

TESTING COMPETING HYPOTHESES FOR CHRONOLOGY AND INTENSITY OF LESSER SCAUP MOLT DURING WINTER AND SPRING MIGRATION

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Abstract. We examined chronology and intensity of molt and their relationships to nutrient reserves (lipid and protein) of Lesser Scaup (*Aythya affinis*) to test predictions of two competing hypotheses. The “staggered cost” hypothesis states that contour-feather molt is nutritionally costly and should not occur during nutritionally costly periods of the annual cycle unless adequate nutrients are available. The “breeding plumage” hypothesis states that prealternate molt must be complete prior to nesting, regardless of nutrient availability. Males and females were completing prebasic molt during winter (Louisiana) and had similar molt intensities. Females underwent prealternate molt during spring migration (Illinois and Minnesota) and prebreeding (Manitoba) periods; 53% and 93% of females were in moderate to heavy molt in Minnesota and Manitoba, respectively, despite experiencing other substantial nutritional costs. Intensity of prealternate molt was not correlated with lipid reserves even though females, on average, were nutritionally stressed. Molt intensity was not negatively correlated with protein reserves at any location. Chronology and intensity of prealternate molt varied little and were not temporally staggered from other nutritionally costly events. Prealternate molt did not influence nutrient reserves, and nutrient reserves likely were not the ultimate factor influencing chronology or intensity of prealternate molt of females. We surmise that nutrients required for prealternate molt come from exogenous sources and that the “staggered cost” hypothesis does not explain chronology of prealternate molt in female Lesser Scaup; rather, it appears that molt must be complete prior to nesting, consistent with the “breeding plumage” hypothesis.

Key words: duck, feather, incubation, migration, molt, plumage, waterfowl.

Evaluación de Hipótesis Alternativas sobre Cronología e Intensidad de la Muda en *Aythya affinis* durante la Migración de Primavera e Invierno

Resumen. Examinamos la intensidad y cronología de la muda y su relación con las reservas de nutrientes (lípidos y proteínas) en *Aythya affinis* con el fin de evaluar las predicciones de dos hipótesis. La hipótesis de “costo discontinuo” predice que la muda de las plumas de contorno es nutricionalmente costosa, por lo que no debería ocurrir durante los periodos del ciclo anual que son nutricionalmente costosos, a menos de que haya disponibilidad adecuada de nutrientes. La hipótesis de “plumaje reproductivo” predice que la muda prealterna debe completarse antes de la anidación, independientemente de la disponibilidad de nutrientes. Encontramos que la intensidad de la muda de machos y hembras que completaron la muda prebásica durante el invierno (Louisiana) fue similar. Las hembras entraron en muda prealterna durante la migración de primavera (Illinois y Minnesota) y antes de comenzar la anidación (Manitoba); 53 y 93% de las hembras en Minnesota y Manitoba, respectivamente, presentaban muda moderada a alta a pesar de otros costos nutricionales substanciales. La intensidad de la muda prealterna no se correlacionó con las reservas de lípidos a pesar de que las hembras, en promedio, se encontraban bajo estrés nutricional. En ninguna localidad hubo correlación negativa entre la intensidad de la muda y la reserva de proteínas. La cronología e intensidad de la muda prealterna no varió mucho y no se alternaron temporalmente con otros eventos nutricionalmente costosos. La muda prealterna no influyó la reserva de nutrientes y muy probablemente las reservas de nutrientes no fueron el principal factor que influyó la cronología o intensidad de la muda prealterna de las hembras. Deducimos que los nutrientes requeridos para la muda prealterna provienen de fuentes exógenas y que la hipótesis de costo discontinuo no explica la cronología de la muda prealterna de las hembras de *A. affinis*. Más bien, parece que la muda debe completarse antes de la anidación, de forma consistente con la hipótesis de plumaje reproductivo.

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INTRODUCTION

Adult ducks generally molt their feathers twice a year (i.e., prebasic and prealternate molts); during each molt, they replace contour feathers (body feathers including head and neck; Humphrey and Parkes 1959, Pyle 2005). In early fall, ducks typically enter into prebasic molt, molting into their basic (brighter) plumage (Pyle 2005). Female ducks typically begin prealternate molt (molting into their drabber alternate plumage) in spring, whereas males begin in late summer (Billard and Humphrey 1972, Lovvorn and Barzen 1988, Pyle 2005).

Contour-feather molt can be an energetically and nutritionally costly period for birds because of thermal losses and feather growth/development (King 1980). Individual ducks have some plasticity in the chronology of molt in relation to nutritional costs because chronology or intensity of molt varies with the condition of the habitat they use (Heitmeyer 1985, 1987, Miller 1986). Heitmeyer (1985) suggested that molt is nutritionally costly and that its costs are temporally staggered with other energetically costly events in the annual cycle (e.g., egg laying and incubation; the “staggered cost” hypothesis). Furthermore, Heitmeyer (1987) suggested that the intensity of molt may be staggered among feather regions to defray the costs associated with a completely simultaneous molt. Indeed, females of *Aythya* complete prealternate molt of contour feathers just prior to egg laying and incubation, whereas males undergo this molt later during summer (Billard and Humphrey 1972, Lovvorn and Barzen 1988, Hohman and Crawford 1995).

Since the proposal of the “staggered cost” hypothesis, the importance of the spring migration period for nutrient acquisition has been well documented for waterfowl (Ebbinge and Spaans 1995, Anteau and Afton 2004, Arzel et al. 2006, Devries et al. 2008). Spring migration and the prebreeding period are nutritionally costly periods of the annual cycle (Lovvorn and Barzen 1988, Austin et al. 1998, Anteau and Afton 2004, Newton 2007). Lovvorn and Barzen (1988) stated that individuals that are nutritionally stressed should stagger molt with other costly events, but if adequate exogenous sources of energy and nutrients are available, they may not stagger molt. Furthermore, they defined stress as “a situation when demands of one event (physiological, behavioral, or otherwise) are great enough to interfere with desirable allocation of resources to other processes.” Heitmeyer (1985) and Lovvorn and Barzen (1988) suggested that the mechanism behind the “staggered cost” hypothesis is a proximate-nutritional trigger enabling individuals to regulate the onset or intensity of molt on the basis of their current nutrient reserves or food availability.

Lesser Scaup (*Aythya affinis*) are mainly carnivorous. Females historically accumulated 50% and 9% of the lipid reserves used for egg laying and incubation, respectively, during spring migration and soon after arrival on breeding areas (Afton and Ankney 1991, Afton and Paulus 1992). Currently, female scaup catabolize lipids and have low lipid reserves

(Anteau and Afton 2004, 2009a, 2011, Strand 2005); they also have reduced availability and quality of their forage and low foraging efficiency (Anteau and Afton 2006, 2008a, b, 2009b, Strand et al. 2008). Therefore, in contrast to situations encountered in previous studies of molt and nutrient reserves of *Aythya*, female Lesser Scaup currently are nutritionally stressed during spring migration, as defined by Lovvorn and Barzen (1988). Therefore, if molt poses a substantial endogenous cost to female scaup, the “staggered cost” hypothesis predicts that females, on average, should not molt during spring migration and prebreeding periods, or during egg laying and incubation. However, it is possible that superior individuals have access to adequate endogenous or exogenous reserves and may molt. Thus, under the “staggered cost” hypothesis, there should be a positive relationship between reserves and intensity of prealternate molt because only the fittest individuals can afford to initiate molt. Furthermore, we should expect wide variation in chronology and intensity of prealternate molt.

Alternatively, color and structural differences between females’ basic and alternate plumages (Bowles 1917, Heitmeyer 1987) may have evolved to make the plumage more cryptic (Heitmeyer 1987) or enhance its ability to insulate eggs (Cole 1979) (hereafter the “breeding plumage” hypothesis). This hypothesis predicts that prealternate molt of breeding females should be completed prior to egg laying and incubation, regardless of nutritional-cost overlaps among molt, migration, pairing, and acquisition of nutrients and energy. Thus, under this hypothesis, chronology of molt generally should be fixed, varying no more than that of nest-initiation dates. Furthermore, under the “breeding plumage” hypothesis, we predict that all females should be in intense molt at the end of spring migration and during the prebreeding period.

Understanding the nutritional cost of molt is difficult in observational studies because nutrition might influence the chronology of molt (Heitmeyer 1985, Lovvorn and Barzen 1988, Hohman et al. 1992). However, if the chronology of prealternate molt is relatively fixed, as predicted by the “breeding plumage” hypothesis, the intensity of molt should be negatively correlated with nutrient reserves if it were costly to endogenous reserves or unrelated if costs of molt can be met from exogenous sources of nutrients.

In this paper, we examine chronology and intensity of molt and their relationships to nutrient reserves (lipid and protein) of Lesser Scaup to test predictions of the “staggered cost” and “breeding plumage” hypotheses. First, we examined chronology and intensity of contour-feather molt in female and male scaup at four locations in the Mississippi Flyway during winter, spring migration, and prebreeding (between arrival on breeding areas and nest initiation). We evaluated whether female scaup molt during spring migration and prebreeding, i.e., nutritionally stressful periods, or whether they temporally stagger molt to avoid additional nutrient costs during these periods. Second, we examined relationships between molt inten-

sity and endogenous nutrient and energy reserves (lipid and protein) of female and male scaup.

For males, completion of prebasic molt (molting into brighter plumage) is a prerequisite for pairing (Hohman et al. 1992), and this molt typically begins in early fall (Pyle 2005). Accordingly, the chronology of prebasic molt in males may be driven by processes similar to the "breeding plumage" hypothesis described for females. However, scaup form pair bonds during spring migration, which is later than that of other duck species (Weller 1965, Hohman et al. 1992). Thus, male scaup may have more flexibility and variability in the chronology of prebasic molt than do other ducks, as predicted by the "staggered cost" hypothesis. We included males in our analyses to estimate the proportion of males still undergoing prebasic molt in late winter and to examine whether the chronology of completion was influenced by nutrient reserves.

METHODS

STUDY AREA AND COLLECTION OF SPECIMENS

We selected four collection locations that represent important areas of wintering, spring stopover, and breeding along a contiguous migration path within the Mississippi Flyway, as determined by band-recovery data, sightings of color-marked scaup, and historical accounts (Thompson 1973, Afton and Hier 1985, Afton et al. 1991, Pace and Afton 1999, Havera 1999). Our collections of prebreeding scaup were from a single prairie-parkland breeding area. Specifically, we collected 30 male and 30 female scaup (unless otherwise noted) in 2000 at four locations ($n = 240$): (1) southern Louisiana (near Lake Pelto, south of Cocodrie; 12 February–4 March); (2) Illinois (Pool 19 of the Mississippi River between Hamilton and Niota; 13–15 March; 29 males and 31 females); (3) northwest Minnesota [Thief Lake Wildlife Management Area (WMA), Agassiz National Wildlife Refuge, and Roseau River WMA; 15–25 April]; and (4) west of Erickson, Manitoba (between Sandy Lake and Elphinstone, and the area 35 km south of these points; 1–15 May). These locations were described in detail by Rogers (1964), Thompson (1973), Hohman (1985), Pace and Afton (1999), and Anteau and Afton (2004).

We randomly collected scaup with a shotgun by sneaking or spotlighting to avoid condition biases associated with using decoys (Pace and Afton 1999). In Louisiana, we collected scaup just prior to their departure. In Illinois and Minnesota, we collected during the middle of spring migration, when relatively large numbers of scaup were using these spring stopover areas (Anteau and Afton 2004). We initiated collecting in Manitoba when resident scaup first arrived and immediately began using small ponds (see below) and completed collections well before the start of rapid follicle growth in females. We limited collections in Minnesota and Manitoba to paired individuals. We determined pair status of individuals prior to collection with criteria outlined in Afton (1985).

We further limited collections in Manitoba to isolated pairs on smaller ponds which, as determined by observations of marked individuals, constitutes a sample of resident breeders (Anteau and Afton 2004).

BODY COMPOSITION AND PROPORTION OF CONTOUR-FEATHER MOLT

We weighed specimens (± 1 g; fresh body mass) immediately after collection, and then we labeled, double bagged, froze, and transported them to the laboratory for further dissections. In the laboratory, we took the following morphometrics on each specimen: total length (± 1 mm), from tip of longest rectrix to tip of bill with bird stretched on its back; wing length (± 1 mm; Carney 1992); and tail length (± 1 mm), from body to tip of longest rectrix. We conducted dissections, carcass homogenizations, preparation of samples for body-composition analyses, and calculation of nutrient-reserve levels exactly as described by Anteau and Afton (2004).

We used grab sampling to assess the proportion of contour-feather molt, sampling approximately 1 cm² of feathers in each grab (Titman et al. 1990). We sampled each subregion with one grab (Titman et al. 1990). We counted blood quills (i.e., growing feathers) and total feather quills for each grab under a lighted magnifying glass. We calculated the proportion of molt for each subregion by dividing the number of blood quills by the total number of quills.

The regions and subregions quantified were (1) head (subregions: crown, cheek, throat, upper and lower dorsal neck, and upper and lower ventral neck); (2) flank (subregions: lower side breast, side belly, and flank); (3) breast (subregions: collar, upper back, upper breast, and upper side breast); (4) belly (subregions: lower breast, upper belly, lower belly, abdomen, and vent); (5) back (subregions: interscapular, midback, lower back, rump, side-rump, and leg); (6) scapulars; and (7) humeral tract (see Titman et al. 1990: fig. 1, Hohman and Crawford 1995).

STATISTICAL ANALYSES

Patterns of contour-feather molt. We used a repeated-measure ANOVA (PROC MIXED; SAS Institute 2002) to analyze intensity of contour-feather molt by feather region, sex, location, and a priori selected interactions (sex-by-location, sex-by-feather region, location-by-feather region, and sex-by-location-by-feather region). We included feather subregion within region as a fixed blocking term to control for the variability of molt within a feather region. We specified the subject (experimental unit) as the individual bird in the repeated statement (SAS Institute 2002) to ensure that proper degrees of freedom were used for all tests. We square-root-transformed molt proportions to conform model residuals to normality. We back-transformed least-squares mean proportions of molt for significant ($\alpha = 0.05$) main effects or interaction(s).

Relationship between molt intensity and nutrient reserves. When assessing nutritional costs of molt, we controlled

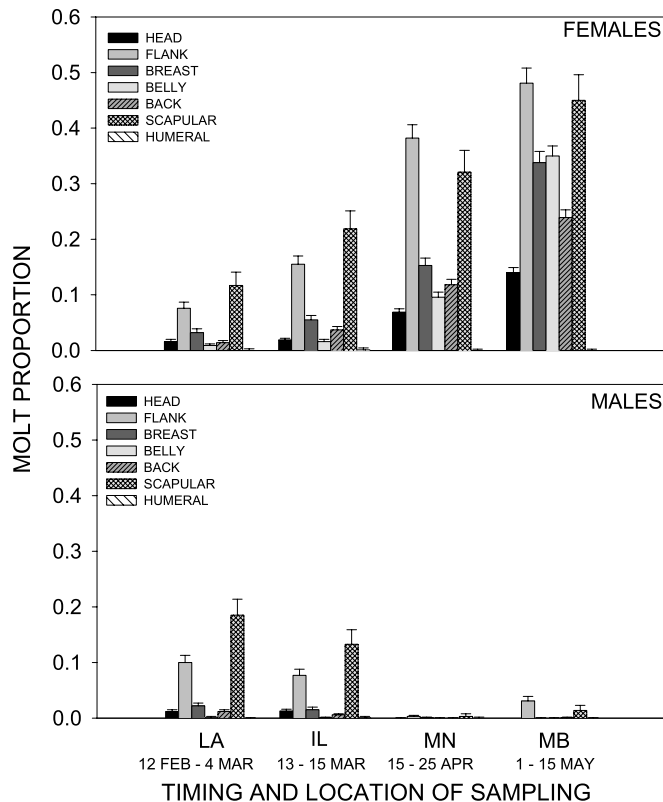


FIGURE 1. Least-squares means of proportions of molt (number of feathers molting divided by the total number of feathers sampled; \pm SE) by contour-feather region for female and male Lesser Scaup collected during 2000 at a wintering area in Louisiana (LA), spring-stopover areas in Illinois (IL) and Minnesota (MN), and a breeding area in Manitoba (MB).

for feather sizes within feather regions because larger feathers require more nutrients than do smaller ones (Hohman 1993, Hohman and Crawford 1995). Accordingly, we calculated a variable, adjusted molt (AMOLT), to index molt intensity with respect to nutrient requirements for feather growth. AMOLT was a single weighted value for each bird, which we calculated by weighting each regional mean intensity by the proportion of dry feather mass of that region represented (Hohman 1993, Hohman and Crawford 1995). We used Hohman and Crawford's (1995) regional feather mass from Ring-necked Ducks (*Aythya collaris*) to weight our regional means. We excluded molt of the humeral coverts from AMOLT because molt proportions in this region were negligible (Fig. 1). To show what percent of individuals were experiencing differing intensities of molt, we categorized AMOLT of individuals as minimal (<5%), light (5–20%), moderate (21–50%), and heavy (>50%) and plotted these categories by location and sex (see Fig. 2), as in Lovvorn and Barzen (1988).

We tested for a relationship between AMOLT and nutrient reserves separately for each sex because males and females were molting into different plumages during spring. For each sex, we ran a separate principal components analysis

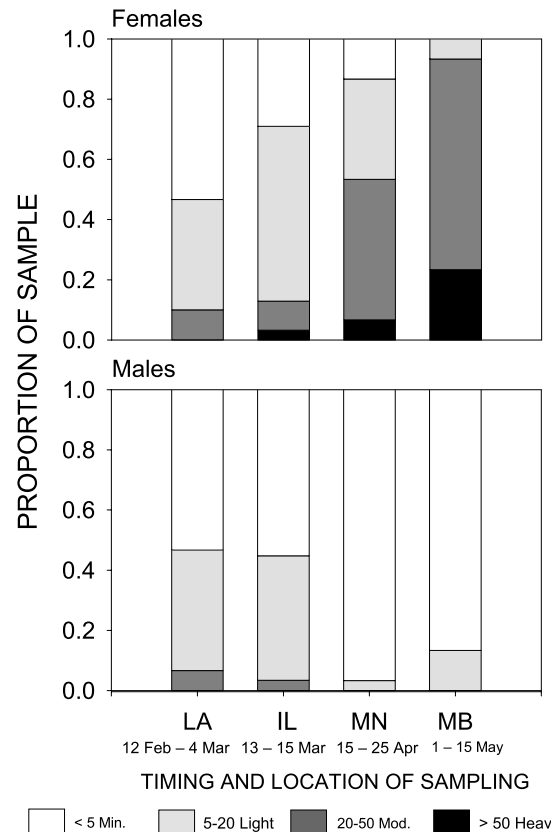


FIGURE 2. Proportions of female and male Lesser Scaup in each molt-intensity class for birds collected during 2000 at a wintering area in Louisiana (LA), spring-stopover areas in Illinois (IL) and Minnesota (MN), and a breeding area in Manitoba (MB). The intensity of molt of each individual was categorized on the basis of a mean of molt proportions from each feather region, weighted by the proportional feather mass of that region (AMOLT; see methods).

of the correlation matrix for all morphometrics (PROC PRINCOMP; SAS Institute 2002), and used the first principal component scores (PC1) to index body size (Afton and Ankney 1991, Anteau and Afton 2004). We tested for a relationship between AMOLT and lipid and protein reserves by using separate ANCOVAs (PROC GLM; SAS Institute 2002); each ANCOVA included location as a class variable, AMOLT and PC1 as covariates, and location-by-AMOLT as an interaction. We used an α level of 0.05 for all statistical tests.

RESULTS

PATTERNS OF CONTOUR-FEATHER MOLT

We detected a significant sex-by-location-by-region interaction in the analysis of molt proportions ($F_{18, 1392} = 10.66$, $P < 0.001$); feather subregion within feather region also was significant ($F_{20, 4778} = 11.06$, $P < 0.001$). Females consistently had greater proportions of molt than did males at all feather regions and collection locations, except at Louisiana (Fig. 1). Proportions and intensities of contour-feather molt of females were greatest in northern collection locations, whereas those

of males were greatest in southern collection locations (Figs. 1, 2). In Manitoba, intensity of molt was moderate or heavy for 93% of females (Fig. 2). In males and females at all locations, flank and scapular regions generally had greater proportions of molt than did other regions (Fig. 1). Humeral covert molt was negligible in males and females at all locations and regions (Fig. 1).

RELATIONSHIP BETWEEN MOLT INTENSITY AND NUTRIENT RESERVES

Lipid reserves. In the principal component analysis of females, factor loadings for PC1 ranged from 0.54 to 0.61; PC1 accounted for 62% of the variation in morphometrics. PC1 was not correlated with lipid reserves of females ($P > 0.05$), so we did not include it in our final model. Our final model explained 58% of the observed variation in lipid reserves of females. AMOLT was correlated with lipid reserves of females; however, correlations varied by location (AMOLT-by-location interaction; $F_{3,113} = 5.26$, $P = 0.002$). In Louisiana AMOLT was negatively correlated with lipid reserves (estimate = -292.7 , $SE = 69.0$, $t = -4.24$, $P < 0.001$); however, slopes were similar to zero at all other locations.

In the principal component analysis for males, factor loadings for PC1 ranged from 0.53 to 0.64; PC1 accounted for 55% of the variation in morphometrics. PC1 was not correlated with lipid reserves of males ($P > 0.05$), so we did not include it in our final model. Our final lipid-reserve model, with the effects location ($F_{3,114} = 31.29$, $P < 0.001$) and AMOLT ($F_{1,114} = 4.18$, $P = 0.043$), accounted for 47% of the variation observed in males. AMOLT was negatively correlated with lipid reserves (estimate = -179.5 , $SE = 87.9$) of males during winter and spring migration.

Protein reserves. The final protein-reserve model for females accounted for 51% of the observed variation. PC1 was correlated with protein in the ANCOVA for females (estimate = 4.0 , $SE = 0.6$, $F_{1,112} = 39.58$, $P < 0.001$). AMOLT was correlated with protein reserves of females; however, correlations varied by location (AMOLT-by-location interaction; $F_{3,112} = 2.97$, $P = 0.035$). AMOLT was positively correlated with protein reserves of females in Illinois (estimate = 32.4 , $SE = 13.7$, $t = 2.38$, $P = 0.019$) and Minnesota (estimate = 23.1 , $SE = 10.1$, $t = 2.28$, $P = 0.025$), but appeared uncorrelated in Louisiana and Manitoba ($P > 0.165$).

The final protein-reserve model of males, with the effects location ($F_{3,113} = 3.47$, $P = 0.019$) and PC1 ($F_{1,113} = 16.90$, $P < 0.001$), accounted for 21% of the variation observed; however, there was weak, but insignificant, positive correlation between AMOLT (estimate = 35.9 , $F_{1,113} = 3.19$, $P = 0.077$) and protein reserves of males.

DISCUSSION

NUTRITIONAL CONTEXT FOR MOLT OF LESSER SCAUP

Currently, female scaup catabolize lipids and have relatively low lipid-reserve levels during spring migration throughout

the upper Midwest, an area where historically they maintained or gained reserves (Anteau and Afton 2004, 2009a, 2011). The nutritional value of forage that scaup consume in the upper Midwest currently is low and probably has declined from historical levels (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Anteau and Afton 2006, 2008a, Strand et al. 2008). Moreover, scaup likely search more for food (within and among wetlands) and consume less food than they did historically (Afton and Hier 1991, Afton et al. 1991, Anteau and Afton 2008b, 2009b). Therefore, for female scaup, nutritional costs of spring migration throughout the upper Midwest likely interfere with the accumulation of nutrient reserves for breeding. Together, these results provide strong evidence that females are nutritionally stressed during spring migration, and present a unique opportunity to contrast this current situation to previous studies of molt in *Aythya*.

Spring migration and the prebreeding period are nutritionally costly parts of the annual cycle. During spring migration ducks of the genus *Aythya* have great nutritional and energetic costs from migratory flights, the need to accumulate nutrients, courtship, pair maintenance, aggressive social interactions, and early development of ovarian follicles, all of which occur during a period of unpredictable and often inclement weather (Lovvorn and Barzen 1988, Austin et al. 1998, Anteau and Afton 2004, Newton 2007). During the prebreeding period, the birds have similar costs; migration is over, but there are increases in the frequency of aggressive social interactions and the intensity of ovarian follicle development (Afton 1984, 1985, Afton and Ankney 1991).

PATTERNS OF CONTOUR-FEATHER MOLT

We draw three basic inferences concerning molts of scaup during winter and spring, on the basis of our results and qualitative observations of molt in context of other studies (Billard and Humphrey 1972, Lovvorn and Barzen 1988, Hohman and Crawford 1995). First, female scaup wintering in Louisiana and males throughout winter and spring appear to be completing their prebasic molt because (1) percentages of scaup observed molting were relatively low, (2) proportions of feathers molting also were low, and (3) molt proportions and intensities of males generally decreased from south to north. Second, females clearly undergo prealternate molt (into their drabber plumage) during spring migration and prebreeding. Third, for males, the “staggered cost” and “breeding plumage” hypotheses do not compete with respect to chronology and intensity of prebasic molt because most males molt well before the pair-formation period.

All females were molting and 93% were in moderate to heavy molt very soon after their arrival on the breeding site in Manitoba. Accordingly, these data are inconsistent with the “staggered cost” hypothesis because nutritionally stressed females are molting during a period of great nutritional costs. Furthermore, females did not noticeably stagger the intensity of molt across feather regions to defray the costs of a simultaneous molt (cf. Heitmeyer 1987), suggesting that

spring molt was not very costly or that molt had to be completed prior to a period that would allow staggering among feather regions or both. Undoubtedly many scaup stopping on migration areas in Illinois and Minnesota breed in areas other than our Manitoba site. We assume that females arriving on other breeding areas have similar or greater intensities of molt or are closer to completion of prealternate molt than are those we observed in Manitoba because our site is near the southern edge of the breeding range (Austin et al. 1998).

We expected that, under the "breeding plumage" hypothesis, chronology of prealternate molt completion would vary like that of nest initiation. Unfortunately, we did not collect females late enough to estimate the chronology of molt completion. Some females had initiated prealternate molting in Illinois, and all but one female had initiated prealternate molt in Minnesota, indicating that females had initiated prealternate molt sometime during the 32 days between 14 March and 15 April. Afton (1984), Brook (2002), and Koons and Rotella (2003) observed that nest-initiation dates of Lesser Scaup vary over a range of 25, 38, and 33 days, respectively. Accordingly, the chronology of prealternate molt initiation is consistent with our expectations. However, the "breeding plumage" hypothesis could regulate the intensity of prealternate molt of females because the selection pressure driving the "breeding plumage" hypothesis is the chronology of molt completion. Indeed, all females molted and had high intensity of molt in Manitoba suggesting that (1) intensity of molt is greater for birds that initiated molt later, (2) prealternate molt cannot be skipped, and (3) molt must be complete prior to egg laying, all of which are consistent with predictions of the "breeding plumage" hypothesis.

Chronology and propensity to breed are influenced by nutrient thresholds prior to breeding (Esler et al. 2001, Martin et al. 2009). The propensity of scaup to breed currently may be low because nutrient thresholds may not be met due to poor habitat conditions on spring migration routes and at breeding areas (Esler et al. 2001, Martin et al. 2009). There may be a selective pressure for nonbreeding females to also skip prealternate molt or at least temporally stagger the costs of molt, so that they do not occur during migration. However, we did not observe any females skipping or delaying prealternate molt apparently because (1) prealternate in females cannot be skipped or delayed, even by those that will not breed or (2) the first nutrient threshold for breeding occurs just prior to initiation of molt, when female scaup had relatively high nutrient reserves and were at stopover areas supplying adequate food (e.g., Illinois; Anteau and Afton 2009a).

RELATIONSHIP BETWEEN MOLT INTENSITY AND NUTRIENT RESERVES

The observed negative correlations between lipid reserves and prebasic molt in Louisiana (males and females) and throughout spring (males) probably were not caused by nutritional demands of molt because molt intensities were near background

levels. For these birds, the chronology of molt appeared highly variable, and, on average, they had relatively large lipid reserves and seemingly abundant food resources in Louisiana and Illinois (Anteau and Afton 2004). Therefore, these negative correlations may be caused by less fit individuals initiating or completing prebasic molt later. Accordingly, the chronology of prebasic molt might be regulated by a nutrient trigger, which would be consistent with the "staggered cost" hypothesis. However, we did not expect the "breeding plumage" hypothesis to have relevance to the chronology of prebasic molt of females, and the two hypotheses do not compete in explaining the chronology of prebasic molt for males because costly portions of molt are complete well before spring pairing.

Protein reserves were not negatively correlated with AMOLT at any location; it appears that spring prealternate molt of females does require depletion of endogenous protein reserves. We observed a positive relationship between AMOLT and protein reserves of females migrating through Illinois and Minnesota, paralleling findings of Lovvorn and Barzen (1988). Given that these locations were where prealternate molt began, perhaps the onset of molt is acutely triggered by protein, providing support for the "staggered cost" hypothesis. For example, females with more endogenous or exogenous protein might initiate molt slightly sooner or molt more intensely. However, there was no relationship between protein reserves and molt intensity of females in Manitoba, where nearly all females were undergoing moderate to heavy molt and all females had initiated molt. Together these results suggest that a protein trigger for the initiation of molt is limited within the confines of other potential endogenous or exogenous triggers (e.g., circannual rhythms or photoperiod; Lovvorn and Barzen 1988, Gwinner 1990, Berthold 1993) as an evolved timing mechanism for the "breeding plumage" hypothesis. For example, molt intensity may increase in those birds that initiated prealternate molt later, regardless of protein-reserve levels, so that molt is complete before breeding.

Our data suggest that the chronology of prealternate molt of female Lesser Scaup is relatively fixed, especially near the final stages of molt, and that it was neither appreciably delayed nor skipped. Therefore, if molt were nutritionally costly to endogenous reserves, we would expect a negative relationship between prealternate molt and nutrient reserves for female scaup migrating across the upper Midwest. Accordingly, the lack of relationship between AMOLT and lipid reserves during spring migration and prebreeding is consistent with the idea that prealternate molt is not costly to endogenous lipid reserves. However, we cannot rule out the possibility that endogenous or exogenous nutrients influenced the onset of molt slightly (as it appeared in protein), which could cloud interpretations of the influence of molt upon nutrient reserves.

Costs of molt include various nutrients and energy, but it appears that scaup met those requirements through exogenous sources. During spring migration birds engage in hyperphagia

in order to accumulate lipid reserves required for breeding (Bairlein 1990, Berthold 1993). Lesser Scaup mainly consume protein-rich foods during spring migration (Afton et al. 1991, Anteau and Afton 2006, 2008) while they attempt to accumulate lipid reserves (Anteau and Afton 2009a, 2011). Given that feathers are composed primarily of protein (Heitmeyer 1988, Hohman et al. 1992), if females have “excess” protein or specific amino acids in their diet during spring, it may help them meet their protein requirements associated with molt. However, our Minnesota and Manitoba samples contained eight females that were noticeably emaciated (weighing <650 g); these individuals had initiated molt and clearly did not have excess protein. Female ducks of other species may utilize endogenous and exogenous nutrients for prealternate molt differently from Lesser Scaup because scaup have diets with relatively high protein content during spring migration and prebreeding (Krapu and Reinecke 1992, Anteau and Afton 2006, 2008). Accordingly, further research is needed to determine whether prealternate molt is costly to endogenous nutrient reserves during spring migration in birds that consume carbohydrate-rich diets or how nutrition during molt may influence feather growth or structure (Hohman et al. 1995, 1997).

CONCLUSION

The “breeding plumage” hypothesis is not relevant to the chronology or intensity of prebasic molt (into brighter plumage) of female Lesser Scaup, and it appears that males complete the costly portion of prebasic molt well before pairing. Indeed, chronology or intensity of prebasic molt of both females and males may have been regulated by a nutritional trigger, consistent with predictions of the “staggered cost” hypothesis. Furthermore, there was some evidence that protein reserves may influence the initiation of prealternate molt of females during migration. However, chronology and intensity of prealternate molt of females arriving at their breeding area was ultimately consistent with a relatively fixed chronology, suggesting that molt must be complete prior to breeding and is consistent with the “breeding plumage” hypothesis.

The first key prediction of the “staggered cost” hypothesis, that molt is costly, appears not to be met for prealternate molt of females. Furthermore, the second key prediction of the “staggered cost” hypothesis, that molt is staggered with other nutritionally costly events, is also not met for prealternate molt of females because nutritionally stressed females are molting during a period of great nutritional costs. In total, our results suggest that selection pressures associated with the “breeding plumage” hypothesis ultimately supplant those of the “staggered cost” hypothesis in regulating the ultimate chronology and intensity of prealternate molt of female Lesser Scaup. Last, given that the chronology of prealternate molt appears relatively fixed, understanding the mechanism that regulates it is important to evaluating the full effects of climate change on the breeding chronology of ducks.

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