RESEARCH ARTICLE

Functional Ecology   BRITISH ECOLOGICAL SOCIETY

Body mass and triglycerides predict departure of free-living nomadic pine siskins

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Handling Editor: Justin Boyles

Abstract

1. Facultative migrations are observed across vertebrate taxa, include irruptive and nomadic movements, and occur in response to ephemeral and unpredictably variable resources. While the physiology underlying seasonal, obligate migrations is thoroughly studied, much less is known about the physiological mechanisms of facultative movements. We test two hypotheses in a free-living, nomadic bird, the pine siskin (*Spinus pinus*).

2. The Prepare Hypothesis predicts that, like obligate migrants, siskins increase fuel stores to prepare for migratory movements and elevations of baseline corticosterone (CORT) support departure. The Escape Hypothesis predicts that siskins do not prepare for departure, body condition declines as food availability declines, and stress-related levels of CORT induce escape from resource-poor areas.

3. Under the controlled lab conditions of previous studies, food restriction induces declines in body condition and increases in CORT and locomotor activity, supporting the Escape Hypothesis. This study evaluates the ecological relevance of these captive findings by testing the Prepare and Escape Hypotheses in the field for the first time.

4. During two fall field seasons, we radio-tagged siskins and tracked their local movements using handheld and automated telemetry. We assess how body condition and CORT relate to feeding behaviour [estimated via plasma triglycerides (TRIG)], space use and departure.

5. We do not find support for either the Prepare or Escape Hypothesis, but rather observe an intermediate pattern. Birds with higher TRIG, and therefore greater food intake, are more likely to depart. Birds in poor condition stay longer near the field site; however, above a threshold body mass, body condition does not predict departure.

6. These findings suggest moderate energy stores are necessary for departure, but movement decisions depend on other factors among birds with sufficient fuel. Siskin movements are physiologically distinct from both obligate and fugitive movements, and we discuss how food availability and body condition interact to drive different types of movement.

1 | INTRODUCTION

Facultative migrations often occur in response to resource availability that varies unpredictably in space and time. Thus, these movements, observed across taxa and around the globe, are characterized by unpredictable timing and destination (Teitelbaum & Mueller, 2019; Watts et al., 2018). Facultative movements are commonly observed among birds in arid environments (Davies, 1984; Ward, 1971) and among those that feed on conifer seeds (e.g. red crossbills (*Loxia curvirostra*), pine siskins (*Spinus pinus*) and common redpolls (*Acanthis flammea*); (Newton, 2006a)). Conifer trees produce seed crops in boom-bust cycles, and the fall and winter southward movements of boreal seed-eating birds occur during years of low seed availability (Bock & Lepthien, 1976; Koenig & Knops, 2001). Because the masting cycles of cone production are often synchronous across large areas (Koenig & Knops, 1998), birds dependent on these seeds may need to travel thousands of kilometres in search of an abundant source of food (Koenig & Knops, 1998; Newton, 2006b), raising questions about how they accomplish long-distance flights from areas with presumably poor feeding conditions and through potentially unfamiliar landscapes.

Captive studies have investigated facultative migratory physiology by manipulating food availability (i.e. the presumptive proximate migratory cue) and recording the effects on body condition, activity and corticosterone (CORT) levels (Cornelius et al., 2010; DeSimone et al., 2021; Robart et al., 2019). These studies focus on CORT, the primary glucocorticoid in birds, because it underlies increases in activity and coordinates animals' responses to energetic demands, making it a likely candidate hormone underlying facultative migrations. Baseline CORT levels rise in anticipation of the energetic demands of predictable life history transitions, including fledging and dispersal (Belthoff & Dufty Jr., 1998; Heath, 1997; Sprague & Breuner, 2010) and seasonal, obligate migrations (Bauer & Watts, 2021; Eikenaar et al., 2017, 2020; Piersma et al., 2000). In response to unpredictable stressors, stress-induced levels of CORT initiate an emergency response (Wingfield et al., 1998). For instance, food-restricted white-crowned sparrows (*Zonotrichia leucophrys gambelii*) have higher levels of CORT and are more active than fed controls (Lynn et al., 2003). Furthermore, exogenous CORT increases locomotor activity in captivity (Breuner et al., 1998; Cash & Holberton, 1999) and activity ranges in the field (Breuner & Hahn, 2003). Thus, birds exhibit two types of movement with distinct physiological mechanisms: predictable movements that can be anticipated and prepared for, and escape movements made in direct response to a stressor.

These two patterns of CORT action are incorporated into the Prepare and Escape Hypotheses, which make explicit predictions about the relationships among body condition, CORT and food availability prior to departure in facultative migrants (DeSimone et al., 2021). The Prepare Hypothesis predicts that individuals are sensitive to changes in food availability such that they can anticipate departure and prepare by depositing fuel stores before local food availability is depleted. We would expect body mass to increase as food availability declines, and baseline levels of CORT to rise in anticipation of departure, as in obligate migrants. The Escape Hypothesis predicts that birds respond directly to insufficient food, rather than changes in food over time. Thus, body condition would decline as food becomes scarce, and stress-related CORT levels would initiate an escape response (i.e. departure).

Studies of captive pine siskins and red crossbills in the fall and winter found overall support for the Escape Hypothesis, with lower body condition, greater hopping activity, and higher CORT levels among birds experiencing marked decreases in food availability (Cornelius et al., 2010; DeSimone et al., 2021; Robart et al., 2019). Furthermore, siskins' increases in activity were not sensitive to changes in food availability over multiple days, but rather to the amount of food received on a given day, and the time of day when they ran out of food (DeSimone et al., 2021). These nomadic finches also show patterns of moderate seasonal fattening during phases of the annual cycle with consistent nomadism (Cornelius et al., 2021; Cornelius & Hahn, 2012), which for pine siskins peaks in the spring (April–May) and fall (September–October; Dawson, 2020). Spring movements likely function to return an individual to its breeding range after fall and winter movements (Robart et al., 2018; Watts et al., 2017). Fall movements may relocate siskins to areas with a suitable seed crop for the overwintering phase. Notably, seasonal increases in fat stores in crossbills and siskins are not as substantial as those observed in obligate migrants (Alerstam & Lindström, 1990; Cornelius et al., 2021).

The unpredictable nature of facultative movements makes them logistically challenging to study in the field. Previous studies have related the nomadic and irruptive movements of birds and ungulates to resource availability and climatic conditions (Bock & Lepthien, 1976; Koenig & Knops, 2001; Mueller et al., 2011; Olson et al., 2010; Pedler et al., 2014; Strong et al., 2015), or have examined the physiology of avian nomads in captivity (Cornelius et al., 2010; DeSimone et al., 2021; Robart et al., 2019). Others have used geolocators and stable isotope analysis to identify the scale of movements of crossbills in Europe (Alonso et al., 2017; Arizaga et al., 2014). But studies relating physiology to the movement patterns of free-living nomadic species are generally lacking (Watts et al., 2018). This study aims to test the Prepare and Escape Hypotheses in free-living nomadic birds. During August – September of 2019 and 2020, we tracked the local movements of pine siskins in relation to their body mass, fat deposition and CORT levels. It is difficult to manipulate and measure food availability at a large scale in the wild, so we instead measured triglyceride (TRIG) levels of each individual. TRIG is the storage form of fat, formed in the liver and transported to adipocytes. During fat catabolism, TRIG

is broken into its glycerol and fatty acid components (Guglielmo, 2018; McWilliams et al., 2004). Thus, circulating plasma TRIG reliably reflects fat deposition and can be used to assess habitat quality and foraging intensity (Guglielmo et al., 2005; Jenni-Eiermann & Jenni, 1994). However, it is worth noting that factors other than food availability could influence body condition and movement, including social information (Cornelius, 2022), parasite or contaminant load (Ackerman et al., 2019; Dawson & Bortolotti, 2000; Jiménez-Peñuela et al., 2019) and age and sex (Ellegren, 1991). Overall, we aim to determine how body condition, fuel deposition and CORT interact to influence pine siskin movement. They may prepare for movement (i.e. increase body mass, TRIG and baseline levels of CORT prior to departure) or rather escape (i.e. low body mass and TRIG, with stress-induced CORT levels, prior to departure). In contrast to previous captive research, studying free-living siskins ensures that both food availability and movement behaviours vary in biologically relevant ways. This is the first study that we are aware of that integrates physiological and movement data to better understand nomadic movements in the wild.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted fieldwork on MPG Ranch in Florence, MT (46.669, −114.026) during August–September of 2019 and 2020. There were four main areas where we observed pine siskins. The floodplain of the Bitterroot River and the seasonal creek draws have a mixture of deciduous and coniferous trees. An open area of the ranch contains fields of annual (*Helianthus annuus*) and perennial (*Helianthus maximiliani*) sunflowers and crops for grazing. A higher elevation area is primarily a mixed coniferous forest. During both years of the study, we commonly observed pine siskins in sunflower patches and in cottonwoods near the floodplain and rarely observed siskins feeding on cones.

2.2 | Capture and sampling

We captured birds between 07:00 and 11:00 using standard mist nets and pine siskin playback recordings. We continuously monitored the nets to note exact capture time and extract birds immediately. No bird was captured more than once.

Up to 125 μl of blood were collected from the brachial vein using 30G needles. Blood samples were kept on ice in the field and were centrifuged in the lab within 6 h to separate plasma from red blood cells. Plasma was aliquoted: plasma used for CORT analysis was stored at −20°C and plasma for TRIG analysis was stored at −60°C. Only blood samples collected <3 min from capture were included in analyses involving CORT (Romero & Reed, 2005); all blood samples were included in TRIG analyses.

Birds were aged as HY or AHY using plumage characteristics as in Pyle (1997). We visually scored fat stores on a scale from 0 to 5 (Moore & Kerlinger, 1987) and pectoralis muscle on a scale from 0 to 3 (Bairlein, 1995). We measured various morphometrics and weighed each bird to the nearest 0.1 g on a digital scale. We scaled body mass with the length of the exposed culmen (Peig & Green, 2009; $F_{1,37} = 5.92$; $p = 0.02$).

All procedures were conducted under permits and approval from the University of Montana IACUC (AUP 050-19 and 009-20EGDBS-040120), the state of Montana (2019-018-W and 2020-025-W), and the federal government (#23206).

2.3 | Radiotelemetry

In total, 40 pine siskins (2019: $n = 21$; 2020: $n = 19$) were fitted with nano-tags (Lotek NTQB2-2 with a 13 s burst interval) using standard leg-loop harnesses (Rappole & Tipton, 1991) and elastic thread (Gütermann elastic thread #5019). Tags weighed <3% body mass of each individual.

Birds were localized using handheld telemetry receivers (Lotek SRX-800). We localized each bird at least 2 h since its previous localization to (1) minimize disturbance to the bird and (2) ensure greater independence among points. When possible, we recorded the exact location of the individual using GPS units (189 of 426 localizations; Garmin GPSMAP 64st). When the bird was inaccessible or on private property, we triangulated its position using the coordinates and azimuth of 3 or more detections. We used Locate III software (Nams, 2005; Version 3.34) to calculate the triangulated locations; points with large MLE estimates (>0.05 km^2) were excluded. MLE estimates of triangulated locations averaged 0.00093 km^2 ± 0.0036 (two standard deviations).

We employed an array of automated telemetry Motus stations (Birds Canada, 2022) on MPG Ranch (2019: $n = 6$; 2020: $n = 5$) and throughout the Bitterroot Valley to the south (2019: $n = 4$; 2020: $n = 3$) to provide additional monitoring (Figure S1). These stations continuously recorded the presence/absence of tagged individuals, and these data were used in combination with our handheld telemetry data to estimate individuals' departure times. In total, 38 birds were detected by at least one Motus station.

We analysed telemetry data in five ways to assess movement patterns and space use. (1) We estimated departure time as either the time of the last handheld telemetry detection of the individual, or the last time it was detected by a Motus station in Montana, whichever came later. We calculated 'days to departure' as the time difference between capture and departure. (2) We used ArcMAP (version 10.6.1) to calculate the minimum convex polygon area for all of the localizations of each bird ('total polygon') and (3) for only the localizations 0–2 days after capture ('3-day polygon'). (4) We used the distHaversine function in R package GEOSPHERE (Hijmans et al., 2019) to calculate the distance between consecutive localizations for each bird. (5) We estimated a total distance travelled per unit time, by summing the distances among consecutive points for each bird, and dividing by the amount of time (hrs) between the first and last localizations.

2.4 | Corticosterone assay

Plasma CORT levels were measured using an Enzyme Linked Immunoassay (ELISA) kit (cat. No. 25-0412, Enzo Life Sciences). 2000 cpm of 3H-CORT was added to samples to estimate recovery. CORT was extracted from plasma using a double ether extraction. Ether was evaporated off in a 50°C water bath. Sample was reconstituted in 260–400 μl assay buffer for a final dilution of 1:20–1:25. Recoveries averaged 64.1 ± 0.05% (mean ± SD); samples were corrected to 100% for analysis.

Assays were run as described in Patterson et al. (2011). Briefly, 100 μl of extracted, diluted sample were assayed in triplicate if possible, and in duplicate when plasma volume was limiting. Each plate included a standard curve (20,000 to 15.63 pg/ml). An external CORT standard was run in triplicate on each plate to quantify inter-plate variation. Plates were read at 405 nm corrected at 595 nm. Intra- and inter-plate coefficients of variation (CVs) were 11.25% and 12.33%, respectively. All samples were within the detectability limit for each assay.

2.5 | Triglyceride assay

We quantified glycerol and total triglyceride using kits and a slightly modified protocol, as in Guglielmo et al. (2002). We thawed plasma samples on ice and diluted them three-fold with 0.9% saline (Sigma Aldrich S8776). Triglyceride assays were run in duplicate in 96-well microplates (Falcon 353910). A glycerol standard curve (Sigma Alrdich G7793) was included on each plate, with values ranging from 2.82 mmol/L to 0.17 mmol/L and a blank (0.0 mmol/L). 5 μl sample (or standard) and 240 μl glycerol reagent (Sigma Aldrich F6428) were added to each well and read at 540 nm in a microplate spectrophotometer (ThermoFisher Multiskan Ascent 51118407) after incubating for 10 min at 37°C. 60 μl of triglyeride reagent (Sigma Aldrich T2449) were added to each well, and the plate was read again at 540 nm after another 10 min incubation at 37°C. All wells were corrected by blank wells, and concentrations were determined by comparison with the standard curve. Within individual CVs averaged 8.08%.

2.6 | Statistical analysis

All statistical analyses were run in RStudio (version 1.3.1093), models were assessed using the PERFORMANCE package (Lüdecke et al., 2021), and figures were produced using ggplot2 (Wickham, 2016, Version 3.3.6).

We log-transformed CORT, TRIG, days to departure and distance travelled per time in all analyses to satisfy normality assumptions. To test the relationship between CORT and energetic state, we built GLMs examining the effect of logTRIG on logCORT and the effect of scaled body mass on logCORT. We also constructed a GLM to test whether logTRIG predicts scaled body mass. Initial models included capture Julian day, capture time and year as covariates, but only significant covariates remained in the final model, as noted in the Results section.

We used GLMs to test the effect of physiology on departure timing. Models tested whether logCORT at capture predicted logDays to Departure, and whether logTRIG at capture predicted logDays to Departure. We initially included capture Julian day, capture time and year as covariates, but only retained significant covariates, which are noted in the Results section. A GLM relating scaled body mass to logDays to Departure had heteroskedastic and non-normally distributed residuals, leading us to try a breakpoint analysis. Using the CHNGPT package (Fong et al., 2017), we identified a breakpoint in the relationship between logDays to Departure and scaled body mass. We used GLMs to test the relationship between logDays to Departure and scaled body mass for points above and below this breakpoint. We used an F-test to compare the variances of points to the left and right of the breakpoint.

Next we used GLMs to assess the effect of physiological metrics on various movement metrics. Each model tested the effect of one physiological metric (logCORT, logTRIG or scaled body mass) on one movement metric (Total Polygon Area, 3-day Polygon Area or Distance Travelled Per Time). We initially included capture Julian day and year as covariates, but only retained significant variants in the final model, as noted in the Results. We also initially included the total number of localizations of an individual as a covariate in the models with Distance Travelled Per Time, but removed it because it was non-significant and did not contribute to the model fit. We included a quadratic term in the model relating scaled body mass to Distance Travelled Per Time because this term had a $p = 0.050$ and greatly improved the model's R^2.

Finally, to test the relationship between logDistance Travelled Per Time and logDays to Departure, we built a GLMM with Bird ID as a random effect and Year as a covariate.

3 | RESULTS

All statistical model results are summarized in Table 1.

3.1 | Physiological metrics

The range, mean and standard error of body mass, TRIG and CORT are summarized in Table 2. CORT levels were not predicted by TRIG (Table 1; Figure 1a) or by scaled body mass (Table 1; Figure 1b). TRIG levels did not predict scaled body mass (Table 1; Figure 1c).

Fat and muscle scores did not predict scaled body mass, TRIG, CORT, or days to departure (Table 1). Julian day did not relate to body mass, TRIG, CORT, fat or muscle score (Table 1).

3.2 | Physiology and departure timing

CORT levels did not predict days to departure (Table 1; Figure 2a). Birds with higher TRIG levels departed sooner after capture (Table 1; Figure 2b).

TABLE 1 Model statistics (F-statistic with degrees of freedom, β and p-value) for all analyses described in the Results. Significant p-values are in bold text

Parameter	Model terms	$F_{(df)}$	β	p
Physiological metrics				
CORT	~TRIG	$_{(1,27)}$ 0.33	−0.08	0.57
	~scaled mass	$_{(1,28)}$ 0.37	0.01	0.55
	~Fat score	$_{(1,28)}$ 0.50	0.04	0.48
	~Muscle score	$_{(1,27)}$ 4.11	−0.09	0.05
	~Julian day	$_{(1,28)}$ 0.24	−0.001	0.63
Scaled mass	~TRIG	$_{(1,35)}$ 0.37	0.69	0.55
	~Fat score	$_{(1,37)}$ 0.01	0.03	0.92
	~Muscle score	$_{(1,37)}$ =0.91	0.35	0.35
	~Julian day	$_{(1,37)}$ =0.04	0.003	0.85
TRIG	~Fat score	$_{(1,35)}$ =2.11	0.07	0.16
	~Muscle score	$_{(1,35)}$ =0.61	0.04	0.44
	~Julian day	$_{(1,35)}$ =0.25	0.001	0.62
Fat score	~Julian day	$_{(1,37)}$ 1.19	0.01	0.28
Muscle score	~Julian day	$_{(1,35)}$ 1.05	0.01	0.31
Physiology and departure timing				
Days to departure	~CORT	$_{(2,27)}$ 2.20	−0.08	0.91
	+Year		0.43	**0.046**
	~TRIG	$_{(2,34)}$ 6.36	−0.81	**0.04**
	+Year		0.37	**0.03**
	~Scaled mass (<13.32)	$_{(1,22)}$ 5.03	−0.17	**0.04**
	~Scaled mass (>13.32)	$_{(1,13)}$ 0.58	−0.22	0.46
	~Fat score	$_{(2,36)}$ 3.94	0.01	0.93
	+Year		0.46	**0.008**
	~Muscle score	$_{(2,34)}$ 0.17	−0.06	0.65
	+Year		0.42	**0.02**
Physiology and movement patterns				
Distance travelled over time	~scaled mass	$_{(2,29)}$ 2.19	1.33	**0.048**
	+scaled mass^2		−0.05	0.05
	~CORT	$_{(1,22)}$ 0.87	0.44	0.36
	~TRIG	$_{(1,28)}$ 3.39	0.52	0.08
Total polygon area	~scaled mass	$_{(2,25)}$ 3.99	1.17	0.13
	+Julian day of capture		−0.16	**0.03**
	~CORT	$_{(2,19)}$ 4.43	7.25	0.35
	+Julian day of capture		−0.21	**0.01**
	~TRIG	$_{(2,23)}$ 2.86	−2.48	0.60
	+Julian day of capture		−0.16	**0.03**
3-day polygon area	~scaled mass	$_{(1,19)}$ 0.10	0.05	0.75
	~CORT	$_{(1,18)}$ 0.37	0.67	0.55
	~TRIG	$_{(1,17)}$ 1.38	−1.19	0.26
Movement and departure				
Days to departure	~distance between localizations	$_{(1325.8)}$ 9.53	−0.18	**0.002**
	+Year		0.43	**0.002**
	+Bird ID (random effect)			

TABLE 2 Range, mean and standard error of the body mass, triglyceride and corticosterone levels of all pine siskins included in analyses

	Range	Mean	SE
Body mass (g)	11.43–14.60	12.78	0.13
TRIG (mmol/L)	0.55–5.29	1.51	0.14
CORT (ng/ml)	1.15–3.61	1.99	0.13

We identified a breakpoint in the relationship between scaled body mass and days to departure (Figure 2c). Higher scaled body mass predicted fewer days to departure among birds with scaled body masses below 13.32 g (Table 1) while days to departure did not vary with scaled body mass among heavier birds (Table 1). The variance in days to departure was also significantly smaller among birds lighter than 13.32 g compared with birds with scaled body masses higher than the breakpoint ($F_{14,23} = 6.01$; $p = 0.0002$).

3.3 | Physiology and movement patterns

Scaled body mass predicted the distance birds travelled over time (Table 1; Figure 3), with birds of intermediate mass travelling further than both lighter and heavier individuals. Scaled body mass did not relate to our other spatial metrics: total polygon area or 3-day polygon area (Table 1). We found no relationships between CORT and the total polygon area, 3-day polygon area, or the distance travelled per time (Table 1). TRIG did not relate to these spatial metrics either (Table 1).

3.4 | Movement and departure

On average, for each bird, the distance between consecutive localizations increased as departure time approached (Table 1; Figure 4).

3.5 | Long-distance movements

In 2020, three individuals were detected by Motus stations out-of-state. One hatch-year siskin was detected 940 km away in Colorado 5 days after its last Montana detection. Two after-hatch-years flew east: one was detected in Wisconsin 26 days after Montana departure (2086 km); one was detected in Ontario 36 days after Montana departure (2529 km). Each of these birds was last detected by a Montana Motus station in the middle of the night, indicating nocturnal departures from our study area.

4 | DISCUSSION

Facultative and nomadic movements are poorly understood and clarifying the environmental and physiological cues underlying these movements is critical to understanding the evolution and diversity of migratory strategies. This study is the first to investigate
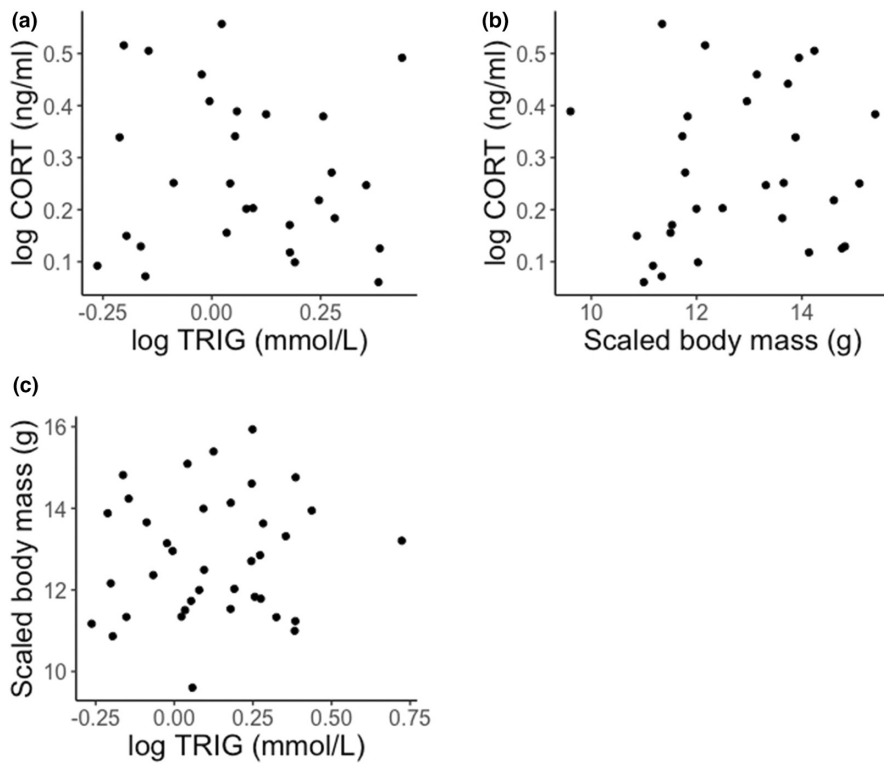
FIGURE 1 Corticosterone was not predicted by (a) plasma triglycerides or (b) scaled body mass. Plasma triglycerides did not predict scaled body mass (c).
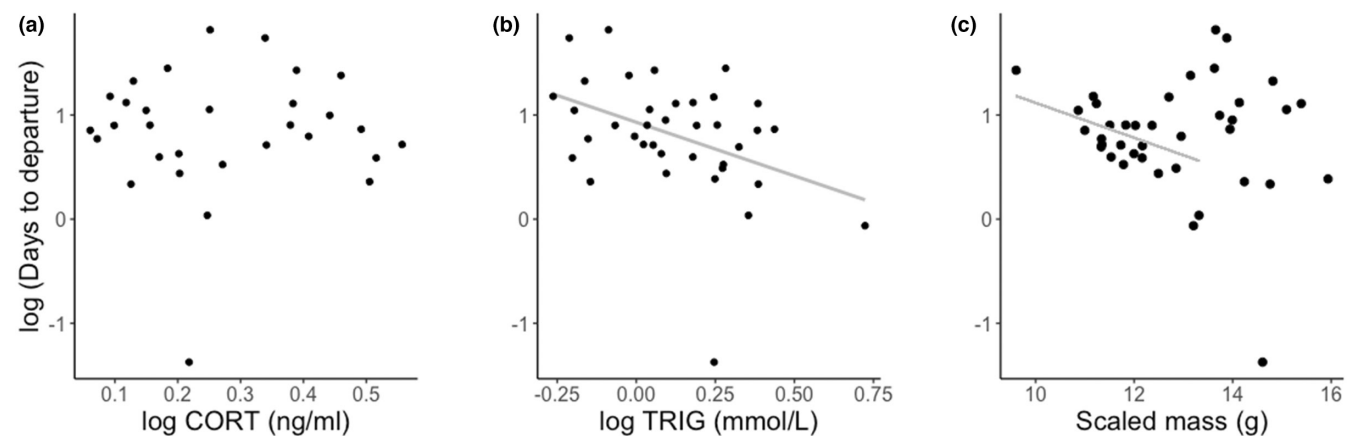

FIGURE 2 Physiology and departure timing. (a) Corticosterone did not predict log-transformed departure timing. (b) Birds with higher levels of triglycerides departed sooner after capture. (c) Scaled body mass negatively correlated with days to departure among birds below the breakpoint at 13.32 g; departure did not relate to scaled body mass among heavier birds.

the physiology of nomadic migrants in relation to their movement in the wild. We tested whether birds fuel up before flight (Prepare Hypothesis) or rather leave an area when food resources and internal body stores are depleted (Escape Hypothesis). We found that individuals had higher TRIG levels as they neared departure (Figure 2b), indicating that foraging success or energetic condition relate to departure decisions. However, we found that scaled body mass only predicts departure among birds below a breakpoint mass (Figure 2c). Birds with lower body mass stayed around the field site longer, but at masses above the breakpoint, mass did not predict departure. Together these results suggest that moderate energy stores are necessary for departure, but movement decisions depend on other factors among birds with sufficient fuel. Our results do not

fully support either the Prepare or Escape Hypotheses. Instead, we observed an intermediate pattern: siskins need adequate – but not large – fuel stores to initiate departure.

In contrast to this field study, captive studies demonstrate support for the Escape Hypothesis and show clearer relationships among body condition, food availability and activity (DeSimone et al., 2021; Robart et al., 2019). In these captive studies, siskins experiencing low food availability in the fall lose body mass and show increases in CORT and activity levels. We integrate Bennetts and Kitchens's (2000) hypothesis relating behaviour to food availability (Figure 5a) and the framework of allostasis (McEwen & Wingfield, 2003; Figure 5b) to explain the discrepancy between captive studies and our field results. Bennetts and Kitchens hypothesize that the probability of movement or departure
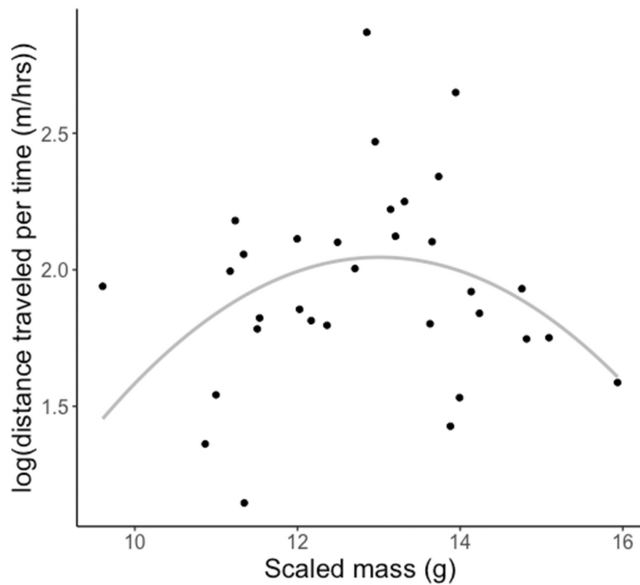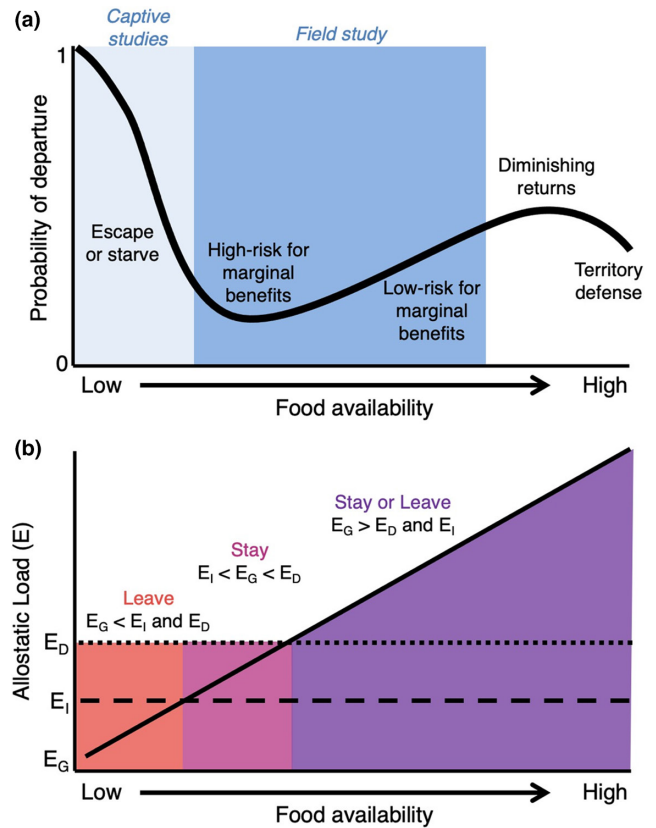
FIGURE 3 An individual's scaled body mass predicted the estimated total distance travelled during their time spent at the field site. On average, birds of intermediate body mass travelled further distances than both lighter and heavier individuals.
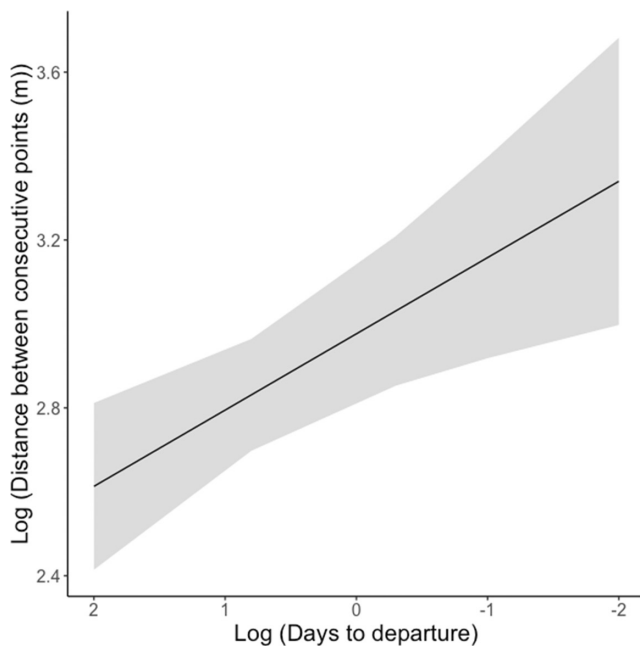
FIGURE 4 The distance (m) between consecutive localizations of an individual increased as departure time neared. Note the inverted x-axis, with departure time approaching from left to right.

FIGURE 5 (a) Hypothesized departure probability along a gradient of food availability. The light-blue-shaded area indicates the region previously tested and observed by captive studies. The dark-blue-shaded area indicates the region likely observed in this field study. Adapted with permission from Bennetts and Kitchens (2000), © OIKOS 2000. (b) Allostatic load or energetic requirements (E) along the same food availability gradient. E_G is the amount of energy available in the environment; E_I is energy required for normal daily activities; E_D is the extra energy needed to depart and find or explore new habitat. Siskins are predicted to leave due to allostatic overload when $E_G < E_I$ ('Escape or Starve' region of a; red region of b). A siskin can remain in an area when $E_G > E_I$ (pink and purple regions of b), though leaving is risky when $E_D > E_G$ ('High-risk for marginal benefits' region of a; pink region of b). See main text for further explanation.

is expected to vary in relation to food availability. Allostasis predicts organismal responses to the environment by relating the energy available in the environment (energy gained; E_G) to an individual's daily energetic needs (E_I) (McEwen & Wingfield, 2003), to which we add the energy required for departure (E_D; Figure 5b). When food availability is critically low, birds must leave their current area or die. In this case, $E_G < E_I$, the animal is in allostatic overload, and it initiates an emergency life history response (McEwen & Wingfield, 2003). At

moderately low food availability, birds are less likely to depart: they do not have sufficient fuel stored for flight ($E_G < E_D$) but can still subsist on local food resources ($E_G > E_I$). As food availability increases, the risk of movement decreases and, thus, the probability of departure increases ($E_G > E_I$ and E_D). At high levels of food availability, the probability of departure decreases again because birds benefit from maintaining high-quality territories. Astheimer et al. (1992) observed such interactions between physiology, food availability and movement: although fasted, captive, white-crowned sparrows with CORT implants significantly increased their perch hopping activity, CORT-implanted sparrows with available food dramatically reduced their activity levels.

We believe this framework helps reconcile captive and field results and can help predict facultative departure probability. Captive studies have tested siskins' responses to low food availability and found

support for the Escape Hypothesis. Birds in these studies were likely in the 'escape or starve' region of Figure 5a ($E_G < E_I$). Captive siskins increase activity when they have little or no food remaining each day, and CORT levels only increase among birds experiencing sustained food reductions (DeSimone et al., 2021). Our field results fit within the central region of Figure 5a. Birds in poor energetic condition stayed in the area for up to 27 days ('high-risk for marginal benefits'; $E_I < E_G < E_D$). Birds with heavier body masses had the fuel necessary to depart if they chose to, but body mass did not relate to departure among these birds ('low-risk for marginal benefits'; $E_G > E_D$). In our study, birds with higher TRIG levels were closer to departure time, corresponding to the transition from high-risk to lower-risk movements.

Furthermore, the combined results of this study and those of DeSimone et al. (2021) suggest that, as departure probability increases, variation of departing individuals' body condition increase. For instance, the average mass of pine siskins at the start of the DeSimone et al. (2021) captive study was 14.56 g, much heavier than the wild-caught birds of this study, and siskins experiencing a variety of food restriction regimes increased activity during times of day when food availability was critically low or absent. In the present field study, departure was limited to those individuals with sufficient stored fuel. In other words, when food availability is critically low, all individuals depart, regardless of their energetic condition, while only those in good condition depart areas with moderate food availability.

We found no relationships between CORT levels and various metrics of movement behaviour. This was unexpected, as previous studies have linked CORT with locomotor activity in captivity (Breuner et al., 1998; Cash & Holberton, 1999), activity ranges in the field (Breuner & Hahn, 2003; Jessop et al., 2018) and predictable transitions to life stages associated with increases in activity, such as fledging (Heath, 1997; Sprague & Breuner, 2010), dispersal (Belthoff & Dufty Jr., 1998) and obligate migration (Eikenaar et al., 2017, 2020; Löhmus et al., 2003; Piersma et al., 2000). In this study, we do not know CORT levels at the moment of departure, and physiology at capture may be too far removed temporally from physiological drivers of departure. For instance, CORT is only elevated in the hours before departure in northern wheatears (*Oenanthe oenanthe*), an obligate migratory passerine. Future experimental work with exogenous CORT could explicitly test its effect on nomadic and irruptive movements.

On average, siskins increased the distance travelled between consecutive localizations as they neared departure time (Figure 4). This result suggests that siskins may explore a broader area when deciding when to depart and where to go next. We also found that birds of intermediate body masses travelled the furthest distances around our field site (Figure 3). One explanation is that light and heavy birds may restrict their movement to conserve energy or remain in an area with abundant resources, respectively. Finer-scale temporal and spatial data could reveal more information about what kind of environmental or social information siskins may gather during these pre-departure movements. Furthermore, because body condition did not predict departure among birds with sufficient fuel, future studies could investigate other climatic, environmental or social factors that may inform siskins' departure

decisions. Nomadic finches are often social, form flocks and likely share information with each other about food availability or to coordinate group movements. Captive pine siskins and red crossbills vocalize more frequently when food-restricted (Robart et al., 2019; Smith et al., 1999), social information alters crossbill physiology (Cornelius, 2022; Cornelius et al., 2010, 2018), and wild pine siskins increase their call rate when departing from a foraging area (S. Sriraman, unpublished data).

Siskin movements during the timeframe of our study could represent expanding home ranges, juvenile dispersal, seasonal movements in search of suitable overwintering habitat or irruption. The Motus telemetry network has spatial and temporal limitations that somewhat restrict our ability to characterize siskins' movements. At the time of this study, Motus stations were very sparsely distributed throughout the western United States (Birds Canada, 2022). Additionally, the batteries of the nano-tags we used are estimated to last about 3 months after initial activation (Lotek Wireless, 2022). However, we do not believe the birds' movements were simply foraging forays or home range expansions because once they left our monitoring area, they rarely returned. Among the 39 birds for which we have departure data, only 4 (10%) were re-detected in Montana within the nano-tag's 3-month lifespan. Most (82% of the birds we aged) were hatch-years, so these post-breeding movements could represent juvenile dispersal. The siskins we tracked were primarily found foraging in sunflower fields and cottonwoods, and anecdotally, overall siskin abundance declined over the course of the season. Siskins may have departed the site in search of food sources that would last through the winter. Body mass and fat stores did not vary with Julian day among these birds, meaning that seasonal fattening did not occur, had already occurred before the start of our study, or that our predominantly juvenile population does not prepare for movement in the same way as adults (Cornelius et al., 2021). Finally, three individuals made long-distance, out-of-state movements, with nocturnal Montana departures, likely representing nomadic or irruptive movements (Watson et al., 2011). These movements were observed in 2020, which was a nation-wide irruption year for many North American finches, including pine siskins (Gyekis, 2021; Mandelbaum, 2020).

For the first time, we integrate physiological and movement data in a nomadic migrant. We conclude that siskins' local movements are clearly distinct from both obligate migrations, which involve extensive physiological preparations, and fugitive migrations, which are initiated in response to a large and sudden disturbance. Our study also illustrates the importance of testing captive findings in the wild, where both food availability and movement behaviour vary in ecologically relevant ways. Finally, we demonstrate that the frameworks of Bennetts and Kitchens (2000) and allostasis (McEwen & Wingfield, 2003) can help predict how physiology and food availability interact to elicit different movement probabilities.

AUTHOR CONTRIBUTIONS

Joely DeSimone: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Visualization, Funding Acquisition. Beverly Domschot: Investigation. Megan Fylling:

Resources, Funding Acquisition, Writing – Review and Editing. William Blake: Resources, Writing – Review and Editing, Creagh Breuner: Conceptualization, Methodology, Writing – Review and Editing, Supervision.

CONFLICT OF INTEREST
The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2v6wwpzsk (DeSimone et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: DeSimone, J. G., Domschot, B. S., Fylling, M. A., Blake, W. M., & Breuner, C. W. (2022). Body mass and triglycerides predict departure of free-living nomadic pine siskins. *Functional Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2435.14238