

RESEARCH ARTICLE

Physiology and behavior under food limitation support an escape, not preparative, response in the nomadic pine siskin (*Spinus pinus*)

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ABSTRACT

Migration allows animals to use resources that are variable in time and/or space, with different migratory strategies depending on the predictability of resource variation. When food varies seasonally, obligate migrants anticipate and prepare for migration. In contrast, facultative migrants, whose movements are unpredictable in timing and destination, may prepare for either migration or escape when resources are depleted. We propose and test two alternative hypotheses regarding the behavioral and physiological responses of facultative migrants to declining food availability. (1) The prepare hypothesis predicts that facultative migrants prepare for departure by increasing fuel stores in response to declining food availability, and elevations of baseline corticosterone (CORT) facilitate increased activity. (2) The escape hypothesis predicts that facultative migrants do not prepare for departure, body condition declines as food availability declines, and stress-induced levels of CORT induce escape behavior when both energetic condition and food resources are low. We conducted a 16-day experiment, measuring body composition (using quantitative magnetic resonance), activity (using force perches) and baseline CORT in pine siskins (*Spinus pinus*) given *ad libitum* food or a slow decline, fast decline or randomly changing amount of food. Our results support the escape hypothesis: body condition declined as food declined, decreases in body and fat mass were associated with increases in baseline CORT, and activity increased only when food availability was low. This work suggests that facultative migration in autumn allows birds to escape low-resource areas and that the underlying physiological mechanisms differ from those driving both seasonal, obligate migrations and spring nomadic movements.

KEY WORDS: Body composition, Corticosterone, Irruption, Locomotor activity, Migration, Pine siskin

INTRODUCTION

Migration enables animals to use resources that are heterogeneous in time and/or space (Lack, 1968; Alerstam et al., 2003; Dingle and Drake, 2007; Somveille et al., 2019). Different migratory strategies largely depend on whether resource variation is predictable or unpredictable (Mueller and Fagan, 2008; Newton, 2012). For instance, the seasonal migrations of birds are often synchronized with the seasonal phenology of temperature or rainfall patterns that correlate with food availability (Alerstam and Enckell, 1979;

Newton and Dale, 1996a,b), and which can be predicted by photoperiod and endogenous rhythms (Gwinner, 1996; Dingle and Drake, 2007; Moller et al., 2008; MacPherson et al., 2018). These movements – called obligate migration – are highly predictable in terms of timing, distance and destination within and among individuals and years (Newton, 2012).

When migratory departure is predictable, animals can anticipate and therefore prepare for the energetic challenges of a long-distance journey, depositing fuel stores while local food resources are still present. Before the onset of obligate migrations, birds eat more (King and Farmer, 1965), increase fat and muscle mass (King and Farmer, 1965; Marsh, 1984), and exhibit nocturnal restlessness in captivity, which is hopping or wing-whirring behavior indicative of readiness for flight (Agatsuma and Ramenofsky, 2006; Eikenaar et al., 2014). Changes in photoperiod, which serve as a reliable indicator of seasonal changes in food availability, proximately cue these migratory preparations (Jenni and Schaub, 2003; Cornelius et al., 2013), though the timing of departure is often refined by supplementary and synchronizing cues (Jacobs and Wingfield, 2000; Jenni and Schaub, 2003; Cornelius et al., 2013).

In contrast, when resources vary unpredictably in space and/or time, the animals that rely on these resources are often facultative migrants, with characteristically unpredictable timing and destination of movements (Newton, 2012). Facultative movements include nomadic and fugitive migrations: nomadic migrations are associated with potentially abundant but ephemeral resources, while fugitive movements are characterized by an escape response to a labile perturbation (Watts et al., 2018). Facultative migrants include nomadic raptors that prey on rodents (Lack, 1954; Galushin, 1974), desert birds that track unpredictable rainfall events and subsequent patches of food (Ward, 1971; Davies, 1984; Wiens, 1991), and birds that feed on conifer seeds (Newton, 2006). Conifers produce cone crops sporadically in time and space, though often synchronously across broad geographic ranges (Koenig and Knops, 1998). Birds that rely on conifer seeds are often nomadic, irruptive migrants and may travel hundreds of kilometers in search of an abundant food source (Koenig and Knops, 1998; Newton, 2006).

Although the physiology of obligate migration has been studied for decades, the physiology of facultative migrations remains more obscure. Low food availability, exacerbated by competition, is thought to be the proximate cue initiating many facultative migrations (Lack, 1954; Bock and Lepthien, 1976), because in these species, photoperiod is not always an informative indicator of spatial and temporal patterns of food availability. Observational studies reveal that years with poor seed crops correspond with irruptions of boreal seed-eating birds (Bock and Lepthien, 1976; Koenig and Knops, 2001). Interestingly, many nomadic migrants are sensitive to photoperiod, and they accumulate fat and become more active in response to spring (but not autumn) photoperiod (Pohl and West, 1976; Cornelius and Hahn, 2012; Robart et al., 2018). However, low food availability may still be necessary to

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initiate departure in these species. Captive red crossbills (*Loxia curvirostra*) and pine siskins (*Spinus pinus*) experiencing food restriction increase activity in winter and spring but not autumn (Cornelius et al., 2010; Robart et al., 2019).

Like obligate migration, facultative migrations likely involve the integration of both external cues (e.g. food availability, environmental conditions, social information) and internal cues (e.g. energetic stores) to time migratory behaviors. Thus, in developing hypotheses about the regulation of facultative migratory behavior and physiology, we include the endocrine system, because hormones coordinate rapid, whole-organism responses to both external and internal challenges (Martin et al., 2011). Corticosterone (CORT), the main avian glucocorticoid, is a prime candidate because it can mediate locomotor behavior at two distinct levels that can be differentiated experimentally.

First, elevated levels within the baseline range of CORT support the increased energetic demands of predictable challenges and life history stage transitions (Wada, 2008), such as hatching and parturition (Challis, 2000; McLean and Smith, 2001), fledging and dispersal (Heath, 1997; Belthoff and Dufty, 1998; Sprague and Breuner, 2010), and, importantly, obligate migratory departure (Löhms et al., 2003; Eikenaar et al., 2017, 2020). In obligate migrants, CORT stimulates fat deposition and mobilizes protein for fuel (Gray et al., 1990). Baseline CORT increases with body mass (Piersma et al., 2000) and migratory restlessness (Löhms et al., 2003), and predicts departure from a stopover site (Eikenaar et al., 2017). In summary, elevations in baseline CORT in obligate migrants with sufficient fuel stores can promote migratory departure.

Second, CORT levels can significantly increase in response to unpredictable perturbations, such as harsh storms (Wingfield et al., 1983, 1998; Landys et al., 2006). These stress-related levels initiate an emergency life history stage, whereby the animal diverts energy away from immediately unnecessary processes, such as reproduction, and toward short-term survival (Wingfield et al., 1998). In these situations, CORT promotes escape behavior and fugitive migration in response to a stressor (Breuner et al., 1998; Breuner and Hahn, 2003).

Thus, CORT can mediate increases in activity either in anticipation of predictable life history stage transitions or in reaction to unpredictable situations. We propose two competing hypotheses to explain the regulation of facultative migration by examining the relationships among CORT, body condition and locomotor activity in response to declining food availability: the prepare hypothesis and the escape hypothesis.

Under the prepare hypothesis, facultative migrants anticipate and prepare for departure just as obligate migrants do. Individuals could prepare if they are sensitive to changes in food availability such that they deposit fuel stores before local food availability is depleted. In this case, (1) we expect body mass to increase as food availability declines, possibly mediated by an increase in food intake and/or a reduction in energetic expenditure and activity. (2) We expect baseline CORT to be elevated in anticipation of departure, playing a similar role as in obligate migrants ready for flight or nestlings ready to fledge. Therefore, (3) we predict body condition and CORT to be positively correlated as food availability decreases and migratory activity increases. Under this scenario, facultative migration is similar to obligate migration in terms of physiological preparation, but the birds respond to a different proximate cue: rather than preparing in response to changing photoperiod like an obligate migrant, facultative migrants initiate migratory preparations in response to changing food availability.

Alternatively, under the escape hypothesis, facultative migrants may express a stress response and escape behavior in low-resource

areas. In this case, we would not expect the birds to perceive and respond to changes in food availability, but rather to the absence of food when resources are very low. Here, (1) we predict that body condition will decline as food availability does. A bird in poor energetic condition in an area with low food availability will initiate an emergency life history stage, so that (2) stress-elevated CORT levels (i.e. circulating levels that approximate those achieved in response to a standardized stressor) promote increased locomotor activity indicative of escape behavior. Therefore, (3) we predict body condition and CORT to be inversely related as food declines and activity increases.

We tested the physiological and behavioral responses to declining food availability in a facultative migrant, the pine siskin. To distinguish the hypotheses, we experimentally manipulated food availability for captive pine siskins and measured hopping activity, body composition and CORT responses. Two groups received food that declined at two different steady rates over the course of the 16-day experiment, allowing us to detect any rate dependence to the birds' responses. An additional random group received an unpredictable amount of food each day so that we could differentiate the effects of declining versus fluctuating food availability. A control group received *ad libitum* food throughout the experiment.

Captive red crossbills and pine siskins exposed to sudden reductions in food quantity or quality have shown decreases in body condition, increases in CORT and, at certain times of year, increases in activity (Cornelius et al., 2010; Robart et al., 2019). Here, we slowly reduced food availability over 16 days to more explicitly test the sensitivity of birds' responses to changes – rather than simply reductions – in food availability. Furthermore, the continuous activity data we collected allow for a more comprehensive and nuanced analysis of the effect of changing food availability on behavior. Finally, the novel addition of a random group in this study enables us to (1) differentiate responses to predictable versus unpredictable changes in food availability and (2) assess whether physiological responses to food restriction are sensitive to changes in food availability over multiple days, or just the food received on a given day.

MATERIALS AND METHODS

Bird capture and housing

Twenty-eight pine siskins (*Spinus pinus*) were captured using mist nets and playback in Missoula, MT, USA, between 5 and 19 October 2018 and banded with unique color band combinations for identification in captivity. They were collected under permits from US Fish and Wildlife Service (permit 23228) and Montana Fish, Wildlife, and Parks (permit 2018-089-W). Birds were housed at the Field Research Station at Fort Missoula, with two individuals per cage, separated by an opaque plexiglass cage divider, allowing for auditory, but not visual, contact between pairs. Cage space per bird was 30.5×25.5×33 cm. Cages were placed inside sound-attenuating chambers (MED-OFA-022, Med Associates Inc., Fairfax, VT, USA) so that a quiet researcher could be in the room without disturbing the birds, though birds could still hear each other's calls. Birds were held under an approximately 10 h:14 h light:dark photoperiod, similar to that of 1 November 2018 in Missoula, MT, with no dim light overnight. Ambient temperature in the housing rooms was ~22°C. Birds were provided with *ad libitum* water and Roudybush Small Bird Daily Maintenance Diet (Roudybush, Woodland, CA, USA) until the beginning of the food manipulation, as described below. Birds were given at least 2 weeks to acclimate to captivity and 1 week to acclimate to the isolation chambers before the start of the experiment. All housing

and experimental protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Protocol 010-18CBOBE-032018).

Food manipulation

After acclimation to captivity, we measured the food intake of each bird for 3 days before the start of the experiment; we weighed the amount of food provided to each bird at lights on (~300% of their daily intake), and subtracted the amount of food remaining in their food dish or on the floor of their cage the next morning. The average of these 3 days of *ad libitum* feeding represents each bird's daily average food intake (3.85 ± 0.04 g; mean \pm s.e.m.).

We randomly assigned birds to one of four treatment groups (Fig. 1): control, slow decline, fast decline and random. Control birds received 300% of their daily average food intake; slow decline birds received 2% less food each day (98% of their daily average food intake on day 0–68% on day 15); fast decline birds received 4% less food each day (96–36%); and random birds received a random amount of food between 72 and 135% each day. On experimental day 15, all birds received *ad libitum* food when returned to their cages after blood sampling and body composition analyses.

On day 3 among the slow decline group, the amount of food provided was mistakenly calculated as 92% of one pre-experimental day's food intake, rather than 92% of the average daily pre-experimental food intake, such that the group's average provided food on day 3 was 89.9%, but ranged from 76.1 to 100.4%.

Because finches are known to communicate information about food quantity to each other (Cornelius et al., 2010, 2018), birds in different food treatments were housed in different rooms. Owing to space limitations, the experiment was conducted in two parts: control and slow decline birds 1–20 November 2018; fast decline and random birds 29 November–18 December 2018. Photoperiod remained the same throughout the study. Four first-round control birds were used as two fast decline and two random individuals in the second round of the experiment.

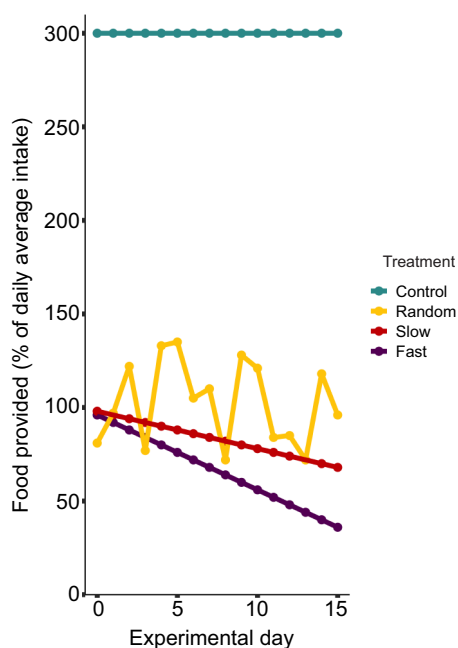


Fig. 1. Experimental food manipulation. Control birds received 300% of their daily average food intake; fast decline birds received 4% less food each day; slow decline birds received 2% less food each day; and random birds received between 72% and 135% of their daily average intake.

Physiological measurements

Five days before and every 4 days after the start of the food manipulation, we collected three physiological measurements. Starting approximately 1.5 h after lights on, we took baseline blood samples from each individual for hormone analyses. Blood samples were collected by puncturing the brachial vein with a 26.5 gauge needle within 3 min of opening the door of the sound-attenuation chambers. Up to three-quarters of a heparinized capillary tube (about 55 μ l) was collected each time to limit blood loss over the course of the experiment. Additional bleeding was staunched with cotton, or when necessary, cotton and styptic powder. Next, we weighed each bird to the nearest 0.01 g and visually scored fat stores on a scale of 0 to 5 (Moore and Kerlinger, 1987) and pectoralis muscle size on a scale of 0 to 3 (Bairlein, 1995). Finally, we scanned them in a quantitative magnetic resonance (QMR) machine (EchoMRI, Houston, TX, USA). The QMR reports the grams of fat mass, lean mass and body water of an individual after a rapid (~90 s), non-invasive scan (Guglielmo et al., 2011). Physiological data collection was completed within 4 h of lights on.

Activity monitoring

We used custom-made force perches instrumented with 120 Ω strain gauges (EA-06-125BT-120, Micrometrics-Measurements, Raleigh, NC, USA) arranged in a full-bridge configuration to measure any vertical force made upon the perch (Tobalske et al., 2004). Thus hops onto and off of the perch were recorded as peaks in the data, and two distinct baselines represented either a bird sitting still on the perch or an empty perch. The perches consisted of a 36 cm wood dowel, 1 cm in diameter, with two brass strips 2.5 cm long, 6 mm wide and 0.08 mm thick (5024682, K&S 0.032 in \times 1/4 in, ACE Hardware) inserted near each end of a 14 in long wooden dowel where the strain gauges were applied. We attached dowel connectors from the brass strips to the wires composing the cages of the birds. The strain gauge signals (V) were conditioned and amplified using a Vishay 2100 signal conditioner and 2120B amplifier. Analog output from the amplifier was sampled at 100 Hz using Axoscope (v8.1) and an Axon Instruments Digidata 1322A analog/digital converter, and stored for analysis on a computer. Resonant frequency of the unloaded perches was ~100 Hz, significantly higher than the time intervals of interest for hops. Thirty minutes of pre-experimental visual observation confirmed that almost all of the hops birds made were either onto or off of the perch; thus the perch data reflect total hopping activity.

Activity analysis

Perch output was analyzed in RStudio (Version 1.2.1335) by calculating the derivative squared of the reported voltages with respect to time, such that the steep increases/decreases in voltage of hops on/off the perch were represented by highly positive squared derivatives. We then calculated the number of local maxima above a threshold value of 20 (determined by visualization of a subset of the data), with the limitation that local maxima must be more than 0.25 s apart to avoid counting a single hop as multiple ones.

Daytime data were divided into blocks of time representing each hour after lights came on. Nighttime data blocks represent each hour after lights went off. Because data recorded while a researcher was in the bird room were removed, each hour chunk does not always represent 60 min of continuous data collection. Thus we converted the number of hops per time block to the number of hops per 10 min for each block. Activity on day 15 (the last day of the study) was removed from analyses because all birds received *ad libitum* food after physiological data were collected that morning. Changes in

activity (Δ activity) represent the hops per 10 min on a given experimental day at a given hour after lights on minus the average hops per 10 min at that same time over the course of four pre-experimental days.

We plotted average Δ activity by hours after lights on for the control, slow decline and fast decline treatment groups, with a different line per experimental day. The random group was excluded from this analysis because their activity patterns depended on food availability on a given day, and examining changes in activity over time does not make sense for this group. We fit non-linear sine curves (nls in R) to these data for each individual bird (i.e. a curve for every experimental day, for every individual), assuming that the entire 10 h period represented one cycle (i.e. 2π radians). We extracted from these curves the amplitude (which represents the height of the curve) and phase (which represents the midpoint between the trough and peak of the cycle). We averaged the amplitude and phase for each experimental day by treatment. We fitted a linear regression to assess the relationship between the amplitude and phase of these sine curves over the course of the experiment for each treatment.

In *post hoc* analysis, we divided the day into ‘morning’ and ‘afternoon’ to separately investigate activity patterns during these times. ‘Morning’ represents the first 5 h after lights on, and ‘afternoon’ is the latter 5 h.

CORT analysis

Plasma CORT levels were detected using an Enzyme Linked Immunoassay (ELISA) kit (cat. no. 25-0412, Enzo Life Sciences). First, CORT was extracted from plasma using a double ether extraction after addition of 2000 cpm of 3H-CORT to estimate recovery. Ether was evaporated off in a 50°C water bath. Sample was reconstituted in 135–425 μ l assay buffer for a final dilution of 1:20 or 1:25. Recoveries averaged $75.8 \pm 0.01\%$; samples were corrected to 100% for analysis.

Assays were run as described in Patterson et al. (2011). In brief, 100 μ l of extracted, diluted sample was assayed in triplicate if possible, and in duplicate or singly when plasma volume was limiting. A standard curve ($20,000$ to 15.63 pg ml^{-1}) was included in triplicate (100 μ l per well) on each plate. An external CORT standard was also run in triplicate on each plate to assess inter-plate variation. Color reaction was read at 405 nm corrected at 595 nm. Intra- and inter-plate coefficients of variation (CVs) were 10.2 and 20.5%, respectively. Average assay detectability was 0.514 ng ml^{-1} ; samples below the assay’s detectability limit ($n=6$) were assigned the mean detection limit of their respective assay.

Statistical analysis

We calculated changes in various physiological metrics (i.e. Δ CORT, Δ body mass, Δ fat mass and Δ lean mass) as the value on a given experimental day subtracted from the value on the pre-experimental day –5. We used GLMMs (R package lmerTest in conjunction with lme4, Type III ANOVA with Satterthwaite’s method) to analyse: the relationship between visual muscle score and experimental day; the relationship between Δ lean mass and experimental day; the relationships between Δ CORT and Δ body mass, Δ fat mass, and Δ lean mass; and the change in morning and afternoon activity in relation to percentage food reduction. In these models, bird ID was included as a random effect unless otherwise noted. Overall models included treatment as an interaction term when significant, but when calculating treatment-specific *P*- and β -values, treatment groups were analyzed separately. In assessing changes in lean mass on day 15, 95% confidence intervals of the average Δ lean mass that do not include 0 are considered to represent

significant ($P < 0.05$) changes in mass. When we compared the slopes of the linear relationships between percentage food reduction and changes in morning and afternoon activity across treatment groups, non-overlapping 95% confidence intervals for the slope parameters were considered to be significantly different. Figures were created using the ggplot2 and cowplot packages.

Sample sizes

Eight birds were assigned to each treatment group. One random bird was removed from the experiment owing to a pre-existing illness. Birds in very poor body condition (i.e. depleted fat stores, concave pectoralis muscles, and body mass $\sim 75\%$ of their initial mass) were removed from the experiment: three fast decline birds were removed on experimental day 12 and two on day 13.

The refrigerator where assay reagents were stored malfunctioned during the time that the second assay plate was run, and the samples from this plate had higher CVs and had markedly higher CORT levels than the other five plates. These samples included control birds on experimental days 3, 7 and 11 ($n=16$), and Slow Decline birds on day 7 and 11 ($n=14$). We removed these samples from analyses involving CORT or Δ CORT values.

One bird from the fast decline group was removed from analyses involving Δ activity because its perch was broken and repaired between the pre-experimental and experimental days, and the Δ activity was an outlier likely because of a change in perch sensitivity. One bird from the control group was not included in activity analyses because its perch was non-functional during the pre-experimental days, so no Δ activity value was possible.

RESULTS

Body composition and food availability

Treatment groups differed in their change in body and fat mass over the course of the experiment. As food availability declined, birds in food reduction treatments lost body mass and fat mass (Fig. 2A,B, Table 1); fast decline birds lost body and fat mass at a faster rate (Table 1). Control and random birds showed no change in body

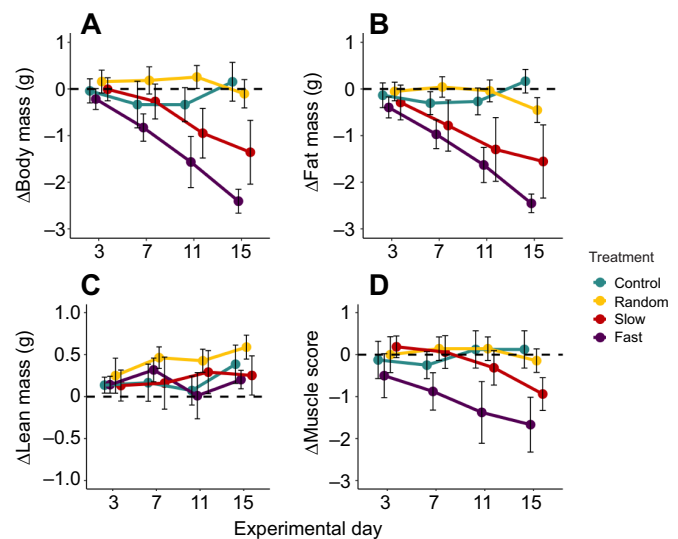


Fig. 2. Changes in body composition compared with pre-experimental values for each group throughout the experiment. Slow decline ($n=8$) and fast decline ($n=8$) birds lost body mass (A) and fat mass (B), and had decreased muscle scores (D) as food availability declined. Among control ($n=8$) and random birds ($n=7$), there was a significant increase in lean mass (C) over time. Means and 95% CI are shown for each group. See Table 1 for statistical analyses of these data.

Table 1. Statistics for Δ body mass, Δ fat mass, Δ lean mass and Δ muscle score over the course of the experiment (days 3–15) for each treatment group

Parameter	Treatment group	<i>F</i>	β [95% CI]	<i>P</i>
Δ Body mass (g)	Control	$F_{1,23}=0.54$	0.01 [−0.03, 0.05]	0.47
	Slow	$F_{1,23}=92.51$	−0.12 [−0.14, −0.09]	<0.0001
	Fast	$F_{1,18.34}=112.50$	−0.19 [−0.22, −0.15]	<0.0001
	Random	$F_{1,20}=2.97$	−0.02 [−0.04, 0.00]	0.1
	Treatment \times day	$F_{3,84.50}=32.34$		<0.0001
Δ Fat mass (g)	Control	$F_{1,23}=7.64$	0.02 [0.01, 0.04]	0.01
	Slow	$F_{1,23}=77.81$	−0.11 [−0.13, −0.08]	<0.0001
	Fast	$F_{1,18.2}=196.39$	−0.18 [−0.20, −0.15]	<0.0001
	Random	$F_{1,20}=15.96$	−0.03 [−0.05, −0.02]	<0.001
	Treatment \times day	$F_{3,84.23}=63.68$		<0.0001
Δ Lean mass (g)	Control	$F_{1,23}=4.45$	0.02 [0.00, 0.03]	0.05
	Slow	$F_{1,23}=1.81$	0.01 [−0.01, 0.03]	0.19
	Fast	$F_{1,25}=0.32$	0.01 [−0.04, 0.02]	0.58
	Random	$F_{1,20}=12.37$	0.02 [0.01, 0.04]	0.002
	Treatment \times day	$F_{3,85.41}=2.12$		0.1
Δ Muscle score	Control	$F_{1,23}=4.24$	0.03 [0.00, 0.06]	0.05
	Slow	$F_{1,23}=33.39$	−0.09 [−0.13, −0.06]	<0.0001
	Fast	$F_{1,18.72}=18.12$	−0.11 [−0.16, −0.06]	<0.001
	Random	$F_{1,20}=0.40$	−0.01 [−0.04, 0.02]	0.53
	Treatment \times day	$F_{3,84.73}=13.92$		<0.0001

F- and *P*-values are shown for the treatment \times day interaction term in the overall model. See Fig. 2 for visualization of these data.

mass over time (Fig. 2A, Table 1). Control birds showed a slight, significant increase in fat mass and random birds showed a decrease in fat mass over time (Fig. 2B, Table 1). Absolute values of body, fat and lean mass for each treatment group over the course of the experiment are shown in Fig. S1B–D.

Visual scores of pectoralis muscle size declined for fast decline and slow decline birds, but not control or random birds as the experiment progressed (Fig. 2D, Table 1). In spite of this, all treatments showed a significant, slight increase in average lean mass – as measured by the QMR – when comparing day 15 with the pre-experimental day −5 (day 15 mean Δ lean mass [95% CI]; control: 0.39 g [0.16, 0.61]; slow decline: 0.25 g [0.02, 0.49]; fast decline: 0.20 g [0.09, 0.31]; random: 0.59 g [0.45, 0.73]; Fig. 2C). Over the course of the experiment, there was an overall significant increase in whole body lean mass, driven by the control and random groups (overall: $F_{1,88.62}=6.97$, $\beta=0.01$ [0.00, 0.02], $P=0.01$; Fig. 2C; see Table 1 for statistics per treatment; interaction term not included in model).

CORT and food availability

Among the experimental days during which birds experienced reduced food availability, elevations in CORT were only observed in birds experiencing sustained food reductions (Fig. 3A; percentage food reduction \times treatment: $F_{2,36.21}=3.53$, $P=0.04$). CORT levels increased with percentage food reduction in the fast decline group ($F_{1,17.3}=9.47$, $\beta=0.05$ [0.02, 0.08], $P=0.007$) and the slow decline group ($F_{1,3}=0.30$, $\beta=0.02$ [0.01, 0.02], $P=0.02$) but not the random group ($F_{1,18}=1.95$, $\beta=-0.04$ [−0.10, 0.02], $P=0.18$). CORT levels were not related to food availability in the control group ($F_{1,7.81}=0.80$, $\beta=1.55$, $P=0.40$). Absolute levels of CORT for each treatment group over the course of the experiment are shown in Fig. S1A.

Body composition and CORT

The relationship between increases in CORT and changes in body and fat mass differed among treatment groups (Δ mass \times treatment: $F_{3,62.45}=4.12$, $P=0.01$; Δ fat mass \times treatment: $F_{3,60.14}=3.06$, $P=0.03$). Increases in CORT were best predicted by declines in

body and fat mass within the fast decline group (Fig. 3B–D; body mass: $F_{1,18.2}=16.04$, $\beta=-1.11$ [−1.68, −0.57], $P<0.001$; fat mass: $F_{1,18}=18.29$, $\beta=-1.27$ [−1.87, −0.68], $P<0.001$; lean mass: $F_{1,18.7}=1.14$, $\beta=-1.20$ [−3.62, 0.99], $P=0.30$) and slow decline group (body mass: $F_{1,3}=17.36$, $\beta=-0.29$ [−0.43, −0.12], $P=0.02$; fat mass: $F_{1,3}=10.82$, $\beta=-0.25$ [−0.41, −0.05], $P=0.05$; lean mass: $F_{1,5.7}=0.32$, $\beta=-0.48$ [−3.06, 1.32], $P=0.59$). The sample size of slow decline individuals with repeated CORT measures is small ($n=4$), so we do not show the data here. There were no significant relationships between changes in body composition and changes in CORT in the random group (body mass: $F_{1,14.3}=1.15$, $\beta=-0.59$ [−1.67, 0.49], $P=0.30$; fat mass: $F_{1,14.7}=0.31$, $\beta=-0.33$ [−1.54, 0.88], $P=0.59$; lean mass: $F_{1,21.6}=0.48$, $\beta=-0.59$ [−2.25, 1.05], $P=0.49$) or control group (body mass: $F_{1,7.6}=2.09$, $\beta=1.09$ [−0.67, 2.55], $P=0.19$; fat mass: $F_{1,7.9}=0.06$, $\beta=0.29$ [−2.51, 2.82], $P=0.80$; lean mass: $F_{1,4.3}=6.24$, $\beta=3.16$ [−0.34, 5.61], $P=0.06$). The relationships between changes in CORT and changes in body, fat and lean mass for individuals in all treatment groups are shown in Fig. S2.

Activity over time

Changes in daytime activity over the course of the experiment differed among treatment groups (Fig. 4; day \times treatment: $F_{3,380.08}=8.00$, $P<0.0001$). The slow decline and fast decline groups slightly, though significantly, decreased morning activity as the experiment progressed (slow: $F_{1,97}=24.37$, $\beta=-5.85$ [−8.18, −3.51], $P<0.0001$; fast: $F_{1,103.1}=4.37$, $\beta=-1.97$ [−3.83, −0.11], $P=0.04$). There was no relationship between change in morning activity and experimental day in the random ($F_{1,97}=0.0$, $\beta=-0.00$ [−1.15, 1.14], $P=0.99$) or control groups ($F_{1,83}=3.18$, $\beta=-1.36$ [−2.86, 0.14], $P=0.08$).

Changes in afternoon activity also differed among treatment groups (Fig. 4; day \times treatment: $F_{3,375.61}=23.96$, $P<0.0001$). Slow decline and fast decline groups significantly increased afternoon activity as the experiment progressed (slow: $F_{1,97}=23.46$, $\beta=7.38$ [4.38, 10.38], $P<0.0001$; fast: $F_{1,99.2}=89.24$, $\beta=17.34$ [13.71, 20.94], $P<0.0001$; random: $F_{1,97}=3.55$, $\beta=2.73$ [−0.12, 5.59], $P=0.06$; control: $F_{1,83}=0.07$, $\beta=-0.31$ [−2.58, 1.95], $P=0.79$). The mean

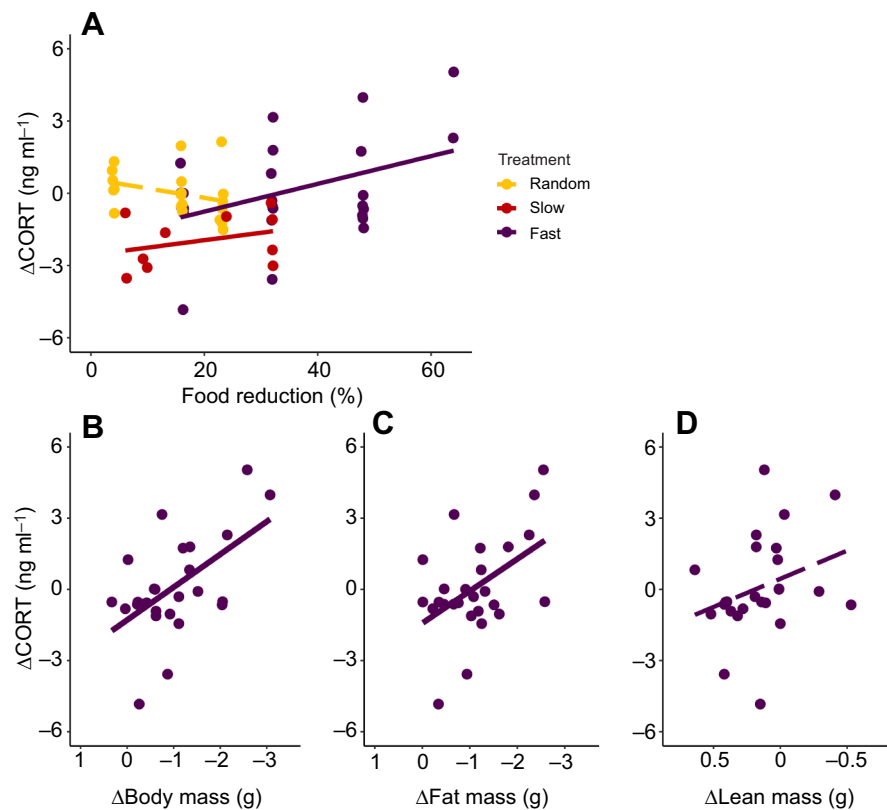


Fig. 3. Change in corticosterone (CORT) levels in relation to reduced food availability and body composition. (A) CORT levels increased as birds experienced greater food reductions, as seen within the fast decline ($n=8$, $P=0.007$) and slow decline groups ($n=6$, $P=0.02$). There was no significant relationship between Δ CORT and percentage food reduction within the random group ($n=7$, $P=0.18$). Declines in (B) body mass ($n=8$, $P<0.001$) and (C) fat mass ($n=8$, $P<0.001$) predict increases in CORT among fast decline birds; changes in (D) lean mass ($n=8$, $P=0.30$) do not predict CORT elevations in these birds. In B–D, note the inverted x-axes, with greater decreases in mass to the right.

amplitude of the sine curves fitted to the change in activity significantly increased over the experimental days in the fast decline and slow decline groups, and at a faster rate within the fast decline group (slow: $\beta=9.56$ [7.98, 11.14], $P<0.0001$; fast: $\beta=13.88$ [9.06, 18.69], $P<0.0001$; control: $\beta=1.74$ [−1.52, 5.00], $P=0.27$). The mean phase of the sine curves increased (shifted earlier in the day) over time in the fast and slow decline groups, and at a faster rate within the fast decline group (slow: $\beta=0.05$ [0.03, 0.08], $P<0.001$; fast: $\beta=0.07$ [0.06, 0.08], $P<0.0001$; control: $\beta=0.05$ [−0.61, 0.72], $P=0.86$), such that the phase occurred 1 h earlier between days 9 and 10 in the fast decline group and by day 12 in the slow decline group. Almost no nocturnal activity was observed in any treatment group, and with no change over time. The birds were not provided with low levels of light overnight, which enhances nocturnal activity (Ramenofsky et al., 2008). We therefore cannot test for an effect of experimental treatment on nocturnal behavior, and do not present these data here.

Activity and food availability

Among experimental days involving food reductions in the slow decline, fast decline and random groups, reductions in morning activity as percentage food reduction increased differed among treatment groups (Fig. 5A; percentage food reduction \times treatment: $F_{2,240.39}=10.43$, $P<0.0001$). There was no difference in slope between the random and fast decline groups (mean β [95% CI]; fast: $\beta=-0.49$ [−0.95, −0.02]; random: $\beta=0.28$ [−0.74, 1.30]), but the slow decline group had a significantly steeper negative slope ($\beta=-2.93$ [−4.12, −1.74]). In the afternoon, activity increased with food reduction across all three treatment groups (Fig. 5B; $F_{1,246.7}=139.14$, $\beta=4.23$ [3.53, 4.94], $P<0.0001$; % food reduction \times treatment interaction term not included) and to a similar extent across groups (fast: $\beta=4.33$ [3.43, 5.24]; slow: $\beta=3.61$ [2.07, 5.15]; random: $\beta=4.81$ [2.62, 6.99]).

Activity and CORT

We found no significant relationship between change in CORT and the change in morning activity (overall: $F_{1,43.3}=2.53$, $\beta=4.92$ [−1.48, 10.86], $P=0.12$; Δ CORT \times treatment interaction not included) or change in afternoon activity (overall: $F_{1,62}=0.49$, $\beta=-4.87$ [−18.14, 8.39], $P=0.48$; Δ CORT \times treatment interaction not included).

Random group food intake

On the four experimental days when random birds were provided $>100\%$ of their pre-experimental daily average food intake immediately following days of food restriction ($<100\%$), random birds did not increase food intake above their pre-experimental level. The average difference in food consumed on these post-food restriction days and their pre-experimental average food intake was -0.044 ± 0.08 g (mean \pm s.e.m.).

DISCUSSION

Our results support the escape hypothesis, suggesting that irruptive migratory physiology is distinct from obligate migratory physiology: whereas obligate migrants undergo extensive preparations for flight, pine siskins express escape behavior to flee areas with insufficient resources, even when provided with ‘advance notice’ of deteriorating conditions through a gradual decline in food availability. Consistent with our predictions, we found that body mass and fat mass declined with food availability (Fig. 2A,B) and, in birds experiencing prolonged food reductions, declines in body and fat mass predicted increases in CORT (Fig. 3B,C). Afternoon activity increased with food reduction, and to the same extent across the slow decline, fast decline and random groups (Fig. 5B), indicating that changes in activity were not sensitive to changes in food availability over multiple days, but rather to the amount of food received on a given

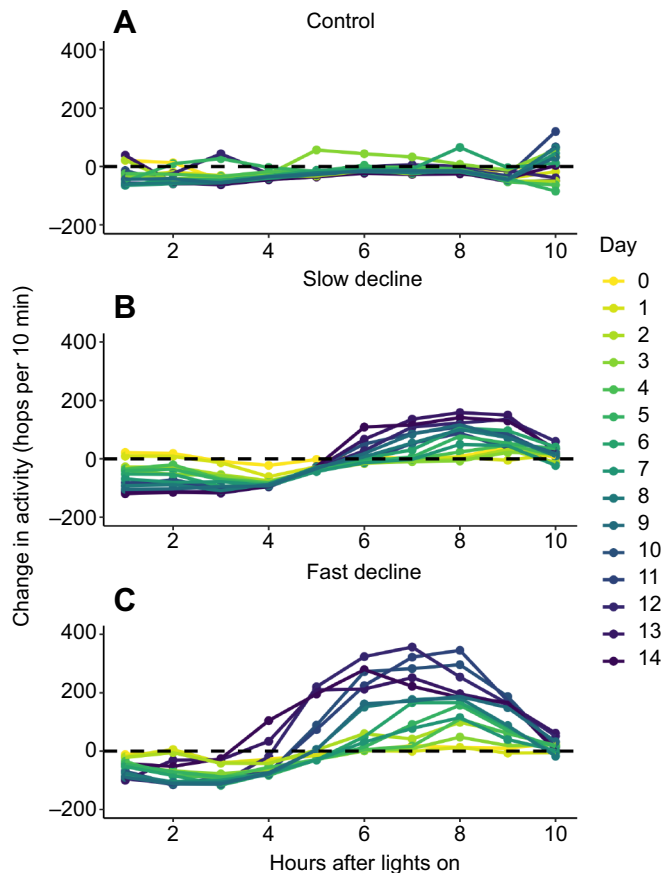


Fig. 4. Change in daytime activity patterns over time. Each point represents the treatment group's average change in activity during a given hour, with color representing experimental day. In contrast to control birds (A; $n=6$), slow decline (B; $n=7$) and fast decline birds (C; $n=8$) significantly changed their daytime activity over the course of the experiment, with slight decreases in morning activity, and significant increases in afternoon activity as the experiment progressed. The mean amplitude of the sine curves fitted to these data increased over the course of the experiment for slow decline ($P<0.0001$) and fast decline birds ($P<0.0001$) but not control birds ($P=0.86$).

day. Pine siskins were also sensitive to the time of day when they ran out of food. As the experiment progressed and they received less food, birds in the fast decline and slow decline groups increased activity earlier in the day (Fig. 4B,C). Finally, birds in the random group did not compensate for days of food restriction by increasing food intake when provided with abundant food the following day. Other studies show that birds often increase food intake, mass or fat stores when experiencing unpredictable food regimes (Witter et al., 1995; Cuthill et al., 2000; Reneerkens et al., 2002; Bauer et al., 2011; Cornelius et al., 2017), further suggesting that siskins respond to insufficient food availability by moving rather than fattening. One caveat is that these captive birds carried greater fat stores than they did in the wild, possibly limiting the effect of intermittent reductions in provided food. In summary, pine siskins exposed to experimental declines in food supply in autumn do not show preparative fueling, they are not sensitive to declines in food availability but rather its absence, and low food availability reduces body condition, increases CORT levels and initiates increased activity.

Under a different food manipulation protocol, Robart et al. (2019) also concluded that siskins do not prepare for autumn movements. In their study, captive siskins in the spring and autumn experienced a reduction in food quality and then a 25% reduction in food

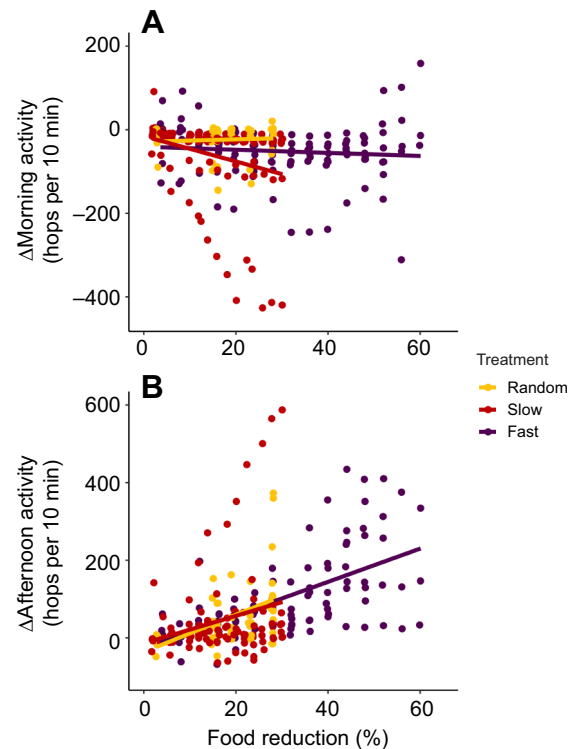


Fig. 5. Changes in activity in relation to food reduction. (A) Morning activity slightly decreased with greater food reductions, and to greater extent within the slow decline ($n=7$, $\beta=-2.93$ [$-4.12, -1.74$]) group compared with the fast decline ($n=8$, $\beta=-0.49$ [$-0.95, -0.02$]) and random groups ($n=6$, $\beta=0.28$ [$-0.74, 1.30$]). (B) Afternoon activity increased with food reduction ($P<0.0001$), and to the same extent across the fast decline ($n=8$, $\beta=4.33$ [$3.43, 5.24$]), random ($n=6$, $\beta=4.81$ [$2.62, 6.99$]) and slow decline groups ($n=7$, $\beta=3.61$ [$2.07, 5.15$]).

quantity. Food-restricted birds showed increased baseline CORT and decreased body condition, and in the spring (but not the autumn), exhibited increases in activity. Robart et al. (2019) suggested that siskins are less behaviorally sensitive to changes in food availability in the autumn, or that their lower body condition in the autumn limits any increases in energy expenditure and activity. Our results are not consistent with these possibilities. We observed marked increases in activity in the autumn, and increases in activity became even more pronounced as food availability declined and body condition worsened. In Robart et al.'s (2019) study, changes in activity may have occurred outside the time it was recorded, or the exposure of food-restricted birds to the vocalizations of control birds may have attenuated their behavioral response to food reductions (Cornelius et al., 2010).

In our study, although the visual muscle scores of slow and fast decline birds decreased over time, there was no change in total lean mass as measured by the QMR. It is possible that the pectoralis muscles appeared smaller over time owing to a depletion of intramuscular fat rather than a loss of lean tissue. Redfern et al. (2004) found that fat and muscle scores were correlated among sedge warblers (*Acrocephalus schoenobaenus*) captured at a banding station, but fat and pectoralis muscle mass were unrelated among dissected individuals. This discrepancy suggests that fat stores may affect visual muscle scores. Another possibility is that there was an increase in some other component of lean mass, such that the QMR reported no overall change in lean mass despite a decrease in pectoralis mass.

CORT underlies increases in activity in two ways, with elevations of baseline CORT promoting increased activity associated with predictable life history stage transitions (as in the prepare hypothesis), and stress-related elevations promoting escape behavior in response to unpredictable stressors (as in the escape hypothesis) (Landys et al., 2006). CORT binds with different affinity to two tissue-level receptors, which allows for these distinct organismal responses to different concentrations of CORT (Reul and de Kloet, 1985; Sapolsky et al., 2000). While our other results support the escape hypothesis, CORT levels did not reach the stress-related levels expected under this hypothesis and previously measured in pine siskins (mean \pm s.e.m. 12.20 ± 1.86 ng ml⁻¹; J. DeSimone unpublished data; Astheimer et al., 1992; Knutie and Pereyra, 2012). This result is consistent with that of Robart et al. (2019), with food-restricted siskins exhibiting only modest elevations in CORT. One possibility is that CORT does not play a mechanistic role in siskin movements in response to food reductions, or that downstream processes, such as receptor levels, are responsible for their migratory behaviors (but see Watts et al., 2019). However, across the avian literature, CORT is correlated with activity during the processes of fledging (Sprague and Breuner, 2010), dispersal (Belthoff and Dufty, 1998), obligate migration (Löhms et al., 2003; Eikenaar et al., 2020) and escape behavior (Breuner et al., 1998; Breuner and Hahn, 2003). We therefore think it more likely that we did not observe a relationship between CORT and activity as a function of experimental design rather than biology. We collected blood samples approximately 2 h after lights on, when birds always had food remaining in their dishes, even among fast decline birds on day 15. Sampling birds while they had food would have allowed us to detect changes in physiology in response to birds' perception of and sensitivity to changes in food availability over time, rather than their response to the absence of food. Instead, changes in activity were not apparent until later in the day, when birds had little or no food remaining. CORT physiology during these times could have been very different from what we measured.

Pine siskins gained significant body mass while acclimating to captivity. The average mass of these siskins when captured in the wild was 12.65 ± 0.11 g (mean \pm s.e.m.), while their average pre-experimental mass (5 days before the start of the food manipulation) was 14.56 ± 0.22 g. Had birds started the experiment in their original body condition, we may have observed even stronger responses to food declines, stronger relationships between changes in CORT and body composition, and declines in lean mass once fat stores were depleted.

The apparent lack of preparation for migration in pine siskins has several possible, non-mutually exclusive implications, all related to the idea that they may not need to make long-distance flights before finding the next available food source. First, siskins may be sufficiently generalist such that, even if their current food source is depleted, they are likely to find patches of suitable alternative food sources on their way to their next destination, negating the need to deposit fuel before departure. Second, areas of low food availability may not be as synchronous as suggested by Koenig and Knops (1998), so that there are patches of food across the landscape and siskins never have to travel far before encountering a food source. Third, siskins could further reduce the need for additional fuel stores if they know where they are going, so they reach their next destination efficiently. This option could be possible if siskins can remember the locations of food patches encountered in the past, or remember areas with past environmental conditions that may favor present food availability. They could also make exploratory excursions from their current area, while local food remains and

refueling is possible, to gather information about broader-scale food availability before departing (Bennetts and Kitchens, 2000). Decisions about flight direction or destination could be enhanced by social information if flocks are able to come to a consensus based on their collective information (Seeley and Buhrman, 1999; Cornelius et al., 2010). Finally, search efficiency of scarce, patchy food sources can be improved with social behavior, as information about food availability can be transferred among neighboring conspecifics, and because foraging conspecifics are likely easier to detect while in flight than conifer seeds (Egert-Berg et al., 2018).

Facultative migratory finches are often social, and public information shared among individuals can alter the behavior and physiology of group members (Smith et al., 1999; Cornelius et al., 2010, 2018). Thus, group behavior in the wild could alter the behavioral and physiological relationships we observed in captive individuals. However, group membership of pine siskin flocks is highly dynamic in the wild (J. DeSimone, personal observation). It is more likely that departure decisions are made individually based on public information, rather than groups arriving at a democratic consensus.

In conclusion, our experimental test supports the escape hypothesis and excludes the prepare hypothesis. Our study characterizes autumn facultative movements as distinct from obligate migrations, and even from spring nomadic movements, and more representative of escape behavior in response to low food availability. A clearer understanding of facultative migratory physiology can open the door for future integrative hypotheses and studies of the broad spectrum of migratory behaviors, how they relate to one another, and their ecological and evolutionary implications.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.G.D.; Methodology: J.G.D., B.W.T., C.W.B.; Formal analysis: J.G.D.; Investigation: J.G.D.; Resources: B.W.T., C.W.B.; Writing - original draft: J.G.D.; Writing - review & editing: J.G.D., B.W.T., C.W.B.; Visualization: J.G.D.; Supervision: C.W.B.; Funding acquisition: J.G.D.

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Data availability

Raw data are available in the Dryad digital repository (DeSimone et al., 2021): qz621jmdm.

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.238774.supplemental>

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