

Glucocorticoids and activity in free-living arctic ground squirrels: Interrelationships between weather, body condition, and reproduction

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ABSTRACT

The dynamic relationship between glucocorticoids and behavior are not well understood in wild mammals. We investigated how weather, body condition, and reproduction interact to affect cortisol levels and activity patterns in a free-living population of arctic ground squirrels (*Urocitellus parryi*). As a proxy for foraging and escape behaviors, collar-mounted accelerometers and light loggers were used to measure above-ground activity levels and the amount of time squirrels spent below the surface, respectively. Fecal cortisol metabolites (FCMs) were quantified to assess glucocorticoid secretion in squirrels. Male and female squirrels differed in above-ground activity levels and time spent below-ground across the active season, with males being most active during mating and females most active during lactation. We also found that female, but not male, squirrels exhibited seasonal variation in FCM levels, with concentrations highest during mid-lactation and lowest after the lactation period. In female squirrels, the seasonal relationships between breeding stage, activity, and FCM levels were also consistent with changes in maternal investment and the preparative role that glucocorticoids are hypothesized to play in energy mobilization. Body condition was not associated with FCM levels in squirrels. As predicted, deteriorating weather also influenced FCM levels and activity patterns in squirrels. FCM concentrations were affected by an interaction between temperature and wind speed when seasonal temperatures were lowest. In addition, above-ground activity, but not time spent below-ground, positively correlated with FCM levels. These results suggest that, although ground squirrels avoid inclement weather by remaining below-ground, activation of the stress axis may stimulate foraging activity.

1. Introduction

Across their life cycles, organisms make constant behavioral and physiological adjustments that enable fitness-critical life-history transitions while also accommodating disruptive perturbations that have direct effects on individual survival. The concept of allostasis describes glucocorticoids (corticosterone and cortisol; hereafter, 'GCs') as the primary physiological mediator that helps animals balance this trade-off between survival and reproduction (McEwen and Wingfield, 2003). When using allostasis to understand stress within an ecological framework, metabolic demands of animals are integrated according to inputs from both predictable and unpredictable events to determine changes in GC secretion (McEwen and Wingfield, 2010; Wingfield, 2005).

Many experimental studies have revealed the general role GCs play in metabolic regulation as well as behavioral adjustments characteristic of energy maintenance (Koch et al., 2002; Landys, 2004; Landys et al.,

2006). One major function of GCs is to promote gluconeogenesis (Dallman et al., 1993; Exton, 1979; Hasselgren, 1999), and the Energy Mobilization hypothesis posits that GC concentrations will be highest during time points with the highest energetic demands (Romero, 2002). For example, GCs generally increase in response to cold environmental temperatures across vertebrate species (de Bruijn and Romero, 2018) and also increase during energetically demanding breeding stages such as pregnancy (Michel et al., 2011) and lactation (Boswell et al., 1994; Kenagy and Place, 2000). Furthermore, GCs can directly influence behavior through both genomic (Joëls and de Kloet, 1994; Webster and Cidlowski, 1999) and non-genomic (Mikics et al., 2004) mechanisms. In a series of studies on black-legged kittiwakes (*Rissa tridactyla*), increases in circulating corticosterone levels caused by food shortages have been shown to drive increases in time spent flying/foraging (Angelier et al., 2007), decreases in time spent attending/guarding nests (Angelier et al., 2009; Kitaysky et al., 2001), and reduced reproductive

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productivity (Buck et al., 2007). While these and other, primarily experimental, studies have revealed the importance of the stress response in balancing energy budgets, interactions between organisms and their natural environments are complex and much remains unknown about how the stress axis and behavior is integrated in the field.

A number of biotic and abiotic factors can influence the energy balance of free-living animals and result in changes in GC secretion and behavior (de Bruijn and Romero, 2018; Romero, 2002; Studd et al., 2020). Prolonged seasonal elevations of GCs are suggested to be adaptive responses that facilitate anticipatory changes associated with the energetic demands of reproduction (Kenagy and Place, 2000; Love et al., 2014; Nunes et al., 2006). Superimposed on predictable changes in reproductive timing, organisms must also be able to respond to unpredictable changes in weather (Jacobs and Wingfield, 2000; Wingfield, 2008). Deteriorating environmental conditions have been shown to have direct effects on foraging opportunities and thermal exchange rates (Cartar and Morrison, 1997; Chappell, 1980; Grubb, 1975; Hilton et al., 1999; Kelly et al., 2002; Raine, 1983), and the role of GCs in modulating responses to inclement weather is well documented across vertebrates (reviewed in de Bruijn and Romero, 2018; Wingfield and Ramenofsky, 2011). For example, fecal glucocorticoid levels of female baboons (*Papio cynocephalus*) of Amboseli, Kenya were elevated during the dry season when temperatures are high and food and water become scarce (Gesquiere et al., 2008). Compounded with these factors is body condition, which serves as a proxy of energy balance and can also influence the ability of organisms to carry out reproduction and withstand acute stressors such as inclement weather (Landys et al., 2006). Body condition has been shown to influence breeding decisions (Béty et al., 2003; Naulleau and Bonnet, 1996) and outcomes (Chastel et al., 1995; Moe et al., 2002) of animals, and both baseline and reactive levels of GCs are likely related to physical condition (Fokidis et al., 2011; Heath and Dufty, 1998; Hennin et al., 2016; Kitaysky et al., 1999; Williams et al., 2008; Wingfield et al., 2011). In one notable study, Breuner and Hahn (2003) developed a model describing how weather, GCs, and body condition affect behavioral adjustments in white-crowned sparrows (*Zonotrichia leucophrys oriantha*). Elevated GC levels were shown to facilitate different behavioral responses depending on the favorability of weather conditions. Moreover, the magnitude of GC secretion in response to a stressor was also greater in birds with low, compared to high, fat reserves. Collectively, this suggests that the stress response and its functions in behavioral modulation are sensitive to changes in both weather and physical condition.

To date, most field studies examining the dynamics of stress physiology and behavior have been performed in songbirds and very few in mammals. While many functions of GCs are generally considered conserved across taxa, differences in life-history and ecology play a major role in shaping the trajectories of GC secretion, evidenced by species exhibiting different, often opposing, physiological and behavioral responses to GC manipulation (Crossin et al., 2016; Landys et al., 2006). Life-history differences may explain why avian, but not mammalian, species consistently show annual rhythms in GC secretion that peak during breeding (Romero, 2002). Moreover, birds and mammals differ greatly in their metabolic requirements, ability to store energy reserves (Nagy, 1987), and the scaling of their GC levels with body mass (Francis et al., 2018). Further, because birds can fly (unlike most mammals), they can more readily use locomotion as a means to escape environmental stressors, e.g., irruptive migrations. While GCs appear to promote locomotor activity and feeding behavior across vertebrate species (Astheimer et al., 1992; Cash and Holberton, 1999; Dallman et al., 2004; Sandi et al., 1996), the directionality of these effects are context-dependent and likely vary with patterns of energy availability and utilization between species (reviewed in Landys et al., 2006). For example, GC administration increased activity of white-crowned sparrows following a 24-h fast but decreased activity when birds were held with ad libitum food (Astheimer et al., 1992). As such, generalizing results from studies largely conducted in passerines to other vertebrate species

may be confounded by the distinctive life-history strategies and ecology of avian species.

Semi-fossorial rodents, such as ground squirrels, may provide a useful system for investigating the relationship between the stress axis and behavior in free-living mammals that utilize thermally-favorable refugia to “wait out” environmental perturbations. Ground squirrels partition aspects of their behavior between surface and subterranean activities, and during the active season, ground squirrels face a trade-off between their ability to forage above-ground versus escaping predators and inclement weather by remaining below-ground (Williams et al., 2016). Along with patterns of behavior, ground squirrel species also exhibit predictable seasonal changes in body mass and condition (Boswell et al., 1994; Buck and Barnes, 1999a; Sheriff et al., 2013) and baseline GC secretion (Boonstra et al., 2001b; Kenagy and Place, 2000; Nunes et al., 2006), coincident with changes in reproduction-associated energy demands. Because fitness of ground squirrels living in seasonal environments benefit from high investment during a short breeding season, the GC-mediated stress response likely plays an important role in balancing the demands of reproduction against responses to inclement weather. Taken together, this suggests that reproductive state, body condition, and weather conditions likely interact to determine changes in GC secretion and behavior in ground squirrels. Similar to what has been observed in birds, acute elevations of GC secretion in squirrels may also trigger behavioral responses that help individuals return to normal life-history function.

In this study, we describe both seasonal and acute patterns of GC secretion in a free-living population of arctic ground squirrels (*Urocitellus parryii*). We used collar-mounted accelerometers and light loggers to measure above-ground overall dynamic body acceleration (ODBA), a measure of total movement of an animal that increases with increasing activity levels (Halsey et al., 2008, 2009). Above-ground ODBA (hereafter, activity) was used as a proxy for surface activity levels, which we assume is primarily driven by foraging behavior, except in early spring, when males are moving to locate receptive females. Light loggers were used to determine when squirrels were below the surface to model behavioral patterns of escape and avoidance. In addition, we quantified fecal cortisol metabolites (FCMs) from field-collected samples, a well-established and non-invasive method for assessing the average daily levels of circulating cortisol (Palme, 2019). The goal of this study was to investigate the relative influence of weather conditions, reproduction, and body condition on GC secretion and activity patterns. First, we describe seasonal variation of FCM concentrations, above-ground activity, and time spent below-ground, predicting that differences between males and female ground squirrels would reflect sex-dependent seasonal differences in the timing of reproductive investment. Based on the general role of GCs in the maintenance of energy balance, we hypothesized that unfavorable thermal conditions will increase male and female FCMs and decrease above-ground activity levels, and elevated FCM concentrations would be found in animals with lower body condition. While GCs have been shown to stimulate foraging behavior in birds, we hypothesized that, due to the ability of squirrels to store large amounts of fat and escape inclement weather, GCs would suppress above-ground activity and increase time spent below-ground.

2. Methods

2.1. Study species

Arctic ground squirrels are the northern-most hibernating small mammal, spending 7–9 months a year sequestered in perennial hibernacula constructed in the active layer above the permafrost. During an active season which lasts between 3 and 5 months, squirrels mate, reproduce, raise young and replenish endogenous fat reserves in preparation for overwinter survival. Upon termination of hibernation, males remain underground for 3–5 weeks, feeding on cached food and

undergo gonadal growth and spermatogenesis (Barnes, 1996; Buck and Barnes, 1999a). Males will then emerge from hibernacula 11–14 days before females (Sheriff et al., 2011) at body masses no different than before entering hibernation (Buck and Barnes, 1999a), during which intense intraspecific competition associated with defense of reproductively receptive females occurs (Buck and Barnes, 2003). Females are impregnated within 2–3 days of ending heterothermy (Williams et al., 2013), as males immediately intercept, mate with, and begin mate guarding females. Gestation and lactation last approximately 26 and 28–35 days, respectively (Williams et al., 2011). Ground squirrel pups will remain below-ground until weaning which occurs 4–5 weeks after parturition (Buck and Barnes, 1999a).

2.2. Field data

Our study was conducted between April 13 and August 4, 2016 at Atigun River (68°27' N, 149°21' W; elevation 812 m), a long-term study site located 20 km south of Toolik Field Station, in the northern foothills of the Brooks Range, Alaska. Squirrels were trapped using Tomahawk live-traps (Tomahawk Trap Co.) during four separate deployments across the active season from April 14–28, May 20–June 4, July 2–12, and July 30–August 3. Due to low trapping success during late-season, usable data for statistical analysis was only procured from April 14–July 12. Trapping efforts were carried out from 11:00 to 17:00 daily, and traps were checked for animals every 1–2 h. Fresh feces were collected upon capture of each animal for analysis of FCMs. All fecal samples collected were from the first capture of the day and samples from individual animals were collected at least 48 h apart. Fecal samples were collected during the first three deployment stages, which were representative of three different seasonal stages of squirrel activity. Because male and female squirrels were found in equal numbers upon first arrival at our study site, and because first captured males were found with enlarged and descended testes, we are confident that our first series of FCM collections, which occurred during mid-spring, are likely representative of late-mating and early-gestational activities. As such, we hereafter describe the seasonal stages of FCM collection as mid-spring/early-gestation, late-spring/mid-lactation, and mid-summer/post-lactation.

Squirrels were anesthetized in the field using isoflurane vapors. After immobilization, animals were weighed and reproductive condition was visually assessed; animals were also sampled for blood (~1 ml) via cardiac puncture for use in other studies. All squirrels were marked with a uniquely numbered aluminum ear tag and a PIT-tag. We deployed collars affixed with an accelerometer and light logger on 13 individuals (six females and seven males). A total of 524 animal-days of usable data were collected across all animals with an average of 40 ± 24.4 (standard deviation [SD]) days collected from each individual. Light loggers and accelerometers wrapped in heat-shrink tubing were epoxied to collars constructed from zip ties sheathed within plastic tubing. Fully built collars weighed approximately 9 g. Total processing time ranged between 5 and 10 min and squirrels were subsequently released at site of capture following arousal from anesthesia.

2.3. Devices

We used light loggers (Intigeo-C56 light loggers, Migrate Technology Ltd., Cambridge, UK) which measure ambient light intensity and enabled determination of when animals were either above- or below-ground. Light loggers were programmed to measure light intensity every minute and record maximum values every 1 or 5 min. Animals were assumed to be below-ground when recorded light intensity was less than or equal to 2 lx (dark) and above ground when light intensity was > 2 lx (light).

We used accelerometers (axy-3 loggers, TechnoSmart Europe srl., Rome, Italy) to investigate the activity patterns of arctic ground

squirrels. Accelerometers continuously measured and recorded acceleration on three orthogonal axes at 10 Hz. To give a measure of dynamic acceleration, a 3 s running average was subtracted from the corresponding measurements of acceleration on each axis to account for the static effect of gravity (Shepard et al., 2008; Wilson et al., 2006). The absolute value of the dynamic acceleration was then summed on all three axes, providing the measure of ODBA (Wilson et al., 2006).

2.4. Environmental data

We used a weather station (HOBO U30-NRC, Onset Computer Corporation, Bourne, MA) located on our study site to measure various environmental parameters known to affect the rates of thermal exchange in small mammals including: ambient temperature (°C), solar radiation (W/m), wind speed (m/s), and rainfall (mm). The interaction between wind speed and ambient temperature was also included as an effect in our analysis. Measurements were taken and recorded in 15-min intervals throughout the year. Rainfall was measured with tipping buckets and characterized as a categorical variable of daily accumulated rainfall (0 mm = absent, > 0 mm and < 2 mm = moderate, and ≥ 2 mm = high) (Williams et al., 2016). Major snowfall events were detailed by an observer who was present during the entirety of the study and were recorded as a categorical variable (present/absent).

2.5. FCM analysis

Fecal samples were collected in the field from trapped animals, with most animals producing fresh feces upon approach. Samples already present in traps were no older than 1–2 h. Collected samples were immediately stored on ice packs until transferred to Toolik Field Station and frozen at -80 °C at the end of the day. All samples were placed and transported on dry ice from Toolik Field Station to Flagstaff, AZ at the end of the summer field season. Fecal samples were freeze-dried using a lyophilizer for 24 h and homogenized with a mortar and pestle. We extracted FCMs from 0.05 ± 0.003 g of dry feces by adding 1 ml of 80% methanol, vortexing for 30 min, centrifuging for 15 min at 1000 g, and collecting the supernatant which was subsequently stored at -80 °C until assay.

We used a 11-oxoetiocholanolone enzyme immunoassay (EIA) to quantify FCMs in the fecal extracts; cross-reactivity of the antibody and details of the assay are described in Palme and Möstl (1997) and Möstl et al. (2002). This assay has been successfully validated in arctic ground squirrels (Sheriff et al., 2012). A 7-point serial dilution of the standard was performed to create the standard curve. In addition to the standard curve, each plate contained nonspecific binding and total binding wells, high and low concentration pool sample extracts, and unknowns (diluted 1:50 with assay buffer). All samples were assayed in duplicate. Intra- and inter-assay variation for all assays ($n = 13$) were 4.24% and 14.73%, respectively. FCMs are expressed as nanograms per gram of dry fecal weight.

2.6. Statistical analysis

All analyses were completed using R statistical software (version 3.2.4; <http://www.R-project.org/>). We examined patterns in body mass and condition across seasonal stages and the relationship of body condition to FCM levels in males and females. A total of 50 and 36 morphometric observations were recorded from 31 females (samples per individual: 1.61 ± 0.9) and 18 males (samples per individual: 2 ± 1.4), respectively. To determine body condition, we extracted residuals from regressions of body mass on zygomatic arch width separately for males and females using ordinary least squares (Dobson et al., 1999; Jakob et al., 1996; Schulte-Hostedde et al., 2005; Werner et al., 2015). This index of animal body condition, which provides an estimate of animal energy reserves (protein and fat) that are independent of size (Schulte-Hostedde et al., 2005), was used in

subsequent analyses to investigate seasonal patterns in body condition and its effect on FCM levels. While intrauterine mass may confound measures of maternal body condition, FCM values collected in this study represent early-gestation, when maternal weight gain is lowest (Finlay et al., 2015). We performed linear mixed-effects (LME) models within each sex to examine patterns of body mass and condition across seasonal stages, including individual identity (ID) as a random effect. Differences in body mass and condition between stages were estimated using Tukey post-hoc tests.

A total of 182 fecal samples [113 samples from 32 females (samples per individual: 3.53 ± 1.4) and 69 samples from 18 males (samples per individual: 3.83 ± 1.9)] were collected and analyzed for FCM content. Normality of FCMs was assessed using normal quantile-quantile plots and values were log-transformed to normalize the distribution of the residuals. Because we only recorded morphometric measurements from a subsample of total trapped individuals, FCM samples were only used in the analysis to understand the relationship between cortisol secretion and body mass and condition if samples were collected within one day of morphometric measurement, producing 28 observations from 15 males (samples per individual: 1.87 ± 1.1) and 40 observations from 24 females (samples per individual: 1.67 ± 0.9), respectively. To examine the effect of body condition on FCM levels, we performed separate LME models within each sex, including FCM levels as the response variable, body condition and seasonal stage as main effects, and ID as a random effect.

To examine patterns of FCM concentrations across the annual cycle, we performed LME models with ID as a random effect. Due to significant covariance between environmental conditions and seasonal stage ($P < 0.001$ for all weather parameters), these effects were examined in different models. First, we compared the effect of seasonal stage on FCM concentrations separately for males and females. Tukey post-hoc tests were then performed to estimate differences in FCMs among seasonal stages. To determine the influence of environmental conditions and sex on FCMs, a separate LME model was performed for each seasonal stage (mid-spring $N = 65$, late-spring $N = 80$, mid-summer $N = 37$) and included sex and environmental parameters as main effects. During the first stage, mid-spring, estimated variances of the random effect was zero, so a general linearized model without random effects was used instead. Moreover, rain was only included as a factor for late-spring and mid-summer models, as FCM samples were not collected on rainy days during other stages. No FCM samples were collected during days with snowfall events.

We performed penalized cubic splines (package 'mgcv'; Wood, 2017) using generalized additive models to account for the nonlinear nature of activity across the year, allowing smooths to vary by sex and designating ID and day of year (factor) as random effects. For analyzing tracking data from April 17 through July 2, two splines were applied to model average daily above-ground ODBA and proportion of day spent below-ground separately. In the model for average daily above-ground ODBA, snow, sex, and average daily rain were included as parametric terms and were calculated as average values for when squirrels were above-ground, i.e., ODBA per unit time above-ground. In addition, day of year, average solar radiation, temperature, and wind speed were included as nonparametric terms. For modeling proportion of day spent below-ground, we included the same parametric and nonparametric terms as the prior model, except environmental variables were instead averaged across all times of the day. Lastly, to examine the relationship between FCMs and animal activity, we collected 34 fecal samples from animals wearing collars at time of sampling. For subsequent analyses, we averaged measures of animal activity (above-ground ODBA and time spent below-ground) across morning hours (5:00–11:00) to remove timeframes during which animal trapping occurred. We performed two generalized linear models with above-ground ODBA and time spent below-ground as different response variables and FCMs, sex, stage, and the interaction between sex and stage as main effects. Lastly, we computed and reported analysis of variance tables with F-tests and

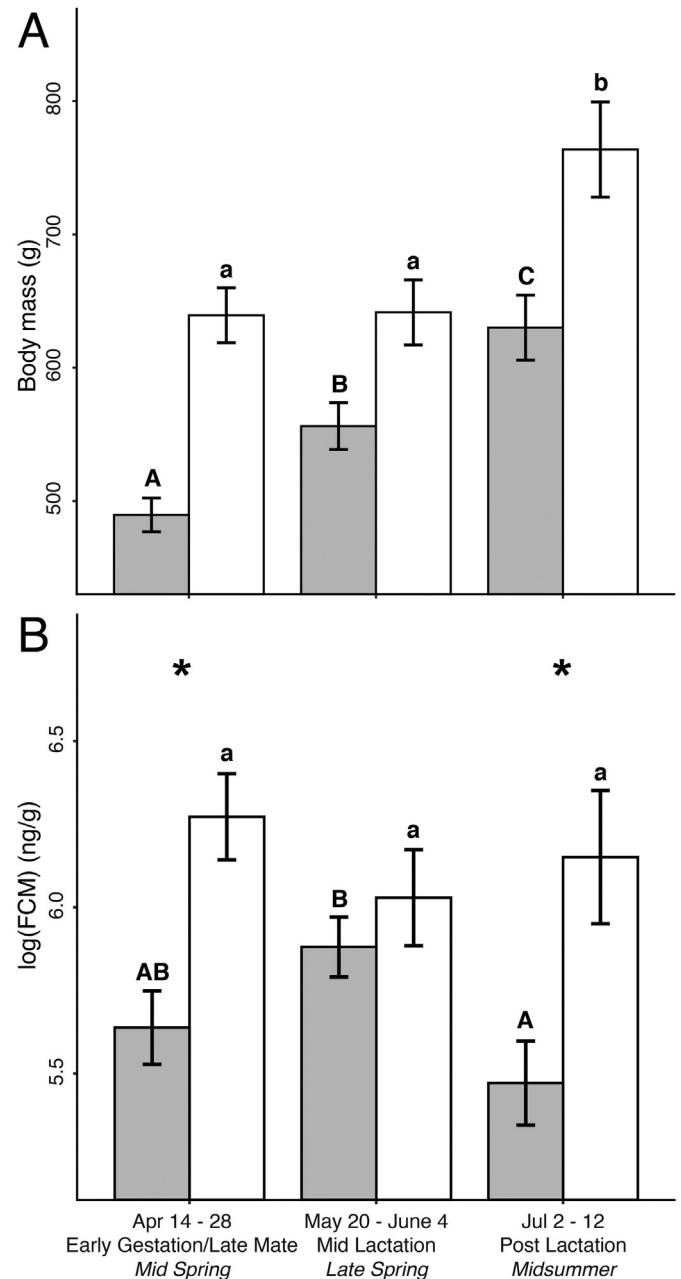


Fig. 1. Body mass (A) and log-transformed fecal cortisol metabolite (FCM) levels (B) (LS means \pm SE) in female (shaded bars, body mass $N = 50$; FCM $N = 113$) and male (open bars, body mass $N = 36$; FCM $N = 69$) arctic ground squirrels during three separate seasonal states across the active season. Sex differences were only examined in (B), where asterisks represent significant differences in FCM concentrations between sexes. Uppercase letters represent significant differences in body mass or FCM levels for females and lowercase for males, as determined by post hoc tests ($P < 0.05$).

p -values for our fitted mixed models using the Satterthwaite's method to estimate degrees of freedom. Using the package 'effectsize' (Ben-Shachar et al., 2020), we computed partial eta-squared (η_p^2) for effect size and used Cohen's d (Cd) measure of effect size for pairwise comparisons.

3. Results

3.1. Body mass and condition

Body mass varied by seasonal stage in males ($F_{2,23} = 7.92$, $P = 0.003$, $\eta_p^2 = 0.41$) and females ($F_{2,26} = 21.68$, $P < 0.0001$, $\eta_p^2 = 0.63$). Males did not differ in body mass between mid-spring (least squares means = 639 ± 20.5 [standard error; SE] g) and late-spring (642 ± 24.4 g), but significantly increased in weight during mid-summer (764 ± 35.7 g) (mid-spring vs late-spring: $P = 0.002$, $Cd = -1.26$; mid-spring vs mid-summer: $P < 0.0001$, $Cd = -2.21$; late-spring vs mid-summer: $P = 0.02$, $Cd = -1.18$) (Fig. 1a). Overall, female squirrels increased their body mass by 29% from April to July. Females body mass was lowest during mid-spring (490 ± 12.7 g), intermediate during late-spring (556 ± 17.5 g), and highest during mid-summer (630 ± 24.3 g) (mid-spring vs late-spring: $P > 0.99$, $Cd = -0.04$; mid-spring vs mid-summer: $P = 0.004$, $Cd = -1.37$; late-spring vs mid-summer: $P = 0.01$, $Cd = -1.37$) (Fig. 1a). Body condition indices were estimated as residuals in a regression of body mass on structural size and calculated separately for each sex. Regressions for both males and females were significant (males: $F_{1,35} = 19.73$, $r^2 = 0.34$, $P < 0.0001$, females: $F_{1,49} = 14.41$, $r^2 = 0.21$, $P = 0.0004$), suggesting that skeletal size explains more of the variation in body mass in males than females. Significant seasonal variation in body condition was found in both male ($F_{2,22} = 5.23$, $P = 0.014$, $\eta_p^2 = 0.32$) and female ($F_{2,30} = 20.24$, $P < 0.0001$, $\eta_p^2 = 0.58$) ground squirrels. Similar to patterns in body mass, we found that female body condition was highest during mid-summer (79.09 ± 19.4 residuals in grams) and lowest during mid-spring (-34.16 ± 10.3 residuals in grams) (mid-spring vs late-spring: $P = 0.003$, $Cd = -1.19$; mid-spring vs mid-summer: $P < 0.0001$, $Cd = -1.99$; late-spring vs mid-summer: $P = 0.03$, $Cd = -1.02$). Male body condition was highest during mid-summer (101.2 ± 38.3 residuals in grams) (mid-spring vs late-spring: $P = 85$, $Cd = 0.22$; mid-spring vs mid-summer: $P = 0.045$, $Cd = -1.02$; late-spring vs mid-summer: $P = 0.02$, $Cd = -1.28$). Body condition did not predict FCM levels in males ($F_{1,16} = 0.01$, $P = 0.91$, $\eta_p^2 = 0.00$) or females ($F_{1,36} = 0.06$, $P = 0.82$, $\eta_p^2 = 0.00$).

3.2. Fecal cortisol metabolites: comparisons

In females, FCM concentrations differed significantly between seasonal stages ($F_{2,96} = 5.35$, $P = 0.006$, $\eta_p^2 = 0.10$); female FCM concentrations were highest during late-spring/mid-lactation and lowest during mid-summer/post-lactation (mid-spring vs late-spring: $P = 0.12$, $Cd = -0.39$; mid-spring vs mid-summer: $P = 0.52$, $Cd = 0.21$; late-spring vs mid-summer: $P = 0.01$, $Cd = 0.61$) (Fig. 1b). On the other hand, male FCM concentrations did not significantly vary across the active season ($F_{2,66} = 0.79$, $P = 0.46$, $\eta_p^2 = 0.02$) (mid-spring vs late-spring: $P = 0.42$, $Cd = 0.31$; mid-spring vs mid-summer: $P = 0.87$, $Cd = 0.13$; late-spring vs mid-summer: $P = 0.87$, $Cd = -0.12$) (Fig. 1b). We found that male FCM levels were significantly higher than females during the mid-spring/early-gestation and mid-summer/post-lactation stages (mid-spring, $F_{1,59} = 13.47$, $P = 0.001$, $\eta_p^2 = 0.19$; mid-summer, $F_{1,27} = 9.09$, $P = 0.006$, $\eta_p^2 = 0.25$) (Table 1). The influence of weather on FCM concentrations was dependent on seasonal stage (Table 1), with FCM levels during the mid-spring (average temperature -5 °C) stage responding most to changes in weather (Table 1a). During this period, FCM levels were significantly affected by ambient temperature ($F_{1,59} = 5.28$, $P = 0.03$, $\eta_p^2 = 0.08$), wind speed ($F_{1,59} = 4.93$, $P = 0.03$, $\eta_p^2 = 0.08$), and the interaction between temperature and wind speed ($F_{1,59} = 7.12$, $P = 0.01$, $\eta_p^2 = 0.11$) (Table 1a). During late-spring (average temperature 6 °C), days with precipitation > 2 mm positively influenced FCM levels in animals ($F_{2,60} = 9.1$, $P = 0.0004$, $\eta_p^2 = 0.23$) (Table 1b). During mid-summer (average temperature 14 °C), no environmental parameters were found to affect FCM concentrations (Table 1c).

Table 1

Parameter estimates (95% CI and P -values) of sex and various environmental variables on fecal cortisol metabolite (FCM) concentrations in arctic ground squirrels. Results are grouped [(a) $N = 65$; (b) $N = 80$; (c) $N = 37$] by three seasonal stages in which collar deployments and feces collection took place.

Stage	Parameter	Estimate[95% CI]	P-value
(a) Early Gestation Mid Spring (Apr 14–Apr 28)	Sex	Male 0.628[0.293, 0.963] Female 0	0.0005
	Temperature (°C)	-0.074[-0.137, -0.011]	0.025
	Wind Speed (m/s)	0.103[0.012, 0.193]	0.03
	Temp × Wind	0.042[0.011, 0.0719]	0.01
	Solar Rad (W/m ²)	-0.009[-0.023, 0.005]	0.21
	(b) Mid Lactation Late Spring (May 20–Jun 4)	Sex	Male 0.242[-0.069, 0.553] Female 0
Temperature (°C)		-0.035[-0.181, 0.11]	0.64
Wind Speed (m/s)		0.319[0.002, 0.635]	0.053
Temp × Wind		0.013[-0.026, 0.051]	0.52
Rain > 2 (mm/day)		1.15 [0.526, 1.773] 0–2 0.674[-0.242, 1.59] 0 0	0.0006 0.15
Solar Rad (W/m ²)		0.001[-0.001, 0.003]	0.30
(c) Post Lactation Midsummer (Jul 2–Jul 12)	Sex	Male 0.697[0.244, 1.151] Female 0	0.006
	Temperature (°C)	-1.820[-4.444, 0.803]	0.18
	Wind Speed (m/s)	-20.18[-49.37, 9.013]	0.19
	Temp × Wind	1.609[-0.714, 3.932]	0.18
	Rain > 2 (mm/day)	-0.739 [-2.776, 1.315] 0–2 NA 0 0	0.49 NA NA
	Solar Rad (W/m ²)	-0.010 [-0.032, 0.012]	0.39

3.3. Activity

Our two generalized additive models, with above-ground ODBA (activity) and time spent below-ground as different response variables, explained 72.4% and 83.7% of total deviance, respectively. Male and female arctic ground squirrels showed seasonal patterns in above-ground ODBA (Fig. 2a) and time spent below-ground (Fig. 2b). Our models, which included sex as a parametric term, did not find differences between males and females in either above-ground ODBA (Table 2a) or time spent below-ground (Table 2b). However, as indicated by significant interactions between sex and day of year, all measures of activity changed nonlinearly across the season for males and females, except for males from the model of time spent below-ground. (Table 2). Above-ground ODBA (Fig. 2c) in males was estimated to be significantly higher during late-April and lower from May through June when compared to females. Females tended to spend more time below-ground than males during late-April and mid-May and less time below-ground from mid-June through early-July (Fig. 2d).

We found that above-ground ODBA and time spent below-ground also varied by environmental variables (Table 2 and Fig. 3). In our first model, above-ground ODBA decreased during snow events, while rainfall had no effect on above-ground ODBA (Table 2a). In addition, nonparametric smoothing terms for solar radiation and wind speed were also significant, suggesting that above-ground activity patterns of squirrels are influenced by the environmental conditions that they encounter while on the surface. Above-ground ODBA in squirrels tended to increase at low- to moderate levels of solar radiation and decrease at higher levels of solar radiation (Fig. 3a). Squirrels also tended to increase levels of surface activity as wind speeds increased (Fig. 3a). In our second model, parameter estimates for rainfall and snow significantly affected the amount of time squirrels spent below-ground (Table 2b). Specifically, rain above 2 mm and snow events increased time spent below-ground, while rain between 0 and 2 mm had no effect on time spent below-ground. All nonparametric smooth terms of weather variables, except wind speed, were also significant (Table 2b). Generally, time spent below-ground decreased as solar radiation and ambient temperature increased (Fig. 3b).

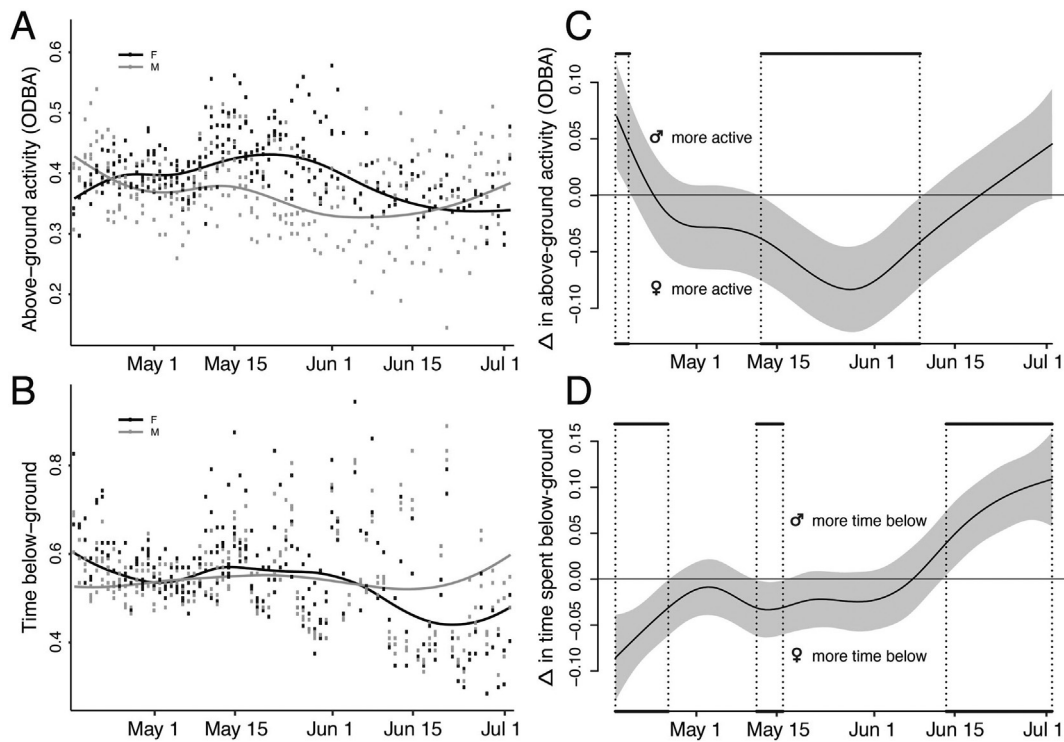


Fig. 2. Left panel: Predicted changes in above-ground overall dynamic body acceleration (ODBA) (A) and time spent below-ground (B) in female (black, $N = 256$ observations from six individuals) and male (gray $N = 268$ observations from seven individuals) arctic ground squirrels across the active season. The solid lines represent fitted mean predictions and dots represent raw values for measures of activity. Right panel: Estimated differences in smooths comparing male and female arctic ground squirrels for measures of above-ground ODBA (C) and time spent below-ground (D) across the active season. The solid line represents mean predictions for difference between male and females with 95% confidence interval. Positive values are interpreted as males being greater than females and negative values as females being greater than males. Intervals enclosed by dashed lines indicate time intervals with significant sex differences. The Y-axis shows the differences in partial residuals for sex covariates generated by regressing the response on the other covariates in the model.

We examined the effect of FCM levels on measures of morning activity using linear models that also included sex, seasonal stage, and the interaction between sex and season as predictor variables. Our models revealed that morning levels of above-ground ODBA ($F_{1,27} = 5.04$, $P = 0.03$, $\eta_p^2 = 0.16$) varied with FCM concentrations, with activity increasing as FCM concentrations increased (Fig. 4). Interestingly, no relationship was found between FCM concentrations and morning levels of time spent below-ground in squirrels ($F_{1,27} = 3.12$, $P = 0.09$, $\eta_p^2 = 0.16$).

4. Discussion

Changes in weather, reproduction, and body condition can all influence the energy balance of animals within their environment. The purpose of this study was to explore how these factors might interact to drive seasonal and reactive patterns of GC secretion and activity in a free-living semi-fossorial rodent. Because male and female arctic ground squirrels differ significantly in their timing of reproductive investment, we predicted that differences in FCM levels and activity patterns would reflect sex-specific differences in seasonal energy

Table 2

General additive mixed model summaries for (a) above-ground overall dynamic body acceleration (ODBA) and (b) time spent below-ground in arctic ground squirrels. Summary statistics of smoothing terms are shown in first four columns and parametric terms are shown in last three columns. Day of year is represented as ‘doy’.

Smooth terms	Effective degrees of freedom	F-statistic	P-value	Parameters	Estimate[95% CI]	P-value
(a) Above-ground ODBA						
s(doy):Female	5.976	14.793	< 0.0001	Sex	Male -0.028[-0.0627,0.0068]	0.116
s(doy):Male	5.851	8.935	< 0.0001		Female 0	
s(Solar Radiation)	3.483	6.793	< 0.0001	Rain	> 2 -0.0049[-0.0242,0.0144]	0.619
s(Temperature)	1.000	0.990	0.320		0-2 0.0028[-0.0114,0.0170]	0.698
s(Windspeed)	1.001	3.944	0.0476		0 0	
				Snow	Present -0.0608[-0.0905,-0.0311]	< 0.0001
					Absent 0	
(b) Time spent below ground						
s(doy):Female	6.082	7.787	< 0.0001	Sex	Male -0.0059[-0.0307,0.0189]	0.6411
s(doy):Male	4.316	1.976	0.0583		Female 0	
s(Solar Radiation)	2.792	29.416	< 0.0001	Rain	> 2 0.0395[0.0070,0.0721]	0.0177
s(Temperature)	1.001	44.551	< 0.0001		0-2 -0.0101[-0.0453,0.0251]	0.5735
s(Windspeed)	1.844	1.233	0.3333		0 0	
				Snow	Present 0.20[0.1429,0.2571]	< 0.0001
					Absent 0	

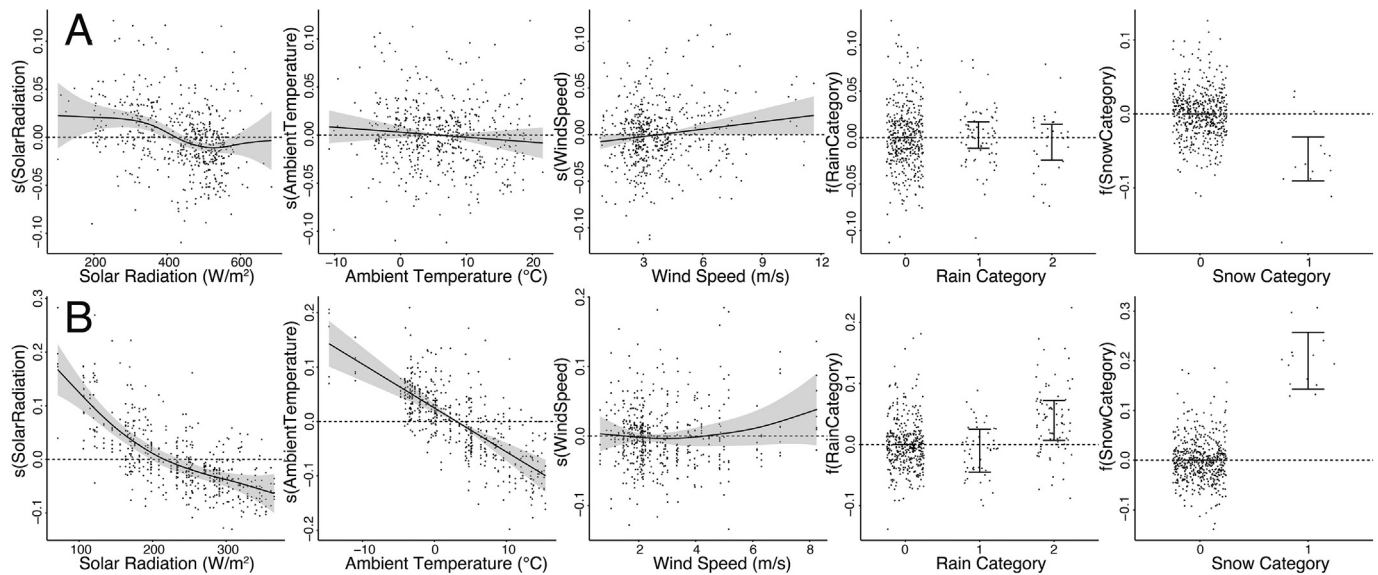


Fig. 3. Environmental predictors of daily above-ground overall dynamic body acceleration (ODBA) (A) and time spent below-ground (B) based on generalized additive models. Solid line represents predicted fit for smooth covariates (left to right) solar radiation, ambient temperature, and wind speed with shaded areas representing 95% confidence intervals. Error bars represent 95% confidence intervals for factor covariates rain category and snow events. Y-axis represents partial residuals for each covariate generated by regressing the response on other covariates.

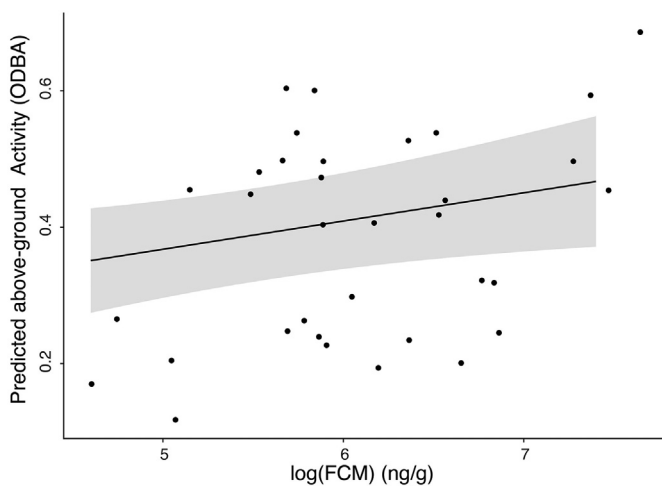


Fig. 4. Estimates of the marginal effects of fecal cortisol metabolites (FCMs) on above-ground overall dynamic body acceleration (ODBA) in arctic ground squirrels. Effects were estimated from generalized linear models which included sex, seasonal stage, and the interaction between sex and stage ($N = 34$). Line represents predicted values of the response variable with changes in FCM concentration and shaded areas represent 95% confidence intervals.

requirements. Due to the energy mobilization and maintenance functions of GCs and its effect on behavior, we also predicted high FCM levels would be associated with lower body condition, inclement weather, more time spent below-ground, and lower levels of above-ground activity. We found that: (1) female, but not male, squirrels showed seasonal variation in FCM levels, with highest values during mid-lactation; (2) both above-ground activity and time spent below-ground varied seasonally depending on sex; (3) body condition failed to predict FCM levels; (4) inclement weather was associated with higher FCM levels only early in the season, when temperatures were lowest; and (5) FCM levels were positively correlated with above-ground activity but not time spent below-ground. Collectively, our results demonstrate that the abiotic and biotic factors that determine the metabolic requirements of mammals may also influence the correlative relationships between GC secretion and patterns of squirrel behavior.

Because factors such as environmental conditions, reproduction, and body condition can all vary similarly on a seasonal scale and may be confounding, we also acknowledge the limitations associated with making causal inferences about specific seasonal phenomena from only one year of data. Nonetheless, at least in the year of this study, adjustments in ground squirrel physiology and behavior appeared to be primarily determined by predictable seasonal requirements which differed between the sexes.

4.1. Seasonal patterns of FCM and activity

Seasonally elevated baseline GC secretion is hypothesized to play an important preparatory role in helping animals anticipate the requirements associated with life-history transitions and reproduction (McEwen and Wingfield, 2010; Romero, 2002). As the northern-most hibernating small mammal, arctic ground squirrels have a single opportunity per year for reproduction before focus shifts to increasing mass sufficiently for over-winter survival. Strong sexual selection has also likely driven the evolution of important sex-specific differences in the expression and timing of life-events across the short active season of this species. As a reflection of the seasonal routines of arctic ground squirrels, we found that male and female squirrels showed different seasonal patterns of FCM levels and activity.

Our results were similar to other studies revealing elevated GC levels during lactation in female arctic ground squirrels (Boonstra et al., 2001a; Sheriff et al., 2017) and other rodent species (Boswell et al., 1994; Dantzer et al., 2010; Kenagy and Place, 2000; Smith et al., 2012). Lactation is the most metabolically demanding period of a mammal's life-history (Fletcher et al., 2012; Kenagy et al., 1989), and seasonal elevations in GCs during this time may be important in both the mobilization of energy stores as well as regulating adjustments to foraging behavior. Increases in GCs have also been linked to suckling (Walker et al., 1992) as well as facilitating milk production (Casey and Plaut, 2007; Motil et al., 1994). In the present study, lactating females had the highest levels of FCMs, above-ground activity, and also showed seasonal elevations in time spent below-ground. During this time, females face a trade-off between foraging above-ground and tending to young underground. Our results were consistent with findings from Williams et al. (2016) that found that lactating arctic ground squirrels increase

the frequency of their forays below-ground and become more active per unit time. GCs have known effects on foraging behavior in mammals (Landys et al., 2006), and the positive association found here between FCM levels and activity in lactating females supports the hypothesis that GCs modulate energy acquisition and mobilization in association with the heightened physiological state of reproduction.

Given that both male and female squirrels were active upon first arrival at our study site, it is unlikely that captured male FCM concentrations were representative of peak breeding (Sheriff et al., 2011), which may have occurred up to a week prior. While there was no significant difference in male FCM concentration from mid- to late-April compared to other stages, mean values were slightly higher, suggesting that FCM values during this time may reflect the tail end of the breeding season. The lack of seasonal trends in FCM levels of males, but not females, is likely a reflection of sex-specific biases in reproductive investment and the polygynous/promiscuous mating system of arctic ground squirrels (Lacey et al., 1997). High basal GC levels in males likely only occur during the short breeding interval (Delehanty and Boonstra, 2011) and may serve an adaptive value in helping squirrels maintain energy balance during increased activity (Sandi et al., 1996), as well as vigilance (Roelofs et al., 2007), and aggression (Mikics et al., 2004). Indeed, male above-ground activity was highest and time spent below ground was lowest during mid-April, followed by respective downward and upward trends that occurred over the following weeks, suggesting that males were exiting the breeding season when our study began.

4.2. Relationship between FCMs and body condition

Stress-related GC levels are known to drive weight loss in animals (e.g., Akana et al., 1992). Contrary to our predictions, we found no relationship between FCM concentrations and male or female body condition, suggesting that squirrels were not in a stress-induced catabolic state. Changes in body condition have been shown to induce biphasic responses in GC secretion, with dramatic increases in GC concentrations only apparent when body condition crosses a threshold of deterioration (Le Ninan et al., 1988; Romero and Wikelski, 2001). Sustained elevations in GCs due to starvation and food shortage occur when a shift in energy production from fatty acid metabolism (phase II starvation) to the breakdown of essential proteins (phase III starvation) occurs (Cherel et al., 1988; Dallman et al., 1993). As such, species with greater fat storage capacity should remain in phase II for longer periods of time, with delayed effects of deteriorating body condition on GC secretion. For example, small birds maintain relatively low amounts of fat when compared to mammals and can enter phase III starvation in only a couple days (e.g., Rodríguez et al., 2005). Arctic ground squirrels, which fluctuate their body fat percentages across an eight-fold range (Lee et al., 2011), may be capable of metabolizing energy from endogenous lipid reserves for extended periods of time before mounting a stress response.

It is also possible that changes in baseline GC secretion serves a function in regulating predictable changes in body mass. Arctic ground squirrels, among other rodent species adapted to seasonal environments, likely possess endocrine mechanisms that regulate changes in seasonal adiposity (Nunes et al., 2006; Scherbarth and Steinechner, 2010). Consistent with other findings on seasonal body mass dynamics of arctic ground squirrels (Buck and Barnes, 1999a), both male and female squirrels appeared to consistently increase in body mass and condition throughout the year. However, these increases did not parallel observed changes in FCMs, which were more variable and differed depending on sex. Moreover, comparisons of patterns in FCMs with above-ground activity suggest that GCs are not involved increases in foraging for pre-hibernation fattening. It is possible that our sampling intervals were not properly adjusted to capture trends in how FCMs and body condition covary, as rates of weight gain should be most rapid after July at our study site (Buck and Barnes, 1999a; Sheriff et al.,

2013). While basal GC concentrations may drive changes in body mass through changes in metabolism and food intake (Boswell et al., 1994; Green et al., 1992; Nunes et al., 2006; Strack et al., 1995), more research is needed to determine the causal relationship between GCs and programmed weight gain in hibernators.

4.3. Effects of weather on FCMs and activity

Our results indicate that weather conditions influence patterns of GC secretion in arctic ground squirrels, but this effect is dependent on season. Notably, main effects of weather on FCM concentrations were most prominent during the first collection interval in mid-spring, when temperatures were lowest (-5°C compared to 6°C and 14°C during late-spring and mid-summer, respectively). During mid-spring, our analyses suggest that the effect of temperature on FCM concentration is dependent on wind speed, with the relationship between FCMs and temperature positive under high winds and negative during low winds. This result is difficult to interpret, but may be due to the fact that values of ambient temperature during this time ranged from being well above (0.4°C) to well below (-20°C) the seasonal average temperature of squirrel burrows (-7 to -11°C) (Buck and Barnes, 1999b). Squirrels may gain a thermal advantage by spending more time in burrows when ambient temperatures are below burrow temperatures, only interfacing with surface wind conditions during higher ambient temperatures. This hypothesis is corroborated by our finding that squirrels appear to spend more time below ground when temperatures are below 0°C , and we found no effect of windspeed on time spent below-ground. In a recent study, Studd et al. (2020) showed that activity levels of endotherms likely increase exponentially as ambient temperatures approach the thermal neutral zone. Further studies are necessary to explore the influence of accessibility to thermal refugia and other environmental buffers on the dynamics of the stress response and behavior.

We suggest four possible explanations for the lack of FCM response to environmental conditions during the rest of the season from late-spring to mid-summer. First, ambient air temperatures during late-spring and mid-summer, when compared to mid-spring, were much closer to the lower critical temperature of arctic ground squirrels (18°C) (Chappell, 1981), and conditions found in the year of this study may not have been extreme enough to induce increases in GC secretion. Second, because behavioral thermoregulation via changes in activity patterns are suggested to help animals balance their energy budgets (Studd et al., 2020; Terrien, 2011; Zhang et al., 2019), squirrels may be able to rely on compensatory behavioral adjustments alone to meet changes in their metabolic requirements. Our results, along with those from Williams et al. (2016), suggest that thermoregulatory conditions are an important driver in determining arctic ground squirrel activity patterns. As such, squirrels may be able to escape unfavorable environmental conditions on the surface by moving below-ground or decreasing overall activity levels, without mounting a stress response. Third, seasonal changes in body fat percentage, which contributes to available energetic reserve and thermal resistance, may influence thresholds for the GC-mediated stress response to inclement weather. Indeed, we found that male and female arctic ground squirrels increased in body mass and condition throughout the year, and FCMs were most affected by weather conditions when both ambient temperature and body condition were lowest. Finally, sensitivity of the GC-mediated stress response to environmental stressors may be affected by reproduction (Wingfield and Sapolsky, 2003), an event that encompasses a significant portion of the short active season of arctic ground squirrels. Male arctic ground squirrels spend the beginning of the season in intense competition for mates, and female arctic ground squirrels spend roughly half of their season undergoing gestation and lactation. During times of reproduction, the sensitivity of the stress response is attenuated in mammals. Stress-induced GC concentrations are markedly lower during pregnancy and lactation (Lightman et al., 2001; Stern et al., 1973), and male arctic ground squirrels have been

shown to maintain breeding physiology and behavior despite chronically high levels of circulating cortisol (Boonstra et al., 2001b).

4.4. Relationship between FCMs and activity

To our knowledge, no studies have examined how GCs might influence the daily activity patterns of a free-living mammalian species. Here, we show that higher FCM concentrations predicted higher levels of above-ground activity, but not time spent below-ground, during morning hours. Given that our model controlled for the effects of sex and season, this relationship likely reflects the relationship between behavior and acute elevations in GCs. While our initial prediction was that high FCM concentrations would be associated with squirrels employing a “sit-and-wait” strategy and spending more time below-ground, it may be prudent to also acknowledge that the impacts of GCs on behavior are sensitive to both concentration (Silverin, 1986) and the context of the stressor (Haller et al., 1997; Nephew et al., 2003). It is conceivable that, at least in the year of this study, acute elevations in GC concentrations may play a more important role in facilitating behaviors related to energy acquisition rather than escape and avoidance. Indeed, the stimulatory and permissive effects that GCs exert on feeding behavior have been well documented in laboratory rats (la Fleur, 2006; Santana et al., 1995). Moreover, because FCMs provide an integrated measure of circulating cortisol across the day while patterns of above- and below-ground behaviors vary on different temporal scales, it can be unclear how different measures of activity are represented within variation in FCMs. Although our analysis suggests that circulating cortisol levels influence foraging behavior in squirrels, the directionality of this relationship should be taken as tentative as the opposite may also be true. Lastly, we urge caution in the interpretation of these results because of our limited sample size of collared animals from which FCMs were also collected.

4.5. Conclusions

Throughout their daily and seasonal routines, activation of the stress axis serves a role in helping animals energetically reconcile demands from both the predictable and unpredictable components of their fluctuating environment. For free-living animals, it becomes important to consider the unique life-histories and reproductive strategies of species when interpreting how GC's effects are manifested in changes in physiology and behavior. Our findings from arctic ground squirrels suggest that patterns in GC secretion and behavior are primarily driven by predictable seasonal changes in reproduction. The main limitation to this study was partite sampling of FCMs across the active season, which precludes more in-depth analyses of its relationship with activity. Nonetheless, our results demonstrate the efficacy of emerging animal tracking technologies in elucidating the relationships between GCs and behavior in previously difficult to study free-living mammals.

Ethics statement

This study adhered to animal-care protocols and was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC no. 340270). Work at our study sites was also permitted by the Alaska Department of Fish and Game (Permit 16–013) and the Bureau of Land Management (Permit F-94817).

Author contributions

VYZ, CTW, and CLB contributed to the development of the concept. VYZ captured animals and collected field data. RP created antibodies and protocols for assays. VYZ analyzed data, drafted figures, and wrote the initial manuscript with input for CTW and CLB. All authors contributed to revisions of the manuscript.

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Declaration of competing interest

The authors declare no competing interests.

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