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Older mothers follow conservative strategies under predator pressure: The adaptive role of maternal glucocorticoids in yellow-bellied marmots

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ABSTRACT

When the maternal environment is a good predictor of the offspring environment, maternal glucocorticoid (GC) levels might serve to pre-program offspring to express certain phenotypes or life-history characteristics that will increase their fitness. We conducted a field study to assess the effects of naturally occurring maternal GC levels on their offspring in yellow-bellied marmots (*Marmota flaviventris*) subjected to different predator pressures. Maternal fecal corticosteroid metabolites (FCM) were positively correlated with predator pressure. Predators had both direct and indirect effects on pups. We found that older mothers with higher FCM levels had smaller and female-biased litters. Moreover, sons from older mothers with high FCM levels dispersed significantly more than those from older mothers with low FCM levels, whereas the opposite pattern was found in pups from younger mothers. These age-related effects may permit females to make adaptive decisions that increase their pups' fitness according to their current situation.

1. Introduction

The environment where an animal develops may generate long-lasting fitness consequences (Lindström, 1999; Metcalfe and Monaghan, 2001). Parents can modify the conditions experienced by their offspring during both prenatal and postnatal stages and thus alter their offspring's phenotype (Cameron, 2004; Grant, 2007; Mousseau and Fox, 1998). These non-genetic modifications can be behavioral – e.g., by increasing licking and grooming rates, mothers reduce the offspring's anxiety later in life (Kappeler and Meaney, 2010), or physiological – e.g., through maternal hormones (Cadby et al., 2010). Whereas most of the behavioral influences of mothers on offspring have been discussed from an adaptive perspective, physiological effects have been commonly assumed to be inevitable byproducts of disease, pollutants, or an unavoidable consequence of the stress response (Bernardo, 1996; Brummelte and Galea, 2010; Kofman, 2002).

GCs are released in response to stressful events, such as following an encounter with a predator (Cockrem and Silverin, 2002; Hawlena and Schmitz, 2010; Monclús et al., 2009; Sheriff et al., 2010). Although GCs play an important role in the mobilization of energy for the fight or flight response (Matteri et al., 2001; von Holst, 1998), they diffuse from the mother to the offspring, and under prolonged stressful situations, GCs have harmful effects that may include hippocampal damage, suppression of the immune system, decreased growth rates, and negative effects on reproductive function (Götz and Stefanski, 2007; Lin et al., 2006; Maule and Vanderkooi, 1999). Therefore, predators might indirectly decrease an individual's fitness (Abrams, 1995; Naddafi et al., 2007; Preisser et al., 2005; Werner and Peacor, 2003).

However, maternal GCs could be used to adaptively prepare offspring to do well in the situation in which they will be born and raised (Love and Williams, 2008; Olofsson et al., 2009). Persistent stressful conditions, such as the chronic presence of predators, might be an informative cue about the environment that the offspring will experience, and parents could increase their fitness by adjusting their offspring phenotypes to the current conditions. To do so, parents can reduce their overall reproductive investment or specifically invest in those phenotypes that either cope better with the stressor (Mashoodh et al., 2009), or are more likely to disperse and escape from it (Johnson, 1988; Romero and Wikelski, 2001). For example, several studies have shown that high maternal GCs can reduce litter size and alter litter sex ratios (Götz et al., 2008; Love et al., 2005; Warner et al., 2009). Parents may benefit by reducing parental effort as this might increase their probability of survival and future reproduction. Offspring may benefit from being in a smaller litter if this is translated into more nutrients allocated to each pup, which may create more competitive individuals that have a higher pre-weaning body mass (König et al., 1988). Ultimately, offspring in better condition will benefit if they have a higher probability of survival until adulthood (Cote et al., 2006; Warner et al., 2009).

Whereas many studies have dealt with the effects of maternal GCs in fluctuating environments, fewer have explored the effects of chronic prenatal stress. We explored this topic, using data from a long-term study of free-living and individually marked yellow-bellied marmots

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(*Marmota flaviventris*). Marmots are the common prey of many predators, and predator pressure differs among colonies (Van Vuren, 2001). Firstly, we assessed the effect of predator pressure on the GC levels of adult females living in different environments. We expected to find that females experiencing higher predator pressure would have higher fecal corticosteroid metabolites (FCM). Secondly, we contrasted two alternative hypotheses. The first is that maternal GCs constitute an indirect effect of predators. In this case we would expect to find a decrease in offspring and/or mother's fitness associated with maternal GCs. The second is that mothers prepare their offspring for the conditions into which they will be born, buffering the effects of the predators, and increasing their own, or their offspring's, fitness.

2. Materials and methods

2.1. Study species

We studied the marmot populations in and around the Rocky Mountain Biological Laboratory, located in the East River Valley, in Gunnison County, Colorado, USA (Armitage, 2010). All the marmots were individually marked and we followed their fate from weaning to death. Marmots have been studied at this location for nearly 50 years, and their social and family groups are known. The marmots live along an elevational gradient, with five colonies up-valley and five colonies down- valley. Annual phenology (emergence from hibernation, mating and emergence from the natal burrows) occur, on average, two weeks earlier in the colonies down-valley (Blumstein, 2009; Van Vuren and Armitage, 1991). For this study we used offspring from 57 litters from 41 adult female marmots (119 females and 134 males). From these, 73 females where from down-valley colonies and 46 were from up-valley colonies, whereas 93 males were from down-valley colonies and 41 were from up-valley colonies.

2.2. Trapping procedures

Between 2002 and 2009, marmots were routinely trapped in Tomahawk live-traps (details in Blumstein et al., 2010). Subjects were individually ear-tagged the first time they were trapped, and an individual symbol was drawn in the back, with Nyanzol cattle dye, for observational purposes. Body mass and reproductive status were recorded each time an individual was trapped. We also collected hair for later DNA parentage assignment.

All the procedures described above were studied 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.

2.3. Observational procedures

Marmot colonies were observed using binoculars and spotting scopes most days during the times of peak activity (07:00–10:00; 16:00–19:00) from mid April to mid September annually. These behavioral observations allowed us to determine the date that an animal emerged from hibernation, as well as the date when the pups emerged from their natal burrow.

2.4. Predator pressure

We used the frequency of predator sightings per colony during regular observations to calculate a predator pressure index. We used only data from mid-April to the end of June, as this is the period of time when the vegetation is short and predators can be easily sighted if they are present. From this frequency, we calculated the median; colony years (a colony observed for a year) with values below the median were considered low predator pressure areas, whereas colonies with values above the median were considered high predator pressure areas. All the observers were trained to identify the different predators around the Rocky Mountain Biological Laboratory, and we believe that intra-observer differences did not account for the differences found.

2.5. Life-history traits

We calculated the growth rate for each individual as the slope of the regression of body mass and age, because marmot juveniles gain mass linearly during the first weeks (Lenihan and Van Vuren, 1996). We only used those marmots that were captured at least three times over more than 20 days.

Our intensive and extensive observation and trapping effort allowed us to know the fate of most individuals. Juveniles remain in the vicinity of their burrow soon after natal emergence. Yearlings do not disperse until the new litters of that year begin to emerge (typically 2 months after emergence from hibernation). Thus, we inferred juvenile mortality if they were no longer seen or trapped around their burrows before entrance into hibernation. Overwinter mortality was scored if: 1) a subject was observed and/or trapped at the end of one season, and 2) it was neither observed nor trapped during the next season.

In marmots, most of the males and about half of the females disperse as yearlings (Armitage, 1991). Because dispersers typically leave around the time of natal emergence of the new pups, we considered that an animal dispersed if it: 1) survived the winter, and therefore it was observed or trapped as a yearling, and 2) was neither observed nor trapped after that year's natal pup emergence.

2.6. Maternal fecal corticosteroid metabolites

2.6.1. Sample collection and analysis

We collected feces from traps in May, a time when adult females are pregnant, during the morning trapping. Marmots were in the traps for no longer than 2 h (07:00–09:00). Fecal samples were stored on ice in zipped bags and, once in the laboratory (not more than 2 h later), they were frozen at −20 °C. Before analysis, the samples were homogenized and a subsample of 0.2 g was extracted with 90% aqueous ethanol. The extract was analyzed with a double-antibody ^{125}I radioimmunoassay kit (MP Biomedicals, Costa Mesa, CA), FCM levels were measured (for further details, see Blumstein et al., 2006). The kit has been validated for the species, and the physiological validation is in progress (Smith et al. in prep).

The resulting FCM levels were split into a low and high group using the median cut.

2.7. Statistical analysis

We performed all analyses with the function lmer from the package lme4 from the software package R, version 2.10.1 (R Development Core Team, 2009). We ensured that the variances were homogeneous and that the distribution of the residuals of all the models followed a normal distribution by visually checking normal probability plots and by Shapiro–Wilk tests. Litter sex composition was $\log_{10}$-transformed.

First, we tested whether maternal FCM were related to environmental and intrinsic factors. We assessed each female's pregnancy retrospectively. In marmots, pregnancy lasts 30 days and the newborn are in the nest for 25 days (Armitage, 2003). For each female we averaged the FCM values (for each female we collected on average 3 values) obtained during the whole pregnancy to reduce the effect of gestation on FCM levels. We fitted generalized linear mixed models (GLM) with a binomial distribution linked by a logit function. We included predator pressure (high or low), the age of the individual (≤ 3 or >3), and the interaction between both factors, the location where the animal lived (down-valley or up-valley), and the social group size as fixed factors, and the individual and the year as crossed random factors to control for the repeated measures.

Second, we tested the relationship between maternal FCM and different life-history traits of the offspring. For the different life-history traits, we included in the models maternal FCM (low or high), maternal age as fixed factors and litter identity and the location where the animal lived (up or down valley) as random factors, to control for the potential dependency among the individuals from the same litter, and for location effects. Maternal body mass might explain some of the life-history traits. However, in marmots, body mass and age are highly correlated, and we only included the age as maternal characteristic. We fitted general linear mixed models to test for the effects of maternal FCM on litter sex composition [$\log_{10}$-transformed]. The program R does not directly provide p-values for LMM calculated with this package. Thus, we calculated p-values and parameter estimates by Markov-chain Monte Carlo sampling based on 10,000 simulation runs (Baayen et al., 2008) using restricted maximum likelihoods. Because the residuals followed a binomial distribution, we fitted generalized linear mixed models to test for the effects of maternal FCM on litter size, growth rate, survival and dispersal.

3. Results

Predator pressure differed among colonies. High predator pressure colonies had, on average 0.41 predator sightings per observation day, whereas the average in low predator pressure colonies was 0.12 sightings per observation day.

3.1. Maternal FCM

The median cut that separated low from high maternal FCM was 161 ng/g of feces (low FCM: mean $= 114.76 \pm 32.99$ SD; high FCM mean $= 244.69 \pm 71.87$ SD). Maternal FCM increased with predator pressure ($\beta = 9.989$, $Z = 2.943$, $n = 38$, $p = 0.003$). Neither the age of the mother, nor the group size affected maternal FCM levels (maternal age: $\beta = -4.189$, $Z = -1.482$, $n = 38$, $p = 0.138$; group size: $\beta = -1.227$, $Z = -0.827$, $n = 38$, $p = 0.408$). The interaction between predator pressure and group size, and between predator pressure and maternal age were non-significant ($\beta = 0.552$, $Z = 0.196$, $n = 38$, $p = 0.845$; $\beta = 2.040$, $Z = 0.442$, $n = 38$, $p = 0.659$, respectively) and were removed from the final model.

3.2. Litter size

Litter size was influenced by both maternal FCM levels, and by maternal age (FCM: $\beta = 10.273$, $Z = 2.738$, $n = 41$, $p = 0.006$; age: $\beta = 7.060$, $Z = 2.895$, $n = 41$, $p = 0.004$) and by the interaction of both factors ($\beta = -6.735$, $Z = -2.017$, $n = 41$, $p = 0.043$). Older mothers with higher FCM levels had smaller litter sizes (Fig. 1), but younger mothers had similar litter sizes regardless of FCM levels. However, the day that juveniles emerged from their natal burrow did not have a significant effect on litter size ($\beta = -0.064$, $Z = -0.483$, $n = 41$, $p = 0.629$).

3.3. Litter sex composition

Maternal FCM or maternal age alone did not affect litter sex composition (FCM: $\beta_{MCMC} = 0.054$, $n = 41$, $p_{MCMC} = 0.423$; age: $\beta_{MCMC} = -0.073$, $n = 41$, $p_{MCMC} = 0.299$). However, the interaction between both factors was significant ($\beta_{MCMC} = -0.274$, $n = 41$, $p_{MCMC} < 0.001$): older females with high FCM levels had female-biased litters (Fig. 2), whereas younger mothers had slightly male-biased litters independently of maternal FCM.

3.4. Growth rate

We found no effects of maternal FCM, maternal age, group size or sex on offspring growth rates (FCM: $\beta = 0.130$, $Z = 0.200$, $n = 105$, $p = 0.841$; age: $\beta = 0.628$, $Z = -0.963$, $n = 105$, $p = 0.335$; group size: $\beta = 0.179$, $Z = 0.586$, $n = 105$, $p = 0.558$; sex: $\beta = 0.197$, $Z = 0.419$, $n = 105$, $p = 0.675$). The interaction between maternal FCM and age was non-significant ($\beta = 0.964$, $Z = -0.717$, $n = 105$, $p = 0.473$) and was removed from the final model.

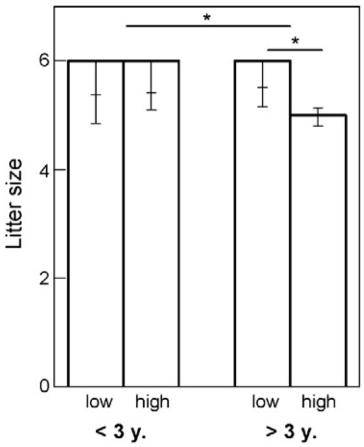

Fig. 1. The effect of maternal fecal corticosteroid metabolites [FCM low or high] and maternal age [≤3 years old or >3 years old] on litter size in yellow-bellied marmots. The figures illustrate median ± S.E. See text for statistics.

3.5. Survival

During their first active season, pup mortality was related to predator pressure ($\beta = 1.354$, $Z = 2.430$, $n = 121$, $p = 0.015$; Fig. 3), whereas maternal age and the sex of the pup did not explain pup mortality (maternal age: $\beta = 0.068$, $Z = 0.154$, $n = 121$, $p = 0.877$; sex: $\beta = -0.375$, $Z = -0.862$, $n = 121$, $p = 0.389$), and neither did colony size ($\beta = 0.003$, $Z = 0.282$, $n = 121$, $p = 0.788$). The interaction between maternal age and FCM was non-significant ($\beta = -0.262$, $Z = -0.280$, $n = 121$, $p = 0.780$) and was removed from the final model.

For those pups that survived to hibernation, over-winter survival was independent of maternal FCM levels ($\beta = -0.651$, $Z = -1.555$, $n = 170$, $p = 0.120$), maternal age ($\beta = -0.333$, $Z = -0.781$, $n = 170$, $p = 0.434$), and the pup's sex ($\beta = -0.289$, $Z = -0.752$, $n = 170$, $p = 0.435$). The interaction between FCM and maternal age was non-significant and was removed from the final model ($\beta = 0.018$, $Z = 0.021$, $n = 170$, $p = 0.984$).

3.6. Dispersal

For female yearlings, FCM levels ($\beta = -0.300$, $Z = -0.558$, $n = 60$, $p = 0.577$), maternal age ($\beta = -0.867$, $Z = -1.599$, $n = 60$,

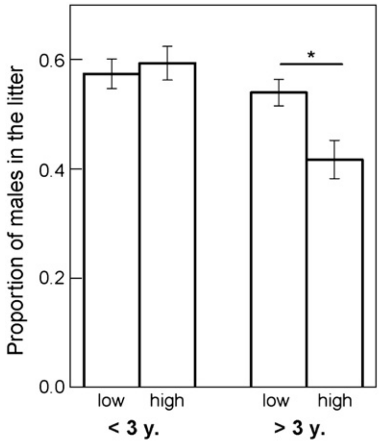

Fig. 2. The effect of maternal age [≤3 years old or >3 years old] and FCM levels [low or high] on litter sex composition in yellow-bellied marmots. The figure illustrates mean ± S.E. See text for statistics.

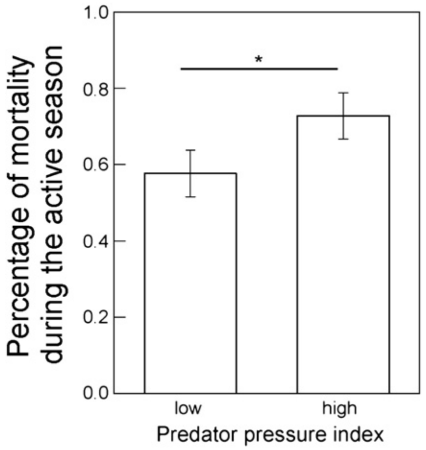

Fig. 3. The relationship between the percentage of pup mortality during the summer and predator pressure in yellow-bellied marmots. The figure illustrates mean ± S.E. See text for statistics.

$p = 0.110$), and colony size ($\beta = 0.025$, $Z = 0.856$, $n = 60$, $p = 0.392$) did not influence dispersal. The interaction between maternal FCM and age was also non-significant and was removed from the final model ($\beta = 0.251$, $Z = 0.231$, $n = 60$, $p = 0.818$).

However, for sons, maternal age ($\beta = -4.626$, $Z = 2.188$, $n = 66$, $p = 0.029$) and the interaction between maternal FCM and age ($\beta = 5.751$, $Z = 2.162$, $n = 66$, $p = 0.031$) predicted the probability of dispersal (Fig. 4). Neither colony size ($\beta = -0.006$, $Z = -0.100$, $n = 66$, $p = 0.920$), nor maternal FCM ($\beta = -2.430$, $Z = -1.305$, $n = 66$, $p = 0.192$) had a significant effect on dispersal. Sons from younger mothers with high FCM levels dispersed significantly less than those from younger mothers with low FCM levels ($\beta = -0.339$, $Z = -2.413$, $n = 28$, $p = 0.021$), whereas the opposite pattern was found in sons from older mothers ($\beta = 0.369$, $Z = 2.044$, $n = 38$, $p = 0.051$).

4. Discussion

Events during early development can have long-lasting effects. Young animals are especially vulnerable to predator pressure (Chase, 1999). Indeed, pups born into colonies with high predator pressure had higher mortality rates during the summer than those from low predator pressure colonies. Moreover, we could also detect indirect effects of predators that acted through maternal FCM and depended on the age of the mother. The presence of predators increased FCM levels in mothers, and this triggered long-term effects on their offspring. Because marmots faced similar predator pressure within a season, we expected that mothers could use this information to prepare their offspring. Indeed, we found that older females from high predator pressure colonies had smaller and female-biased litters. We did not find any effect of maternal FCM on growth or over-winter survival, but we did find that younger females with high FCM levels had sons that were less likely to disperse than those of younger females with low FCM levels, whereas older females with high FCM levels had sons that were more likely to disperse than those of older females with low FCM levels. We discuss how these age-dependent strategies might be adaptive for the mothers, and possibly also for the offspring.

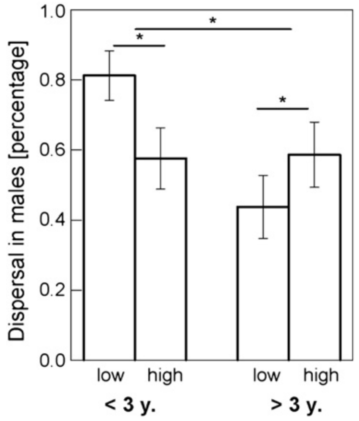

Fig. 4. The effect of FCM levels [low or high] and age of the mother [≤3 years old or >3 years old] on dispersal rates of male juveniles. The figure illustrates mean ± S.E. See text for statistics.

A positive relationship between predator pressure and GC levels is commonly seen in vertebrates (Monclús et al., 2009; Scheuerlein et al., 2001; Sheriff et al., 2009). Generally, an individual's assessment of predation risk is translated into both a physiological stress response as well as antipredator behavior (von Borell and Ladewig, 1992). The perception of a stressful situation activates the sympathetico-adrenomedullary system and the hypothalamic pituitary adrenocortical (HPA) axis (Matteri et al., 2001; Möstl and Palme, 2002; von Holst, 1998). These increase levels of catecholamines and GCs in the blood, which help mobilize energy, which in turn modulates the behavioral response (Sapolsky, 1992; von Holst, 1998).

During early developmental stages, the occurrence of high levels of GCs might have strong organizational and activational effects on a developing fetus (Braastad, 1998). In vertebrates, GCs pass from the mother to her offspring through passive diffusion from the mother's bloodstream (Gil, 2008; Welberg and Seckl, 2001). Thus, mothers may have no means to reduce the impact of GCs in their offspring. Even if this an undesirable side-effect of viviparity, parents, under stressful situations, might still try to make the best out of a bad situation. For example, litter reduction might be an adaptive strategy in a long-lived multiparous mammal, such as the yellow-bellied marmot. By reducing current reproductive effort during stressful conditions, marmots might increase their chances of survival and of future reproduction, since both traits trade-off with current reproduction (Candolin, 1998; Ghalambor and Martin, 2000; Magnhagen, 1991). Additionally, offspring might directly benefit from being able to obtain more milk. This should lead to a higher pre-weaning body mass (König et al., 1988; Rödel et al., 2008), and enhance the pup's competitive ability and chances of over-winter survival (Van Vuren and Armitage, 1991).

One mechanism of litter reduction is embryonic mortality. Male embryos are known to be more sensitive to GCs, resulting in smaller and female-biased litters (Arck, 2001; Clutton-Brock et al., 1985; Krackow, 1990). Indeed, this pattern also is seen in birds; female European starlings (*Sturnus vulgaris*) injected with corticosterone had smaller and female-biased broods (Love and Williams, 2008), but only when the treatment was coupled with reduced maternal provisioning rates. We found a slightly different pattern in yellow-bellied marmots. In marmots, age is a good predictor of maternal body condition; younger mothers weigh less than older mothers (Huang et al., 2011). Interestingly, only older and more stressed females had smaller, female-biased litters; younger females had male-biased litters and FCM had no effect on litter size. Overall, it seems that the effects are species-specific and context-dependent (Love et al., 2005; Rubolini et al., 2005; Warner et al., 2009).

Taken together, our results suggest that older females reduce their reproductive effort, whereas younger females do not. There is a trade-off between current and future reproduction, and it has been suggested that in long-living species, younger animals should invest in future reproduction, decreasing the risk for themselves at the cost of decreasing the fitness of the offspring (Candolin, 1998; Ghalambor and Martin, 2000). However, yellow-bellied marmots do not seem to follow this strategy; females gain higher individual fitness when they start reproducing earlier, and early reproduction does not seem to carry survival costs (Oli and Armitage, 2003).

While GCs may be responsible for differential survival during the prenatal period, during the postnatal stage early exposure to GCs might generate adaptive consequences. Several studies have shown that offspring from prenatally stressed mothers have higher survival rates (Cote et al., 2006; Gagliano and McCormick, 2009; Warner et al., 2009). In yellow-bellied marmots, those pups that survived until hibernation did not differ in over-winter survival. It seems that in marmots, mortality due to maternal GCs acts at earlier stages, while over-winter survival is affected by other factors (Ozgul et al., 2010).

Other life-history traits might be affected by maternal GCs, such as dispersal. Younger females, which normally have lower body condition and lower social rank (Huang et al., 2011), might benefit from investing in the dispersing sex (males) because the philopatric sex (females) might be outcompeted by the offspring of higher ranking females (Cockburn et al., 1985). Accordingly, in yellow-bellied marmots, offspring from younger females with low FCM levels were more likely to disperse. However, offspring from both younger and older mothers with high FCM levels showed similar dispersal rates. However, within a maternal age-class, sons from older mothers with high FCM levels dispersed more than those from older mothers with low FCM levels. Offspring might increase their fitness by dispersing and escaping from the unfavorable situation (Clobert et al., 1994; Johnson, 1988; Romero and Wikelski, 2001). This might be especially important in situations where predator pressure is the main stressor. In domestic chicks, corticosterone injections into eggs led to reduced development of visual lateralization, and this reduced lateralization reduced the ability to detect aerial predators (Freire et al., 2006). Because marmots are preyed by both terrestrial and aerial predators (Van Vuren, 2001), dispersal might be a good strategy to increase the probability of survival. In younger mothers, offspring from high FCM mothers were less likely to disperse than those from low FCM mothers. A possible explanation might be that these sons, which come from male-biased litters, might have some advantages. In male-biased litters, individuals usually have higher testosterone levels because of intra-uterine masculinization (Clark et al., 1992; Ryan and Vandenbergh, 2002). Males with higher testosterone levels might have enhanced competitive abilities and thus be able to successfully monopolize resources. Such males might become successful satellite males around their natal colonies (Drickamer, 1996).

In conclusion, we found mixed evidence for adaptive prenatally stressed phenotypes. Yellow-bellied marmots followed two different strategies depending on their age, which might be related to their environment and their assessments of their state. Older marmots followed a conservative strategy, whereby they decreased reproductive effort in terms of litter size. They probably increased their own fitness by reducing reproductive effort, and maybe their offspring fitness by having sons with higher dispersal rates. On the other hand, younger females seemed to increase their offspring fitness, but not their own, by having male-biased litters which might outcompete the offspring from higher ranking females. Whether this is sufficient evidence of them preparing their offspring for the current environment should be explored further in future studies.

Acknowledgments

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