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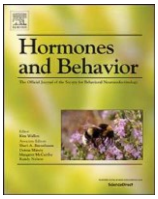

Correlates of maternal glucocorticoid levels in a socially flexible rodent

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ABSTRACT

While it is generally accepted that social isolation has detrimental effects on social species, little is known about the importance of social interactions in less social species–particularly for wild reproductive females. We studied socially-flexible yellow-bellied marmots (*Marmota flaviventer*) and asked whether features of the social environment are associated with maternal fecal glucocorticoid metabolite (FGM) concentrations. Since changes in maternal baseline glucocorticoids may have positive or negative consequences for offspring fitness, we were also interested in estimating their relationship with measures of reproductive success. We fitted generalized linear mixed effects models to a dataset including maternal FGM measurements, social network metrics, maternal/alloparental care, and pup FGM and survival. Agonistic interactions were positively associated with maternal FGM levels, while mothers that engaged in relatively more affiliative interactions had reduced FGM levels when living in environments with low predator pressure. Pups associated with mothers exhibiting high FGM levels had low annual survival rates, received less maternal/alloparental care and had higher FGM levels. Interestingly, offspring from mothers with high FGM levels were more likely to survive the summer when born in small litters. In sum, social interactions likely influence and are influenced by glucocorticoid levels of facultatively social females. Potential benefits of social bonds may be context-specific, and agonistic interactions may be tightly correlated with fitness. Female marmots exhibiting high FGM levels had overall low reproductive success, which is predicted by the cort-fitness hypothesis. However, under adverse conditions, offspring summer survival can be maximized if pups are born in small litters.

1. Introduction

The social environment—defined as the set of all interactions between an individual and its conspecifics—may challenge individuals but may also promote well-being and/or modify their ability to cope with adversity (Beery and Kaufer, 2015; Cohen, 2004; Holt-Lunstad et al., 2010). In nature, ecological and demographic factors modify social environments (Armitage and Downhower, 1974; Barash, 1974; Blumstein, 2013; Iossa et al., 2008; Klein et al., 2017; Negrin et al., 2016; Ondrasek et al., 2015; Pasinelli and Walters, 2002), and the degree to which social changes impact individuals depends on a variety of contextual factors, including group size, type of interactions, species social organization, sex and age (Anisman and Merali, 1999; Cohen, 2004; Hall, 1998; Palanza et al., 2001).

The consequences of the social environment on individuals are often studied by manipulating group composition or structure in captive, domesticated species (Cruces et al., 2014). Such studies may not be applicable to wild populations since artificially selected lineages may have altered social phenotypes (Chalfin et al., 2014; Künzl et al., 2003; Künzl and Sachser, 1999), and behavioral and endocrine responses have evolved in contexts characterized by multiple stressors. In addition, most in situ studies have been conducted on highly social mammals. For instance, while it is generally accepted that social isolation is a risk factor for mortality, and affiliative behavior lowers stress levels in social species (House et al., 1988; Sapolsky et al., 1997; Holt-Lunstad et al., 2010; Cruces et al., 2014), little is known about the effects of the social environment on individuals of less social species (Ferron, 1985; Maher, 2009; Yoerg, 1999). In fact, Blumstein et al. (2018) found that the strength of affiliative social relationships is negatively associated with longevity in yellow-bellied marmots (*Marmota flaviventer*), emphasizing that studies on less social species may provide insightful perspectives in this field.

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Furthermore, physiological and behavioral responses to social conditions have been mostly studied in males (Palanza et al., 2001; Palanza and Parmigiani, 2017; Pittet et al., 2017; Taylor et al., 2000). Yet, sex differences in the perception of the social environment are expected due to sex-specific social roles (Kudielka and Kirschbaum, 2005; Palanza et al., 2001; Palanza and Parmigiani, 2017; Stroud et al., 2002). Since female mammals generally invest more in their offspring, female responsiveness to social variation may be essential for the wellbeing of both females and their young (Taylor et al., 2000). In this respect, the strength and stability of female social bonds may be key predictors of fitness (Palanza and Parmigiani, 2017; Stroud et al., 2002; Taylor et al., 2000).

Exposure to challenging conditions that disrupt homeostasis and cause mental or physical tension promotes the activation of pathways that culminate in the production of glucocorticoid hormones (Anisman and Merali, 1999; Cruces et al., 2014; Sapolsky et al., 2000; Sheriff et al., 2010). Due to their role in coping responses, glucocorticoid hormones (GC) and their metabolites are often used to measure stress levels in ecological and psychosocial studies (Sheriff et al., 2010; Sheriff and Love, 2013; Wey et al., 2015). Here, we evaluate how both affiliative and agonistic aspects of the social environment are associated with maternal fecal glucocorticoid metabolites (FGM) levels in facultatively social, yellow-bellied marmots.

Wild female marmots can live alone or form kin groups (Armitage and Schwartz, 2000). While large group sizes are characterized by more agonistic interactions and reproductive suppression (Armitage and Schwartz, 2000), group living may also have advantages since solitary females occupy suboptimal environments (Armitage and Downhower, 1974) and exhibit more vigilant behavior than females in groups (Mady and Blumstein, 2017). Group living may be particularly important to mothers and their offspring (Blumstein et al., 2016) because pups are extremely vulnerable to predators (Wey and Blumstein, 2012). Although Wey and Blumstein (2012) found no relationship between social context and FGM levels in females, their analysis did not use information on reproductive status, which may be an important determinant of female sensitivity to variation in the social environment (Ralph and Tilbrook, 2016; Reeder et al., 2004; Tu et al., 2005).

Assuming that GC levels vary according to the magnitude of environmental challenges, and that individuals facing greater challenges have lower fitness, the cort-fitness hypothesis predicts that baseline GC levels will be negatively associated with long-term survival and/or reproductive success (Bonier et al., 2009a, 2010). Due to conflicting results in different taxa (Bonier et al., 2009b; Dipietro et al., 2006; Maguire and Mody, 2016; Sapolsky et al., 2000; Whirledge and Cidlowski, 2010), the efficiency of GC as a proxy of fitness should be validated in each species (Bonier et al., 2010). In yellow-bellied marmots, high concentrations of FGM are associated with an increased risk of mortality (Wey et al., 2015). However, females with higher FGM levels wean larger litters (Blumstein et al., 2016), indicating a higher reproductive output. Because about half of the pups are either killed by predators or fail to survive their first winter (Armitage and Downhower, 1974), the relationship between maternal FGM levels and offspring survival should be further investigated for a better understanding of female reproductive success under sub-optimal conditions.

Maternal response to sub-optimal conditions may be adaptive when it reliably prepares offspring for their future environments (Sheriff and Love, 2013). Cues received during early life trigger developmental plasticity that may be beneficial later in life (Bateson et al., 2014). In this regard, maternal care may provide such cues (Klaus et al., 2013) and is known to directly affect offspring development and brain function (Curley et al., 2011; Curley and Champagne, 2016; Luby et al., 2012; Weaver et al., 2004). Female yellow-bellied marmots engage in maternal care by grooming and interacting affiliatively with offspring, as well as by alarm calling (Blumstein et al., 1997). Female marmot FGM levels have been shown to be significantly associated with litter size, offspring sex ratio, dispersal behavior and personality (Monclús et al., 2011; Petelle et al., 2017). We ask whether maternal care, measured through female-pup interactions and maternal antipredator behavior, is associated with maternal FGM levels.

Here, we use long-term data on a wild population to study the association between the social environment and FGM levels of facultatively social females, and the impact of their FGM levels on offspring fitness. To do so, we (1) estimated the association between maternal FGM levels and social network metrics calculated from affiliative and agonistic interactions; (2) investigated whether female FGM levels are associated with their antipredator behavior and interactions with pups; and (3) measured the association between maternal FGM and both offspring FGM levels and offspring survival.

2. Methods

2.1. Data collection

We analyzed 10 years (2005–2012, 2014, 2015) of behavioral and trapping data collected from females and their offspring in free-living yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (38°57′N, 106°59′W; 2900 m elevation; Gunnison County, Colorado, USA; Blumstein, 2013). This research was performed under the University of California, Los Angeles Institutional Animal Care and Use protocol (2001–191-01, renewed annually) and with permits from Colorado Parks and Wildlife (TR917, renewed annually).

Trapping sessions occurred biweekly from May to mid-September (details in Blumstein et al., 2016; Wey et al., 2015). We trapped marmots with Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) baited with Purina Omolene 100 Horse Feed (Purina Mills, LLC, Gray Summit, MO). At each capture, we recorded individual identification through fur mark and two uniquely numbered metal ear-tags (Monel self-piercing fish tags #3, National Band and Tag, Newport, KY, United States); individual sex and reproductive status; time and date of capture. We also collected hair and, when available, fecal material (Armitage, 1982). Fecal samples were collected from May to the end of July, only when feces were both fresh and could be clearly associated with the trapped individual, and were stored on ice and frozen at −20 °C within 2 h. Unique dorsal fur marks were drawn using black Nyanzol fur dye to identify individuals from afar during behavioral observations.

Weather permitting, we performed daily behavioral observations during times of peak activity (0700–1000, and 1600–1900 h; Armitage, 1962) from mid-April to mid-September. Observers used binoculars and 15–45× spotting scopes, being positioned 20–150 m from marmot groups (Blumstein et al., 2009; Yang et al., 2017). Observers recorded individual identity, type of behavior, location and predator presence in an all-occurrence sampling scheme (details in Blumstein et al., 2009). Behavior types included alarm calling and 32 types of intraspecific interactions, grouped as agonistic for aggressive behaviors or affiliative for amicable ones (ethogram in Blumstein et al., 2009). For each interaction, we recorded the identity of initiators and recipients. We also quantified time allocated to antipredator vigilance with 2-min focal observations on foraging individuals (details in Blumstein et al., 2004, 2010). Focals were scored in JWatcher 1.0 (Blumstein and Daniel, 2007).

To test how maternal fecal glucocorticoid metabolites (FGM) levels are associated with the social context and pup care, FGM and survival, we fitted (generalized) linear mixed effects models. The variables included in the models are explained below.

Maternal and pup FGM – Free glucocorticoid hormones (GC), which are biologically active, are metabolized by the liver and excreted via urine and feces (Palme, 2005; Touma and Palme, 2005). Because of the accumulation of GC metabolites in the gut, FGM concentrations are less sensitive to episodic fluctuations in the hypothalamo-pituitary-adrenal axis activity, thus being less influenced by short-term stressors (Sheriff et al., 2010; Touma and Palme, 2005). Therefore, FGM concentrations are an easy, effective, and non-invasive method to access changes in plasma free-GC concentrations in response to conditions that may last from several hours to days (Palme, 2005; Sheriff et al., 2010; Smith et al., 2012; Touma and Palme, 2005).

Smith et al. (2012) validated this method in both captive and wild yellow-bellied marmots, describing significant rise in FGM levels with stressors (biological and physiological validation) and significant effects of year, season, time of day, sex, age, reproductive status and individual identity. We use extensive, long-term individual level data collected from this yellow-bellied marmot population (Blumstein, 2013) to control for these additional effects on GC levels that could confound our ability to isolate an effect of interest (Djurhuus et al., 2004; Palme, 2005; Sapolsky et al., 2000). Thus, we used FGM concentrations as a proxy of baseline stress levels (Palme, 2005; Sapolsky et al., 2000; Sheriff et al., 2010; Smith et al., 2012; Touma and Palme, 2005). Marmot FGM levels rise 24 h after capture (Smith et al., 2012), therefore we only analyzed samples collected during an individual's first capture of each trapping session. FGMs were extracted using a double-antibody ^{125}I radioimmunoassay kit (RIA; MP Biomedicals, Costa Mesa, CA) from samples within 6 months of collection (Smith et al., 2012). Details are described in Appendix A of Blumstein et al. (2006). Briefly, we boiled 0.2 g of thawed feces in 90% aqueous ethanol at 80 °C, centrifuged the solution, decanted the supernatant and repeated the procedure. Supernatants were dried in a vacuum centrifuge and reconstituted with 1 ml of Absolute ethanol. We used 12.5 μl of this concentrated solution in a corticosterone RIA that was cross-reactive with cortisol but not other steroid hormones. RIAs were run in duplicate and if the CV was $>$ 10% we reran samples.

FGM concentration data were used differently depending on the model fitted. We used: (1) FGM concentrations measured from each fecal sample; (2) the mean of FGM concentrations from samples collected before a given female's litter emerged (hereafter, FGM before emergence mean); and (3) the mean of FGM concentrations from samples collected after a given female's litter emerged (hereafter, FGM after emergence mean).

Pup care – Female-pup interaction and antipredator behavior were used as proxies for pup care. In marmot matrilines, more than one female can breed in a season, and these share burrows and nurse non-offspring (Armitage and Gurri-Glass, 1994). Consequently, interactions among any female and any pup in a social group may represent pup care and have an important role in offspring phenotypic variation, as observed in other species (Bauer et al., 2015; Birnie et al., 2013; Branchi et al., 2006; Curley et al., 2009; Fleming et al., 2002; Sayler and Salmon, 1969). Thus, we measured whether reproductive females were observed interacting with pups or not during a season, including both mother-offspring and potential alloparental interactions (Blumstein and Armitage, 1999). Vigilance was measured as the proportion of time mothers spent vigilant in each 2-min focal animal sample. Propensity to alarm call was quantified based on observations of mothers seen calling or not during a season.

Maternal age and litter emergence date – We analyzed only mothers of known age (i.e., they had been monitored since birth). We also recorded the emergence date for each litter, defined as the first day in which the first pup from a litter was seen above ground. Because females are observed and trapped frequently, we are able to detect lactating females and potential burrows with pups. Groups with lactating females are observed closely, and most litters were found as soon as they emerged.

Social attributes – We used observed social interactions between all females older than one year to create two separate social networks, one that only considered affiliative interactions and one that only considered agonistic interactions. From each social network, we calculated 10 social attributes that captured various dimensions of marmot social behavior (Fuong et al., 2015; Wey and Blumstein, 2012), which are *degree* (in and out), *strength* (in and out), *closeness* (in and out), *betweenness centrality*, *eigenvector centrality*, *embeddedness*, and *clustering coefficient*:

- *Degree* represents the number of social partners an individual has. It is a directed measure such that in-degree represents the number of individuals that initiated an interaction with the focal animal while out-degree represents the number of individuals with which the focal animal initiated an interaction (Wasserman and Faust, 1994).
- *Strength* represents the total number of interactions the focal individual received (in-strength) or initiated (out-strength) regardless of the number of social partners (Barrat et al., 2004).
- *Closeness* represents how closely the focal individual is connected to every other individual in the network and is calculated as the reciprocal of the sum of the shortest path lengths between a focal and every other individual (Wasserman and Faust, 1994; Wey et al., 2008). A shortest path length of 1 represents individuals that interacted directly with each other while a shortest path length of 2 represents individuals that are most closely connected to each other through one other individual. By including indirect social connections, *closeness* is a measure that reflects how a focal individual can influence (out-closeness) or be influenced by (in-closeness) individuals in the social network, even if they do not interact directly. The closer individuals are connected, the more influence they will have on one another.
- *Betweenness centrality* estimates how much focal individuals connect all other individuals in a network, and is therefore a measure of an individual's importance in maintaining group stability as well as its role as a potential "bridge" in information transfer. It is calculated as the proportion of shortest path lengths in the network that include the focal individual (Wey et al., 2008).
- *Eigenvector centrality* ranks individuals based on the quality of their connections. An individual has a high eigenvector centrality if it is connected to other high-ranking individuals. It is calculated as the eigenvector associated with the maximal eigenvalue of an adjacency matrix (Bonacich, 2007).
- *Embeddedness* is a measure of integration into a group. It identifies the greatest size of the cohesive subgroups to which the focal individual belongs (Moody and White, 2003). Cohesive subgroups are groups within the greater social network in which each individual is independently connected to every other individual.
- *Clustering coefficient* reflects how densely the network is clustered around a focal individual. It uses the number of observed connections among the focal individual's neighbors over the total possible connections (Wey et al., 2008).

Although the social networks included non-reproductive females, only reproductive females were considered focal individuals. All social attributes were calculated in igraph package 0.7.0 (Csardi and Nepusz, 2006) and R 3.3.1 (R Development Core Team, 2016). Because many of these social attributes are correlated (Wey and Blumstein, 2012), we used a principal component analysis to reduce them into uncorrelated measures (extractions based on eigenvalue $>$ 1 with varimax rotation; SPSS 21.0; IBM Corp., Armonk, NY; IBM Corp 2012).

Group size – Social groups are formed by individuals living in close proximity and more associated among themselves than with other individuals in the population (Maldonado-Chaparro et al., 2015). We used data from individuals seen or trapped at least five times in a given year. We calculated the simple ratio index (SRI, Cairns and Schwager, 1987) from live-trapping and observation data for each pair of marmots using Socprog (Whitehead, 2009). We established the number and identity of individuals belonging to social groups with the random walk algorithm in Map Equation (Rosvall et al., 2009).

Litter size – Estimated during behavioral observations and trapping sessions. Relationships were further confirmed with parentage analysis, using DNA extracted from hair samples. We genotyped pups and females with 8–12 microsatellite markers and estimated mother-offspring pairs using CERVUS 3.0 (Kalinowski et al., 2007). Details can be found in Blumstein et al. (2010).

Pup survival – We obtained three estimates of pup survival rates per litter: summer, winter, and annual survival. Summer survival was calculated as the number of pups that survived until the end of the active season divided by litter size. Winter survival was the number of pups observed or trapped in the following summer divided by the number of pups that survived their first summer. Annual survival was the number of pups observed or trapped in the following summer divided by litter size.

Predator index – Following Monclús et al. (2011), we calculated predator index as the proportion of observation sessions in which predators were recorded, from April to June. Locations were classified as having high or low predator presence based on a median cut. Predators included: red fox (*Vulpes vulpes*), coyote (*Canis latrans*), American badger (*Taxidea taxus*), American black bear (*Ursus americanus*), domestic dog (*Canis lupus familiaris*), and several species of raptors and mustelids (Van Vuren, 2001).

2.2. Statistical analysis

According to the distribution of the dependent variable, we fitted linear mixed effects models (LMMs) or generalized linear mixed effects models with binomial distribution (binomial GLMMs). We used a top-down approach for model selection following Zuur et al. (2009). Initial models contained random effects (individual identity and year), fixed effects and interactions (Table S1), which were selected based on data availability and biological relevance. The optimal fixed component was found by dropping variables one-by-one and, in each turn, performing likelihood ratio tests (LMM) or analysis of deviance tests (binomial GLMM) to compare nested models. We computed the marginal and conditional R squared values for all final models to understand how much of the data variance is being explained by fixed and random effects.

We transformed variables as necessary, and scaled and centered continuous explanatory variables so that estimates would be comparable. Specific data transformations in each model can be found in the Supplementary File S2. We evaluated the assumptions of the models by visually inspecting the correlation among variables, qq plots of residuals, plots of residuals with fitted values, and plots of residuals with each explanatory variable (present or not in the final model). We also calculated Cook's distance to look for influential observations and checked model fit by plotting fitted with observed values of the dependent variable. We used standardized residuals for LMMs, and deviance residuals for binomial GLMMs. For a better evaluation of plots with residuals from the binomial GLMMs, re- siduals were separated in groups of five based on the order of fitted values, and the average of these groups were used in the plots. Analyses were carried out in R 3.4.4 (R Core Team, 2018) using the packages lme4 1.1–14 (Bates et al., 2015), and lmerTest 3.0–1 (Kuznetsova et al., 2017). Plots were generated using the packages ggplot2 3.0.0 (Wickham, 2016) and ggpubr 0.1.7. (Kassambara, 2018).

To test how the social context is associated with maternal FGM levels, we fitted separate LMMs for affiliative and agonistic interactions. Affiliative interactions are more common in yellow-bellied marmots than agonistic behavior, so we analyzed the data separately because of the differences in sample size. The fixed effects of the initial models (i.e., first step of the model selection) were group size, litter size, metrics from social networks, predator index, maternal age and time/day of capture in which the fecal sample was collected. Interactions between fixed effects can be found in Table S1. The dependent variable was maternal FGM concentrations measured from each fecal sample (ng/ml).

To test the association between maternal FGM levels and pup care, we fitted binomial GLMMs for each measure of pup care: alarm calling, vigilance and female-pup social interactions. For the models using alarm calling and female-pup interactions, fixed effects were maternal FGM after emergence, litter size, maternal age, predator index and total time spent observing each social group. For the model using vigilance data, fixed effects included: maternal FGM after emergence, litter size, maternal age, predator index, and time/day in which the focal was performed. Interactions between fixed effects can be found in Table S1.

To study the influence of maternal FGM levels on pup survival, we fitted binomial GLMMs for each measure of pup survival: summer, winter, and annual survival. The models included maternal FGM after emergence, litter size, maternal age, and predator index as fixed effects.

Finally, to investigate the effect of maternal FGM levels on pup FGM levels, we fitted two LMMs to the pup FGM concentration data (ng/ml). In one model we used maternal FGM before emergence and, in the other, maternal FGM after emergence mean as fixed effects. Common fixed effects for both models were litter size, predator index, maternal age, and time/date of capture in which the fecal sample was collected.

3. Results

3.1. Maternal fecal glucocorticoid metabolites (FGM) levels

3.1.1. How are maternal FGM levels associated with affiliative interactions?

The female-affiliative social network analysis included 51 unique females and represented 87 breeding events over 10 years. Females had an average of 2.52 FGM measurements per active season (*SD* = 1.41, *n* = 219 individual measurements). Social groups averaged 13.36 individuals (*SD* = 7.92; range 3–34), litter size averaged 4.36 pups (*SD* = 1.81, range 1–10), and the average maternal age was 4.37 years (*SD* = 2.51, range 2–12). The principal components analysis explained 74.6% of the variation in affiliative social metrics. The principal components can be interpreted as popularity ($PC1_{AFF}$), which included degree (in and out), closeness (in and out), and eigenvector centrality; relationship strength ($PC2_{AFF}$), which included strength (in and out);

Table 1

Factor loadings for each component of the principal component analysis on social metrics from affiliative and agonistic networks. High loading values are in bold.

Social metrics	Affiliative networks			Agonistic networks		
	PC1 (popularity)	PC2 (relationship strength)	PC3 (group cohesiveness)	PC1 (aggression initiated)	PC2 (aggression received)	PC3 (group cohesiveness)
In-degree	**0.85**	0.18	−0.14	0.18	**0.93**	0.11
Out-degree	**0.84**	0.28	0.01	**0.95**	−0.02	0.00
In-strength	0.21	**0.90**	0.07	−0.19	**0.88**	0.14
Out-strength	0.20	**0.91**	0.10	**0.52**	−0.02	0.38
In-closeness	**0.87**	0.12	−0.13	0.55	**0.68**	0.23
Out-closeness	**0.84**	0.21	0.15	**0.88**	0.01	0.12
Betweenness centrality	0.19	−0.19	**−0.63**	0.43	−0.15	**−0.81**
Eigenvector centrality	**0.85**	−0.04	0.12	**0.68**	0.29	−0.12
Embeddedness	0.21	0.28	**0.72**	0.22	0.36	**0.75**
Clustering coefficient	0.02	−0.35	**0.80**	0.20	0.03	**0.84**

Table 2
Results from linear mixed effects models explaining variation in maternal stress levels (measured through fecal glucocorticoid metabolite concentrations) in a wild yellow-bellied marmot population. Models differed by the inclusion of social network metrics based on affiliative or agonistic interactions.

Affiliative networks			Agonistic networks		
Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P
Intercept	−0.11 ± 0.26	0.681	Intercept	−0.03 ± 0.36	0.937
$PC3_{AFF}$	−0.03 ± 0.07	0.681	$PC1_{AGO}$	0.20 ± 0.08	0.014
Litter size	0.19 ± 0.06	0.001	Litter size	0.22 ± 0.07	0.004
Predator index (low)	0.03 ± 0.14	0.843	$PC2_{AGO}$	0.21 ± 0.08	0.007
Time of capture	0.16 ± 0.05	0.001	Time of capture	0.19 ± 0.07	0.005
Day of capture	−0.13 ± 0.05	0.005	Day of capture	−0.22 ± 0.06	<0.001
$PC3_{AFF}$: Predator index	−0.25 ± 0.11	0.020			

Affiliative networks			Agonistic networks		
Random effect	Variance	SD	Random effect	Variance	SD
Mother identity	0.02	0.13	Mother identity	0.01	0.10
Year	0.60	0.78	Year	0.97	0.98

and group cohesiveness ($PC3_{AFF}$), which included clustering, embeddedness, and betweenness (Table 1).

Our final model included $PC3_{AFF}$ (group cohesiveness), litter size, predator index, time/date of individual capture, and the interaction between $PC3_{AFF}$ and predator index (Table 2). The interaction between $PC3_{AFF}$ and predator index explained significant variation in maternal FGM levels ($p = 0.020$, Table 2). In low predation pressure environments, females with high group cohesion had somewhat lower FGMs than females with low group cohesion (Fig. 1). In contrast, there was no apparent association between group cohesion and FGMs in high predation environments. Litter size was positively associated with maternal FGM ($p = 0.001$), and both day and time of capture affected FGM levels (Table 2). Female identity and year (random effects) explained much of the variation in maternal FGM, because this model had a marginal R^2 of 0.10 and a conditional R^2 of 0.66. By comparing estimates in this model, we infer that the interaction between group cohesiveness and predator index was the fixed effect with the strongest effect on maternal FGM, followed by litter size (Table 2).

3.1.2. How are maternal FGM levels associated with agonistic interactions?

The female-agonistic dataset included 32 unique females that represented 42 breeding events over 8 years. Females had an average of 2.74 FGM measurements per season ($SD = 1.52$, $n = 115$ individual FGM samples). Groups averaged 15.22 individuals ($SD = 8.60$; range 3–34). The principal components analysis explained 75.5% of the variation in affiliative social metrics. The principal components can be interpreted as aggression initiated ($PC1_{AGO}$), which included out-degree, out-closeness, out-strength, and eigenvector centrality; aggression received ($PC2_{AGO}$), which included in-degree, in-closeness, and in-strength; and group cohesiveness ($PC3_{AGO}$), which included clustering, embeddedness, and betweenness (Table 1).

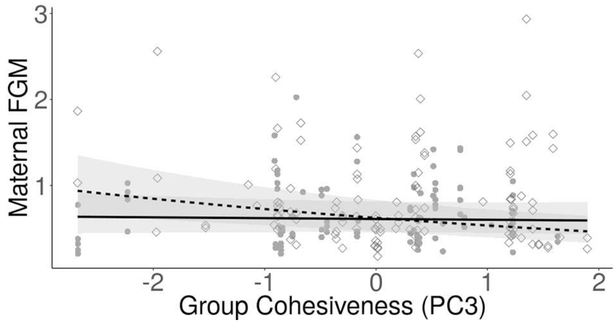

Fig. 1. Relationship between maternal fecal glucocorticoid metabolite concentrations (ng/ml) and group cohesiveness, a principle component characterized by affiliative clustering, embeddedness, and betweenness. The dashed line and diamond shaped points illustrate environments with low predator indices, while the continuous line and the filled circles illustrate environments with high predator indices. Points represent the actual data, while lines were generated with predicted probabilities from a linear mixed effects model. To generate predictions from the model, all other variables were set to the mean. Buffers illustrate the 95% confidence intervals. Importantly, observed values do not control for significant variation explained by the model.

Our final model included $PC1_{AGO}$ (aggression initiated), $PC2_{AGO}$ (aggression received), litter size, and time/day of individual capture (Table 2). After controlling for FGM seasonal and daily variation, maternal FGM levels were positively associated with aggression initiated, aggression received and litter size ($p = 0.014$, 0.007 and 0.004, respectively; Table 2, Fig. 2). Female identity and year explained a significant portion of the variation in maternal FGM levels; this model had a marginal R^2 of 0.13 and a conditional R^2 of 0.74. In addition to day of capture, litter size was the fixed effect with highest estimates, followed by $PC2_{AGO}$ and $PC1_{AGO}$, respectively (Table 2).

3.2. Pup care

3.2.1. Does maternal FGM explain variation in the probability of a mother emitting an alarm call?

This dataset included 59 unique mothers involved in 91 breeding events. We only positively identified 30 mothers that alarm called following pup emergence. Our final model was no different from the null model, and annual effects explained more of the variation than maternal identity (Table 3).

3.2.2. Does female FGM explain variation in whether females are ever seen interacting with pups?

From the 90 reproductive events of 58 females observed during 10 years, females were observed interacting with pups in 49 events. In our final model, maternal FGM after emergence and predator index were negatively associated with the occurrence of female-pup interactions ($p = 0.032$ and 0.001, respectively; Table 3). This result suggests that mothers are less likely to interact with pups when exhibiting high FGM levels or at locations with high predation pressure. Individual identity and year seem not to have an effect on female-pup interactions (Table 3). This model had a marginal R^2 of 0.22 and a conditional R^2 of 0.22.

3.2.3. Does maternal FGM explain variation in time mothers allocate to vigilance?

We collected 71 focals from 24 females with pups over 7 years, with an average of 2.09 focals per female per year. The final model had only

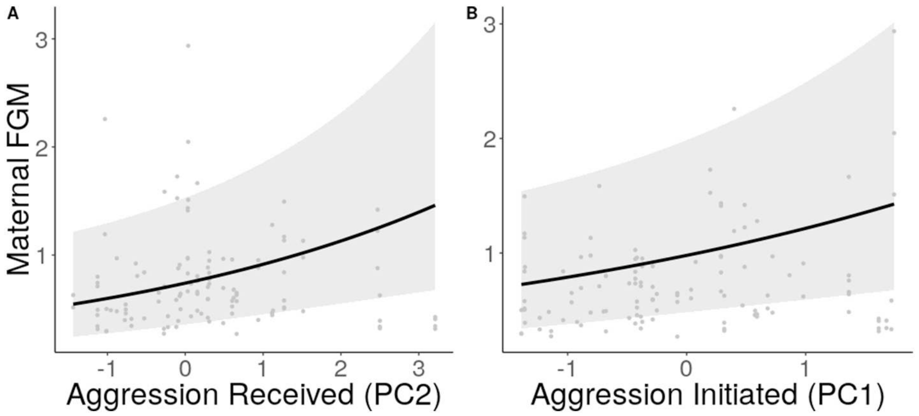

Fig. 2. Relationship between maternal fecal glucocorticoid metabolite concentrations (ng/ml) and aggression received (A) and aggression initiated (B). Aggression received (PC2) was inferred from a principal component on which in-degree, in-closeness, and in-strength were loaded; and aggression initiated (PC1) was defined by out-degree, out-closeness, out-strength, and eigenvector centrality. Points represent the actual data, while lines were generated with predicted probabilities from a linear mixed effects model. To generate predictions from the model, all other variables were set to the mean. Buffers illustrate the 95% confidence intervals. Importantly, the points of observed values are not controlled for significant variation explained by the model.

one fixed effect, the predator index, suggesting that mothers spend less time being vigilant in environments with lower predator pressure ($p = 0.028$; Table 3). The random effects explained no variation in vigilance. This model had a marginal R^2 of 0.20 and a conditional R^2 of 0.20.

3.3. Pup FGM levels

The model using the average maternal FGM before emergence included 227 FGM measurements from 148 pups of 43 mothers across 7 years, while the model using maternal FGM after emergence included 217 FGM measurements from 139 pups of 40 mothers across 7 years. Interestingly, maternal FGM was positively associated with pup FGM levels only when it was calculated as a mean before emergence ($p = 0.028$; Table 4). Mothers with high FGM levels before pup emergence had pups with high FGM, while maternal FGM levels measured after pup emergence had no effect on pup FGM levels. The random effect of year explained more of the variation in pup FGM levels than maternal or pup identity. The model using maternal FGM before emergence had a marginal R^2 of 0.05 and a conditional R^2 of 0.65.

3.4. Offspring survival

Offspring survival was measured for 91 litters from 59 females across 10 years. In the final models, maternal FGM after emergence was negatively associated with measurements of winter and annual survival ($p < 0.001$ and $= 0.001$, respectively; Table 5, Fig. 3). For the model fitted to summer survival data, we found a negative effect of predator index ($p = 0.031$), where pups were more likely to survive in environments with low predator pressure, and a significant effect of the interaction between maternal FGM after emergence and litter size ($p = 0.011$, Table 5). During the active season, large litters from females with low FGM levels had higher chance of survival than smaller litters, but this pattern was inverted if females had high FGM concentration (Fig. 4). In addition, the random effects of mother identity and year explained no variation in any measurements of survival. The marginal R^2 for the summer survival model, winter survival model and annual survival model were 0.57, 0.23 and 0.25, respectively.

4. Discussion

4.1. Associations between social interactions and maternal fecal glucocorticoid metabolites (FGM) levels

Overall, we found that social conditions are associated with maternal FGM levels in wild female yellow-bellied marmots. These results contrast with Wey and Blumstein (2012), who conducted similar social network measurements on a smaller sample from the same yellow-bellied marmot population and found no association of social interactions with female FGM levels. Wey and Blumstein (2012) analyzed females at different life stages but did not include information about individual reproductive status in the models, which is an important factor that explains female sensitivity to environmental and social conditions in other species (Mora et al., 1996; Palanza et al., 2001; Ralph and Tilbrook, 2016; Reeder et al., 2004; Tu et al., 2005). The discrepancy of our results suggests that reproductive female marmots are more responsive to their social environment, however this should be tested directly.

Maternal FGM levels were associated with position in agonistic networks; mothers both initiating and receiving agonistic interactions had increased FGM levels, so agonistic behavior clearly has an important role in female fitness and marmot social organization. Lea et al. (2010) found that measures of initiated aggression were positively associated with both longevity and lifetime reproductive success, while

Table 3

Results from generalized linear mixed effects models explaining variation in pup care in a wild yellow-bellied marmot population. Models differed by the proxies used to access pup care: alarm calling, female-pup interactions, and proportion of time allocated to vigilance while foraging.

Alarm calling			Female-pup interactions			Vigilance		
Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P
Intercept	−1.63 ± 0.94	0.084	Intercept	−0.52 ± 0.31	0.092	Intercept	−1.15 ± 0.43	0.008
–	–	–	Maternal FGM after emergence	−0.52 ± 0.24	0.032	Predator index (low)	−1.85 ± 0.85	0.028
–	–	–	Predator index (low)	1.57 ± 0.48	0.001	–	–	–

Alarm calling			Female-pup interactions			Vigilance		
Random effect	Variance	SD	Random effect	Variance	SD	Random effect	Variance	SD
Mother identity	0.01	0.09	Mother identity	0.00	0.00	Mother identity	0.00	0.00
Year	5.65	2.38	Year	0.00	0.00	Year	0.00	0.00

Table 4

Results from linear mixed effects models explaining variation in pup stress levels (measured through fecal glucocorticoid metabolite concentrations - FGM) in a wild yellow-bellied marmot population. Models differed by the calculation of the fixed effect related to maternal stress levels: maternal FGM before emergence (included only samples preceding pup emergence) and maternal FGM after emergence (included only samples following pup emergence).

Maternal FGM before emergence			Maternal FGM after emergence		
Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P
Intercept	−0.57 ± 0.17	0.013	Intercept	−0.50 ± 0.20	0.044
Maternal FGM before emergence	0.12 ± 0.05	0.028	–	–	–
Random effect	Variance	SD	Random effect	Variance	SD
Mother identity	0.02	0.15	Mother identity	0.02	0.15
Pup identity	0.01	0.08	Pup identity	0.01	0.10
Year	0.17	0.41	Year	0.25	0.50

received agonistic interactions were negatively correlated to lifetime reproductive success. Female marmots can be hierarchically ranked based solely on the relative number of wins against opponents in agonistic interactions, and dominant females exhibit lower FGM levels (Blumstein et al., 2016).

Under low predation pressure, group cohesiveness was weakly associated with reduced maternal FGM, but may potentially act as a social buffer by reducing effects of external stressors (Cohen, 2004; Kiyokawa and Hennessy, 2018). The conditional and weak relationship between social buffering and predator pressure represented in Fig. 1 suggests that affiliative bonds may not significantly alter maternal FGM levels under some scenarios. Maldonado-Chaparro et al. (2015) found that yellow-bellied marmots lose influence over conspecifics as group size increases, indicating some fragility of social bonds in this socially flexible rodent.

The affiliative metrics associated with maternal FGM were undirected and unweighted, indicating that a female marmot can be affected or affect a social network by simply being connected to others, independently of the number of interactions or the identity/dominance rank of individuals. Although evidently there are limitations to the effects of social bonds in marmots, there may be collective context-specific benefits, which could explain previous observations of marmots exhibiting higher sociality in harsher environments (Armitage, 2014; Barash, 1974; Blumstein, 2013). Sociality can buffer individuals from the impact of environmental changes in other taxa (Keiser et al., 2014; Pinter-Wollman et al., 2009), and the benefits of marmot social behavior may occur not only during hibernation (as reported in Alpine marmots, *M. marmota*, but not yellow-bellied marmots–e.g., Allainé, 2000; Arnold, 1988; Ruf and Arnold, 2000) but also in the active season.

Recent studies of yellow-bellied marmots have identified overwinter survival (Yang et al., 2017) and longevity costs (Blumstein et al., 2018) of sociality. The potential positive fitness effects of social buffering could balance out these negative effects and be a factor that explains affiliative social interactions in yellow-bellied marmots. Despite the restricted number of behavioral studies with less social mammals, some species seem to benefit from social behavior. Young 13-lined ground squirrels (*Ictidomys tridecemlineatus*)—an undomesticated and asocial species—have capacity for social reward (Lahvis et al., 2015). Social contact is also important for the maintenance of female estrous cycle in solitary kangaroo rats (*Dipodomys heermanni*; Yoerg, 1999). Previously isolated kangaroo rats behave more socially after several encounters with conspecifics (Yoerg, 1999). In more social species, positive outcomes of social bonds on female fitness are more pronounced (Cameron et al., 2009; Silk et al., 2003, 2009, 2010; Vander Wal et al., 2015). Since advantages of sociality are context dependent (Lahvis et al., 2015; Silk, 2007), identifying which conditions differ among less and more social species may reveal the conditions that have selected for more complex social systems in ancestral species.

4.2. Associations between female FGM levels and pup care

The influence of adult stress on parental care is still underexplored when compared to the effects of individual early experiences on phenotypes (Darnaudéry and Maccari, 2008; Pittet et al., 2017). In wild marmots, we found that FGM levels are associated with pup care: females with high FGM levels are less likely to interact with pups. Previous studies reported similar findings on other species. For instance, mothers in low quality environments or with high stress levels engage in more offspring-directed aggression in guinea pigs and rats (*Rattus*

Table 5

Results from generalized linear mixed effects models explaining variation in offspring survival in a wild yellow-bellied marmot population. Models differed by the different calculations of survival: summer survival, winter survival and annual survival.

Summer survival			Winter survival			Annual survival		
Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P	Fixed effect	Estimate ± SE	P
Intercept	0.02 ± 0.33	0.964	Intercept	0.25 ± 0.23	0.281	Intercept	−0.40 ± 0.24	0.098
Maternal FGM after emergence	−0.74 ± 0.30	0.015	Maternal FGM after emergence	−0.98 ± 0.27	<0.001	Maternal FGM after emergence	−1.06 ± 0.30	0.001
Litter size	−0.66 ± 0.35	0.061	–	–	–	–	–	–
Predator index (low)	1.11 ± 0.51	0.031	–	–	–	–	–	–
Maternal FGM after emergence: Litter size	−1.09 ± 0.43	0.011	–	–	–	–	–	–
Summer survival			Winter survival			Annual survival		
Random effect	Variance	SD	Random effect	Variance	SD	Random effect	Variance	SD
Mother identity	0.00	0.00	Mother identity	0.00	0.00	Mother identity	0.00	0.00
Year	0.00	0.00	Year	0.00	0.00	Year	0.00	0.00

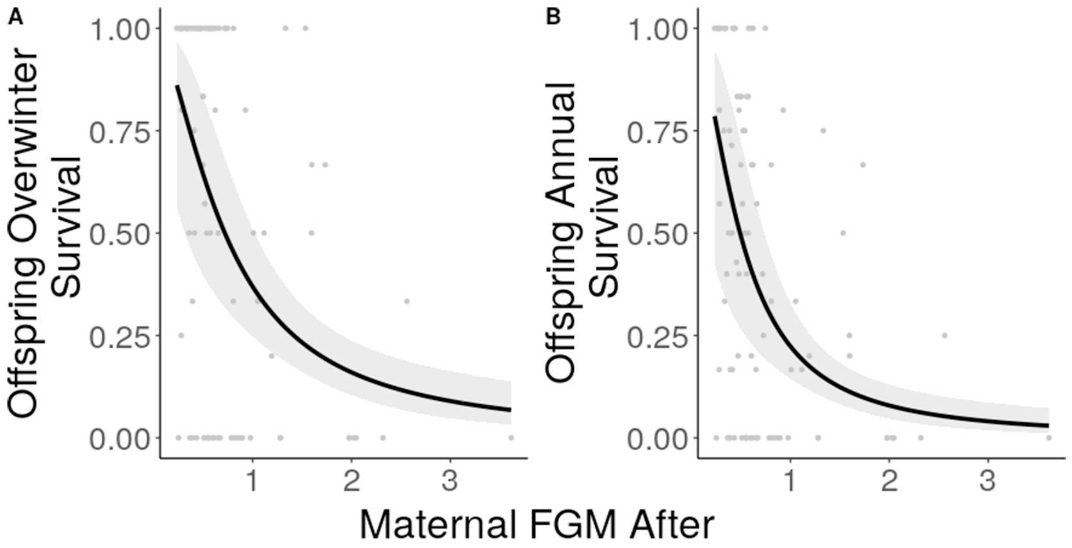

Fig. 3. Relationship of offspring overwinter (A) and annual (B) survival with maternal FGM measured after pups emerged (fecal glucocorticoid metabolite concentrations (ng/ml)). Points represent the actual data, while lines were generated with predicted probabilities from a linear mixed effects model. Buffers illustrate the 95% confidence intervals. Importantly, the points of observed values are not controlled for significant variation explained by the model.

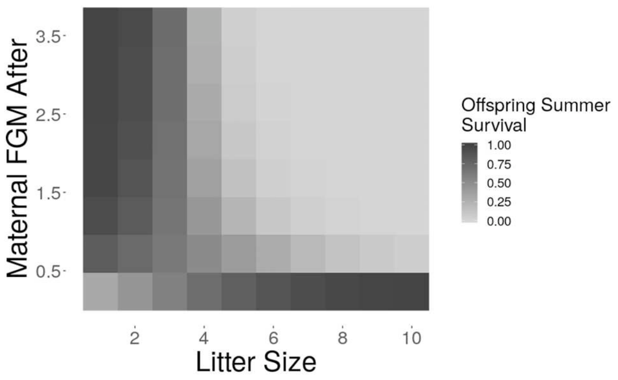

Fig. 4. Relationship between offspring summer survival, litter size and maternal FGM measured after pups emerged (fecal glucocorticoid metabolite concentrations (ng/ml)). The heatmap was generated with predicted probabilities from a linear mixed effects model. To generate predictions from the model, all other variables were set to the mean if continuous or to a fixed value if categorical (Predator index set as high).

rattus and *Cavia aperea*; Klaus et al., 2013; Rosenblum and Andrews, 1994). The artificial shortening of photoperiod, restraining experiments and administration of corticosterone reduce maternal care in rats, leading to a decrease of frequency and duration of nursing and licking/grooming interactions (Brummelte and Galea, 2010; Champagne and Meaney, 2006; Toki et al., 2007). Pittet et al. (2017) found no effects of chronic social partner instability on rat maternal care. However, when exposed to male intruders, females increased maternal care, indicating a variation in maternal behavior response according to stressor type or combination.

Our measures of female-pup interactions were taken at least 30 days after birth, which may not have been the most sensitive period for behavioral imprinting, since significant effects of pup care on pup development occur within the first weeks of life (Curley and Champagne, 2016) and the frequency of female-pup interactions decreases with pup age (Peña and Champagne, 2013). However, if the strength of female-pup bonds decrease at a similar rate among litters, the differences in pup care found after pup emergence may still reflect differences in within-burrow pup care among litters.

4.3. *Associations between female FGM levels and pup FGM levels*

Female yellow-bellied marmots produce at most one litter per year, reproduce as soon as they emerge from hibernation, have approximately a 30-day long gestation, and lactate another 25–30 days (Armitage, 2014; Blumstein and Armitage, 1998). Pups emerge from burrows nearly weaned (Frase and Hoffmann, 1980), so maternal FGM measured before pup emergence may quantify stress during both pregnancy and lactation. Only maternal stress measured during this period was significantly associated with pup FGM levels, suggesting that events during pregnancy and lactation may have long-term effects on pup behavior and neuroendocrine development (Curley and Champagne, 2016; Darnaudéry and Maccari, 2008). This finding is consistent with previous studies in yellow-bellied marmots, where lactating females with high FGM levels produced less docile pups (Petelle et al., 2017), a personality trait stable across life stages (Petelle et al., 2013).

Therefore, perinatal maternal FGM has an overall positive association with offspring FGM levels in marmots, but it is important to consider that differences in the type and intensity of stressors, pup sex (Curley and Champagne, 2016; Darnaudéry and Maccari, 2008), pup genotype (Pan et al., 2018), and within-litter variation in maternal care (Hasselt et al., 2012; Pan et al., 2014) are expected to modify the intensity and direction of maternal effects on pup stress responses. Since glucocorticoid hormones are involved in many metabolic pathways, the mechanism behind the influence of maternal FGM on offspring traits may essentially involve any pathway known to affect pup development, which can include hormone transmission via the placenta (Mairesse et al., 2007) and milk (Dettmer et al., 2018; Hinde et al., 2015), microbiota sharing via nursing (Daft et al., 2015; Ubeda et al., 2012), and behavioral imprinting (Bauer et al., 2015; Curley and Champagne, 2016; Darnaudéry and Maccari, 2008; Liu et al., 1997).

4.4. *Associations between maternal FGM levels and pup survival*

Although females with high FGM levels wean larger litters (Blumstein et al., 2016), their pups are significantly less likely to survive. Mothers with high FGM levels produced offspring with lower winter and annual survival. Random effects of mother identity explained no variation in the models, suggesting that external factors have an important role in pup survival. In addition to having a low annual reproductive success, mothers with high FGM levels have low overwinter survival (Wey et al., 2015), which reinforces that FGMs are reliable proxies for female fitness in free-living yellow-bellied marmots and supports the cort-fitness hypothesis (Bonier et al., 2009a, 2010). A negative association between glucocorticoid baseline levels and fitness has been found in other species, such as mice (Maguire and Mody, 2016), barn swallows (*Hirundo rustica*; Jenni-Eiermann et al., 2008), and tufted puffins (*Fratercula cirrhata*; Williams et al., 2008). However, associations between fitness and baseline glucocorticoids give conflicting results depending on the species, individual life history stage and sex (Bonier et al., 2009a, b).

In addition, the effects of litter size on offspring summer survival are contingent on maternal FGM levels: when mothers have high FGM levels, individuals born into small litters have higher summer survival than individuals born into larger litters. Interestingly, Monclús et al. (2011) reported that, under stressful conditions, older females were more likely to produce smaller litters than younger mothers. By using both results together, it is possible to hypothesize that older females are able to increase offspring survival likelihood by programming litter sizes according to environmental conditions. This suggested hypothesis follows the rationale of the experience constraint hypothesis (Curio, 1983; Forslund and Part, 1995), where female marmots could learn from experience how to use physiological or environmental cues to increase pup fitness. We may not expect that females are able to cognitively determine the number of pups they will give birth to, however pups spend approximately a month after birth within the burrow, and mothers could actively reduce their litter size by not feeding or killing some young.

Experienced mothers have increased reproductive success compared to inexperienced females in other species (Broussard et al., 2008; Colas, 1999; Dwyer and Lawrence, 2000; Künkele and Kenagy, 1997; Lunn et al., 1994; Schino and Troisi, 2005; Snyder et al., 2016; Sunderland et al., 2008; Wang and Novak, 1994; Zedrosser et al., 2009). Previous work has shown that the interaction between maternal age and FGM also determines offspring personality (Petelle et al., 2017), and, if changes on offspring phenotype enhance their fitness, marmot maternal behavior may support the Predictive Adaptive Response (PAR) hypothesis. According to the PAR hypothesis, maternal stress responses may be adaptive if stress levels reliably prepare offspring for their future environments, which has been observed across mammals, reptiles and fishes (Bateson et al., 2014; Sheriff and Love, 2013). Since this hypothesis was not directly tested in this study, future work should test whether older female marmots actually adopt strategies to enhance litter survival.

4.5. Conclusions

Physiological stress, measured through fecal glucocorticoid metabolites (FGM) levels, in free-living mothers of a facultatively social mammal is seemingly associated with both affiliative and agonistic interactions with conspecifics, which may have critical consequences for offspring survival. Agonistic interactions are key for yellow-bellied marmot social organization and have a positive association with maternal FGM. Female affiliative behavior may be collectively advantageous depending on the social group's environmental context. An increase in maternal FGM levels during pregnancy and lactation is associated with high FGM levels in pups, which may cause life-long changes in offspring behavior. Litters in social groups with mothers exhibiting high FGM levels throughout the active season received less maternal and/or alloparental care. Females with high FGM levels had offspring with lower annual survival and therefore have an overall lower reproductive success, which supports the cort-fitness hypothesis. Mothers under adverse conditions may, however, maximize offspring fitness by producing small litters.

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Declaration of competing interest

None.

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