Habitat type influences endocrine stress response in the degu (*Octodon degus*)

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ABSTRACT

While many studies have examined whether the stress response differs between habitats, few studies have examined this within a single population. This study tested whether habitat differences, both within-populations and between-populations, relate to differences in the endocrine stress response in wild, free-living degus (*Octodon degus*). Baseline cortisol (CORT), stress-induced CORT, and negative feedback efficacy were measured in male and female degus from two sites and three habitats within one site during the mating/early gestation period. Higher quality cover and lower ectoparasite loads were associated with lower baseline CORT concentrations. In contrast, higher stress-induced CORT but stronger negative feedback efficacy were associated with areas containing higher quality forage. Stress-induced CORT and body mass were positively correlated in female but not male degus across all habitats. Female degus had significantly higher stress-induced CORT levels compared to males. Baseline CORT was not correlated with temperature at time of capture and only weakly correlated with rainfall. Results suggest that degus in habitats with good cover quality, low ectoparasite loads, and increased food availability have decreased endocrine stress responses.

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1. Introduction

The stress response is linked with an animal's ability to survive and cope in its environment. Activation of the endocrine stress response results in increased levels of circulating glucocorticoids, such as corticosterone and cortisol (CORT). CORT has many different physiological effects including increased glucose mobilization, increased cardiovascular tone, and inhibition of physiological processes that are not necessary for immediate survival, such as immune and reproductive functions (Sapolsky et al., 2000). While increased CORT secretion is beneficial in the short-term, exposure to high levels of CORT over long periods is thought to be detrimental (McEwen, 1998; Sapolsky et al., 2000). Field studies often measure concentrations of plasma CORT or fecal glucocorticoid metabolites to assess the relative health of animal populations (Cockrem, 2005; Creel et al., 1997; Mason, 1998; Wasser et al.,

1997). While CORT levels may be good indicators of an animal's health, the stress response also reflects the interaction between an animal's physiology and environment (Romero et al., 2009). Animals may modulate their endocrine stress response to better cope with their specific environment, and more research is needed to determine how the stress response varies with environmental factors.

Many studies have examined the effects of habitat on the endocrine stress response. Researchers have studied this interaction by comparing CORT concentrations of species sampled from geographically distinct populations (Lindstrom et al., 2005; Mateo, 2006; Mueller et al., 2007; Romero et al., 2006; Silverin et al., 1997) or along altitudinal clines (Addis et al., 2011; Bears et al., 2003; Busch et al., 2011; Hik et al., 2001; Sheriff et al., 2012). There has been recent interest in the effect of human-induced habitat changes on the endocrine stress response, and investigators have focused on how habitat fragmentation (Rangel-Negrin et al., 2009), urban environments (Fokidis et al., 2011; French et al., 2008; Zhang et al., 2011), and other anthropogenic effects (Homan et al., 2003; Hopkins and DuRant, 2011) influence CORT levels in wild, free-living animals. Since most studies examining the relationship between habitat type and the endocrine stress response have used populations that are geographically distinct, differences

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in CORT between habitats could be attributed to genetic differences. The hypothesis that habitat type affects the stress response within a single population, reflecting phenotypic plasticity, has been relatively less examined.

Habitat type has been reported to influence the stress response in a number of ways. Low food availability can cause increased baseline and stress-induced CORT in wild birds (Buck et al., 2007; Clinchy et al., 2004; Kitaysky et al., 1999). Food availability is linked to body mass or condition, and several studies have found body mass to be negatively correlated with baseline and stress-induced CORT (Cabezas et al., 2007; Clinchy et al., 2004; Fokidis et al., 2011; Kitaysky et al., 2007; Nunes et al., 2002; Schoech et al., 2007). Studies have shown that predator density can be positively correlated with CORT concentrations (Boonstra and Singleton, 1993; Clinchy et al., 2004; Rogovin et al., 2006; Scheuerlein et al., 2001). Within single populations, where predator density should not significantly vary, the amount and availability of suitable cover may better correlate with differences in the stress response between habitat types. Dense, overhead cover may prevent detection by aerial predators, but lateral cover that obstructs sightlines may make animals more at risk to terrestrial predators (Ebensperger and Hurtado, 2005). The lack of adequate and appropriate cover would be predicted to increase required vigilance (Vasquez et al., 2002), which could lead to decreased foraging efficiency or an increase in the number of foraging bouts. However, the cost of increased vigilance could be buffered by the fact that degus may forage socially and will respond to con-specific alarm calls (Ebensperger et al., 2006; Vasquez, 1997). Regardless, cover quality could increase the animal's allostatic load (McEwen and Wingfield, 2003) by affecting predator detection. An animal's allostatic load could also be affected by ectoparasites, which inflict metabolic and immune costs (Lehmann, 1993; Nilsson, 2003) or by poor weather conditions that could decrease food availability. An increased allostatic load could in turn result in an augmented stress response (McEwen and Wingfield, 2003; Romero et al., 2009).

Degus (*Octodon degus*) are social, semi-fossorial rodents that occupy a variety of habitats. We used degus to test whether local habitat type affects the endocrine stress response by measuring baseline CORT, stress-induced CORT, and negative feedback. We examined degus of both sexes at two sites, with one site comprising three habitats abutting each other and presumably within the dispersal distance of the population. We predicted that the stress response would vary more between sites rather than within sites, partly because of local climate but also because of genetic differences between populations (Predictions summarized in Table 1). At each habitat, we quantitatively measured cover availability and degu ectoparasite load, and qualitatively measured food availability. We predicted that degus from habitats with high cover

availability and low ectoparasite loads would have lower allostatic load, resulting in decreased baseline and stress-induced CORT. We are unaware of previous studies examining the impact of cover availability or ectoparasite loads on negative feedback, but we predicted a response paralleling baseline and stress-induced CORT. We also predicted that degus from habitats with high food availability would have decreased baseline CORT, decreased stress-induced CORT, and increased negative feedback. Several studies have found significant relationships between CORT and body mass (Cabezas et al., 2007; Fokidis et al., 2011; Heath and Dufty, 1998; Schoech et al., 2007) so we also examined whether body mass correlated with baseline CORT, stress-induced CORT, and negative feedback efficacy. We predicted that body mass would be negatively correlated with baseline CORT but positively correlated with stress-induced CORT and negative feedback efficacy. We also investigated the relationship between baseline CORT with temperature and rainfall, since weather has been shown to affect baseline CORT (Astheimer et al., 1992; Romero et al., 2000). We predicted that degus sampled immediately after a precipitation event would have decreased baseline CORT since precipitation and food availability are positively correlated.

2. Methods

2.1. Study animal and habitats

We studied degus (*Octodon degus*) because they occupy a variety of habitats, they are diurnal, and their main stress hormone, cortisol, has been successfully measured in wild populations (Kenagy et al., 1999). This study examined degus in two populations, with one of those populations using three different habitats. One population was located near Santiago, Chile at Estación Experimental Rinconada de Maipú (33°23′S, 70°31′W, altitude 495 m), hereafter referred to as Rinconada, a field station managed by the Universidad de Chile. Rinconada is characterized by a sparse, relatively open matorral habitat. Similar to the chaparral of Southern California, the matorral is typified by large, grassy areas with occasional shrubs and acacia trees (*Acacia cavens*). Within Rinconada, we trapped degus at three habitats within close proximity of each other: (1) the "Field" habitat, which was a sparsely vegetated valley bottom (tree cover <10%), (2) the "Boulder" habitat, which was a gently sloping hillside littered with large rocks of varying size, and (3) the "Tree" habitat, a flat, grassy area with many acacia trees (tree cover >50%). Dispersal is not sex biased and male and female degus settle within 30–40 m on average from their burrows of origin (Quirici et al., 2011a). Maximum dispersal distances reach up to 200 m within 2 months (Quirici et al., 2011b). The second population was located at Parque Nacional Fray Jorge (3038′S, 71°40′W, altitude 200 m), hereafter referred to as Fray Jorge, a semi-arid, cactus-dominated site approximately 350 km northwest of Rinconada. Average annual rainfall is 133 mm at Fray Jorge (Gutierrez et al., 2010) and 236 mm at Rinconada. Because reproductive state can affect the degu stress response (Kenagy et al., 1999), we trapped degus during the early stages of gestation in the austral winter from June 23rd–July 2nd (Field), July 5th–7th (Boulder), July 12th–18th (Tree), and July 22nd–30th (Fray Jorge) 2011.

2.2. Trapping, blood sampling, and individual condition measurements

Degus were live trapped with Tomahawk traps (Tomahawk Live Trap Company, Tomahawk, WI, USA) baited with plain, rolled oats. Traps were placed near burrow entrances and along runways. Traps were opened prior to emergence from burrows (approximately one hour after sunrise) and were closed at least three hours before sunset (0845–1500 h). During this time, 3–5 observers

Table 1
Upper panel summarizes predictions of stress response variation between and within populations. Middle panel shows predicted, relative levels of CORT concentrations and negative feedback for each habitat variable. The lower panel displays predicted trend directions of body mass and rainfall with baseline (BL) CORT, stress-induced (SI) CORT, and negative feedback.

Comparison	Variation in stress response		
Between populations	High		
Within populations	Low		
Variable	BL CORT	SI CORT	Neg. feedback
High cover availability	Low	Low	Strong
Low ectoparasite load	Low	Low	Strong
High food availability	Low	Low	Strong
Body mass	Negative	Positive	Positive
Time since rainfall	Positive		

watched traps with binoculars so that the exact time of capture would be known. Degus were then bled for a baseline blood sample (~60 μL) within three minutes of capture since CORT levels start to increase after this time (Romero and Reed, 2005). Blood samples were taken from the saphenous vein and collected with microhematocrit capillary tubes. Because of the high vegetation density at Fray Jorge, observers would quietly sit by sets of traps and listen for sound of the trap door shutting. Any degus trapped unnoticed were excluded from CORT data analysis.

Following collection of baseline blood samples, degus were returned to traps, carried to a shady area, and left in the closed traps covered with a towel. Degus were then ear-tagged for identification purposes, sexed, and weighed to the nearest 0.1 g. Stress-induced blood samples (~30 μL) were taken 30 min after capture. Capture and restraint has been shown to be a reliable acute stressor for free-living rodents (Nunes et al., 2006; Place and Kenagy, 2000; Romero et al., 2008; Vera et al., 2011). After collecting stress-induced blood samples, degus were then injected intra-peritoneally with a 1 mg/kg body weight dose of dexamethasone (Vedco, St. Joseph, MO). Dexamethasone is a synthetic glucocorticoid and is an effective way to measure negative feedback. Degus were returned to traps and a final blood sample (~60 L) was taken 90 min later. We chose 90 min as a compromise between the two-hour DEX tests on other wild mammals (Boonstra and Singleton, 1993) and a desire to decrease the total processing time on our animals.

Blood samples were placed in a cooler with cold packs immediately after collection. Samples were centrifuged within 9 h of collection at approximately 230 G for 2 min. Hematocrit, the ratio of packed red blood cells to total blood volume, was determined by measuring samples to the nearest 0.1 mm with calipers. Plasma was stored at −20 °C until further analysis. All plasma samples were then measured for CORT with I^{125} radioimmunoassay kits (Corti-Cote Solid Phase Component System, MP Biomedicals LLC, Irvine, CA). Samples were assayed in duplicate. Distilled water was added to plasma to bring the total volume up to 25 μL. The assay sensitivity was 0.7 ng/mL and the intra- and inter-assay variation were 5.0% and 6.5%, respectively.

Degus were combed (Burger et al., 2012) over a bucket filled with 95% ethanol and dead ectoparasites were then collected and counted to determine ectoparasite load. The most common ectoparasites infecting degus at Rinconada are the exotic fleas *Leptopsylla segnis* and *Xenopsylla cheopis* (Burger et al., 2012). After sample collection, degus were returned to a burrow opening at the site of capture. All animal protocols were approved by the Institutional Animal Care and Use Committee at Tufts University.

2.3. Habitat measurements

We sampled the trapping area at each site using line intersect transects to quantify the ecological characteristics of each habitat (Canfield, 1941). The dominant habitat feature was recorded every two meters along six to ten parallel 50 m transects that were spaced 10 m apart. The total number of transects sampled was determined by the size of the trapping area. All habitat features were grouped into five categories: tree/shrub (provides cover), edible vegetation, bare ground, dead grass (inadequate to provide cover) and other features (such as rocks, cacti, burrows, etc.). Occasionally, multiple habitat features were noted at the same sample point (e.g. if dead grass was found under the canopy of a tree). The relative frequency (%) of each feature along the transects was then calculated to determine the ecological composition of each habitat.

To further assess availability of cover (object or vegetation, besides burrows, that would offer concealment or protection from predators), the proximity to the nearest structure that provided

cover was determined at all burrow systems where degus were captured (Hayes et al., 2007). The distance was taken to the nearest tenth of a meter from the approximate center of the burrow system to the closest edge of cover. Structures included in this assessment were typically higher than 0.5 m above ground.

Soil penetrability was measured at each burrow opening where degus were caught using a hand-held soil penetrometer (Lang Penetrometer Inc., Gulf Shores, AL, USA). Soil penetrability is the measurement of the force needed to penetrate soil to specific depth. This serves as an indicator of soil hardness and can estimate the difficulty of soil excavation (Lacey and Wieczorek, 2003; Vleck, 1979). Penetrability was assessed one meter away from each burrow opening in a randomly selected cardinal direction, and was measured on the same day as capture in order to reduce the impact of daily variation in soil moisture content.

Hourly temperature and daily precipitation reports for the three habitats at the Rinconada field site were obtained from the NOAA National Data Center (NNDC) DS3505 Hourly Global Surface Data Reports for Pudahuel, Chile. The Pudahuel weather station, located 15 km to the northeast of the Rinconada trapping area, was the closest climate reporting center to the study area. The 2005–2008 rainfall data from the Pudahuel weather station was used to determine average annual rainfall at Rinconada. Daily precipitation data for Parque Nacional Fray Jorge were provided by the Corporación Nacional Forestal (CONAF) from data collected onsite by park employees. Total daily precipitation was typically greater than 4 mm or less than 1 mm. We only included days with precipitation equal to or greater than 4 mm in our analyses because trace amounts of rainfall below 1 mm supply a similar amount of moisture as overnight dew and plant guttation (Hughes and Brimblecombe, 1994). The fact that our correlations were much weaker when we included precipitation less than 4 mm supports the idea that trace rainfall, dewfall, and guttation are difficult to distinguish biologically.

2.4. Statistical analyses

Statistical analyses were performed using SPSS (Version 19.0) and JMP (Version 5.0.1a). Integrated CORT after DEX injection was calculated by subtracting the stress-induced CORT value from the CORT value 90 min after the DEX injection, multiplying by 90 min, and dividing by two (Dickens et al., 2009), thus estimating the total relative decrease of integrated CORT between DEX injection and sampling. Due to animal escape during processing and sample loss during centrifugation, we did not always collect a full stress series for each animal. Therefore, our sample sizes are different for each measured variable. We analyzed each CORT variable separately because baseline CORT, stress-induced CORT, and negative feedback have been shown to be regulated independently (Hodgson et al., 2007; Landys et al., 2006; Reul et al., 1987; Romero, 2006). We used two-way ANOVAs to determine the main effects of habitat, sex, and a habitat by sex interaction on baseline CORT, stress-induced CORT, integrated CORT after DEX injection, hematocrit, and body mass. Only integrated CORT after DEX injection was normally distributed, so other data were either log (baseline CORT, hematocrit and body mass) or square root (stress-induced CORT) transformed. We added 3.5, the product of the dilution factor (5) and the sensitivity (0.7 ng/mL) of our CORT assay, to baseline CORT values of zero prior to log transformation. All data that met homogeneity assumptions were analyzed with Fisher's LSD post-hoc tests. Data that did not meet homogeneity assumptions were analyzed with Games-Howell post-hoc tests (the non-parametric form of Fisher's LSD post-hoc tests) (Norusis, 2007).

Data transformation failed to obtain normal distributions for distance to cover, soil penetrability, and ectoparasite load data. Consequently, we used Kruskal–Wallis tests to determine the

effect of habitat on distance to cover and soil penetrability. We used the Scheirer–Ray–Hare extension of the Kruskal–Wallis test (SRHE Kruskal–Wallis, a non-parametric equivalent of a two-way ANOVA) (Scheirer et al., 1976) to determine the effect of habitat, sex, and the interaction between habitat and sex on ectoparasite load. Significant interactions were analyzed with paired Mann–Whitney tests with a Bonferroni correction ($p < 0.0083$).

One-way ANCOVAs were used to determine if body mass was correlated with baseline CORT, stress-induced CORT, and integrated CORT after DEX injection, and whether these relationships were affected by habitat and sex. We also used one-way ANCOVAs to determine if time since the last significant rainfall greater than 4 mm was correlated with baseline CORT and hematocrit, and if temperature at time of capture was correlated with baseline hematocrit. We also tested whether these relationships were affected by habitat and sex. Before running ANCOVAs, we confirmed that data met all normality, homoscedasticity, and homogeneity-of-regression assumptions. After analysis, unstandardized, standardized, and studentized residuals were tested for normality, and studentized residuals were plotted against predicted values to check for constant variance (Norusis, 2007). Because many vertebrates have diel CORT rhythms (Gardiner and Hall, 1997; Romero and Rich, 2007; Spieler and Noeske, 1984), we used linear regression to test whether time of day correlated with baseline CORT.

3. Results

3.1. Habitat differences

Qualitative differences between habitat subtypes were confirmed with vegetation transect data; the Tree and Fray Jorge habitats had more tree/shrubs and edible vegetation compared to the Field and Boulder habitats, while the Boulder habitat had more rocks compared to all other habitats (Table 2). Burrows in which degus were captured at the Field habitat were significantly further from cover than burrows at other habitats (Kruskal–Wallis test; $H_3 = 42.75$, $p < 0.001$, paired Mann–Whitney post-hoc tests all $ps < 0.001$) (Table 2). Burrows used by degus at Fray Jorge were under bushes or within thick vegetation, so all Fray Jorge degus were captured under some type of cover. Soil was significantly more penetrable at Fray Jorge compared to the other habitats (Kruskal–Wallis test; $H_3 = 53.91$, $p < 0.001$, paired Mann–Whitney post-hoc tests all $ps < 0.001$) (Table 2), a difference most likely due to the sandier soil conditions at this site (Skaff, personal observation).

3.2. Stress response measurements

Baseline CORT was affected by habitat (two-way ANOVA; $F_{3,79} = 3.11$, $ps = 0.031$) (Fig. 1). Degus at Fray Jorge had lower baseline CORT than degus at the Field, Boulder, and Tree habitats (Fisher's LSD all $ps < 0.05$). There was not a significant sex or a sex by habitat interactive effect on baseline CORT (two-way ANOVA, effect of sex; $F_{1,79} = 1.31$, $p = 0.129$, effect of sex∗habitat;
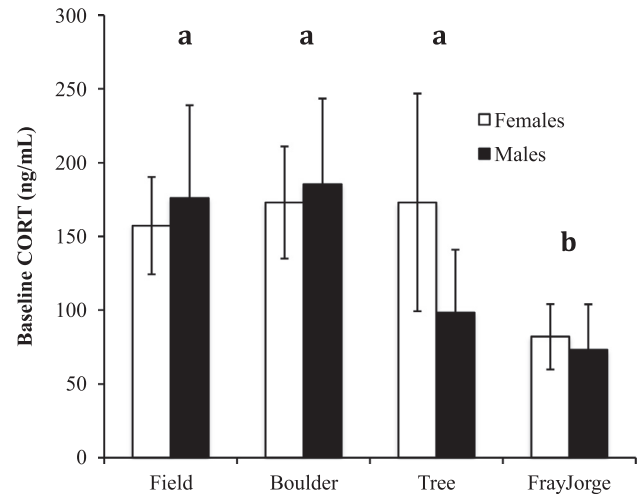

Fig. 1. Mean (±SE) plasma baseline CORT concentrations of female and male degus at the Field ($n = 16$ and 10), Boulder ($n = 10$ and 14), Tree ($n = 11$ and 6), and Fray Jorge ($n = 13$ and 7) habitats, respectively. There were no significant sex differences. Different letters indicate significant habitat differences.
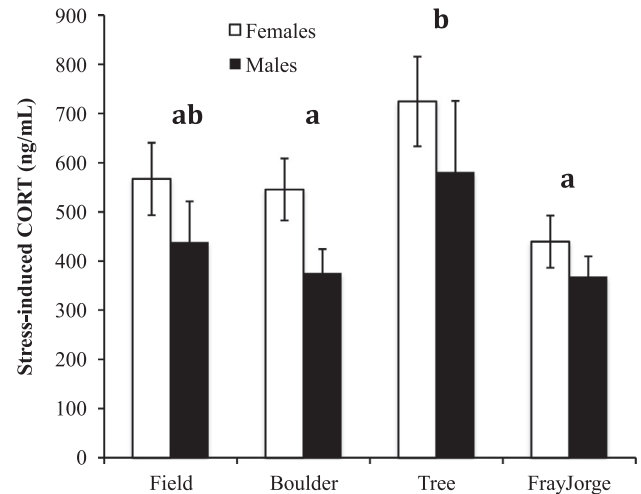

Fig. 2. Mean (±SE) plasma stress-induced CORT concentrations of female and male degus at the Field ($n = 16$ and 9), Boulder ($n = 12$ and 17), Tree ($n = 10$ and 6), and Fray Jorge ($n = 15$ and 6) habitats, respectively. Females had significantly higher stress-induced CORT across habitats. Different letters indicate significant habitat differences.

$F_{3,79} = 0.09$, $p = 0.966$). Baseline CORT was not affected by time of day ($F_{1,83} = 0.344$, $r^2 = 0.004$, $p = 0.559$).

Stress-induced CORT was also affected by habitat (two-way ANOVA; $F_{3,85} = 2.87$, $p = 0.041$) (Fig. 2). Degus at the Tree habitat had higher stress-induced CORT compared to degus at the Boulder and Fray Jorge habitats (Fisher's LSD all $ps < 0.05$). Female degus also had higher stress-induced CORT compared to males across all habitats (two-way ANOVA; $F_{1,85} = 5.85$, $p = 0.018$). However,

Table 2
Habitat composition of the Field, Boulder, Tree, and Fray Jorge habitats determined from vegetation transects. Distance to cover from burrow and soil penetrability values are means (±SE). Sample sizes are in parentheses. Values followed by letters indicate significant habitat differences.

Habitat	% Bare ground	% Edible vegetation	% Tree/shrub	% Dead grass	% Rock/other	Distance to cover from burrow (m)		Soil Penetrability (kPa)	
Field	57.6	16.0	5.9	19.4	1.0	7.5 ± 1.3[a]	(22)	2518.9 ± 441.1	(25)
Boulder	56.6	11.5	0.0	23.0	9.0	0.3 ± 0.1	(16)	2323.1 ± 426.1	(29)
Tree	12.1	44.2	17.1	26.7	0.0	0.7 ± 0.3	(10)	2142.5 ± 441.1	(17)
FrayJorge	41.4	21.6	29.9	3.4	3.7	0 ± 0	(14)	651.9 ± 411.0[a]	(21)

the sex by habitat interaction on stress-induced CORT was not statistically significant (two-way ANOVA, $F_{3,85} = 0.27$, $p = 0.848$).

Integrated CORT after DEX injection was affected by habitat (two-way ANOVA; $F_{3,76} = 5.00$, $p = 0.003$) (Fig. 3). Degus at the Tree habitat had a larger decrease in integrated CORT after DEX injection compared to degus at the Field, Boulder, and Fray Jorge habitats (Fisher's LSD all $ps < 0.05$). A larger decrease indicates stronger efficacy of negative feedback. There were no significant effects of sex or a sex by habitat interaction on integrated CORT after DEX injection (two-way ANOVA, effect of sex; $F_{1,76} = 0.87$, $p = 0.353$, effect of sex∗habitat; $F_{3,76} = 0.92$, $p = 0.434$).

3.3. Individual condition measurements

Body mass significantly differed between habitats (two-way ANOVA; $F_{3,83} = 26.69$, $p < 0.001$) (Table 3). Degus at the Tree habitat were significantly larger and degus at the Fray Jorge habitat were significantly smaller compared to all other habitats (Games-Howell all $ps < 0.01$). Body mass was not affected by sex or a sex by habitat interaction (two-way ANOVA, effect of sex; $F_{1,86} = 1.18$, $p = 0.281$, effect of sex∗habitat; $F_{3,86} = 0.41$, $p = 0.743$).

Hematocrit was affected by habitat (two-way ANOVA; $F_{3,78} = 3.90$, $p = 0.012$) (Table 3). Degus at the Field habitat had significantly lower hematocrit compared to degus at the Tree and Fray Jorge habitats (Fisher's LSD all $ps < 0.05$). Hematocrit was not affected by a main effect of sex or a sex by habitat interaction (two-way ANOVA, effect of sex; $F_1 = 0.28$, $p = 0.596$, effect of sex∗habitat; $F_{3,78} = 2.46$, $p = 0.069$).

Ectoparasite load significantly differed between habitats (SRHE Kruskal–Wallis, effect of habitat; $x^2_{(3)} = 18.57$, $p < 0.001$) (Table 3). Degus at the Fray Jorge habitat had significantly lower ectoparasite

Fig. 3. Mean (±SE) integrated CORT after DEX injection of female and male degus at the Field ($n = 15$ and 9), Boulder ($n = 9$ and 15), Tree ($n = 10$ and 5), and Fray Jorge ($n = 15$ and 6) habitats, respectively. There were no significant sex differences. Different letters indicate significant habitat differences. Note that a larger decrease indicates stronger efficacy of negative feedback.

Table 3
Differences in body mass, hematocrit, and ectoparasite load of degus from the Field, Boulder, Tree, and Fray Jorge habitats. Values are represented as means (±SE) with samples sizes in parentheses. There were no significant sex differences so sexes were combined. Values followed by letters indicate significant habitat differences.

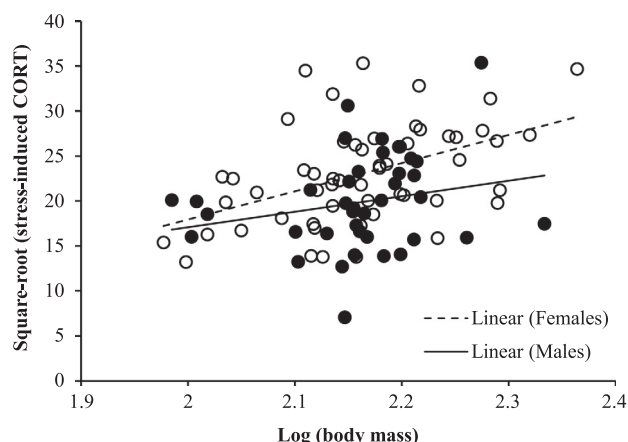| Habitat	Body mass (g)	Hematocrit	Ectoparasite load
Field	148.6 ± 2.8 (25)	0.70 ± 0.01[a] (25)	1.92 ± 0.43 (25)
Boulder	147.5 ± 2.8 (30)	0.74 ± 0.02[ab] (26)	3.31 ± 0.92 (29)
Tree	177.8 ± 6.0[a] (18)	0.76 ± 0.02[b] (17)	1.50 ± 0.50 (18)
FrayJorge	119.5 ± 4.4[b] (21)	0.76 ± 0.02[b] (18)	0.10 ± 0.07[a] (20)

Fig. 4. Relationship between plasma stress-induced CORT and body mass in female (open circles) ($F_{1,53} = 14.81$, $r^2 = 0.218$ $p < 0.001$) and male (closed circles) ($F_{1,36} = 1.90$, $r^2 = 0.050$, $p = 0.176$) degus. The equation for the female and male best-fit lines are $y = 31.368x-44.795$ and $y = 17.243x-17.406$, respectively.

loads compared to degus from all other habitats (paired Mann–Whitney post-hoc tests all $ps < 0.001$). Ectoparasite load was not affected by a main effect of sex or a sex by habitat interaction (SRHE Kruskal–Wallis, effect of sex; $x^2_{(1)} = 0.01$, $p = 0.916$, effect of habitat∗sex; $x^2_{(3)} = 1.26$, $p = 0.739$).

3.4. Body mass and stress response relationship

Body mass did not have a significant effect on baseline CORT (one-way ANCOVA, $F_{1,73} = 1.35$, $p = 0.25$) or integrated CORT after DEX injection (one-way ANCOVA, $F_{1,78} = 0.44$, $p = 0.51$).

Body mass had a significant effect on stress-induced CORT (one-way ANCOVA, $F_{1,87} = 5.14$, $p = 0.026$). Sex had a significant effect on the relationship between body mass and stress-induced CORT (one-way ANCOVA, effect of sex; $F_{1,87} = 6.35$, $p = 0.014$) so we ran separate linear regressions for males and females (Fig. 4). Females exhibited a significant, positive correlation between stress-induced CORT and body mass ($F_{1,53} = 14.81$, $r^2 = 0.218$, $p < 0.001$) while males did not ($F_{1,36} = 1.90$, $r^2 = 0.050$, $p = 0.176$).

3.5. Temperature and rainfall effects

Time since the last rainfall greater than 4 mm had a significant effect on baseline CORT (one-way ANCOVA, effect of rainfall; $F_{5,82} = 6.03$, $p = 0.0163$). Sex had a significant effect on the relationship between baseline CORT and the time since the last rainfall greater than 4 mm (one-way ANCOVA, effect of sex; $F_{5,82} = 4.10$, $p = 0.0465$) therefore, we conducted linear regressions separately for males and females. Females had a statistically significant negative relationship between baseline CORT and time since the last rainfall greater than 4 mm ($F_{1,48} = 6.95$, $r^2 = 0.129$, $p = 0.0113$) while males did not ($F_{1,33} = 2.10$, $r^2 = 0.0617$, $p = 0.157$).

Baseline hematocrit and temperature at capture had a weak, positive correlation ($F_{1,81} = 4.82$, $r^2 = 0.055$, $p = 0.031$). Time since the last rainfall greater than 4 mm did not have a significant effect on baseline hematocrit (one-way ANCOVA, effect of rainfall; $F_{5,84} = 0.0932$, $p = 0.337$).

4. Discussion

Although habitat has been suggested as a possible cause of differences in CORT, there has been little previous research examining whether natural habitat differences can alter a species' stress response while minimizing potential genetic influences (Hik et al.,
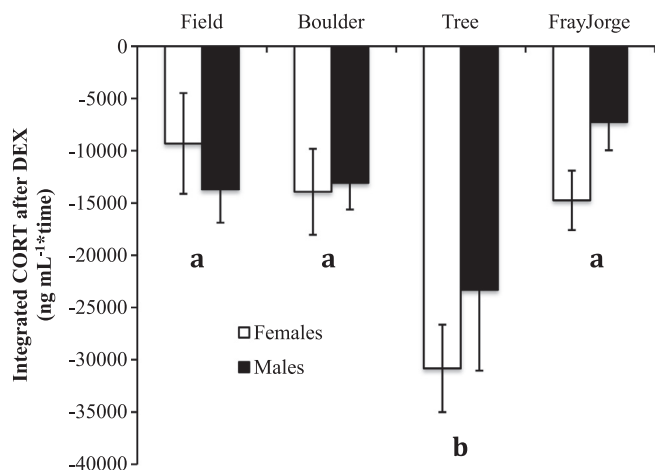
2001; Lewanzik et al., 2012; Mateo, 2007). This study used wild, free-living degus to explore whether the stress response differed between natural habitats. We found significant differences in ecological, stress response, and individual condition variables between habitats, with more variation between-populations than within-populations. We also found significant correlations between baseline CORT and hematocrit with weather variables, and a significant correlation between body mass and the stress response (Summarized in Table 4). These findings suggest that habitat type influences the stress response, either through direct habitat features or indirect effects mediated by physiological traits.

Baseline CORT concentrations are often used as an index of an animal's health or stress level (Bonier et al., 2009). Degus from the Fray Jorge habitat had lower baseline CORT and body mass compared to degus from all other habitats. The positive correlation between baseline CORT and body mass is opposite to what most within-population studies have found (Cabezas et al., 2007; Fokidis et al., 2011; Schoech et al., 2007), however there was no significant relationship between body mass and baseline CORT across all habitats. Lower baseline CORT in Fray Jorge degus could also be driven by cover availability. While the Fray Jorge habitat did not have significantly more cover compared to the Boulder or Tree habitats, the cover at Fray Jorge may have been of higher quality. Dense vegetation and thorny, low-lying shrubs at the Fray Jorge habitat may be more advantageous for predator avoidance compared to the rocks in the Boulder habitat and the acacias in the Tree habitat, which could obstruct views of ambush predators like foxes and eagles (Ebensperger and Hurtado, 2005). Belding's ground squirrels at densely vegetated habitats exhibit lower fecal CORT compared to squirrels in more open habitats (Mateo, 2007). The type and relative quality of a habitat's cover can affect predator detection (Boinski et al., 2003; Griesser and Nystrand, 2009), and several studies have found a positive correlation between predator abundance and baseline CORT (Boonstra and Singleton, 1993; Clinchy et al., 2004; Rogovin et al., 2006; Scheuerlein et al., 2001). While Rinconada and Fray Jorge populations are known to share some species of aerial and terrestrial degu predators, we did not measure specific predator composition and abundance in our different habitats, and both of these factors could influence baseline CORT levels in degus.

Baseline CORT could also be correlated with ectoparasite load. Ectoparasites inflict metabolic and immune costs on hosts (Lehmann, 1993; Nilsson, 2003), which could be reflected in glucocorticoid concentrations, and degus at the Fray Jorge habitat had significantly lower baseline CORT and ectoparasite loads compared to degus at other habitats. However, the vast majority of studies have found no relationship between ectoparasite load and baseline or fecal CORT (Bize et al., 2009; Eggert et al., 2010; Grutter and Pankhurst, 2000; Lobato et al., 2008; Monello et al., 2010; Raouf et al., 2006). Degus at Rinconada are almost entirely infected by exotic ectoparasites (Burger et al., 2012) and preliminary assessment of parasites suggests that exotic fleas also infect degus at Fray Jorge (Burger, personal communication). It is possible that exotic ectoparasites may exert greater metabolic and immune costs than native ectoparasites, which could be reflected in baseline CORT levels. These patterns provide insight into the mechanistic link between ectoparasite load and lower body condition and fitness (Burger et al., 2012). Lower ectoparasite loads at Fray Jorge could be explained by the sandier soil, which could be more effective for removing ectoparasites during dust bathing (Borchelt et al., 1976) and less favorable for development of fleas in the free-living larval stage.

Based on the distance between Fray Jorge and Rinconada, it is also possible that the differences in baseline CORT are due to genetic differences. Several studies have demonstrated that geographically distinct populations can display differences in the stress response (Lindstrom et al., 2005; Mateo, 2006; Romero, 2006; Silverin et al., 1997) and there is evidence that certain aspects of the stress response are heritable (Baugh et al., 2012; Carere et al., 2003; Cockrem et al., 2010; Evans et al., 2006; Harri et al., 2003). Genetic differences, however, cannot explain the different responses across the three habitats at Rinconada because the habitats were close in proximity.

Stress-induced CORT concentrations are often used as a measure of an animal's ability to respond to a stressor (Breuner et al., 1999). While a strong and rapid stress response may be adaptive in the short-term (Cabezas et al., 2007), the inability to turn off the stress response can lead to decreased fitness (Boonstra et al., 1998; Romero and Wikelski, 2010). Degus from the Tree habitat had higher stress-induced CORT than degus from the Boulder and Fray Jorge habitats, and stronger negative feedback than degus from all other habitats. Increased stress-induced CORT, negative feedback, and body mass in the degus at the Tree habitat could be linked to food availability. While we did not collect any quantitative measures of food availability, our qualitative vegetation transects showed that the Tree habitat had a higher percentage of edible vegetation compared to all other habitats. Studies using captive American kestrels (Heath and Dufty, 1998) and curve-billed thrashers (Fokidis et al., 2011) have shown a positive relationship between food abundance and stress-induced CORT. How-

Table 4
Upper panel summarizes the results of tests of the hypothesis that the stress response varies by habitat type. Relative levels of habitat, stress, and morphological measurements are listed for each habitat with significant differences noted by different superscript letters. Levels within parentheses indicate higher perceived quality. Lower panel summarizes the relationship between body mass and the stress response, and the relationships between baseline CORT and hematocrit with weather variables. Statistically significant trends are listed with the direction of the linear relationship and whether the trend was consistent across all habitats and sexes.

Variable	Habitat			
	Field	Boulder	Tree	FrayJorge
Baseline CORT				Low[a]
Stress-induced CORT		Low[a]	High[b]	Low[a]
*Females higher than males				
Negative feedback efficacy			High[a]	
% Edible vegetation			High	
Cover availability	Low[a]			(High)
Soil penetrability				High[a]
Body mass			High[a]	Low[b]
Ectoparasite load				Low[a]

Trend	Direction	Habitats	Sexes
Stress-induced CORT & body mass	Positive	All	Females
Baseline CORT & time since rainfall	Negative	All	Females
Hematocrit & temperature at capture	Positive	All	Both

ever, the opposite trend has been found in studies using wild birds (Clinchy et al., 2004; Kitaysky et al., 2007) and food supplementation did not affect stress-induced CORT levels in Florida scrub jays (Schoech et al., 2007) or Belding's ground squirrels (Nunes et al., 2002). Hik et al. (2001) reported higher stress-induced CORT levels in arctic ground squirrels that inhabited an alpine habitat versus a boreal forest habitat, yet found no differences in food availability between the sites. However, the male squirrels were significantly heavier in the alpine habitat compared to the boreal forest habitat. Negative feedback efficacy has also been positively correlated with food availability (Heath and Dufty, 1998; Romero and Wikelski, 2010).

It is unlikely that cover availability is related to stress-induced CORT and negative feedback efficacy in degus since the Field habitat was the only habitat that significantly differed in distance to cover measurements, while only the Tree habitat significantly differed from other habitats in stress-induced CORT and negative feedback. Several studies have shown a positive relationship between stress-induced CORT and predation pressure (Boonstra and Singleton, 1993; Clinchy et al., 2004) but because the Rinconada habitats were so close to each other (<600 m), it is unlikely that predation pressure was stronger at the Tree habitat compared to the Field and Boulder habitats.

Our results showed that across habitats, female degus had significantly higher stress-induced CORT compared to males. While Kenagy et al. (1999) found no difference in stress-induced CORT levels between male and female degus during the mating season, their samples were collected at least three weeks earlier than samples collected during this study. Since our females were captured later, some may have already been pregnant and gaining weight, although there were no body mass differences between males and females. For female degus, stress-induced CORT increases during pregnancy (Bauer, unpublished data) and peaks during lactation (Kenagy et al., 1999). If our females were already pregnant, their stress-induced CORT levels may have already been increasing, and this may also explain why only females show a significant correlation between body mass and stress-induced CORT. Prior studies indicate that stress-induced CORT and negative feedback are positively correlated with body mass (Fokidis et al., 2011; Heath and Dufty, 1998; Schoech et al., 2007). Our data supports this trend, with female degus from the Tree habitat weighing more than female degus from all other habitats. Alternatively, as female degus gain weight during pregnancy they become very rotund and may be more susceptible to predation. Increased stress-induced CORT may help pregnant degus better respond to predation attempts.

Hematocrit was significantly lower at the Field habitat compared to the Tree and Fray Jorge habitats. These differences may be partially due to temperature, as the Field habitat had significantly lower temperatures at time of capture than all other habitats and had the lowest average hematocrit. We also found a positive correlation between temperature at capture and hematocrit across habitats. This relationship seems to be consistent with the effects of body water volume contraction or dehydration. As the temperature increases, water is more likely to be lost through respiration (Getz, 1968). In some circumstances, this may lead to relative polycythemia or the apparent increase in hematocrit due to a reduction in plasma (Pearson, 1991).

Baseline CORT concentration can be positively correlated with the amount of precipitation (Foley et al., 2001). Our results depict an opposite relationship in which baseline CORT decreased with increasing time since the last rainfall greater than four millimeters. Although one study assessing the impact of rainfall on CORT concentrations in marmosets did corroborate our findings (Cunha et al., 2007), we cannot rule out that our relationship is the result of the order in which the habitats were sampled. A relatively large amount of precipitation fell while we sampled habitats at the Rinconada site, while much less fell during our time sampling Fray Jorge. Alternatively, degus stay underground if it is raining; so increased baseline CORT during periods of high precipitation could be explained by decreased foraging time.

Degus are social, plural-breeding mammals that live in groups ranging from one to twelve adult individuals (Hayes et al., 2009). Because social dynamics can influence the stress response (Silk, 2007), it is possible that differences in the degu CORT response are due to group size and composition. Habitat type can affect group size and composition (Maher and Burger, 2011; Rubenstein, 2007), which supports the hypothesis that habitat type may mediate the CORT response through differences in sociality (Blumstein, 2010). While we did not determine average group size and composition at each habitat in this study, it appears that social groups at Fray Jorge tend to be larger than at Rinconada (Burger, personal communication). By manipulating group sizes and CORT levels at different habitats, future studies could tease apart the relationships between habitat type, sociality, and the CORT response.

5. Conclusions

Results from this study demonstrate that the endocrine stress response in degus differs between populations and habitat types, either directly through habitat features or indirectly through physiological processes. Differences in the stress response between habitats do not necessarily imply that certain habitats are more "stressful" than others. Animals may be modulating their stress response to better cope with their specific environment. This distinction could be determined by measuring other markers of stress such as immune function, cardiovascular function, and changes in stress-related behaviors.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ygcen.2013.02.036.

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