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ENERGETIC COSTS AND STRATEGIES OF POST-JUVENAL MOLT IN AN EQUATORIAL BIRD, THE RUFOUS-COLLARED SPARROW (*ZONOTRICHIA CAPENSIS*)

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Abstract · Many tropical birds have slow-paced life history strategies, exhibiting lower metabolic rates, reduced annual investment in reproduction, and longer lifespans relative to birds at higher latitudes. Life history strategies have been relatively well documented in adult individuals in the tropics, but we know comparatively little about the immature life history stage. Here we examine strategies of feather replacement (molt) and fattening in immature Rufous-collared Sparrows (*Zonotrichia capensis*) in a high elevation equatorial population, following a parallel, previous study on an arctic congener, the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). In captivity, Rufous-collared Sparrows incurred energetic costs of experimentally induced feather growth, similar to those previously described for *Zonotrichia* at higher latitudes. In contrast, free-ranging immature Rufous-collared Sparrows in natural molt had fat stores that declined over time, opposite to patterns evident in arctic *Zonotrichia* that fatten before migration. Equatorial birds in good condition molted more heavily (controlling for fat stores), suggesting that body condition limits the intensity of molt. Heavily molting equatorial sparrows also had lower amounts of fat (controlling for body condition), suggesting a trade-off between allocation of resources to fat stores versus feather growth. Molt progressed slowly in Rufous-collared Sparrows relative to previously described patterns in their arctic congener, which is concordant with a slower pace-of-life syndrome in tropical, as compared with high latitude, birds.

Resumen · Costos energéticos y estrategias de muda post-juvenil en un ave ecuatorial, el Chingolo (*Zonotrichia capensis*)

Muchas especies de aves tropicales presentan historias de vida lenta, exhibiendo bajas tasas metabólicas, esfuerzo reproductivo anual reducido, y mayor longevidad que las especies que habitan en latitudes más altas. La variación en historia de vida en especies tropicales ha sido bien documentada para individuos adultos, pero sabemos comparativamente poco de los individuos inmaduros. Aquí estudiamos las estrategias de muda y deposición de grasa en individuos inmaduros de Chingolo (*Zonotrichia capensis*) en una población ecuatorial de altura y comparamos los resultados con un estudio similar realizado en una población ártica del congénere Chingolo Coroniblanco (*Zonotrichia leucophrys gambelii*). En cautiverio, individuos juveniles de *Z. capensis* incurrieron costos energéticos debidos a la muda inducida, similar lo encontrado en *Z. leucophrys gambelli*. En contraste, *Z. capensis* inmaduros mudando en libertad presentaron depósitos de grasa que disminuyeron a lo largo del tiempo, lo opuesto a *Z. l. gambelii*, que deposita más grasa antes de migrar. *Z. capensis* inmaduros en buen estado nutricional (controlando por diferencias en deposición de grasa) mudaron de manera más intensa, lo que sugiere que el estado nutricional limita la muda. Individuos inmaduros de *Z. capensis* mudando de manera intensa presentaron menor cantidad de grasa depositada (controlando por diferencias en estado nutricional), lo que sugiere un balance entre la deposición de grasa y la muda. La muda fue más lenta en la población ecuatorial de *Z. capensis* comparado con la de *Z. l. gambelii*, lo que concuerda con lo esperado debido a la historia de vida más lenta en aves tropicales.

Key words: Energetic costs · Feather growth · Latitude · Post-juvenal molt · Rufous-collared Sparrow

INTRODUCTION

Many tropical vertebrates have slow-paced life history strategies that are evident at many stages of their life cycles (Conover 1992, Lovegrove 2000, Robinson et al. 2010). For example, tropical bird embryos and nestlings develop slower, parental care of fledglings is longer, adult lifespan is greater, annual reproductive investment (including clutch size) is lower, adult metabolic rates are slower, and investment in adult survival is greater compared with birds at higher latitudes (Moreau 1944, Ricklefs 1976, Ricklefs 1997, Ghalambor & Martin 2001, Martin 2002, Wiersma et al. 2007, Robinson et al. 2008, Ricklefs 2010, Robinson et al. 2010). Life history theory predicts, and empirical evidence demonstrates, that reproductive maturation is delayed and the juvenile and immature stages are prolonged in organisms with slow paced life histories (Gadgil & Bossert 1970, Stearns 1976, Hutchings 1993, Lankford et al. 2001). Beyond slowed maturation, we know comparatively little about the immature life history stages of tropical organisms. Nonetheless, the immature stage represents an important life history stage in most organisms. Events that occur during the immature stage (e.g., mortality) can strongly influence the evolution of life history strategies (Reznick et al. 1990, Robinson et al. 2010). At a minimum, an improved understanding of the immature stage would provide a more comprehensive view of how life history strategies vary with latitude.

High levels of mortality and dispersal often characterize the immature period (Magrath 1991, Newton 1998, Naef-Daenzer et al. 2001), but beyond this we know little about the specific challenges facing immature individuals, particularly in tropical taxa. In many bird species, immature individuals replace body feathers (hereafter, *post-juvenal molt*) and accumulate fat stores for the energetic demands associated with their transition to reproductive maturity. These challenges are not unique to the immature life history stage, but are important obstacles that must be surpassed on the route to reproductive maturity. Both feather growth and the accumulation of fat stores are energetically costly (Murphy & King 1992, Lindstrom et al. 1993, Witter & Cuthill 1993, Schieltz & Murphy 1995, Wojciechowski & Pinshow 2009), and thus immature birds might exhibit trade-offs in allocation of resources to these two processes (Lindstrom et al. 1994, Rubolini et al. 2002, Bonier et al. 2007). Appropriate allocation of resources to each of these processes can have important fitness consequences because both feather quality and fat stores influence survival (Nilsson & Svensson 1996, Pfister et al. 1998, Hemborg 1999). Among all of the competing functions that birds invest in, feather growth might have a relatively significant impact on fitness. In most passerine birds, complete body feather molt occurs only once annually. Thus, the quality of body feathers can impact the bird for an entire year, potentially influencing mating and reproductive success, energy bal-

ance, thermoregulation, and survival (Weathers & Sullivan 1989, Nilsson & Svensson 1996, Dawson et al. 2000, Serra et al. 2007).

Almost all of what we know about selective pressures on immature birds comes from studies of northern temperate and arctic species. However, the majority of species are tropical and the suite of selective pressures facing immature birds in the tropics undoubtedly differs from those facing birds at higher latitudes. Thus, generalizations based on studies of temperate zone species might be inadequate. For example, many high latitude birds migrate further, experience greater seasonal variation in temperatures and food availability, suffer higher annual mortality, and invest more annually in reproduction (Ghalambor & Martin 2001, Faaborg et al. 2010, Ricklefs 2010). These differing selective pressures might underlie distinct strategies of resource allocation and trade-offs in immature birds occurring at high latitudes compared to the tropics, perhaps following the pace-of-life syndrome seen in adults.

Here we replicate a previous study conducted on arctic (69°N) White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) (Bonier et al. 2007) on a high elevation equatorial population of the congeneric Rufous-collared Sparrow (*Zonotrichia capensis*). Bonier et al. (2007) found that the post-juvenal molt in sparrows in the Arctic is intense, rapid, and energetically expensive. Arctic *Zonotrichia* sparrows replace all of their body feathers simultaneously, resulting in rapid progression of molt and significant costs of feather growth. Arctic sparrows are limited in the amount of time available to both molt and accumulate fat prior to the onset of cold temperatures and snow cover that coincides with their southward migration (Figure 1). In contrast, the focal equatorial population of Rufous-collared Sparrows occurring in the Andes Mountains (3300 m a.s.l.) of Ecuador is nonmigratory and experiences climatic conditions that do not deteriorate dramatically as the season progresses (Figure 1). Given these differences in seasonal variation in climate and migration behaviors, we predicted that equatorial birds would experience reduced time and energetic constraints, compared with their arctic congener, while progressing through the post-juvenile molt period. These relaxed constraints might thus result in reduced trade-offs, reduced resource allocation to fattening and post-juvenal molt, and a less hurried pace of progression through the post-juvenal molt. Alternatively, costs and constraints might be conserved in the genus *Zonotrichia* or be fundamental to post-juvenal molt and fattening, and thus might be incurred independent of the environment. If so, then we expect to find similar costs, constraints, and trade-offs in arctic and equatorial *Zonotrichia*.

In this study, we combined an observational field study with a controlled captive experiment to address the following questions: Do equatorial sparrows: (1) experience significant energetic costs of body feather growth?, (2) accumulate fat stores during the post-
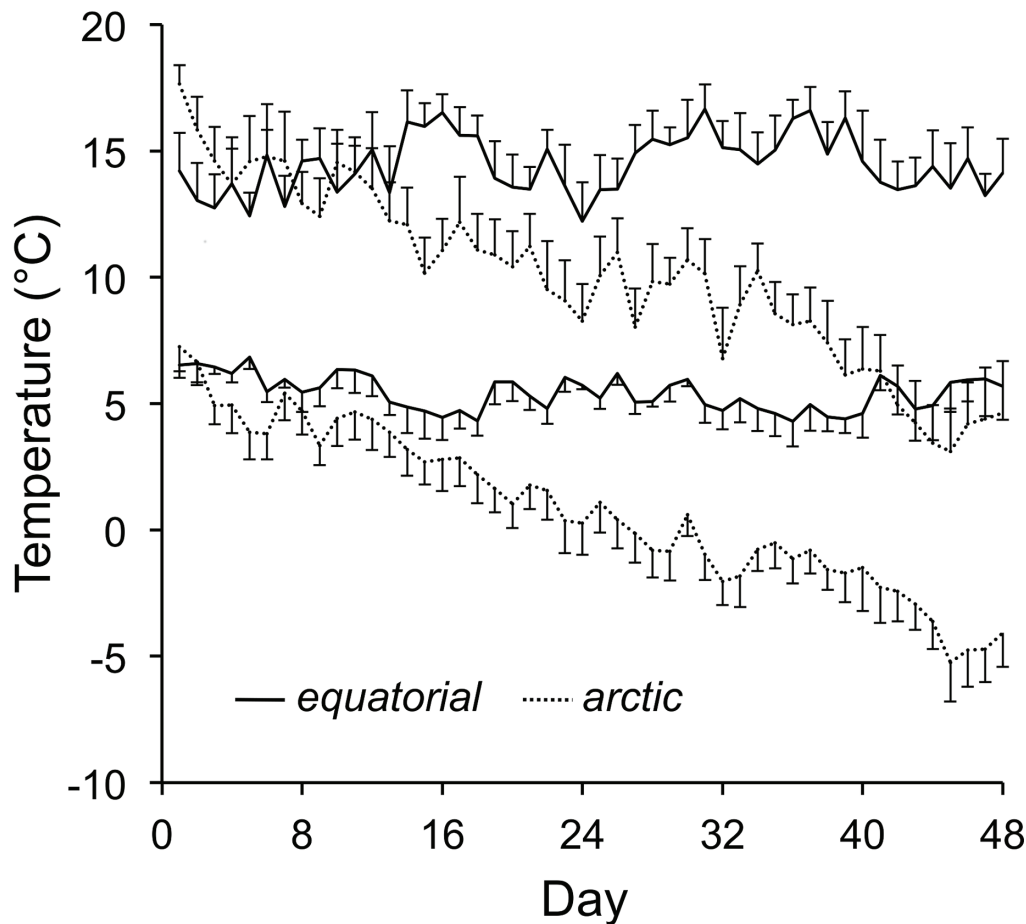
Figure 1. Daily mean maximum and minimum air temperatures experienced during the post-juvenile period by Rufous-collared Sparrows (*Zonotrichia capensis*) at Papallacta, Napo Province, Ecuador, 0°21'S, 78°8'W, 3300 m a.s.l.: solid lines, data from 2002–2006 (ITM), 1 = 15 December, and White-crowned Sparrows (*Zonotrichia leucophrys*) at Toolik Lake, Alaska, USA, 68°36'N, 149°18'W, 700 m a.s.l.: dashed lines, data from 1988–2002 (Shaver & Laundre 2003), 1 = 1 August. Data are presented as daily mean plus (maximum temperature) or minus (minimum temperature) standard error.

juvenile period?, (3) trade-off between allocation of resources to fat stores and feather growth?, and (4) progress through the post-juvenile period similarly (e.g., on a similar schedule and following similar patterns of change in molt intensity) to their arctic congener, the White-crowned Sparrow?

METHODS

Study species. The Rufous-collared Sparrow is the only tropical representative of the genus *Zonotrichia* (family Emberizidae), and is widespread and common throughout much of Central and South America from southern Mexico to Tierra del Fuego (Rising & Jaramillo 2016). We conducted our field study on a population near the town of Papallacta, Napo Province, Ecuador (0°21'S, 78°08'W, 3300 m a.s.l.). This population of Rufous-collared Sparrows is nonmigratory and breeds seasonally, with peaks of breeding activity occurring from October through December, in association with seasonal patterns of rainfall (Moore et al. 2004, Moore et al. 2005). Immature Rufous-collared Sparrows in Papallacta begin to forage independently of their parents within approximately 20 days follow-

ing fledging from their nests, often moving locally (within ~ 1 km of nest sites) in flocks with other immature conspecifics (FB, PRM pers. observ.). Rufous-collared Sparrows at Papallacta can begin the post-juvenal molt as soon as 47 days following fledging from the nest (based on observations of 3 banded nestlings recaptured as molting immatures).

Captive study. We captured 18 juvenile birds at Papallacta between 7 February and 14 March 2008 and assigned 9 birds each to a control or experimental (feather plucked) group. Several birds were actively molting, and so we allowed 3 months in captivity for all birds to complete natural molt and acclimate to captivity before starting the experiment. We balanced groups by sex and morphometric measures, so that sexes were equally represented across groups and mean fat score, body mass, tarsus length, and wing length did not differ between groups. Male and female birds in this population cannot be distinguished by plumage, but they do show size dimorphism, so we initially estimated sex using wing length. For example, in 2006–2007 known adult females sampled in this population had a mean wing

length of 62.5 mm (range 59.2–65.4 mm, N = 29) as compared to 66.5 mm mean wing length for adult males (range, 61.5–69.3 mm, N = 29). We assessed the accuracy of this sexing method by laparotomy and direct visual inspection of the gonads following completion of the experiment confirming that our groups were balanced by sex, with 3 females and 6 males in each group. Birds were transferred to Quito, Ecuador (0°8'S, 78°27'W, 2900 m a.s.l.) and individually housed in wire cages (42L x 40W x 45H cm) randomly placed on shelves (0.7 or 1.3 m off the floor) in a 3.6L x 2.4W x 2H m indoor room. The room was illuminated with natural light supplemented with incandescent lights on timers (12:12h L:D). Temperature in the room ranged from 12.6–17.5°C and was monitored with a temperature datalogger at 30 minute intervals throughout the experiment (mean = 14.5, SD = 1.1°C). Captive sparrows were fed a 50/50 mix of Trill Canary and Finch Mix (Mars, Inc., McLean, VA) and SuperMaxi Alpiste (100% Canary grass *Phalaris canariensis* seed). The Trill mix contained a mix of seeds, including Canary grass seed, and a pellet fortified with vitamins A, D, and E.

To determine baseline (pre-feather removal) rates of food intake, we provided each bird with a fixed amount of food and then reweighed and replaced the food every two days between 5 and 11 June 2008. We used dishes fitted with partial covers to minimize removal of food independent of consumption, and any food on the bottom of the cages was also collected every two days and added to the remaining food prior to weighing. We then used the cumulative measure of food removed from the dish to calculate a mean daily food intake for each bird (g of food). On 12 June, we assessed levels of natural feather growth for each bird; natural feather growth was absent for most birds, or quite low as they completed their post-juvenal molt (mean natural feather growth 2.9% across all birds). On 20 June we measured body mass (± 0.1 g with a Pesola spring scale), wing length, and tarsus length (± 0.1 mm with a caliper), and assigned each bird a fat score based on visual inspection of stores of fat in the furculum (on a scale from 0–5, following Wingfield & Farner 1978) and removed body feathers (mean 0.49 g, range 0.42–0.65 g dried feather mass) from birds assigned to the experimental group, with feather removal evenly distributed across the nape, flanks, back, breast, and belly. We handled birds in the control group similarly, but did not remove feathers. We waited 10 days and again measured daily food intake from 30 June–6 July using the same methods to determine post-feather removal food intake. We based this timing for measurement of food intake on our previous study in White-crowned Sparrows, where feather growth lasted approximately 28 days following feather removal (Bonier et al. 2007). This timing was expected to have allowed time for birds to invest considerable energy in feather replacement, but to still be actively replacing feathers. On 7 July, we assessed the level of body molt (artificially and naturally

regrowing feathers), and on 8 July we again measured tarsus length, body mass, and fat score, and also performed laparotomies on all birds to visually inspect gonads to confirm their sex (see above). To minimize inter-observer bias, feather removal, all measurements, and laparotomies were conducted by TWS. We note that with this protocol, we cannot distinguish between costs directly involved with feather growth and those resulting from increased thermoregulatory demands associated with decreased insulation. These costs are often similarly indistinguishable in nature, and would be predicted to be higher in free-ranging birds that often experience lower ambient temperatures and higher intensities of feather growth than those experienced by the captive birds.

Field study. We captured 92 immature Rufous-collared Sparrows in Papallacta between 15 December 2006 and 23 January 2007 using seed-baited mist nets. We captured 50 of these birds more than once (mean number of captures for all birds 1.75, range 1–4) and sampled them similarly at each capture. Specifically, we measured body mass (± 0.1 g with a Pesola spring scale), wing and tarsus length (± 0.1 mm with a caliper), and assigned each bird a fat score (as above, on a scale from 0–5, following Wingfield & Farner 1978). Additionally, we quantified the intensity of body feather molt using the same scoring method described in Bonier et al. (2007). Briefly, we estimated the proportion of all body feathers that were actively being replaced (as indicated by the presence of sheathed feathers) across seven regions of the body (wing coverts, back, nape, head, breast, belly, and flanks) and then calculated the mean percentage of actively growing body feathers across the bird's body to arrive at one body molt score for each bird. Each bird was also fitted with a numbered leg band along with a unique combination of colored leg bands to permit subsequent identification. To minimize inter-observer bias, all measurements including fat, molt, and plumage scores were made by FB (who also made all measurements for the previous arctic study).

We collected a small (< 150 μL) blood sample through alar venipuncture into heparinized microcapillary tubes for subsequent genetic analyses to identify the sex of each bird. We used a PCR-based method that permits sexing of birds based on a size polymorphism of the CHD-W and CHD-Z genes (for details, see Griffiths et al. 1998). To verify accuracy of this method, we also genetically sexed samples from 5 known male and 3 known female adults. All of our genetically assigned sexes agreed with the known sex of these individuals.

Statistical analyses. *Question 1: Do equatorial sparrows experience significant energetic costs of body feather growth?* We tested if equatorial birds experience significant energetic costs of body feather growth by comparing changes in body condition, fat

scores, and food intake between birds that had experimentally lost feathers and were actively replacing them, with control birds that had not. We compared measures for experimental and control birds using two-sample Kruskal-Wallis tests because the data were not normally distributed. We predicted that if body feather growth is energetically costly, then Rufous-collared Sparrows that were actively replacing feathers would have reduced fat scores, reduced body condition, and/or increased daily food intake relative to controls. Throughout both the captive and field study, we employ size-corrected mass (calculated as [body mass/tarsus length]) as an estimate of body condition following Bonier et al. (2007), with the assumption that this metric provides an estimate of level of stored resources, and that a bird with more stored resources is in better condition than a bird with fewer stored resources. The use of size-corrected mass as an index of condition is controversial (Green 2001, Merila et al. 2001, Peig & Green 2009, Schamber et al. 2009). However, our use of size-corrected mass allowed us to maintain consistency with our prior study, and this index correlated strongly with other candidate body condition metrics, including uncorrected body mass (r = 0.83), residuals of a linear regression of body mass on tarsus length (r = 0.90), and Thorpe-Lleonart scaled mass index (following Peig & Green 2009, r = 0.90) (data from Ecuador field study, N = 92 birds). We analyzed and interpreted fat stores and body condition separately, as these two indices can vary independently (Sherry 2000) and might provide different information about the energetic costs of feather growth and strategies of energy storage. We used the comparison of molt measures to confirm that our treatment did stimulate feather growth, and to provide quantification of naturally occurring feather replacement, which was ongoing at low levels in some of the birds prior to the beginning of the study.

Question 2: Do equatorial sparrows accumulate fat stores during the post-juvenile period? To determine if free-ranging equatorial Rufous-collared Sparrows accumulate fat stores during the post-juvenile period, we first tested if fat scores were significantly greater than zero, indicative of a significant storage of furcular fat. For birds captured more than once, we used a mean fat score. We used a one-sample Wilcoxon signed rank test, because data were non-normally distributed. We also conducted a one-sample Wilcoxon signed rank test on the change in fat score per day (calculated as [last fat score – first fat score] / number of days between capture) for the 50 birds that we captured more than once, to determine if they progressively accumulated fat during the post-juvenal period (i.e., mean change in fat score > 0).

Question 3: Do equatorial sparrows trade-off between allocation of resources to fat stores and feather growth? To determine if free-ranging equatorial Rufous-collared Sparrows exhibit a trade-off between allocation of resources to fat stores and feather growth, we used Spearman partial correlation

analyses of the relationship between fat score, body condition, and molt score. We employed nonparametric tests because data were non-normally distributed. To test for sex effects, we first ran analyses separated by sex. Results did not differ among males and females, and thus data from males and females were combined in our final analyses. We predicted that heavily molting birds would have lower fat scores and/or body condition if equatorial sparrows trade-off resource allocation between fat accumulation and feather growth.

Question 4: Do equatorial sparrows progress through the post-juvenile period similarly to arctic sparrows? To determine if free-ranging equatorial birds progress through the post-juvenile period similarly to arctic birds, we first used three linear regressions with molt score, fat score (scaled relative to a maximum score of 5), and body condition as the dependent variables and the day of capture (with first date of sampling at each site set equal to 1), site (arctic or equatorial), and an interaction term (site by day of capture) as factors to explore population-level patterns of progression through the post-juvenile period. We used mean values for individuals captured more than once to avoid pseudoreplication. Because molt score and fat score are bounded between zero and one, we first modeled the error distribution as a binomial distribution. Preliminary analysis indicated strong under-dispersion, so the final analysis was conducted using a quasi-binomial distribution. Body condition is bounded between zero and infinity, and the data indicated a variance that increases proportional to the mean, suggesting a Poisson error distribution. Preliminary analysis again indicated strong under-dispersion, so the final analysis was done using a quasi-Poisson error distribution. We note that molt score does not permit assessment of stage of progression through feather replacement. For example, birds might have similar scores when they are starting the molt (and intensity is increasing) and when they are nearing the end of the molt (and intensity is decreasing). However, the relationship between molt score and day of sampling provides information on how intensity of molt changes through the season and also how synchronously the birds progress through molt. In all of the above analyses, a significant interaction effect would indicate a difference in progression through the post-juvenile period between the two sites.

We supplemented the above across-individual analyses with an analysis of changes in molt score within individuals captured more than once. We examined within-individual patterns using linear regressions of the change in molt score (calculated as [last-measured molt score – first-measured molt score]) with median day between captures, duration in days between captures, site, and two interaction terms (site by duration and site by median day) as factors. We report results from the highest order simplified model with statistical significance. A significant effect of either interaction term would indicate differences
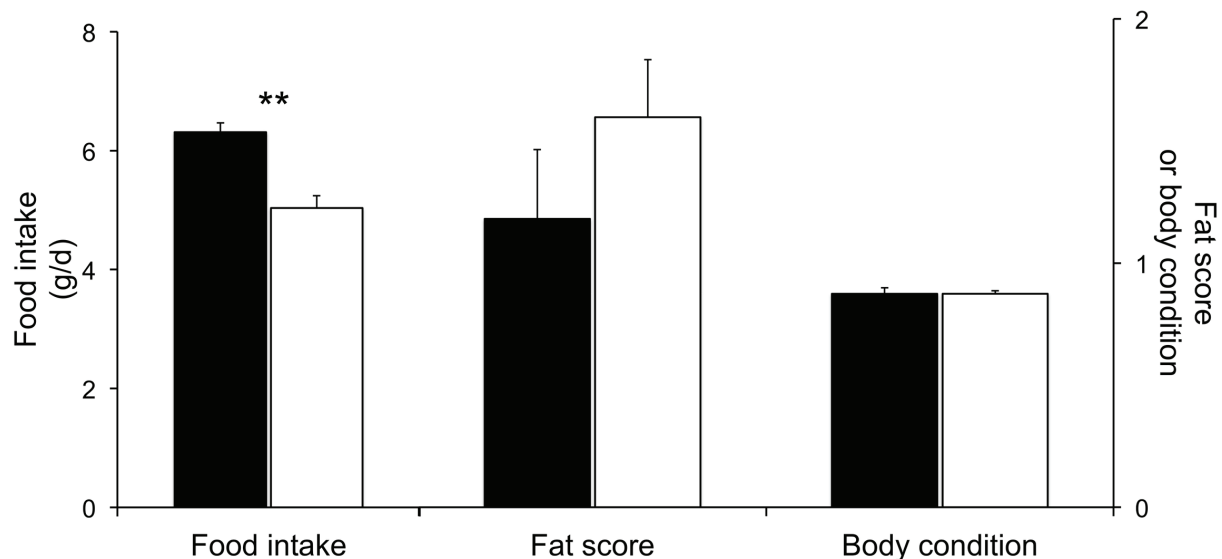
Figure 2. Daily food intake (left-hand axis), and fat score and body condition (size-corrected mass, right-hand axis) (all values given as mean + SE) in equatorial Rufous-collared Sparrows (*Zonotrichia capensis*) that were replacing body feathers (black bars) vs. control birds (open bars). Feather-replacing birds consumed 25% more food than controls (t = 4.90, asterisks indicates P = 0.0002, N = 9 treatment birds, 9 control birds), though their fat scores and body condition did not differ.

in progression through post-juvenile molt between the two sites.

RESULTS

Captive study. *Question 1: Do equatorial sparrows experience significant energetic costs of body feather growth*? Before beginning the feather removal experiment, control and experimental birds did not differ in any of the measures we assessed (fat score, Z = 0.41, P = 0.68; molt score, Z = 0.33, P = 0.74; body condition, t = -0.44, P = 0.68; daily food intake, Z = 0.62, P = 0.54, N = 9 treatment, 9 control birds). Our feather removal protocol was effective in inducing feather replacement – experimental birds had higher body molt scores than control birds (control birds, mean molt score = 0.3%; experimental birds, mean molt score = 24.9%; Z = 3.70, P = 0.0002). The level of feather replacement found within our experimental birds is within the range of molt scores observed in free-ranging Rufous-collared Sparrows in post-juvenal molt (mean 20.6%, range 0.1–70.7%). During the period of feather growth, feather-replacing birds consumed 25% more food per day than controls (Figure 2; t = 4.90, P = 0.0002). Despite this increase in food intake, control and experimental birds did not differ in fat score or body condition (Figure 2; fat score, Z = -1.33, P = 0.18; body condition, t = -0.01, P = 1.00).

Field study. *Question 2: Do equatorial sparrows accumulate fat stores during the post-juvenile period?* Immature Rufous-collared Sparrows had significant amounts of stored furcular fat (S = 1827.5, P < 0.0001, N = 92 birds). However, the birds did not progressively accumulate fat during the post-juvenile period (S = -98.0, P = 0.16, N = 50 birds). In fact, birds

tended to have lower fat scores on subsequent captures, indicative of an overall loss of fat as the season progressed (mean change in fat score per day -0.02, range -0.30–0.14).

Question 3: Do equatorial sparrows trade-off between allocation of resources to fat stores and feather growth? Heavily molting equatorial sparrows had lower fat scores than birds with lower molt scores (Figure 3a, nonparametric partial correlation, controlling for relationship with body condition; Spearman's ρ = -0.23, P = 0.03, N = 92 birds), suggesting a trade-off between allocation of resources to fat stores versus feather growth. Heavily molting equatorial birds had higher estimates of body condition than birds with lower molt scores (Figure 3c, nonparametric partial correlation, controlling for relationship with fat score; Spearman's ρ = 0.52, P < 0.0001, N = 92 birds).

Question 4: Do equatorial sparrows progress through the post-juvenile period similarly to arctic sparrows? The progression of post-juvenal molt differed between arctic and equatorial *Zonotrichia* sparrows (Figure 4a, linear regression with quasi-binomial distribution, interaction of day of capture by site; t = -6.50, P < 0.0001, N = 92 equatorial, 205 arctic birds). Specifically, equatorial birds showed no significant changes to their intensities of molt through the season (t = -1.56, P = 0.12), whereas arctic birds showed a significant decline in molt intensity as the season progressed (t = -6.50, P < 0.0001). Average molt scores differed among sites (t = 11.40, P < 0.0001), with a greater proportion of feathers molting simultaneously on arctic birds. We found a similar pattern when analyzing changes in molt score within individuals captured more than once. The duration of time between captures influenced change in molt score in
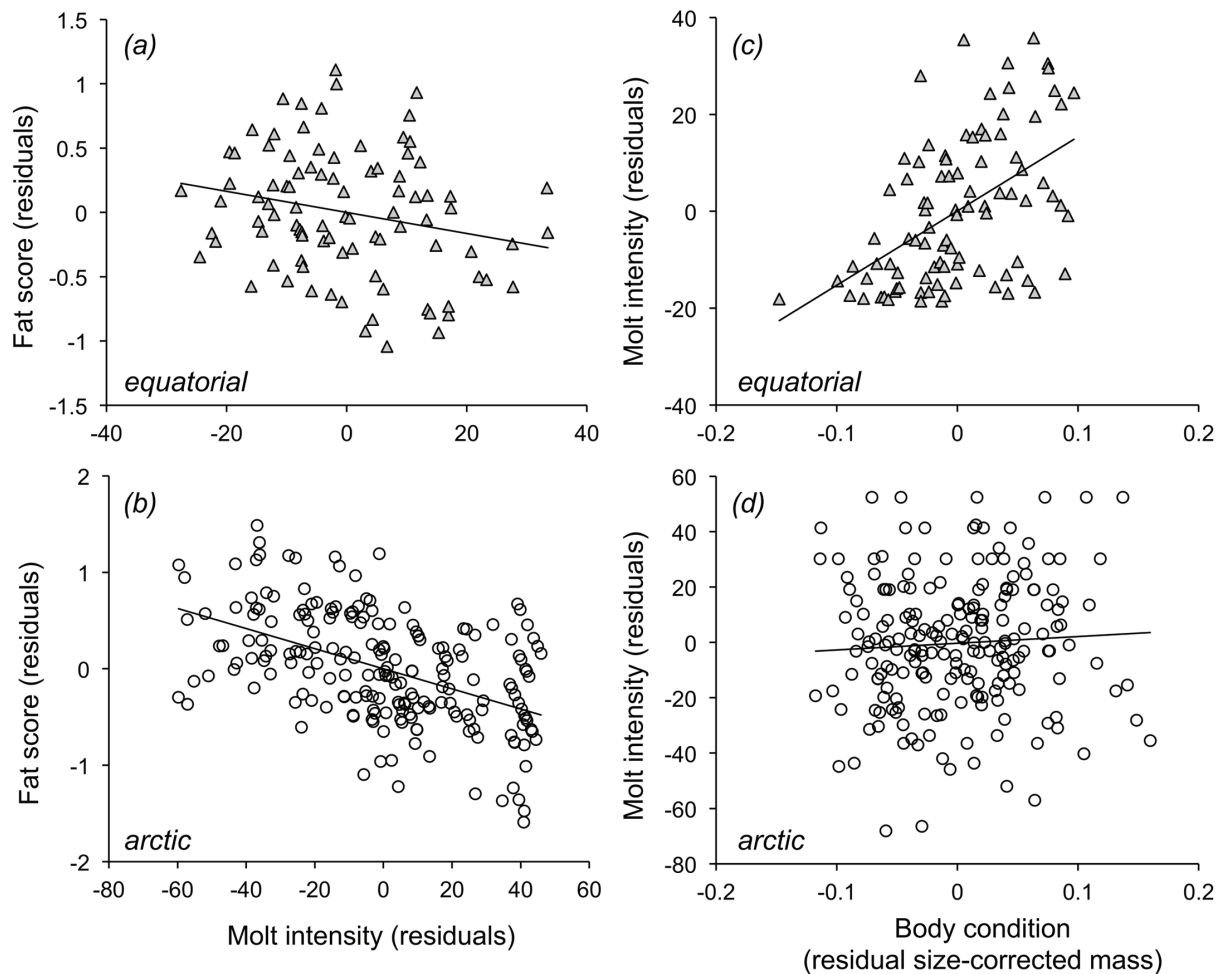
Figure 3. (a) Scatter plot of the relationship between molt intensity (residual molt score) and fat score in juvenile equatorial Rufous-collared Sparrows (*Zonotrichia capensis*) (nonparametric partial correlation, controlling for size-corrected mass; Spearman's ρ = -0.23, P = 0.03, N = 92 birds). Heavily molting birds had lower fat scores than birds with lower molt scores. (b) Scatter plot of the relationship between molt intensity (residual molt score) and fat score in juvenile arctic White-crowned Sparrows (*Zonotrichia leucophrys*) (nonparametric partial correlation, controlling for size-corrected mass; Spearman's ρ = -0.48, P < 0.0001, N = 205 birds). Heavily molting birds had lower fat scores than birds with lower molt scores. (c) Scatter plot of the relationship between body condition (residual size-corrected mass) and molt intensity (residual molt score) in juvenile equatorial Rufous-collared Sparrows (nonparametric partial correlation, controlling for fat score; Spearman's ρ = 0.52, P < 0.0001, N = 92 birds). Birds in better condition had higher molt scores. (d) Scatter plot of the relationship between body condition (residual size-corrected mass) and molt intensity (residual molt score) in juvenile arctic White-crowned Sparrows (nonparametric partial correlation, controlling for fat-score; Spearman's ρ = 0.12, P = 0.08, N = 205 birds). Birds in better condition had similar molt scores as birds with lower body condition. Note: Partial correlation analyses were conducted separately for the two species, thus residuals are not calculated similarly and are not quantitatively comparable.

arctic sparrows differently than change in molt score in equatorial birds (Figure 4b, linear regression, interaction of duration in days between captures by site; t = 3.85, P = 0.0002, N = 50 equatorial, 52 arctic birds) with molt score in the equatorial birds showing no significant change between captures (t = 0.99, P = 0.33) and molt score in the arctic birds showing a significant decline (t = 3.85, P < 0.0001).

DISCUSSION

Equatorial Rufous-collared Sparrows are closely related to their north temperate-arctic *Zonotrichia* congeners (Barker et al. 2015), but are confronted by

dramatically different selective environments. Equatorial sparrows exhibited many similarities and important differences in their progression through the post-juvenile period as compared with their arctic congeners. First, we found that both equatorial and arctic *Zonotrichia* that we studied experience significant energetic costs of feather growth (Bonier et al. 2007). In our captive study, equatorial Rufous-collared Sparrows that were replacing body feathers increased food consumption, but had similar fat scores and body conditions, relative to controls (Figure 2). The increase in food intake in feather replacing birds likely reflects direct (e.g., protein required for feather growth) and indirect (e.g.,
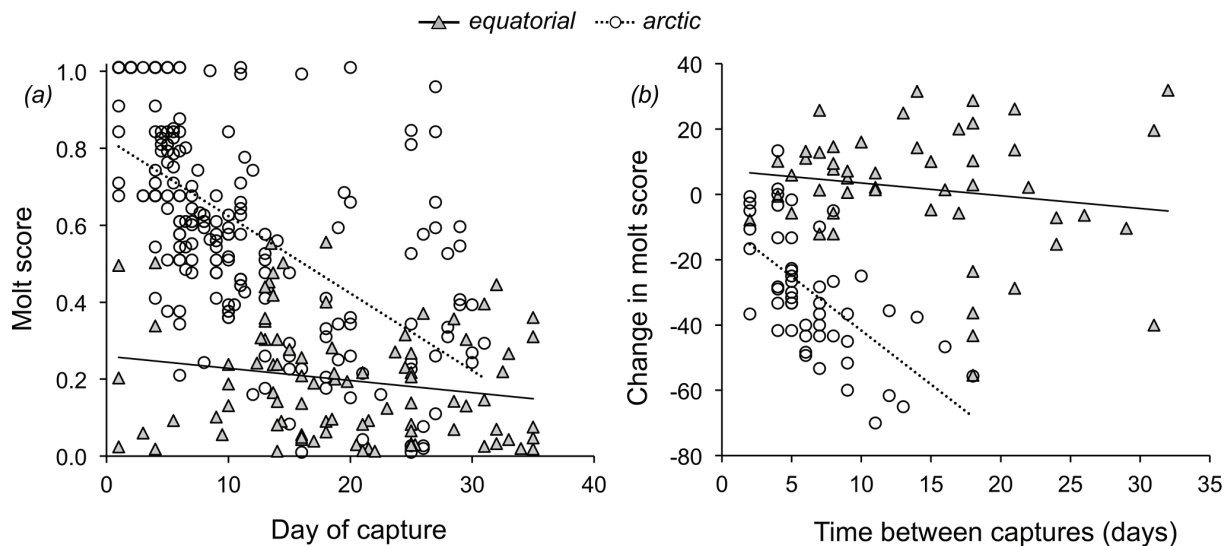
Figure 4. (a) Scatter plot of the relationship between day of capture and molt score in equatorial Rufous-collared Sparrows (*Zonotrichia capensis*, shaded triangles, 1 = 20 December 2006) and arctic White-crowned Sparrows (*Zonotrichia leucophrys*, open circles, 1 = 1 August 2004) (linear regression with quasi-binomial distribution, interaction of day of capture by site; t = -6.50, $P < 0.0001$, N = 92 equatorial, 205 arctic birds). Molt scores for arctic birds declined with progression through the season while molt scores in equatorial birds did not change. (b) Scatter plot of the relationship between the number of days between first and last capture and the change in molt score in equatorial Rufous-collared Sparrows (shaded triangles) and arctic White-crowned Sparrows (open circles) that were captured more than once (linear regression, interaction of duration in days between captures by site; t = 3.85, P = 0.0002, N = 50 equatorial, 52 arctic birds). Molt scores for arctic birds declined with number of days between captures, whereas change in molt scores in equatorial birds was unrelated to number of days between captures.

thermoregulatory) costs associated with feather growth. These energetic costs might define an important and fundamental constraint on progression through post-juvenal molt. Second, we found that equatorial sparrows possess significant fat stores. Interestingly, these fat stores tend to decline rather than accumulate during the post-juvenile period, in contrast to the pattern of pre-migratory fattening found in arctic-breeding migratory species. Third, we found that Rufous-collared Sparrows in good condition molted more feathers simultaneously than did birds in poor condition (Figure 3c). We also found evidence for an allocative trade-off between molt and fat accumulation: heavily molting birds had low fat scores (Figure 3a). Finally, we found that equatorial sparrows appear to maintain constant and low levels of feather replacement, resulting in a slow progression through molt (Figure 4). Thus, our findings suggest that patterns of molt in arctic and equatorial *Zonotrichia* sparrows are shaped by selection, but the energetic costs of feather growth are constrained. Similarly, in a recent study of molt in adults of several species of Neotropical passerines, Guallar et al. (2016) suggest both ecological adaptations and phylogenetic constraint explain variation in timing and patterns of molt among species.

Equatorial Rufous-collared Sparrows are not confronted by time constraints or energetic demands of the same intensity seen in high latitude congeners – these birds do not migrate, and climatic conditions do

not deteriorate dramatically as the season progresses (Figure 1). Thus, when confronted with the task of replacing body feathers, the birds exhibit a slow and steady approach. The most heavily molting equatorial bird that we sampled was replacing 71% of its feathers, and mean molt scores were only 21% in equatorial sparrows (compared to 100% feather molt observed in 54 of 205 individuals, and mean molt scores of 59% in arctic *Zonotrichia*; Bonier et al. 2007). By reducing the number of feathers being replaced concurrently, equatorial birds should experience reduced energetic costs of molt at any given time, and show a less pronounced trade-off between molt and fat stores (Figure 3). In addition to reduced energetic costs, benefits of a slower molt might include production of higher quality feathers, as reduced feather quality has been linked to rapid molt in other bird species (Dawson et al. 2000, Serra 2001, Serra et al. 2007). Thus, arctic birds might be forced to trade speed for quality, whereas tropical birds, being less time constrained, might be able to grow higher quality feathers.

Surprisingly, equatorial Rufous-collared Sparrows in better condition had higher molt scores, replacing more feathers simultaneously than birds in worse condition. This pattern suggests that equatorial birds molt more rapidly if they are in sufficiently good condition and have sufficient resources to do so. We saw no such relationship in the Arctic, perhaps because all arctic *Zonotrichia* molt as rapidly as possible regardless of condition (Bonier et al. 2007). On the equator,

birds that progress through the post-juvenal molt more quickly may be at an advantage, but the costs of failing to molt rapidly on the equator are likely less severe than in the arctic.

To our knowledge, the post-juvenal molt of closely related birds has been compared across latitude in only one other system. The comparative biology of captive stonechats (*Saxicola torquatus* and *S. rubicola*) derived from African- and central European-breeding populations, respectively, has been extensively studied (Wikelski et al. 2003, Versteegh et al. 2008, Helm et al. 2009), including strategies of post-juvenal molt (Helm & Gwinner 1999). In this system, captive birds derived from equatorial populations similarly displayed a slower progression through the post-juvenal molt than European-derived birds. In contrast to our findings, the maximum intensity of molt did not differ in the stonechats; both northern and equatorial-derived birds displayed simultaneous replacement of body feathers in all plumage areas during peak molt intensity (Helm & Gwinner 1999). Interestingly, Helm & Gwinner (1999) provide evidence for heritable differences in molt strategies between the populations, suggesting these different strategies may have evolved due to divergent selection in dramatically different environments.

The patterns of molt and fattening that we observed in Rufous-collared Sparrows, and their differences with those observed in an arctic congener, correspond well to their selective environments, with arctic *Zonotrichia* showing evidence of stronger selection for, and trade-offs between, rapid molt and fattening prior to deteriorating climatic conditions and the onset of migration. In contrast, equatorial Rufous-collared Sparrows showed evidence for reduced constraints on molt and fattening despite similar costs of feather replacement. The strong trade-offs evident in arctic compared to equatorial *Zonotrichia* support the importance of seasonal changes in climate driving the evolution of life history strategies of arctic-breeding birds, and suggest that equatorial Rufous-collared Sparrows, and perhaps other equatorial birds, are subject to less intense selection by climate, allowing for a slower-paced progression through the post-juvenile period.

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