong advantage for at least one parent, and probably some advantage for both parents, to retain primaries for up to one month posthatch. The finding that parental male and female Tundra Swans initiate molt an average of 19–21 days after hatch is consistent with the predator defense constraint.

The constraint of brooding young. Brooding, during which primaries are used to shelter young, may also favor the delay of molt by breeding females for about three weeks posthatch. In Northern Hemisphere geese and swans, females alone are responsible for brooding, young are typically brooded periodically during the first 14 (geese) or 21 (swans) days of life (Kear 1970), and both members of breeding pairs in most species begin molt after this period (Cramp and Sim-

mons 1977, Bellrose 1980). Although the delay of molt by breeding females is consistent with the constraint of brooding young, the concurrent delay by breeding males suggests that some other factor is also acting, at least on males.

The constraint of a short breeding season. The short breeding season on the Colville River Delta may force more overlap of breeding and molt, and thus result in more synchrony between mates and between breeders and nonbreeders, than might be advantageous if only the constraints discussed above are considered. The constraints of a short breeding season are indirectly energetic; i.e., they involve the energetic consequences of flightlessness (or the lack of feathers) rather than the direct energetic cost of molt. For example, the colder temperatures and thus greater costs of thermoregulation during late summer may favor an earlier molt in midsummer. Also, late molt may overlap with the initial stages of premigratory fattening, and flightless individuals will presumably be less efficient at travel to abundant food sources. Third, the timing of molt is probably constrained by the risk of being flightless at the time of permanent fall freeze-up, which is highly variable from year to year. In the three years of this study, breeding females had fully-grown primaries an average of only six (± 1) days before their cygnets fledged (mean fledging date = 7 September, fledging at 60 days posthatch is assumed; Bellrose 1980).

Note that if the constraints of energetics, brood defense, and a short breeding season acted equally on breeding males and females, then males (which take one day longer to molt) should initiate molt an average of about one day before females. Also, if there were some advantage to mates in regaining flight simultaneously, the date of molt initiation of mates should be correlated. However, breeding males initiated molt three days before their mates, on average, and there was no tendency for the timing of molt of breeding males to be correlated with that of their mates (Fig. 4).

Insights from other Anserinae. Several lines of evidence from other Northern Hemisphere geese and swans suggest that energetic constraints alone are not sufficient to explain the timing of molt. First, in direct contrast to predictions based on energetics alone, breeding females initiate molt before breeding males in Giant Canada Geese (Hanson 1965), Lesser Snow Geese (*Chen caerulescens caerulescens*, Palmer 1972), Mute Swans in Europe (approx. 25 days, Beekman 1991) and

Michigan (45 days, Wood and Gelston 1972), Whooper Swans (*Cygnus cygnus*) in Iceland (1–2 days, Rees et al. 1991), and some Trumpeter Swans (several weeks, see below). Among Northern Hemisphere swans, only Tundra Swans (this study) and some Trumpeter Swans fit the energetics-based prediction that females should initiate molt later than their mates.

Second, the degree of asynchrony between mates in Mute Swans and Trumpeter Swans is best explained by the constraint of brood defense or territory defense and is not explained by energetic constraints. In Mute Swans, breeding males initiate molt about 25 days after their mates have initiated molt, resulting in very little overlap in flightlessness between the sexes. Beekman (pers. comm.) and Kear (1972) suggested that this asynchrony ensures that at least one parent is capable of brood defense, and that the larger male, which is primarily responsible for brood protection in Mute Swans (Kear 1972), will have fully-feathered wings when the brood is younger and more vulnerable.

Similarly, in Trumpeter Swans there is little overlap in flightlessness between members of a pair. Typically one sex initiates molt within two weeks after hatch and the other sex molts several weeks later (Banko 1960, Hansen et al. 1971, Page 1976, Bollinger 1982, and references below). Interestingly, the male molts earlier than the female in some pairs and later than the female in others. This has been documented in southern Alaska (Hansen et al. 1971; P. Henson, pers. comm.), Idaho (P. Henson, pers. comm.), and Montana (D. Lockman, pers. comm.). The cause of this variation is unknown, but it always results in very little overlap in molt between mates. This suggests that asynchrony, per se, is advantageous, perhaps either to facilitate territory defense or brood protection, but that the relative strengths of energetic or non-energetic constraints acting on males and females differ among pairs.

Finally, the timing of molt is probably constrained by season length, regardless of what other energetic or non-energetic constraints are operating. For example, the hatch-to-molt interval varies as a function of season length among populations of Canada Geese. In southern portions of the range, parents postpone molt for up to one month after hatch, whereas in the Arctic, parents initiate molt only two weeks after hatch; parents in each area regain flight at about the same time as do their young (Bellrose 1980; see also Barry

1966). Similarly, the degree of molt asynchrony between mates in swan species varies as a function of season length: the more southerly breeding species, Mute and Trumpeter Swans, tend to be more asynchronous than the sub-arctic- and arctic-breeding species of Tundra, Bewick's (*C. columbianus bewickii*) and Whooper Swans.

In summary, my results are consistent with the need for primaries during territory and brood defense. Evidence from Northern Hemisphere geese and swans suggests that patterns of molt asynchrony within and among species result, at least in part, from non-energetic constraints. Understanding the selective forces that have shaped the timing of molt in waterfowl is a rich, and largely unexplored field. Much remains to be learned from studies that document the timing of molt while quantifying both potential non-energetic and energetic constraints.

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