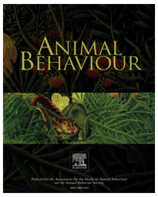
Animal Behaviour 112 (2016) 1–11

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Fitness and hormonal correlates of social and ecological stressors of female yellow-bellied marmots

Daniel T. Blumstein [a], [b], *, Kathryn N. Keeley [a], Jennifer E. Smith [c]

[a] *Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA, U.S.A.*
[b] *The Rocky Mountain Biological Laboratory, Crested Butte, CO, U.S.A.*
[c] *Department of Biology, Mills College, Oakland, CA, U.S.A.*

ARTICLE INFO

Article history:
Received 22 February 2015
Initial acceptance 20 March 2015
Final acceptance 30 September 2015
Available online
MS. number: A15-00144R2

Keywords:
ecological stressor
glucocorticoid
reproductive success
reproductive suppression
social rank
social stressor
yellow-bellied marmot

The effects of social and ecological stressors on female reproductive success vary among species and, in mammals, previous reviews have identified no clear patterns. However, few studies have simultaneously examined the relation between social rank and stressors and the relationships among rank, stressors and reproductive success. We used a long-term data set to study free-living facultatively social yellow-bellied marmots, *Marmota flaviventris*, to isolate the relationship between female social dominance rank and faecal glucocorticoid metabolite (FGM) levels (our measure of basal stress) in adult females. In addition, we examined whether rank and FGM levels were associated with reproductive success by quantifying the probability of an individual successfully weaning a litter and, for those who did, litter size. High-ranking females had lower FGM levels and larger litters. However, females with the highest FGM levels were significantly more likely to wean a litter. Importantly, body condition (as measured by previous year's mass) was also positively associated with breeding and with weaning larger litters. Thus, although low-ranking females probably experienced more social stressors than high-ranking females and although adult females often delayed their first reproduction until they were of a sufficient mass, our results suggest that elevated baseline FGM levels failed to mediate reproductive suppression. Perhaps, in species like marmots that have only a single chance per year to reproduce, reproductive suppression should be rare. These results highlight the importance of social status, body condition and predator abundance on determining reproductive success in highly seasonal breeders.

In vertebrates, the hypothalamic–pituitary–adrenal (HPA) axis modulates reactions to stressors by producing glucocorticoid hormones and restoring homeostasis (Reeder & Kramer, 2005). Glucocorticoid production upon encountering a stressor varies among species and among individuals and may be a repeatable trait within individuals (Martínez-Mota, Valdespino, Rebolledo, & Palme, 2008; Ramamoorthy & Cidlowski, 2013; Rensel & Schoech, 2011; Smith, Monclús, Wantuck, Florant, & Blumstein, 2012; Tilbrook, Turner, & Clarke, 2000). Glucocorticoid responses may be influenced by a number of factors, including social factors (e.g. there are documented relationships between social rank and glucocorticoid levels; discussed below), factors associated with body condition (Williams, Kitaysky, Kettle, & Buck, 2008) and ecological factors (e.g. predators and food availability; Creel, Dantzer, Goymann, & Rubenstein, 2013).

The relationship between dominance and glucocorticoids is particularly complex, varying enormously with respect to the species involved, the breeding system, ecological contexts and the means by which rank is achieved and maintained (Creel et al., 2013). It is generally accepted that in relatively closed societies, socially dominant individuals have better access to resources and mates than do subordinates (Appleby, 1980) and that dominants may direct aggressive behaviour (including aggressive threats) towards subordinates to maintain their rank, discourage retaliatory attacks or cause eviction (Ellis, 1995; Stockley & Bro-Jørgensen, 2011). However, even though socially dominant individuals benefit from their increased priority of access to resources due to their social status and, often as a result, reproductive dominance (defined here as increased reproductive success), high-ranking individuals may experience high costs associated with the maintenance of social rank (Creel, 2001; Gesquiere et al., 2011; Muller & Wrangham, 2004). For instance, reproductively dominant females

---

* Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90025-1606, U.S.A.

E-mail address: marmots@ucla.edu (D. T. Blumstein).

http://dx.doi.org/10.1016/j.anbehav.2015.11.002

among cooperatively breeding mammals, such as in African wild dogs, *Lycaon pictus* (Creel, 2001), meerkats, *Suricata suricatta* (Carlson et al., 2004), ringtailed lemurs, *Lemur catta* (Cavigelli, 1999; Cavigelli, Dubovick, Levash, Jolly, & Pitts, 2003), wolves, *Canis lupus* (Sands & Creel, 2004; but see McLeod, Moger, Ryon, Gadbois, & Fentress, 1996), and common marmosets, *Callithrix jacchus* (Saltzman, Schultz-Darken, Scheffler, Wegner, & Abbott, 1994) have higher glucocorticoid levels than do conspecific subordinates. This is probably because reproductively dominant females are involved in more agonistic interactions to maintain their high rank than are subordinates. Conversely, other studies have found that socially subordinate individuals may experience elevated glucocorticoid levels compared to their dominant counterparts, perhaps due to reduced access to food and social support, frequent harassment and reproductive suppression (Cavigelli & Chaudhry, 2012). Such a pattern is seen in some primates (reviewed by Abbott et al., 2003), alpine marmots, *Marmota marmota* (Hackländer, Möstl, & Arnold, 2003), African elephants, *Loxodonta africana* (Foley, Papageorge, & Wasser, 2001), and spotted hyaenas, *Crocuta crocuta* (Goymann et al., 2001). In addition to these opposite patterns, other studies have found no relationships between female social rank and glucocorticoid levels (ringtailed lemurs: Starling, Charpentier, Fitzpatrick, Scordato, & Drea, 2010; meerkats: Barrette, Monfort, Festa-Bianchet, Clutton-Brock, & Russell, 2012; common marmoset monkeys: Abbott, 1984; golden lion tamarins, *Leontopithecus rosalia*: Bales, French, Hostetler, & Dietz, 2005; Syrian hamsters, *Mesocricetus auratus*: Chelini, Palme, & Otta, 2011; baboons, *Papio hamadryas ursinus*: Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; white rhinoceros, *Ceratotherium simum simum*: Metrione & Harder, 2011; mandrills, *Mandrillus sphinx*: Setchell, Smith, Wickings, & Knapp, 2008; Ethiopian wolves, *Canis simensis*: van Kesteren et al., 2013).

Notably, we have listed multiple studies that documented different patterns for the same species, such as in ringtailed lemurs, meerkats and common marmosets. Given this variation and the multitude of studies suggesting different patterns, generalizations about social rank and glucocorticoid levels are not obvious.

Furthermore, because high glucocorticoid levels are a plausible mechanism of reproductive failure (Bonier, Martin, Moore, & Wingfield, 2009; Johnson, Kamilaris, Chrousos, & Gold, 1992; Moberg, 1985; Munck, Guyre, & Holbrook, 1984; Sapolsky, 1992; Scarlata et al., 2012; Welsh & Johnson, 1981), it is meaningful to look beyond the rank–stress relationship to better understand the direct relationships between stressors and reproductive success. In particular, female reproductive success can be meaningful to examine because of the frequently high rates of reproductive failure in female mammals (Wasser & Barash, 1983). In many group-living animals, not all individuals breed or produce surviving offspring, and reproductive suppression is a common reason for this (Abbott, 1987; Arnold & Dittami, 1997; Kaplan, Adams, Koritnik, Rose, & Manuck, 1986; Rood, 1980; Wasser & Barash, 1983). In some systems, the socially dominant female is also the reproductively dominant female. Furthermore, because socially subordinate females are usually the ones that are reproductively suppressed, it is often inferred that suppression is a direct result of social stressors caused by the unpredictable harassment, intimidation, evictions and violence by the reproductively dominant female(s) (Abbott et al., 2003; Hackländer et al., 2003; Louch & Higginbotham, 1967; Mendl, Zanella, & Broom, 1992; Young et al., 2006). Reduced access to food resources, although indirect, could be another mechanism of suppression (Ellis, 1995), especially since dominant females have better body condition than their subordinates due to increased access to food (Huang, Wey, & Blumstein, 2011).

Whereas social subordinates may have reduced reproductive success because of the actions of more dominant individuals, suppressing others may itself be costly and may therefore not be always be favoured by natural selection. Indeed, Bell, Nichols, Gilchrist, Cant, and Hodge (2012) found that when socially dominant banded mongooses, *Mungos mungo*, suppressed subordinates, the offspring born to dominant females weighed less than those born to dominant females that did not suppress others. To avoid such costs, female reproductive suppression is absent altogether in some carnivores, such as in the African lions, *Panthera leo*, living in egalitarian societies, because aggression is hypothesized to be disadvantageous and cub survival depends on cooperative defence against infanticidal males (Packer, Pusey, & Eberly, 2001).

There is therefore substantial variation among and within species in the relationships between stress and reproduction. Some studies have reported links between low social rank, high stress and suppression (Hackländer et al., 2003; Louch & Higginbotham, 1967; Wasser & Barash, 1983), while others have found no relationship between reproductive success and a female's glucocorticoid levels (Beehner, Nguyen, Wango, Alberts, & Altmann, 2006; Sapolsky, Romero, & Munck, 2000; Setchell et al., 2008; Weingrill, Gray, Barrett, & Henzi, 2004). Given this variation among species, it is difficult to make generalizations among taxa. Empirical studies that simultaneously track multiple social and ecological variables in free-living wild mammals are therefore warranted to tease apart the mechanisms and fitness correlates of female–female competition.

We studied the relationship between social rank and faecal glucocorticoid metabolite (FGM) levels and the relationship between glucocorticoid levels and reproduction in plural breeding yellow-bellied marmots, *Marmota flaviventris*. Yellow-bellied marmots are an interesting system in which to study this because they are facultatively social and hibernate throughout the winter, which creates an important constraint on fitness (Armitage, 1998, 2010, 2014). Marmot colonies contain one to multiple matrilines of adult females and their offspring. Cooperation and competition within colonies is concentrated within family groups. Close kin exchange the highest rates of affiliative and agonistic interactions; these patterns emerge early in ontogeny at the pup stage and persist into adulthood (Smith, Chung, & Blumstein, 2013). On average, fewer than 50% of females wean a litter in a given year (e.g. Blumstein & Armitage, 1998). Prior research suggests that younger and less dominant adult females may be reproductively suppressed (e.g. 2-year-old females reproduce only 34% of the time), and may thus reproduce at later ages, especially if they remain in the same groups as their reproductively dominant mothers (Armitage, 1998, 2010). Interestingly, delaying the age of first reproduction beyond the age of 2 years, however, is rare, and body mass, rather than age, per se, is a strong predictor of reproductive success among adults (Lenihan & Vuren, 1996). Previous studies have also shown that environmental variation (Schwartz, Armitage, & Vuren, 1998), age (Ozgul, Oli, Olson, Blumstein, & Armitage, 2007), predation pressure (Monclús, Tiulim, & Blumstein, 2011) and parity (e.g. if the animal has previously produced offspring or not; see Oli & Armitage, 2003) can influence reproductive success. Thus, we therefore employed a holistic approach here to integrate these variables into a single study based on almost a decade's worth of field data to isolate the effects of rank and stress on female reproduction.

Our study builds upon earlier research on this species to address fundamental and highly debated questions. First, after controlling for variation in environmental factors, age classes, predation pressure, colony size and breeding status, we aimed to understand the specific relationship between social rank and FGM level (our validated measure of baseline stress; Smith et al., 2012) in adult female marmots. Second, we aimed to understand whether FGM levels were associated with reproductive success by investigating each individual's probability of breeding as well their annual reproductive success, which we measured as the number of emergent young.

Based on what is known about the social system of yellow-bellied marmots, we predicted the following. Because individuals are facultatively social and live in groups that can be described by dominance hierarchies, we expected a relationship between social rank and the degree to which individuals experienced stressors. Thus, if female–female competition is a stressor, then we expected variation in FGM levels as a function of female social rank, and we predicted that (socially) low-ranking reproductively mature females in this plural breeding species should have higher glucocorticoid levels than those of socially dominant females. Huang et al. (2011) previously found no effect of an individual's overall social dominance rank (based on outcomes of agonistic interactions with all adult male and female group-mates) on reproductive success of adult female marmots. Nevertheless, theory predicts that female reproductive success should be most strongly shaped by intrasexual competition among female mammals in social systems in which females compete within matrilines (Stockley & Bro-Jørgensen, 2011).

Here we therefore inquired whether female–female competition (measured as adult female agonistic rank, after controlling for group size; see Huang et al., 2011, and methods below) in combination with interindividual variation in responses to stressors may together explain previously documented patterns of reproductive suppression observed among adult female yellow-bellied marmots (e.g. Armitage, 1998, 2014). Stressors triggered by female–female competition in combination with ecological stressors may together explain reproductive failure and/or skew among adult female marmots if reproductive success is reduced as a consequence of low social rank and/or elevated FGM levels. We therefore predicted that females with elevated FGM levels (i.e. young, low-ranking females), low body mass and increased exposure to predators would have the lowest reproductive success. Because we expected larger colonies to attract more predators within an active season, we also included colony size and its interaction with predator abundance as predictor variables in our models. While larger females are dominant to smaller females, there was substantial variation in our data set to permit us to isolate the effect of these variables statistically (none of the correlations among mass, rank and predators exceeded 0.25).

METHODS

Field Methods

To determine the relationships among social rank, stress and reproductive suppression, we studied the social interactions of yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL, 38°57′N, 106°59′W) in Gunnison County, Colorado, U.S.A. (Armitage, 2010; Blumstein, 2013). For these analyses, we focus on data collected on wild individuals over 9 years (2003–2011) at five colony sites (Bench, Gothic Townsite, Picnic, Marmot Meadow, and River) located in and around the RMBL. Colony sites are geographical locations that contain one or more marmot social groups; social groups are defined by space use overlap and contain one or more breeding age females (who are related), typically a single male, young of the year, and predispersal yearlings of both sexes.

We live-trapped marmots in Tomahawk traps that we placed around marmot burrow entrances for a few consecutive days every other week. At each trapping event, we recorded an individual's mass, sex, age, reproductive status (by scoring nipple development as ‘present’, ‘swollen’ or ‘lactating’; Armitage & Wynne-Edwards, 2002; we conservatively estimated that 9% of females that failed to wean a litter were scored as ‘lactating’) and collected faeces (when present). The first time a subject was trapped, we collected a hair sample for subsequent parentage assignment (Blumstein, Wey, & Tang, 2009). Marmots were also marked permanently with eartags the first time they were captured and their dorsal pelage was dyed (and redyed when required) with a unique fur mark for visual recognition from afar (see Armitage, 1982).

Social Factors Affecting Glucocorticoid Levels

Glucocorticoid metabolites can be reliably extracted from marmot faeces (Smith et al., 2012). We opportunistically collected faeces at trapping events and stored them on ice in plastic bags. Samples were frozen within 2 h of collection at −20 °C and steroid hormones were extracted within 6 months of collection at the University of California Los Angeles (details in Monclús et al., 2011; Smith et al., 2012). Details of sample preparation and glucocorticoid assay are in Appendix A of Blumstein, Patton, and Saltzman (2006). We collected faecal samples each time an individual defecated in a trap or in a bag. To be conservative, we only used the first faecal sample collected from each weekly trapping session to assess basal FGM levels ($N = 278$; mean ± SD = 30.8 ± 15.79 samples/year). We did this because repeated capture can result in trap stress and elevated FGM levels in marmots (Smith et al., 2012). For each individual ($N = 60$; mean ± SD = 14.1 ± 6.33 individuals/year), we calculated the annual glucocorticoid measure by averaging the combination of each of these single samples collected from each biweekly trapping session.

To determine an individual's social rank, we observed marmots both in the morning (0700–1000 hours) and in the afternoon (1600–1900 hours), when marmots are most active (Armitage, 1962). We observed marmots at distances of 20–150 m (Huang et al., 2011) to avoid influencing the marmots' behaviour. We observed marmots in all five colonies for a total of 8762 h over the 9 years (mean ± SD = 973.6 ± 246.30 h/year). Because social groups and colonies vary in their composition annually through births, deaths and dispersal, we analysed the data for each colony separately for each year. Colonies contained one or more social groups, defined by space use overlap, and also varied annually. Following Huang et al. (2011), we calculated rank based on the subset of individuals in a colony that were observed to interact; for females, these almost always were restricted to other social group members.

During observations, we recorded both affiliative and agonistic interactions, although for this study, we focused only on agonistic interactions because we were interested in the link between aggressive interactions and stress response. We defined agonistic interactions as those that were aggressive and accompanied by biting, chasing or fighting (see ethogram in Wey & Blumstein, 2012). For each social interaction, we recorded the instigator and the victim, as well as the winner and the loser of the interaction. These data allowed us to calculate social dominance hierarchies for adult females using the Clutton-Brock index (CBI).

For a given subject, the CBI considers the total number of wins and losses against each opponent (Clutton-Brock, Albon, Gibson, & Guinness, 1979). The CBI is more applicable to the study of yellow-bellied marmots than other metrics of dominance, like David's score (DS), or the frequency-based dominance index (FDI), because it is better suited for species with relatively few observed interactions and does not use the rate of interaction in its calculation (Bang, Deshpande, Sumana, & Gadagkar, 2010). The index is defined as $\mathrm{CBI} = (B + b + 1)/(L + l + 1)$, where B is the total number of ‘losers’ (individuals that previously lost an interaction) that an individual has ‘beaten’, b is the total number of individuals that the ‘losers’ (B) have ‘beaten’, L is the total number of ‘winners’ (individuals that previously won an interaction) that have ‘beaten’ the individual, and *l* is the total number of individuals that have 'beaten' the 'winners' (*L*).

Using the CBI, we then calculated relative rank, a measure that accounts for differences in the number of individuals in a hierarchy by standardizing each rank with respect to the total number of individuals (Huang et al., 2011). We ordered the CBI values from lowest to highest and then divided absolute rank by the total number of individuals. In the relative ranking data, the lowest rank was always zero and the highest rank was always one for each hierarchy.

We determined social rank based solely the two-way interactions between females that were of reproductive age (2 years or older; Oli & Armitage, 2003). In our calculations we excluded male interactions because our objective was to understand reproductive suppression in females only. For the 9 years and the 45 colony-years (each of five colonies studied over 9 years) analysed, all had sufficient two-way interactions to allow us to calculate ranks for one or more social groups based on our parameters of age and sex. However, there were some dominance hierarchies that could not be used because there were no observed interactions to base rank upon because breeding-age females in the group were not observed to interact aggressively with each other. For our analyses we assume that rank relationships were stable within years. However, social rank very well could change from year to year given differences in group composition and agonistic interactions.

The Relationship between Glucocorticoid Levels and Reproductive Success

Our second goal was to understand what factors influenced breeding, and specifically whether stress (as measured by FGM level) was a likely mechanism underlying reproductive success. We examined this in two ways: first, by testing whether glucocorticoid metabolite levels affected the probability of breeding and second, by testing whether glucocorticoid metabolite levels and/or female social rank best predicted the number of young weaned (a measure of annual reproductive success). Because litters from different females may be mixed (Armitage, 1989; Olson, Blumstein, Pollinger, & Wayne, 2012), we assigned offspring to their mother's molecularly (details in Blumstein et al., 2009). Briefly, we extracted DNA from hair and used 12 microsatellite markers to assign maternity using Cervus 3.0 (Kalinowski, Taper, & Marshall, 2007) with 95% confidence (see Blumstein, Lea, Olson, & Martin, 2010). Our pedigree included 60 adult females (ca. 14 individuals were studied each year) and their 306 confirmed offspring.

Statistical Analysis

We fitted generalized linear mixed-effects models (GLMMs) to evaluate our questions. Following Smith et al. (2012), FGM levels were ln transformed. To study the relationship between social rank and stress, our dependent variable was the annual FGM level. For this model, we entered each set of predictor variables associated with each trapping event (time of day, day of the year; see below) for which FGMs were collected to assess their effects on average annual FGM values for each subject based on a Gaussian distribution. To study the relationship between social stress and the probability of breeding, our dependent variable was whether a female successfully weaned a litter; these effects were modelled using the binomial distribution. To study the relationship between social stress and litter size, our dependent variable was the number of offspring weaned; these effects were modelled using the Poisson distribution.

Each model contained nine fixed effects, each of which was entered as a separate predictor variable (rather than as an annual measure so as to capture seasonal factors that might influence variation in FGM values), as follows: (1) whether or not the individual reproduced in the previous year; (2) the hour the glucocorticoid sample was collected (there is seasonal and daily variation in FGM; Smith et al., 2012); (3) an individual's mass at the current trapping event (i.e. when the particular faeces were collected for FGM extraction); (4) the date the glucocorticoid sample was collected; (5) an individual's body mass as estimated on 15 August the previous year (because previous year's mass is correlated with reproductive success: Lenihan & Vuren, 1996; for a description of the linear mixed modelling approach used to estimate body mass, see Ozgul et al., 2010); (6) the number of predators seen during observations between April and July that year (the number of predators encountered can influence FCM levels: Boonstra, Hik, Singleton, & Tinnikov, 1998; Monclús et al., 2011); (7) colony size; (8) female relative rank and/or (9) female rank and FGM levels, depending on the model tested.

In addition, because female marmots can reproduce at 2 years of age but may be reproductively suppressed (Blumstein & Armitage, 1999), we tested for the effects of age by creating a binary variable that separated potentially reproductive females into two categories: 2 years old versus >2 years old. We tested for all two-way interactions and only included these terms when it increased the fit of our model using the Akaike Information Criterion (AIC).

Each model also contained three random effects: the colony that an individual belonged to, female identity and year. These were included to explain location, individual and seasonal differences that may account for variation in FGM levels. We tested for two-way interactions and retained interaction terms only when doing so increased the fit of our model (within 2 AIC values of our best model). Values for excluded terms were based on adding each term to our final models. We set our alpha to 0.05 and report the results of two-tailed tests.

We elected to not analyse our data with a formal path analysis because to do so we would have had to remove about 15% of our data and risk overfitting a structural equation model. Given the relatively small effect sizes we report from the GLMM (see below), we wished to retain as much power as possible and thus conducted the GLMM.

Ethical Note

All procedures were approved under research protocol ARC 2001-191-01 as well as permits issued by the Colorado Division of Wildlife. The research protocol was approved by the University of California Los Angeles Animal Care Committee on 13 May 2002 and renewed annually. After trapping, individuals were released immediately at the trap location. Marmots were in traps no longer than 2–3 h, and typically for much less time than that. Traps were shaded with vegetation on warm days. Marmot handling was brief (typically 5–15 min depending upon the data to be collected) and marmots were not injured during handling. All marmots were handled while inside of a conical cloth-handling bag to reduce stress. We swabbed ears with alcohol before tagging individuals to reduce the chance of infection. Observations were conducted at distances chosen to not overtly affect marmot behaviour.

RESULTS

Our final data set contained 147 breeding events from 60 unique adult female marmots, collected over 9 years and from our five colonies (mean ± SD = 15.8 ± 10.34 breeding events/year). There

Table 1
Factors affecting faecal glucocorticoid metabolite levels in female yellow-bellied marmots

Fixed effects	Estimate±SD	*P*
Reproduced in previous year	0.0617±0.4616	0.8935
Hour of faecal sample collection	0.0006±0.0034	0.8401
Mass at current trapping event	0.0001±0.0001	0.1305
Day of year of faecal sample collection	**−0.0018±0.0009**	**0.0480**
Mass in previous year	**0.0002±0.0001**	**<0.0001**
2 years of age	**0.2323±0.0409**	**<0.0001**
Relative female social rank	**−0.1269±0.0524**	**0.0162**
Predator abundance	**0.0277±0.0079**	**0.0005**
Colony size	**0.0129±0.0033**	**<0.0001**
Predator abundance∗colony size	**−0.0005±0.0001**	**0.0001**

Significant outcomes are shown in bold.

were a total of 485 pups weaned over the 9 years from all females (mean ± SD = 53.9 ± 40.37 pups weaned/year). Main predators that visited the sites included black bears, *Ursus americanus*, coyotes, *Canis latrans*, mountain lions, *Puma concolor*, red foxes, *Vulpes vulpes*, and various raptors. On average (±SD), we detected and identified predators at these colony sites on 19 ± 12.87 days/year, but this varied by colony.

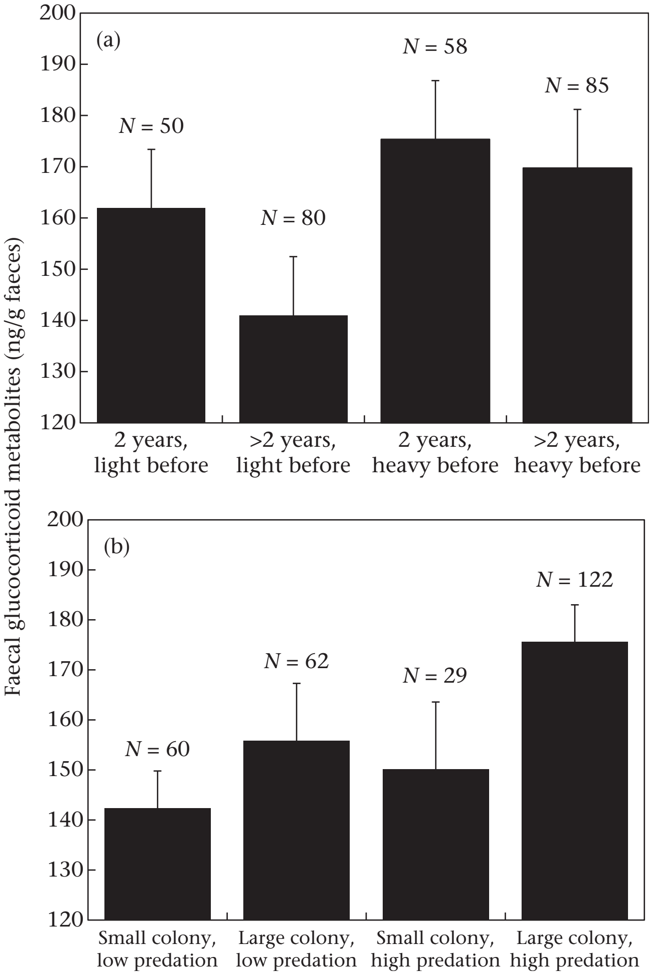


Figure 1. Mean faecal glucocorticoid metabolite concentration in female yellow-bellied marmots as a function of (a) age (2 years old vs >2 years old) and previous-year body mass (light before: 2500–3500 g; heavy before: 3500–4500 g) and (b) colony size (small: <50 marmots; large: >50 marmots) and predator abundance (low: <22 predators; high: >22 predators). We entered body mass, colony size and predator abundance as continuous variables directly into our statistical model (Table 1). Sample sizes above bars indicate the number of faecal samples for females in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

Factors Affecting Glucocorticoid Levels

After controlling for variation accounted for by our random variables, six of our fixed effects and one interaction between them significantly explained variation in average annual faecal glucocorticoid metabolite levels (Table 1). When considered together, FGM levels significantly increased when females were heavier in the previous year (Fig. 1a), when they were 2 years old (rather than >2 years; Fig. 1a), when they were of lower rank (Fig. 2), when there were more predators in the area (Fig. 1b) and when they were found in larger colonies (Table 1, Fig. 1b). This was the case after controlling for the day of sample collection; FGM levels declined across the season (Table 1). Colony size modulated the effect of predator abundance (Table 1). The addition of other interactions did not significantly explain variation in FGM levels. All random effects were significant (year: $\chi^2_1 = 224.7$, $P < 0.0001$; colony: $\chi^2_1 = 13.7$, $P = 0.0002$; marmot identity: $\chi^2_1 = 26.5$, $P < 0.0001$).

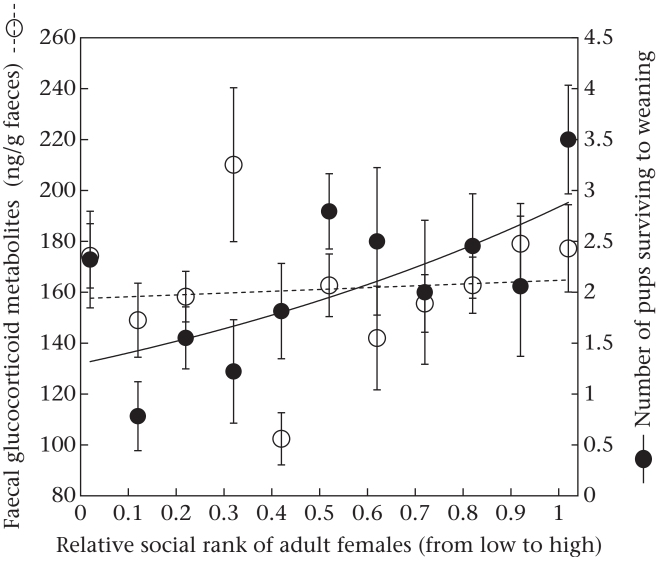


Figure 2. Effects of relative social rank on faecal glucocorticoid metabolite concentration (open circles) and number of pups surviving to weaning (black circles) in female yellow-bellied marmots ranked from lowest (0) to highest (1). Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

Table 2
Factors affecting the probability that adult female yellow-bellied marmots successfully weaned a litter

Fixed effects	Estimate±SE	*P*
Reproduced in previous year	**136.8±63.940**	**0.0324**
Hour of faecal sample collection	−0.020±0.073	0.7817
Mass at current trapping event	−0.002±0.001	0.2650
Day of year of faecal sample collection	−0.001±0.022	0.9709
Mass in previous year	**0.005±0.001**	**<0.00001**
2 years of age	**−3.058±0.943**	**0.0012**
Relative female social rank	−0.481±1.346	0.7207
Predator abundance	**−0.109±0.046**	**0.0177**
Colony size	**0.658±0.224**	**0.0033**
Faecal glucocorticoid metabolite (FGM) level	**6.474±3.155**	**0.0402**
FGM levels∗colony size	**−0.116±0.045**	**0.0105**
FGM levels∗reproduced in previous year	**−30.450±13.740**	**0.0267**

Significant outcomes are shown in bold.

The Relationships Between Glucocorticoid Levels and Reproductive Success

After controlling for a variety of variables that might influence the probability of breeding, six of our fixed effects and two interactions between them explained significant variation in probability that adult female marmots reproduced (Table 2). The variability of these data was consistent with that expected for the binomial distribution (e.g. the dispersion parameter of 0.311 was less than 1). Females were more likely to wean a litter if they were heavier in the previous August (Fig. 3), if they lived in larger colonies (Figs. 4b and 5a), if they had higher FGM levels (Fig. 5a, b) and if they reproduced in previous years (Table 2, Fig. 5b). Adult females were also significantly less likely to wean a litter if they were 2 years of age (rather than >2 years; Fig. 3), and less likely to wean a litter when more predators were present (Table 2, Fig. 4a). There were significant negative interactions between FGM levels and both colony size and whether or not a female weaned a litter in the previous year (Table 2). However, reproductive failure could not be explained by social rank, a variable that failed to explain whether an adult female weaned a litter (Table 2). All random effects were significant (year: $\chi^2_1 = 13.3$, $P = 0.0003$; colony: $\chi^2_1 = 24.2$, $P < 0.0001$; marmot identity: $\chi^2_1 = 48.6$, $P < 0.0001$).

In contrast, the number of pups weaned was influenced by four measured main effects, including social rank, and three interactions (Table 3). The variability of these data was consistent with that expected for the Poisson distribution (e.g. the dispersion parameter of 0.784 was less than 1). Weaning litter sizes were larger when females were of higher social rank (Fig. 2), they had higher FGM levels (Table 3, Fig. 6a), they lived in larger colonies (Fig. 6a), they reproduced in the previous year (Fig. 6b) and they were heavier in the previous year (Fig. 7a). The effect of FGM levels on litter size, however, was modulated by colony size and whether or not a female reproduced in the previous year (Table 3). For marmots that successfully reproduced the previous year, litters were larger if females were heavier when trapped in the previous August prior to hibernation, and if they were of higher relative social rank within their colonies (Table 3). Similarly, for 2-year-olds, litters were smaller as predator abundance increased (Table 3, Fig. 7b). As with the tendency to wean a litter or not, all random effects were significant (year: $\chi^2_1 = 39.5$, $P < 0.0001$; colony: $\chi^2_1 = 61.0$, $P < 0.0001$; marmot identity: $\chi^2_1 = 128.0$, $P < 0.0001$).

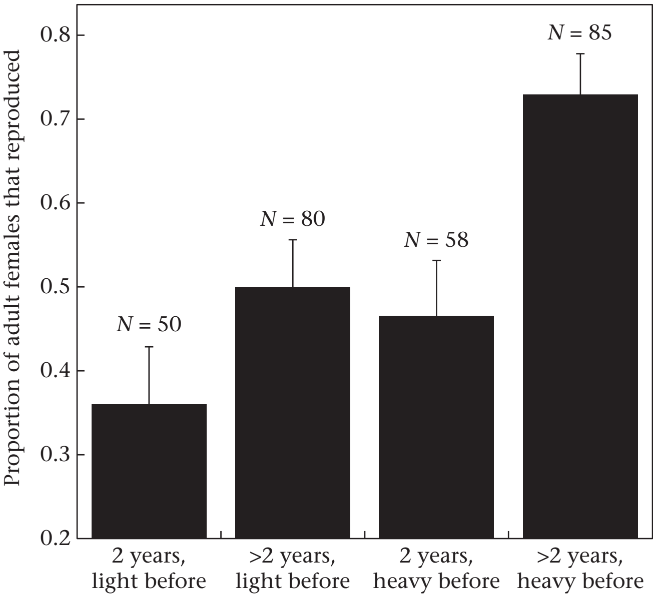


Figure 3. Effects of previous-year body mass (light before: 2500–3500 g; heavy before: 3500–4500 g) and age (2 years old vs >2 years old) on the probability that female yellow-bellied marmots would wean a litter in the current year. We entered body mass as a continuous variable directly into our statistical model (Table 2). Sample sizes above bars indicate the number of females sampled in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

DISCUSSION

To better understand the influences of social stressors and their associations with reproductive success, we investigated the probability of weaning a litter and the annual reproductive success of 60 female yellow-bellied marmots studied over 9 years. Importantly,

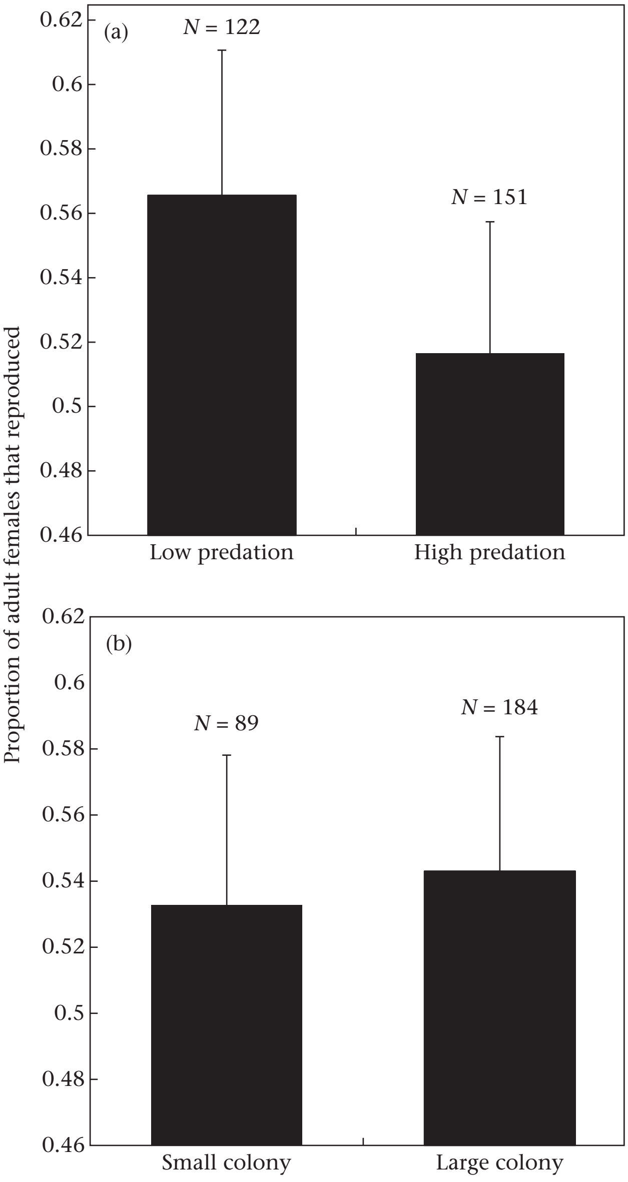


Figure 4. Effects of (a) predator abundance (low: <22 predators; high: >22 predators) and (b) colony size (small: <50 marmots; large: >50 marmots) on the probability that adult female yellow-bellied marmots would wean a litter in the current year. We entered colony size and predator abundance as continuous variables directly into our statistical model (Table 2). Sample sizes above bars indicate the number of females sampled in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

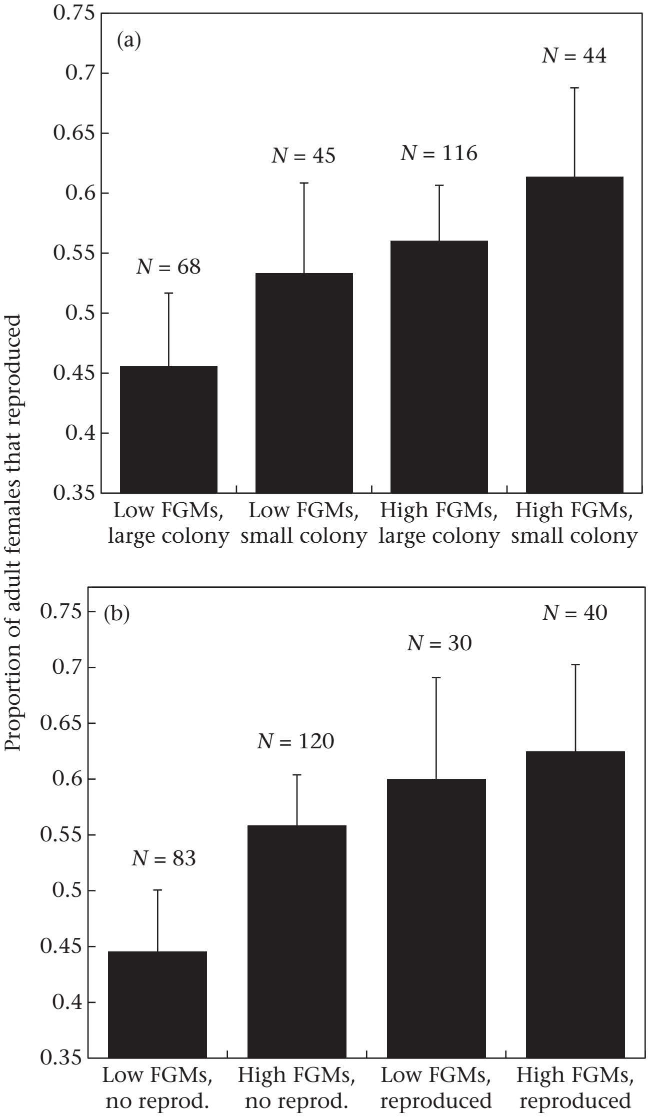


Figure 5. Effects of faecal glucocorticoid metabolite concentration (low FGMs: <128 ng/g faeces; high FGMs: ≥128 ng/g faeces), (a) colony size (large: >50 marmots; small: <50 marmots) and (b) reproductive success in the previous year on the probability that female yellow-bellied marmots would wean a litter in the current year. We entered FGM and colony size as continuous variables directly into our statistical model (Table 2). Sample sizes above bars indicate the number of females sampled in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

Table 3
Factors affecting the number of yellow-bellied marmot pups surviving to weaning

Fixed effects	Estimate±SE	*P*
Reproduced in previous year	**34.97±13.32**	**0.0087**
Hour of faecal sample collection	−0.0102±0.0132	0.4372
Mass at current trapping event	−0.0002±0.0002	0.1366
Day of year of faecal sample collection	−0.0031±0.0035	0.3872
Mass in previous year	**0.0008±0.0002**	**0.0002**
Relative female social rank	**0.5259±0.2539**	**0.0384**
2 years of age	0.2652±0.3363	0.4303
Predator abundance	0.0078±0.0081	0.3341
Colony size	**0.1964±0.0444**	**<0.00001**
Faecal glucocorticoid metabolite (FGM) level	**2.218±0.6253**	**0.0004**
FGM levels*colony size	**−0.0355±0.0091**	**<0.00001**
FGM levels*reproduced in previous year	**−9.0480±2.875**	**0.0016**
Mass at current trapping event *reproduced in previous year	**0.0021±0.0009**	**0.0146**
2 years of age*predator abundance	**−0.0788±0.0181**	**<0.00001**

Significant outcomes are shown in bold.

we found that as a female's social rank increased, her FGM levels significantly decreased, but this was a relatively small effect that was only detected after controlling for other variables that explained variation in FGM levels. This is notable because similar patterns have also been documented in many cooperative breeders (Cavigelli & Chaudhry, 2012). From this finding, we infer that low-ranking females experience more stressors than high-ranking females. Indeed, social competition among female kin is intense within matrilines; social competition emerges early in ontogeny and persists into adulthood (Smith et al., 2013).

Social rank also influenced the number of offspring successfully weaned in a season (but not reproductive failure), with high-ranking producing the most offspring. Our finding that females with high social status, based on agonistic interactions, produced more offspring than did low-ranking females has similarly been documented in ungulates (e.g. mountain goats, *Oreamnos americanus*: Côté & Festa-Bianchet, 2001), carnivores (e.g. spotted hyaenas: Holekamp, Smale, & Szykman, 1996) and primates (e.g. gelada baboons, *Theropithecus gelada*: Dunbar & Dunbar, 1977). Low-ranking females may produce fewer offspring because of differences in access to resources, amount of social support, body condition, group size and/or increased agonistic interactions (Abbott et al., 2003; Appleby, 1980; Cabezas, Blas, Marchant, & Moreno, 2007; Foley et al., 2001; Hackländer et al., 2003).

Taken together, our findings about ‘stress’ levels and reproductive output are therefore in accordance with classic captive studies on aggresion, rank and physiological stress responses that support the ‘stress of subordination’ hypothesis (reviewed by Creel et al., 2013). However, high FGM levels were also correlated with increased reproductive success: higher FGM levels were correlated with increased likelihood of successful reproduction as well as litter size. This finding is inconsistent with many findings of no relationship between stress levels and reproductive success (reviewed in: Boonstra, 2013; Creel, 2001; Sapolsky et al., 2000). Our findings are important because they support the emerging view, such as that expressed recently by Creel et al. (2013), that the effects of social stressors on the HPA axis are complex. Our empirical findings therefore contribute to important data from wild populations of mammals necessarily to advance this area of science forward.

Social rank was correlated with our measure of physiological stress, but it failed to predict the probability of breeding. The relationships we identified between FGM and social rank and FGM and reproductive success may at first appear contradictory (high-ranking females had lower FGM levels and the probability of breeding was positively correlated with FGM, suggesting that high-ranking females have a lower probability of breeding). However, our finding that females living in large colonies had elevated annual FGM levels and produced the most offspring is likely attributed to a surge in glucocorticoids during reproduction. In adult female marmots, FGM levels vary with reproductive state and are highest during pregnancy and lactation (Smith et al., 2012). Ebensperger et al. (2011) found similar results in degus, *Octodon degus*. In particular, adult female cortisol levels appear to rise as offspring are weaned, which seems to be associated with an increased propensity to produce alarm calls (Blumstein, Steinmetz, Armitage, & Daniel, 1997), but not with other factors such as group size or number of females. Perhaps the measure of probability of breeding (whether or not the female weaned pups) should include pups lost before the pups' emergence. Unfortunately, such assignments are nearly impossible for obligate hibernators, such as marmots, under

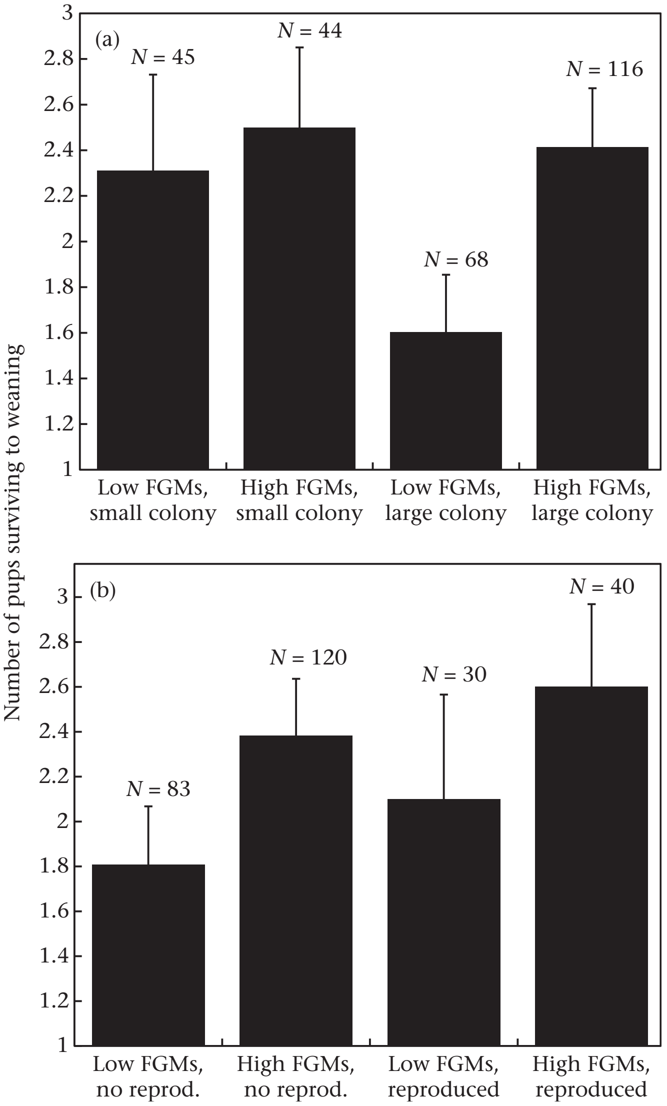


Figure 6. Effects of faecal glucocorticoid metabolite concentration (low FGMs: <128 ng/g faeces; high FGMs: ≥128 ng/g faeces), (a) colony size (large: >50 marmots; small: <50 marmots) and (b) previous-year reproductive success on the number of offspring that female yellow-bellied marmots weaned in the current year. We entered FGM and colony size as continuous variables directly into our statistical model (Table 3). Sample sizes above bars indicate the number of females sampled in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

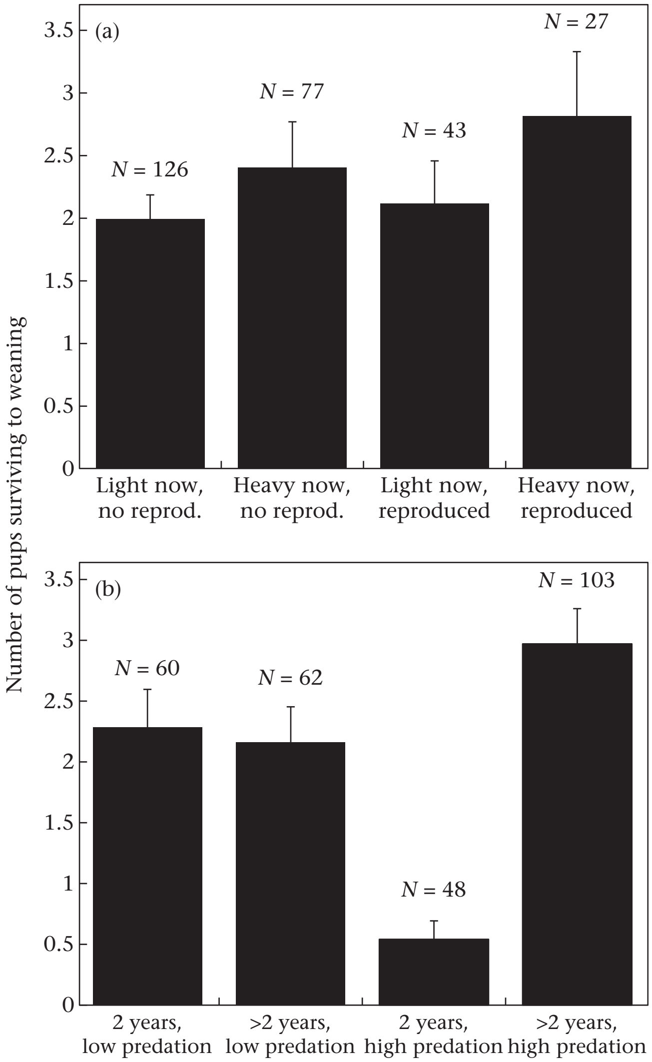


Figure 7. Effects of (a) current-year body mass (light now: 1000–3000 g; heavy now: 3001–5000 g) and previous-year reproductive success and (b) predator abundance (low: <22 predators; high: >22 predators) and female age (2 years old vs >2 years old) on the number of offspring that female yellow-bellied marmots weaned in the current year. We entered body mass as a continuous variable directly into our statistical model (Table 3). Sample sizes above bars indicate the number of females sampled in each category. Error bars represent raw standard errors around the mean for each category (for illustrative purposes).

natural conditions. This would require live-trapping of marmots with bait that would prematurely prime metabolic processes prior to snow-melt and the start of the growing season in their high-elevation habits. Such an effort would not only confound the reproductive outputs, but would probably be dangerous for the marmots. Given some uncertainty about the cause of preweaning failure (litter reabsorption versus preweaning predation), we elected to define breeders as those who successfully weaned a litter, but we recognize that at least 9% of females that failed to wean a litter were scored as lactating. We therefore call for future research in a more controlled setting than is possible under field conditions, such as in a laboratory, to unravel these complex patterns. Additional studies may therefore be able to disentangle the relative effects of preweaning predation and reabsorption to explain these seemingly contradictory results.

These inconsistent patterns may also suggest that female reproductive outcomes in yellow-bellied marmots are more strongly mediated by ecological factors than by stressors associated with social status. Indeed, an individual's mass from the previous year was correlated with increased FGM levels and both metrics of reproductive success. Our finding here that FGM levels increased with the number of predator visits is consistent with a growing body of evidence revealing the potential sublethal effects of predators on prey (e.g. Brooks, Gaskell, & Maltby, 2009; Creel & Christianson, 2008; Pangle, Peacor, & Johannsson, 2007). Our finding that the probability of weaning a litter decreased as the observed number of predators increased is consistent with studies showing that high predator-induced ‘stress’ directly impairs reproductive function in snowshoe hares, *Lepus americanus* (Boonstra et al., 1998; Sheriff, Krebs, & Boonstra, 2009). Given that marmots consistently reside at the same burrows, marmots may similarly suffer from sublethal effects from predator-induced stressors. In contrast, Creel, Winnie, and Christianson (2009) found that wolf presence limits reproduction in elk, *Cervus* *elaphus*; wolves drive elk to forage on suboptimal diets. Perhaps ecological factors associated with foraging decisions also influence body mass, which, in turn, influences FGM levels and reproductive success in marmots. Moreover, because predator abundance may also contribute directly to pup mortality via predation, carefully designed field experiments are needed to investigate the mechanisms responsible for this observed pattern in marmots and other rodents.

Rodent reproductive success often increases with age in wild mammal populations (King & Allainé, 2002; King, Festa-Bianchet, & Hatfield, 1991). Accordingly, 2-year-old marmots (the age of reproductive maturity; Oli & Armitage, 2003) in the current study had higher FGM levels and were less likely to reproduce than older females. Thus, 2-year-old females, which are often socially and reproductively subordinate to their mothers, might delay their age of first reproduction. Armitage (1998) suggested that older adult female marmots may reproductively suppress 2-year-olds. However, because we found no interactions between being a 2-year-old and FGM levels, it is unlikely that FGM mediates reproductive failure. Instead, we found an interesting, nonadditive effect of predator abundance on the number of offspring weaned by 2-year-olds and by older females. That is, 2-year-olds appeared to be particularly sensitive to the risks of high predator abundance, rearing disproportionally small litters under the risk of high predation. This raises the possibility that 2-year-olds are most vulnerable to the nonlethal effects of predators and/or the least prepared to successfully protect their offspring from predators. Because adult females belonging to both age categories apparently similarly perceived large numbers of predators as intense stressors (additive effect of predators on FGM levels of females that were 2 years old and >2 years old), our findings are instead most consistent with the notion that the loss of offspring born to inexperienced mothers is due to direct predation rather than to nonlethal effects of mothers being 'stressed' by high predator abundance.

Moreover, the significant interaction between body mass and whether an individual reproduced the previous year highlights the importance of condition-related factors affecting reproductive success. Thus, the reproductive skew that Armitage (1998) proposed may be due to factors other than social rank, such as female body condition and predator abundance found to be important in our current study. By contrast, for males, Huang et al. (2011) identified a correlation between rank and reproductive success. Further study of male–male competition is clearly warranted.

As reviewed in the Introduction, differences in stress level, dominance rank and reproductive success are seen among taxa, and even within species. These connections are clearly complex, and research has found both positive and negative relationships between social stress and reproductive success (Bonier et al., 2009; Brann & Mahesh, 1991; Crespi, Williams, Jessop, & Delehanty, 2013). There are multiple potential causes for these variable relationships. For example, Brann and Mahesh (1991) noted that reproductive outcome is in part a function of whether the stress is acute or chronic because acute stressors may facilitate corticosteroid production and enhance fertility. By contrast, chronic stressors may have a more inhibitory effect on reproduction, by preventing sexual maturation and impairing pregnancies.

Although it may be premature to make generalizations about the effects of stressors and social rank on reproductive success, our study highlights the value of longitudinal empirical studies relating three features of social living in relevant ecological contexts: social rank, baseline stress and reproductive success. Whether socially induced or induced through predator threat, females that enter hibernation at low body mass may reduce their investment in young to conserve valuable resources. Perhaps in species that only have a single chance per year to reproduce, like marmots, socially mediated reproductive suppression should be rare, and thus, social rank or other social stressors may only reduce offspring number rather than restrict annual reproductive bouts altogether. Regardless, these results highlight the importance of body condition and other environmental factors, such as predator abundance, on the reproductive success of highly seasonal breeders.

Acknowledgments

We thank all the marmoteers since 2001 who helped collect these data. D.T.B was supported by the National Geographic Society (grant number 8140-06), the University of California Los Angeles (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the National Science Foundation (IDBR-0754247 and DEB-1119660 to D.T.B., as well as DBI 0242960 and 0731346 to the Rocky Mountain Biological Laboratory). J.E.S. was supported by funds from Faculty Development Funds and from the Provost's Office at Mills College as well as by fellowships from the American Association of University Women, the Institute for Society and Genetics at the University of California Los Angeles and the American Philosophical Society. We also thank several anonymous referees whose astute comments helped us improve previous versions of this manuscript.

References

Abbott, D. H. (1984). Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. *American Journal of Primatology, 6*, 169–186.

Abbott, D. H. (1987). Behaviourally mediated suppression of reproduction in female primates. *Journal of Zoology, 213*, 455–470.

Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., et al. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior, 43*, 67–82.

Appleby, M. C. (1980). Social rank and food access in red deer stags. *Behaviour, 74*, 294–309.

Armitage, K. B. (1962). Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour, 10*, 319–331.

Armitage, K. B. (1982). Yellow-bellied marmot. In D. E. Davis (Ed.), *CRC handbook of census methods for terrestrial vertebrates* (pp. 148–149). Boca Raton, FL: CRC Press.

Armitage, K. B. (1989). The function of kin discrimination. *Ethology Ecology & Evolution, 1*, 111–121.

Armitage, K. B. (1998). Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. *Journal of Mammalogy, 79*, 385–393.

Armitage, K. B. (2010). Individual fitness, social behavior, and population dynamics of yellow-bellied marmots. In I. Billick, & M. V. Price (Eds.), *The ecology of place: Contributions of place-based research to ecological understanding* (pp. 134–154). Chicago, IL: University of Chicago Press.

Armitage, K. B. (2014). *Marmot biology: Sociality, individual fitness, and population dynamics*. Cambridge, U.K.: Cambridge Univesity Press.

Armitage, K. B., & Wynne-Edwards, K. E. (2002). Progesterone concentrations of wild-caught yellow-bellied marmots. In K. B. Armitage, & V. Y. Rumiantsev (Eds.), *Holarctic marmots as a factor of biodiversity: Proceedings of the Third International Conference on Marmots, Cheboksary, Russia, 25–30 August 1997* (pp. 41–47). Moscow: ABF.

Arnold, W., & Dittami, J. (1997). Reproductive suppression in male alpine marmots. *Animal Behaviour, 53*, 53–66.

Bales, K. L., French, J. A., Hostetler, C. M., & Dietz, J. M. (2005). Social and reproductive factors affecting cortisol levels in wild female golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology, 67*, 25–35.

Bang, A., Deshpande, S., Sumana, A., & Gadagkar, R. (2010). Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices. *Animal Behaviour, 79*, 631–636.

Barrette, M.-F., Monfort, S. L., Festa-Bianchet, M., Clutton-Brock, T. H., & Russell, A. F. (2012). Reproductive rate, not dominance status, affects fecal glucocorticoid levels in breeding female meerkats. *Hormones and Behavior, 61*, 463–471.

Beehner, J. C., Nguyen, N., Wango, E. O., Alberts, S. C., & Altmann, J. (2006). The endocrinology of pregnancy and fetal loss in wild baboons. *Hormones and Behavior, 49*, 688–699.

Bell, M. B., Nichols, H. J., Gilchrist, J., Cant, M. A., & Hodge, S. J. (2012). The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses. *Proceedings of the Royal Society B: Biological Sciences, 279*, 619–624.

Blumstein, D. T. (2013). Yellow-bellied marmots: insights from an emergent view of sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*, 20120349.

Blumstein, D. T., & Armitage, K. B. (1998). Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behavioral Ecology, 9*, 8–19.

Blumstein, D. T., & Armitage, K. B. (1999). Cooperative breeding in marmots. *Oikos, 84*, 369–382.

Blumstein, D., Lea, A., Olson, L., & Martin, J. (2010). Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. *Journal of Evolutionary Biology, 23*, 879–887.

Blumstein, D. T., Patton, M. L., & Saltzman, W. (2006). Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters, 2*, 29–32.

Blumstein, D. T., Steinmetz, J., Armitage, K. B., & Daniel, J. C. (1997). Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Animal Behaviour, 53*, 173–184.

Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological Sciences, 276*, 3007–3012.

Bonier, F., Martin, P. R., Moore, I. T., & Wingfield, J. C. (2009). Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution, 24*, 634–642.

Boonstra, R. (2013). Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Functional Ecology, 27*, 11–23.

Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs, 68*, 371–394.

Brann, D. W., & Mahesh, V. B. (1991). Role of corticosteroids in female reproduction. *FASEB Journal, 5*, 2691–2698.

Brooks, A. C., Gaskell, P. N., & Maltby, L. L. (2009). Sublethal effects and predator–prey interactions: implications for ecological risk assessment. *Environmental Toxicology and Chemistry, 28*, 2449–2457.

Cabezas, S., Blas, J., Marchant, T. A., & Moreno, S. (2007). Physiological stress levels predict survival probabilities in wild rabbits. *Hormones and Behavior, 51*, 313–320.

Carlson, A. A., Young, A. J., Russell, A. F., Bennett, N. C., McNeilly, A. S., & Clutton-Brock, T. (2004). Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Hormones and Behavior, 46*, 141–150.

Cavigelli, S. A. (1999). Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour, 57*, 935–944.

Cavigelli, S. A., & Chaudhry, H. S. (2012). Social status, glucocorticoids, immune function, and health: can animal studies help us understand human socioeconomic-status-related health disparities? *Hormones and Behavior, 62*, 295–313.

Cavigelli, S. A., Dubovick, T., Levash, W., Jolly, A., & Pitts, A. (2003). Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior, 43*, 166–179.

Chelini, M. O. M., Palme, R., & Otta, E. (2011). Social stress and reproductive success in the female Syrian hamster: endocrine and behavioral correlates. *Physiology & Behavior, 104*, 948–954.

Clutton-Brock, T. H., Albon, S., Gibson, R., & Guinness, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour, 27*, 211–225.

Côté, S. D., & Festa-Bianchet, M. (2001). Reproductive success in female mountain goats: the influence of age and social rank. *Animal Behaviour, 62*, 173–181.

Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution, 16*, 491–497.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution, 23*, 194–201.

Creel, S., Dantzer, B., Goymann, W., & Rubenstein, D. R. (2013). The ecology of stress: effects of the social environment. *Functional Ecology, 27*, 66–80.

Creel, S., Winnie, J. A., & Christianson, D. (2009). Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 12388–12393.

Crespi, E. J., Williams, T. D., Jessop, T. S., & Delehanty, B. (2013). Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? *Functional Ecology, 27*, 93–106.

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior, 53*, 254–265.

Dunbar, R. I. M., & Dunbar, E. P. (1977). Dominance and reproductive success among female gelada baboons. *Nature, 266*, 351–352.

Ebensperger, L. A., Ramírez-Estrada, J., León, C., Castro, R. A., Tolhuysen, L. O., Sobrero, R., et al. (2011). Sociality, glucocorticoids and direct fitness in the communally rearing rodent, *Octodon degus*. *Hormones and Behavior, 60*, 346–352.

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology, 16*, 257–333.

Foley, C., Papageorge, S., & Wasser, S. (2001). Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology, 15*, 1134–1142.

Gesquiere, L. R., Learn, N. H., Simao, M. C. M., Onyango, P. O., Alberts, S. C., & Altmann, J. (2011). Life at the top: rank and stress in wild male baboons. *Science, 333*, 357–360.

Goymann, W., East, M. L., Wachter, B., Höner, O. P., Möstl, E., Van't Holf, T. J., et al. (2001). Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences, 268*, 2453–2459.

Hackländer, K., Möstl, E., & Arnold, W. (2003). Reproductive suppression in female alpine marmots, *Marmota marmota*. *Animal Behaviour, 65*, 1133–1140.

Holekamp, K. E., Smale, L., & Szykman, M. (1996). Rank and reproduction in the female spotted hyaena. *Journal of Reproduction and Fertility, 108*, 229–237.

Huang, B., Wey, T. W., & Blumstein, D. T. (2011). Correlates and consequences of dominance in a social rodent. *Ethology, 117*, 573–585.

Johnson, E. O., Kamilaris, T. C., Chrousos, G. P., & Gold, P. W. (1992). Mechanisms of stress: a dynamic overview of hormonal and behavioral homeostasis. *Neuroscience & Biobehavioral Reviews, 16*, 115–130.

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology, 16*, 1099–1106.

Kaplan, J. R., Adams, M. R., Koritnik, D. R., Rose, J. C., & Manuck, S. B. (1986). Adrenal responsiveness and social status in intact and ovariectomized *Macaca fascicularis*. *American Journal of Primatology, 11*, 181–193.

van Kesteren, F., Paris, M., Macdonald, D. W., Millar, R., Argaw, K., Johnson, P. J., et al. (2013). The physiology of cooperative breeding in a rare social canid; sex, suppression and pseudopregnancy in female Ethiopian wolves. *Physiology & Behavior, 122*, 39–45.

King, W. J., & Allainé, D. (2002). Social, maternal, and environmental influences on reproductive success in female alpine marmots (*Marmota marmota*). *Canadian Journal of Zoology, 80*, 2137–2143.

King, W. J., Festa-Bianchet, M., & Hatfield, S. E. (1991). Determinants of reproductive success in female Columbian ground squirrels. *Oecologia, 86*, 528–534.

Lenihan, C., & Vuren, D. V. (1996). Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). *Canadian Journal of Zoology, 74*, 297–302.

Louch, C. D., & Higginbotham, M. (1967). The relation between social rank and plasma corticosterone levels in mice. *General and Comparative Endocrinology, 8*, 441–444.

Martínez-Mota, R., Valdespino, C., Rebolledo, J. A. R., & Palme, R. (2008). Determination of fecal glucocorticoid metabolites to evaluate stress response in *Alouatta pigra*. *International Journal of Primatology, 29*, 1365–1373.

McLeod, P. J., Moger, W. H., Ryon, J., Gadbois, S., & Fentress, J. (1996). The relation between urinary cortisol levels and social behaviour in captive timber wolves. *Canadian Journal of Zoology, 74*, 209–216.

Mendl, M., Zanella, A. J., & Broom, D. M. (1992). Physiological and reproductive correlates of behavioural strategies in female domestic pigs. *Animal Behaviour, 44*, 1107–1121.

Metrione, L. C., & Harder, J. D. (2011). Fecal corticosterone concentrations and reproductive success in captive female southern white rhinoceros. *General and Comparative Endocrinology, 171*, 283–292.

Moberg, G. P. (1985). Influence of stress on reproduction: measure of well-being. In G. P. Moberg (Ed.), *Animal stress* (pp. 245–267). Bethesda, MD: American Physiological Society.

Monclús, R., Tiulim, J., & Blumstein, D. T. (2011). Older mothers follow conservative strategies under predator pressure: the adaptive role of maternal glucocorticoids in yellow-bellied marmots. *Hormones and Behavior, 60*, 660–665.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology, 55*, 332–340.

Munck, A., Guyre, P. M., & Holbrook, N. J. (1984). Physiological functions of glucocorticoids in stress and their relation to pharmacological actions. *Endocrine Reviews, 5*, 25–44.

Oli, M. K., & Armitage, K. B. (2003). Sociality and individual fitness in yellow-bellied marmots: insights from a long-term study (1962–2001). *Oecologia, 136*, 543–550.

Olson, L., Blumstein, D., Pollinger, J., & Wayne, R. (2012). No evidence of inbreeding avoidance despite demonstrated survival costs in a polygynous rodent. *Molecular Ecology, 21*, 562–571.

Ozgul, A., Oli, M. K., Olson, L. E., Blumstein, D. T., & Armitage, K. B. (2007). Spatiotemporal variation in reproductive parameters of yellow-bellied marmots. *Oecologia, 154*, 95–106.

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science, 293*, 690–693.

Pangle, K. L., Peacor, S. D., & Johannsson, O. E. (2007). Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology, 88*(2), 402–412.

Ramamoorthy, S., & Cidlowski, J. A. (2013). Exploring the molecular mechanisms of glucocorticoid receptor action from sensitivity to resistance. *Endocrine Development, 24*, 41–56.

Reeder, D. M., & Kramer, K. M. (2005). Stress in free-ranging mammals: integrating physiology, ecology, and natural history. *Journal of Mammalogy, 86*, 225–235.

Rensel, M. A., & Schoech, S. J. (2011). Repeatability of baseline and stress-induced corticosterone levels across early life stages in the Florida scrub-jay (*Aphelocoma coerulescens*). *Hormones and Behavior, 59*, 497–502.

Rood, J. P. (1980). Mating relationships and breeding suppression in the dwarf mongoose. *Animal Behaviour, 28*, 143–150.

Saltzman, W., Schultz-Darken, N. J., Scheffler, G., Wegner, F. H., & Abbott, D. H. (1994). Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology & Behavior, 56*, 801–810.

Sands, J., & Creel, S. (2004). Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour, 67*, 387–396.

Sapolsky, R. M. (1992). Neuroendocrinology of the stress response. In J. B. Becker, S. M. Breedlove, & D. Crews (Eds.), *Behavioral endocrinology* (pp. 287–324). Cambridge, MA: MIT Press.

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews, 21*, 55–89.

Scarlata, C. D., Elias, B. A., Godwin, J. R., Powell, R. A., Shepherdson, D., Shipley, L. A., et al. (2012). Relationship between fecal hormone concentrations and reproductive success in captive pygmy rabbits (*Brachylagus idahoensis*). *Journal of Mammalogy, 93*, 759–770.

Schwartz, O. A., Armitage, K. B., & Vuren, D. (1998). A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology, 246*, 337–346.

Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Factors affecting fecal glucocorticoid levels in semi-free-ranging female mandrills (*Mandrillus sphinx*). *American Journal of Primatology, 70*, 1023–1032.

Sheriff, M. J., Krebs, C. J., & Boonstra, R. (2009). The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology, 78*, 1249–1258.

Smith, J. E., Chung, L. K., & Blumstein, D. T. (2013). Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots. *Animal Behaviour, 85*, 715–725.

Smith, J. E., Monclús, R., Wantuck, D., Florant, G. L., & Blumstein, D. T. (2012). Fecal glucocorticoid metabolites in wild yellow-bellied marmots: experimental validation, individual differences and ecological correlates. *General and Comparative Endocrinology, 178*, 417–426.

Starling, A. P., Charpentier, M. J., Fitzpatrick, C., Scordato, E. S., & Drea, C. M. (2010). Seasonality, sociality, and reproduction: long-term stressors of ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior, 57*, 76–85.

Stockley, P., & Bro-Jørgensen, J. (2011). Female competition and its evolutionary consequences in mammals. *Biological Reviews, 86*, 341–366.

Tilbrook, A., Turner, A., & Clarke, I. (2000). Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. *Reviews of Reproduction, 5*, 105–113.

Wasser, S. K., & Barash, D. P. (1983). Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Quarterly Review of Biology, 58*, 513–538.

Weingrill, T., Gray, D. A., Barrett, L., & Henzi, S. P. (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior, 45*, 259–269.

Welsh, T. H., Jr., & Johnson, B. H. (1981). Stress-induced alterations in secretion of corticosteroids, progesterone, luteinizing hormone, and testosterone in bulls. *Endocrinology, 109*, 185–190.

Wey, T. W., & Blumstein, D. T. (2012). Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology, 66*, 1075–1085.

Williams, C. T., Kitaysky, A. S., Kettle, A. B., & Buck, C. L. (2008). Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *General and Comparative Endocrinology, 158*, 29–35.

Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C., & Clutton-Brock, T. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 12005–12010.