



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 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.

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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

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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 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, 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

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