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PRE-MIGRATORY LIFE HISTORY STAGES OF JUVENILE ARCTIC BIRDS: COSTS, CONSTRAINTS, AND TRADE-OFFS

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Abstract. Many young birds on the Arctic tundra are confronted by a challenging task: they must molt their feathers and accumulate fat stores for the autumn migration before climatic conditions deteriorate. Our understanding of the costs and constraints associated with these stages is extremely limited. We investigated post-juvenal molt and premigratory fattening in free-ranging juvenile White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) on the Arctic tundra. We found evidence for trade-offs between premigratory fat accumulation and molt: heavily molting birds had significantly less fat. Birds increased the rate of fat accumulation as the season progressed, but we found no evidence of a similar increase in rate of molt. Using a controlled captive study to isolate the energetic costs of body feather replacement, we found no difference in fat or size-corrected mass of birds actively growing body feathers as compared to controls. Molting birds, however, consumed 17% more food than controls, suggesting a significant cost of body feather growth. Our results provide evidence of significant costs, constraints, and trade-offs associated with post-juvenal molt and premigratory fat accumulation in young Arctic birds.

Key words: Arctic tundra; fat accumulation; juvenile birds; post-juvenal molt; Toolik Lake, Alaska; trade-offs; White-crowned Sparrow; Zonotrichia leucophrys gambelii.

INTRODUCTION

Every year, several hundred million birds, from more than 280 species, migrate to their primary breeding grounds on the Arctic tundra (Callaghan et al. 2004*a*). Many of these birds raise offspring that are confronted by a challenging task: they must replace their body feathers and accumulate fat stores for the autumn migration before climatic conditions on the tundra deteriorate. Although successful progression through molt and accumulation of fat prior to migration may be critical to a bird's survival (Nilsson and Svensson 1996, Pfister et al. 1998, Hemborg 1999, Helm and Gwinner 2006), our understanding of the costs and constraints associated with these stages is extremely limited, particularly for juvenile birds.

Climatic conditions on the Arctic breeding grounds quickly deteriorate during the late summer (Fig. 1), creating a selective environment that may favor rapid progression through the premigratory stages, but energetic costs, physiological constraints, and resource availability may limit the rate at which a bird can replace its feathers and accumulate fat stores. Given constraints on time and resources, we may expect the potential for trade-offs between molt and fattening, particularly if both are energetically costly. Although the energetic cost of the adult post-breeding, or postnuptial, molt, which involves replacement of all of the flight and body feathers as well as much of the integument and components of the blood and bone (King and Murphy 1990), is generally accepted (Ginn and Mellville 1983, Murphy and King 1992, Lindström et al. 1993, Schieltz and Murphy 1995), the cost of the post-juvenal molt, which involves replacement of body feathers alone, is not known (but see Rubolini et al. 2002).

We explored molt and premigratory fattening, two critical life history events prior to autumn migration, in free-ranging juvenile White-crowned Sparrows (*Zonotrichia leucophrys gambelii*; see Plate 1) at the northern limit of their breeding range (Chilton et al. 1995). We addressed two questions central to an understanding of

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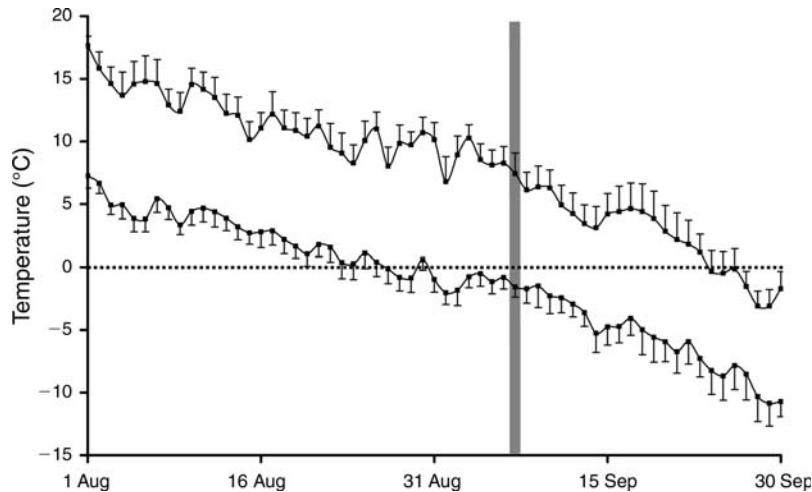
Fig. 1. Daily mean maximum and minimum air temperatures at the Toolik Lake, Alaska, USA, field site from 1988 through 2002. Data are presented as daily mean plus (maximum temperature) or minus (minimum temperature) standard error. The vertical shaded line marks the date at which all birds sampled for this study would have completed the post-juvenal molt, as estimated using the mean rate of progression through molt calculated from birds captured more than once ($N = 52$ birds). Temperature data are from Shaver and Laundre (2003).

the costs, constraints, and trade-offs of these premigratory life history events: (1) do juvenile birds trade off between investment of energy in molt vs. premigratory fattening? and (2) does the rate of progression through these events change later in the season as time becomes more limiting? Following our field study, we performed a controlled captive study designed to isolate the energetic costs of body feather replacement in immature Z. l. gambelii.

Methods

Field study

We conducted the field study near Toolik Lake north of the Brooks Range in Alaska (68°36′ N, 149°18′ W) during August 2004, near the northern limit of the breeding distribution of Z. l. gambelii (Chilton et al. 1995). We trapped 205 juvenile birds using seed-baited potter traps and mist nets. For clarity, we define juvenile birds as those birds still at least partially in juvenal plumage, which is the plumage found in birds from the age at fledging through completion of the post-juvenal molt. We recorded body mass (± 0.1 g) with a Pesola scale (Pesola, Baar, Switzerland), tarsus length (± 0.1 mm) with a caliper, fat score by inspecting visible subcutaneous fat stores in the furculum (interclavicular depression) (scale 0–5, see Wingfield and Farner 1978 for details), and body feather molt score (scale 0–100%), and fit each bird with a numbered leg band as well as a unique combination of colored leg bands, permitting subsequent individual identification. Because birds store most of their fat subcutaneously, fat score is a reliable indicator of total body fat content, particularly if interobserver variation is controlled (Krementz and Pendleton 1990); thus all fat scores were made by F. Bonier.

We scored molt using a method that involves estimating the percent of feathers that are actively being replaced (as indicated by presence of sheathed feathers) out of the total number of body feathers that could be replaced in seven regions of the body: wing coverts, back, nape, head, breast, belly, and flanks (Rohwer 1986). Within each of these seven body regions, we estimated percentage molt by counting the number of sheathed (vs. unsheathed) feathers in five small areas of approximately 20 body feathers each, thus sampling across the majority of the bird's body to arrive at total molt scores. We took the mean of the percentage of feather replacement across all seven regions to arrive at one combined body molt score. For example, if a bird were replacing 20% of the wing coverts, 10% of the back feathers, 50% of the nape feathers, 15% of the head feathers, 25% of the breast feathers, 75% of the belly feathers, and 5% of the flank feathers, its final molt score would be the mean of these seven values, 28.6%.

We estimated the rate of progression through molt and fattening for individual birds using measures from 52 birds that we recaptured during the study. For these birds, we calculated a daily rate of change in molt and fat score by dividing change in these scores by the number of days between captures. We recaptured four birds twice, and for these birds we calculated the rate of change in molt and fat score using data from the first and last captures. In Z. l. gambelii, the earliest stages of molt are characterized by a rapid increase in molt scores to a maximum of 100% of all body feathers being actively replaced. Because of the timing of our sampling, which began after all birds had achieved maximal molt scores, repeated sampling revealed a decline in molt score with date. We observed a between-captures increase in molt score in only 3.8% of recaptured

individuals ($N = 2$ individuals) and a decrease in fat score in 11.5% of recaptures ($N = 6$ individuals). This evidence suggests that changes in these scores represent a biologically relevant measure of progression through post-juvenal molt and premigratory fattening. We note that change in molt score does not directly measure rate of feather replacement, but instead is a measure of progression through molt, as all birds' molt scores approach zero with completion of molt.

We took a small blood sample (<250 μL) from each bird using alar vein puncture for assay of hormone levels (not reported here) and for use in molecular sexing. Because juvenile *Z. l. gambelii* are not sexually dimorphic, we sexed them using a simple PCR-based technique (detailed in Griffiths et al. 1998). We then tested for sex effects on all of the measured parameters using two-tailed *t* tests. Because we found no sex effects, we conducted all subsequent analyses with data for males and females combined.

We predicted that, if energy is a limiting factor, birds must trade off between fattening and molting, and heavily molting birds would therefore have lower fat scores and/or body condition, as estimated by size-corrected mass (body mass/tarsus length) (Freeman and Jackson 1990). We first investigated the relationship between these three parameters and time, using linear regression of each metric on day of capture, with the first day of sampling, 1 August, equal to 1. We then tested for evidence of trade-offs by quantifying the relationships between size-corrected mass, fat score, and molt score using partial correlations controlling for the effect of day of sampling. To determine if rate of fattening or rate of progression through molt changed later in the season, we used regressions of change in molt and fat score on median date between captures for those birds that were captured more than once. All data were normally distributed. Because we conducted multiple statistical tests on nonindependent data, we adjusted alpha levels using a sequential Bonferroni correction (five tests [Rice 1989]).

Captive study

During September 2004, we captured 20 immature *Z. l. gambelii* as they passed through central Washington State, USA during autumn migration. These birds are referred to as immature rather than juvenile because they had all completed the post-juvenal molt, and were all in the first basic plumage of first-year, nonbreeding birds. We transported these birds to the University of Washington in Seattle, where they were held for the duration of the study. We housed birds individually in $45 \times 45 \times 45$ cm cages in a room with a photo cycle adjusted to simulate naturally shortening days that would be found on the birds' wintering grounds in southwestern North America, and with ambient temperature maintained at 22°C (± 1°C). We provided birds with ad libitum access to food and fresh water throughout the study. We sexed the captive birds using

the PCR-based method described previously (Griffiths et al. 1998), and then randomly assigned birds to either a control or treatment group, balancing the groups in relation to sex, fat score, and size-corrected mass (body mass/tarsus length).

Following a one-week period of acclimation, we induced body feather production by removing approximately 600 body feathers from each of the treatment group birds. We evenly distributed feather removal across the bird's back, flanks, breast, and belly. Mean ($\pm$SD) dry mass of removed feathers was 586 ± 9.3 mg, which is approximately 32.5% of the total feather mass in this species (Chilgren 1977, King and Murphy 1990). This percentage of the total feather mass is conservatively within the range of feathers being actively replaced at one time during molt, as observed in the field component of our study (mean 59.3%, range 0–100%). Feather removal involved handling each bird for approximately five minutes, so we handled control birds similarly for the same amount of time without removing any of their feathers.

To minimize potential measurement bias, an assistant who was unaware of the hypothesis being tested recorded fat scores and body mass of all captive birds every three to four days. We also monitored food intake by weighing food before and after consumption for seven days during and seven days following the period of feather production. All of the birds completed feather replacement within 28 days.

We predicted that if body feather growth is energetically costly, birds replacing plucked feathers would have lower fat scores, lower size-corrected body mass, and/or increased food intake relative to controls. We compared mean size-corrected body mass and mean daily food intake during the period of feather replacement using two-tailed *t*-tests, and mean fat score using a two-tailed Mann-Whitney *U* test, because data were not normally distributed. We used mean size-corrected body mass and fat score data across 8 measurements taken during the 28-day feather replacement period, and mean daily food intake data from seven consecutive days of food intake measurements taken during the feather replacement period.

Results

Field study

Molt score declined with day of sampling ($F_{1, 203} = 118.35$, $P < 0.0001$, $N = 205$ birds), as would be predicted as birds progress through the post-juvenal molt. Fat score tended to increase, but was not well predicted by day of sampling ($F_{1, 203} = 2.47$, $P = 0.12$, $N = 205$ birds). As predicted, heavy body molt was correlated with lower fat scores (Fig. 2b, partial correlation controlling for day of sampling, $R = -0.54$, $P < 0.0001$, $N = 205$ birds). There was no relationship between molt score and size-corrected body mass ($R = -0.05$, $P = 0.49$, $N = 205$ birds). We recaptured 52 birds between 2 and 18 days (mean 6.6 ± 3.6 days) following initial capture. The relationship between rate of fatten-
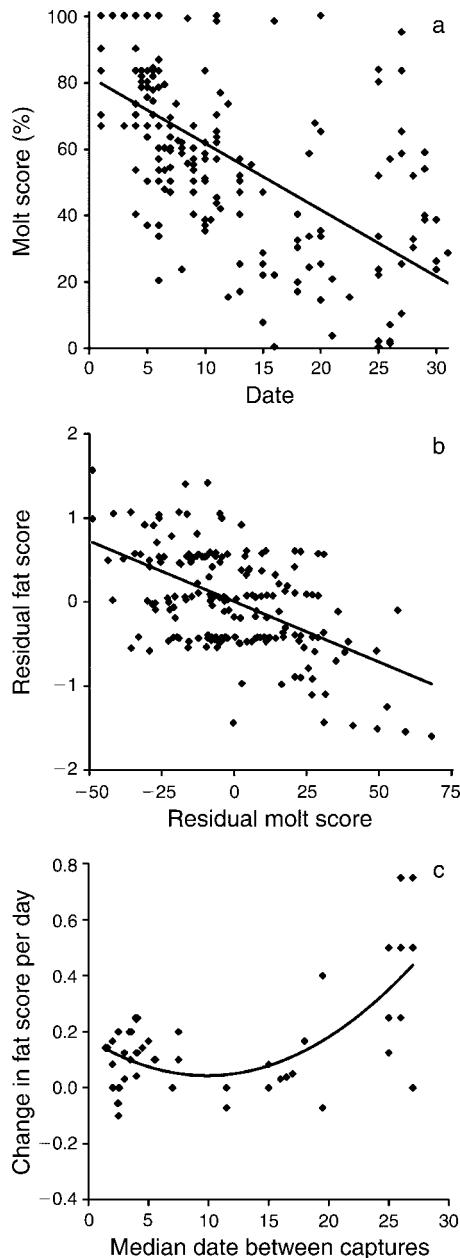
FIG. 2. (a) Scatter plot of the relationship between molt score and date (1 = 1 August = first day of sampling) in juvenile *Zonotrichia leucophrys gambelii* (linear regression of molt score on date, $F_{1,203} = 118.35$, $P < 0.0001$, $N = 205$). Molt score (mean percentage of feather replacement across seven body regions) declined as the season progressed. (b) Scatter plot of the relationship between fat scores and intensity of molt (residuals of fat score and molt, controlling for date) in juvenile *Z. l. gambelii* (partial correlation controlling for day of sampling, $R = -0.54$, $P < 0.0001$, $N = 205$). Fat score (scale 0–5) is based on visible subcutaneous fat stores in the furculum. Heavily molting birds had lower fat stores. (c) Regression of the rate of fattening (change in fat score per day) on the median date between captures (1 = 1 August) for birds that were captured more than once (quadratic regression, $F_{2,49} = 16.25$, $P < 0.0001$, $N = 52$). For example, if a bird was caught on 4 August and then again on 8 August, its median date between captures was 6 August. Birds increased the rate of fat accumulation as the season progressed.

ing and median date between captures was best fit by a quadratic regression, as the data displayed a nonlinear pattern, and the R^2 value for quadratic regression exceeded that of linear regression. The birds' rate of fattening increased with median date between captures (Fig. 2c, quadratic regression, $F_{2,49} = 16.25$, $R^2 = 0.40$, $P < 0.0001$, $N = 52$ birds; equation: $y = 0.04 - 0.0002x + 0.001[x - 13.0577]^2$). Rate of progression through molt did not change with date (linear regression, $F_{1,50} = 0.04$, $R^2 = 0.001$, $P = 0.85$, $N = 52$ birds).

Captive study

Molting birds consumed 17% more food than controls (Fig. 3; $t_{18} = 2.83$, $P = 0.01$, $N = 10$ treatment birds, 10 control birds). Despite the marked difference in food intake, experimental and control birds did not differ in size-corrected body mass or fat score (body mass, $t_{18} = 0.04$, $P = 0.97$; fat score, $U = 44$, $P = 0.64$). Food intake following the period of feather replacement did not differ between groups ($t_{18} = 0.72$, $P = 0.49$).

DISCUSSION

Juvenile *Zonotrichia leucophrys gambelii* on the Arctic tundra are confronted by two challenging tasks: to undergo the post-juvenal molt and fatten before climatic conditions deteriorate. Given constraints on time and resources, we predicted that birds would trade off between investment in feather growth and fat accumulation. Further, we predicted that as the season progressed and time became more limiting, birds would increase their rates of fat accumulation and progression through molt.

We found strong evidence that juvenile *Z. l. gambelii* trade off between molt and fattening: heavily molting birds had significantly lower fat scores after controlling for the effects of sampling date (Fig. 2b). Similar correlations have been found in several avian species
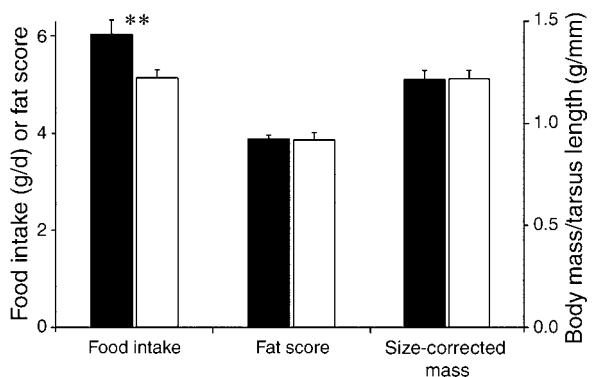

FIG. 3. Daily food intake and fat score (left-hand axis), and size-corrected body mass (right-hand axis) (all values given as mean + SE) in *Z. l. gambelii* for birds that were replacing body feathers (black bars) vs. control birds (open bars). Feather-replacing birds consumed 17% more food than controls ($t_{18} = 2.83$, ** $P = 0.01$, $N = 10$ treatment birds, 10 control birds), though their fat scores and body mass did not differ.

PLATE 1.   An adult male White-crowned Sparrow. This species has a broad breeding distribution in North America. At the northern limit of the distribution, White-crowned Sparrows need to be very flexible to cope with the vagaries of the sometimes harsh climate in the Arctic. Photo credit: J. C. Wingfield.

(King et al. 1965, Dolnik and Blyumental 1967, Lindström et al. 1994, Merilä 1997, Schaub and Jenni 2000, Rubolini et al. 2002). Our captive study provided further evidence of an energetic cost of feather growth: feather-replacing birds consumed 17% more food than controls during feather replacement (Fig. 3). Following feather growth, food intake levels declined and did not differ between experimental and control groups. Fat scores and size-corrected body mass did not differ between groups, suggesting that the entirety of the nutrients derived from excess food consumption during feather replacement was devoted to increased energetic demands associated with feather replacement. Overall, evidence for a trade-off between fat accumulation and feather growth in wild but not captive birds, coupled with the dramatic increase in food consumption in captive birds as they replaced their feathers, suggests that food resources are limiting for young *Z. l. gambelii* in nature. This limitation could be manifested directly through food availability, or through an interaction with other factors (e.g., costs of foraging, predation, climate), in either case resulting in an evolutionary trade-off in allocation of limited resources.

Despite the fact that captive birds were housed at temperatures well above ambient temperatures found on the Arctic molting grounds, we cannot distinguish between costs involved with feather growth and those resulting from increased thermoregulatory demands associated with decreased insulation. These costs are similarly indistinguishable in nature. Indeed, thermoregulatory costs may be highest in free-ranging birds in the Arctic, where maximum ambient temperatures at the time of the post-juvenal molt rarely exceed 15°C (Fig. 1). Captive birds were induced to replace only about 33% of their body feathers, compared to 100% of the body feathers replaced during the post-juvenal molt. In combination, these facts suggest that our estimate of an energetic cost of body feather growth is conservative. Our experiment does not replicate natural molt, thus physiological differences associated with life history stage are not controlled, and may have affected our results. For example, naturally molting birds may physiologically prepare for the energetic costs of feather growth, which contrasts with the unpredicted, forced feather replacement in our experiment. This difference should not, however, cause an overestimation of the energetic cost of feather growth, but may influence how birds allocate resources prior to and during feather growth.

We did not find any evidence that *Z. l. gambelii* are capable of increasing their rate of progression through molt later in the season, suggesting a basic constraint on the rate of feather growth. Morton et al. (1969) found indirect evidence suggesting a similar lack of increase in rate of molt in free-ranging juvenile *Z. l. gambelii* sampled at 64.8° N, contrasting with experimental evidence of a decrease of duration of postnuptial molt in captive adult *Z. l. gambelii* exposed to shortened day lengths found by Moore et al. (1982) and a decreased duration of postnuptial molt in free-ranging adult *Z. l. gambelii* with late-fledged clutches found by Wingfield and Farner (1979). These two findings are not necessarily contradictory, the differences potentially caused by age-related factors. The rate of molt in adult birds is

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often measured using rate of growth of primary flight feathers, whereas only body feathers are replaced during post-juvenal molt. Further, adult birds can decrease the total duration of molt by replacing more primaries simultaneously (Wingfield and Farner 1979), whereas juvenile *Z. l. gambelii* in our study were often actively replacing all of their body feathers at once, providing no opportunity for increase. The rate of post-juvenal molt has been found to be flexible in the chaffinch, *Fringilla coelebs*, and the stonechat, *Saxicola torquata*, increasing in response to shortened day length and late hatching date (Dolnik and Gavrilov 1980, Helm et al. 2005). The post-juvenal molt in *Z. l. gambelii* is one of the fastest known, however, with a duration of only 22–45 days (Morton et al. 1969), compared with 44–133 days in captive Chaffinches (Dolnik and Gavrilov 1980) and ~20–110 days in captive Stonechats (Helm et al. 2005). Further increasing the rate of molt could potentially compromise the quality of body feathers, as has been found in the primary wing feathers of other species (Dawson et al. 2000, Hall 2000, Dawson 2004), negatively influencing fitness through reduced overwinter survival and future reproductive success (Nilsson and Svensson 1996).

In contrast with our observation of no change in the rate of progression through molt, we found evidence that *Z. l. gambelii* increased their rate of fat accumulation as the premigratory period progressed. The benefits of increasing storage of fat prior to the energetically expensive southward migration are obvious, but the potential costs of an increased rate of fattening are unknown. To increase allocation to fat stores, birds must either divert energy from other demands, or increase resources available for allocation. Similar flexibility in rate of fattening but not rate of molt was found by Lindström et al. (1994) in an experimental study of the effects of day length on rate of molt and fat accumulation in adult Bluethroats, *Luscinia svecica*, another Arctic-breeding passerine bird. Together, the findings of this study and that of Lindström et al. (1994) suggest a constraint on molt rate, likely related to a reduction of quality in rapidly produced feathers.

In this paper, we have taken a physiological perspective to address an ecological question, bringing together field and experimental data to reveal basic costs, constraints, and trade-offs associated with molt and fattening in juvenile birds. Similar approaches have revealed basic trade-offs between allocation of resources to molt and reproduction (Nilsson and Svensson 1996, Hemborg et al. 1998, Sanz 1999), immune function and reproduction (Nordling et al. 1998, Ilmonen et al. 2000, Greenman et al. 2005, but see Williams et al. 1999), and secondary sexual characters (including behavioral traits) and parental effort (Gustafsson et al. 1995, Stoehr and Hill 2000, Lynn et al. 2002). These repeated patterns of trade-offs suggest that fundamental physiological constraints may underlie many ecological phenomena, and illustrate the strength of combining a physiological and

ecological approach to address important biological questions.

The majority of Arctic-breeding bird populations are currently declining, and models suggest that more dramatic declines will occur in response to continued climate change (Callaghan et al. 2004b). Our results suggest that some juvenile birds face resource limitations that constrain their ability to complete successful molt and fully fatten prior to departure for their southward migration. Any climatic changes that increase resource or time constraints on juvenile birds could have catastrophic effects on survival. For example, if warming temperatures cause plants to fruit and seed early (Arft et al. 1999), resource availability could decline during the energetically expensive premigratory stages. At present, however, we have little understanding of the interactions between climate change, breeding and premigratory phenology, and resource availability and cannot therefore accurately predict the impacts of future changes in Arctic climate.

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