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

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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 focused on both of these relationships simultaneously—the one 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 metabolites (FGM) levels (our measure of basal stress) in adult females. In addition, we asked 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 August mass) was also positively associated with breeding and with weaning larger litters. Thus, although low-ranking females likely experienced more social stressors than did high-ranking females and adult females often delayed their first reproduction until they were of a sufficient mass, our data suggest that elevated baseline FGM levels failed to mediate reproductive suppression. Perhaps, in species like marmots that only have 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.

Keywords: social rank, social stressors, ecological stressors, reproductive success, reproductive suppression, yellow-bellied marmots, glucocorticoids

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 their subordinates (Appleby, 1980), and that dominants may engage in aggressive behaviour (including aggressive threats) directed toward 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; Muller & Wrangham, 2004; Gesquiere et al., 2011). For instance, reproductively dominant females among cooperatively

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

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

Furthermore, because high glucocorticoid levels are a plausible mechanism of reproductive failure (Johnson, Kamilaris, Chrousos, & Gold, 1992; Moberg, 1985; Sapolsky, 1992; Munck, Guyre, & Holbrook, 1984; Welsh & Johnson, 1981; Scarlata et al., 2012; Bonier, Martin, Moore, & Wingfield, 2009), 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 or females (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 were lighter 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 hypothesised to be disadvantageous, and cub survival depends on cooperative defense 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 report links between low social rank, high stress, and suppression (Hackländer et al., 2003; Louch & Higginbotham, 1967; Wasser & Barash, 1983), while others find 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 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 matriline 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 et al. 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. two-year old females reproduce only 34% of the time), and may thus reproduce at later ages, especially if they remain the same groups as their reproductively dominant mothers (Armitage, 1998, 2010). Interestingly, delaying the age of first reproduction beyond the age of two, 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 faecal glucocorticoid metabolites (FGM) levels [our validated (Smith et al., 2012) measure of baseline stress] in adult female marmots. Second, we aimed to understand whether FGM levels were associated with reproductive success by

investigating at the probability of breeding as well as an individual's 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 female reproductive success should be most strongly shaped by intrasexual competition among female mammals in social systems in which females compete within matriline (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 inter-individual 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 elevated FGM levels of low-ranking females of young ages, low body masses, and exposed to high number of predators

should 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 interactions 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 between 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, USA (Armitage, 2010; Blumstein, 2013). For these analyses, we focus on data collected on wild individuals over nine years (2003-2011) at five different marmot colony sites (Bench, Gothic Townsite, Picnic, Marmot Meadow, and River) located in and around the RMBL. Colony sites are geographic 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 pre-dispersal 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 & Wynn-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 ear tags the first time they were captured and their dorsal pelage was dyed (and re-dyed 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 the marmot's faeces (Smith et al., 2012). Faeces were opportunistically collected at trapping events at the RMBL, stored on ice in plastic bags, frozen within two hours of collection at -20°C, and steroid hormones extracted within six months of collection at UCLA (details in Monclús, Tiulim, & Blumstein, 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 first faecal sample collected from each weekly trapping session to assess basal FGM levels ($n = 278$; mean = 30.8 samples per year, standard deviation = 15.79). We did this because Smith et al. (2012) found repeated captures of the same marmot sometimes results in trap stress and elevated FGM levels upon the subsequent capture. For each individual ($n = 60$; mean = 14.1 individuals per year, standard deviation = 6.33), we calculated the annual glucocorticoid measure by averaging the combination of each of these single samples collected from each of the bi-weekly trapping sessions.

To determine an individual's social rank, we observed the marmots both in the mornings (0700-1000 h) and in the afternoons (1600-1900 h), which are the periods when marmots were most active (Armitage, 1962). We observed the animals at distances that varied from 20 to 150 m (Huang et al., 2011); these distances were selected to not influence the marmots' behaviour. We

observed marmots in five colonies for a total of 8,762 hours over the nine years (mean = 973.6 hours per year, standard deviation = 246.30). Because social groups and colonies vary in their composition annually through births, deaths, and dispersal, each colony each year was analyzed separately. 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, though for this study, we focused on only agonistic interactions because we were interested in the link between aggressive interactions and stress response. These were defined as those that were aggressive and accompanied by biting, chasing, or fighting (ethogram in Wey & Blumstein, 2012). For each social interaction, we recorded the instigator and victim, as well as the winner and 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 Clutton-Brock Index considers both the total of number individuals the subject has “beaten” as well as those it lost to, rather than just one or the other (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 interactions in its calculation (Bang, Deshpande, Sumana, & Gadagkar, 2010). The index is defined:

$$CBI = (B + b + 1) / (L + l + 1)$$

where, (B) is the total number of “losers” (individuals that have lost an interaction) that the individual has “beaten”, (b) is the total number of marmots that the “losers” [(B)] have “beaten”, (L) is the total number of “winners” (individuals that have won an interaction) that have “beaten” the individual, and (l) is the total number of marmots that have “beaten” the marmots 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 who were of reproductive age (two 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 nine years and 45 colony years (a marmot colony studied over a year) analyzed, all had sufficient two-way interactions to be able 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 if stressors, as measured by FGM levels 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, DNA was extracted from hair and we 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 generalised linear mixed effects models to evaluate our questions. Following Smith et al. (2012), FGM levels were natural log transformed. To study the relationship between social rank and stress, our dependent variable was the annual FGM levels. For this model, we entered each set of predictor variables associated with each trapping events (time of day, day of the year, see below) for which FGMs were collected to assess their annual effects on the 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): whether or not the individual reproduced in the previous year; the hour the glucocorticoid sample was collected (there is seasonal and daily variation in FGM; Smith et al., 2012); an individual's mass at the current trapping event (that is, when the particular faeces were collected for FGM extraction); the date the glucocorticoid sample was collected; an individual's mass that was estimated on 15 August the previous year (because previous year's mass is correlated with reproductive success; Lenihan & Vuren, 1996; see Ozgul et al. (2010) for a description of the linear mixed modeling approach used to estimate body mass); the number of predators seen during observations between April and July that year (predator visitation can influence FCM levels; Boonstra, Hik, Singleton, & Tinnikov, 1998; Monclús et al., 2011); the colony size; and the female's relative rank and or rank and FGM levels depending on model tested.

In addition, we tested for the effects of age by creating a binary variable that separated potentially reproductive females into two categories: 1) two years old and 2) greater than two years old. This is because two-year old females may reproduce but they may also be reproductively suppressed (Blumstein & Armitage, 1999), so we wanted a distinction between the two. 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 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 (AIC values

within 2 of our best model). Values for excluded terms are 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 over-fitting 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 UCLA 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 what data needed to be collected) and marmots were not injured during this 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 nine years and from our five colonies (mean = 15.8 breeding events per year, standard deviation = 10.34. There were a total of 485 pups weaned over the nine years from all

females (mean = 53.9 pups weaned per year, standard deviation = 40.37). 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, we detected and identified predators about 19 days each year at these colony sites, but this varied by colony (standard deviation = 12.87).

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 (Figure 1a), when they were two years old (rather than > 2 years, Figure 1a), when they were lower ranked (Figure 2), when there were more predators around (Figure 1b), and when they were found in larger colonies (Table 1; Figure 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-square = 224.7, d.f. = 1, $P < 0.0001$; colony: Chi-square = 13.7, d.f. = 1, $P = 0.0002$; marmot identity: Chi-square = 26.5, d.f. = 1, $P < 0.0001$).

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 those expected for the binomial distribution (e.g., the dispersion parameter of 0.311 is less than 1.0). Females were more likely to wean a litter if they were heavier in the previous August (Figure 3), if they lived in larger colonies (Figures 4b, 5a), if they had higher FGM levels (Figures 5a,b), and if they reproduced in previous years (Table 2; Figure 5b). Adult females were also significantly less likely to wean a litter if they were two years of age (rather than > 2 years; Figure 3), and less likely to wean a litter when more predators were present (Table 2, Figure 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-square = 13.3, d.f. = 1, $P = 0.0003$; colony: Chi-square = 24.2, d.f. = 1, $P < 0.0001$; marmot identity: Chi-square = 48.6, d.f. = 1, $P < 0.0001$).

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 those expected for the Poisson distribution (e.g., the dispersion parameter of 0.784 is less than one). Weaning litter sizes were larger when females were higher ranked socially (Figure 2), heavier in the previous year (Figure 7a), they lived in larger colonies (Figure 6a), they reproduced in the previous year (Figure 6b), and when they had higher FGM levels (Table 3, Figure 6a). The effect of FGM levels of 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 they were heavier when trapped in the previous August prior to hibernation, and if adult females were of higher relative social rank within their colonies (Table 3). Similarly, for two year olds, litters were smaller as predator

abundance increased (Table 3, Figure 7b). As with the tendency to wean a litter or not, all random effects were significant (Year: Chi-square = 39.5, d.f. = 1, $P < 0.0001$; Colony: Chi-square = 61.0, d.f. = 1, $P < 0.0001$; Marmot Identity: Chi-square = 128.0, d.f. = 1, $P < 0.0001$).

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 nine years. Importantly, we found that as a female's social rank increased, her FGM levels significantly decreased, but this was a relatively small effect that only was 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 stressor than high-ranking females. Indeed, social competition among female kin is intense within matriline; social competition emerges early in ontogeny and persisting into adulthood (Smith, Chung, & Blumstein, 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, produce 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). This could be explained by inadequate 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 aggression, 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 correlated with 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 is 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 levels 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 emit 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 the obligate hibernators, such as marmots, under 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 likely be dangerous for subjects. Given some uncertainty about the cause of pre-weaning failure (litter reabsorption versus pre-weaning 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 pre-weaning 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 predator visitation is consistent with a growing body of evidence revealing the potential sub-lethal effects of predators on prey (e.g. Pangle, Peacor, & Johannsson, 2007; Creel & Christianson, 2008; Brooks, Gaskell, & Maltby 2009). Our finding that the probability of weaning a litter decreased as the number of predators observed 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 sub-lethal effects from predator-induced stressors. In contrast, Creel, Winnie, and Christianson (2009) found wolfpresence 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, two-year old marmots (the age of reproductive maturity; Oli & Armitage, 2003) in the current study had elevated FGM levels and less likely to reproduce than did older females. Thus, two-year old females, who 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 two-year olds. However, because we found no interactions between being a two-year old and FGM levels, it is unlikely that FGM mediates reproductive failure. Instead, we found an interesting, non-additive effect of predator abundance on the number of offspring weaned by two year olds and by older females. That is, two year olds appeared to be particularly sensitive to the risks of high predator abundance, rearing disproportionately small litters under the risk of high predation. This raises the possibility that two year olds are most vulnerable to the non-lethal effects of predators and/or 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 on predators on FGM levels for 2 years and >2 years of age), our findings are instead most consistent with the notion that offspring born to unexperienced mothers were lost to direct predation than non-lethal effects of mothers “stressed” by high predator abundance.

Moreover, the significant interaction between mass and whether an individual reproduced the previous year highlights the importance of condition-related factors affecting reproductive success. Thus, the reproductive skew 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 levels, dominance ranks, 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 of 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 generalisations 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 entering hibernation at low body masses experiencing stressors 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 we should expect social rank or 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 determining reproductive success in highly seasonal breeders.

Acknowledgements

We thank all the marmoteers since 2001 who helped collect these data, and three anonymous reviewers for very constructive comments. D.T.B was supported by the National Geographic Society, UCLA (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the NSF (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 reviewers whose astute comments helped us improve previous versions of this MS.

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773 **Table 1**
774 Factors affecting fecal glucocorticoid metabolite (FGM) levels in female yellow-bellied
775 marmots.

Fixed effects	Estimate $\pm$ Std. Error	P-value
Reproduced in Previous Year	0.0617 $\pm$ 0.4616	0.8935
Hour of Fecal Sample Collection	0.0006 $\pm$ 0.0034	0.8401
Mass at Current Trapping Event	0.0001 $\pm$ 0.0001	0.1305
Day of Year Fecal Sample Collected	-0.0018 $\pm$ 0.0009	0.0480
Mass in Previous August	0.0002 $\pm$ 0.0001	<0.0001
Two Years of Age	0.2323 $\pm$ 0.0409	<0.0001
Relative Female Social Rank	-0.1269 $\pm$ 0.0524	0.0162
Predator Abundance	0.0277 $\pm$ 0.0079	0.0005
Colony Size	0.0129 $\pm$ 0.0033	<0.0001
Predator Abundance * Colony Size	-0.0005 $\pm$ 0.0001	0.0001

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Table 2

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

Fixed effects	Estimate $\pm$ Std. Error	<i>P</i>-value
Reproduced in Previous Year	136.8 $\pm$ 63.940	0.0324
Hour of Fecal Sample Collection	-0.020 $\pm$ 0.073	0.7817
Mass at Current Trapping Event	-0.002 $\pm$ 0.001	0.2650
Day of Year Fecal Sample Collection	-0.001 $\pm$ 0.022	0.9709
Mass in Previous August	0.005 $\pm$ 0.001	<0.00001
Two Years of Age	-3.058 $\pm$ 0.943	0.0012
Relative Female Social Rank	-0.481 $\pm$ 1.346	0.7207
Predator Abundance	-0.109 $\pm$ 0.046	0.0177
Colony Size	0.658 $\pm$ 0.224	0.0033
Fecal Glucocorticoid Metabolite (FGM) level	6.474 $\pm$ 3.155	0.0402
FGM levels * Colony Size	-0.116 $\pm$ 0.045	0.0105
FGM levels * Reproduced in Previous Year	-30.450 $\pm$ 13.740	0.0267

783 **Table 3**

784 Factors affecting the number of yellow-bellied marmot pups surviving to weaning.

Fixed effects	Estimate $\pm$ Std. Error	<i>P</i>-value
Reproduced in Previous Year	34.97 $\pm$ 13.32	0.0087
Hour of Fecal Sample Collection	-0.0102 $\pm$ 0.0132	0.4372
Mass at Current Trapping Event	-0.0002 $\pm$ 0.0002	0.1366
Day of Year Fecal Sample Collection	-0.0031 $\pm$ 0.0035	0.3872
Mass in Previous August	0.0008 $\pm$ 0.0002	0.0002
Relative Female Social Rank	0.5259 $\pm$ 0.2539	0.0384
Two Years of Age	0.2652 $\pm$ 0.3363	0.4303
Predator Abundance	0.0078 $\pm$ 0.0081	0.3341
Colony Size	0.1964 $\pm$ 0.0444	<0.00001
Fecal Glucocorticoid Metabolite (FGM) level	2.218 $\pm$ 0.6253	0.0004
FGM levels * Colony size	-0.0355 $\pm$ 0.0091	<0.00001
FGM levels * Reproduced in Previous Year	-9.0480 $\pm$ 2.875	0.0016
Mass at Current Trapping Event * Reproduced in Previous Year	0.0021 $\pm$ 0.0009	0.0146
Two Years of Age * Predator Abundance	-0.0788 $\pm$ 0.0181	<0.00001

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Figure Legends

Figure 1. Concentrations of fecal glucocorticoid metabolites (FGMs; Mean $\pm$ S.E.) in female yellow-bellied marmots as a function of: **A)** adult female age (2 years or > than 2 years) and mass in the previous August or **B)** colony size and predator abundance. We entered continuous variable of mass, colony size, and predator abundance directly into our statistical model (Table 1). For the purposes of visual representation, in females in were categorized as: A) light (2500 g to 3500 g; white bars) or heavy (3500 g to 4500 g; black bars) in the previous August and B) as occurring in small (<50 marmots) or large (> 50 marmots) colonies subject to low (<22 predators) or high (>22 predators) predation. Sample sizes over each bar indicate the number of fecal samples for females belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 2. Effects of relative social rank on concentrations of fecal glucocorticoid metabolites (FGM; open circles) and on the number of pups surviving to weaning (black circles) in female yellow-bellied marmots ranked from lowest (0.0) to highest (1.0). Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 3. Effects of mass in the previous August and age (2 years or >2 years old) on the probability that adult female yellow-bellied marmots successfully weaned a litter in the current year. We entered continuous variable of mass directly into our statistical model (Table 2). For the purposes of visual representation, in females in were categorized as: light (2500 g to 3500 g; white bars) or heavy (3500 g to 4500 g; black bars) before (in the previous August). Sample sizes

over each bar indicate the females sampled when belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 4. Effects of **A)** predator abundance and **B)** colony size age (2 years or >2 years old) on the probability that adult female yellow-bellied marmots successfully weaned a litter in the current year. We entered colony sizes and predator abundances as continuous variable directly into our statistical model (Table 2). For the purposes of visual representation, in females in were categorized as: occurring in colonies A) subject to low (<22 predators) or high (>22 predators) predation, and in B) small (<50 marmots) or large (> 50 marmots) colonies. Sample sizes over each bar indicate the females sampled when belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 5. Effects of concentrations of fecal glucocorticoid metabolites (FGMs) and **A)** colony size age (2 years or >2 years old) or **B)** whether a female reproduced successfully in the previous year on the probability that adult female yellow-bellied marmot successfully weaned a litter in the current year. We entered FGMs and colony sizes as continuous variable directly into our statistical model (Table 2). For the purposes of visual representation, in females in were categorized as: having low (<128 ng/g feces) or high ($\geq$ 128 ng/g feces) FGMs or occurring in small (<50 marmots) or large (> 50 marmots) colonies. Sample sizes over each bar indicate the females sampled when belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 6. Effects of concentrations of fecal glucocorticoid metabolites (FGMs) and **A)** colony size or **B)** whether a female reproduced successfully in the previous year on the number of offspring that adult female yellow-bellied marmot weaned in the current year. We entered FGMs and colony sizes as continuous variable directly into our statistical model (Table 3). For the purposes of visual representation, in females in were categorized as: having low (< 128 ng/g feces) or high (≥ 128 ng/g feces) FGMs or occurring in small (< 50 marmots) or large (> 50 marmots) colonies. Sample sizes over each bar indicate the females sampled when belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 7. Effects of **A)** mass at current trapping event and whether she reproduced successfully in the previous year or **B)** age (2 years or > 2 years old) and predator abundance on the number of offspring that adult female yellow-bellied marmot weaned in the current year. We entered continuous variable of mass directly into our statistical model (Table 3). For the purposes of visual representation, in females in were categorized as: **A)** light (1000 g to 3000 g; white bars) or heavy (3001 g to 5000 g; black bars) now (at the time of trapping) or subject to low (< 22 predators) or high (> 22 predators) predation. Sample sizes over each bar indicate the females sampled when belonging to each category. Error bars represent raw standard errors around means for each category for illustrative purposes only.

Figure 1.

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864 **Figure 2.**
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Figure 4.

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Figure 6.

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Figure 7.

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