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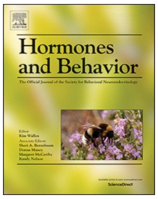

Declining food availability, corticosterone, and migratory response in a nomadic, irruptive migrant

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ABSTRACT

While obligate migrants time their movements to respond to predictable changes in the environment, facultative migration is characterized by more variable movements that are driven by unpredictable changes in resource availability. The proximate cues that trigger facultative migrations and the endocrine mechanisms involved in these responses remain poorly understood, though corticosterone may be a key mediator of facultative migration due to its effects on activity and metabolic processes. We conducted experiments in the fall and spring to examine the response of pine siskins (*Spinus pinus*), a facultative migrant, to a two-stage food restriction. Our goals were to examine whether declining food availability stimulated behavioral and/or physiological changes consistent with a migratory response, whether anticipatory behavioral and physiological adjustments occurred when birds were initially presented with changing food availability, and if observed changes corresponded to changes in circulating corticosterone levels. We found no evidence of preparatory physiological changes for migration, but food-restricted birds in the spring had increased daytime activity indicative of a migratory response. Corticosterone increased at each stage of the restriction and the change in corticosterone corresponded to the magnitude of decline in body condition. Increased corticosterone was also correlated with larger increases in activity during the initial stage of food restriction, but only during the spring, when birds also displayed higher levels of initial body condition. These results suggest that initial energetic state and corticosterone response may interact to determine an individual's behavioral and physiological response to declining food availability and ultimately the facultative migratory response.

1. Introduction

Facultative migrations are those that occur in response to unpredictable fluctuations in resources. These irregular migrations vary in terms of the distance travelled, the direction of orientation, and/or the timing of movements on a year-to-year basis (Newton, 2012, 2006). This form of migration stands in contrast to the more well-known obligate migrations – migrations that are spatially and temporally regular and predictable. Much of what we know about migration, including its endocrine regulation, comes from studies of obligate migration, while many aspects of facultative migration remain poorly understood, despite it occurring across a range of taxonomic groups (Fieberg et al., 2008; Holland, 2006; Newton, 2012, 2006; Plotkin, 2010; Singh et al., 2012). Facultative migrations can take several forms, notably nomadic migration, fugitive migration, and irruptive migration (Watts et al., 2018). Nomadic migration is generally characterized by a greater degree of variability in the timing and/or direction of movement compared to obligate migration, though recent work suggests that nomadic movements have a greater seasonal component and directionality than previously appreciated (Bennetts and Kitchens, 2000; Cornelius and Hahn, 2012; Pedler et al., 2014). Fugitive migration occurs in response to severe environmental perturbation (*e.g.*, storm or drought) and moves animals away from the perturbation. Finally, irruptive migration is characterized by the movement of large numbers of animals out of their typical range in response to poor environmental conditions over relatively large geographic areas; thus, this form of migration may represent a special case of fugitive migration (Watts et al., 2018). However, the extent to which these categories accurately reflect biologically distinct forms or represent points along a continuum remains unresolved, due in large part to a dearth of knowledge about facultative migrations (Watts et al., 2018).

The proximate cues that trigger facultative migrations also remain

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poorly understood. For example, severe storms are known to lead to facultative altitudinal migrations, but it remains unclear whether predictive environmental cues (*e.g.*, temperature, barometric pressure, food availability), internal cues about the animal's physiological state (*e.g.*, body condition), or a combination of these cues trigger a migratory response (Boyle et al., 2010; Breuner and Hahn, 2003; Hahn et al., 2004). Another well-documented form of facultative migration are the irruptive migrations of boreal seed-eating birds. In such species, analyses over large geographic scales indicate that fall and winter movements of birds are often correlated with patterns of abundance of seed cone crops (Bock and Lepthien, 1976; Koenig and Knops, 2001; Strong et al., 2015). While these studies highlight the link between food availability and patterns of facultative migration, few experimental studies have tested whether declining food availability is a proximate cue triggering facultative migration. In one species for which this has been tested, the red crossbill (*Loxia curvirostra*), the results are consistent with reduced food availability stimulating a migratory response (Cornelius et al., 2018, 2010). However, it has also been proposed that some predictive environmental cues (*e.g.*, local population density, less dire changes in food availability) may be important in stimulating physiological preparations for migration and/or migratory behavior (Lack, 1954; Newton, 1973; Watts et al., 2018). The use of such predictive cues would potentially allow birds to make physiological preparations for migration – similar to those made by obligate migrants – while energetic demands are still sustainable, that would in turn support migratory movements once departure occurs. However, it is unclear whether individuals make physiological changes in anticipation of a facultative migration or depart immediately once environmental conditions indicate impending change.

The elevation of circulating corticosterone levels, *via* activation of the hypothalamic-pituitary-adrenal (HPA) axis, has been proposed as a likely mediator of facultative migratory responses (Cornelius et al., 2012; Watts et al., 2018; Wingfield et al., 1998; Wingfield and Ramenofsky, 1997). Unpredictable changes in the environment that lead to increased energetic demands and/or depletion of food resources can result in an animal experiencing an allostatic overload and negative energy balance, which in turn causes an increase in circulating corticosterone and the activation of an emergency life history stage (ELHS; Landys et al., 2006; McEwen and Wingfield, 2003; Watts et al., 2018; Wingfield et al., 1998; Wingfield and Ramenofsky, 1997). Such increases in corticosterone can facilitate increased metabolic demands *via* the promotion of gluconeogenesis and the mobilization of energy reserves (Landys et al., 2004a, 2006; Wingfield et al., 1998; Wingfield and Ramenofsky, 1997), as well as the reduction of metabolic demands during inactive periods, such as at night (Buttemer et al., 1991). In addition to its metabolic effects, corticosterone may also facilitate movement in response to environmental perturbation. Numerous studies have observed concomitant increases in plasma corticosterone levels and locomotor activity (Breuner et al., 1998; Dolnik and Blyumental, 1967; Eikenaar et al., 2014; Krause et al., 2017; Lynn et al., 2003; Meier et al., 1971), though the effects of corticosterone on activity can depend on the energetic state of the animal (Astheimer et al., 1992; Breuner and Hahn, 2003). At levels that are lower than those typical of an ELHS, corticosterone can also play an important role in mediating adjustments in physiology and behavior – for example in response to predictable or manageable energetic demands ("physiological state B," as described in Landys et al., 2006). It is in this context that corticosterone is thought to be important in obligate migration (Cornelius et al., 2012; Landys et al., 2006) and could also be important in mediating the initiation of facultative migration in response to predictive environmental cues or before an ELHS becomes necessary.

In this study, we used the pine siskin as a model to begin to address some of the gaps in our understanding of the regulation of facultative migration. Specifically, we sought to examine (1) whether declining food availability stimulated changes in behavior and/or physiology consistent with a migratory response, (2) whether birds made anticipatory behavioral or physiological adjustments for migration when presented with changing food availability, and (3) whether changes in behavior and physiology corresponded to changes in circulating plasma corticosterone levels consistent with a role for corticosterone in mediating the transition to a facultative migratory state. Pine siskins are a small North American finch whose migratory patterns include both nomadic and irruptive movements. Pine siskins have low site-fidelity (Dawson, 2014; Yunick, 1983) and lack strong directional orientation and timing to movements (Brewer et al., 2006), indicative of nomadic migration. They are also known to irrupt in large numbers to areas outside their typical range (Bock and Lepthien, 1976; Newton, 2006). Pine siskins are observed migrating most commonly in the fall and spring, but movements have been observed at other times of the year, including late summer and winter (Dawson, 2014). Spring movements are stimulated at least partially by increasing day length, as captive pine siskins experiencing naturally changing day lengths display increased levels of nocturnal migratory restlessness, which are proceeded by physiological preparations for migration (Robart et al., 2018; Watts et al., 2017). Spring migration or readiness to migrate in this species may facilitate movement at a time when new food sources are likely to become available, or it may function to return birds to suitable breeding habitat following irruptions. As in other boreal seed-eating birds, irruptive movements of pine siskins have been linked to the declining availability of conifer seed cones and have most commonly been reported in the fall and early winter (Bock and Lepthien, 1976; Koenig and Knops, 2001; Strong et al., 2015) – times of year when the abundance of conifer cone seeds often declines (Burns and Honkala, 1990; Hahn, 1998).

In this study, we experimentally simulated a decline in food availability using a two-stage food restriction in treated birds, while control birds had *ad libitum* access to food. Prior to the start of the experiment, birds had *ad libitum* access to a seed mixture and a pellet diet. In the first stage of the food restriction, we removed the seed mixture, but birds continued to receive pellet diet *ad libitum.* In the second stage of the restriction, food-restricted birds were provided with 75% of their daily intake of pellet diet. This staggered approach allowed us to create a semi-naturalistic food decline, as preferred food items declined first, followed by a more dramatic reduction in resource availability. This approach also allowed us to investigate potential anticipatory behavioral or physiological adjustments for migration since birds were provided with an indicator that food availability was changing, but still had access to sufficient resources to support the metabolic demands of preparatory changes associated with a migratory state. Thus, if declining food availability is a stimulatory cue for migration in this species, we predicted that birds experiencing a food restriction would show behavioral indicators of a migratory state, and possibly physiological changes. Further, if pine siskins make anticipatory adjustments for migration as food availability changes, then we predicted that birds would show changes in behavior and/or physiology indicative of migration during the first stage of the food restriction. Finally, if corticosterone plays a role in mediating the transition to a facultative migratory state in this species, we predicted that corticosterone levels would be elevated in birds that experience a food restriction and that changes in circulating corticosterone levels would correlate to changes in migratory behavior and/or physiology. By examining behavioral, physiological, and endocrine changes that occur in response to declining food availability, this study aims to advance the understanding of the regulatory mechanisms involved in the facultative migrations that many animals use to respond to environmental perturbations.

2. Methods

2.1. Animals

We used wild-caught male pine siskins for this experiment. Birds were collected with permits from the U.S. Fish and Wildlife Service

(MB813248 and MB18234A), California Department of Fish and Wildlife (SC-10677), Washington Department of Fish and Wildlife (Watts 15-155), and Wyoming Game and Fish Department (393). Birds were sexed in the field based on the presence of an enlarged cloacal protuberance; in the absence of this we collected a blood sample that was used to genetically sex the bird (DNA Solutions, Miami, FL). We aged birds (hatch year [HY] or after hatch year [AHY]) based on plumage characteristics and skull ossification (Pyle, 1997). Birds used during the fall food restriction experiment came from 3 capture sites in the western United States (Wrightwood, CA: 34°21′N, 117°37′W; Randle, WA: 46°18′N, 121°32′W; Jackson, WY: 43°28′N, 110°49′W) and consisted of a mixture of HY and AHY birds. We balanced capture site and age across the control and food restriction treatments. Birds used in the spring food restriction experiment came from a single capture site (Los Angeles, CA: 34°07′N, 118°12′W) and were all AHY birds.

We brought birds to Loyola Marymount University in Los Angeles, CA after capture and housed them indoors on a photoperiod that mimicked naturally changing day length locally (34°N latitude). Birds were initially housed in small groups and given *ad libitum* water, grit, a pelleted maintenance diet (Roudybush Small Bird Maintenance Diet; Woodland, CA, hereafter "pellets"), and a preferred seed mixture consisting of nyjer thistle and sunflower seed hearts (hereafter "seeds"). We placed birds in individual cages prior to the start of each experiment (approximately 34 cm (w) x 38.5 cm (l) x 43 cm (h)). Experimental procedures were approved by the Loyola Marymount University Institutional Animal Use and Care Committee (protocol: LMU IACUC 2014 FA 02).

2.2. Experiment overview

We conducted two separate food-restriction experiments, one in the fall and one in the late winter/early spring. The fall experiment was conducted 9 November – 18 December 2015. The spring experiment occurred from 28 February – 9 April 2016. We started with an initial sample size of 28 birds for each experiment. We monitored birds closely during the experiment and removed from the experiment any bird that exhibited poor body condition (below that encountered in healthy free-living birds) so that it could be returned immediately to *ad libitum* food. We had to remove 1 food-restricted bird during both the fall and spring experiments, resulting in samples sizes of 14 control and 13 food-restricted birds for both experiments. The two treatment groups were housed together in experimental rooms such that birds had auditory, but not visual, access to others birds in the room and could hear conspecifics in both treatment groups.

We conducted a two-stage food restriction (Fig. 1) during both experiments. Prior to food manipulation ("Pre") both treatment group were provided with *ad libitum* seeds and pellets. We removed the seeds from the food-restricted birds during the "No Seed" phase, but still provided them with *ad libitum* pellets. The No Seed phase lasted 8 days and we measured the daily intake of pellets for each food-restricted bird during this period. The next phase of the experiment, "Restriction", lasted 6 days and each day we provided food-restricted birds with 75% of their own average daily intake of pellets, as calculated during the No Seed period. A previous study of red crossbills that used a similar food restriction found effects on physiology and behavior in just 3 days (Cornelius et al., 2010). However, captive pine siskins can carry quite large fat deposits at some times of year and preliminary work indicated that a longer (6-day) food restriction might be necessary in order to impose an appreciable energetic challenge (HE Watts, unpublished data). Thus, we chose to use approximately weekly intervals for the food restriction phases, which also facilitated blood sampling, though we expected that the effects of food restriction might vary across that interval as energetic reserves declined. We provided the daily allotment of food in the late morning, after completing any blood collection and body condition measurements in the rooms. At the end of the Restriction period the food-restricted birds were again provided with *ad libitum* seeds and pellets for 2 weeks prior to the final sampling period ("Post").

To ensure that we collected blood samples and body measurements on the same day of the experiment relative to the start, we staggered the start date for groups of birds. Based on space available in the experimental rooms, we divided the birds into 5 (A-E) and 7 (A-G) groups, respectively, for the fall and spring experiments. Each group consisted of an equal number of control and food-restricted birds. On the first calendar day of the experiment, we began data collection for the "A" group, starting data collection for the "B" group the following day. We continued in this manner until data collection for all groups was started.

2.3. Blood sampling and body measurements

Blood samples were collected to measure circulating corticosterone, testosterone and triglyceride levels. Testosterone was measured because it is linked to the development of a spring migratory state (Deviche, 1995; Owen et al., 2014; Tonra et al., 2011; Wingfield et al., 1990), while elevated triglyceride levels can indicate physiological preparation for migration (Jenni-Eiermann and Jenni, 1994; Smith and McWilliams, 2009) and serve as a fuel source during short-term fasts (Jenni-Eiermann and Jenni, 1996). Blood samples were collected at the end of the Pre, Restriction, and Post phases (Fig. 1). The No Seed phase lasted 8 days, but we collected a blood sample (and body measurements) on the 7th day of this phase. This was due to limits on the frequency with which we could collect blood samples and ensured that all blood collections were spaced at least a week apart. We collected blood approximately 2:30 h after the lights came on. We punctured the alar vein and collected ~70–100 μL of blood in heparinized microhematocrit tubes. We collected blood within 3-min of entering a room each day for samples that were used to measure baseline corticosterone levels (Wingfield et al., 1982). We collected samples within 10 min for blood that was used to measure plasma testosterone and triglyceride levels. We stored samples on ice until centrifugation. We collected the plasma and stored it at −20 °C until assayed for corticosterone, testosterone, and triglycerides.

Measures of body condition were collected as indicators of energetic state and as indicators of potential migratory preparations. We recorded body measurements approximately 1–2 h after we collected a blood sample. We measured body mass, furcular and abdominal fat, and flight (pectoralis) muscle size and color. Body mass, body fat, and flight muscle size have been found to increase in pine siskins in preparation for spring nomadic migration (Robart et al., 2018). We recorded body

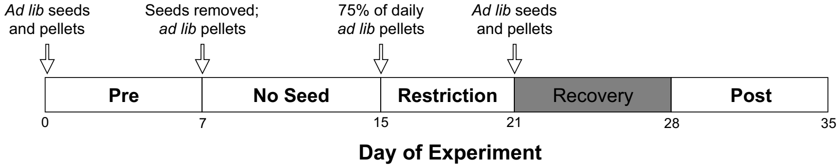

Fig. 1. Schematic of experimental design. Open arrows denote days when food was manipulated for the food-restricted birds. Control birds had *ad libitum* seeds and pellets for the duration of the experiment. Body measurements and blood samples were collected at the end of each phase of the experiment, except for the No Seed phase for which blood collection and body measurements occurred on day 14. Mean activity was calculated for the duration of each phase and also for the first 3-days of the No Seed and Restriction phases. No data collection or sampling occurred during the Recovery phase.

mass to the nearest 0.01 g using an electronic balance. We measured furcular and abdominal fat visually on a scale from 0 (no fat) to 5 (bulging fat) (Wingfield and Farner, 1978). We also visually measured flight muscle size on a scale from 0 (muscle concave with keel very prominent) to 3 (muscle bulging over keel) (Bairlein, 1995). The color of the flight muscle has been observed to lighten during migratory preparations (Robart et al., 2018), and the change in color is believed to be related to increased lipids deposited directly in the muscle fibers (M. Ramenofsky, personal communication). We quantified flight muscle color by comparing the bird's flight muscle to a set of standard color (paint) chips. Birds were scored as a "3" (the lightest, pinkest category) if their muscle color corresponded to the Benjamin Moore paint chip "1287" or lighter. Birds with a muscle color that was best approximated by the Benjamin Moore paint chip "1281" were scored as a "2" (the intermediate category). Birds that had a darker, more maroon color for their flight muscle than the 1281 paint chip were scored as a "1" (the darkest category). We conducted an additional measurement of body fat and muscle size part way through the Restriction period, at the start of day 4, to ensure that the food-restricted birds did not decline in condition too severely. For birds that had a total fat score (furcular + abdominal) of 1 and a muscle size of 1, we increased the daily allotment of pellets to 85% of the bird's average daily intake for the remaining period of the Restriction (2 and 1 birds for the fall and spring experiments, respectively).

2.4. Activity data

We quantified both nocturnal and diurnal activity levels as indicators of migratory behavior, as pine siskins are both nocturnal and diurnal migrants (Dawson, 2014; Robart et al., 2018; Watson et al., 2011; Watts et al., 2017). We collected activity data using passive infrared sensors (Starr Life Sciences Corp., Oakmont, PA). The sensors were placed on top of each cage and attached to a VitalView Data Acquisition System (Starr Life Sciences Corp., Oakmont, PA). Counts of activity were summed in 10-min bins. We calculated mean morning and nocturnal activity for each phase of the experiment (Fig. 1). We confined our analysis of daytime activity to the first 2 h of each day since morning activity can serve as a proxy for overall diurnal patterns of activity (Watts et al., 2017). This ensured that activity data corresponded to times when researchers were not present in the room and the birds had not yet been handled for blood collection or body measurements for the day. We calculated mean morning activity by averaging the 10-min intervals for the first 2 h after the lights had come on the rooms each day. Nocturnal activity typically begins after 23:00 in pine siskins, following a 3 to 4 h quiescence period (Watts et al., 2017). Pine siskins also exhibit pre-dawn activity, which is thought to be different than nocturnal migratory restlessness (Agatsuma and Ramenofsky, 2006; Pérez et al., 2016; Watts et al., 2017). We therefore conservatively calculated nocturnal activity by averaging the 10-min intervals between 23:00 and 3:00. For the Pre and Post phases, we averaged activity for the 7-day period immediately prior to when we collected a blood sample and measured body parameters. The No Seed and Restriction phases were 8 and 6 days, respectively, and we averaged activity for each phase. Since we expected that activity levels might vary across each phase as energetic reserves declined, we also calculated mean activity for the first 3 days of the No Seed and Restriction phases of the experiment to examine whether initial activity patterns were different than activity levels over the entire duration for each of these phases.

2.5. Vocal behavior

During the fall experiment, we recorded the rate of vocalization during the two stages of the food restriction. Given that birds from the two treatment groups could hear each other over the course of the experiment, and that social information may be important in assessing food availability (Cornelius et al., 2018, 2010; Smith et al., 1999), we were interested in quantifying vocal behavior of the birds. Each bird was observed twice, once during the No Seed period and again during the Restriction phase. We observed birds in the afternoon 1–3 days (X +/− SE: 1.85 +/− 0.10 days) after the start of the manipulation for each phase. We began our observations with the "A" group and sampled all birds within a group, ensuring an equal number of control and food-restricted birds were observed each time. After entering the room, we allowed the birds 5 min to acclimate to the presence of the observer – birds were already well habituated to the presence of researchers in the room. We then conducted a 10-min observation for each bird and recorded the total number of calls it made. We were able to distinguish calls made by the focal bird from those emitted by other birds in the room based on movements of the mouth and throat of the focal bird, as well as the direction of the sound. Birds emitted a variety of call types, though no alarm calls were recorded and no singing was observed. Using our observational methods, we could not reliably categorize call types with much detail. Therefore, we tallied all calls as a single category, which excluded alarm calls. One trained observer (MIM) conducted all observations and was blind to treatment.

2.6. Hormone assays

We measured plasma corticosterone (ADI-901-097) and testosterone (ADI-901-065) using enzyme immunoassay kits from Enzo Life Sciences. We ran samples in duplicate, with plasma dilutions and steroid displacement buffer concentrations optimized for pine siskins as previously described (Watts and Hahn, 2012). We ran a corticosterone/testosterone standard in triplicate on each plate to estimate coefficients of variation (CV), with the detection limit calculated for each plate as the upper limit of the 95% confidence interval for the blank wells. For all assays, samples below the detection limit were assigned the mean detection limit of their respective assay.

We ran corticosterone samples in a 1:20 dilution with 1% (of raw plasma volume) steroid displacement buffer with a six-point standard curve ranging from 2000 to 1.95 pg/mL. We ran samples across 3 plates each for the fall and spring experiments. Fall samples had an intra-assay CV of 12.6% and an inter-plate CV of 27.8%, with a mean detection limit of 0.49 ng/mL; the intra-assay CV was 8.4% and inter-plate CV was 5.7% for spring samples, with a mean detection limit of 0.43 ng/mL.

We ran testosterone samples in a 1:20 dilution with 0.5% steroid displacement buffer. Samples were run across 3 plates each for the fall and spring experiments. Testosterone samples for fall had an intra-assay CV of 5.3% and an inter-plate CV of 6.7%, with a mean detection limit of 0.11 ng/mL. Spring testosterone samples had an intra-assay CV of 8.5% and inter-plate CV of 8.2%, with a mean detection limit of 0.20 ng/mL.

We measured plasma triglycerides using an analytical assay for total triglycerides and free glycerol (Sigma-Aldrich Co.). Plasma triglyceride was calculated by subtracting glycerol from the total triglycerides. We attempted to run samples in duplicate; however, 16 and 15 samples from the fall and spring experiments, respectively, were run singly due to limited quantities of plasma. For each experiment samples were run across 2 plates. The fall assay had an intra-assay CV of 10.7% and inter-plate CV of 2.1%; the intra-assay and inter-plate CVs were 12.0% and 11.8%, respectively, for spring samples.

2.7. Statistical analyses

We used JMP Pro 13.0 (SAS Institute Inc.) and R version 3.2.4 (R Development Core Team, 2016) for analyses. We used Principal Components Analyses (PCA) to calculate a composite measure for body condition that included mass and total fat score. We calculated a total of 3 principal components (PCs): one each for the fall and spring experiments, and a PC that contained only the Pre measurements for both the

Table 1
Loading scores for body condition principal components.

Body measure	Fall	Spring	Fall and Spring Pre
Mass (g)	0.96	0.96	0.94
Total fats	0.96	0.96	0.94
Eigenvalue	1.83	1.86	1.75
% variation explained	91.55	92.99	87.34

fall and spring experiments to examine differences in body condition between the 2 seasons (Table 1). We confirmed that Pre levels of activity, body condition, and blood parameters did not differ between the two treatments for both the fall and spring experiments (see supplementary material). To control for inter-individual differences in baseline levels of body condition and hormone levels, we calculated each bird's response to the different phases of the experiment as the change in condition/hormone levels relative to its level during the Pre phase of the experiment. Similarly, for the activity data we calculated the percent change relative to Pre activity levels for the full duration of each sampling period (6–8 days, hereafter "week" activity), and also the percent change using activity for the first 3-days of the No Seed and Restriction phases ("3-day" activity). Since the inclusion of both analyses (3-day and week) inflates the risk of making a Type I error (falsely rejecting the null hypothesis), we present effect sizes along with *p*-values from statistical tests following the recommendation of Nakagawa (2004). We used the raw data, however, for the analyses for plasma triglycerides, and muscle size and color. We were limited by plasma volume for some samples and prioritized assaying corticosterone and testosterone. This resulted in smaller sample sizes of triglycerides measured during the Pre phase (fall: $N = 21$; spring: $N = 9$), limiting our ability to look at change in triglyceride levels. Only a muscle size of 3 and color of 3 is indicative of migratory preparations, so we used the raw data for these measurements to assess whether changes in muscle size and color suggest birds were preparing physiologically for migration. We analyzed data from the fall and spring experiments separately and tested the effects of sampling period, food treatment, and the interaction between sampling period and food treatment. The analysis for the rate of vocalization during the fall only tested the effect of treatment since observations were not conducted during the Pre and Post phases. We used mixed models for most analyses and included bird ID as a random effect (random intercepts). We used the lme4 package (Bates et al., 2015) for linear mixed models (LMMs) and the ordinal package (Christensen, 2015) to analyze muscle size and color using cumulative link mixed models and tested model effects using likelihood-ratio tests. We used the glmmADMB package (Bolker et al., 2012) and negative binomial distribution ("nbinom1") to analyze the rate of vocalizations since the data were over-dispersed and zero-inflated. We used pairwise comparisons to test for differences between sampling points and treatments using the lsmeans package (Lenth, 2016) with Tukey's test for multiple comparisons. We checked for deviations from normality and homoscedasticity by visually inspecting residual plots. Nocturnal activity for neither the fall nor spring was normally distributed. We were unable to transform the fall data to achieve a normal distribution and therefore utilized Wilcoxon tests to test the effect of food treatment on change in nocturnal activity, analyzing each sampling phase separately. To correct for multiple comparisons for each phase, we used the Benjamini and Hochberg false discovery rate (FDR; Benjamini and Hochberg, 1995) at the 0.05 level. We report raw *p*-values and indicate whether comparisons are significant after correction. We performed a Box-Cox transformation on both the week ($\lambda = 0.14$) and 3-day ($\lambda = 0.12$) spring nocturnal activity. We also utilized Box-Cox transformations for the morning activity for both fall (week: $\lambda = 0.43$; 3-day: $\lambda = 0.46$) and spring (week: $\lambda = 0.39$; 3-day: $\lambda = 0.35$). Box-Cox transformations were also used on the body condition PCs for both fall ($\lambda = 1.47$) and spring ($\lambda = 1.69$). There was one outlier each for the fall and spring corticosterone samples. The inclusion of these samples in their respective analyses quantitatively changed the results and were therefore excluded from the final analyses. We used Box-Cox transformations for both the fall ($\lambda = 0.34$) and spring ($\lambda = 0.67$) corticosterone samples. We included plate ID as a random effect (random intercepts) for the fall corticosterone assay to account for the high inter-plate CV. We transformed the fall testosterone data using a Box-Cox transformation ($\lambda = 0.60$). We were unable to transform the spring testosterone data and used Wilcoxon tests to analyze each sampling phase separately; we corrected for multiple comparisons using the Benjamini and Hochberg FDR (FDR = 0.05). We also used Box-Cox transformations for fall and spring ($\lambda = 0.21$) plasma triglyceride levels.

We examined differences in activity, body condition, and blood parameters during the Pre period between the fall and spring experiments for possible seasonal differences. We tested the effect of season and used ANOVAs for the response variables that met assumptions of normality and Wilcoxon tests when non-parametric tests were needed. Muscle size and color, which are ordinal variables, were analyzed using Cochran-Armitage trend tests (Agresti, 2007).

Finally, we also examined the relationship between changes in circulating corticosterone levels and changes in body condition and morning activity for the food-restricted birds. The relationship between change in corticosterone and changes in body condition/activity may be different for the two different phases of the restriction due to differences in allostatic load (Landys et al., 2006). We therefore used LMMs to test the effects of change in corticosterone, phase of restriction, and the interaction between change in corticosterone and phase on the change in body condition and morning activity, analyzing the fall and spring experiments separately.

We report effect sizes where possible. We calculated semi-partial R^2 values for fixed effects and interaction terms for LMMs using the r2glmm package (Jaeger et al., 2016). We report Cohen's *d* for ANOVAs and *r*, calculated as $(\frac{Z}{\sqrt{N}})$, for Wilcoxon tests (Fritz et al., 2012). We are unaware of methods for calculating effect sizes for negative binomial generalized linear mixed models and cumulative link mixed models. Given the multiple levels and unbalanced nature of the muscle size and color data, Agresti (2007) does not recommend utilizing correlation coefficients (*r*) as estimates of effect sizes and we are not aware of alternative methods for calculating effect sizes for ordinal data.

3. Results

3.1. Fall experiment

Morning activity during the week sampling periods was not significantly affected by treatment ($\chi_1^2 = 1.45$, $p = 0.23$, $R^2 = 0.05$), sampling period ($\chi_2^2 = 4.91$, $p = 0.09$, $R^2 = 0.09$), or the interaction between treatment and sampling period ($\chi_2^2 = 2.13$, $p = 0.35$, $R^2 = 0.04$). Morning activity during the first 3 days of the No Seed and Restriction phases varied significantly by sampling period ($\chi_2^2 = 7.32$, $p = 0.03$, $R^2 = 0.13$; Fig. 2a) and was highest during the Restriction phase, although there was no treatment ($\chi_1^2 = 0.74$, $p = 0.39$, $R^2 = 0.03$) or sampling period*treatment interaction ($\chi_2^2 = 1.36$, $p = 0.51$, $R^2 = 0.03$). Nocturnal activity was not significantly different between treatments for any of the time points for either the week activity (No Seed: $Z = -0.78$, $N = 27$, $p = 0.44$, $r = -0.15$; Restriction: $Z = -1.04$, $N = 27$, $p = 0.30$, $r = -0.20$; Post: $Z = -0.07$, $N = 27$, $p = 0.94$, $r = -0.01$; all comparisons not significant after Benjamini and Hochberg correction) or the 3-day activity (No Seed: $Z = -0.61$, $N = 27$, $p = 0.54$, $r = -0.12$; Restriction: $Z = -1.14$, $N = 27$, $p = 0.25$, $r = -0.22$; Post: $Z = -0.07$, $N = 27$, $p = 0.94$, $r = -0.01$; all comparisons not significant after Benjamini and Hochberg correction). The PC for body condition loaded positively for both mass and total fats and explained 91.6% of the variation (Table 1). There was a significant effect of sampling period ($\chi_2^2 = 32.34$, $p < 0.0001$, $R^2 = 0.60$), treatment ($\chi_1^2 = 5.71$, $p = 0.02$, $R^2 = 0.19$), and sampling period*treatment interaction ($\chi_2^2 = 30.91$, $p < 0.0001$, $R^2 = 0.44$) on body condition. Body condition declined significantly in the food-restricted birds during the Restriction phase of the experiment, but was not significantly different relative to the control birds during the other phases of the experiment (Fig. 2b). Flight muscle size declined in the food-restricted birds relative to its size during the Pre and Post periods (sampling period: $\chi_3^2 = 12.24$, $p = 0.007$; treatment: $\chi_1^2 = 1.56$, $p = 0.21$; sampling period*treatment: $\chi_3^2 = 14.32$, $p = 0.003$; Fig. S1a). Flight muscle color did not vary during the experiment ($\chi_3^2 = 4.98$, $p = 0.17$), nor was there a significant effect of treatment ($\chi_1^2 = 0.22$, $p = 0.64$) or sampling period*treatment interaction ($\chi_3^2 = 2.40$, $p = 0.49$). There was a significant effect of sampling period ($\chi_2^2 = 12.57$, $p = 0.002$, $R^2 = 0.22$) and treatment ($\chi_1^2 = 4.98$, $p = 0.03$, $R^2 = 0.18$) on corticosterone, but no sampling period*treatment interaction ($\chi_2^2 = 4.75$, $p = 0.09$, $R^2 = 0.13$). Corticosterone was higher in the food-restricted birds compared to the control birds and was highest during the Restriction phase (Fig. 2c). There was a significant sampling period*treatment effect ($\chi_2^2 = 6.06$, $p = 0.05$, $R^2 = 0.11$) on testosterone, but testosterone remained low throughout the experiment for both groups (sampling period: $\chi_2^2 = 0.53$, $p = 0.77$, $R^2 = 0.02$; treatment: $\chi_1^2 = 0.009$, $p = 0.92$, $R^2 = 0.00$), with only a slight elevation during the Restriction phase in the control birds (Fig. S1c). Triglycerides were lower during the Restriction phase, relative to the other periods during the experiment ($\chi_3^2 = 12.67$, $p = 0.005$, $R^2 = 0.23$; Fig. S1b), but there was no effect of treatment ($\chi_1^2 = 2.45$, $p = 0.12$, $R^2 = 0.12$) or sampling period*treatment interaction ($\chi_3^2 = 4.87$, $p = 0.18$, $R^2 = 0.09$). The food-restricted birds vocalized at a higher rate compared to the control birds (Fig. 2d; Wald $z = 2.27$, $p = 0.02$).

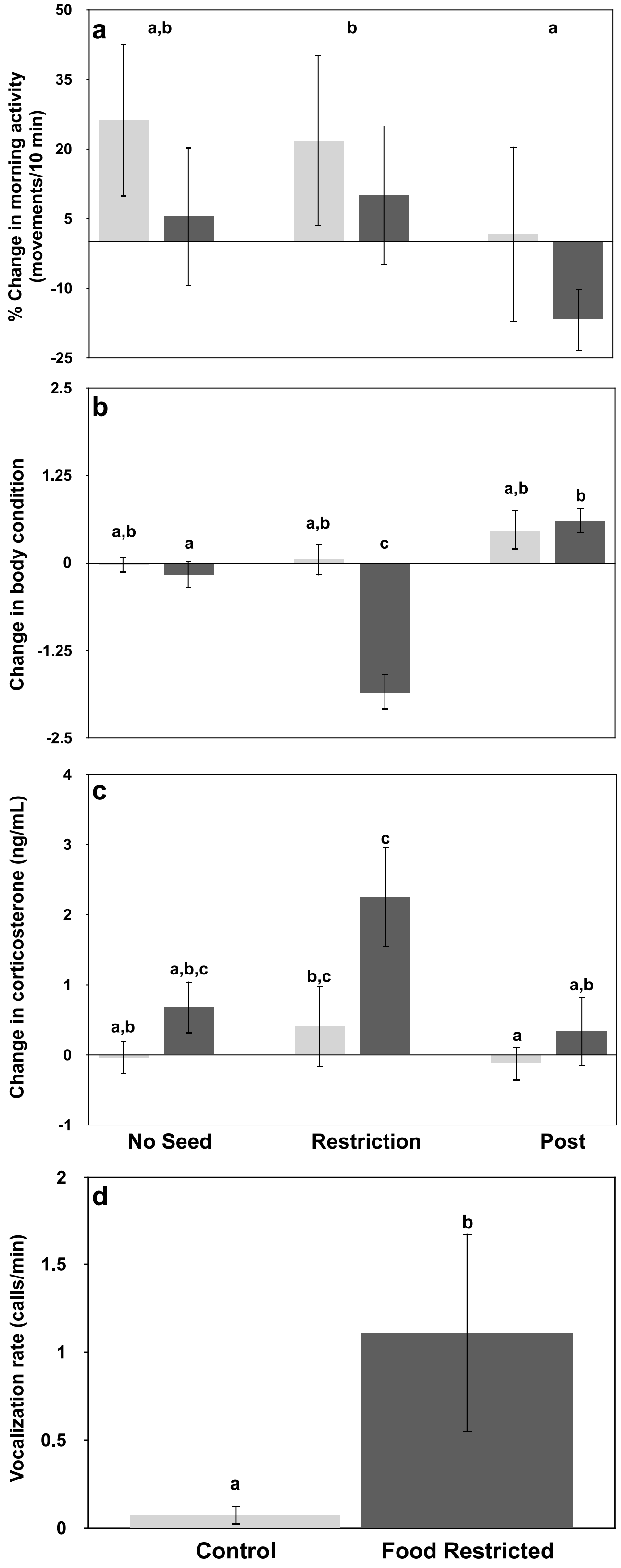

Fig. 2. Change in morning activity (a; during first 3 days of each phase), body condition (b; see Table 1 for PC loading values), corticosterone levels (c), and rate of vocalizations (d) by control (light grey) and food-restricted (dark grey) birds during the fall experiment. Change in response variable is relative to levels measured during the Pre phase of the experiment. Different letters indicate significantly different groups based on pairwise comparisons ($p < 0.05$); letters for morning activity (a) are comparisons only for different sampling periods, as there was no treatment or sampling period*treatment effect. Data presented as means ± 1 sem.

3.2. Spring experiment

The analyses of changes in morning activity for both the week (sampling period*treatment: $\chi_2^2 = 10.60$, $p = 0.005$, $R^2 = 0.18$; sampling period: $\chi_2^2 = 8.56$, $p = 0.01$, $R^2 = 0.18$; treatment: $\chi_1^2 = 0.06$, $p = 0.80$, $R^2 = 0.00$) and 3-day sampling periods (sampling period*treatment: $\chi_2^2 = 16.76$, $p = 0.0002$, $R^2 = 0.27$; sampling period: $\chi_2^2 = 8.64$, $p = 0.01$, $R^2 = 0.21$; treatment: $\chi_1^2 = 0.3$, $p = 0.87$, $R^2 = 0.00$) yielded similar results. The food-restricted birds had a larger increase in morning activity compared to the control birds during the No Seed and Restriction phases (Fig. 3a); this increase in activity relative to the control birds was more pronounced during the No Seed phase for the 3-day activity analysis (Fig. S2a). Changes in nocturnal activity were also similar for the week sampling period and 3-day activity. For the week sampling period there was a significant effect of sampling period ($\chi_2^2 = 23.65$, $p < 0.0001$, $R^2 = 0.39$), treatment ($\chi_1^2 = 5.57$, $p = 0.02$, $R^2 = 0.19$), and sampling period*treatment interaction ($\chi_2^2 = 6.21$, $p = 0.04$, $R^2 = 0.11$) on the change in nocturnal activity. Food-restricted birds had a slight decline in nocturnal activity during the No Seed and Restriction phases, whereas control birds increased their nocturnal activity during each phase relative to their Pre levels (Fig. 3b). There was a significant effect of sampling period ($\chi_2^2 = 27.67$, $p < 0.0001$, $R^2 = 0.42$) and treatment ($\chi_1^2 = 4.90$, $p = 0.03$, $R^2 = 0.17$) on the 3-day nocturnal activity, but no sampling period*treatment effect ($\chi_2^2 = 3.31$, $p = 0.19$, $R^2 = 0.06$). The pattern of changes for both the control and food-restricted birds was similar to nocturnal activity for the week sampling period (Fig. S2b). The PC for body condition during the spring explained 93.0% of the variation in mass and total fats and loaded positively for both measures (Table 1).

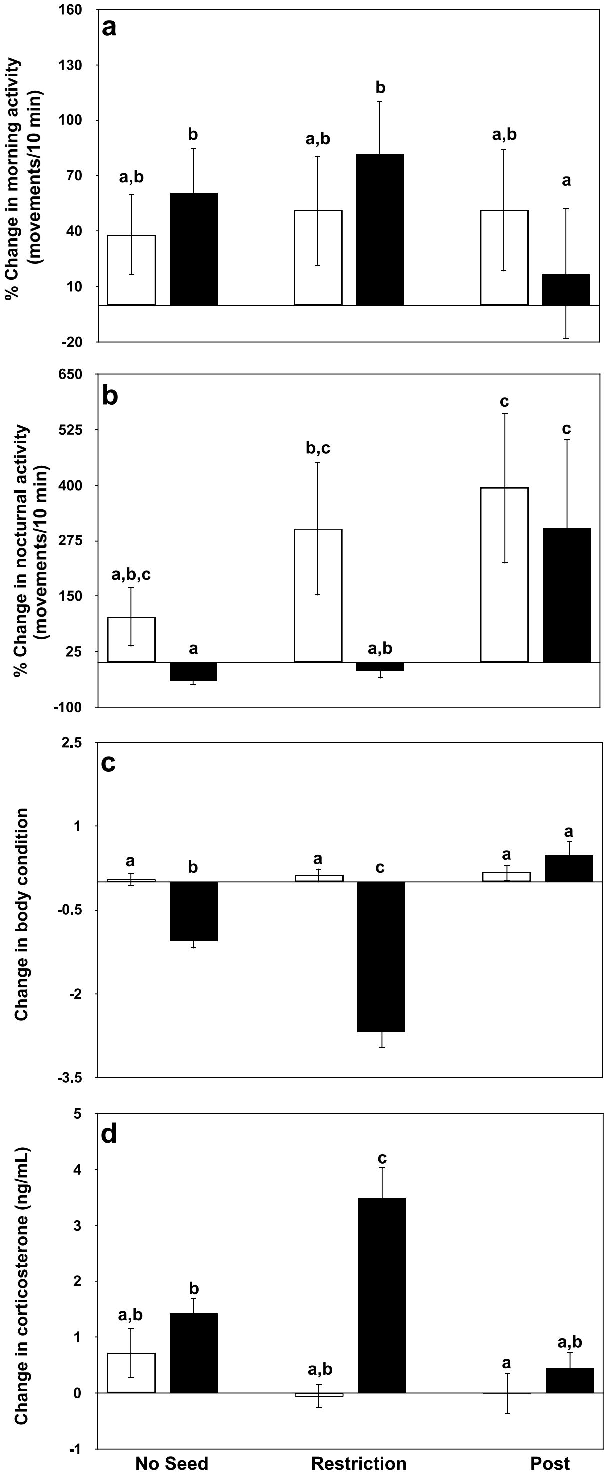

Fig. 3. Change in morning activity (a; for entire period of each phase), nocturnal activity (b; for entire period for each phase), body condition (c; see Table 1 for PC loading values), and corticosterone levels (d) by control (open bars) and food-restricted (closed bars) birds during the spring experiment. Different letters indicate significantly different groups based on pairwise comparisons ($p < 0.05$). Data presented as means ± 1 sem.

Sampling period ($\chi_2{}^2 = 28.27, p < 0.0001, R^2 = 0.69$), treatment ($\chi_2{}^2 = 18.67, p < 0.0001, R^2 = 0.56$), and the interaction between sampling period and treatment ($\chi_1{}^2 = 60.60, p < 0.0001, R^2 = 0.67$) all significantly affected body condition. Body condition for the food-restricted birds declined significantly during the No Seed period and declined even further during the Restriction phase (Fig. 3c). There was a significant effect of sampling period ($\chi_3{}^2 = 15.31$, $p = 0.002$), treatment ($\chi_1{}^2 = 12.02$, $p = 0.005$), and sampling period*treatment ($\chi_3{}^2 = 3562$, $p < 0.0001$) on flight muscle size. Similar to fall, flight muscle size was lowest for the food-restricted birds during the Restriction phase (Fig. S3a). Flight muscle color remained relatively consistent for the control birds during the experiment, but was lighter for the food-restricted birds during the Post phase compared to the color during the Pre phase (sampling period*treatment: $\chi_3{}^2 = 12.29$, $p = 0.006$; sampling period: $\chi_3{}^2 = 13.25, p = 0.004$; treatment: $\chi_1{}^2 = 2.37$, $p = 0.12$; Fig. S3b). There was a significant sampling period*-treatment effect ($\chi_2{}^2 = 19.73$, $p < 0.0001$, $R^2 = 0.40$), as well as significant sampling period ($\chi_2{}^2 = 12.15$, $p = 0.002$, $R^2 = 0.33$) and treatment ($\chi_1{}^2 = 11.17$, $p = 0.0008$, $R^2 = 0.42$) effects on corticosterone. Corticosterone rose for the food-restricted birds during the No Seed period and was significantly higher during the Restriction phase (Fig. 3d). Testosterone did not significantly differ between the treatments during any of the sampling periods (No Seed: $Z = -1.55$, $N = 25$, $p = 0.12$, $r = -0.31$; Restriction: $Z = -0.19$, $N = 25$, $p = 0.85$, $r = -0.04$; Post: $Z = -0.46$, $N = 24$, $p = 0.64$, $r = -0.09$; all comparisons not significant after Benjamini and Hochberg correction). Triglyceride levels were similar for control and food-restricted birds at all time points, except the Restriction phase of the experiment, when food-restricted birds had lower triglyceride levels (sampling period*treatment: $\chi_3{}^2 = 8.09$, $p = 0.04$, $R^2 = 0.16$; sampling period: $\chi_3{}^2 = 8.44$, $p = 0.04$, $R^2 = 0.18$; treatment: $\chi_1{}^2 = 2.73$, $p = 0.09$, $R^2 = 0.10$; Fig. S3c).

3.3. Seasonal differences in baseline parameters

Nocturnal activity during the Pre period did not significantly differ between the fall and spring experiments ($Z = 1.27$, $N = 54$, $p = 0.20$, $r = 0.17$), but morning activity in the Pre period was significantly higher in the fall compared to spring ($F_{1,\ 52} = 20.94$, $p < 0.0001$, Cohen's $d = 1.25$; Table 2). Body condition at the start of the experiment was significantly higher during spring compared to the fall experiment ($F_{1,53} = 17.50$, $p < 0.001$, Cohen's $d = -1.13$). The PC for body condition at the start of both experiments explained 87.3% of the variation in mass and total fats and loaded positively for both body measures (Table 1). The bird with the highest PC value during the spring weighed almost 1.5 g more than the bird with the highest PC value for the fall and also had much larger fat deposits (Table 2). Neither flight muscle size ($Z = -0.50, p = 0.62$) nor flight muscle color ($Z = -1.15$, $p = 0.29$) was significantly different in the Pre period between fall and spring (Table 2). Corticosterone also did not significantly differ between the start of the fall and spring experiments ($Z = 1.32$, $N = 51$, $p = 0.19$, $r = -0.19$; Table 2). However, testosterone ($Z = -2.38$, $N = 51$, $p = 0.02$, $r = 0.33$) and triglycerides ($F_{1,\ 28} = 11.61$, $p = 0.002$, Cohen's $d = -1.36$) were both significantly higher at the start of the spring experiment compared to levels measured at the beginning of the fall experiment (Table 2).

3.4. Relationship between corticosterone and activity/body condition in food-restricted birds

The change in morning activity during the fall was not related to changes in corticosterone levels ($\chi_1{}^2 = 0.28, p = 0.60, R^2 = 0.01$), the phase of restriction ($\chi_1{}^2 = 1.44$, $p = 0.23$, $R^2 = 0.02$), or the interaction between change in corticosterone and phase ($\chi_1{}^2 = 0.57, p = 0.50$, $R^2 = 0.03$). There was a significant change in corticosterone*phase effect on the change in morning activity during the spring (corticosterone*phase: $\chi_1{}^2 = 9.24, p = 0.002, R^2 = 0.43$; corticosterone: $\chi_1{}^2 = 0.03$, $p = 0.87$, $R^2 = 0.01$; phase: $\chi_1{}^2 = 1.32$, $p = 0.25$, $R^2 = 0.56$). Birds that had a larger increase in corticosterone during the No Seed phase increased their activity more compared to birds that has smaller increases in corticosterone (Fig. 4a), while there was a negative

Table 2
Activity levels, body condition, and blood parameters at the start of the fall and spring experiments. The range for body condition is presented as the PC value, with the corresponding mass (g) and total fat score (furcular + abdominal; 0–10) included in parentheses. See Table 1 for PC loading scores.

	Fall		Spring	
	Mean ± sem	Range	Mean ± sem	Range
Nocturnal activity (movements/10 min)	2.22 ± 0.81	0–13.04	6.03 ± 1.93	0–41.67
Morning activity (movements/10 min)	85.76 ± 7.34	17.02–163.60	45.78 ± 4.73	14.42–107.12
Body condition	−0.66 ± 0.21	−2.89 (12.62, 3) – 1.16 (18.42, 6)	0.64 ± 0.23	−1.32 (13.94, 5) – 3.80 (19.9, 10)
Muscle size	1.96 ± 0.10	1–3	2.04 ± 0.11	1–3
Muscle color	1.59 ± 0.10	1–2	1.75 ± 0.10	1–3
Corticosterone (ng/mL)	1.01 ± 0.13	0.32–2.55	1.02 ± 0.19	0.43–4.27
Testosterone (ng/mL)	0.41 ± 0.05	0.11–1.06	0.76 ± 0.12	0.26–2.78
Triglyceride (mmol/L)	1.54 ± 0.14	0.54–2.87	2.29 ± 0.14	1.64–2.97

relationship between change in corticosterone and change in activity during the Restriction phase. For both fall and spring, there were significant effects of change in corticosterone and phase on the change in body condition, but no change in corticosterone*phase effect (fall: corticosterone*phase: $\chi_1^2 = 2.52$, $p = 0.11$, $R^2 = 0.13$; corticosterone: $\chi_1^2 = 6.12$, $p = 0.01$, $R^2 = 0.03$; phase: $\chi_1^2 = 32.32$, $p < 0.0001$, $R^2 = 0.86$; spring: corticosterone*phase: $\chi_1^2 = 0.08$, $p = 0.78$, $R^2 = 0.01$; corticosterone: $\chi_1^2 = 6.77$, $p = 0.009$, $R^2 = 0.08$; phase: $\chi_1^2 = 26.47$, $p < 0.0001$, $R^2 = 0.58$). There was an overall negative correlation between change in corticosterone and change in body condition, while body condition was higher during the No Seed phase compared to the Restriction phase both fall (Fig. 4b) and spring (Fig. 4c).

4. Discussion

The results of these experiments indicate that a decline in food availability leads to increased circulating corticosterone in pine siskins, and increased activity under some conditions. Further, our results do not suggest that pine siskins make physiological preparations in anticipation of facultative migration. Although pine siskins are both diurnal and nocturnal migrants (Dawson, 2014; Robart et al., 2018; Watson et al., 2011; Watts et al., 2017), the increase in activity in food-restricted birds was confined to daytime hours, with very little change in nocturnal activity compared to Pre levels (Table 3). We did not collect detailed behavioral data during these experiments; but in a subsequent study we found that food-restricted pine siskins have a higher frequency of flight behavior in the morning relative to birds with full access to food (AR Robart and HE Watts, unpublished data). This suggests that the increase in morning activity in our experiments is indicative of a migratory response. Such an interpretation is consistent with observed increases in morning activity in association with a migratory state in other species with diurnal migration (Munro and Munro, 1998; Palmgren, 1949). However, diurnal migratory behavior and migratory behavior in response to environmental perturbations, such as fugitive migrations, are not well characterized. This makes interpretation of experimental results difficult, particularly since diurnal migration and/or migration in response to environmental perturbations may differ from predictable nocturnal migration. At present, the literature remains unresolved as to whether particular behaviors are indicative of migration or instead suggestive of an "escape" response (perch-hopping: Astheimer et al., 1992; Breuner et al., 1998; beak-up: Coverdill et al., 2011; Ramenofsky et al., 2008) – however we note that an escape response could reflect a fugitive migratory movement. Ultimately, in the case of pine siskins, diurnal movement in response to declining food availability would facilitate assessment of new habitat to determine resource availability when visibility is best, and allow birds to conserve energetic reserves at night. Experimentally elevated corticosterone levels have been shown to promote nighttime restfulness and reduce metabolic rate in pine siskins (Buttemer et al., 1991). Thus, an increase in daytime, but not nighttime activity, may be mediated by increased corticosterone levels. The absence of a change in nocturnal activity in the food-restricted birds during the spring experiment is notable because the week of the Restriction phase corresponded to the spring equinox, which is when pine siskins have previously been shown to initiate nocturnal migratory restlessness in response to increasing photoperiod (Robart et al., 2018). This suggests that a decline in food availability could affect spring migratory behavior in wild birds, perhaps shifting migratory activity from nighttime to daytime.

While it has been suggested that nomadic migrants may initiate a migratory response to conditions that are less severe than those needed to induce an ELHS (Watts et al., 2018), and thus, may have time to prepare physiologically for impending departure, we did not observe any evidence of physiological preparations for migration in this experiment. Experimental birds showed no increases in body mass, fat deposition, or flight muscle hypertrophy, as would be expected for migratory preparation (Berthold, 2001; Cornelius and Hahn, 2012; Jenni-Eiermann and Jenni, 1994; Landys et al., 2004b; Pohl and West, 1976; Ramenofsky et al., 2017; Robart et al., 2018; Smith and McWilliams, 2009). Although elevated corticosterone levels have been linked to increased foraging effort through a permissive effect on feeding (Landys et al., 2004a; Lõhmus et al., 2003; Pravosudov, 2003; but see Eikenaar, 2017; Gray et al., 1990), food-restricted birds in this experiment did not display changes in the body condition parameters that typically increase in response to migratory fueling, despite being provided with *ad libitum* pellets during the No Seed phase and having increased corticosterone. Thus, it may be that pine siskins respond to indications of an impending perturbation by attempting to flee the current area immediately before conditions decline further, rather than preparing for the increased energetic demands of migratory flight. This may be an adaptive response if the additional time needed for increased fueling ultimately jeopardized departure or if birds have a high probability of encountering food resources once migration is underway.

Irruptions of pine siskins have mainly been observed in the fall and early winter (Bock and Lepthien, 1976; Koenig and Knops, 2001; Strong et al., 2015), and it was therefore surprising that the response of the food-restricted birds was more robust during the spring experiment compared to the fall. During the spring experiment, the food-restricted birds increased their morning activity an average of 71% during the two phases of the restriction compared to their Pre morning activity levels. This contrasts with the fall experiment where morning activity in food-restricted birds initially increased by 5% in the first 3-days of the No Seed phase, then showed an overall 11% decline across the entire No Seed phase, and then a 5% increase in activity during the Restriction phase (with an initial increase of 12% in the first 3 days). Differences in the nature of migratory behavior expressed in the spring *versus* the fall have been described in several obligate migrants (Agatsuma and Ramenofsky, 2006; Fusani and Gwinner, 2004; Ramenofsky et al., 2008). In the case of this study, we suggest that these differences in response between fall and spring may be related to significant differences in both initial (Pre) body condition and morning activity levels between the two experiments. Morning activity during the fall was

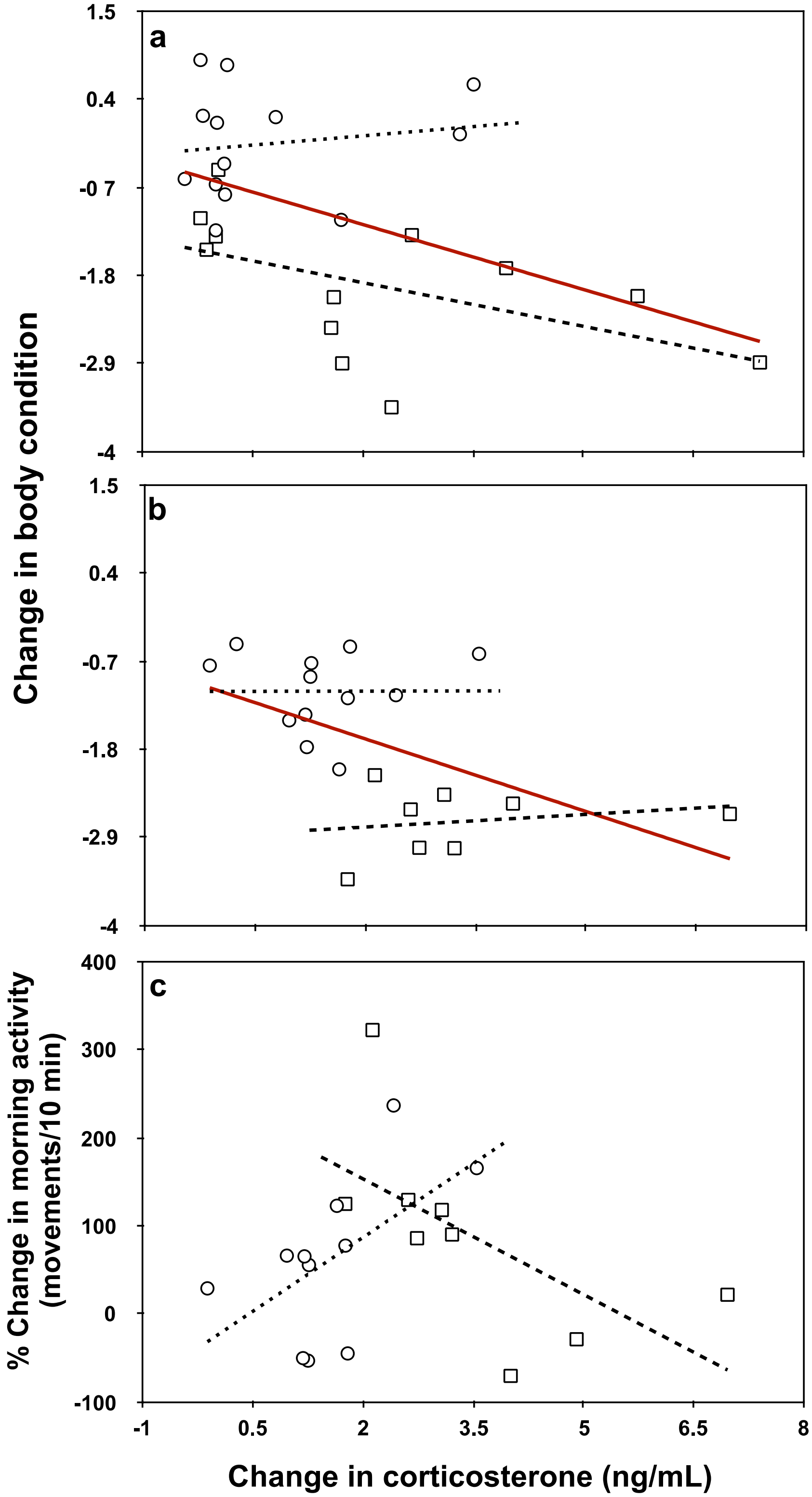

Fig. 4. Relationship between change in body condition and change in corticosterone level for food-restricted birds in fall (a) and spring (b) experiments. Larger increases in corticosterone levels were associated with larger declines in body condition in both experiments (see Table 1 for PC loading values). During the spring experiment, food-restricted birds with larger increases in corticosterone levels during the No Seed phase had larger increases in morning activity, while there was a negative correlation between change in corticosterone and change in activity during the Restriction phase (c). For all panels, the circles and dotted lines indicate response during the No Seed phase and the squares and dashed line represent data for the Restriction phase. The solid line in panels a and b indicate the overall effect of change in corticosterone on change in body condition.

almost twice that of the initial morning activity during the spring experiment, but the fall birds had significantly lower body condition, both in terms of mass and total fat. It is possible that fall birds were already in a migratory state at the start of the experiment, and therefore showed little further change in response to the food restriction. Pine siskins develop clear indicators, both behavioral and physiological, of a spring migratory state (Robart et al., 2018), but it is unknown whether changes in these same parameters would be expected for a fall migratory state, which is not well characterized in pine siskins or other facultative migrants. While the explanation that the fall birds were already in a migratory state is consistent with the behavioral data, if a fall migratory state is similar to a spring migratory state in terms of the physiological preparations, we would have expected the fall birds to be in better body condition with *ad libitum* food (Robart et al., 2018). Energy reserves can influence the decision of whether or not to migrate (Lupi et al., 2017; Sandberg and Moore, 1996), and it is therefore

Table 3
Activity levels (movements/10 min) for food-restricted birds during the fall and spring experiments. Activity is presented as mean ± sem for the week sampling periods.

		Pre	No seed	Restriction	Post
Fall	Morning	89.30 ± 10.34	78.32 ± 11.10	81.73 ± 10.04	75.68 ± 11.37
	Nocturnal	1.78 ± 0.88	1.25 ± 0.87	1.04 ± 0.62	0.87 ± 0.44
Spring	Morning	47.49 ± 7.13	66.88 ± 9.42	73. 84 ± 9.44	45.26 ± 13.19
	Nocturnal	5.50 ± 1.92	1.73 ± 0.74	3. 72 ± 1.41	11.22 ± 3.45

possible that the lower energetic reserves, combined with increased energetic demands of initial higher activity levels, limited the ability of food-restricted birds during the fall to initiate a migratory response to the declining food availability. The fact that the fall birds showed initial increases in activity at each phase of the food restriction that were not maintained across the entire week suggests that birds may only have been able to sustain short-term increases in activity. Another explanation for differences between the fall and spring experiments may be that birds are more sensitive in the spring to changes in resource abundance. The food-restricted birds during the spring experiment had a significant decline in body condition during the No Seed phase despite being provided with *ad libitum* pellets, while the food-restricted birds during the fall experiment exhibited no change in condition until the Restriction phase. The increased sensitivity to food resources in the spring may be associated with spring nomadism or with the transition to breeding. Previous work in pine siskins has found that access to a preferred food item advanced reproductive development in males and resulted in greater affiliation within pairs (Watts and Hahn, 2012). If birds initiated reproduction but then food availability declined such that there were insufficient resources either to feed the developing brood or the adults themselves it would likely result in a failed breeding attempt. While birds in our spring experiment may have been responding to the type of food available (presence or absence of the seed mixture), it is possible that they were responding to the absolute volume of food that was available and/or to the different energetic value that the pellets provided relative to the nutritional value of the seed mixture. Finally, we also cannot rule out the possibility that the different responses of food-restricted birds in the fall and spring experiments were driven by differences between the birds unrelated to season. Several birds were in the final stages of body molt during the fall experiment and this may have prevented them from initiating a migratory response (Watts et al., 2017). However, the birds in molt were balanced between the two treatments and none of the analyses were affected by the exclusion of these birds (data not shown). The fall experiment also contained birds from several sites and two age groups (HY and AHY), while the birds in the spring were all AHY and from a single site. Age can affect several aspects of migration, including orientation, route, and pre-migratory fattening (Hake et al., 2003; Heise and Moore, 2003; Thorup et al., 2003); an interesting avenue for future research would be to investigate whether the sensitivity to environmental perturbations in facultative migrants is age-specific.

Corticosterone increased at each stage of the restriction for the food-restricted birds in both the fall and the spring. For both experiments there was a moderate increase in corticosterone during the No Seed phase, with a larger increase during the Restriction phase. The relationship between change in corticosterone and change in body condition was similar for the fall and spring experiments. Birds that had larger increases in corticosterone had larger declines in body condition and mean body condition was lower during the Restriction phase compared to the No Seed period. The decline in mass and size of fat deposits and drop in plasma triglyceride levels suggest that food-restricted birds were utilizing these energy stores, while the decrease in flight muscle size also suggests that proteins were catabolized for fuel. These changes are consistent with the metabolic effects of corticosterone (Jenni-Eiermann and Jenni, 1996; Landys et al., 2006; Wingfield and Ramenofsky, 1997) and would help mitigate the increased allostatic load by releasing energetic reserves. Corticosterone has also been shown to increase activity in response to a decline in food availability (Astheimer et al., 1992). Here, we found that an increase in corticosterone was correlated with increased activity during the No Seed phase of the spring experiment only. The food-restricted birds at the start of the No Seed phase in the spring had significantly higher body condition compared to food-restricted birds during the fall, and therefore may have had sufficient energetic reserves to deal with the increased metabolic demands required of a facultative migration. Fusani and Gwinner (2004) also found that the migratory response of blackcaps (*Sylvia atricapilla*) to food restriction differed between the spring and fall, and these difference may be due at least in part to differences in body condition. Overall, our results are consistent with a role for corticosterone in mediating a facultative migratory response, but dependent on an individual's energetic state. However, corticosterone manipulation studies are still needed to test these relationships.

Facultative migration, particularly the fugitive form, is often associated with an ELHS, when a severe allostatic overload results in a sharp increase in corticosterone levels and activation of physiological processes that promote survival (Landys et al., 2006; McEwen and Wingfield, 2003; Watts et al., 2018; Wingfield et al., 1998; Wingfield and Ramenofsky, 1997). However, the maximum corticosterone levels measured in this study (8.49 and 7.38 ng/mL for the fall and spring experiments, respectively) are below those that have been reported in either captive (Astheimer et al., 1992) or free-living (Knutie and Pereyra, 2012) pine siskins under stress-induced conditions (> 20 ng/mL). On the other hand, these levels are similar to corticosterone levels measured in red crossbills in response to food restriction (Cornelius et al., 2010) and in several obligate migrant species during the spring migratory period (Eikenaar et al., 2017; Holberton et al., 2008; Schwabl et al., 1991). This contrasts with studies on Gambel's white-crowned sparrows (*Zonotrichia leucophyrs gambelii*) that were fasted for as little as 4 h and had corticosterone levels over 20 ng/mL (Krause et al., 2017; Landys et al., 2004a). We recognize that birds likely perceive the complete removal of food during a fast differently than our experimental design, which restricted their daily food intake to 75% of *ad libitum*. However, food-restricted birds in our study typically had no food remaining in their cups each morning during the Restriction phase and therefore also likely experienced a short-term fast each day before they received their daily allotment of food. The increase in corticosterone in fasted white-crowned sparrows was accompanied by an increase in activity (Krause et al., 2017; Landys et al., 2004a), suggesting birds initiated a facultative migratory response. However, unlike pine siskins and red crossbills that regularly make facultative migrations, Gambel's white-crowned sparrows are obligate migrants and their response to a short-term fast may be indicative of fugitive migration as part of an ELHS. Taken together, these interspecific differences suggest that facultative migrations initiated by nomadic, irruptive migrants in response to declining food availability may be distinct from fugitive migrations initiated by obligate migrants in response to similar conditions.

In both the fall and spring experiments the control birds increased their activity during both phases of the restriction, despite not experiencing any changes in food availability themselves. In the fall experiment the control birds increased their morning activity to a greater degree than the food-restricted birds, although there was not a significant difference between the treatments. Studies of another facultative migrant, red crossbills, have also found that birds with *ad libitum* food increased their activity when a neighbor was food restricted (Cornelius et al., 2010). In red crossbills, increased activity in *ad libitum* fed birds was also associated with an increase in circulating corticosterone, but control pine siskins showed no similar increase in corticosterone during either the fall or spring experiment. Interestingly, exposure to food-restricted neighbors also impacted expression of glucocorticoid and mineralocorticoid receptor mRNA in the brain of red crossbills (Cornelius et al., 2018). Thus, information from conspecifics could influence migratory behavior by influencing sensitivity to glucocorticoids. Given that we prevented birds in our experiments from seeing either other individuals or the food available to other birds, the most likely mechanism whereby control birds could have assessed the food availability of the restricted birds was through vocal communication. During the fall experiment we measured the rate of calling in control and food-restricted birds and found that food-restricted birds vocalized more frequently. Public information in the form of vocalizations is known to increase foraging efficiency (Smith et al., 1999), but our results also suggest that this socially acquired information may influence facultative migratory responses.

In summary, we found that changes in food availability stimulate a behavioral response in pine siskins that is consistent with facultative migration and that pine siskins display a stronger response to changes in food resources during the spring compared to the fall. However, we did not observe changes during the No Seed phase that were consistent with anticipatory physiological adjustments for migration. The results from both the fall and spring experiments indicate that changes in circulating corticosterone levels may facilitate the metabolic demands of an increased allostatic load, but we only found evidence for a role for corticosterone in mediating behavioral changes associated with facultative migration during the spring experiment. Thus, our results indicate that declining food availability can serve as a proximate cue for facultative migration in pine siskins and that corticosterone may play a role in mediating this behavioral response. However, we found no indication that pine siskins show physiological preparations for facultative migration in response to declining food availability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2019.02.007.

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