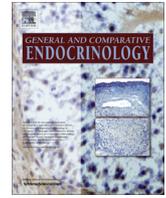




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Fecal cortisol levels predict breeding but not survival of females in the short-lived rodent, *Octodon degus*

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ABSTRACT

The cort-adaptation hypothesis indicates that an association between glucocorticoid (cort) levels and fitness may vary with the extent to which reproduction or breeding effort is a major determinant of cort levels. Support for a context dependent association between cort and fitness comes mostly from relatively long-lived, bird species. We tested the hypothesis that there are gender and context (life-history) specific cort-fitness relationships in *degus*, a short-lived and generally semelparous social rodent. In particular, we used demographical records on a natural population to estimate adult survival through seasons and years and linked that to records of baseline cort (based on fecal cortisol metabolites). We found no evidence for a direct relationship between baseline cort and adult survival across seasons, and this lack of association was recorded irrespective of sex and life history stage. Yet, cort levels during early lactation predicted the probability that females produce a second litter during the same breeding season, supporting a connection between baseline cort levels and breeding effort. Overall, the differential effects of cort on survival and breeding supported that the extent of cort-fitness relationships depends on the fitness component examined.

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1. Introduction

Central to life-history theory is the tenet that resources and available energy are limited, and consequently organisms trade off competing activities and processes to maximize fitness (Roff, 1992; Stearns, 1992). For instance, investment in current reproduction may lead to lower future survival or reproductive success (Garratt et al., 2011; Nilsson and Svensson, 1996; Stearns, 1992). While ecological causes and evolutionary consequences to these trade-offs are relatively well known (Roff, 1992; Stearns, 1992), interest has turned into integrative studies to determine the proximate underpinnings of these relationships (Garratt et al., 2011; Ricklefs and Wikelski, 2002; Selman et al., 2008, 2012). In particular, a key role of glucocorticoids (stress hormones; herein referred to as 'cort') as mediators of a trade off in self-maintenance versus reproduction has been established (Bonier et al., 2009a,b; Lovejoy and Barseyte, 2011).

Glucocorticoid hormones are a main component of the hypothalamus-pituitary-adrenocortical axis (HPA), which in turn is

one of the two major physiological systems used by animals to respond to social and environmental stressors (Nelson, 2011). The phenotypic effects (or expression) of this stress response involves variation in cort concentration, the temporality of cort increase and decrease (negative feedback), and variation in the density and location of cort receptors (Romero, 2002). Since cort typically divert energy from long-term storage for immediate use (Awerman and Romero, 2010; Sapolsky et al., 2000), short-term and seasonal variation in baseline levels of cort (i.e., different allostatic states) represent normal stress responses to predictable and unpredictable effects of stressors that act on the body to increase energy use above some resting or basal level (Ashley and Wingfield, 2012; Bonier et al., 2009a,b; Breuner et al., 2008; Landys et al., 2006; Nelson, 2011; Sapolsky et al., 2000). Thus, short-term (e.g., under acute stress) and seasonal elevations of cort above baseline levels are generally beneficial and do not lower fitness. In contrast, whenever cort remains elevated above baseline for long periods (i.e., chronic stress), the associated metabolic costs may exceed available resources, or make individuals more susceptible to perturbations in the environment (Ashley and Wingfield, 2012; Bonier et al., 2009a,b; Landys et al., 2006), and ultimately lower fitness (Bonier et al., 2009a; Landys et al., 2006; Sapolsky, 1985). Based on these considerations, the cort-fitness hypothesis predicts that

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relatively high baseline cort levels in response to environmental challenges should result in relatively low fitness (Bonier et al., 2009a).

More recently, the cort–fitness hypothesis has been embedded into the cort–adaptation hypothesis to accommodate the fact that the relationship between cort levels and fitness may be contingent upon reproductive (life history) stage of individuals (Bonier et al., 2009a). The cort–adaptation hypothesis posits that high baseline cort levels (i.e., seasonal baseline) are necessary to sustain immediate reproductive challenges (Bonier et al., 2009a,b; Landys et al., 2006). Reproductive individuals are considered to be in good condition when able to sustain elevated levels of baseline cort. The relationship between fitness (e.g., reproductive success) and cort levels is expected to be positive when reproduction is the major determinant of predictable energetic demands relative to ecological factors (Bonier et al., 2009a). Nevertheless, it is clear that maintaining reproductive effort (or investment) during a period over which resources are typically decreasing may compromise subsequent ability to respond to stressors, survive, and breed (Goutte et al., 2010a; Lovejoy and Barsyte, 2011; Satterthwaite et al., 2010). In this sense, we may expect a switch to a negative relationship between current levels of cort and survival as well as future reproductive success.

A mediator role of life history stage on the cort–fitness relationship is supported by recent studies on relatively long-lived birds. Before egg laying (*Passer domesticus*) (Ouyang et al., 2011) or early in incubation (*Tachycineta bicolor*) (Bonier et al., 2009b), baseline cort negatively covaried with the number of offspring subsequently produced and the probability to survive to the following breeding event (only *T. bicolor*). In contrast, baseline cort levels during the period of nestling provisioning positively covaried with offspring produced in both species (Bonier et al., 2009b; Ouyang et al., 2011), implying that life history stage mediates the cort–fitness covariation.

Previous studies that compared the cort–fitness relationships of individuals at different life history states (e.g., breeding vs. non-breeding) also examined different fitness measures. Bonier et al. (2009a) suggested that the extent of cort–fitness relationships depends on the fitness measures used. For example, corticosterone levels of *Rissa tridactyla*, a colonially breeding bird, sampled during the arrival stage reliably predicted laying success, but were less reliable at predicting hatching and fledging success (Lanctot et al., 2003). Thus, it is important to quantify cort–fitness relationships based on proxies similarly related to fitness during the same life history state.

Compared with birds, fewer studies on mammals have examined the cort–fitness covariation (Bonier et al., 2009a). Similar to bird models (Bonier et al., 2009a,b), female mammals with relatively low baseline cort during mating period (i.e., reflecting good condition early in the breeding season) should exhibit relatively higher subsequent survival to lactation, and reproductive success. However, during lactation the relatively high cort levels needed to sustain milk production and parental care duties should correlate with relatively greater current reproductive success in the females (Ebensperger et al., 2011a). In contrast, males with relatively high baseline cort (needed to sustain mate searching and territory defence) should experience relatively high reproductive success yet low subsequent survival. How these relationships in males vary during offspring rearing might depend on the extent to which males provide direct (e.g., offspring grooming, feeding) or indirect (e.g., territory defence) forms of parental care. Positive correlations between cort and reproductive success might be predicted in species with parental males during offspring rearing, yet no relationship might be expected in males of non-parental species at this time.

1.1. Model species and predictions

Herein we examined how individual baseline cort levels relate to survival and breeding frequency (two measures of direct fitness), and how covariation in these fitness variables and cort is contingent upon different breeding life stages of the social rodent, *Octodon degus* (Ebensperger et al., 2004, 2011a; Hayes et al., 2009). Degus inhabit the open savannahs of central Chile, where most females typically breed once per year in early austral winter (June) and give birth to a mean of 6 offspring in early austral spring (September) (Ebensperger and Hurtado, 2005). Occasionally, degus undergo a second breeding event as a result of post partum estrous with conceptions during late December and lactation extending through January (i.e., early austral summer) (Contreras and Bustos-Obrégón, 1977; Rojas et al., 1977). Degus experience a relatively long gestation (ca. 90 days) needed to produce precocial offspring (Long and Ebensperger, 2010). However, and similar to rodent species with altricial offspring, lactation remains as the most energy demanding life history stage in degus (Veloso and Bozinovic, 2000).

Degus exhibit intriguing similarities and differences compared with more “traditional” study models used to examine the connection between life history, fitness, and stress hormones. Typically, 85–90% of male and female adults do not survive to their second year of age in the wild (Ebensperger et al., 2009; Meserve et al., 1993). As a consequence, most individuals breed once in their lifetime, a condition that parallels semelparity in some (mostly male) dasyurid and didelphid marsupials (McDonald et al., 1981; Oakwood et al., 2001; Schmidt et al., 2006). Under these conditions, we may expect explosive reproductive strategies, such as maximal investment in current reproduction at a cost to future reproduction, characteristic of semelparous species. However, the causes of “degu semelparity” seem different from marsupial semelparity. Degu survival and fecundity (number of offspring produced) increase with increasing rainfall (i.e., food abundance) and with decreasing predation rate (Meserve et al., 1993; Previtali et al., 2010), and male and female degus can live and breed over multiple years in captivity (Correa, 2012). These observations suggest a major influence of ecological constraints on survival and reproduction as drivers of degu “semelparity” compared with the physiological effects of an explosive breeding activity that characterize several marsupials (Oakwood et al. 2001; Schmidt et al. 2006).

The relevance of degus to the cort–adaptation hypothesis, typically posited in iteroparous species (Bonier et al., 2009a), is further highlighted by the known endocrine basis of degu reproduction. Two previous studies support an antagonistic association between glucocorticoids and androgens in males (Kenagy et al., 1999; Soto-Gamboa et al., 2005), implying the possibility that long-term elevation of cort may reduce male fertility (Ge et al., 1997). However, females with higher cort levels during early lactation produce more surviving offspring than females with low cort levels, implying a rather positive role of cort to female breeding (Ebensperger et al., 2011a). Thus, and compared with previous studies on birds (Blas et al., 2007; Goutte et al., 2010a; Rivers et al., 2012), degus represent an opportunity to further test the generality of life history stage as a mediator on the cort–fitness relationship in a short-lived, eutherian model species.

During offspring rearing, female degus engage in several forms of communal care, including huddling and retrieving of non-descendent offspring, and communal nursing (Ebensperger et al., 2002, 2007, 2010). Thus, following Silk (Silk, 2007), degus are plural breeders with communal care. During mating time, males spend most of their time chasing other males and receptive females yet do not seem to defend territories during lactation (Ebensperger and Hurtado, 2005; Soto-Gamboa et al., 2005), implying low if any indirect form of care. Lab studies suggest that although

Table 1
Number of burrow systems examined and the number of days that each burrow system was trapped per season (and life history stage of degus) and year of study at Rinconada de Maipú.

Austral season	Life history stage	Burrow systems				Number of days			
		2009	2010	2011	2012	2009	2010	2011	2012
Summer	Non breeding (or second lactation event ^a)	–	38	37	43	–	15	15	16
Winter	Mating	50	42	54	44	35	30	37	35
Spring	Main lactation event	45	40	68	–	44	42	48	–

^a A second breeding event was recorded in January 2010 exclusively (see Results).

male degus huddle over and groom the pups, these direct forms of care do not affect the development of pups (Ebensperger et al., 2010). Given these observations, we consider degus to be a species with extensive maternal yet limited male parental care.

We aimed to test whether the relationship between cort levels and fitness is contingent upon gender and reproductive (life history) stage of degus, a key aspect of the cort-adaptation hypothesis. We derived predictions specific to degus based on the general expectations that current levels of cort should be positively associated to fitness whenever reproduction is the major determinant of current energetic demands, but negatively associated to subsequent survival and reproductive success. With regard to the females, we predicted: (i) cort levels during mating (winter) season should not predict survival from winter through lactation (spring) season; (ii) survival through summer should be negatively associated with spring cort levels, particularly in years with two events of breeding; (iii) the ability of females to exhibit two breeding events within same year should decrease with spring cort levels; and (iv) cort levels during mating season (winter) should not predict survival through next mating season. With regard to the males, we predicted that: (v) survival from winter (mating) through spring decreases with increasing winter cort levels; (vi) spring cort levels should be negatively related to survival through early summer, yet only in years with records of two main breeding events; (vii) cort levels during mating season (winter) should not predict survival through next mating season.

2. Materials and methods

2.1. Demography

We used demographical records across years 2009–2012 on a natural population of degus to examine how variation in survival (males and females) and fertility (females) track variation in cortisol (the main glucocorticoid in degus) (Kenagy et al., 1999; Sheriff et al., 2010). The study site was located at the Estación Experimental Rinconada de Maipú (33°23 S, 70°31 W, altitude 495 m), a field station of Universidad de Chile. This study area is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers (di Castri and Hajek, 1976). We used capture-mark-recapture trapping to determine breeding condition and quantify adult survival. The live trapping protocol was set in the context of a long-term study of degu sociality, and aimed to quantify burrow sharing. Thus, traps were placed at burrow systems, defined as a group of burrow openings surrounding a central location where individuals are repeatedly found during night time telemetry and usually spanning 1–3 m in diameter (Fulk, 1976; Hayes et al., 2007). Given that degus are diurnally active and remain in underground burrows overnight, traps were set prior to the emergence of adults during morning hours (06:00 h). After 1.5 h, traps were closed until the next trapping day. We determined the identity, location, sex, body mass (to 0.1 g) of all degus and reproductive condition of all females (perforated, pregnant, or lactating). Gravid females typically had enlarged abdomens, and fetuses could be de-

tected easily by gentle palpation. Lactation was recorded if females expressed milk in response to gentle squeezing of two randomly selected nipples (Ebensperger et al., 2011b). During trapping, we marked every degu at the time of first capture with a tag on each ear (Monel 1005-1, National Band and Tag Co., Newport, USA). We used two ear tags (with identical ID codes) because this procedure reduced to zero the probability that an animal missed both tags across years. The number of burrow systems and the number of days that each burrow system was trapped per season (and life history stage of degus) and year of study at Rinconada are summarized in Table 1. The total area examined at Rinconada was nearly 2 h and did not vary across seasons or years of study.

2.2. Fecal cortisol metabolite determinations

We used a noninvasive fecal glucocorticoid analysis to extract fecal cortisol metabolites (thereafter FCM) as a means of assessing secretion of cort in degus. To increase our ability to draw general conclusions we restricted this measurement of stress response to adult degus (Goutte et al., 2010a). Fecal glucocorticoid assays reliably reflect endogenous changes in adrenal activity of rodents (Boonstra et al., 2001; Harper and Austad, 2000; Mateo and Cavigelli, 2005), including degus (Soto-Gamboa et al., 2009). In contrast to plasma steroid measurements, fecal steroid measurements represent a cumulative secretion over a number of hours before capture and so may not include the short-term hormonal fluctuations caused by capture and blood drawing (Anestis, 2010; Good et al., 2003). Moreover, FCM has been shown to reflect free cortisol, the biologically active fraction of cortisol (Sheriff et al., 2010), and predict survival in wild mammals (Cabezas et al., 2007; Pride, 2005). Therefore, we used FCM as a measure of baseline cortisol levels.

Fecal samples were obtained from all adult degus once per season (austral winter or spring) at first capture by placing Tomahawk traps on paper towels during processing. While fecal glucocorticoid analysis decreases the variability associated with serum samples from diurnal and pulse secretion patterns (Von der Ohe and Servheen, 2002), we further controlled for hourly variation by means of trapping degus between 06:30 and 08:00 h. All fecal pellets were collected within 2 h of closing traps. Thus, no fecal pellets were collected from degus that spent more than 3.5 h in a trap. A validation study on degus indicated that fecal measurements reflected baseline cortisol levels experienced by individuals 5–6 h before defecation (Soto-Gamboa et al., 2009). Collected feces were immediately stored into Eppendorf tubes with 0.8 mL of 95% ethanol, transported to the lab within 2–3 h, and refrigerated at 5 °C until assayed. Samples were stored for about 1 month before FCM extraction. During spring season, fecal samples of females and males were collected when females were in early lactation.

We extracted FCM with 80% ethanol, as recommended in previous studies (Mateo and Cavigelli, 2005; Soto-Gamboa et al., 2009). Feces were dried in an oven (95 °C; 4–5 h), crushed and homogenized. A 0.01 g portion (only 0.005 g in two samples) of each sample was mixed with 1 mL of 80% ethanol, vortexed for 5 s, and

centrifuged at 3000g for 20 min. Supernatants were removed and stored at -20°C until determination of FCM. Cortisol metabolites in feces were quantified with the Coat-A-Count RIA kit (Siemens Healthcare Diagnostics Inc., Los Angeles, California 90045, USA) in the Radio Immune Essay Laboratory at P. Universidad Católica de Chile. Fecal samples were assessed with the use of steroid-free human serum (standard zero) to provide similar protein environments (Mateo and Cavigelli, 2005; Soto-Gamboa et al., 2009). The intra- and inter-assay coefficients of variation of the immunoassay were 6.5% and 7.5%, respectively.

2.3. Variation in body condition

The effects of chronic stress on fitness may involve reductions in body mass or condition (Blas et al., 2007; Cabezas et al., 2007; Landys et al., 2006; Ricklefs and Wikelski, 2002), typically due to muscle breakdown and increasing catabolic action (Awerman and Romero, 2010). Since body weight is a predictor of body condition in rodents (King and Allainé, 2002), we recorded percent of variation in body weight as a measure of the extent to which body condition decreased (or increased) relative to condition at the beginning of each season. Percent variation in body weight was determined from recapture records within seasons.

2.4. Direct fitness measures

Following previous studies (Blas et al., 2007; Meserve et al., 1993), we quantified survival of adult males and females based on subsequent recapture. This estimate of survival is appropriate in degus for the following reasons: dispersal is not sex biased, animals settle close to their burrows of origin, and recapture rate of adults and offspring is high (i.e., within 30–40 m) (Quirici et al., 2011a,b), implying that survival is unlikely to be underestimated by individuals alive that were not recaptured. Despite this, we used a conservative criterion to record survival. First, degus with only a single capture were considered as non residents and excluded from analysis. Second, every degu known to be alive in winter, summer, or in spring was tallied as 'not survived' only when not recaptured through two or more subsequent trapping seasons.

2.5. Statistical analysis

To examine predictions (i) and (v), we focused on females and males known to be alive during winter (mating time) and that were potentially recaptured during spring (lactation time). To examine predictions (ii), (iv), (vi) and (vii) we focused on females and males known to be alive during spring (lactation time) and that were potentially recaptured during subsequent summer and winter (mating time). Finally, to examine prediction (iii), we focused on females known to be alive in spring and that were potentially noted to exhibit a second pregnancy and lactation during subsequent summer season.

Demographical records from this study indicated that on average less than 5% of adult degus known to be alive in winter (mating) survive to next winter (see Results). Thus, most (ca. 95%) adult females and males in the population at the time of mating were yearlings. Based on this information, we considered individual degus as independent replicates across years, and did not include age of individuals as a factor during statistical analyses.

We used a generalized linear and non linear model approaches to examine the main effects of winter FCM (a continuous predictor), percent variation in body weight during winter (a continuous predictor), sex (male vs. female), and year cohort (2009 vs. 2010 vs. 2011) on degu survival from winter to spring (yes vs. no). We fitted the dependent variable to a Binomial distribution with a Logit link function. Based on our a priori predictions (i) and (iii), we also con-

sidered a winter FCM-by-sex interaction term to the other main effects in the model.

We used a similar approach to examine the main effects of spring FCM (a continuous predictor), percent variation in body weight during spring (a continuous predictor), sex (male vs. female), and year cohort (2009 vs. 2010 vs. 2011) on degu survival from spring to summer (yes vs. no). Again, we fitted the dependent variable to a Binomial distribution with a Logit link function. Based on our a priori predictions (i) and (iii), we also added a spring FCM-by-sex interaction term to the other main effects in the model.

The examination of degu survival to next winter (mating) season was complicated by the fact that few adults from every yearly cohort were recaptured during subsequent winter. For example, no degu known to be alive in 2009 was recaptured in winter 2010, and only five males and one female known to be alive in winter 2010 were recaptured in winter 2011. As a result of this natural, yet unbalanced variation we used a generalized linear and non linear model to test the main effects of spring FCM (a continuous predictor), sex (male vs. female), percent variation in body weight during spring (a continuous predictor), and spring FCM-by-sex interaction on degu survival (yes vs. no) from spring through next winter. Yet, we could not include a main effect of year or any interactions with year in the model.

We used a generalized linear and non linear model approach to examine the main effects of spring FCM and percent variation in body weight during spring (two continuous predictors) on the probability of females to breed twice (yes vs. no). Since females were recorded to breed twice in a season in 2009 but not in other years, we restricted this analysis to 2009 data. However, the addition of female degus examined during years 2010 and 2011 did not change the main findings of this analysis (results not reported). All data are reported as means \pm SE. An α level of $P = 0.05$ was used in all analyses. Analyses were conducted using Statistica 9.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

3. Results

3.1. Overall fitness patterns

A total of 204 different adult degus were examined between winter 2009 and winter 2012, providing 211 data records for subsequent analyses. Only seven animals provided data on two different years. The total number of captures and recaptures was 4525 and averaged 21.4 ± 1.1 captures per degu.

In relation to individuals that were known to be alive in winter (mating) season, $83.0 \pm 2.1\%$ ($n = 3$ years of study) of females and $73.1 \pm 5.4\%$ ($n = 3$ years of study) of males known to be alive in

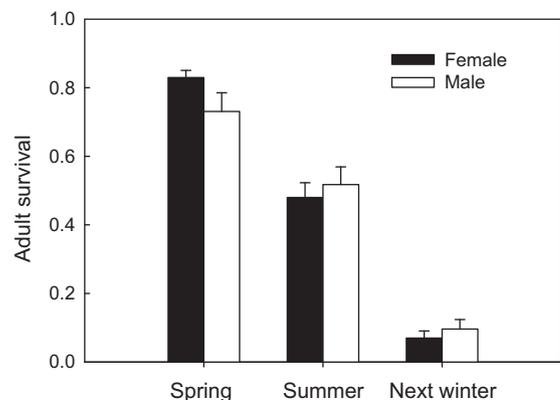


Fig. 1. Proportion of adult male and female degus known to be alive during winter (mating) that survive to the following spring (lactation time), to summer, and to the following winter. Data are means \pm SE ($n = 3$ study years).

Table 2
Results from the generalized linear and non linear models. Bold typing is used to highlight statistically significant effects.

Dependent variable	Effect	df	Wald χ^2	P-value
Survival from mating (winter) to main lactation (spring)	Sex	1	0.0092	0.9234
	Year	2	5.9112	0.0520
	Winter FCM (ng per g)	1	0.1484	0.7001
	Winter percent variation in body weight	1	8.5632	0.0034
	Winter FCM-by-sex interaction	1	0.1048	0.7462
Survival from main lactation (spring) to summer ^a	Sex	1	2.9285	0.0870
	Year	2	0.4051	0.8166
	Spring FCM (ng per g)	1	0.0546	0.8152
	Spring percent variation in body weight	1	3.1294	0.0769
	Spring FCM-by-sex interaction	1	1.9172	0.1662
Survival from main lactation (spring) to next mating (winter)	Sex	1	3.1320	0.0768
	Spring FCM (ng per g)	1	0.0020	0.9641
	Spring percent variation in body weight	1	4.7780	0.0288
	Spring FCM-by-sex interaction	1	2.0055	0.1567
Multiple breeding	Spring FCM (ng per g)	1	5.0272	0.0250
	Spring percent variation in body weight	1	2.2976	0.1296

^a Summer typically represents the non breeding period in degus that do not breed twice during the same year.

winter (mating season) survived to spring (lactation season) on average (Fig. 1). Subsequently, $48.0 \pm 4.3\%$ of females and $51.8 \pm 5.2\%$ of males were known to have survived through summer (Fig. 1). Only $7.0 \pm 2.0\%$ of females and $9.6 \pm 2.8\%$ of males known to be alive in winter survived to subsequent winter (Fig. 1). Female degus exhibited a second pregnancy during spring and subsequent lactation in early summer in 2009 but not in any other year. Thus, 12 out of 26 females (54%) bred twice in 2009.

3.2. Survival from winter (mating) to spring (lactation)

Degu survival (based on recapture) from winter (mating) to spring (lactation) season was unaffected by sex, winter FCM, or a sex-by-winter FCM factor interaction (Table 2). There was a statistically significant main effect of percent variation in body mass on survival, and where male and female survivors more likely were individuals that gained body weight (Fig. 2). On average, degus that survived through spring gained $6.1 \pm 1.2\%$ ($n = 98$) of their body weight through winter, mating season. In contrast, degus that did not survive tended to lose or not experience changes in body weight ($-0.02 \pm 1.4\%$, $n = 52$). A marginally significant effect of year (Table 2) suggested survival from winter through spring during 2009 (64%, or 65 degus) was lower than during 2010 (80%, or 33 degus) and 2011 (90%, or 61 degus).

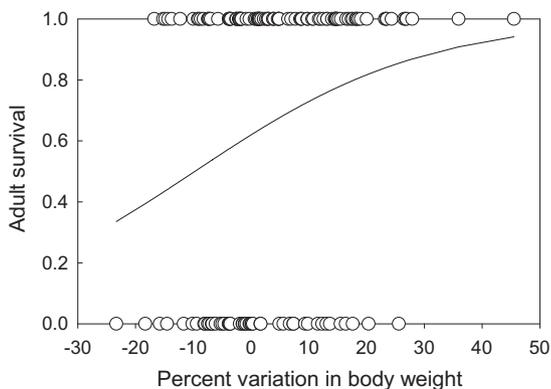


Fig. 2. Probability of survival to spring of adult degus known to be alive in winter as a function of percent variation in body weight during winter.

3.3. Survival from spring (lactation) to summer

Survival of degus from spring to summer was unaffected by year, spring FCM, or a sex-by-FCM factor interaction (Table 2). There were only marginally significant main effects of sex and percent variation in body weight on survival (Table 2). Survival of females (63%, or 52 degus) tended to be lower than that of males (68%, or 52 degus), and male and female survivors gained more body weight ($3.3 \pm 1.0\%$, $n = 93$) than non survivors ($1.1 \pm 1.3\%$, $n = 47$) during spring.

3.4. Survival from spring (lactation) to next winter (mating)

Degu survival from spring to subsequent winter was not affected by spring FCM, or a sex-by-spring FCM factor interaction (Table 2). However, there was a statistically significant main effect of percent variation in body weight on survival, where male and female survivors more likely were individuals that gained body weight than non survivors (Table 2, Fig. 3). On average, degus that survived through next winter gained $8.6 \pm 3.1\%$ ($n = 10$) of their body weight through the previous spring. Animals that did not survive tended to gain $2.1 \pm 0.8\%$ ($n = 130$) of their body weight. There was a marginally significant main effect of sex on survival (Table 2), where females tended to survive less (7%, or 6 females) than males (11%, or 8 males).

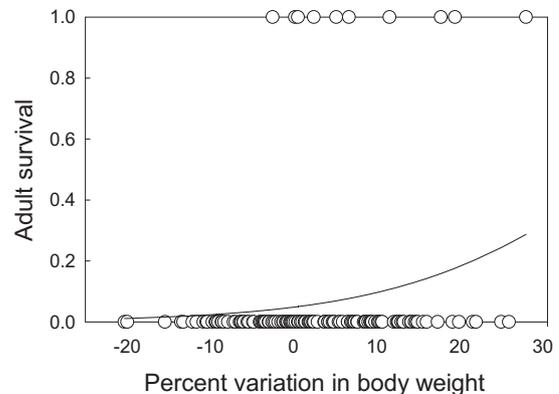


Fig. 3. Probability of survival to subsequent winter of adult degus known to be alive during the previous spring as a function of percent variation in body weight during spring.

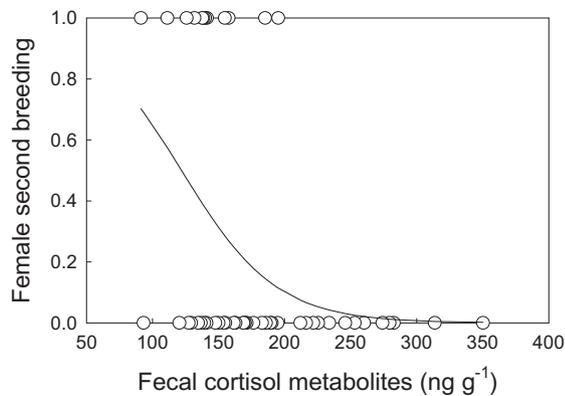


Fig. 4. Probability of adult females to breed twice during spring (with conceptions in early summer) as a function of fecal cortisol metabolites (FCM) measured during early lactation of major spring breeding event.

3.5. Multiple breeding

A total of 83 females were monitored during spring across years of study. Of these, only one female did not show evidence of parturition or lactation. Two females were noted to breed in spring on different, consecutive years.

Multiple breeding within same year took place during 2009 exclusively. We recorded a statistically significant main effect of main lactation, spring FCM on the probability that a female bred twice in 2009 (Table 2). Thus, females that exhibited a second breeding event as a consequence of postpartum estrus had lower FCM levels determined early during spring, main lactation (mean \pm SE = 142.5 ± 8.3 ng g⁻¹, $n = 12$) than females that breed once (mean \pm SE = 207.9 ± 18.2 ng g⁻¹, $n = 14$, Fig. 4). The main effect of percent variation in body weight on multiple breeding was not statistically significant (Table 2). Including FCM and percent variation in body weight recorded during mating (winter) of 2009 to the model did not change these findings and revealed no effect of these factors (not shown).

4. Discussion

4.1. Main findings

Results of this study revealed five main points. First, we found little if any support for a direct connection between baseline cort levels (based on FCM) and adult survival across seasons. Survival across seasons within years is likely a major component of fitness in degus facing extremely low inter annual survival. Second, a lack of association between baseline cort and adult survival was recorded irrespective of sex and life history stage, providing no support to our a-prior predictions based on a life-history and sex dependent association between cort and survival. Third, percent variation in body weight, an estimate of variation in body condition, was a relatively strong predictor of male and female survival from winter to spring, and from spring to subsequent winter. Fourth, results supported a connection between baseline cort levels during early main lactation and the probability that females produce a second litter within same season. In particular, the probability that females bred twice in the same year increased with decreasing cort levels early during main lactation. These findings are intriguing, implying a role of stress response in regulating the semelparity–iteroparity continuum in degus, a eutherian model. Finally, the differential effects of cort on survival and on breeding supported that the extent of cort–fitness relationships depends on the fitness component examined.

4.2. Association between cort levels, fitness, and life history

The cort-adaptation hypothesis states that an association between cort levels and fitness may vary with the extent to which reproduction or breeding effort is a major determinant of cort levels. This tenet is based on the premise that high baseline cort levels (i.e., seasonal baseline) are necessary to sustain current reproductive challenges (Bonier et al., 2009a,b; Landys et al., 2006). During reproductive life history stages, an individual's fitness is expected to increase with increasing cort levels (Bonier et al., 2009a). Whenever other ecological or social factors become the main drivers of cort levels, fitness might be expected either to decrease or not to vary with cort levels. Evidence for a context dependent association between cort and fitness based on life history stage differences is provided nicely by bird studies. For instance, baseline cort levels before or early in incubation negatively covary with subsequent reproductive success and the probability that adults survive to the following breeding season (Bonier et al., 2009b; Ouyang et al., 2011). However, reproductive success increases with increasing cort levels during subsequent nestling provisioning (Bonier et al., 2009b; Ouyang et al., 2011). Our study on a short-lived, mammalian model species adds on the complexity of the cort–fitness relationship in that this association is contingent upon fitness component examined.

Similar to previous studies (Blas et al., 2007; Cabezas et al., 2007; Romero and Wikelski, 2001), degus that were able to maintain or improve body condition were more likely to survive to the next season than degus whose body condition deteriorated. These findings contrasted with the observation that baseline cort was not a predictor of adult degu survival, implying that this measure of stress response is not directly linked to changes in body condition. However, it is possible that other components of the stress response are more directly linked to degu body condition and survival (Lanctot et al., 2003). This possibility is supported by studies on birds and reptiles in which adult survival is predicted by stress-induced cort or the efficiency of negative feedback and not baseline cort (Blas et al., 2007; Romero and Wikelski, 2001, 2010). Yet, other studies report no differences in the association between survival and stress response when different components of stress response are examined (Angelier et al., 2009; MacDougall-Shackleton et al., 2009), implying this issue requires further examination.

Previously we reported that females with higher cort levels during early lactation produced more surviving offspring than females with low cort levels in two out of 3 years examined, implying that the link between circulating cort levels and reproductive effort may be affected by inter-annual variation in environmental conditions (Ebensperger et al., 2011a). Interestingly, there was not a statistically significant relationship between cort during early lactation and reproductive effort in 2009 (Fig. 3 in Ebensperger et al. (2011a)), the year during which we observed multiple breeding (this study). Moreover, during 2009, females with lower cort during lactation were more likely to breed a second time during the same year than females with higher baseline cort during lactation. Taken together, these findings are consistent with the hypothesis that increasing cort levels to sustain current reproductive effort may compromise subsequent fertility and residual fitness (Goutte et al., 2010b). Cort levels may down regulate reproduction through several pathways (Long and Ebensperger, 2010) including the endocrine pathways that regulate reproductive development, zygote production and reproductive behaviors (e.g., Goutte et al., 2010b). The endocrine basis of degu reproduction remains poorly understood (Hayes et al., 2011), yet available evidence supports an antagonistic association between glucocorticoids and reproductive hormones in males (Kenagy et al., 1999; Soto-Gamboa et al., 2005). Thus our findings strongly support a need for similar studies

on other organisms with varying life histories, particularly on the connections between HPA and hypothalamic–pituitary–gonadal (HPG) axes.

Our study did not support gender- or life history stage-dependent associations between cort and adult survival. These results depart from previous suggestions of a negative relationship between current reproductive effort and subsequent survival in longer-lived and typically iteroparous species. Interestingly, the ecology of “semelparity” observed in degus has some similarities and differences to the partial semelparity recorded in dasyurid and didelphid marsupials in which annual male mortality is very high (McDonald et al., 1981; Oakwood et al., 2001; Schmidt et al., 2006). In degus, ecological conditions (e.g., low primary food abundance, high predation rate) seem to be important drivers of this feature for both males and females. Moreover, these ecological conditions seem to mediate the cort–fitness association in the long-term (Breuner et al., 2008). Multiple breeding in degus was linked to baseline cort during early lactation, yet this phenomenon does not occur annually. In dasyurids, predation may be the primary cause of the mortality of females but not in males, in which physiological costs of mating seem to be the driving factor of high mortality (McDonald et al., 1981; Oakwood, 2000; Oakwood et al., 2001). In some dasyurids, females and males experience similar increases in cort (Naylor et al., 2008) whereas in other species, cort levels are not associated with male mortality (Oakwood et al., 2001). These ecological and physiological differences call for studies on other species with contrasting patterns of seasonal or yearly survival (similar to McDonald et al., 1981) including the quantification of different aspects of the stress response. It is possible that inter-annual variation in the relative contributions of ecological conditions and breeding to allostatic load mediate the connection between cort levels or other components of the stress response (Awerman and Romero, 2010; Davis et al., 2008) and fitness.

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