

THE EFFECTS OF LIMITED WINTER FOOD AVAILABILITY
ON THE POPULATION DYNAMICS, ENERGY RESERVES,
AND FEATHER MOLT OF THE SWAMP SPARROW

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ABSTRACT

Small birds likely face energetic challenges in temperate zone winters posed by cold weather coupled with food scarcity. These challenges are often assumed to occur, but are rarely experimentally tested. I hypothesized that the naturally occurring, lower abundances of food in temperate zone winters limit a bird's ability to acquire optimal energy and ultimately limit fitness. In this dissertation, I show that supplementation of food decreased mortality and improved traits potentially associated with future reproductive success of wild swamp sparrows (*Melospiza georgiana*), supporting the hypothesis that winter food abundance limits fitness. These results come from a replicated and controlled food supplementation experiment conducted over three years. First, I demonstrated that following food addition, immigration increased, leading to higher densities, and that all age/sex classes experienced higher survival and maintained larger energy reserves (Chapter I). Survival was positively related to energy reserves, indicating that food availability limits survival through a bird's ability to maintain sufficient fat. In addition to causing mortality in winter, food limitation of energy reserves may carry over to affect future reproductive success by influencing timing of preparations for breeding, including migration. In Chapter II, I show that swamp sparrows decreased fat reserves over each winter, despite unlimited food availability, indicating that they adaptively regulated fat reserves, potentially to balance starvation and depredation risks. Fat reserves of control birds tracked recent temperature and control birds lost muscle throughout the winter, indicating that they were limited by food and were unable to reach optimal fat levels on a daily basis. These

results suggest that limitation of energy reserves by food availability can be influenced by temperature and predator abundance. Lastly, I demonstrated that food abundance limits the timing of molt in the wild (Chapter III), an unprecedented finding. Because molt, migration, and breeding typically do not overlap, early molt might lead to earlier migration and breeding. Therefore, we hypothesize that timing of molt is another mechanism by which winter food abundance can limit reproductive success. These results provide strong evidence that food availability can limit wintering temperate migrants in a variety of ways.

DEDICATION

To all of my mentors past and present.

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ATTRIBUTION

Dr. Russell S. Greenberg, Center Head, Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC 20013. Dr. Russell S. Greenberg was a co-advisor throughout my dissertation research. He is a coauthor on all manuscripts (Chapters I, II, and III) in this dissertation.

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CHAPTER I. EXPERIMENTAL SUPPORT FOR FOOD LIMITATION OF A SHORT-DISTANCE MIGRATORY BIRD WINTERING IN THE TEMPERATE ZONE

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Laila M. Kirkpatrick, and Jeffrey R. Walters

Abstract. The Winter Food Limitation Hypothesis (WFLH) states that winter food abundance contributes to population limitation of migratory birds. Evidence is accumulating that long-distance migratory birds wintering in tropical climates have high overwinter survival probabilities and that winter food limitation mainly affects their fitness non-lethally by limiting energetic reserves necessary for successful reproduction. In contrast, the relative roles of direct mortality vs. indirect effects caused by food limitation have not been investigated thoroughly on short-distance migratory birds wintering in temperate zones, where they face thermal challenges. We performed the first test of the WFLH for a temperate migratory bird in the wild on the swamp sparrow (*Melospiza georgiana*), with a replicated plot-wide food supplementation experiment. In contrast to tropical, but consistent with other temperate-wintering migrants, swamp sparrows on unmanipulated plots showed relatively low apparent survival across the winter. Following food addition, birds i) immigrated to experimental plots, which subsequently supported approximately 50% higher abundances, ii) experienced increases of within-season apparent survival of 7–13%, depending on age/sex class, and iii) had higher scaled mass index values. The last two findings are interrelated because birds with higher scaled mass had higher survival probabilities, further supporting direct effects of winter food limitation. Food limitation of fat reserves might also have an indirect effect on reproductive success by limiting migration

timing. Increases in scaled mass were higher in adult and immature females, suggesting that they are disproportionately affected by food limitation. Evidence of competition supports the hypothesis that effects of winter food limitation are density-dependent. Based on Robust Design Modeling, we found no support for emigration prior to food addition, indicating that our estimates of mortality are unbiased. Global change is likely to affect the energetic equation that underlies winter food limitation in this system.

Key words: abundance; body condition; carry-over effects; density-dependence; population limitation; scaled body mass index; short-distance migratory bird; survival; Winter Food Limitation Hypothesis; WFLH

INTRODUCTION

Identification of factors that contribute to population limitation, and when during the life cycle such factors occur, is central to understanding many aspects of the ecology and evolution of organisms. Limiting factors provide essential information for unraveling the formation and function of complex ecosystems (Vitousek et al. 1997), and resource limitation forms the basis for both natural and sexual selection (Darwin 1859). On the practical side, determining the nature of limiting factors is crucial for developing conservation strategies, especially when planning for global climate change (Langley and Megonigal 2010). Despite this, for most taxa, major limiting factors are assumed to occur, and are not rigorously examined or experimentally tested (Newton 1998).

Identification of important limiting factors has proven particularly challenging for migratory animals, which face potential population limitation at sites that are often hundreds or thousands of kilometers apart. Migratory birds are thought to be limited in winter by habitat loss

and quality, poisoning, hunting, and extreme weather (Baillie and Peach 1992, Rappole and McDonald 1994, Goss-Custard et al. 1995, Newton 1998, Sillett 2000), but critical analyses of the relative importance of these factors are relatively rare. Lack (1954, 1966) and Fretwell (1972) proposed, and Sherry et al. (2005) formalized, the Winter Food Limitation Hypothesis (WFLH), which holds that the abundance of food during the resource poor time of year is probably a dominant source of population limitation for migratory birds. The WFLH states that winter food availability contributes to population limitation of migratory birds in two ways: first, winter food abundance could limit populations directly, locally through emigration or through immediate mortality; and second, winter food abundance could limit population size indirectly, by limiting body condition, which then “carries over” to affect reproductive success in the following breeding season (Marra et al. 1998, Newton 2006).

Evidence supporting the WFLH comes mainly from long-distance insectivorous migrant birds that winter in the tropics. Most results point to food limitation working through indirect effects rather than direct effects. Body condition was positively related to manipulated (Brown and Sherry 2006) and measured (Strong and Sherry 2000) food abundance, and to habitat type (Marra and Holberton 1998, Marra et al. 1998) and weather (Latta and Faaborg 2002), intermediate variables that are probably related to variation in food availability. These documented effects on body condition, in turn, have been shown to influence the performance of birds that is ultimately related to breeding success. Specifically, body condition is thought to limit timing of spring migration departure and subsequently arrival to, and success on, the breeding grounds. This mechanism is supported by relationships between winter habitat quality, migration arrival date, and reproductive success (Norris et al. 2004, Saino et al. 2004, Reudink 2009), and relationships between departure date and winter habitat (Marra et al. 1998), body

condition (Marra et al. 1998), food abundance, and weather (Studds and Marra 2007, Studds and Marra 2011).

Moving from the individual to the population level, observational studies provide mixed support that winter food can directly limit population size of long-distance migrant birds. Sherry et al. (2005) reviewed rapid changes in winter population size following changes in natural food resources, which suggest that food can limit populations locally through immigration and emigration. In contrast, survival of long-distance migratory birds during the stationary phase of winter is high (Marra and Holmes 2001, Sillett and Holmes 2002, Conway et al. 2005) and the one experimental manipulation of food abundance found no evidence of food limiting survival or abundance (Brown and Sherry 2006). Correlations between fecundity and winter weather (Sillett et al. 2000) suggest that mortality caused by winter food limitation is additive rather than compensatory.

All of the above studies pertain to insectivorous temperate zone breeding birds that winter in the tropics. The WFLH has not been tested in the wild on short-distance migratory birds that winter in temperate zones (hereafter referred to as temperate migrants). Temperate migrants, however, often winter under more thermally challenging conditions in which one might expect a larger impact of food supply on individual fitness and population limitation. This is because in addition to a reduced food supply during the winter months (which may be shared by tropical wintering birds facing a dry season), temperate migrants are likely to experience temperatures well below their thermal neutral zones in winter, thus elevating energy needs for thermoregulation (Liknes et al. 2002). Given the reduced food availability and cold temperatures, food limitation could impact temperate migrants primarily through direct mortality. Indeed, resident species experience relatively low winter survival, and food limitation

has been documented in a few species (Brittingham and Temple 1988, Jansson et al. 1981). In addition, temperate migrants that were allowed to gain mass in captivity initiated spring migration earlier (Bridge et al. 2010), suggesting a role for indirect food limitation of reproductive success in temperate migrants.

Although the WFLH is stated in terms of limitation, both direct and indirect effects of food availability could result from either density-independent (“limiting”) or density-dependent (“regulating”) processes. While it is often difficult to distinguish between the two (Newton 1998), competition for resources would suggest density-dependent processes. One sign of competition is the presence of dominance relationships. In many bird species, adults are dominant to immatures and males are dominant to females (Ekman et al. 1981, Smith et al. 1980, Piper and Wiley 1989) and these asymmetries can translate into different intensities of food limitation among age and sex classes. There is support for class-specific magnitudes of food limitation for migratory and resident birds wintering in the temperate zone and migrants in the tropics, which is inconsistently shown in survival (Smith et al. 1980, Jansson et al. 1981, Marra and Holmes 2001, Johnson et al. 2006, but see Brittingham and Temple 1988, Silet and Holmes 2002) and body mass maintenance (Brittingham and Temple 1988, Marra and Holberton 1998, Johnson et al. 2006, but see Brown and Sherry 2006), and consistently shown in migration timing (Marra et al. 1998, Saino et al. 2004, Bridge et al. 2010).

We tested the WFLH with a temperate migrant, the swamp sparrow (*Melospiza georgiana*), using a plot-wide food manipulation experiment. We tested both direct and indirect effects of food limitation by determining if food addition led to increases in 1) abundance through immigration, 2) within-season survival, and 3) body condition, and additionally, 4) if individuals with higher body condition experienced higher survival. We tested for differential

effects of treatment on each age/sex class, which might indicate dominance relationships and density-dependence. Emigration from study plots would artificially inflate mortality estimates, so we tested for emigration based on mark-recapture data.

METHODS

Study species and plots

Swamp sparrows are temperate migrants that spend the summers (approximately May–September) breeding in northeastern North America and migrate short distances to winter primarily in the southeastern United States and in lower numbers along the Pacific Coast of North America (Mowbray 1997, Fig. 1). Swamp sparrows forage primarily on seeds in the winter (Mowbray 1997), along with a few arthropods on warm days and gastropods at our study site (pers. obs). In the spring and summer they shift to a diet dominated by arthropods with some seeds (Mowbray 1997, Olsen pers. comm.). All data were collected in coastal Hyde County, North Carolina during the winter months of January–March, 2008–2010. At this site, *M. m. georgiana*, *M. m. nigrescens* (Greenberg et al. 2007) and potentially *M. m. ericrypta* occur in syntopy. During these periods, temperatures were below the swamp sparrow’s thermal neutral zone (lower limit 24.1°C, Yarbrough 1971), except for 12.5 hours in 2008, 8.5 hours in 2009, and less than two hours in 2010 (Fig. 2), indicating that the environment was thermally challenging and that the sparrows required much energy in order to maintain body temperature (Liknes et al. 2002). We used four study plots (Control 1 and 2, Experimental 1 and 2, referred to as C1, C2, E1, E2; Fig. 1). All plots were separated by at least 3.4 km (mean 27.7 km); we detected no movement of swamp sparrows between them. The habitat was similar at all sites,

composed of an ecotone between low and high brackish marshes, dominated by *Spartina patens*, *Iva frutescens*, *Baccharis halimifolia*, with few a *Myrica cerifera* and small stands of *Phragmites australis* (Fig. A1).

Food manipulation

2008 served as a baseline year in which we collected data at all four plots without manipulating food. We randomly assigned two plots as experimental (E1 and E2) and two plots as controls (C1 and C2) and supplemented food on the experimental plots in 2009 and 2010 (Fig. 1). In order to provide supplemental food for as many individuals on experimental plots as possible, regardless of dominance status (Theimer 1987), we distributed food at the intersections of a grid formed of 9 x 4 lines, with lines separated by 25 m, producing 36 feeding stations per plot. At each station, we maintained a small pile of millet and mealworms (*Tenebrio molitor*). We supplied millet *ad libitum* and replaced mealworms when replenishing millet. In total, over January–March 2009 and 2010, we applied 719.32 kg of millet and 14,389 mealworms to E1 and E2 (Table A1). The amount of food added in 2010 was larger than in 2009 because of loss to occasional flooding. Swamp sparrows were frequently seen eating millet and mealworms from the piles (Fig. A2) and we regularly observed those items in their feces.

Data collection

We captured birds with mist-nets during mark and recapture sessions spaced evenly throughout the study period (January–March) each winter. Throughout the study, we altered the number of recapture sessions per year, days per session, and number of nets used per day to reduce the person-hours required for data collection. We performed five sessions in 2008 and

2009 and four in 2010. Sessions were 3 days long in 2008, and 2 days long in 2009 (except E2: 3 days) and 2010. The number of horizontal meters of net used per day was 216 in all years at C1, 120 at the other plots in 2008, and 150 at the other plots in 2009 and 2010. Plot C1 has been studied with a similar number of daily net meters since 2006 and the number of net meters were smaller at other plots because those plots were smaller. The area of each site and time of netting remained constant across all years. Nets covered approximately 1.2 ha at three plots and 1.8 ha at one plot (C1). We opened nets in the morning before nautical twilight and closed nets after approximately 4 hours, between 1000 and 1100 hrs. Captures were concentrated in the early part of the morning. Upon each bird's capture, we applied a uniquely numbered leg band and three colored bands or recorded the number of a previously applied band, measured body mass to the nearest 0.01 g with an electronic balance and tarsus length to the nearest 0.1 mm with digital calipers, determined age, and collected blood from the brachial vein or feather quills for genetic sexing. We aged birds as immature (1st winter) or adult ($\geq 2^{\text{nd}}$ winter) based on skull pneumatization, face and crown coloration (Danner unpub. data), and wing growth bar alignment (Danner unpub. data). We determined the sex of birds with a PCR-based genetic test (Griffiths et al. 1998, see Appendix B for details).

Analyses

If food limits abundance, survival, and body condition, we would expect increases in each variable following food addition (in 2009 and 2010) on supplemented plots, but no change on control plots. We tested if Treatment, Age, and Sex were important predictors of dependent variables using an information-theoretic approach. For each analysis, we constructed candidate sets of biologically plausible models that described each response variable and then compared

the fit of models to the data using Akaike's Information Criterion (Akaike 1973) corrected for small sample sizes (AICc, Burnham and Anderson 2002). To assess the support for Treatment and other predictor variables, we calculated an evidence ratio for each, which is the probability that the model of interest is the best model in the set compared to that of an appropriate null model. The null model did not include the predictor of interest. Evidence ratios were calculated as the weight of model of interest/weight of appropriate null model. In addition, we described relative fit of models based on Δ AICc scores. To show effect sizes of important variables, we present model average predictions and unconditional standard errors (calculated from all fit models) for each age/sex class considered in the analysis. Model names include only higher-level interactions although all main effects and lower-level interactions are also included in the models. For example, the model titled Treatment * Scaled mass * Age + Sex includes the following terms: Treatment * Scaled mass * Age + Treatment * Scaled mass + Scaled mass * Age + Treatment * Age + Treatment + Scaled mass + Age + Sex.

In contrast, we compared abundance separately on experimental and control plots to test for an effect of Treatment Period (before treatment in 2008 vs. food addition in 2009 and 2010 on experimental plots). This method allowed us to account for differences in abundance among plots and therefore test food limitation using the evidence ratio of Treatment Period. Because apparent survival and recapture probability are latent variables (not directly measured) and scaled mass included a random effect (individual), we took the approach of modeling those parameters as accurately and precisely as possible and then testing hypotheses about food limitation based on evidence ratios and comparison of model average predictions. To increase precision of parameter estimates, we modeled Treatment effects simultaneously at control and

experimental plots, which allows common parameters to be shared between plots (MacKenzie et al. 2006). All analyses were performed in R (R Development Core Team 2011).

Abundance

To test if food limits abundance, we compared fit of generalized linear models that describe the number of individuals captured per session with the variables Treatment, Period and Plot. Treatment Period had two levels, 2008 (no food addition) and 2009/2010 (when food was added to experimental plots). If food limits abundance, we would expect abundance to increase in 2009/2010 on the experimental plots, but not on the control plots. Although differences among plots are not of interest for testing our hypotheses, Plot was included because baseline abundances might differ among them. We analyzed experimental plots separately from control plots to test the effect of Treatment Period through an interaction with Plot. Plots of raw data indicated that abundance did not correlate with session number. To correct for changes in net hours between years, we used only the first and second days of each capture session and adjusted abundance estimates proportionally based on the number of net-hours used per day. We modeled abundance with a gamma error distribution using function `glm` (R Development Core Team 2011) because the data were always greater than zero and not integers (Zuur et al. 2009). We ranked models with AICc using function `aic.tab`, and calculated model average predictions with function `modavgpred` (Mazerolle 2011). Residuals from the saturated model (Plot * Treatment Period) were normally distributed and homoscedastic, indicating that all models in the set had adequate fit.

Because immigration rates following food addition might differ by age class, we also tested the effect of food supplementation on abundance of adults and immatures separately. Two

individuals in the dataset were not aged, so were excluded from these analyses. We did not analyze the sexes separately because 61 individuals (mainly from 2008 and 2009) were not sexed.

Apparent survival

Models describing apparent survival (ϕ) included combinations of the variables Treatment, Plot, Year, Sex, and Age and formed a set of 66 *a priori* models. Support for Treatment or Plot*Year could indicate a treatment effect, though the latter would require comparing model average predictions to determine the directionality and magnitude of the treatment effect. Although habitat appeared similar among sites, it might vary subtly, so we tested for an additive effect of Plot. Because age and sex classes might have different access to food due to dominance relationships, we included additive and interactive effects of Age (immature vs. adult) and Sex. Models describing recapture probability (p) included only additive effects of Plot and/or Treatment, or only the intercept; we had no *a priori* hypotheses that p would vary according to Sex, Age, or Year. All combinations of ϕ and p terms were modeled using 264 Cormack-Jolly-Seber (CJS) models, which were fit and ranked using program MARK (White and Burnham 1999) and the RMark package (Laake 2011). Individuals were given independent encounter histories consisting of 4 or 5 sessions for each year. Because our data set included missing sessions, we were unable to assess overdispersion by calculating \hat{c} . We compared fit of closely ranked models with the likelihood ratio test in Program MARK. Sample sizes of individuals were: 2008: $n = 190$, 2009: 220, 2010: 228, and were roughly equal in number of adults ($n = 328$) and immatures (310), and males (301) and females (337).

Emigration

We hypothesized that food supplementation could reduce emigration from the study plots, which would bias our estimates of apparent survival obtained from CJS analyses. However, if there was no evidence of emigration in 2008 (before food supplementation), we would not need to account for emigration in later years. We therefore tested for emigration from plots within the winter of 2008 with Robust Design Models (Pollock 1982) using RMark and MARK. There were insufficient sampling days to fit robust models for 2009 and 2010. The five mark and recapture sessions per plot in 2008 were considered primary sampling periods, and the three capture days nested in each primary period were considered secondary sampling periods. We compared the fits of two models: Both included constant survival (S) and detection rate (p), and allowed population size (N) to vary by session. In one model we constrained temporary emigration (γ) to be zero and in the other model we allowed random emigration. Temporary emigration (γ) is represented by two different parameters, γ'' and γ' (Kendall et al. 1997). Parameter γ'' is the probability that a bird leaves the plot after session i and does not return for session $i + 1$. Parameter γ' is the probability that a bird not on the plot during session i returns to the plot for session $i + 1$. We were interested in testing emigration from each site overall, regardless of age/sex class, so analyzed all individuals together.

Scaled mass

Because birds at our study site experienced cold and stochastic weather (Fig. 2), we expected birds to accumulate more fat if possible. Therefore, we interpreted higher body mass corrected for structural size as higher body condition. We corrected body mass for structural size using the scaled mass index, following Pieg and Green (2009). As a part of the scaled mass

calculation, we calculated the standardized major axis (SMA) regression slope of mass vs. tarsus length of individuals from control plots. For all scaled mass estimates, we used average tarsus length per individual across all years. For all SMA regressions described here, plots of residual vs. fitted values and quantile-quantile plots of residuals indicated linear and homoscedastic relationships between mass and tarsus.

Despite differing tarsus lengths between the sexes (Danner unpub. data), SMA regression slopes did not differ significantly between them (Males: 2.85, 2.61–3.12 95% CI, n=716, Females: 3.02, 2.80–3.26 95%, n=550, CI, Bartlett-corrected likelihood ratio test, $df=1$, $X^2=0.942$, $p=0.332$, function `slope.com`, Warton and Ormerod 2007). Therefore, we recalculated scaled mass index including both sexes and individuals of unknown sex (n=1,196 total paired measurements of mass and tarsus). The slope of our final scaled mass index (2.95, 2.80–3.11 95% CI) was close to three, which is indicative of isometric body growth (Pieg and Green 2009).

Models describing scaled mass as a response variable included the same combinations of the variables used to estimate apparent survival (Treatment, Plot, Year, Sex, and Age), and formed a set of 66 *a priori* models. All models of scaled mass also included Individual as a random effect to account for repeated sampling, and Ordinal Day, because scaled mass is known to decrease over the season (Danner Chapter II). We fit linear mixed models using function `lmer` (Bates et al. 2011), ranked models with AICc using function `aic.tab`, and calculated model average predictions with function `modavgpred`. Model average predictions were calculated with Ordinal Day set to February 1st. Residuals from the saturated model (Plot * Year * Sex * Age + Ordinal Day + random effect of individual) were normally distributed and homoscedastic, indicating that all models in the set had adequate fit.

Apparent survival dependent on scaled mass

We tested if individuals with higher scaled mass experienced higher apparent survival by testing if adding scaled mass improved the fit and rank of top models from the previous survival analysis. We modeled scaled mass both as an additive effect and as having an interaction with treatment. The former describes a similar effect of scaled mass at all plots (control and experimental) and the latter describes different effects per treatment. Because scaled mass decreases throughout the season (Danner Chapter II), we restricted this analysis to individuals that were first captured in the first or second session per year (n=407) and used each bird's maximum scaled mass for the season. We did not anticipate an effect of scaled mass index on recapture probability, so left the covariates describing recapture probability unchanged.

RESULTS

Abundance

On both experimental plots, abundance increased following food addition (Fig. 3 top). All three models containing Treatment Period were ranked at the top of the set. The top model was 154 times more likely to be the best model in the set than models without Treatment Period (Table C1), indicating support for Treatment Period. Model average predictions indicated that swamp sparrow abundance increased by approximately 57–62% following food addition on E1 and E2, from (means \pm unconditional s.e.) 9.25 ± 0.96 and 9.39 ± 0.98 to 15.03 ± 1.17 and 14.79 ± 1.14 , respectively. On experimental plots, separate analyses for each age class revealed increases for both adults and immatures, with top models containing Treatment Period over 25 and 9 times more likely than null models, respectively (Tables C2 and C3). Model average

predictions indicated that abundances of each age class also increased by roughly 40–82%; adults on E1 and E2: from 4.89 ± 0.65 and 5.44 ± 0.75 to 7.21 ± 0.83 and 8.42 ± 0.96 , respectively, immatures on E1 and E2: from 4.41 ± 0.96 and 4.25 ± 0.83 to 8.03 ± 1.32 and 5.95 ± 1.01 , respectively. Plot was not supported as an important predictor of overall abundance (evidence ratio = 0.3), though there was mild support for plot in the age-specific models (evidence ratios = 1.3–1.4).

On control plots, abundance did not change consistently over time (Fig. 3 bottom). There was no support for an effect of Treatment Period on abundance, shown by lower rank of Treatment Period compared to a null model (Plot) for the analysis with both ages combined (Table C4) and ages modeled separately (Tables C5 and C6). In each of the three analyses for control plots, all models containing Plot were ranked at the top, and were over 1,680 times more likely to be better models in the set than those without Plot, supporting differences in abundance between plots. Model average predictions indicated higher abundances for both age groups on plot C1 (Fig. 3).

Survival

Models including Treatment and Age and/or Sex were ranked at the top of the candidate set and the highest ranked model had significantly better fit compared to the top model lacking Treatment (likelihood ratio test: $\chi^2=3.84$, d.f.=1, $p=0.050$, evidence ratio=2.5, Table C7). For models not including Age or Sex, Treatment had an evidence ratio of 3.5 when compared to the null (Intercept only model) and 4.7 when compared to Year. Model average predictions indicated that in 2008 (before food addition), apparent survival was similar on all plots, ranging from 0.68–0.83 depending on age/sex class. In 2009 and 2010 (when food was added), birds on

experimental plots experienced increases in survival of 0.06–0.09 ($\phi=0.77$ –0.89) and birds on control plots remained similar to 2008 levels ($\phi=0.67$ –0.83, Fig. 4). Age and Sex were present in the top 20 models and evidence ratios of the top model compared to the top model lacking Age and Sex was 5.57, support differences in survival among age/sex classes. Model average predictions showed that the effect of Treatment on age/sex classes was mostly additive (it did not differ among classes). Further, model average predictions showed that in all cases, survival was higher in adults than immatures and higher in females than males. Apparent survival for immature males was noticeably lower than other age/sex classes. The range of survival on experimental plots was slightly lower following food addition (0.13) than under natural conditions (0.16). Recapture probability (p) was best explained by site; the evidence ratio of the top model to the top model without site was 244 (Table 1). Recapture probability ranged from 0.25 on plot E1 to over 0.5 on C1 (Fig. 5). There was no support for an additive effect of Treatment on p (evidence ratio=0.36).

Emigration

The Robust Design model that constrained emigration to zero captured 0.98 of the model weight, providing support that there was no emigration in 2008, before food addition (evidence ratio=65.63, Table 9). The model average survival (S) estimate for January–March 2008 was 0.78 ± 0.03 unconditional s.e. Estimates from the top model included abundance, which ranged from 160.96–231.60 depending on session, and encounter probability, $p = 0.15$.

Scaled mass

The top ranked model explaining scaled mass index accounted for 0.87 of the model weight and included an interaction between Treatment, Sex, and Age (Table C8). This model was $8.647E+07$ times more likely to be the best model in the set than the highest ranked model that did not have an effect of either Treatment or Plot * Year. Support for the top model indicates that scaled mass changed in response to Treatment and that sex/age classes differed in the amount of this change. Models with an interaction between Plot and Year were ranked highly, and accounted for approximately 12% of the model weight, indicating that scaled mass differed by Plot by Year. The top model, however, which included Treatment, was 12.7 times more likely to be the best model in the set compared to the top ranking model with Plot * Year. This indicates that the Plot * Year interaction reflects the Treatment effect rather than differences between Plots within a Treatment.

Model average predictions show that all age/sex classes increased scaled mass when given supplemental food (Fig. 6). On control plots, and before food addition on experimental plots, adult males had higher scaled mass than other age/sex classes. Following food addition, however, adult and immature females increased scaled mass to levels near that of adult males. On experimental plots, immature males showed modest increases in scaled mass in the first year of food supplementation, and larger increases in the second year, though remained below the other age/sex classes.

Survival dependent on scaled mass

Model average predictions show that for all age/sex classes, individuals with higher Scaled mass experienced higher survival probability (Fig. 7). All models with Scaled mass were ranked at the top of the set and the lowest ranked model with Scaled mass had an evidence ratio

of 17 compared to the top model without Scaled mass (Table C10). All models with the Treatment * Scaled mass interaction were ranked above models with additive effects of Scaled mass (evidence ratio of the top interactive and additive models=13). Support for the Treatment * Scaled mass interaction indicates that scaled mass had different effects on survival depending on Treatment. Model average predictions show that experimental birds experienced a quadratic pattern between Scaled mass and survival, where individuals above ~17g experienced survival near 1.0 whereas there was a steep drop in survival below that mass. In contrast, for control birds, the range of survival probabilities was nearly linear in relation to Scaled mass and below predictions for experimental birds above ~17g.

DISCUSSION

Food limitation

Many short distance migratory birds of temperate zones face serious energetic challenges in winter. These species must find enough to eat among reduced and continuously declining food stores (mainly seeds) to survive thermally challenging and unpredictable winter weather. In addition, they must fit into their energetic budgets some preparations for the following breeding season. Because of these challenges, winter food abundance has been hypothesized to limit individual fitness and potentially population sizes of temperate migrants. However, the Winter Food Limitation Hypothesis has not previously been tested experimentally in the wild on a temperate migrant.

Using a plot-level food supplementation experiment, we found that food limits the abundance, survival, and body condition of swamp sparrows in winter. These results provide

strong evidence that food abundance can limit populations of short distance migratory birds wintering in the temperate zone. Abundance of birds increased by approximately 50% on both experimental plots following food addition, indicating that birds immigrated from surrounding areas. Although we detected immigration into the supplemented plots, we observed no movement of individuals among sites.

Apparent survival (ϕ) was approximately 0.67–0.83 during the winter months of January–March under natural conditions, depending on age/sex class. Annual swamp sparrow survivorship ($\phi \pm \text{s.e.}$) is estimated to be 0.45 ± 0.07 for females and 0.52 ± 0.04 for males (Etterson et al. 2011). Monthly probability of survival in January–March (0.87–0.94) is therefore up to 9% lower than that predicted by constant monthly survival throughout the year (0.94–0.95). This disparity indicates that a disproportionate amount of mortality occurs in the winter months, suggesting that winter mortality is additive rather than compensatory and contributes to population limitation. When provided additional food, survivorship during the months of January–March increased by 0.06–0.09 (7–13%), depending on age/sex class, suggesting that lower survivorship in winter is caused by food limitation.

Recapture probability was best explained by Plot, possibly owing to differences in mist net distribution in relation to morning commute routes from roost to forage locations. Habitat structure was similar among plots and therefore likely less important in affecting recapture probability. The lack of a Treatment effect on recapture probability suggests that broad daily movement patterns were unaffected by supplemental food.

Based on Robust Design Models, we found support for a lack of emigration in 2008 (before food manipulation) on all plots. This indicates that the difference in survival that we observed between treatments is not an artifact of reduced emigration from treated plots. Aside

from playing a functional role in estimating survival for this experiment, the lack of emigration indicates that swamp sparrows have high site fidelity throughout the winter, which has not previously been reported for this species. High site fidelity might provide information on patterns of food availability in this system. Both temporal unpredictability and spatial homogeneity of food availability are predicted to promote site fidelity (Switzer 1993). Indeed, food availability is likely temporally unpredictable in this system (food can be covered with snow and ice by erratic weather patterns) but spatially homogenous given the relative homogeneity of the swamp sparrow's winter habitat and lack of insect availability (a spatially heterogeneous resource) during winter. Temporal unpredictability of food could exacerbate food limitation.

Scaled mass index increased on experimental plots when food was supplemented, indicating that food is limiting under natural conditions. Birds carried up to approximately 2g more mass following treatment. On experimental plots, we also found that scaled mass increased by year. The cause of higher scaled mass in 2010 than 2009 is unknown. Although a greater amount of food was supplied in 2010 than 2009, it was supplied *ad libitum* in both years, suggesting that differing degrees of food limitation are not responsible for yearly differences in scaled mass. In addition, birds on control plots had higher scaled mass in 2010, suggesting a factor related to that year affected all plots. 2010 was generally colder than previous seasons, and it is possible that birds adaptively carried more fat to survive these colder conditions (see Chapter II).

Evidence that food limits survival is corroborated by our finding that individuals with higher body condition experienced higher survival probabilities. This relationship confirms the assumption that higher body condition is the mechanism responsible for higher survivorship on

experimental plots. The positive relationship between Scaled mass and survival was evident in both control and experimental birds, but interestingly, we found that the slope and curvature of this relationship differed by Treatment. The relationship was quadratic for experimental birds and nearly linear for control birds. For experimental birds, the increasing quadratic pattern indicates that reaching a threshold of ~17g ensures almost certain survival. For birds above ~16g, experimental birds had higher probabilities of survival than control birds of the same Scaled mass. This suggests that in addition to the fat a bird carries at any given time, food availability affects survival in another way. One possibility is that the continuous supply of food available to experimental birds allowed them to recover quickly after particularly thermally challenging weather episodes and thus increase survival. Alternatively, supplemental food might have allowed experimental birds to maintain sufficient fat levels when much of the natural food base was covered with ice (supplemental food was almost always accessible), while control birds were unable to find food. We also found that experimental birds with masses below average (average mass was ~17g) had lower survival than control birds of the same mass. A potential cause of this unexpected pattern is that the light experimental birds were subordinate while foraging and were outcompeted more often following the large influx of immigrants, resulting in starvation or depredation while foraging in conspicuous locations.

Evidence for density-dependence

The documented effects of food limitation on abundance, survival, and body condition might be controlled through density-independent or density-dependent processes. In the system studied here, density-independent processes might limit populations through changes in food availability, including snow or ice coverage of food, or storms that impose severe

thermoregulatory costs. Density-dependent processes would most likely include interference or exploitation competition for food. Both forms of competition could be based on either contests or scramble behavior. In systems where food depletion is thought to occur through foraging, such as the one described here, it seems likely that exploitation competition could cause or exacerbate food limitation.

Overall, competition for food (and therefore density-dependence) could be supported since supplementation allowed all age/sex classes to successfully immigrate, improve their body condition, and survive better. The strongest evidence for competition was in different scaled mass among the age/sex classes. We found that under natural conditions, adult males had the highest scaled mass, which is consistent with expectations from dominance hierarchies where adult males are dominant to all other classes, and suggests contest interference competition. Dominance relationships have not been reported in swamp sparrows; however, adult-male dominated hierarchies have been found in other species of sparrows in winter (Rohwer et al. 1981, Piper and Wiley 1989). Further supporting contest interference competition, both adult and immature females experienced larger increases in mass than adult males following food addition and as a result converged with adult males, potentially indicating release from subordinate foraging positions. On the other hand, the scaled mass of immature males did not converge upon that of adult males and was maintained lower than the other age/sex classes, perhaps reflecting factors other than dominance. Our finding that sparrows immigrated to experimental plots following food addition is consistent with predictions from Ideal Free and Ideal Despotic Distribution models, which assume that competition limits food availability and therefore the settlement choices of individuals (Fretwell and Lucas 1970, Fretwell 1972). We therefore count food limitation of immigration in this system as tentative evidence of density-

dependence through scramble or interference competition.

Competition was not clearly reflected in survival however. Differences in survival among age/classes potentially suggest competition, though the ranks are inconsistent with the expected adult-male dominated dominance hierarchy, which was generally reflected in scaled mass. In addition, survival of all age/sex classes increased in concert following food addition, suggesting that the asymmetries are not caused by competition. Immature males had the lowest survival probabilities at all times, which was consistent with scaled mass following supplementation, but not under natural conditions. Alternatively, it is possible the models were not precise enough to capture the real differences among age/sex classes.

*Food limitation in temperate migrants,
temperate residents, and long-distance migrants*

The combination of numerical limitation and the potential for carry-over effects suggests that short-distance migrants in the temperate zone experience mechanisms of food limitation reported for both temperate residents and long-distance migrants that winter in the tropics. For temperate residents, food limitation is manifested mainly in mortality, whereas food limitation is thought to play a major role in reproductive success of long-distance migrants through carry-over effects (Marra et al. 1998, Norris et al. 2004). Swamp sparrow winter survival estimates are intermediate to those of resident and long-distance migrants. Monthly winter survival probabilities of passerines are low in temperate residents (~0.85: Jansson et al. 1981, Brittingham and Temple 1988), moderate in temperate migrants (0.87–0.94: this study), and high in short-distance migrants wintering in the subtropics (>0.90, Johnson et al. 2009) and long-distance

migrants wintering in high quality tropical habitats (>0.90, Marra and Holmes 2001, Sillett and Holmes 2002, Conway et al. 2005, Johnson et al. 2006).

Carry-over effects, such as food limitation of migration, have not been well studied in temperate migrants. Recent studies suggest, however, that the size of fat reserves can lead to carry-over effects in a temperate migrant, the dark-eyed junco (*Junco hyemalis*). First, individuals allowed to gain mass while temporarily held in captivity departed earlier for spring migration (Bridge et al. 2010). Second, males with higher mass had higher levels of circulating testosterone in winter (Tonra 2011), which influences timing of breeding preparations before migration and migration itself (Tonra et al. 2011). Further, food availability has been shown to limit the timing of the pre-alternate molt in the swamp sparrow, which might also constrain timing of migration (Chapter III). Combined with our results, these studies suggest that food availability limits migration timing of temperate migrants, potentially leading to lower reproductive success, as observed in long-distance migrants (Aebischer et al. 1996, Currie et al. 2000, Norris et al. 2004).

While the difference in strengths of carry-over effects between temperate migrants and long distance migrants is unknown, it is possible that the former experience greater carry-over effects because of the more energetically challenging weather they face in the winter. In addition, short-distance migrants might have greater plasticity in migration timing than long-distance migrants, which is suggested by a greater change in migration timing in response to global warming (Butler 2003). If so, the greater plasticity in migration timing of temperate migrants could allow greater carry-over effect sizes.

Winter food limitation and climate change

Temperature and food availability are the main factors that determine the extent of food limitation in the temperate zone. Climate directly influences thermoregulatory demands, and indirectly along with atmospheric CO₂ concentrations and nutrient availability, the amount of food available. Overall, warmer winters should reduce energetic demands for thermoregulation and decrease food demands, allowing sparrows to winter farther north (Root 1988). However, some climate models also predict increased variability of winter climate (Field et al. 2012). We found variation in bird abundance and scaled mass both on experimental and control plots, suggesting that fluctuating climatic conditions could lead to variable levels of limitation. Indeed, variations in winter weather have been correlated with variation in survival of birds wintering in the temperate zone (Brittingham and Temple 1988, Goss-Custard 1995), breeding population sizes of long-distance migratory birds (den Held 1981, Szép 1995, Sillett et al. 2000) and associated plant productivity (Saino et al. 2004) in the tropics. Fluctuations in winter conditions will demand plasticity in movement and settlement behavior, but such plasticity already appears to exist in swamp sparrows in winter (this study) and summer (Greenberg 1988) and other temperate zone wintering migrants (Gordon 2000, Butler 2003).

On the other side of the food limitation equation, temperate zone species could be especially susceptible to enhanced food limitation if biomass, particularly seed, production is altered. The effects of climate change on primary productivity and seed production is poorly understood for wetlands. However, it has been demonstrated that increased atmospheric CO₂ leads to short-term increases of biomass production (Reich et al. 2006), especially when accompanied by an increase in N from anthropogenic sources (Luo et al. 2004). Experimental CO₂ and N fertilization in brackish marshes similar to our study plots increased plant growth for two years (Langley and Megonigal 2010). How this affects seed crops is not known, but overall

plant productivity increases could increase seed and invertebrate availability for temperate birds. The position of our study sites, near the mouth of an estuary in a major farming region, makes increases in anthropogenic N fertilization likely. Thus it is possible that food supply for wintering swamp sparrows could increase, which would join rising winter temperatures to support wintering farther north. However, predictive models would have to consider the effects of altered rainfall and its effect on freshwater inputs to brackish marsh systems (Bates et al. 2008). In addition, the short-term increase in productivity documented in the aforementioned study was followed by a shift in community composition that ultimately reduced biomass production (Langley and Megonigal 2010).

Summary

We have shown that food availability can limit population sizes of migratory birds that winter in the temperate zone and potentially carry-over to limit future reproductive success. In addition, we found evidence that immigration and body condition are regulated through competition for food. These findings suggest that temperate migrants experience mechanisms of food limitation reported for both temperate residents and long-distance migrants that winter in the tropics. Global climate change is likely to alter the energetic equation that underlies food limitation in this system.

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LITERATURE CITED

- Aebischer, A., N. Perrin, M. Krieg, J. Studer, and D. R. Meyer. 1996. The Role of Territory Choice, Mate Choice and Arrival Date on Breeding Success in the Savi's Warbler *Locustella luscinioides*. *Journal of Avian Biology* **27**:143-152.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* 1:267-281.
- Baillie, S. R. and W. J. Peach. 1992. Population limitation in Palaearctic-African migrant passerines. *Ibis* **134**:120-132.
- Bates, B. C., Z. W. Kundzewicz, S. Wu, and J. P. Palutikof, editors. 2008. *Climate Change and Water*. IPCC Secretariat, Geneva.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes.
- Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* **145**:484-495.
- Blem, C. 1990. Avian energy storage. *Current Ornithology* **7**:59-113.
- Bridge, E. S., J. F. Kelly, P. E. Bjornen, C. M. Curry, P. H. Crawford, and J. M. Paritte. 2010. Effects of nutritional condition on spring migration: do migrants use resource availability to keep pace with a changing world? *Journal of Experimental Biology* **213**:2424-2429.
- Brown, D. R. and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* **149**:22-32.
- Brittingham, M. C. and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology* **69**:581-589.
- Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis* **142**:389-398.
- den Held, J. D. 1981. Population changes of the Purple Heron in relation to drought in the wintering area. *Ardea* **69**:185-191.
- Etterson, M. A., B. J. Olsen, R. Greenberg, and W. G. Shriver. 2011. Sources, sinks, and model accuracy. Pages 273-290 in J. Liu, V. Hull, A. Morzillo, and J. Wiens, editors. *Sources, Sinks, and Sustainability Across Landscapes*. Cambridge University Press, New York, N.Y.
- Field, C. B., V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G.-K. Plattner, S. K. Allen, M. Tignor, and P. M. Midgley, editors. 2012. *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. Cambridge University Press, Cambridge, United Kingdom.

- Fretwell, S. D. 1972. Populations in a Seasonal Environment. Monographs in Population Biology. Princeton University Press, Princeton, N.J.
- Fretwell, S. D. and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. *Acta Biotheoretica*:16-36.
- Gordon, C. E. 2000. Movement patterns of wintering grassland sparrows in Arizona. *The Auk* **117**:748-759.
- Goss-Custard, J. D., R. T. Clarke, K. B. Briggs, B. J. Ens, K.-M. Exo, C. Smit, A. J. Beintema, R. W. G. Caldow, D. C. Catt, N. A. Clark, S. E. A. Le V. Dit. Durrell, M. P. Harris, J. B. Hulscher, P. L. Meininger, N. Picozzi, R. Prys-Jones, U. N. Safriel, and A. D. West. 1995. Population consequences of winter habitat loss in a migrating shorebird: Pt. 1. Estimating model parameters. *Journal of Applied Ecology* **32**:320-336.
- Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 in A. Keast and E. S. Morton, editors. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D.C.
- Greenberg, R. 1988. Water as a habitat cue for breeding swamp and song sparrows. *Condor* **90**:420-427.
- Greenberg, R., P. P. Marra, and M. J. Wooller. 2007. Stable-isotope (C, N, H) analyses help locate the winter range of the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*). *The Auk* **124**:1137-1148.
- Jansson, C., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* **37**:313-322.
- Johnson, E. I., J. K. DiMicelo, and P. C. Stouffer. 2009. Timing of migration and patterns of winter settlement by Henslow's sparrows. *Condor* **111**:730-739.
- Johnson, M. D., T. W. Sherry, R. T. Holmes, and P. P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conservation Biology* **20**:1433-1444.
- Källander, H. 1981. The effect of provision of food in winter on a population of the great tit *Parus major* and the blue tit *P. caeruleus*. *Ornis Scandinavica* **12**:244-248.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* **78**:563-578.
- Laake, J. 2011. RMark: R Code for MARK Analysis.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London, England.
- Lack, D. and . 1966. *Population studies in birds*. Oxford University Press. , London, England.
- Langley, J. A. and J. P. Megonigal. 2010. Ecosystem response to elevated CO2 levels limited by nitrogen-induced plant species shift. *Nature* **466**:96-99.

- Liknes, E. T., S. M. Scott, and D. L. Swanson. 2002. Seasonal acclimatization in the American Goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor* **104**:548-557.
- Lima, S. L. and E. 67:377–385. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology* **67**:377-385.
- Luo, Y., B. Su, W. S. D. Currie, J. S., A. Finzi, U. Hartwig, B. Hungate, R. E. McMurtrue, R. Oren, W. J. Parton, D. E. Pataki, M. R. Shaw, D. R. Zak, and C. B. Field. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **54**:731-739.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, Burlington, MA.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1988. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**:1884-1886.
- Marra, P. P. and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* **116**:284-292.
- Marra, P. P. and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *The Auk* **118**:92-104.
- Mazerolle, M. J. 2011. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).
- Morse, D. H. 1980. Population limitation: breeding or wintering grounds. Pages 505-516 *in* A. Keast and E. S. Morton, editors. *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation*. Smithsonian Institution Press, Washington, D.C.
- Mowbray, T. B. 1997. Swamp Sparrow. *in* A. Poole, editor. *The Birds of North America Online* Cornell Laboratory of Ornithology, Ithaca.
- Newton, I. 1998. *Population limitation in birds*. Academic Press, San Diego, CA. .
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? . *Journal of Ornithology* **147**:146-166.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. M. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B* **271**:59-64.
- Piper, W. H. and R. H. Wiley. 1989. Correlates of dominance in wintering white-throated sparrows: age, sex and location. *Animal Behaviour* **37**:298-310.
- Peig, J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**:1883-1891.

- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management* **46**:752-757.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rappole, J. H. and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. *The Auk* **111**:652-660.
- Reich, P. B., S. E. Hobbie, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, and J. Trost. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* **440**:922-925.
- Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. *Journal of Avian Biology* **40**:34-41.
- Rohwer, S., P. W. Ewald, and F. C. Rohwer. 1981. Variation in size, appearance, and dominance within and among the sex and age classes of Harris' sparrows. *Journal of Field Ornithology* **52**:291-303.
- Root, T. 1988. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* **15**:489-505.
- Sherry, T. W., M. D. Johnson, and A. M. Strong. 2005. Does winter food limit populations of migratory birds? Pages 414-425 in R. Greenberg and P. P. Marra, editors. *Birds of Two Worlds*. Johns Hopkins University Press, Baltimore, MD.
- Sillett, T. S. and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**:296-308.
- Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. The El Niño Southern Oscillation impacts population dynamics of a migratory songbird throughout its annual cycle. *Science* **288**:2040-2042.
- Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island song sparrow population. *Oecologia* **47**:164-170.
- Strong, A. M. and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology* **69**:883-895.
- Studds, C. E. and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology* **86**:2380-2385.
- Studds, C. E. and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research* **35**:115-122.
- Studds, C. E. and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the

- spring departure programme of a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* **278**:3437-3443.
- Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* **7**:533-555.
- Szép, T. 1995. Relationship between west African rainfall and the survival of central European Sand Martins *Riparia riparia*. *Ibis* **137**:162-168.
- Theimer, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos. *Animal Behaviour* **59**:1883-1890.
- Tonra, C. 2011. The role of breeding preparation in migratory phenology and seasonal interactions in migratory passerines. University of Maine.
- Tonra, C., P. P. Marra, and R. L. Holberton. 2011. Early elevation of testosterone advances migratory preparation in a songbird. *The Journal of Experimental Biology* **214**:2761-2767.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Technical Report: Human Alteration of the Global Nitrogen Cycle: Sources and Consequences. *Ecological Applications* **7**:737-750.
- Warton, D. and J. Ormerod. 2007. smatr: (Standardised) Major Axis Estimation and Testing Routines.
- White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46 Supplement**:120-138.
- Yarbrough, C. G. and C. B. P. 39A:235–266. 1971. The influence of distribution and ecology of the thermoregulation of small birds. *Comparative Biochemistry and Physiology A* **39**:235-266.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in Ecology with R. Springer, New York, N.Y.

Figures legends:

Figure 1. Map of research plots in coastal North Carolina. C1 and C2 were control plots in all years (2008–2010) and E1 and E2 received food supplementations in 2009 and 2010. Inset map shows swamp sparrow breeding (orange) and main nonbreeding (blue) ranges and study area.

Figure 2. Temperatures at the research site (recorded at plot C1) during January–March of the three years of study. Dashed line indicates the lower limit of the swamp sparrow's thermal neutral zone.

Figure 3. Abundance of swamp sparrows at study plots. Mean \pm s.e. Squares = both ages, filled circles = adults, and open circles = immatures. Gray background shading indicates food supplementation.

Figure 4. Apparent survival (ϕ) of swamp sparrows as a function of treatment, plot, year, sex, and age. Model average predictions \pm unconditional s.e. Filled square=adult male, filled circle=adult female, unfilled square=immature male, unfilled circle=immature female. Gray background shading indicates food supplementation.

Figure 5. Recapture probability (p) of swamp sparrows as a function of Plot and treatment. Model average predictions \pm unconditional s.e. Gray background shading indicates food supplementation.

Figure 6. Scaled mass of swamp sparrows. Model average predictions \pm unconditional s.e. Filled square=adult male, filled circle=adult female, unfilled square=immature male, unfilled circle=immature female. Gray shading indicates food supplementation.

Figure 7. Apparent survival (ϕ) of swamp sparrows as a function of scaled mass index for each sex and age class under natural and food supplemented conditions. Model average predictions \pm unconditional s.e. Gray background shading indicates food supplementation. AM = adult male, AF = adult female, IM = immature male, IF = immature female.

Figures:

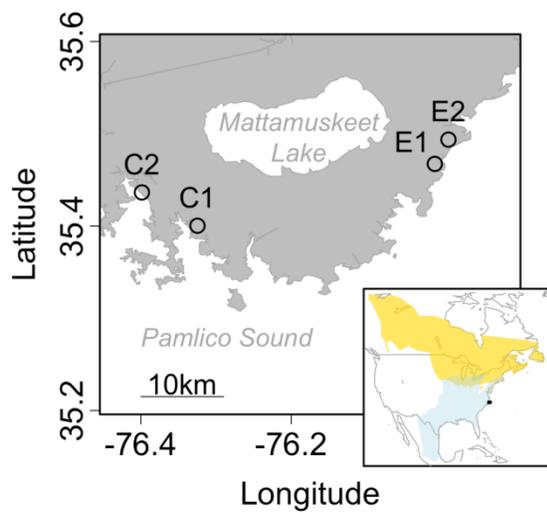


Fig. 1.

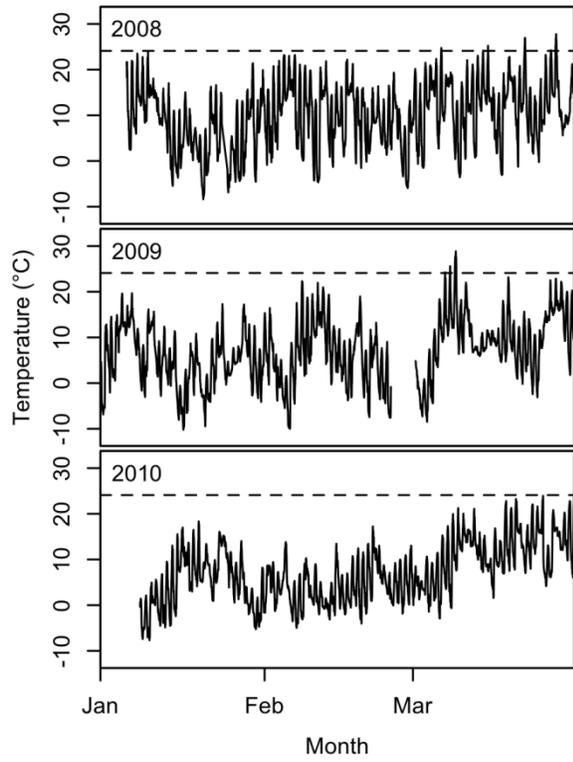


Fig. 2.

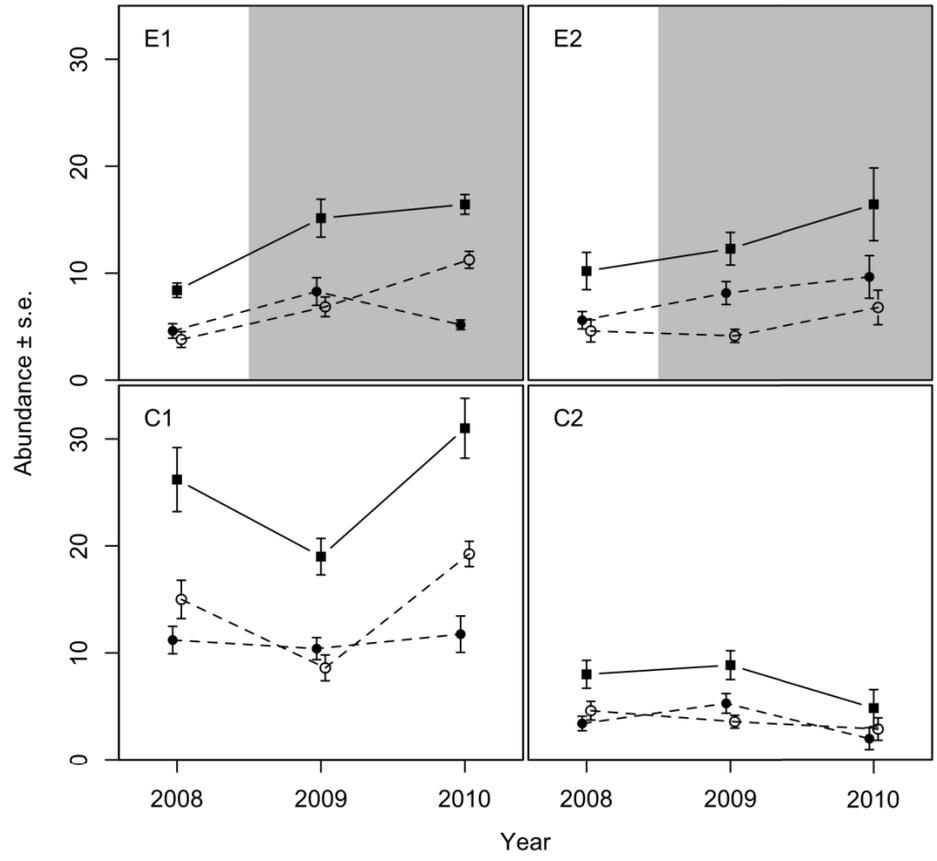


Fig. 3.

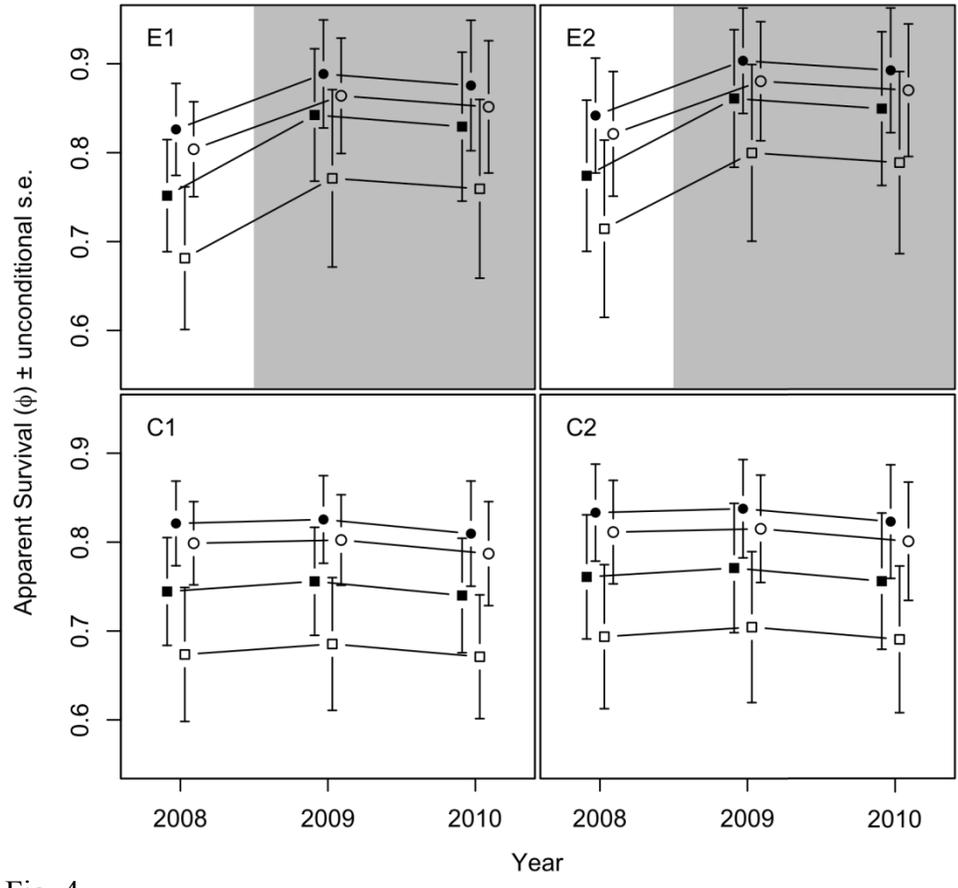


Fig. 4.

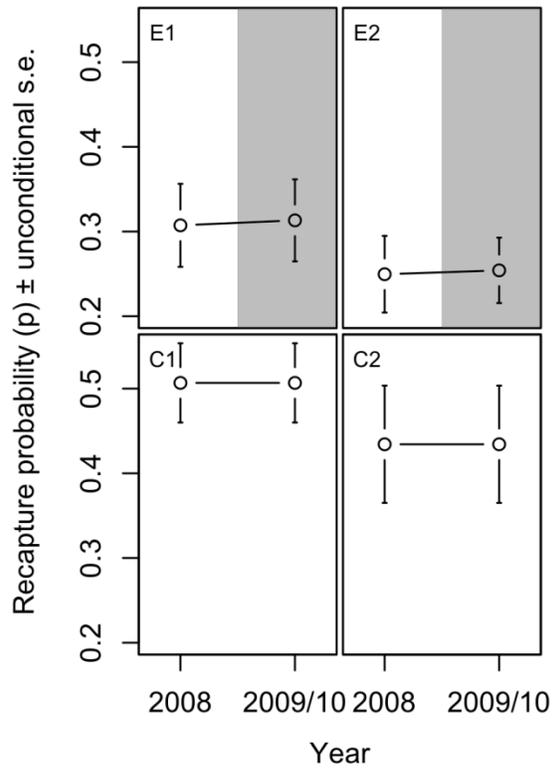


Fig. 5.

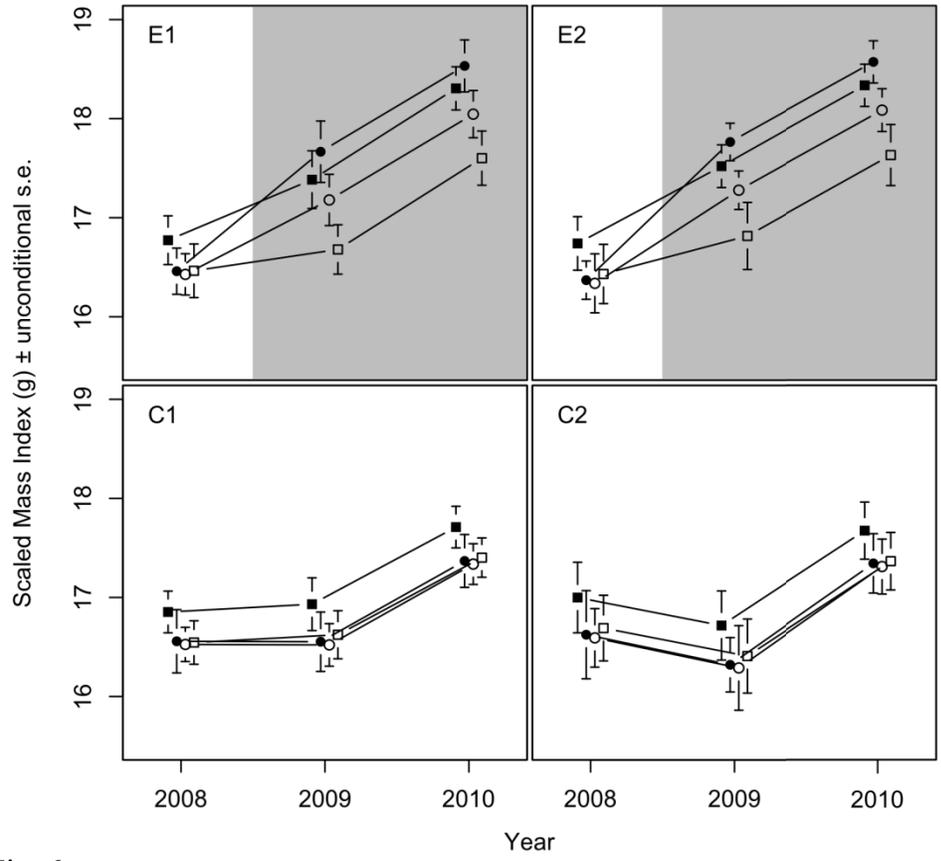


Fig. 6.

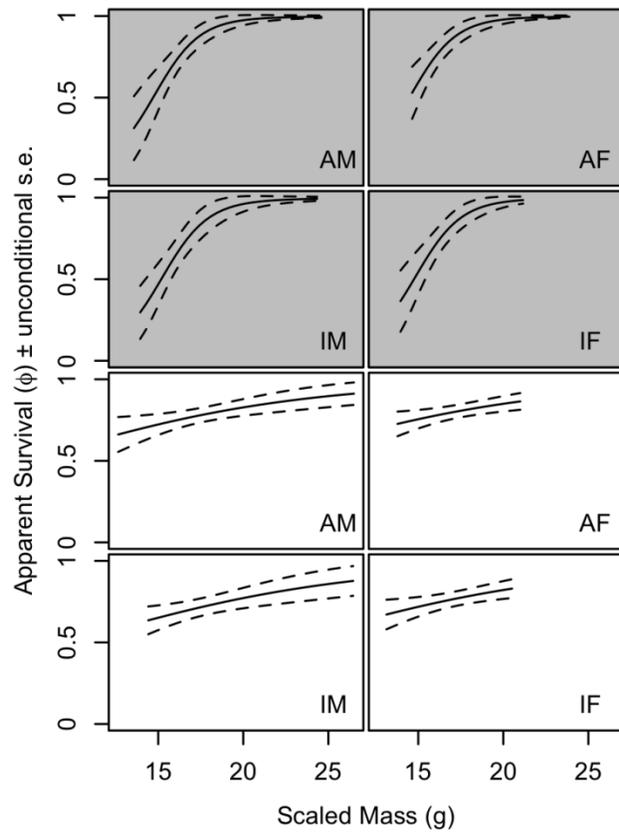


Fig. 7.

Appendix A. Photograph of habitat at research plots, a table showing the quantities of food supplied, and a photograph of a swamp sparrow eating supplemented food.



Figure A1. Photograph of marsh habitat covered in frost at study plot C2. The Pamlico Sound is visible on left.

Table A1. Quantities of food supplemented to experimental plots in 2009 and 2010. No food was added in 2008.

Year	Plot	Millet (kg)	Mealworms (number of individuals)
2009	E1	130.25	2,268
	E2	122.06	2,171
2010	E1	228.26	4,765
	E2	238.74	5,185



Figure A2. A swamp sparrow eating millet at a supplemental food station. Image used with permission of Matt Klostermann.

Appendix B: Genetic methods to determine the sex of swamp sparrows.

We determined the sex of birds with a PCR-based genetic test based on a size polymorphism of the CHD-W and CHD-Z genes (Griffiths et al. 1998). DNA was extracted from frozen blood or feathers using the DNeasy® Blood & Tissue Kit (Qiagen Inc.). Five microliters of frozen whole blood were placed in 200µl of lysis buffer and extracted following the Animal Blood Spin-Column Protocol. Where blood was not available, two feather quills were used as a source of DNA and the above protocol modified as per Bush et al. (2005) with some additional modifications. The quills were digested in 300µl of buffer ATL, 20µl of Proteinase K and 20µl of 1M DTT and incubated at 56°C for 1–4hrs until all solids were dissolved. 300µl of buffer AL was added and samples incubated at 72°C for an additional 10 min. To separate the DNA from other cellular components, 300µl of 100% cold ethanol was added and then DNA purified following the same steps used for blood samples. Amplifications with the primers P2 and P8 (Griffiths et al. 1998) were done in 10µl reactions containing 1X PCR buffer (15 mM Tris-HCl pH 8.0, 50 mM KCl), 5 mM MgCl₂, 200 µM for each dNTP, 0.5µM of each primer, 10X BSA (10mg/ml) and 0.6 units of AmpliTaq®Gold DNA Polymerase. We used the following cycling parameters: one cycle of 5 minutes at 95°C, 30 cycles of 30 seconds at 94°C, 45 seconds at 48°C, 45 seconds at 72°C and one cycle of 5 minutes at 72°C. PCR products were visualized with 3% agarose gel stained with ethidium bromide.

Appendix C: Tables of linear models ranked based on AICc values.

Table C1. Linear models that describe total swamp sparrow abundance on experimental plots. K

= number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Treatment period	3	158.154	0	0.711
Treatment period + Plot	4	160.826	2.673	0.187
Treatment period * Plot	5	162.150	3.997	0.096
Intercept only	2	168.229	10.075	4.613E-03
Plot	3	170.704	12.550	1.338E-03

Table C2. Linear models that describe adult swamp sparrow abundance on experimental plots. K

= number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Treatment period + Plot	4	130.224	0	0.484
Treatment period	3	130.763	0.539	0.369
Treatment period * Plot	5	133.185	2.960	0.110
Intercept only	2	136.738	6.513	0.019
Plot	3	136.750	6.525	0.019

Table C3. Linear models that describe immature swamp sparrow abundance on experimental plots. K = number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Treatment period + Plot	4	138.375	0	0.357
Treatment period * Plot	5	138.638	0.263	0.313
Treatment period	3	139.026	0.651	0.258
Plot	3	142.807	4.432	0.039
Intercept only	2	143.124	4.749	0.033

Table C4. Linear models that describe total swamp sparrow abundance on control plots. K = number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Plot	3	178.548	0	0.738
Plot + Treatment period	4	181.061	2.513	0.210
Plot * Treatment period	5	183.852	5.304	0.052
Intercept only	2	209.323	30.775	1.532E-07
Treatment period	3	211.743	33.196	4.568E-08

Table C5. Linear models that describe adult swamp sparrow abundance on control plots. K = number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Plot	3	145.540	0	0.759
Plot + Treatment period	4	148.275	2.735	0.193
Plot * Treatment period	5	151.091	5.552	0.047
Intercept only	2	165.957	20.417	2.798E-05
Treatment period	3	168.474	22.934	7.948E-06

Table C6. Linear models that describe immature swamp sparrow abundance on control plots. K = number of parameters, w_i = model weight.

Models	K	AICc	Δ AICc	w_i
Plot	3	150.218	0	0.662
Plot + Treatment period	4	152.328	2.109	0.231
Plot * Treatment period	5	153.850	3.632	0.108
Intercept only	2	178.284	28.066	5.326E-07
Treatment period	3	180.485	30.267	1.772E-07

Table C7. Cormack-Jolly-Seber logistic regression models that describe apparent survival (ϕ) and recapture probability (p) for swamp sparrows. K = number of parameters, w_i = model weight.

ϕ	p	K	AICc	Δ AICc	w_i
Treatment + Sex + Age	Plot	8	1543.560	0	0.078
Treatment + Sex * Age	Plot	9	1543.805	0.245	0.069
Treatment + Sex	Plot	7	1543.860	0.300	0.068
Treatment * Age + Sex	Plot	9	1544.030	0.470	0.062
Sex + Age	Plot	7	1545.364	1.803	0.032
Sex * Age	Plot	8	1545.411	1.850	0.031
Treatment + Sex + Age	Treatment + Plot	9	1545.593	2.033	0.028
Treatment * Sex + Age	Plot	9	1545.599	2.038	0.028
Treatment + Sex	Treatment + Plot	8	1545.770	2.210	0.026
Treatment + Sex * Age	Treatment + Plot	10	1545.852	2.291	0.025
Treatment * Sex	Plot	8	1545.898	2.337	0.024
Treatment * Age + Sex	Treatment + Plot	10	1546.003	2.442	0.023
Treatment + Year + Sex	Plot	9	1546.073	2.513	0.022
Sex	Plot	6	1546.270	2.709	0.020
Plot + Sex * Age	Plot	11	1546.305	2.745	0.020
Sex * Age	Treatment + Plot	9	1546.314	2.754	0.020
Sex + Age	Treatment + Plot	8	1546.324	2.764	0.020
Plot + Sex * Age	Treatment + Plot	12	1546.492	2.931	0.018
Treatment + Year + Sex + Age	Plot	10	1546.667	3.106	0.017

Treatment	Plot	6	1547.078	3.517	0.014
Treatment + Year + Sex * Age	Plot	11	1547.128	3.568	0.013
Treatment + Plot + Sex * Age	Plot	12	1547.308	3.748	0.012
Plot + Sex + Age	Plot	10	1547.329	3.769	0.012
Year + Sex	Plot	8	1547.339	3.779	0.012
Treatment + Age	Plot	7	1547.447	3.886	0.011
Sex	Treatment + Plot	7	1547.453	3.893	0.011
Year + Sex * Age	Plot	10	1547.583	4.023	0.010
Treatment * Sex + Age	Treatment + Plot	10	1547.633	4.072	0.010
Year + Sex + Age	Plot	9	1547.649	4.088	0.010
Plot + Sex + Age	Treatment + Plot	11	1547.753	4.193	0.010
Treatment * Sex	Treatment + Plot	9	1547.808	4.248	0.009
Plot + Sex	Plot	9	1547.907	4.347	0.009
Treatment + Plot + Sex + Age	Plot	11	1547.940	4.380	0.009
Treatment * Sex * Age	Plot	12	1548.092	4.532	0.008
Treatment + Year + Sex	Treatment + Plot	10	1548.093	4.532	0.008
Treatment + Year	Plot	8	1548.290	4.730	0.007
Treatment * Age	Plot	8	1548.327	4.767	0.007
Treatment + Plot + Sex	Plot	10	1548.335	4.775	0.007
Treatment + Plot + Sex * Age	Treatment + Plot	13	1548.548	4.988	0.006
Plot + Sex	Treatment + Plot	10	1548.593	5.033	0.006
Plot + Year * Sex + Age	Plot	14	1548.702	5.142	0.006
Treatment + Year + Sex + Age	Treatment + Plot	11	1548.719	5.158	0.006

Year * Sex + Age	Plot	11	1548.775	5.215	0.006
Year * Sex	Plot	10	1548.962	5.401	0.005
Treatment	Treatment + Plot	7	1548.967	5.407	0.005
Year + Sex	Treatment + Plot	9	1548.973	5.412	0.005
Plot + Year * Sex + Age	Treatment + Plot	15	1549.014	5.453	0.005
Year + Sex + Age	Treatment + Plot	10	1549.142	5.582	0.005
Year + Sex * Age	Treatment + Plot	11	1549.148	5.588	0.005
Year * Age + Sex	Plot	11	1549.160	5.600	0.005
Treatment + Year + Sex * Age	Treatment + Plot	12	1549.184	5.623	0.005
Age	Plot	6	1549.194	5.633	0.005
Plot + Year + Sex * Age	Plot	13	1549.296	5.736	0.004
Intercept only	Plot	5	1549.387	5.827	0.004
Treatment + Year + Age	Plot	9	1549.411	5.850	0.004
Plot + Year * Sex	Plot	13	1549.442	5.881	0.004
Treatment + Age	Treatment + Plot	8	1549.460	5.899	0.004
Treatment + Plot + Sex + Age	Treatment + Plot	12	1549.670	6.109	0.004
Plot + Year * Sex * Age	Treatment + Plot	20	1549.903	6.342	0.003
Plot + Year + Sex	Plot	11	1549.930	6.370	0.003
Year	Plot	7	1549.939	6.378	0.003
Plot + Year * Sex * Age	Plot	19	1549.952	6.392	0.003
Year * Sex + Age	Treatment + Plot	12	1550.028	6.468	0.003
Plot + Year + Sex * Age	Treatment + Plot	14	1550.064	6.504	0.003
Plot + Year * Sex	Treatment + Plot	14	1550.067	6.507	0.003

Treatment * Sex * Age	Treatment + Plot	13	1550.104	6.543	0.003
Age	Treatment + Plot	7	1550.164	6.604	0.003
Treatment * Age	Treatment + Plot	9	1550.290	6.729	0.003
Treatment + Year	Treatment + Plot	9	1550.317	6.757	0.003
Plot + Year + Sex + Age	Plot	12	1550.322	6.761	0.003
Treatment + Plot + Sex	Treatment + Plot	11	1550.332	6.771	0.003
Year * Sex	Treatment + Plot	11	1550.441	6.881	0.003
Intercept only	Treatment + Plot	6	1550.547	6.987	0.002
Year * Age + Sex	Treatment + Plot	12	1550.652	7.092	0.002
Year + Age	Plot	8	1550.857	7.297	0.002
Plot + Year + Sex	Treatment + Plot	12	1550.977	7.416	0.002
Plot + Year + Sex + Age	Treatment + Plot	13	1551.122	7.561	0.002
Year	Treatment + Plot	8	1551.411	7.850	0.002
Treatment + Year + Age	Treatment + Plot	10	1551.457	7.897	0.002
Plot * Age + Sex + Year	Plot	15	1551.525	7.965	1.462E-03
Treatment * Sex * Age + Year	Plot	14	1551.586	8.025	1.419E-03
Plot	Plot	8	1551.778	8.218	1.288E-03
Treatment + Plot	Plot	9	1551.968	8.407	1.172E-03
Plot + Age	Plot	9	1551.984	8.423	1.163E-03
Year + Age	Treatment + Plot	9	1552.154	8.594	1.067E-03
Plot + Year * Age + Sex	Plot	14	1552.232	8.671	1.027E-03
Treatment + Plot + Age	Plot	10	1552.386	8.826	9.508E-04
Plot	Treatment + Plot	9	1552.510	8.949	8.938E-04

Year * Age	Plot	10	1552.524	8.964	8.873E-04
Plot + Age	Treatment + Plot	10	1552.532	8.971	8.840E-04
Plot * Age + Sex + Year	Treatment + Plot	16	1552.851	9.291	7.534E-04
Plot + Year * Age + Sex	Treatment + Plot	15	1553.030	9.470	6.889E-04
Plot + Year	Plot	10	1553.057	9.497	6.797E-04
Treatment * Sex * Age + Year	Treatment + Plot	15	1553.641	10.081	5.075E-04
Year * Sex * Age	Plot	16	1553.767	10.207	4.766E-04
Plot + Year	Treatment + Plot	11	1553.846	10.285	4.582E-04
Year * Age	Treatment + Plot	11	1553.866	10.305	4.537E-04
Treatment + Plot	Treatment + Plot	10	1554.011	10.451	4.219E-04
Plot + Year + Age	Plot	11	1554.180	10.620	3.877E-04
Treatment + Plot + Age	Treatment + Plot	11	1554.365	10.805	3.534E-04
Treatment + Plot + Sex	Treatment	8	1554.569	11.008	3.192E-04
Treatment + Sex	Treatment	5	1554.632	11.071	3.093E-04
Plot + Year + Age	Treatment + Plot	12	1554.750	11.190	2.916E-04
Treatment + Plot + Sex + Age	Treatment	9	1555.036	11.476	2.526E-04
Year * Sex * Age	Treatment + Plot	17	1555.124	11.563	2.419E-04
Plot * Sex + Year	Plot	14	1555.329	11.768	2.183E-04
Plot * Sex + Age + Year	Plot	15	1555.602	12.042	1.904E-04
Treatment + Sex + Age	Treatment	6	1555.689	12.129	1.823E-04
Treatment + Plot + Sex * Age	Treatment	10	1555.792	12.231	1.732E-04
Treatment + Sex * Age	Treatment	7	1556.002	12.442	1.559E-04
Treatment * Age + Sex	Treatment	7	1556.072	12.511	1.506E-04

Plot + Year * Age	Plot	13	1556.309	12.748	1.337E-04
Year + Sex	Treatment	6	1556.420	12.860	1.265E-04
Treatment + Plot	Treatment	7	1556.507	12.947	1.211E-04
Treatment * Sex	Treatment	6	1556.658	13.097	1.123E-04
Plot * Sex + Year	Treatment + Plot	15	1556.680	13.120	1.110E-04
Treatment + Year + Sex	Treatment	7	1556.757	13.197	1.069E-04
Plot * Sex + Age + Year	Treatment + Plot	16	1556.766	13.206	1.064E-04
Plot + Year * Age	Treatment + Plot	14	1556.948	13.388	9.714E-05
Year + Sex * Age	Treatment	8	1557.023	13.463	9.356E-05
Plot * Age + Year	Plot	14	1557.216	13.656	8.496E-05
Sex	Treatment	4	1557.217	13.656	8.493E-05
Treatment	Treatment	4	1557.254	13.694	8.335E-05
Plot * Sex * Age + Year	Plot	22	1557.310	13.749	8.107E-05
Treatment + Plot + Age	Treatment	8	1557.391	13.830	7.786E-05
Plot * Year + Sex	Plot	17	1557.404	13.844	7.732E-05
Sex * Age	Treatment	6	1557.540	13.980	7.224E-05
Year + Sex + Age	Treatment	7	1557.544	13.984	7.211E-05
Sex + Age	Treatment	5	1557.605	14.044	6.995E-05
Treatment * Sex + Age	Treatment	7	1557.718	14.157	6.611E-05
Treatment + Year + Sex * Age	Treatment	9	1558.038	14.477	5.634E-05
Treatment + Year + Sex + Age	Treatment	8	1558.134	14.574	5.369E-05
Year * Sex	Treatment	8	1558.171	14.610	5.271E-05
Plot * Age + Year	Treatment + Plot	15	1558.218	14.658	5.147E-05

Plot * Year + Sex * Age	Plot	19	1558.372	14.812	4.766E-05
Year * Age + Sex	Treatment	9	1558.651	15.090	4.147E-05
Treatment + Age	Treatment	5	1558.694	15.134	4.057E-05
Plot * Sex * Age + Year	Treatment + Plot	23	1558.930	15.370	3.606E-05
Year * Sex + Age	Treatment	9	1559.030	15.469	3.430E-05
Year	Treatment	5	1559.055	15.494	3.388E-05
Treatment + Year	Treatment	6	1559.279	15.719	3.029E-05
Treatment * Age	Treatment	6	1559.474	15.914	2.747E-05
Plot * Year + Sex	Treatment + Plot	18	1559.487	15.927	2.729E-05
Intercept only	Treatment	3	1559.700	16.140	2.453E-05
Treatment * Sex * Age	Treatment	10	1560.002	16.442	2.110E-05
Plot * Year	Plot	16	1560.104	16.543	2.005E-05
Plot * Year + Sex * Age	Treatment + Plot	20	1560.193	16.633	1.918E-05
Age	Treatment	4	1560.554	16.993	1.601E-05
Year + Age	Treatment	6	1560.650	17.089	1.526E-05
Plot + Year + Sex	Treatment	9	1560.916	17.355	1.336E-05
Treatment + Year + Age	Treatment	7	1561.052	17.492	1.248E-05
Plot * Year + Age	Plot	17	1561.499	17.938	9.984E-06
Plot + Year + Sex * Age	Treatment	11	1561.644	18.084	9.281E-06
Year * Age	Treatment	8	1561.769	18.209	8.720E-06
Plot + Year + Sex + Age	Treatment	10	1561.797	18.236	8.600E-06
Plot * Age + Sex + Year	Treatment	13	1562.073	18.513	7.490E-06
Plot + Sex	Treatment	7	1562.148	18.588	7.214E-06

Plot * Year	Treatment + Plot	17	1562.172	18.612	7.130E-06
Plot + Sex + Age	Treatment	8	1562.210	18.650	6.995E-06
Plot + Sex * Age	Treatment	9	1562.324	18.764	6.607E-06
Treatment * Sex * Age + Year	Treatment	12	1562.487	18.926	6.091E-06
Year * Sex * Age	Treatment	14	1562.902	19.341	4.949E-06
Plot + Year * Age + Sex	Treatment	12	1563.003	19.442	4.706E-06
Plot + Year * Sex	Treatment	11	1563.120	19.560	4.438E-06
Sex * Age	Intercept only	5	1563.150	19.590	4.371E-06
Sex	Intercept only	3	1563.188	19.628	4.289E-06
Plot + Year	Treatment	8	1563.203	19.643	4.257E-06
Plot * Year * Sex	Plot	28	1563.280	19.719	4.098E-06
Plot * Sex + Age + Year	Treatment	13	1563.490	19.930	3.688E-06
Sex + Age	Intercept only	4	1563.551	19.991	3.578E-06
Plot * Sex + Year	Treatment	12	1563.580	20.020	3.525E-06
Plot * Year + Age	Treatment + Plot	18	1563.582	20.022	3.522E-06
Plot * Sex * Age + Year	Treatment	20	1563.636	20.075	3.429E-06
Plot * Year * Sex + Age	Plot	29	1563.637	20.076	3.428E-06
Plot + Year * Sex + Age	Treatment	12	1563.784	20.224	3.184E-06
Plot + Sex * Age	Intercept only	8	1563.989	20.428	2.875E-06
Plot + Sex + Age	Intercept only	7	1564.102	20.541	2.717E-06
Plot * Year + Sex	Treatment	15	1564.385	20.825	2.357E-06
Plot + Sex	Intercept only	6	1564.396	20.836	2.344E-06
Plot	Treatment	6	1564.444	20.883	2.290E-06

Plot + Year + Age	Treatment	9	1564.496	20.936	2.230E-06
Treatment + Plot + Sex + Age	Intercept only	8	1564.521	20.960	2.203E-06
Treatment + Plot + Sex * Age	Intercept only	9	1564.529	20.969	2.194E-06
Treatment + Sex * Age	Intercept only	6	1564.679	21.119	2.035E-06
Treatment + Sex	Intercept only	4	1564.844	21.283	1.875E-06
Plot + Age	Treatment	7	1564.899	21.338	1.824E-06
Treatment + Plot + Sex	Intercept only	7	1564.934	21.373	1.792E-06
Treatment + Sex + Age	Intercept only	5	1565.091	21.530	1.657E-06
Intercept only	Intercept only	2	1565.310	21.750	1.484E-06
Plot * Year * Sex	Treatment + Plot	29	1565.407	21.847	1.414E-06
Plot + Year + Sex	Intercept only	8	1565.506	21.946	1.346E-06
Year + Sex	Intercept only	5	1565.691	22.130	1.227E-06
Plot * Year * Sex + Age	Treatment + Plot	30	1565.783	22.223	1.172E-06
Plot + Year * Age	Treatment	11	1565.824	22.263	1.148E-06
Treatment + Year + Sex	Intercept only	6	1565.866	22.305	1.124E-06
Treatment + Year + Sex * Age	Intercept only	8	1565.898	22.338	1.106E-06
Plot + Year + Sex * Age	Intercept only	10	1565.930	22.370	1.089E-06
Plot + Year + Sex + Age	Intercept only	9	1566.036	22.476	1.033E-06
Plot * Year	Treatment	14	1566.067	22.506	1.017E-06
Age	Intercept only	3	1566.149	22.588	9.762E-07
Plot	Intercept only	5	1566.168	22.607	9.669E-07
Year + Sex * Age	Intercept only	7	1566.230	22.669	9.373E-07
Treatment * Age + Sex	Intercept only	6	1566.247	22.687	9.292E-07

Plot + Age	Intercept only	6	1566.287	22.727	9.108E-07
Treatment * Sex	Intercept only	5	1566.421	22.861	8.518E-07
Treatment + Plot	Intercept only	6	1566.490	22.929	8.231E-07
Treatment + Plot + Age	Intercept only	7	1566.494	22.934	8.212E-07
Treatment * Sex + Age	Intercept only	6	1566.670	23.109	7.523E-07
Year * Sex	Intercept only	7	1566.695	23.135	7.427E-07
Year + Sex + Age	Intercept only	6	1566.726	23.166	7.313E-07
Treatment + Year + Sex + Age	Intercept only	7	1566.773	23.213	7.143E-07
Plot * Year + Sex * Age	Treatment	17	1566.833	23.273	6.933E-07
Plot + Year	Intercept only	7	1566.879	23.318	6.777E-07
Plot * Age + Year	Treatment	12	1566.894	23.333	6.726E-07
Treatment	Intercept only	3	1566.948	23.388	6.545E-07
Plot + Year * Age + Sex	Intercept only	11	1567.038	23.478	6.257E-07
Plot * Age + Sex + Year	Intercept only	12	1567.127	23.566	5.986E-07
Year * Sex + Age	Intercept only	8	1567.324	23.763	5.425E-07
Year * Age + Sex	Intercept only	8	1567.385	23.824	5.262E-07
Year	Intercept only	4	1567.421	23.861	5.167E-07
Plot * Year + Age	Treatment	15	1567.614	24.053	4.692E-07
Treatment + Age	Intercept only	4	1567.668	24.108	4.566E-07
Plot + Year * Sex	Intercept only	10	1567.675	24.115	4.550E-07
Plot * Sex + Age + Year	Intercept only	12	1567.773	24.213	4.333E-07
Plot + Year + Age	Intercept only	8	1567.791	24.231	4.294E-07
Treatment + Year	Intercept only	5	1567.864	24.303	4.141E-07

Plot + Year * Sex + Age	Intercept only	11	1567.935	24.375	3.995E-07
Plot + Year * Sex * Age	Treatment	17	1568.068	24.508	3.739E-07
Plot * Sex + Year	Intercept only	11	1568.367	24.807	3.219E-07
Plot * Year * Sex	Treatment	26	1568.619	25.058	2.839E-07
Treatment * Age	Intercept only	5	1568.867	25.307	2.508E-07
Year + Age	Intercept only	5	1568.873	25.312	2.500E-07
Plot + Year * Age	Intercept only	10	1569.063	25.502	2.274E-07
Treatment * Sex * Age	Intercept only	9	1569.074	25.514	2.261E-07
Plot * Year * Sex + Age	Treatment	27	1569.171	25.611	2.154E-07
Treatment + Year + Age	Intercept only	6	1569.244	25.683	2.077E-07
Plot * Sex * Age + Year	Intercept only	19	1569.282	25.722	2.037E-07
Year * Age	Intercept only	7	1569.626	26.065	1.716E-07
Plot * Year * Age + Sex	Plot	29	1569.953	26.392	1.457E-07
Plot * Age + Year	Intercept only	11	1570.449	26.889	1.137E-07
Treatment * Sex * Age + Year	Intercept only	11	1570.558	26.997	1.077E-07
Year * Sex * Age	Intercept only	13	1570.638	27.078	1.034E-07
Plot + Year * Sex * Age	Intercept only	16	1571.839	28.279	5.674E-08
Plot * Year * Age + Sex	Treatment + Plot	30	1572.096	28.535	4.991E-08
Plot * Year * Age	Plot	28	1574.298	30.738	1.659E-08
Plot * Year + Sex	Intercept only	14	1574.358	30.798	1.610E-08
Plot * Year	Intercept only	13	1575.334	31.774	9.883E-09
Plot * Year + Sex * Age	Intercept only	16	1575.463	31.903	9.267E-09
Plot * Year * Age + Sex	Treatment	27	1575.844	32.283	7.661E-09

Plot * Year * Age	Treatment + Plot	29	1576.415	32.855	5.757E-09
Plot * Year + Age	Intercept only	14	1576.622	33.061	5.192E-09
Plot * Year * Sex + Age	Intercept only	26	1578.421	34.860	2.112E-09
Plot * Year * Sex	Intercept only	25	1578.650	35.090	1.883E-09
Plot * Year * Age	Treatment	26	1579.420	35.860	1.281E-09
Plot * Year * Sex * Age	Plot	52	1581.550	37.990	4.417E-10
Plot * Year * Sex * Age	Treatment + Plot	53	1583.821	40.260	1.419E-10
Plot * Year * Sex * Age	Treatment	50	1585.421	41.861	6.377E-11
Plot * Year * Age + Sex	Intercept only	26	1585.796	42.236	5.286E-11
Plot * Year * Age	Intercept only	25	1588.344	44.783	1.479E-11
Plot * Year * Sex * Age	Intercept only	49	1593.568	50.008	1.085E-12

Table C8. Linear mixed models that describe scaled mass index of swamp sparrows. K = number of parameters, w_i = model weight. All models include Individual as a random effect and Ordinal Day.

Models	K	AICc	Δ AICc	w_i
Treatment * Sex * Age + Year	13	3965.608	0	0.719
Plot * Year + Age	16	3969.086	3.478	0.126
Plot * Year * Sex + Age	28	3970.291	4.684	0.069
Plot * Year + Sex + Age	17	3971.132	5.524	0.045
Plot * Year + Sex * Age	18	3972.118	6.510	0.028
Treatment + Year + Age	8	3976.073	10.465	3.840E-03
Plot * Year	15	3976.339	10.731	3.361E-03
Treatment + Year + Sex + Age	9	3978.023	12.415	1.448E-03
Treatment + Year + Sex * Age	10	3978.131	12.524	1.372E-03
Plot * Year + Sex	16	3978.354	12.746	1.227E-03
Plot * Year * Sex	27	3979.972	14.364	5.465E-04
Treatment + Year	7	3981.044	15.436	3.198E-04
Treatment + Year + Sex	8	3982.939	17.331	1.240E-04
Plot * Year * Age	27	3983.909	18.301	7.635E-05
Plot * Year * Age + Sex	28	3985.998	20.390	2.686E-05
Plot * Year * Sex * Age	51	4000.868	35.260	1.586E-08
Plot + Year * Age	12	4002.331	36.724	7.627E-09
Year * Age	9	4003.295	37.687	4.712E-09
Plot + Year * Age + Sex	13	4004.290	38.682	2.865E-09

Year * Age + Sex	10	4005.179	39.571	1.836E-09
Plot * Age + Year	13	4007.071	41.463	7.131E-10
Plot + Year + Sex * Age	12	4007.271	41.663	6.454E-10
Plot + Year + Age	10	4007.532	41.924	5.663E-10
Year + Sex * Age	9	4007.704	42.096	5.197E-10
Year + Age	7	4007.904	42.296	4.702E-10
Plot * Age + Sex + Year	14	4008.884	43.276	2.881E-10
Plot + Year + Sex + Age	11	4009.275	43.667	2.369E-10
Year + Sex + Age	8	4009.528	43.920	2.088E-10
Plot * Sex * Age + Year	21	4010.447	44.839	1.318E-10
Plot + Year	9	4010.757	45.150	1.129E-10
Plot * Sex + Age + Year	14	4010.775	45.167	1.119E-10
Plot + Year * Sex * Age	18	4011.206	45.598	9.022E-11
Year	6	4011.450	45.842	7.985E-11
Year * Sex * Age	15	4012.301	46.693	5.219E-11
Plot + Year + Sex	10	4012.441	46.833	4.866E-11
Year + Sex	7	4012.989	47.382	3.698E-11
Plot + Year * Sex + Age	13	4013.352	47.745	3.084E-11
Year * Sex + Age	10	4013.571	47.963	2.765E-11
Plot * Sex + Year	13	4013.909	48.301	2.336E-11
Treatment * Sex * Age	11	4014.110	48.502	2.112E-11
Treatment * Age	7	4015.079	49.472	1.301E-11
Plot + Year * Sex	12	4016.196	50.588	7.443E-12

Year * Sex	9	4016.618	51.010	6.026E-12
Treatment * Age + Sex	8	4017.020	51.412	4.928E-12
Treatment + Plot + Age	9	4018.325	52.718	2.566E-12
Treatment + Plot + Sex + Age	10	4020.301	54.693	9.555E-13
Treatment * Sex + Age	8	4021.555	55.947	5.104E-13
Treatment + Plot + Sex * Age	11	4022.104	56.496	3.880E-13
Treatment + Plot	8	4026.743	61.136	3.814E-14
Treatment + Age	6	4027.571	61.963	2.521E-14
Treatment + Plot + Sex	9	4028.733	63.126	1.410E-14
Treatment * Sex	7	4029.367	63.759	1.027E-14
Treatment + Sex + Age	7	4029.535	63.927	9.443E-15
Treatment + Sex * Age	8	4031.473	65.865	3.584E-15
Treatment	5	4036.263	70.655	3.268E-16
Treatment + Sex	6	4038.246	72.639	1.212E-16
Plot + Age	8	4094.746	129.138	6.528E-29
Age	5	4096.255	130.647	3.069E-29
Plot + Sex + Age	9	4096.768	131.160	2.375E-29
Sex + Age	6	4098.276	132.668	1.117E-29
Plot + Sex * Age	10	4098.782	133.174	8.677E-30
Sex * Age	7	4100.294	134.686	4.074E-30
Plot	7	4107.617	142.009	1.047E-31
Intercept only	4	4109.365	143.757	4.369E-32
Plot + Sex	8	4109.644	144.036	3.800E-32

Sex 5 4111.381 145.773 1.594E-32

Table C9. Robust models that describe survival (S), temporary emigration (γ'' and γ'), encounter probability (p), and abundance for swamp sparrows in 2008. K = number of parameters, w_i = model weight. Dots indicate that parameters are constrained to constant values.

S	γ''	γ'	p	N	K	AICc	Δ AICc	w_i
.	0	0	.	Session	7	-715.621	0	0.985
.	Time	Time	.	Session	11	-707.253	8.368	0.015

Table C10. Cormack-Jolly-Seber logistic regression models that describe apparent survival (ϕ) and recapture probability (p) for swamp sparrows with respect to scaled mass index and other variables. K = number of parameters, w_i = model weight.

ϕ	p	K	AICc	Δ AICc	w_i
Treatment * Scaled mass + Sex + Age	Plot	10	1315.628	0	0.334
Treatment * Scaled mass + Age	Plot	9	1315.636	0.008	0.332
Treatment * Scaled mass + Sex * Age	Plot	11	1316.443	0.815	0.222
Treatment * Scaled mass * Age + Sex	Plot	13	1320.628	5.000	0.027
Treatment + Sex + Age + Scaled mass	Plot	9	1320.703	5.075	0.026
Treatment + Sex * Age + Scaled mass	Plot	10	1320.706	5.078	0.026
Treatment + Age + Scaled mass	Plot	8	1321.887	6.258	0.015
Treatment * Age + Sex + Scaled mass	Plot	10	1321.913	6.285	0.014
Treatment + Sex + Age	Plot	8	1327.621	11.993	8.305E-04
Treatment + Sex * Age	Plot	9	1328.112	12.484	6.498E-04

Treatment * Age + Sex	Plot	9	1328.595	12.967	5.104E-04
Treatment + Age	Plot	7	1329.079	13.451	4.006E-04

CHAPTER II. ADAPTIVE FAT REGULATION WHEN FOOD IS LIMITING:
EXPERIMENTAL EVIDENCE OF A FAT REGULATION THRESHOLD

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Abstract. Many birds of the temperate zone increase and then decrease the size of fat reserves over the course of a winter. Adaptive fat models explain these changes as a strategy of fattening to avoid starvation during cold weather and of fat regulation to avoid depredation. Adaptive fat regulation has rarely been tested experimentally in the wild. Further, fat reserves of several species are limited by food availability in winter, though it is unknown if birds adaptively regulate fat when food is limiting. In a temperate zone system where food is known to limit fat levels in winter, we hypothesized that 1) optimal levels of fat are constantly refined based on shifting starvation and predation risks (which is consistent with other adaptive fat models), but that 2) fat fluctuates under this optimal level on a daily basis when food availability is limited. We call this the Fat Regulation Threshold Hypothesis. This hypothesis is novel in that it distinguishes between optimal and actual fat reserves. We tested the Fat Regulation Threshold Hypothesis by measuring temporal changes in scaled mass, furcular fat, abdominal fat, and pectoral muscle of swamp sparrows (*Melospiza georgiana*) over three winters with a controlled and replicated food supplementation experiment.

Birds with access to supplemental food gained scaled mass through the coldest part of the winter and then lost scaled mass and fat (but not pectoral muscle) as temperatures warmed, supporting adaptive fat regulation. In contrast, control birds had lower scaled mass, fat, and muscle, each of which decreased at a steeper slope than in experimental birds. In addition,

scaled mass of control birds positively tracked recent temperature, which determines energetic demands for thermoregulation, indicating that energy stores were limited by food. Scaled mass and fat of experimental and control birds converged near the end of each winter, suggesting that while control birds adaptively regulated optimal fat levels over the course of the season, actual fat levels were limited by food availability. These results provide experimental support for adaptive fat regulation in the wild and the first evidence that actual fat reserves are limited by food availability while optimal levels are adaptively regulated.

Key words: Adaptive fat regulation; adaptive mass; Fat Regulation Threshold Hypothesis; cumulative logit model; linear model; food limitation; food supplementation experiment; migratory bird; winter ecology

INTRODUCTION

The ability to maintain appropriate energy stores is essential for most animals to survive winter. Fat deposits are especially important for small birds, which are highly susceptible to mortality from hypothermia and starvation because of high metabolic rates and high surface area-to-volume ratios that allow a proportionally large amount of heat loss (Kendeigh 1970, Bennett and Harvey 1987). During cold nights, small birds have been shown to catabolize fat that equals >10% of their body weight (Chaplin 1974, Haftorn 1992). Similarly, fat reserves are necessary to avoid starvation during interruptions in foraging when food is covered with snow or ice (Ketterson and King 1977, Rogers and Reed 2003).

A growing body of evidence shows that small birds adjust fat reserves to meet anticipated energetic demands. Many temperate zone birds have been shown to carry more fat in winter

than other seasons (King and Farner 1966, Clark 1979, Lehikoinen 1987, Haftorn 1989, Koenig et al. 2005). Maintenance of large fat reserves is thought to increase depredation risk, however, by necessitating more time foraging (Ekman 1986, Brodin 2001, Dierschke 2003), or reducing predator evasion ability (Blem 1975, Kullberg et al. 1996, reviewed in Lind et al. 2010). Models of adaptive fat regulation explain changes in fat reserves as a strategy to balance risks of starvation and depredation (Lima 1986, Houston and McNamara 1993, reviewed in Brodin 2007). Adaptive fat regulation models predict inverse relationships between size of fat reserves and temperature, interruptions in foraging, and risk of predation. Controlled experiments of captive birds demonstrate inverse relationships between size of fat reserves and temperature (Ekman and Hake 1990, Rogers 1995, Cuthill et al. 2000) and food predictability (Ekman and Hake 1990, Cuthill et al. 2000). The few experimental tests of adaptive fat regulation in the wild provide additional support. Macleod et al. (2005) found that fat levels were inversely related to artificial predator abundance and Rogers et al. (1993) showed that fat levels of birds from three locations converged to similar levels following translocation to a common environment.

Adaptive fat regulation might occur at both long (seasonal) and short (weekly or daily) timescales. Seasonally, birds are hypothesized to adjust fat to meet the maximum expected energetic costs and predation risks (Lima 1986) and this is supported with observational data (Evans 1969, Dawson and Marsh 1986). On a shorter scale, birds have been shown to adjust fat based on temperature of recent days (King and Farner 1966, Bednekoff et al. 1994, Rogers et al. 1993, Rogers 1995).

It is not well known if or how small birds in winter adjust energy reserves at either seasonal or shorter timescales when food abundance is limited. In the most severe case, limited food abundance might entirely limit a bird's ability to adjust fat between seasons and days.

Alternatively, birds might adjust optimal fat levels based on a balance of starvation and predation risks, but be unable to reach those levels on a daily basis. In this scenario, optimal fat level could be viewed as a threshold, above which fat is down-regulated and under which fat levels vary depending on short-term fluctuations in food availability and weather. We call this second hypothesis the Fat Regulation Threshold Hypothesis. This hypothesis explicitly distinguishes optimal and actual fat levels, an important distinction from other models of adaptive fat regulation. Neither hypothesis regarding fat regulation when food is in limited availability (simple food limitation and The Fat Regulation Threshold) has been tested experimentally, despite the fact that food has been shown to limit fat reserves in multiple species in winter (Brittingham and Temple 1988, Rogers and Heath-Coss 2003, Brown and Sherry 2006, Chapter I).

We asked if birds regulate fat in winter when food is limiting. We have shown previously (Chapter I) that migratory swamp sparrows (*Melospiza georgiana*) overwintering in the temperate zone increased body mass following food supplementation, indicating that fat levels are limited by food. Observations indicate that mass declined throughout the late winter, though it is unknown if the decline was a result of adaptive fat regulation or food limitation resulting from diminishing food supply.

We hypothesized that in this system, swamp sparrows 1) adaptively regulate optimal fat levels over the course of the season, but 2) fluctuate under this optimal level on a daily basis when food availability is limited. To test these hypotheses, we compared changes of scaled mass, subcutaneous fat, and muscle of birds on replicate study plots with natural and supplemented food abundances throughout three winters. Over the course of each winter, as temperatures warm, decreases in scaled mass and fat on control plots would support either

adaptive fat regulation or simple food limitation. In contrast, decreases of scaled mass and fat over time on supplemented plots would indicate adaptive fat regulation. Because birds catabolize muscle for energy after fat reserves have been depleted (Cherel et al. 1988, Jenni-Eiermann and Jenni 1996, 1997), loss of muscle throughout the winter would support food limitation. Within a shorter timeframe, adaptive fat regulation would be indicated by an inverse relationship between fat and recent temperature. Alternatively, food limitation of daily fat levels would be shown by a positive correlation between fat and ambient temperature.

METHODS

Data Collection

We studied the change in energetic reserves of swamp sparrows (*Melospiza georgiana*) over three winters (January–March 2008–2010) in coastal North Carolina, USA. During these periods, temperatures were below the swamp sparrow's thermal neutral zone (lower limit 24.1°C, Yarbrough 1971) except for 12.5 hours in 2008, 8.5 hours in 2009, and less than two hours in 2010, indicating the sparrows required much energy in order to maintain body heat (Liknes et al. 2002).

This study was part of a large food supplementation experiment. See Chapter I for details regarding study plots, data collection, and food manipulation. We captured (with mist nets), marked, and recaptured birds on four similar study plots in brackish marshes near Swanquarter and Engelhard, NC. Mist nets covered approximately 1.2 ha at three plots and 1.8 ha at one plot. We measured body mass, fat, and muscle of each individual at each capture. Mass was quantified to the nearest 0.01g using an electronic balance and corrected for structural size

(tarsus, 0.1mm precision) by calculating the scaled mass index following Peig and Green (2009) using package *smatr* (Warton et al. 2011) in R (R Development Core Team 2012). Fat was quantified by visually inspecting subcutaneous fat deposits between the bones of the furcula (“furcular fat”) and fat covering the abdomen, from the sternum to cloaca (“abdominal fat”, see Table A1 for fat classes, Fig. A1). Rogers et al. (1991) found that similar visible fat classes were positively and significantly related to lipid index (grams ether-soluble lipid/gram lean dry mass) in dark-eyed juncos. Muscle was scored based on size of the pectoralis in relation to the keel and was observed visually and tactically, by rolling a finger over the breast to feel the muscle and keel (see Table A1 for muscle classes). We recorded mass, and fat and muscle scores in the morning (within four hours of civil daylight), so the sizes of energy reserves represent that which was not used throughout the night for thermoregulation (Rogers and Reed 2003).

In 2009 and 2010, we supplemented food at two plots (E1 and E2) and left two as controls (C1 and C2). Supplemental food was distributed at the intersections of a grid formed of 9 lines x 4 lines, with lines separated by 25 m, producing 36 feeding stations per plot. This design was intended to allow as many individuals to access food as possible, regardless of social rank (Theimer 1987). Food consisted of millet *ad libitum* and mealworms (*Tenebrio molitor*) every time we replenished millet. More food was distributed in 2010 than in 2009 because of occasional flooding. Swamp sparrows were frequently seen eating millet and mealworms from the piles and we regularly observed those items in their feces.

Analyses

To characterize patterns of temporal change in scaled mass, furcular fat, abdominal fat and muscle, we tested if ordinal date within a year (“Day”, January 1 = 1) predicts each variable.

Because smoothed temperature patterns showed a quadratic relationship with time, we fit some models with a quadratic Day term (Day^2). To determine if energy stores were lost at different rates depending on Treatment, we tested for interactions between $\text{Day} * \text{Treatment}$ and $\text{Day}^2 * \text{Treatment}$. We compared models with and without variables of interest by ranking them with AICc and calculating the evidence ratio (Burnham and Anderson 2002). The evidence ratio is based on model weights (w_i) and is calculated as the probability that the model of interest (e.g. Day) is the best in the model set over the probability that the null model (e.g. lacking Day) is the best in the set. A previous analysis (see Chapter I) found that differences in scaled mass among age/sex classes differed by treatment, so we included an additive effect of $\text{Treatment} * \text{Age} * \text{Sex}$ in all models to improve precision of parameter estimation. Previous analyses also found that scaled mass differed by year, so we included the factor variable Year in each model. Lastly, because each individual was measured multiple times throughout each winter, we included a random intercept effect of individual in each model.

We fit linear models of scaled mass using normal error distributions with package lme4 (Bates et al. 2011). The saturated model ($\text{scaled mass} = \text{Day} * \text{Treatment} + \text{Day}^2 * \text{Treatment} + \text{Treatment} * \text{Sex} * \text{Age} + \text{Year}$) showed appropriate fit based on diagnostic plots, indicating appropriate fit in nested models (Zuur et al. 2009). We treated fat and muscle scores as ordinal data as suggested by Hailman (1965, 1969) and (Rogers 1991). We tested if fat and muscle were correlated to scaled mass index and to one another (both treatments combined) using polyserial (ordinal vs. continuous data) and polychoral (ordinal vs. ordinal data) correlations, using package polycor (Fox 2010). Further, we performed cumulative logit regressions with package ordinal (Christensen 2011) with scaled mass as a predictor of fat and muscle scores, with individual as a random effect. According to the cumulative logit models, consecutive thresholds between scores

were not equidistant, indicating that the fat and muscle score data were indeed ordinal rather than interval (ranges: Furcular fat=1.12–2.76g, Abdominal fat=1.66–3.90g, Muscle=2.90–3.36g). We fit models of fat and muscle change over time with cumulative logit models and tested goodness of fit of top cumulative logit models with deviance following Christensen (2011).

To test if scaled mass is adjusted in response to, or limited by, recent temperature, we compared the top model from the scaled mass analysis described above with similar models containing additive and interactive temperature terms. We did not test the effect of temperature on fat and muscle because these models had poor goodness of fit. For this analysis, we modeled experimental and control birds separately to eliminate the Treatment variable and therefore greatly reduce the number of variables in each model. We used mean minimum temperature of the current day and a range of prior days (T_{\min}), because Rogers et al. (1994) found similar variables to best predict mass of dark-eyed juncos. The range of days averaged was 1–14 (referred to as T1–T14). T_{\min} was not well correlated with Day, though the relationship improved with timeframe length (r^2 including interactive effect of Year: 0.20–0.43), so we centered T1–T14, Day, and Day² for further analyses. In addition, we tested for an effect of T_{\min}^2 to determine if fat is regulated or limited differently at different temperatures. T_{\min} and T_{\min}^2 were included as additive and interactive effects. Daily temperature minima were recorded at Cherry Point, NC, 50 km away from the study sites in similar habitat (National Climate Data Center 2012). Minimum temperatures from Cherry Point were highly correlated to a smaller, fragmented data set recorded at one of our study plots. Preliminary analyses using temperatures from the study plots gave very similar results to those presented here.

To visualize these models, we calculated model average predictions and unconditional standard errors for linear models with package AICcmodavg (Mazerolle 2011) and for

cumulative link models following Hostetler et al. (2011) and Burnham and Anderson (2002).

We also present parameter estimates from the top ranked models (B for unstandardized variables and β for centered variables). Parameter estimates from cumulative link models are presented in the scale of ordered logits (otherwise known as ordered log odds), which are interpreted as the change in probability of moving to the next higher level of the dependent variable with a unit increase in the independent variable.

Model names include only higher-level interactions although all main effects and lower-level interactions are also included in the models. For example, the model titled Day + Treatment * Age * Sex includes the following terms: Day + Treatment + Age + Sex + Treatment * Age + Treatment * Sex + Age * Sex + Treatment * Age * Sex.

RESULTS

Under both natural and food supplemented conditions, scaled mass declined overall as the winter progressed (Fig. 1). The model that included Day*Treatment + Day²*Treatment was ranked at the top of the set (Table B1). The evidence ratio for an effect of Day was 9.75E34, providing strong support that scaled mass changed by Day. The evidence ratio that the pattern of change was quadratic in at least one Treatment was 70, and the evidence ratio that the change differed by Treatment was also 70. Model average predictions (Fig. 1) and parameter estimates from the top model show that control birds lost scaled mass throughout the entire winter ($-0.01\text{g}/\text{Day} \pm 0.007$) and that this loss was almost linear ($B_{\text{Day}}^2 = -0.00009 \pm 0.00008$). In contrast, experimental birds gained scaled mass throughout the early winter ($0.06\text{g}/\text{Day} \pm 0.02$) and lost scaled mass later ($B_{\text{Day}}^2 = -0.0006 \pm 0.0002$). Scaled mass was higher in experimental birds throughout the season, though the two groups converged at the beginning and end of the

study periods. There was evidence of variation in scaled mass among years. Compared to 2008, scaled mass was similar in 2009 ($-0.002 \text{ g} \pm 0.14 \text{ s.e.}$), but higher in 2010 (0.84 ± 0.16).

Furcular and abdominal fat were positively correlated with scaled mass ($\rho \pm \text{s.e.}$): 0.538 ± 0.022 , 0.523 ± 0.023 , respectively (Fig. 2). Pectoral muscle did not correlate with scaled mass: $\rho = 0.282 \pm 0.031 \text{ s.e.}$ Cumulative link models, which included a random effect of individual, indicated that as scaled mass increased, there was an increase in probability of transition to higher levels of furcular fat ($B=0.96 \pm 0.07 \text{ s.e.}$, evidence ratio= $9.370e79$, Table B2), abdominal fat ($B=0.85 \pm 0.06 \text{ s.e.}$, evidence ratio= $1.24e68$, Table B3), and muscle ($B=0.36 \pm \text{s.e. } 0.05$, evidence ratio= $7.873e13$, Table B4). Fat scores were correlated to one another ($\rho=0.88 \pm 0.009 \text{ s.e.}$) and, to a lesser degree, muscle (furcular: $\rho=0.42 \pm 0.03 \text{ s.e.}$, abdominal: $\rho=0.41 \pm 0.03 \text{ s.e.}$).

Fat levels declined throughout the winters for both Treatments (Figs. 3 and 4). Models with Day*Treatment were ranked highest for both furcular and abdominal fat indicating that fat decreased differently by Treatment. The evidence ratios for an effect of Day were $> 3E22$ and for an interaction with Treatment were > 82 (Tables B5 and B6). For furcular fat, model average predictions (Fig. 3) and top model parameter estimates (on the ordered log odds scale) indicate declines that were shallower on experimental plots ($B = -0.03/\text{Day} \pm 0.007 \text{ s.e.}$) than control plots (-0.05 ± 0.005). Model average predictions also show a slight decrease in magnitude of decline late in the winter, even though models with Day² made up a small percentage of the overall model weight (0.008%). Similar to the patterns of furcular fat loss, experimental birds had shallower declines of abdominal fat (Fig 4., $-0.02/\text{Day} \pm 0.006 \text{ s.e.}$) than control birds (-0.05 ± 0.005). Models containing Day² received 12% of the model weight and this is shown in Fig. 4 by a slight increase in rate of abdominal fat loss in experimental birds as the winters progressed and a slight decrease in rates of loss in control birds. Similar to scaled mass, we found higher

values of fat in 2010 than in 2008 and 2009 (Figs. 3 and 4, Furcular $B_{\text{Year } 2010} = 0.72 \pm 0.23$ s.e., Abdominal $B_{\text{Year } 2010} = 1.09 \pm 0.23$).

Muscle levels declined throughout the winter very slightly or not at all in experimental birds ($B = -0.004 \pm 0.007$ s.e.) and declined at higher rates in control birds (-0.02 ± 0.005 , Fig. 5). Similar to both measures of fat, models with Day*Treatment were ranked highest for muscle (evidence ratio = 20), supporting differential rates of fat change by Treatment. In contrast to between-Year variation in fat reserves, we found that muscle levels were lower in 2009 and 2010 ($B_{\text{Year } 2009} = -1.41 \pm 0.25$ s.e., $B_{\text{Year } 2010} = -1.27 \pm 0.25$) than in 2008.

Previous temperature affected scaled mass of control birds but not experimental birds. For experimental birds, the top ranked model lacked T_{min} , and the evidence ratio of the second ranked model (which contained T7) was 0.76 (Table B8). In contrast, for control birds, there was strong support for an effect of recent temperature on scaled mass (evidence ratio of top model to null = $9.72E8$, Table B9). The top four models included T5 and T6; these two variables are highly correlated ($r^2=0.98$). The top two models included T5 + T5² and T6 + T6², and there was some support for the quadratic terms (evidence ratios for both = 4). Model average predictions (Fig. 7) and top model parameter estimates show that scaled mass of control birds is positively related to recent temperature, and that the rate of increase is higher at higher temperatures ($\beta_{T5} = 0.05\text{g}/1^\circ\text{C} \pm 0.009$ s.e., $\beta_{T5^2} = 0.004 \pm 0.002$).

DISCUSSION

Adaptive fat regulation

Our study is the first to experimentally test and find adaptive fat regulation in the temperate zone by ruling out sole control of fat reserves by food limitation. We found that both scaled mass and fat reserves declined in experimentally supplemented and control birds as the winters progressed. Decline of these variables in experimental birds despite *ad libitum* food supplementation indicates that adaptive regulation rather than food limitation was the driving force. In addition, maintenance of muscle in experimental birds throughout the winters provided further support that fat was regulated rather than limited. Adaptive fat regulation in experimental birds suggests that control birds also adaptively regulate optimal fat levels throughout the course of the winter. In particular, decline in fat of experimental birds indicates that the large fat reserves in both treatments at the beginning of the year are a result of adaptive regulation (“winter fattening”). Three other food supplementation experiments in temperate winters included measures of body mass or fat, but did not compare change in these values by treatment in relation to date and they did not measure muscle, so it is unclear if those changes in fat are due to adaptive regulation or food limitation (Smith et al. 1980, Brittingham and Temple 1988, Rogers and Heath-Coss 2003).

Scaled mass was indicative of fat, shown by correlations between those measures and that they decreased over time largely in concert. Scaled mass did not correlate well with muscle, further indicating that changes in scaled mass observed in this study are mainly representative of changes in fat reserves. Correlation between scaled mass and fat is not found in all systems (Dawson and Marsh 1986, Strong and Sherry 2000) and might reflect the dependency of small ground-foraging birds on fat deposits when ice and snow cover food resources (Rogers and Smith 1993). Despite a strong correlation between scaled mass and fat, the increase in scaled mass during the first month following food addition was not paralleled by increases in fat scores.

Experimental birds did show weakly quadratic abdominal fat loss, potentially reflecting the pattern of scaled mass. One potential reason for this discrepancy is that fat measurements were much less precise than mass measurements, suggesting that one would be more likely to detect complex patterns of temporal change in scaled mass than fat.

Food limitation of fat reserves

Multiple results also indicated that food limited the size of fat reserves of control birds. First, the positive correlation between fat reserves of control, but not experimental, birds and minimum temperature averaged over the previous 5–6 days suggests that control birds lost fat when temperatures were low and thermoregulatory costs were high and that they deposited fat when temperatures warmed. The energetic challenges posed by cold weather might have been exacerbated by a correlated reduction in food availability over the short term. On cold days, food might have been covered by ice or snow and on the warmest days invertebrates might have been more active, particularly at the beginning and end of the winters. We hypothesize that experimental birds were able to maintain steady fat reserves despite fluctuations in temperature because they were able to replenish their fat reserves constantly.

Second, the decline of muscle and the faster rates of loss of scaled mass and fat in control compared to experimental birds strongly supports food limitation. Decline in muscle of control birds suggests they were unable to rebuild muscle following catabolism (possibly during extreme cold events) and possibly that they directed energy to fat deposition instead of muscle anabolism. For wintering swamp sparrows, maintaining sufficient fat reserves might be more important than maintaining large flight muscles given that fat provides more energy per gram than muscle (Cherel et al. 1988). In addition, the importance of flight muscles for movement might be

reduced for swamp sparrows in winter; long flights (>50m) occur during morning and evening commutes between roosts and foraging locations, while movement throughout the rest of the day is mainly composed of running, hopping, and very short flights (Danner pers. obs.).

Fat gain following food addition could be evidence of food limitation, but is also predicted by adaptive fat regulation models for stochastic environments (Lima 1986). The adaptive fat regulation model for energetically challenging and stochastic environments (such as winter at our site) predicts that birds should gain fat when food becomes more abundant because the increased feeding rate allows for shorter foraging time and thereby a reduction in depredation risk (Lima 1986). Therefore, the higher mass and fat of swamp sparrows when food was supplemented are not sufficient evidence of either simple food limitation or adaptive fat regulation. However, because we found evidence of food limitation in this system, we can infer that the increases in mass and fat following food supplementation resulted at least in part from relaxed food limitation. It is possible that adaptive fat regulation allowed the increase in fat of experimental birds above some unknown threshold. As expected, our results do not support an alternate adaptive fat regulation model formulated for environments that are predictable between days (Houston and McNamara 1993), which predicts reductions in fat reserves following food supplementation.

Two food supplementation studies in temperate winters also found increases in mass or fat following food addition (Brittingham and Temple 1988, Rogers and Heath-Coss 2003) and one did not (Smith et al. 1980). Without complementary analyses, it is hard to know if mass gain in those studies was a result of adaptive regulation or food limitation. Brittingham and Temple (1988) stated that their results were in accord with adaptive fat regulation. Rogers and Heath-Coss (2003) reasoned that fat gain was caused by adaptive regulation rather than limitation

because gains in fat were slight. In contrast, we found predicted increases in scaled mass of over 1 gram, which is 6.25% of a 16g bird's body mass.

A Fat Regulation Threshold

The combined results of fat regulation and limitation suggest that regulation occurs only above a certain threshold and that below this threshold, food availability limits fat reserves. Therefore, these results support the Fat Regulation Threshold Hypothesis. In addition to our findings, an adjustable fat regulation threshold is also supported by fat reserve patterns observed in captive birds. There are many examples of captive birds that maintain a steady mass while provided unlimited food and then increase mass drastically in preparation for migration (e.g. King and Farner 1959, Tonra et al. 2011).

Adaptive fat regulation is thought to be widespread in wild birds, though we provide the first documentation of food limitation occurring in a season when adaptive regulation has also been documented. A key result indicating food limitation of fat was that the scaled mass of control birds tracked recent temperatures. Several studies have found negative correlations between fat reserves and recent temperature, indicating adaptive fat regulation on a short timescale (King and Farner 1966, Bednekoff et al. 1994, Rogers et al. 1993, Rogers 1995). Other studies found no correlation between recent temperature and fat reserves (Dawson and Marsh 1986). It is possible that birds in our system are particularly susceptible to fat loss because of intense winter storms and low food availability. In addition, the surface water that covers large portions of the marshes at our plots froze frequently, possibly making food inaccessible more often than on terra firma. Alternatively, a modeling approach such as ours, which includes large sample sizes and high temporal resolution, and accounts for differences

among age/sex classes, individuals, and years, might be necessary to detect some short-term relationships between fat reserves and temperature.

Fitness consequences of food limitation of fat reserves

Fat reserves are important for small birds to survive in winter. I (Chapter I) found that individuals with larger fat reserves and those with access to supplemented food experienced higher survival. Similarly, Jansson et al. (1981) and Brittingham and Temple (1988) found that birds with access to supplemented food had higher survival during winter, presumably as a result of increased fat reserves. In addition, limitation of fat reserves on a daily basis indicates that tradeoffs exist with other energetically costly functions. Danner et al. (Chapter III) found that supplemented swamp sparrows molted earlier than control birds, which might allow earlier migration, breeding territory acquisition, and subsequently higher breeding success (Norris et al. 2004).

Summary

We found that a combination of adaptive fat regulation and food limitation controls the fat reserves of a migratory bird wintering in the temperate zone. Swamp sparrows adaptively regulated fat levels throughout the winter, though on a daily basis, food limitation prevented them from reaching optimal fat levels, thus supporting the Fat Regulation Threshold Hypothesis. These results are the first to show simultaneous seasonal adaptive regulation and daily limitation of fat reserves and have important implications for understanding energetic requirements and tradeoffs in winter.

LITERATURE CITED

- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using Eigen and syntax classes. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>
- Bednekoff, P. A., H. Biebach, and J. Krebs. 1994. Great tit fat reserves under unpredictable temperatures. *Journal of Avian Biology* 25(2):156–160.
- Bennett, P.M. and P. H. Harvey. 1987 Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213:237–363.
- Brodin, A. 2001. Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation? *Animal Behaviour* 62:993–999.
- Brodin, A. 2007. Theoretical models of adaptive energy management in small wintering birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:1857–1871.
- Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* 149:22–32.
- Blem, C. R. 1975. Geographic variation in wing-loading of the House Sparrow. *Wilson Bulletin* 87:543–549.
- Brittingham, M. C. and S. A. Temple. 1988. Impacts of supplemental feeding rates on survival of Black-capped Chickadees. *Ecology* 69:581–589.
- Chaplin, S. B. 1974. Daily energetics of the Black-capped Chickadee *Parus atricapillus*, in winter. *Journal of Comparative Physiology* 89:321–330.
- Cherel, Y., J.-P. Robin, and Y. L. Meho. 1988. Physiology and biochemistry of long-term fasting in birds. *Canadian Journal of Zoology* 66:159–166.
- Christensen, R. H. B. 2011. Analysis of ordinal data with cumulative link models – estimation with the R-package ordinal. <http://cran.r-project.org/web/packages/ordinal/index.html>
- Clark, G. A., Jr. 1979. Body weights of birds: a review. *Condor* 81:193–202.
- Cuthill, I. C., S. A. Maddocks, C. V. Weall, and E. K. M. Jones. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behavioral Ecology* 11(2):189–195.
- Dawson, W. R. and R. L. Marsh. 1986. Winter fattening in the American goldfinch and the possible role of temperature in its regulation. *Physiological Zoology* 59(3):357–368.
- Dierschke, V. 2003. Predation hazard during migratory stopover: are light or heavy birds at risk? *Journal of Avian Biology* 34:24–29.
- Ekman, J. 1986. Tree use and predator vulnerability of wintering passerines. *Ornis Scandinavica* 17:261–267.

- Ekman, J. B. and M. K. Hake. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris*) during periods of unpredictable foraging success. *Behav. Ecol.* 1:62–67.
- Evans, P. R. 1969. Winter fat deposition and overnight survival of yellow buntings (*Emberiza citrinella* L.). *J. Anim. Ecol.* 38:415–423.
- Fox, J. 2010. polycor: Polychoric and polyserial correlations. R package version 0.7-8. <http://CRAN.R-project.org/package=polycor>
- Haftorn, S. 1992. The diurnal body weight cycle in titmice *Parus* spp. *Ornis Scand.* 23, 435–443.
- Hailman, J. P. 1965. Notes on quantitative treatments of subcutaneous lipid data. *Bird Banding* 36:14–20.
- Hailman, J. P. 1969. The continuing problem of fat classes as a "Rule of thumb" for identifying interval and ratio data. *Bird Banding* 40:321–322.
- Hostetler, J. A., D. P. Onorato, B. J. Bolker, W. E. Johnson, S. J. O'Brien, D. Jansen, and M. K. Oli. 2011. Does genetic introgression improve female reproductive performance? A test on the endangered Florida panther. *Oecologia*. DOI 10.1007/s00442-011-2083-0
- Houston, A. I. and J. M. McNamara. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* 24:205–219.
- Jenni-Eiermann, S. and L. Jenni. 1996. Metabolic differences between the postbreeding moulting and migratory periods in feeding and fasting passerine birds. *Funct Ecol* 10:62–72.
- Jenni-Eiermann, S. and L. Jenni. 1997. Diurnal variation of metabolic responses to short-term fasting in passerine birds during the postbreeding, molting and migratory period. *Condor* 99:113–122.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72(1):60–65.
- Ketterson, E. D. and J. R. King. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). - *Physiol. Zool.* 50(2): 115-129.
- King and Farner 1959. Premigratory changes in body weight and fat in wild and captive male white-throated sparrows. *The Condor.* 61(5): 315-324.
- King, J. R. and D. S. Farner. 1966. The adaptive role of winter fattening in the white-crowned sparrow with comments on its regulation. *The American Naturalist* 100(914):403–418.
- Koenig, W. D., E. L. Walters, J. R. Walters, J. S. Kellam, K. G. Michalek, and M. S. Schrader. Seasonal body weight variation on five species of woodpeckers. *Condor* 107:810–822.
- Kullberg, C., T. Fransson, and S. Jakobsson. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society of London, Series B*, 263:1671–1675.

- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica* 18:216–226.
- Liknes, E. T., S. M. Scott, and D. L. Swanson. 2002. Seasonal acclimatization in the American goldfinch revisited: To what extent do metabolic rates vary seasonally? *The Condor* 104:548-557.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology* 67:377–385.
- Lind, J., S. Jakobsson, and C. Kullberg. 2010. Impaired predator evasion in the life history of birds: behavioral and physiological adaptations to reduced flight ability. *Current Ornithology* 17:1–30.
- Macleod, R., A. G. Gosler, and W. Cresswell. 2005. Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* 74:956–964.
- Mazerolle, M. J. 2011. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.14. <http://CRAN.R-project.org/package=AICcmodavg>.
- National Climatic Data Center. 2012. Global Summary of the Day. Version 7. <http://www7.ncdc.noaa.gov/CDO/cdo>
- Norris, R. D, P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B:Biological Sciences* 271(1534):59–64.
- Peig, J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891.
- Piper, W. H. and R. H. Wiley. 1989. Correlates of dominance in wintering white-throated sparrows: age, sex and location. *Animal Behaviour* 37(2):298–310.
- R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rogers, C. M. 1991. An evaluation of the method of estimating body fat by quantifying visible subcutaneous fat. *J. Field Ornithol.* 62: 349–356.
- Rogers, C. M. 1995. Experimental evidence for temperature-dependent winter lipid storage in the dark-eyed junco (*Junco hyemalis oregonus*) and song sparrow (*Melospiza melodia morphna*). *Physiological Zoology* 68(2):277–289.
- Rogers, C. M. and R. Heath-Coss. 2003. Effect of experimentally altered food abundance on fat reserves of wintering birds. *Journal of Animal Ecology* 72:822–830.
- Rogers, C. M., V. Nolan, and E. D. Ketterson. 1993. Geographic variation in winter fat of dark-eyed juncos: Displacement to a common environment. *Ecology* 74(4):1183–1190.
- Rogers, C. M. and A. K. Reed. 2003. Does avian winter fat storage integrate temperature and

- resource conditions? A long-term study. *Journal of Avian Biology* 34(1):112–118.
- Rogers, J. N. M. and C. R. Smith. 1993. Life-history theory in the nonbreeding period: Trade-offs in avian fat reserves? *Ecology* 74(2):419–426.
- Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island song sparrow population. *Oecologia* 47:164–170.
- Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology* 69:883–895.
- Theimer, T.C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos. *Animal Behaviour* 59:1883–1890.
- Tonra, C., Marra, P.P., Holberton, R.L. 2011. Early elevation of testosterone advances migratory preparation in a songbird. *The Journal of Experimental Biology* 214:2761-2767.
- Witter, M. S. and I. C. Cuthill. 1993. The ecological costs of avian fat storage. *Philosophical Transactions: Biological Sciences*. 340(1291):73–92.
- Yarborough, C. G. 1971. The influence of distribution and ecology of the thermoregulation of small birds. *Comparative Biochemistry and Physiology A* 39:235-266.

Figure legends:

Figure 1. Scaled mass change over time within three winters. Raw data are shown as gray dots and multiple measures for individuals are connected with lines. Solid black line represents model average predictions for adult males with unconditional standard errors shown by dashed lines.

Figure 2. Correlations between scaled mass and fat.

Figure 3. Furcular fat change over time in three winters. Raw data are shown as gray dots and multiple measures for individuals are connected with lines. Solid black line represents model average predictions for adult males with unconditional standard errors shown by dashed lines.

Figure 4. Abdominal fat change over time in three winters. Raw data are shown as gray dots and multiple measures for individuals are connected with lines. Solid black line represents model average predictions for adult males with unconditional standard errors shown by dashed lines.

Figure 5. Muscle change over time in three winters. Raw data are shown as gray dots and multiple measures for individuals are connected with lines. Solid black line represents model average predictions for adult males with unconditional standard errors shown by dashed lines.

Figure 6. Scaled mass of control birds in relation to mean minimum temperature of the preceding five days. Raw data are shown as gray dots and multiple measures for individuals are connected

with lines. Solid black line represents model average predictions for adult males with unconditional standard errors shown by dashed lines.

Figure 7. Scaled mass predicted values from models that account for recent temperature. Black lines represent predicted values \pm unconditional s.e. and blue lines represent trace of mean minimum temperature from the previous five days.

Figures:

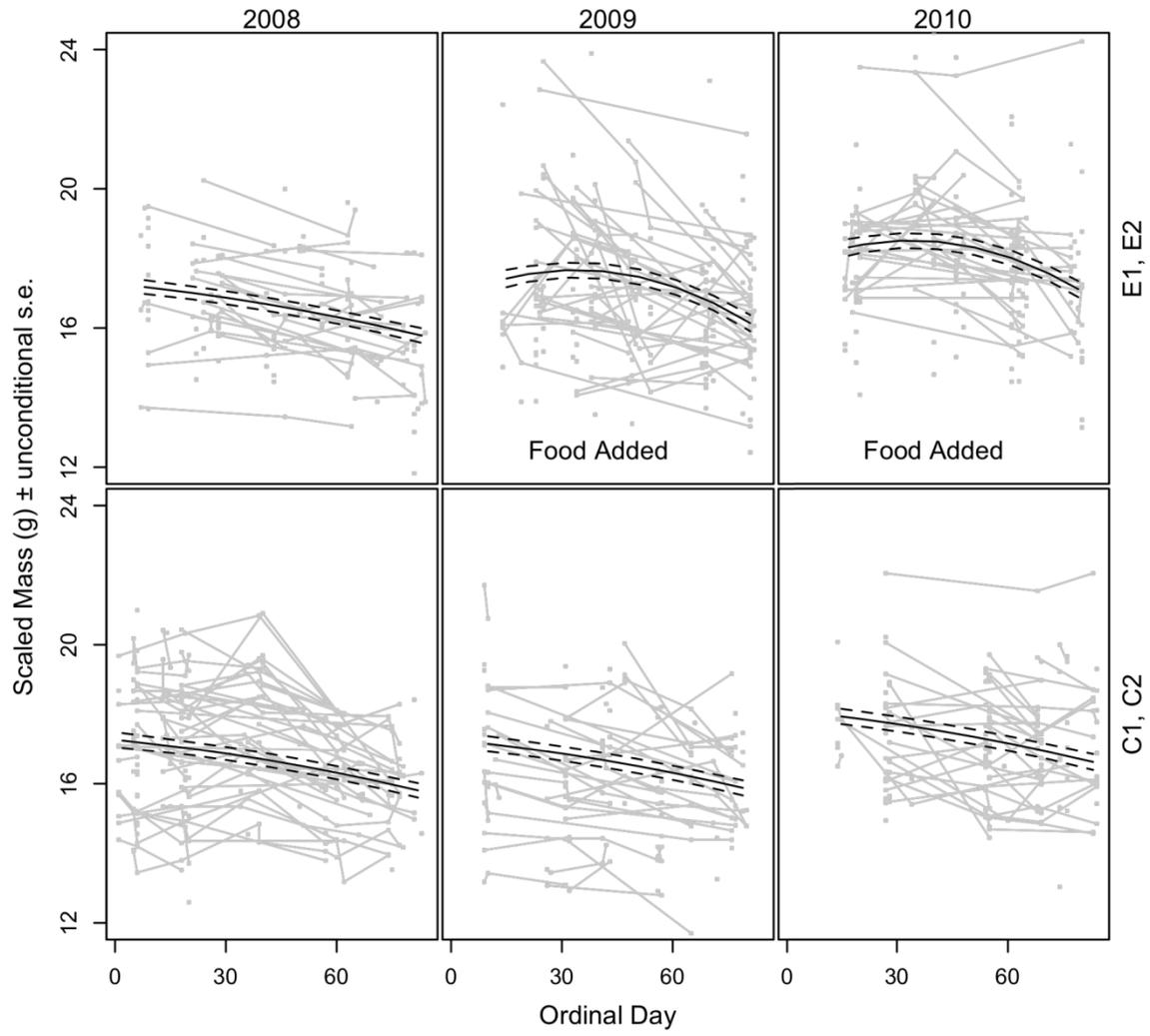


Fig. 1

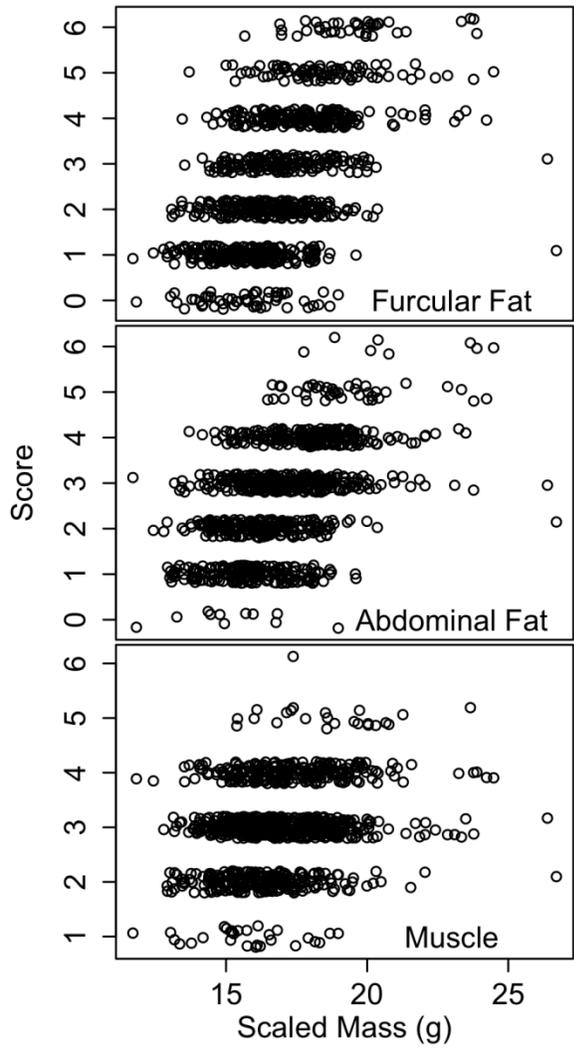


Fig. 2

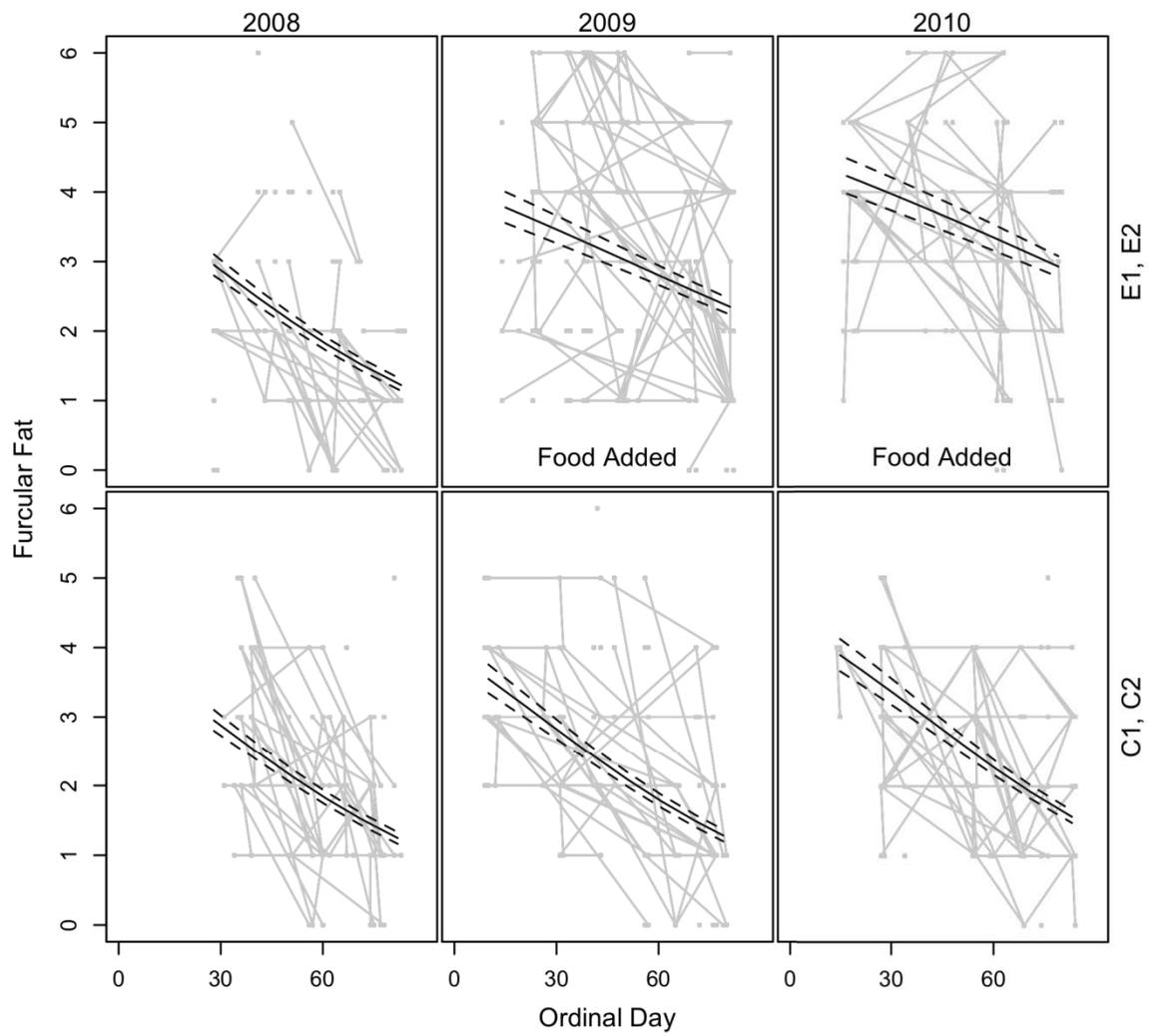


Fig. 3

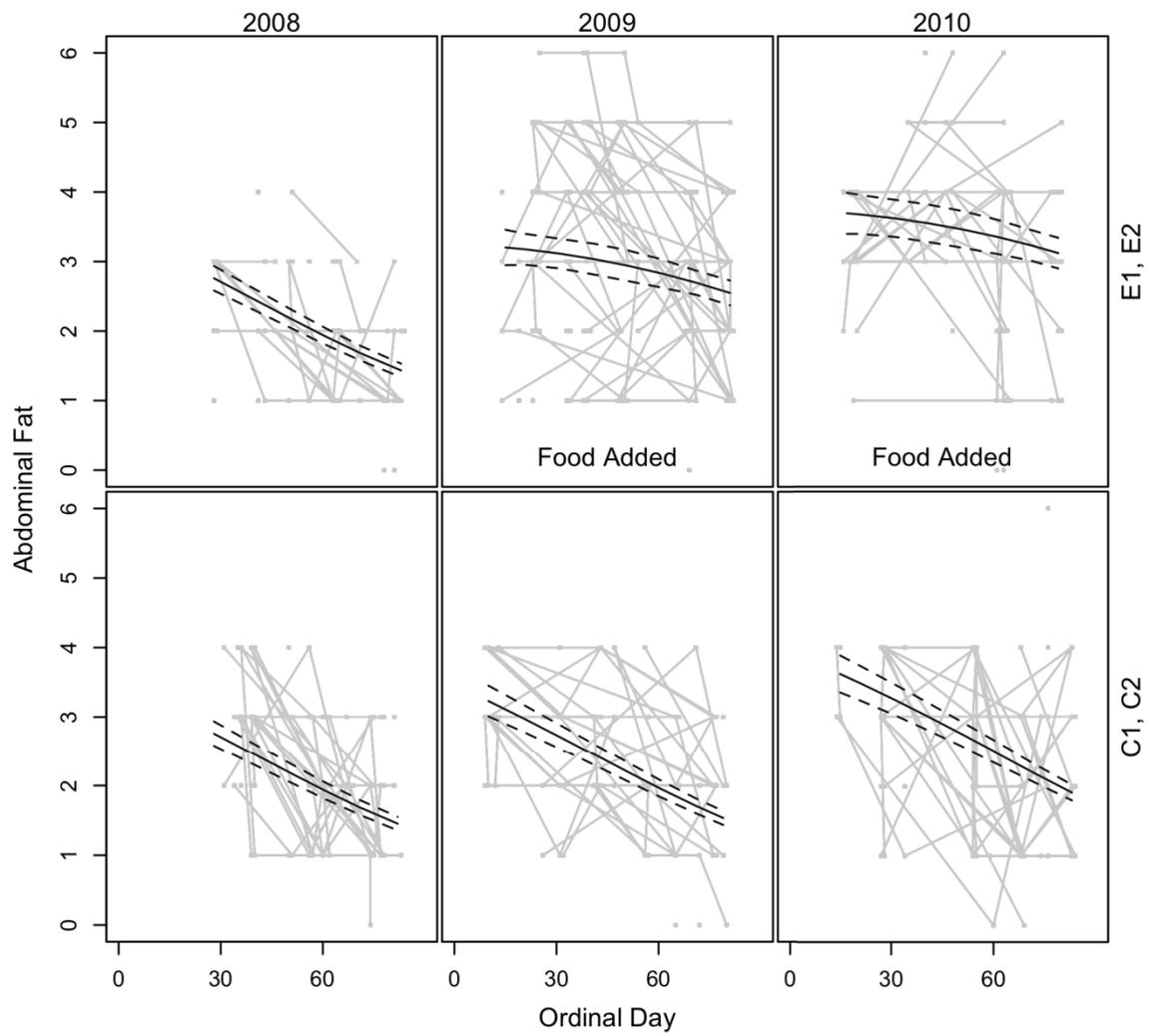


Fig. 4.

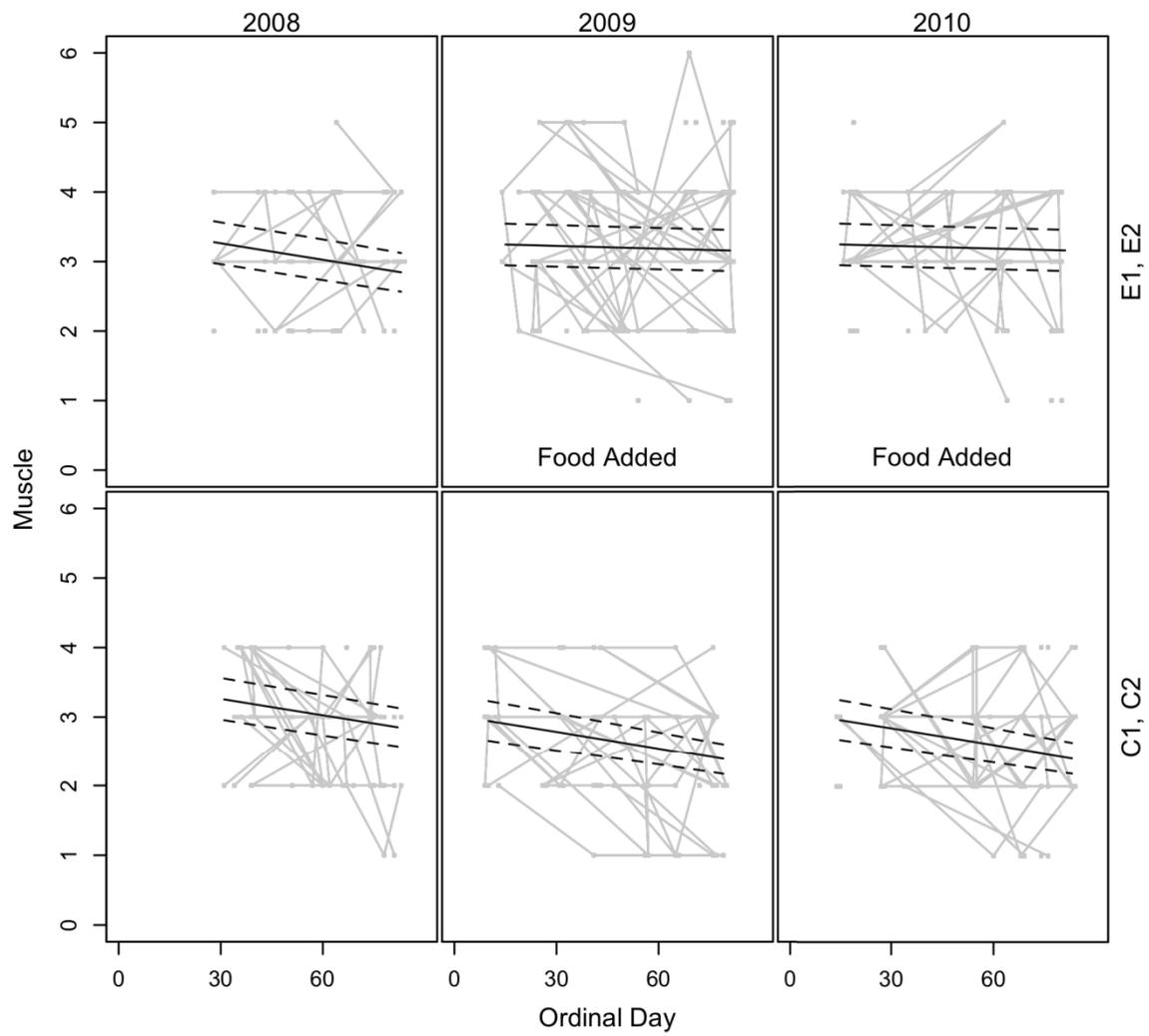


Fig. 5.

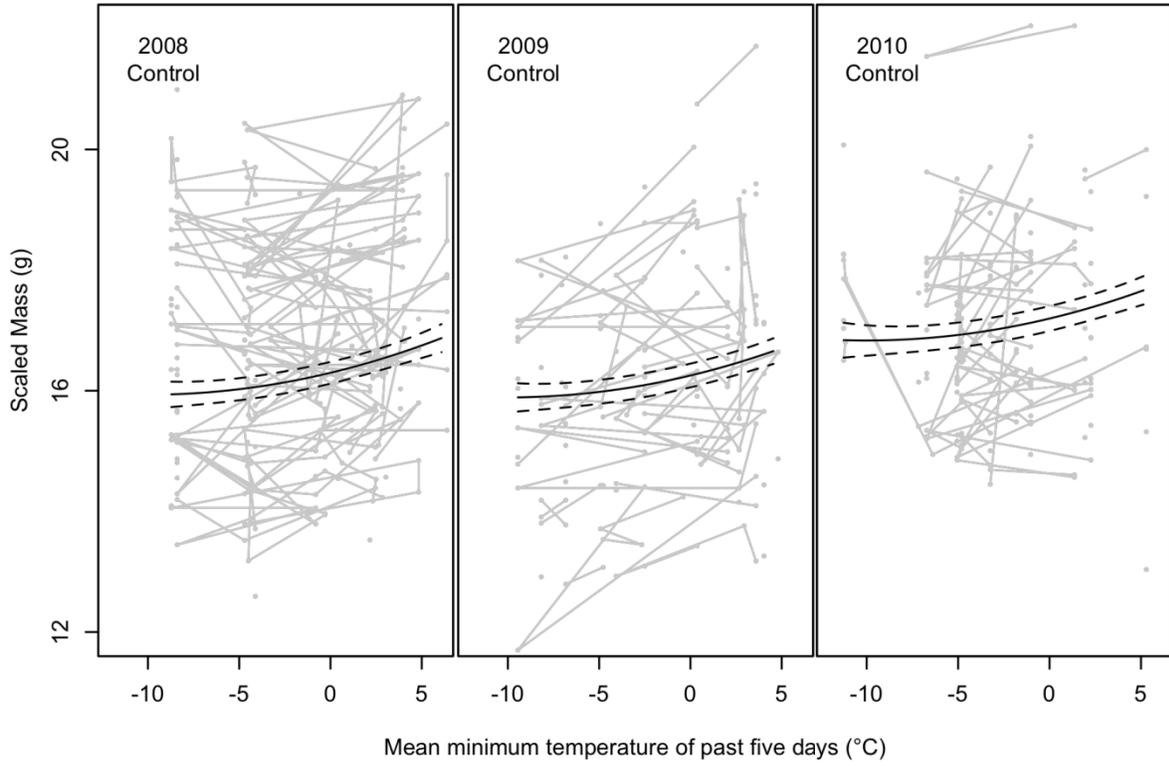


Fig. 6.

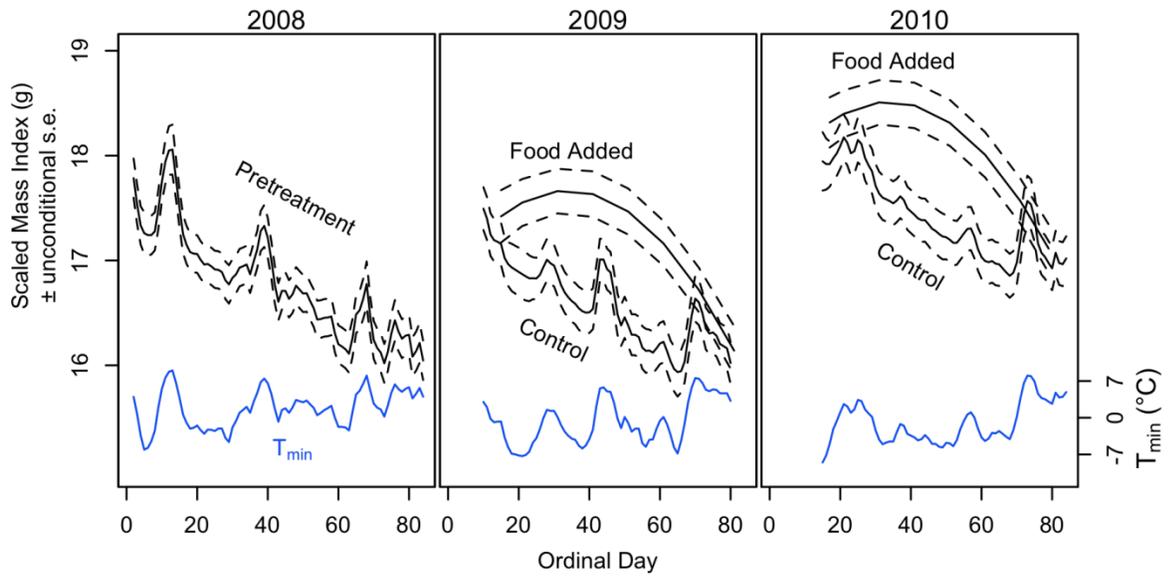


Fig. 7.

Appendix A: A table of scoring criteria for fat and muscle levels and images of low and high scores.

Table A1. Scoring criteria for fat and muscle.

Score	Furcular Fat	Abdominal Fat	Muscle
0	No visible fat	No visible fat	No pectoralis (never observed)
1	Fills <25% of furculum	Light under ribcage, none on abdomen	Keel very prominent, ribs detectable
2	Fills 26–50% of furculum	Heavy under ribcage, none abdomen	Keel very prominent, ribs not detectable
3	Fills 51–75% of furculum	Under ribcage, partially covering abdomen	Keel prominent
4	Fills 76–99% of furculum	Under ribcage, completely covering abdomen	Almost flush with keel
5	Flush with furculum	On abdomen even with ribcage	Flush with keel (cannot feel keel)
6	Convex (exceeding furculum)	Convex (exceeding the ribcage)	Convex (pectoralis exceeding keel)

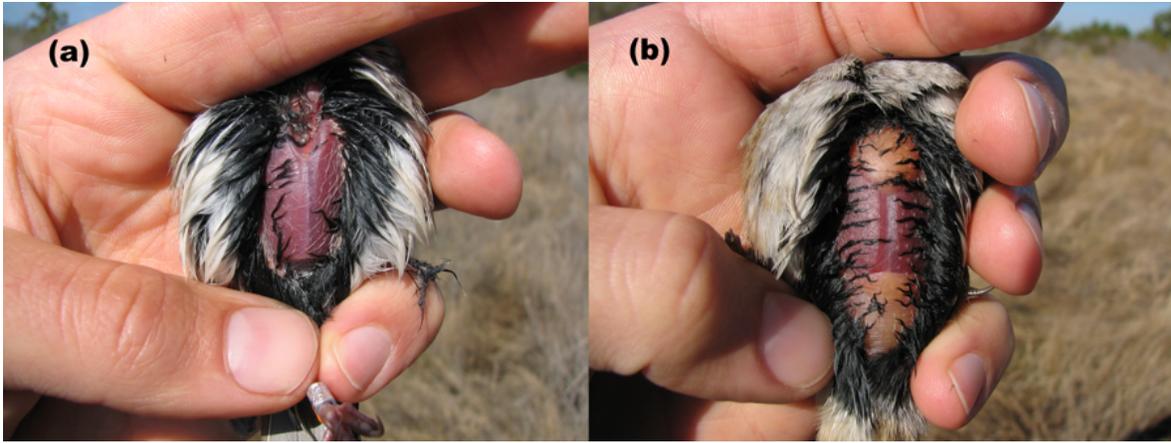


Fig. A1. Representative images of fat and muscle scores. Head is held between index and middle fingers. Ventral feathers are parted to show (a) a lean bird, where furcular fat=1, abdominal fat=1, and muscle=3, and (b) and a heavy bird, where furcular fat, abdominal fat, and muscle=6.

Appendix B: Tables of ranked models that describe change in scaled mass, fat, and muscle.

Table B1. Linear mixed models that describe scaled mass index of swamp sparrows. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and Individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day * Treatment + Day ² * Treatment + Treatment * Sex * Age	16	3978.087	0	0.985
Day + Day ² + Treatment * Sex * Age	14	3986.542	8.455	0.014
Day + Treatment * Sex * Age	13	3995.100	17.013	1.992E-04
Day * Treatment + Treatment * Sex * Age	14	3996.281	18.194	1.104E-04
Treatment * Sex * Age	12	4139.222	161.134	1.010E-35

Table B2. Cumulative logit mixed models that describe furcular fat in relation to scaled mass in swamp sparrows. K = number of parameter and w_i = model weight. All models include individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Scaled Mass	8	3020.970	0	1
Intercept only	7	3389.253	368.282	1.068E-80

Table B3. Cumulative logit mixed models that describe abdominal fat in relation to scaled mass in swamp sparrows. K = number of parameter and w_i = model weight. All models include individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Scaled Mass	8	2687.617	0	1
Intercept only	7	3001.196	313.579	8.078E-69

Table B4. Cumulative logit mixed models that describe muscle in relation to scaled mass in swamp sparrows. K = number of parameter and w_i = model weight. All models include individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Scaled Mass	8	2257.429	0	1
Intercept only	7	2321.423	63.994	1.27E-14

Table B5. Cumulative logit mixed models that describe change in furcular fat of swamp sparrows in relation to day. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and Individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day * Treatment + Treatment * Sex * Age	19	3083.351	0	0.988
Day + Treatment * Sex * Age	18	3092.111	8.760	0.012
Day * Treatment + Day ² * Treatment + Treatment * Sex * Age	21	3102.094	18.743	8.410E-05
Day + Day ² + Treatment * Sex * Age	19	3116.539	33.187	6.140E-08

Treatment * Sex * Age	17	3265.366	182.015	2.950E-40
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Table B6. Cumulative logit mixed models that describe change in abdominal fat of swamp sparrows in relation to day. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and Individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day * Treatment + Treatment * Sex * Age	19	2740.016	0	0.882
Day * Treatment + Day ² * Treatment + Treatment * Sex * Age	21	2744.041	4.025	0.118
Day + Treatment * Sex * Age	18	2758.861	18.846	7.130E-05
Day + Day ² + Treatment * Sex * Age	19	2774.576	34.561	2.760E-08
Treatment * Sex * Age	17	2878.369	138.353	7.990E-31

Table B7. Cumulative logit mixed models that describe change in muscle of swamp sparrows in relation to day. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and Individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day * Treatment + Treatment * Sex * Age	18	2249.324	0	0.952
Day + Treatment * Sex * Age	17	2255.283	5.959	0.048
Treatment * Sex * Age	16	2270.603	21.280	2.278E-05
Day * Treatment + Day ² * Treatment + Treatment * Sex * Age	20	2276.090	26.766	1.466E-06
Day + Day ² + Treatment * Sex * Age	18	2283.790	34.467	3.120E-08

Table B8. Linear mixed models that describe change in scaled mass of experimentally supplemented swamp sparrows in relation to mean minimum temperature. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day + Day ² + Sex * Age	9	1647.477	0	0.130
Day + Day ² + T7 + Sex * Age	10	1648.021	0.544	0.099
Day + Day ² + T1 + Sex * Age	10	1648.292	0.815	0.086
Day + Day ² + T6 + Sex * Age	10	1648.355	0.878	0.084
Day + Day ² + T3 + Sex * Age	10	1648.567	1.090	0.075
Day + Day ² + T2 + Sex * Age	10	1648.708	1.231	0.070
Day + Day ² + T4 + Sex * Age	10	1649.001	1.524	0.061
Day + Day ² + T14 + Sex * Age	10	1649.202	1.725	0.055
Day + Day ² + T8 + Sex * Age	10	1649.245	1.768	0.054
Day + Day ² + T5 + Sex * Age	10	1649.295	1.818	0.052
Day + Day ² + T13 + Sex * Age	10	1649.564	2.087	0.046
Day + Day ² + T12 + Sex * Age	10	1649.573	2.095	0.046
Day + Day ² + T10 + Sex * Age	10	1649.573	2.095	0.046
Day + Day ² + T11 + Sex * Age	10	1649.574	2.097	0.045
Day + Day ² + T9 + Sex * Age	10	1649.575	2.098	0.045
Day + T14 + T14 ² + Sex * Age	10	1655.328	7.851	2.561E-03
Day + T13 + T13 ² + Sex * Age	10	1655.841	8.364	1.982E-03

Day + T12 + T12 ² + Sex * Age	10	1657.863	10.385	7.214E-04
T13 + T13 ² + Sex * Age	9	1660.200	12.723	2.241E-04
Day + T11 + T11 ² + Sex * Age	10	1660.538	13.061	1.893E-04
T14 + T14 ² + Sex * Age	9	1660.933	13.456	1.554E-04
Day + T13 + Sex * Age	9	1662.498	15.021	7.110E-05
Day + T9 + Sex * Age	9	1662.707	15.229	6.400E-05
Day + T10 + Sex * Age	9	1662.765	15.288	6.220E-05
Day + T12 + Sex * Age	9	1662.981	15.504	5.580E-05
Day + T11 + Sex * Age	9	1663.159	15.682	5.110E-05
Day + T14 + Sex * Age	9	1663.180	15.703	5.050E-05
Day + T5 + Sex * Age	9	1663.435	15.958	4.450E-05
Day + T10 + T10 ² + Sex * Age	10	1663.444	15.967	4.430E-05
T12 + T12 ² + Sex * Age	9	1663.789	16.312	3.730E-05
Day + T4 + Sex * Age	9	1663.812	16.335	3.680E-05
Day + T5 + T5 ² + Sex * Age	10	1663.867	16.390	3.580E-05
Day + T8 + Sex * Age	9	1664.046	16.568	3.280E-05
T13 + Sex * Age	8	1664.327	16.849	2.850E-05
Day + T3 + Sex * Age	9	1664.522	17.045	2.580E-05
Day + T6 + Sex * Age	9	1664.526	17.049	2.580E-05
Day + T9 + T9 ² + Sex * Age	10	1664.596	17.119	2.490E-05
Day + T7 + Sex * Age	9	1664.750	17.273	2.300E-05
Day + T1 + T1 ² + Sex * Age	10	1664.833	17.356	2.210E-05
Day + T2 + Sex * Age	9	1664.834	17.356	2.210E-05

Day + T1 + Sex * Age	9	1664.937	17.460	2.100E-05
Day + T8 + T8 ² + Sex * Age	10	1665.694	18.217	1.440E-05
T14 + Sex * Age	8	1665.728	18.251	1.410E-05
Day + T4 + T4 ² + Sex * Age	10	1665.781	18.304	1.380E-05
Day + T2 + T2 ² + Sex * Age	10	1666.151	18.674	1.140E-05
T12 + Sex * Age	8	1666.294	18.817	1.060E-05
Day + T3 + T3 ² + Sex * Age	10	1666.496	19.019	9.620E-06
Day + T7 + T7 ² + Sex * Age	10	1666.542	19.065	9.400E-06
Day + T6 + T6 ² + Sex * Age	10	1666.559	19.081	9.330E-06
T11 + T11 ² + Sex * Age	9	1667.452	19.975	5.970E-06
T11 + Sex * Age	8	1667.745	20.268	5.160E-06
T10 + Sex * Age	8	1667.899	20.422	4.770E-06
T9 + Sex * Age	8	1668.783	21.306	3.070E-06
T10 + T10 ² + Sex * Age	9	1669.719	22.242	1.920E-06
T9 + T9 ² + Sex * Age	9	1670.869	23.392	1.080E-06
T8 + Sex * Age	8	1672.819	25.341	4.080E-07
T8 + T8 ² + Sex * Age	9	1674.611	27.134	1.660E-07
T5 + Sex * Age	8	1676.543	29.066	6.330E-08
T7 + Sex * Age	8	1676.579	29.101	6.220E-08
T5 + T5 ² + Sex * Age	9	1676.580	29.103	6.220E-08
T6 + Sex * Age	8	1676.803	29.326	5.560E-08
T7 + T7 ² + Sex * Age	9	1678.315	30.838	2.610E-08
T6 + T6 ² + Sex * Age	9	1678.772	31.294	2.080E-08

T4 + Sex * Age	8	1681.210	33.732	6.140E-09
T4 + T4 ² + Sex * Age	9	1682.806	35.328	2.770E-09
T3 + Sex * Age	8	1685.732	38.255	6.400E-10
T3 + T3 ² + Sex * Age	9	1687.438	39.961	2.730E-10
T2 + Sex * Age	8	1690.367	42.889	6.310E-11
T2 + T2 ² + Sex * Age	9	1691.226	43.749	4.100E-11
T1 + T1 ² + Sex * Age	9	1691.989	44.511	2.800E-11
T1 + Sex * Age	8	1692.748	45.271	1.920E-11

Table B9. Linear mixed models that describe change in scaled mass of control swamp sparrows in relation to mean minimum temperature. K = number of parameter and w_i = model weight. All models include Year as a fixed effect and individual as a random effect.

Models	K	AICc	Δ AICc	w_i
Day + T5 + T5 ² + Sex * Age	11	2230.354	0	0.597
Day + T6 + T6 ² + Sex * Age	11	2232.783	2.429	0.177
Day + T5 + Sex * Age	10	2233.097	2.744	0.152
Day + T6 + Sex * Age	10	2235.395	5.042	0.048
Day + T4 + Sex * Age	10	2238.111	7.757	0.012
Day + T4 + T4 ² + Sex * Age	11	2238.603	8.250	0.010
Day + T7 + T7 ² + Sex * Age	11	2241.666	11.312	2.088E-03
Day + T7 + Sex * Age	10	2243.005	12.652	1.069E-03
Day + T3 + Sex * Age	10	2245.630	15.276	2.878E-04
Day + T3 + T3 ² + Sex * Age	11	2247.002	16.649	1.449E-04

Day + T8 + T8 ² + Sex * Age	11	2248.578	18.225	6.589E-05
Day + T8 + Sex * Age	10	2251.180	20.826	1.795E-05
Day + T2 + Sex * Age	10	2256.159	25.805	1.488E-06
Day + T9 + T9 ² + Sex * Age	11	2256.224	25.870	1.441E-06
Day + T9 + Sex * Age	10	2257.668	27.314	7.000E-07
Day + T2 + T2 ² + Sex * Age	11	2257.701	27.347	6.886E-07
Day + T10 + Sex * Age	10	2263.836	33.482	3.205E-08
Day + T10 + T10 ² + Sex * Age	11	2265.077	34.724	1.722E-08
Day + T1 + Sex * Age	10	2265.100	34.747	1.703E-08
Day + T1 + T1 ² + Sex * Age	11	2267.123	36.770	6.192E-09
Day + T11 + Sex * Age	10	2267.786	37.433	4.445E-09
Day + T11 + T11 ² + Sex * Age	11	2269.772	39.419	1.647E-09
Day + T12 + Sex * Age	10	2270.464	40.111	1.165E-09
Day + T13 + Sex * Age	10	2271.044	40.690	8.721E-10
Day + T14 + Sex * Age	10	2271.096	40.742	8.496E-10
Day + Sex * Age	9	2271.744	41.390	6.144E-10
Day + T12 + T12 ² + Sex * Age	11	2272.429	42.076	4.362E-10
Day + T13 + T13 ² + Sex * Age	11	2273.056	42.702	3.189E-10
Day + T14 + T14 ² + Sex * Age	11	2273.088	42.734	3.139E-10
T6 + T6 ² + Sex * Age	10	2394.328	163.974	1.478E-36
T5 + T5 ² + Sex * Age	10	2394.437	164.084	1.399E-36
T14 + T14 ² + Sex * Age	10	2394.639	164.285	1.265E-36
T13 + T13 ² + Sex * Age	10	2397.944	167.591	2.424E-37

T12 + T12 ² + Sex * Age	10	2398.703	168.349	1.659E-37
T7 + T7 ² + Sex * Age	10	2401.070	170.717	5.077E-38
T5 + Sex * Age	9	2403.738	173.385	1.337E-38
T6 + Sex * Age	9	2403.788	173.435	1.304E-38
T4 + T4 ² + Sex * Age	10	2404.274	173.921	1.023E-38
T11 + T11 ² + Sex * Age	10	2405.212	174.859	6.401E-39
T14 + Sex * Age	9	2405.240	174.886	6.313E-39
T4 + Sex * Age	9	2405.907	175.554	4.521E-39
T13 + Sex * Age	9	2406.208	175.854	3.890E-39
T7 + Sex * Age	9	2406.366	176.013	3.594E-39
T12 + Sex * Age	9	2406.879	176.525	2.782E-39
T1 + Sex * Age	9	2407.632	177.279	1.909E-39
T8 + T8 ² + Sex * Age	10	2407.836	177.483	1.724E-39
T8 + Sex * Age	9	2408.158	177.804	1.468E-39
T11 + Sex * Age	9	2408.521	178.167	1.224E-39
T3 + Sex * Age	9	2408.551	178.198	1.206E-39
T1 + T1 ² + Sex * Age	10	2408.592	178.238	1.181E-39
T2 + Sex * Age	9	2408.868	178.515	1.029E-39
T10 + Sex * Age	9	2409.111	178.757	9.114E-40
T9 + Sex * Age	9	2409.122	178.768	9.064E-40
T10 + T10 ² + Sex * Age	10	2409.180	178.826	8.804E-40
T3 + T3 ² + Sex * Age	10	2409.978	179.624	5.908E-40
T2 + T2 ² + Sex * Age	10	2410.421	180.067	4.734E-40

$T9 + T9^2 + \text{Sex} * \text{Age}$	10	2411.178	180.825	3.241E-40
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CHAPTER III. WINTER FOOD LIMITS TIMING OF PRE-ALTERNATE MOLT
IN A SHORT-DISTANCE MIGRATORY BIRD

Raymond M. Danner, Russell S. Greenberg, Julie E. Danner, and Jeffrey R. Walters

Summary

1. Molt is critical for fitness for many organisms for several reasons: it allows growth and maintains the function of the integument for protection, thermoregulation and communication.
2. Feather molt in birds is costly and therefore typically does not overlap with migration or reproduction. In spring, the rapid succession of pre-alternate molt, migration (if a migrant), and breeding, suggests that timing of molt could constrain the initiation of breeding. A tradeoff between time spent molting and breeding might also limit molt quality.
3. The proximate basis for the timing of pre-alternate molt initiation is not well known, though it typically occurs during a resource poor time of year. Food limitation combined with fitness consequences of molting earlier suggests that plasticity in timing of pre-alternate molt in response to food abundance should be advantageous.
4. We experimentally tested, for the first time, if food abundance influences the timing of molt in the wild. We conducted a controlled food supplementation experiment on free-living swamp sparrows (*Melospiza georgiana*) preceding and during the time of natural pre-alternate molt.

5. Supplemented birds began molting the body, face, and crown earlier than control birds (11, 14, and 8 days earlier, respectively) indicating that food abundance limits the initiation of molt. Along with interannual variation, these results indicate that photoperiod is not the sole cue for initiation of molt.
6. Swamp sparrows molted in sequence, starting with the body, followed by the crown 9 days later, and the face 11 days later. The presence of a sequence further suggests energetic limitation of molt and possibly a strategy to molt the most important regions first or during the optimal time for growth.
7. This study is the first to experimentally demonstrate that food abundance can: i) limit pre-alternate molt timing and ii) limit molt timing of any kind in the wild. It is only the second to experimentally show that food limits molt in any context, prior study having been in captivity. The implications of these findings are broad. Food limitation of molt timing could cascade through other life history stages in the annual cycle and ultimately affect reproductive success.

Key-words: Food-limitation, Carry-over effects, molt sequence

Introduction

Molt is critical for fitness for many organisms. Molt allows body growth in amphibians, reptiles and invertebrates, and maintains the function of the integument for protection, thermoregulation, and communication. Seasonal molt allows animals to adapt their integument throughout the year for expected changes in environmental conditions. For species with distinct

breeding seasons, seasonal molt also allows sexual signals to be displayed during specific times of the year.

Molt is costly for birds. Growth of new feathers and associated tissues requires large amounts of energy and nutrients (Payne 1972, King and Murphy 1990, Dietz et al. 1992, Lindström et al. 1993, Bonier et al. 2007) and skin exposed during molt increases thermoregulatory demands through heat loss (Lustick 1970, Klaassen 1995, Murphy 1996). Loss of flight feathers reduces flight performance (Swaddle and Witter 1997, Vega Rivera et al. 1998), which may incur further energetic costs and higher susceptibility to depredation.

Feather molt is thought to be sufficiently energetically costly that it does not overlap with other life history stages. Breeding and migration, both of which are major energetic investments (Ricklefs et al. 1996, Williams 2005 and Berthold 1975, Alerstam 1993, Wikelski et al. 2003, respectively) rarely overlap with molt in temperate zone species (Morton and Welton 1973, Kjellén 1994, Stutchbury et al. 2011). The mutual exclusivity of these stages is thought to be an adaptation to balance energy costs (Kendeigh 1949, Hemborg and Lundberg 1998).

The need to allocate a portion of the annual calendar to molt leads to another great potential cost of molt, its constraint on the timing of other fitness related activities in the annual calendar. Many passerines breed soon after pre-alternate molt (Jenni and Winkler 1994, Poole 2005, Pyle 1997), suggesting that molt could constrain timing of breeding. In addition, many short- and long-distance migratory passerines that breed in the temperate and arctic zones molt soon before migrating in both spring and fall. The close succession of molt and migration, and the correlated timing of these events within individuals studied in fall (Pulido and Coppack 2004, Stutchbury et al. 2011), suggests molt could limit the timing of migration. Migration timing can influence fitness; individuals of both sexes that arrive at their breeding locations earlier in the

spring have been shown to acquire higher quality breeding territories and subsequently have higher reproductive success (Cristol 1995, Aebischer et al. 1996, Currie et al. 2000, Norris et al. 2004).

The potential for pre-alternate molt timing to limit the initiation of breeding suggests a tradeoff between the amounts of time allotted to each activity. This tradeoff may be the reason pre-alternate molt is typically limited in extent, often restricted to the head (“a partial molt”, Pyle 1997). A longer duration of molt, however, might also provide fitness benefits to birds. First, a longer duration could allow more extensive molt, which could be a cue preferred by mates or confer structural benefits, such as thermoregulation. Second, a longer duration of molt has been shown to result in the production of higher quality feathers (Dawson 2004, Dawson et al. 2000, Griggio et al. 2009), which could also be selected by mates or provide benefits associated with structural integrity.

Factors controlling the initiation of pre-alternate molt are not well understood. An endogenous program has been found for pre-basic molt in some species (Dolnik and Gavrillov 1980, Gwinner 2003), though there is no evidence for such control over pre-alternate molt. Gonadal hormones are required for completion of pre-alternate molt, though not initiation (Hannon and Wingfield 1990, Peters et al. 2000). Photostimulation led to the initiation of pre-alternate molt in several species in captivity (Miyasaki 1934, Brown and Rollo 1940, Leshner and Kendeigh 1941, Keast 1953, Miller 1954, Farner and Medwaldt 1955), though abnormalities such as overlap with gonadal development, lack of molt in some individuals, and molt of feathers not typically molted suggests that other controlling factors exist (Payne 1972).

Despite widespread agreement that life history stages are usually mutually exclusive because of energy limitations, the role of food abundance in influencing molt timing has received

very little attention, particularly for pre-alternate molt. A small amount of observational evidence shows that pre-alternate molt is delayed in years with adverse weather conditions (Mulder and Magrath 1994) and that individuals with higher body mass (and presumably larger energy stores) start molt sooner (Piersma and Jukema 1993, Mulder and Magrath 1994). There have been no experimental tests of food limitation of pre-alternate molt initiation, though this molt occurs in a time of year when food is generally thought to be limiting (Fretwell 1972, Brittingham and Temple 1988, Chapter I). Regarding pre-basic molt, three experimental manipulations of diet quality in captive birds found that food-deprived birds did not delay molt (Murphy, King, and Lu 1988, Murphy and King 1991, Pap et al. 2008) and a fourth showed delayed pre-basic molt in males, but not females (Meijer 1991).

Another form of evidence for food limitation of pre-alternate molt could be an ordered sequence of molt by feather region, such as is found in pre-basic molt (Pyle 1997); reducing the number of simultaneously molting feathers would reduce energetic costs per unit time that result from feather production (Freed and Caan 2012) and increased thermoregulatory demands from exposed skin (Lustick 1970, Klaassen 1995, Murphy 1996). Indeed, extended molt occurs in numerous species when food availability is low both in the field (Freed and Caan 2012) and in captivity (Murphy, King, and Lu 1988, Murphy and King 1991, Pap et al. 2008). In addition, if food resources are limited, we hypothesize that a sequence of molt might be a strategy to ensure that the most important molt is either completed first or when conditions are optimal. Currently, too few detailed accounts of pre-alternate molts exist for such analyses.

The combination of food limitation during the time of pre-alternate molt and fitness consequences potentially associated with the timing of molt suggests that plasticity in timing of molt in response to variation in food should be advantageous. We tested this hypothesis in the

swamp sparrow (*Melospiza georgiana*), a species for which winter resources have been shown to be limiting (Chapters I and II) and which undergoes a pre-alternate molt. The swamp sparrow's pre-alternate molt is partial and is thought to be restricted mainly to the head, including the face and crown, and occasionally the body (Dwight 1900, Pyle 1997). This molt leads to the acquisition of a patch of bright feathers on the crown (mostly in males, Greenberg 1988), which is thought to be sexually selected (Olsen et al. 2008, 2009). Molt is thought to be particularly important for marsh-dwelling species such as the swamp sparrow because they experience high rates of feather wear from abrasion and feather degrading bacteria (Burt and Ichida 1999). Our study population consists of a large proportion of coastal plain swamp sparrows (*Melospiza georgiana nigrescens*, Greenberg et al. 2007), which have a high prevalence and abundance of feather degrading bacteria during the breeding season (Peele et al. 2009).

We experimentally tested if winter food abundance limits timing of feather molt during the time of naturally occurring pre-alternate molt. To test for the existence of food limitation, we performed a plot-level food supplementation experiment over two years. If food abundance limits molt, we would expect earlier molt when food is supplemented. In addition, we tested if molt of different feather regions was ordered or occurred simultaneously, which could provide further support of food limitation and insights to strategies of molt under food limitation.

Methods

Data Collection

We studied the pre-alternate molt of swamp sparrows (*Melospiza georgiana*) captured over two winters (January–March 2009 and 2010) in coastal North Carolina, USA. Although

timing of the pre-basic molt of swamp sparrows has been studied in detail (Ballentine and Greenberg 2010), timing of the pre-alternate molt is not well known. Based on an examination of museum skins collected over many sites and years, Dwight (1900) determined that pre-alternate molt of males and females occurs in late February–April.

We supplemented food at two of four study plots in brackish marshes near Swanquarter and Engelhard, NC. Supplemental food was distributed at the intersections of a grid formed of 9 lines x 4 lines, with lines separated by 25 m, producing 36 feeding stations per plot. Food consisted of millet ad libitum and mealworms (*Tenebrio molitor*) every time we replenished millet. Swamp sparrows were frequently seen eating millet and mealworms from the piles and we regularly observed those items in their feces. We captured (with mist nets), marked, and recaptured birds at each plot throughout the study period. Mist nets covered approximately 1.2 ha at three plots and 1.8 ha at one plot. In addition to molt status (below), we determined age and sex of each individual captured. See Chapter I for details regarding study plots, food manipulation, and data collection other than molt.

The earliest ordinal date of molt (“Day”, January 1 = 1) was quantified in three regions of the birds based on the hypothesis that molt in each region would have different consequences. We identified active molt as sheathed feathers, which were observed while blowing air to part the feathers. First, we recorded molt on the head, because it is expected for most individuals. Molt in this region consisted of the face (from the proximal edge of the bill to the auriculars) and the throat and is referred to as face molt. Second, we recorded body molt separately because it occurs only on some individuals, and therefore may constitute additional molt that is possible only when conditions are favorable. We classified the body as molting if we detected molt in

one the following regions: back, rump, sides, flanks, nape. Third, we recorded crown feather molt because of its putative function in sexual signaling.

Analyses

To identify variables that predicted molt, we constructed several biologically plausible models that described body, face, and crown molt and then selected the best models with an information-theoretic approach. The set of candidate models was the same for each region of molt, consisting of 20 linear models based on the global model: Earliest molt date = Treatment + Age * Sex + Year. If food limits the timing of molt, we would expect molt to occur earlier on treated plots and for the variable Treatment to be supported. Because ages and sexes might have different molt schedules, we included additive effects of Age, Sex and Age * Sex in some models. All models with Age * Sex also include the main effects of Age and Sex. Because of interannual differences in weather (Chapters I and II) and most likely natural food abundance, we tested for an additive effect of Year.

Global models fit with a Normal distribution had poor fit, so we used a Gamma error structure with an inverse link, which is appropriate for positive, continuous data (Zuur et al. 2009). All models were fit with function glm in R (R Development Core Team 2012). Dispersion parameters of the global models indicated underdispersion (body: 0.06, face: 0.02, and crown: 0.01).

Models were ranked based on their AIC (Akaike Information Criterion) scores corrected for small sample sizes (AICc, Burnham and Anderson 2002) with package AICcmodavg (Mazerolle 2011). We assessed the value of each predictor variable by its evidence ratio, which is calculated as the probability (or “model weight”) of the model containing that variable divided

by the probability of an appropriate null model, which did not contain the variable of interest. To examine the effect size produced by important variables, we calculated model average parameter estimates \pm unconditional standard errors. Further, we calculated and plotted model average predictions \pm unconditional standard errors to visualize the effect sizes of important variables.

To determine if molt occurs in a sequence ordered by region, we tested if molt start date differed by region. For this test, we fit a linear model that included Molt region (Body, Face, and Crown) and variables shown to be important in the previous analyses. To account for individual variation in molt initiation, we included individual as a random effect. We fit this model with a Gamma distribution using function `glmmPQL` in package `MASS` (Venables and Ripley 2002) after finding poor fit with a Normal distribution. Because function `glmmPQL` uses quasi-likelihood and does not produce AIC values, we were unable to use the information-theoretic approach for this test and instead present Wald t-statistics and associated p-values. Because we observed more molting individuals on experimental plots and control birds might have initiated molt after our last sampling effort, an effect of earlier molt in experimental birds would be conservative.

Results

Overall, we measured molt in 539 individuals, of which the majority were on experimental plots. The number of birds that molted/total per treatment were: 2009 control: 7/147, experimental: 71/163; 2010 control: 38/114 experimental: 71/115.

Body Molt

Body molt began earlier on Experimental plots in both 2009 and 2010 (Fig. 2). The earliest experimental birds began molting on day 19 in 2009 and day 34 in 2010 (mid-January to early February), whereas control birds did not begin molting until 46 days (day 65) and 20 days later (day 54), respectively (mid-February to early March). Model comparison showed strong support for an effect of Treatment (evidence ratio = 23.4, Table 1) and the model averaged parameter estimate indicated that among birds that did molt, experimental birds molted earlier on average ($B = -10.57 \text{ days} \pm 2.88 \text{ unconditional s.e.}$). Year was in the top model and had an evidence ratio of 1.3, indicating weak support of an effect of Year, and the model average parameter estimate indicated molt was earlier in 2010 ($B = -5.57 \pm 3.09$). There was no support for Age, Sex, nor Age*Sex, which had evidence ratios of 0.35, 0.35, and 0.04, respectively.

Face molt

Face molt began earlier on Experimental plots in both 2009 and 2010 (Fig. 3). The earliest experimental birds began molting on day 69 in 2009 and day 35 in 2010, whereas control birds did not begin molting until 11 days (day 80, one individual) and 33 days later (day 58), respectively. Model comparison showed strong support for an effect of Treatment (evidence ratio = 26.1, Table 2) and the model averaged parameter estimate indicated that experimental birds molted earlier on average ($B = -13.94 \text{ days} \pm 3.09 \text{ unconditional s.e.}$). Year was in the top 10 models and had an evidence ratio of 2,003, and the model average parameter estimate indicated molt was earlier in 2010 ($B = -14.71 \pm 0.92$). There was no support for Age, Sex, nor Age*Sex, which had evidence ratios of 0.50, 0.32, and 0.04, respectively.

Crown molt

Crown molt began earlier on Experimental plots in both 2009 and 2010 (Fig. 4). The earliest experimental birds began molting on day 69 in 2009 and day 61 in 2010, whereas control birds did not begin molting until 7 days (day 76, one individual) and 8 days later (day 69), respectively. Model comparison showed strong support for an effect of Treatment (evidence ratio = 101, Table 3) and the model averaged parameter estimate indicated that experimental birds molted earlier on average ($B = -8.21 \text{ days} \pm 2.09 \text{ unconditional s.e.}$). Year was in the top four models and had an evidence ratio of 14.6, and the model average parameter estimate indicated molt was earlier in 2010 ($B = -5.53 \pm 4.38$). There was no support for Age, Sex, nor Age*Sex, which had evidence ratios of 0.32, 0.32, and 0.05, respectively.

Sequence of molt

We found that molt occurred in a sequence, where molt of the body started first, followed by the crown ($B = 8.69 \text{ days later} \pm 2.64 \text{ s.e.}, t_{139} = -3.54, p < 0.0001$) and then the face ($B = 10.73 \pm 2.64, t_{139} = -4.48, p < 0.0001$). A similar model that contained an interaction of Molt region and Treatment showed that, in relation to body molt, timing of face ($t_{137} = -1.4, p = 0.164$) and crown molt ($t_{137} = -0.815, p = 0.164$) did not differ by Treatment.

Discussion

Food limitation of molt

We found that swamp sparrows given supplemental food initiated pre-alternate molt earlier on the body, face, and crown than individuals foraging on natural abundances of food. These results provide the first experimental evidence that food abundance can limit pre-alternate

molt timing. These results are also the first to demonstrate in the wild that food limits timing of any molt. In the only other study showing that molt timing is dependent on diet, Meijer (1991) found that pre-basic molt was delayed in male, but not female, European starlings (*Sternus vulgaris*) while on poor diets in captivity. These results contrast with the three other experimental studies of pre-basic molt of captive white-crowned sparrows (*Zonotrichia leucophrys*, Murphy, King, and Lu 1988, Murphy and King 1991) and house sparrows (*Passer domesticus*, Pap et al. 2008), which found no effect of diet on molt timing despite losses in body mass of up to 20–38% (near lethal levels).

The discrepancy between our finding that food limits molt timing of swamp sparrows in spring, and that food generally does not limit molt timing in the fall, might be related to the ecological factors that characterize those life history stage transitions. In the fall, the start of molt appears to be limited by the end of breeding. Fall molt generally occurs soon after the end of breeding activity (Morton and Morton 1990, Morton 1992) and molt can be delayed by late-season breeding activities (Morton 1992, Hemborg and Merila 1999, Newton and Rothery 2005, Stutchbury et al. 2011, see discussion of hormonal mechanisms in *Cues for initiation of pre-alternate molt* below). In addition, molt timing of juvenile birds is influenced by hatch date (Bojarinova et al. 1999). Breeding activities are generally limited by food (Martin 1987). Given the immediate fitness benefits of extending breeding activities to produce another brood or to care longer for existing young, and that relationships between fall molt and fitness are indirect (e.g. Reudink et al. 2009), birds presumably will elect to increase fitness by continuing to breed if food is available rather than cutting breeding short to start molting. Therefore, in the fall, we would expect high food abundances to lead to longer breeding efforts, which could delay molt.

Pre-alternate molt, on the other hand, precedes the breeding stage and follows several months devoted primarily to survival during a resource poor time of year, when food limits survival (Jansson et al. 1981, Brittingham and Temple 1988, Chapter I) and fat reserves (Chapters I and II). Given the direct fitness benefits of breeding as early as possible, we expect high food abundances to cause pre-alternate molt to occur earlier so that breeding can begin earlier. Food limitation of spring molt timing likely interacts with thermoregulatory costs imposed by cold ambient temperatures, however; in the temperate zone, molt might not be energetically feasible until shortly before breeding or migration because of the high energetic demands and low level of food abundances. The importance of pre-alternate molt might differ between species, being higher in those like swamp sparrows that have high rates of abrasion. If so, we might expect greater plasticity in molt timing in species that experience greater feather wear such as the swamp sparrow.

In addition to potentially increasing fitness by lengthening the breeding season or improving territory location, earlier molt might also allow for the growth of feathers of higher quality and more extensive molt. Studies employing manipulation of photoperiod found that time of molt initiation is inversely related to the duration of molt (Dawson 2004) and that feathers resulting from short durations of molt are smaller, lighter, and less colorful than those molted over longer periods of time (Dawson 2004, Dawson et al. 2000, Griggio et al. 2009). These results suggest that birds with access to abundant food and that start molting earlier would produce higher quality feathers. Our study design did not allow us to measure molt duration. We hypothesize that the experimental birds, which began molt earlier, would continue to molt longer than those on the control plots and thus produce higher quality feathers in addition to advancing departure date. Because longer duration of molt likely results in lower energy cost per

unit time compared to shorter molt, more extensive molt might also be possible, though there is currently no evidence for this hypothesis.

Earlier start of pre-alternate molt might also be a strategy to ensure that molt is completed if there is a chance that it could be interrupted. Molt interruption is a common phenomenon caused by reductions in food availability and sudden needs to migrate and breed (Murphy 1996). If earlier molt is a strategy to deal with interruption, we would predict that molt timing adjustment by food would be most likely to occur in environments that are characterized by unpredictable breaks in foraging and fluctuations in energy expenditures, such as the storm-driven climates of the temperate zone winter. During our study periods at our study sites, the frequency of freezing temperatures and snowfall that would reduce food availability decreased later in the season, but could occur anytime, potentially encouraging a strategy of starting molt earlier.

We did not find age/sex class-specific timing of molt initiation, suggesting that all classes share the same limitations and strategies to deal with them. Danner (Chapter I) found that for the birds used in the present study, food limitation of body condition and survival probability differed by age/sex class. Body condition was similar among classes on control plots, but was higher in adults and immature females than immature males on plots with added food. Immature males also had the lowest survival probabilities in both treatments. Therefore, we expected immature males to molt later. Immature experimental males did show a lack of early crown molt in 2009, but it was not supported statistically, and this pattern was not seen in 2010 or in other molt regions. Assuming there is a tradeoff between molt and survival, that immature males did not molt later than other age/sex classes suggests molt is more important for them than survival probability. Molting feathers that produce sexual signals may be especially important

determinants of reproductive success of first year males, which have not previously established breeding territories.

Cues for initiation of pre-alternate molt

Food availability is not the primary cue for molt in swamp sparrows; if it were, birds would have started molting immediately after food addition. Food abundance could provide “supplementary information” used to fine-tune the timing that is set by a primary cue (Hahn et al. 1992). Aside from a strictly visual cue, the larger fat reserves caused by food addition could potentially act as a cue for molt. Primary cues for pre-alternate molt are unknown. Captive swamp sparrows (B. Ballentine pers. comm.), like several other species (Miyasaki 1934, Brown and Rollo 1940, Leshner and Kendeigh 1941, Keast 1953, Miller 1954, Farner and Medwaldt 1955) begin pre-alternate molt when exposed to increasing photoperiod and constant temperature and food supplies, suggesting that photoperiod or an endogenous cycle plays a role. Likewise, photostimulation induces pre-basic molt (Dolnik and Gavrilov 1980, Helm and Gwinner 2006, Dawson and Goldsmith 1984, Nolan and Ketterson 1990), and evidence suggests it is mediated by peak prolactin concentrations (Dawson 2006, Kuenzel 2003). Prolactin levels are low, however, during pre-alternate molt (Dawson and Goldsmith 1984, Wingfield and Goldsmith 1990). Testosterone induces pre-alternate molt in male willow ptarmigan (*Lagopus lagopus*, Stokkan 1979, Hannon and Wingfield 1990, but see Stokkan and Sharp 1980) and male superb fairy-wrens independently of photoperiod (Peters et al. 2000). Therefore, food limitation of pre-alternate molt in males could be mediated by testosterone. Tonra (2011) found that male American redstarts (*Setophaga ruticilla*) with high mass in winter had higher levels of testosterone, suggesting that food availability limits the amount of circulating testosterone, which

provides a potential mechanism for food availability to limit molt timing. Hormonal factors affecting pre-alternate molt in females have not been identified. Our finding that molt initiation dates did not differ among age/sex classes suggests that a factor other than (or in addition to) testosterone is also involved for males.

Sequence of molt

Swamp sparrows molted major regions of the body sequentially, suggesting further support for food limitation of molt. Body feathers were molted first, followed by the face, and then the head. Sequential molt might be a strategy to reduce energetic costs. Swamp sparrows began to molt body feathers before the face and crown, while temperatures were still low and insects had not yet emerged. Molt of body feathers might incur lower thermoregulatory costs than the face or crown because body feathers are longer and wider, and when overlaid, can cover and potentially insulate bare patches resulting from missing feathers. In contrast, a sparrow's face releases a large amount of heat even when not molting (see pictures in Greenberg et al. Accepted) and the shorter crown feathers do not completely cover adjacent bare patches during molt (Danner unpub. data).

In addition, sequential loss of feathers might ensure that the most important molt occurs first or at the optimal time for feather growth. In swamp sparrows, we might expect crown molt to be most important given its putative uses in signaling (Olsen et al. 2008, 2010), and also the face and throat because of seasonal changes in coloration in both sexes, which suggests they contain sexual signals related to breeding. Indeed, we found the range of molt initiation to be the smallest for the face and crown. These regions molted after the body, suggesting that swamp sparrows do not molt the most important body regions first, but rather at the optimal time for feather growth. Molt of the crown and face might coincide with elevated testosterone levels in

males (see discussion in *Cues for initiation of pre-alternate molt*). Given these hypothetical strategies, we consider the existence of sequential molt as additional, tentative support for food limitation. Currently, too few studies of detailed molt sequences exist to address these hypotheses (Bridge 2011). Future research should focus on relationships between detailed molt sequences, food availability, heat loss, and circulating hormone concentrations.

Literature Cited

- Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D.R. (1996) The Role of Territory Choice, Mate Choice and Arrival Date on Breeding Success in the Savi's Warbler *Locustella luscinioides*. *Journal of Avian Biology*, **27**, 143-152.
- Alerstam, T. (1993) *Bird Migration*. Cambridge University Press, New York, NY.
- Ballentine, B. & Greenberg, R. (2010) Common garden experiment reveals genetic control of phenotypic divergence between swamp sparrow subspecies that lack divergence in neutral phenotypes. *PLoS One*, **5**, e10229 10221-10226.
- Berthold, P. (1975) Migration control and metabolic physiology. *Avian Biology* (eds D.S. Farner & J.R. King). Academic Press, New York, NY.
- Bonier, F.B., Martin, P.R., Jensen, J.P., Butler, L.K., Ramenofsky, M. & Wingfield, J.C. (2007) Pre-migratory life history stages of juvenile arctic birds: Costs, constraints, and trade-offs. *Ecology*, **88**, 2729-2735.
- Bojarinova, J.G., Lehikoinen, E. & Eeva, T. (1999) Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. *Journal of Avian Biology*, **30**, 437-446.
- Bridge, E.S. (2011) Mind the gaps: What's missing in our understanding of feather molt. *Condor*, **113**, 1-4.
- Brittingham, M.C. & Temple, S.A. (1988) Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology*, **69**, 581-589.
- Burt, E.H. & Ichida, J.M. (1999) Occurrence of feather-degrading bacilli in the plumage of birds. *The Auk*, **116**, 364-372.
- Cristol, D.A. (1995) Early arrival, initiation of nesting, and social status: an experimental study of breeding female red-winged blackbirds. *Behavioral Ecology*, **6**, 87-93.
- Currie, D., Thompson, D.B.A. & Burke, T. (2000) Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis*, **142**, 389-398.
- Dawson, A. (2004) The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in common starlings *Sturnus vulgaris*. *Ibis*, **146**, 493-500.
- Dawson, A. (2006) Control of molt in birds: Association with prolactin and gonadal regression in starlings. *General and Comparative Endocrinology*, **147**, 314-322.
- Dawson, A. & Goldsmith, A.R. (1984) Effects of gonadectomy on seasonal changes in plasma LH and prolactin concentrations in males and female starlings (*Sturnus vulgaris*). *Journal of Endocrinology*, **100**, 213-218.
- Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C. & Eccleston, L. (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society B*, **267**, 2093-2098.

- Dietz, M.W., Daan, S. & Masman, D. (1992) Energy requirements for molt in the kestrel *Falco tinnunculus*. *Physiological Zoology*, **65**, 1217-1235.
- Dolnik, V.R. & Gavrillov, V.M. (1980) Photoperiodic control of the molt cycle in the Chaffinch (*Fringilla coelebs*). *The Auk*, **97**, 50-62.
- Dwight, J.D. (1900) The Sequence of Plumages and Moults of the Passerine Birds of New York. *Annals of the New York Academy of Sciences*, **13**, 73-369.
- Freed, L.A. & Cann, R.L. (2012) Changes in timing, duration, and symmetry of molt of Hawaiian forest birds. *PLoS One*, **7**, e29834 29831-29816.
- Fretwell, S.D. (1972) Populations in a Seasonal Environment. *Monographs in Population Biology*. Princeton University Press, Princeton, N.J.
- Greenberg, R. (1988) Seasonal plumage dimorphism in the swamp sparrow. *Journal of Field Ornithology*, **59**, 149-154.
- Greenberg, R., Cadena, V., Danner, R.M. & Tattersall, G.J. (Accepted) Heat loss may explain bill size differences between birds occupying different habitats. *PLoS One*.
- Greenberg, R., Marra, P.P. & Wooller, M.J. (2007) Stable-isotope (C, N, H) analyses help locate the winter range of the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*). *The Auk*, **124**, 1137-1148.
- Griggio, M., Serra, L., Licheri, D., Campomori, C. & Pilastro, A. (2009) Molt speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology*, **22**, 782-792.
- Gwinner, E. (2003) Circannual rhythm in birds. *Current Opinion in Neurobiology*, **13**, 770-778.
- Hahn, T.P., Swingle, J., Wingfield, J.C. & Ramenofsky, M. (1992) Adjustments of the prebasic molt schedule in birds. *Ornis Scandinavica*, **23**, 314-321.
- Hannon, S.J. & Wingfield, J.C. (1990) Endocrine correlates of territoriality, breeding stage, and body molt in free-living willow ptarmigan of both sexes. *Canadian Journal of Zoology*, **68**, 2130-2134.
- Helm, B. & Gwinner, E. (2006) Timing of molt as a buffer in the avian annual cycle. *Acta Zoologica Sinica*, **52(Supplement)**.
- Hemborg, C. & Lundberg, A. (1988) Costs of overlapping reproduction and molt in passerine birds: an experiment with the pied flycatcher. *Behavioral Ecology and Sociobiology*, **43**.
- Hemborg, C. & Merila, J. (1999) Reproductive investment and molt-breeding overlap in the collared flycatcher *Ficedula albicollis*: an experimental approach. *Annales Zoologici Fennici*, **36**, 1-9.
- Jansson, C., Ekman, J. & von Brömssen, A. (1981) Winter mortality and food supply in tits *Parus* spp. *Oikos*, **37**, 313-322.
- Jenni, L. & Winkler, R. (1994) *Moult and ageing of European Passerines*. Academic Press Limited, London.

- Kendeigh, S.C. (1949) Effect of temperature and season on energy resources of the English sparrow. *The Auk*, **66**, 113-127.
- King, J.R. & Murphy, M.E. (1990) Estimates of the mass of structures other than plumage produced during molt by white-crowned sparrows. *Condor*, **92**, 839-843.
- Kjellén, N. (1994) Molt in relation to migration in birds—a review. *Ornis Svecica*, **4**, 1-24.
- Klaassen, M. (1995) Molt and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicula* and the East African *S. t. axillaris*. *Oecologia*, **104**, 424-432.
- Lindström, A., Visser, G.H. & Daan, S. (1993) The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology*, **66**, 490-510.
- Lustick, S. (1970) Energy requirements of molt in cowbirds. *The Auk*, **87**, 742-746.
- Mazerolle, M.J. (2011) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).
- Meijer, T. (1991) The effect of a period of food restriction on gonad size and molt of male and female Starlings *Sturnus vulgaris* under constant photoperiod. *Ibis*, **133**.
- Morton, G.A. & Morton, M.L. (1990) Dynamics of pre-basic molt in free-living mountain white-crowned sparrows. *Condor*, **92**, 813-828.
- Morton, M.L. (1992) Control of pre-basic molt in the mountain white-crowned sparrow: a perspective from field data. *Ornis Scandinavica*, **23**, 322-327.
- Morton, M.L. & Welton, D.E. (1973) Postnuptial molt and its relation to reproductive cycle and body weight in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*). *Condor*, **75**, 184-189.
- Mulder, R.A. & Magrath, J.L. (1994) Timing and pre-alternate molt as a sexually selected indicator of male quality in superb fairy-wrens (*Malurus cyaneus*). *Behavioral Ecology*, **5**, 393-400.
- Murphy, M.E. (1996) Energetics and Nutrition of Molt. *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 158-198. Chapman and Hall, New York, N.Y.
- Murphy, M.E. & King, J.R. (1991) Protein intake and the dynamics of the pre-basic molt in White-crowned Sparrows *Zonotrichia leucophrys gambelli*. *Canadian Journal of Zoology*, **69**, 2225-2229.
- Murphy, M.E., King, J.R. & Lu, J. (1988) Malnutrition during the pre-basic molt of White-crowned Sparrows: feather growth and quality. *Canadian Journal of Zoology*, **66**, 1403-1413.
- Newton, I. & Rothery, P. (2005) The timing, duration and pattern of molt and its relationship to breeding in a population of the European greenfinch *Carduelis chloris*. *Ibis*, **147**, 667-679.
- Nolan, V. & Ketterson, E.D. (1990) Effect of long days on molt and autumn migratory state of site-faithful dark-eyed juncos held at their winter sites. *Wilson Bulletin*, **102**, 469-479.

- Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.M. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B*, **271**, 59-64.
- Olsen, B.J., Greenberg, R., Fleischer, R.C. & Walters, J.R. (2008) Extrapair paternity in the swamp sparrow, *Melospiza georgiana*: male access or female preference? *Behavioral Ecology and Sociobiology*, **63**, 285-294.
- Olsen, B.J., Greenberg, R., Liu, I.A., Felch, J.M. & Walters, J.R. (2010) Interactions between sexual and natural selection on the evolution of a plumage badge. *Evolutionary Ecology*, **24**, 731-748.
- Pap, P.L., Vágási, C.I., Czirják, G.A. & Barta, Z. (2008) Diet quality affects pre-basic molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? *Canadian Journal of Zoology*, **86**, 834-842.
- Payne, R.B. (1972) Mechanisms and control of molt. *Avian Biology* (eds D.S. Farner & J. King), pp. 103-155. Academic Press, New York, N.Y.
- Peele, A.M., Burt Jr., E.H., Schroeder, M.R. & Greenberg, R.S. (2009) Dark color of the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*) may be an evolutionary response to occurrence and abundance of salt-tolerant feather-degrading bacilli in its plumage. *The Auk*, **126**, 531-535.
- Peters, A., Astheimer, L.B., Boland, C.R.J. & Cockburn, A. (2000) Testosterone is involved in acquisition and maintenance of sexually selected male plumage in superb fairy-wrens, *Malurus cyaneus*. *Behavioral Ecology and Sociobiology*, **47**, 438-445.
- Piersma, T. & Jukema, J. (1993) Red breasts as honest signals of migratory quality in a long-distance migrant, the bar-tailed godwit. *Condor*, **95**, 163-177.
- Poole, A. (2005) The Birds of North America Online. Cornell Laboratory of Ornithology Ithaca, N.Y.
- Pulido, F. & Coppack, T. (2004) Correlation between timing of juvenile moult and onset of migration in the blackcap, *Sylvia atricapilla*. *Animal Behaviour*, **68**, 167-173.
- Pyle, P. (1997) *Identification guide to North American birds. Part I Columbidae to Ploceidae*. Slate Creek Press, Bolinas, CA.
- R Development Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reudink, M.W., Studds, C.E., Marra, P.P., Kyser, T.K. & Ratcliffe, L.M. (2009) Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. *Journal of Avian Biology*, **40**, 34-41.
- Ricklefs, R.E. (1996) Avian energetics, ecology, and evolution. *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 1-30. Chapman and Hall, New York, N.Y.
- Stokkan, K.A. (1979) Testosterone and daylength-dependent development of comb size and breeding plumage of male willow ptarmigan (*Lagopus lagopus lagopus*). *The Auk*, **96**, 106-115.

- Stokkan, K.A. & Sharp, P.J. (1980) Seasonal changes in the concentration of plasma luteinizing hormone and testosterone in willow ptarmigan (*Lagopus lagopus lagopus*) with observations on the effect of permanent short days. *General and Comparative Endocrinology*, **40**, 109-115.
- Stutchbury, B.J.M., Gow, E.A., Done, T., MacPherson, M., Fox, J.W. & Afanasyev, V. (2011) Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 131-137.
- Swaddle, J.P. & Witter, M.S. (1997) The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): and experimental approach. *Canadian Journal of Zoology*, **75**, 1135-1146.
- Tonra, C. (2011) The role of breeding preparation in migratory phenology and seasonal interactions in migratory passerines. Ph.D., University of Maine.
- Vega Rivera, J.H. (1998) Pattern and chronology of prebasic molt for the wood thrush and its relation to reproduction and migration departure. *Wilson Bulletin*, **110**, 384-392.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, Fourth edn. Springer, New York, N.Y.
- Wingfield, J.C. & Goldsmith, A.R. (1990) Plasma levels of prolactin and gonadal steroids in relation to multiple-brooding and reneating in free-living populations of the song sparrow, *Melospiza georgiana*. *Hormones and Behavior*, **24**, 89-103.
- Williams, T.D. (2005) Mechanisms underlying the costs of egg production. *BioScience*, **55**, 39-48.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in Ecology with R*. Springer, New York, N.Y.

Tables

Table 1. Rank of models describing earliest recorded date of body molt of swamp sparrows (top models and null). K = number of parameters and w_i = model weight. For full model set, see Table S1.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	1253.225	0	0.291
Treatment	3	1253.808	0.582	0.217
Treatment + Age + Year	5	1255.303	2.078	0.103
Treatment + Sex + Year	5	1255.322	2.097	0.102
Intercept only	2	1259.528	6.302	0.012
Treatment + Age * Sex + Year	7	1259.612	6.387	0.012

Table 2. Rank of models describing earliest recorded date of face molt of swamp sparrows (top models and null). K = number of parameters and w_i = model weight. For full model set, see Table S2.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	515.483	0	0.470
Treatment + Age + Year	5	516.887	1.405	0.233
Treatment + Sex + Year	5	517.741	2.258	0.152
Treatment + Age * Sex + Year	7	521.681	6.198	0.021
Intercept only	2	530.688	15.205	2.347E-04

Table 3. Rank of models describing earliest recorded date of crown molt of swamp sparrows (top models and null). K = number of parameters and w_i = model weight. For full model set, see Table S3.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	519.520	0	0.512
Treatment + Age + Year	5	521.795	2.275	0.164
Treatment + Sex + Year	5	521.799	2.278	0.164
Treatment + Age * Sex + Year	7	525.380	5.860	0.027
Intercept only	2	528.760	9.240	5.043E-03

Figure Legends

Figure 1. A swamp sparrow molting throat, face, and crown feathers as part of prealternate molt in eastern North Carolina. Image used with permission of Jeff Lewis.

Figure 2. Earliest detected body molt of swamp sparrows at study plots. Model average predictions \pm unconditional standard errors in black, the first identified molt per individual (raw data) are shown in gray.

Figure 3. Earliest detected face molt of swamp sparrows at study plots. Model average predictions \pm unconditional standard errors in black, the first identified molt per individual (raw data) are shown in gray.

Figure 4. Earliest detected crown molt of swamp sparrows at study plots. Model average predictions \pm unconditional standard errors in black, the first identified molt per individual (raw data) are shown in gray.

Figures



Fig 1. Photo by Jeff Lewis, used with permission.

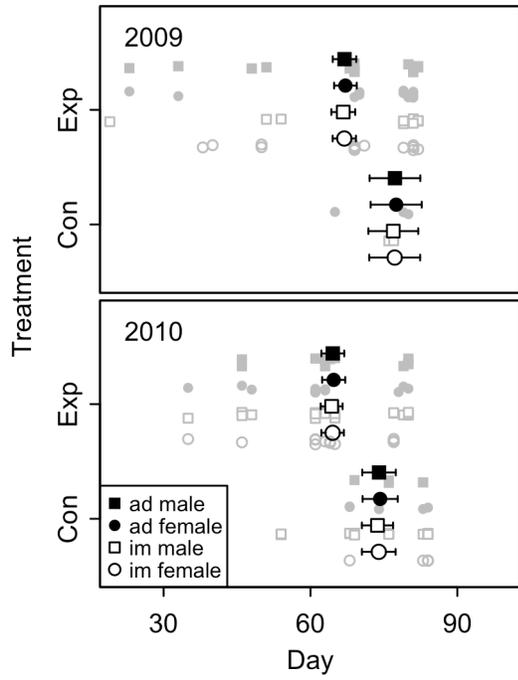


Fig 2.

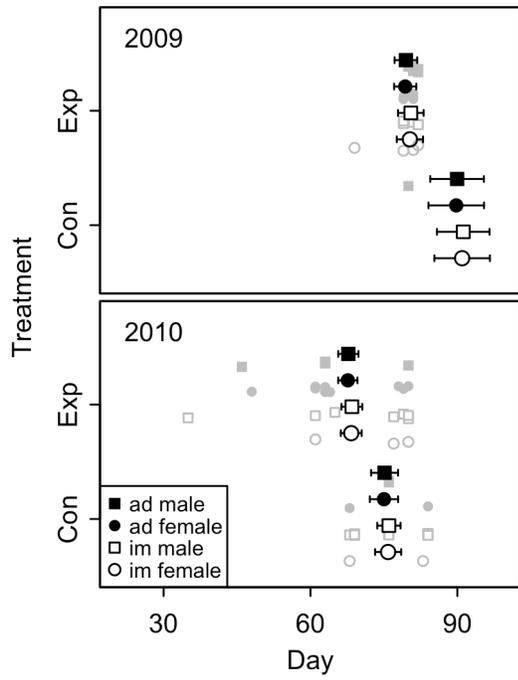


Fig 3.

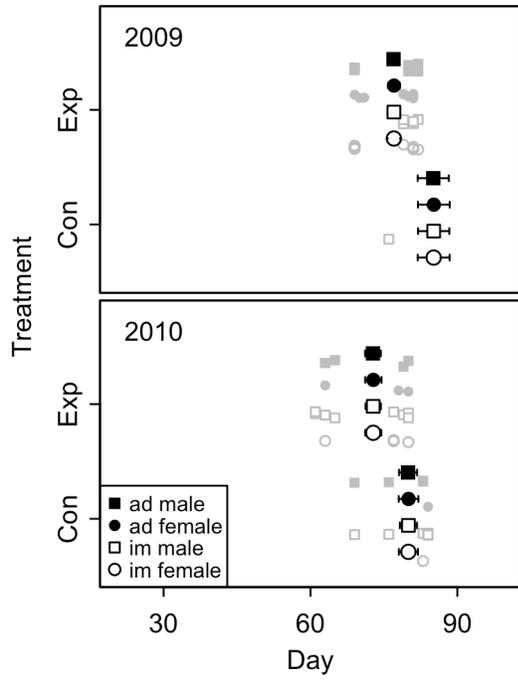


Fig 4.

Appendix (Supporting Information)

Table S1. Rank of models describing earliest recorded date of body molt of swamp sparrows (full set). K = number of parameters and w_i = model weight.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	1253.225	0	0.291
Treatment	3	1253.808	0.582	0.217
Treatment + Age + Year	5	1255.303	2.078	0.103
Treatment + Sex + Year	5	1255.322	2.097	0.102
Treatment + Age	4	1255.709	2.483	0.084
Treatment + Sex	4	1255.754	2.529	0.082
Treatment + Age + Sex + Year	6	1257.442	4.217	0.035
Treatment + Age + Sex	5	1257.731	4.505	0.031
Intercept only	2	1259.528	6.302	0.012
Treatment + Age * Sex + Year	7	1259.612	6.387	0.012
Treatment + Age * Sex	6	1259.830	6.605	0.011
Year	3	1261.236	8.010	0.005
Age	3	1261.601	8.375	0.004
Sex	3	1261.605	8.379	0.004
Sex + Year	4	1263.315	10.090	0.002
Age + Year	4	1263.348	10.122	0.002
Age + Sex	4	1263.704	10.478	0.002
Age + Sex + Year	5	1265.456	12.231	0.001
Age * Sex	5	1265.738	12.512	0.001

Age * Sex + Year	6	1267.457	14.231	0.000
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Table S2. Rank of models describing earliest recorded date of face molt of swamp sparrows (full set). K = number of parameters and w_i = model weight.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	515.483	0	0.470
Treatment + Age + Year	5	516.887	1.405	0.233
Treatment + Sex + Year	5	517.741	2.258	0.152
Treatment + Age + Sex + Year	6	519.289	3.807	0.070
Treatment + Age * Sex + Year	7	521.681	6.198	0.021
Age + Year	4	522.045	6.562	0.018
Year	3	522.115	6.632	0.017
Sex + Year	4	523.329	7.846	9.302E-03
Age + Sex + Year	5	524.008	8.525	6.624E-03
Age * Sex + Year	6	526.331	10.848	2.073E-03
Intercept only	2	530.688	15.205	2.347E-04
Treatment	3	531.781	16.298	1.359E-04
Age	3	532.442	16.959	9.767E-05
Sex	3	532.453	16.971	9.709E-05
Treatment + Sex	4	533.901	18.418	4.708E-05
Treatment + Age	4	533.912	18.429	4.682E-05
Age + Sex	4	534.489	19.006	3.509E-05
Treatment + Age + Sex	5	536.159	20.676	1.522E-05

Age * Sex	5	536.593	21.110	1.226E-05
Treatment + Age * Sex	6	538.259	22.777	5.326E-06

Table S3. Rank of models describing earliest recorded date of crown molt of swamp sparrows (full set). K = number of parameters and w_i = model weight.

Model	K	AICc	Δ AICc	w_i
Treatment + Year	4	519.520	0	0.512
Treatment + Age + Year	5	521.795	2.275	0.164
Treatment + Sex + Year	5	521.799	2.278	0.164
Treatment + Age + Sex + Year	6	524.138	4.618	0.051
Treatment	3	524.881	5.360	0.035
Treatment + Age * Sex + Year	7	525.380	5.860	0.027
Treatment + Sex	4	526.835	7.314	0.013
Treatment + Age	4	526.988	7.468	0.012
Intercept only	2	528.760	9.240	5.043E-03
Treatment + Age + Sex	5	529.003	9.483	4.465E-03
Year	3	529.818	10.298	2.971E-03
Treatment + Age * Sex	6	530.601	11.080	2.009E-03
Sex	3	530.878	11.358	1.749E-03
Age	3	530.912	11.391	1.719E-03
Sex + Year	4	531.760	12.239	1.125E-03
Age + Year	4	531.906	12.385	1.046E-03
Age + Sex	4	533.092	13.571	5.782E-04

Age + Sex + Year	5	533.900	14.379	3.860E-04
Age * Sex	5	534.012	14.492	3.649E-04
Age * Sex + Year	6	534.457	14.937	2.921E-04

CHAPTER IV. CONCLUSIONS

It is often said that challenges are defining factors in one's life. Challenges are ubiquitous throughout the lives of most species. Uncovering the challenges that carry fitness consequences (those that cause mortality or affect future reproductive success) and learning how organisms respond to those challenges are major goals of organismal biology. Understanding these challenges provides information on how organisms interact with each other and their environment, the selection pressures they face, and how they can be conserved.

Winters in the temperate zone are thought to impose energetic challenges on many small animals. Temperate zone winter weather is driven by storms at unpredictable frequencies and is characterized by temperatures that lie below the thermoneutral zone of endotherms, resulting in elevated thermoregulatory demands. Further, prey items are generally scarce at this time of year. Vegetation growth is drastically reduced and as a result, the abundance of vegetation, including seeds, is depleted throughout the winter. Invertebrates become scarce after entering diapause or migrating. Lastly, the relatively short photoperiods reduce foraging time. The combination of increased thermoregulatory costs and reduced food availability and foraging time could result in challenges to acquiring sufficient energy in temperate winters.

Energetic challenges posed by temperate winter conditions may be particularly acute for small passerine birds that forage on the ground. Small passerines have high surface area-to-volume ratios, which allows relatively high heat loss, and causes high mass-specific basal metabolic rates (Kendeigh 1970, Bennett and Harvey 1987). For ground foraging birds, ice and snow can cause interruptions in foraging when prey items are covered. Despite this co-occurrence of increased thermoregulatory costs and food scarcity for small birds, only a handful

of studies have experimentally examined the challenges posed by food limitation of birds in temperate winters (Smith et al. 1980, Jansson et al. 1981, Brittingham and Temple 1988, Rogers and Heath-Coss 2003).

In this dissertation, I studied if and how limited food availability in winter is a challenge to a small ground foraging bird, the swamp sparrow (*Melospiza georgiana*). With a focus on the potential for food to limit fitness, I hypothesized that food abundance can influence mortality rates and preparation for reproduction in the following breeding season. I tested these hypotheses by evaluating if food abundance has the ability to affect population density, survival, energy (fat) regulation strategies, and feather molt. Figure 1 illustrates the links that I identified between winter food abundance and fitness, along with the associated chapter numbers.

In Chapter I, I found that winter food availability limits density, survival, and energy reserves of swamp sparrows. Individuals with larger fat reserves experienced higher survival probabilities, indicating that the mechanism of food limitation of survival was the maintenance of sufficient fat. Food supplementation led to immigration and reduced mortality, indicating that food abundance can limit populations immediately. We were unable to test for differences in annual survival however, because annual return rates between 2009 and 2010 were low (experimental plots: 10% and 21%; control plots: 4% and 15%). Food limitation of fat reserves also suggests that food abundances can carry-over to affect breeding performance in the following summer. The combination of numerical limitation and the potential for carry-over effects suggests that temperate migrants experience mechanisms of food limitation reported for both temperate residents (numerical limitation: Jansson et al. 1981, Brittingham and Temple 1988) and long-distance migratory species that winter in the tropics (carry-over effects: Marra et al. 1998, Norris et al. 2004).

Maintenance of sufficient fat is important for winter survival (Chapter I) and departure timing for spring migration (Bridge et al. 2010), both of which can affect fitness (Norris et al. 2004). Therefore, strategies of fat reserve regulation and a bird's ability to successfully carry out those strategies could have fitness consequences. In Chapter II, I found that swamp sparrows regulated fat reserves when food was unlimited. The level of fat maintained by experimental birds was potentially optimized as a balance between risks of starvation and depredation (Lima 1986, Houston and McNamara 1993). In contrast, we concluded that control birds were unable to reach optimal fat levels on a daily basis because of food limitation. Food limitation was evident in that scaled mass of control birds tracked recent temperature and control birds lost muscle throughout the winter. In contrast, scaled mass of experimental birds did not track recent temperature and muscle size remained constant throughout the season. These results suggest that limitation of energy reserves by food availability can be influenced by temperature and predator abundance.

Molt is energetically costly and therefore typically does not overlap with migration or reproduction. In spring, the rapid succession of pre-alternate molt, migration (if a migrant), and breeding suggests that timing of molt could constrain the initiation of breeding. We showed for the first time that food abundance influences the timing of molt in the wild. Supplemented birds began molting the body, face, and crown earlier than control birds (11, 14, and 8 days earlier, respectively) indicating that food abundance limits the initiation of pre-alternate molt. Three feather regions molted in sequence, further suggesting food limitation of molt. These results suggest that food limitation of molt could cascade through other life history stages in the annual cycle and ultimately affect reproductive success.

Evidence of winter food limitation has both basic and far-reaching implications. The identification of limiting factors lies at the core of our understanding of a species' ecology and related fitness consequences can help uncover selection pressures that species face. Many links that we identified likely lead to fitness (Figure 1), indicating that winter food availability should drive selection on traits that provide advantages in foraging or thermoregulation. Selection related to winter food availability and energetic costs has been documented in only a few well-known cases (Boag and Grant 1983, Fleischer and Johnston 1988), potentially because it is rarely known if food is actually limiting.

Winter food limitation in swamp sparrows may help explain described variation in bill morphology of emberizid sparrows. Tidal marsh-endemic sparrow taxa, including the coastal plain swamp sparrow (*Melospiza georgiana nigrescens*) are characterized by larger bills than terrestrial relatives (Greenberg and Droege 1990, Grenier and Greenberg 2005). Winter food limitation might drive this pattern if larger bills confer a foraging advantage in tidal marshes but not other winter habitats. In addition, Greenberg and Olsen (2010) found a high degree of sexual dimorphism in bill size in tidal marsh species compared to inland relatives and hypothesized that the dimorphism resulted from sexual selection or niche divergence. Winter food limitation could drive niche divergence to reduce intraspecific competition, of which we found evidence (Chapter I). Such studies of selection should consider seasonal change in bill size, however, which has been observed in swamp sparrows (Danner unpub. data) and other tidal marsh sparrow taxa (Greenberg, Etterson, and Danner unpub. data) and shows that bills are typically largest in the summer.

In addition to testing *a priori* hypotheses, this research generated several new hypotheses and should stimulate diverse research. In Chapter I, I found that bird density is limited by food

availability. Research into territoriality and dominance relationships would to help understand if this limitation of density is controlled through density-independent or density-dependent processes and if food limitation leads to habitat segregation by age and sex, as found in some migratory species in winter (Marra and Holmes 2001). Chapter II provides evidence for the new hypothesis that birds regulate fat only when it reaches an optimal level. Previous studies of adaptive fat regulation have not considered the difference between optimal and actual fat levels, and this distinction provides a new perspective that must be considered when interpreting the sizes of fat reserves and could be readily tested with a series of controlled laboratory experiments. In Chapter III, we found the first evidence that food availability limits pre-alternate molt timing in birds. Future research should focus on the physiological mechanisms by which food limits molt, the thermoregulatory challenges imposed by molt in cold weather, and test if molt timing does indeed limit timing of migration and breeding.

In conclusion, these results provide strong evidence that food can limit wintering temperate migrants in a variety of ways. The combination of energetically challenging winter weather, low food availability, and the process of migration make temperate migrants susceptible to both immediate and carry-over effects of food limitation, indicating that they experience challenges in winter characteristic of both temperate residents and long-distance migrants. These findings help to place temperate migrants in ecological and evolutionary spectra regarding overwintering strategies and provide bases for much additional research.

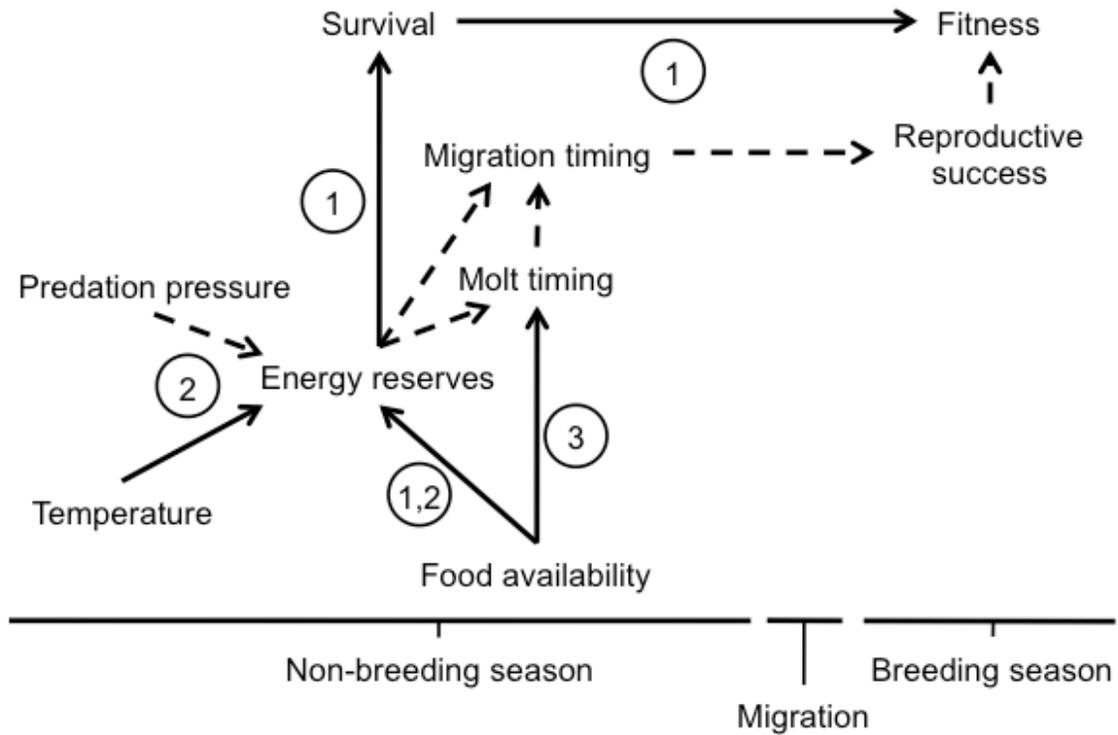


Figure 1. Conceptual model of links between winter food availability and fitness. Solid lines = links that are supported in this dissertation (chapter numbers in circles). Dashed lines = links that are thought to exist based on published research regarding other species. The dashed lines between i) energy reserves and molt timing and ii) molt timing and migration timing represent hypotheses that I make in Chapter III.

Literature Cited

- Bennett, P. M. and P. H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *Journal of Zoology* **213**:237-363.
- Boag, P. T. and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches. (Geospizinae) in the Galapagos. *Science* **214**:82-85.
- Bridge, E. S., J. F. Kelly, P. E. Bjornen, C. M. Curry, P. H. Crawford, and J. M. Paritte. 2010. Effects of nutritional condition on spring migration: do migrants use resource availability to keep pace with a changing world? *Journal of Experimental Biology* **213**:2424-2429.
- Brittingham, M. C. and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology* **69**:581-589.
- Fleischer, R. C. and R. F. Johnston. 1982. Natural selection on body size and proportions in house sparrows. *Nature* **298**:747-749.
- Greenberg, R. and S. Droege. 1990. Adaptations to tidal marshes in breeding populations of the swamp sparrow. *Condor* **92**:393-404.
- Greenberg, R. and B. J. Olsen. 2010. Bill size and dimorphism in tidal-marsh sparrows: island-like processes in a continental habitat. *Ecology* **91**:2428-2436.
- Grenier, J. L. and R. Greenberg. 2005. A biogeographic pattern in sparrow bill morphology: Parallel adaptation to tidal marshes *Evolution* **59**:1588-1595.
- Houston, A. I. and J. M. McNamara. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* **24**:205-219.
- Jansson, C., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* **37**:313-322.
- Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor* **72**:60-65.
- Lima, S. L. and E. 67:377-385. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology* **67**:377-385.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1988. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**:1884-1886.
- Marra, P. P. and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *The Auk* **118**:92-104.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. M. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B* **271**:59-64.
- Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island song sparrow population. *Oecologia* **47**:164-170.