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The effect of maternal glucocorticoid levels on juvenile docility in yellow-bellied marmots

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ABSTRACT

Maternal effects can have significant and long-term consequences on offspring behavior and survival, while consistent individual differences (i.e., personality) can have profound impacts on individual fitness. Thus, both can influence population dynamics. However, the underlying mechanisms that determine variation in personality traits are poorly understood. Maternal effects are one potential mechanism that may explain personality variation. We capitalized on a long-term study of yellow-bellied marmots (*Marmota flaviventris*) to identify maternal effects on juvenile docility. To do so, we partitioned the variance in juvenile docility using a quantitative genetic modeling approach to isolate potential maternal effects. We also directly tested whether maternal stress, measured through fecal glucocorticoid metabolite levels during lactation of 82 mothers, was associated with offspring docility. Docility scores were estimated for 645 juveniles trapped between 2002 and 2012. We found an interaction between maternal glucocorticoid levels and dam age on juvenile docility. We also found significant maternal, litter, permanent environment, and year effects. These results suggest that a mother's life history stage interacts with stress to influence offspring personality. This early life influence can have long lasting effects on an individual's docility throughout life.

1. Introduction

Understanding the potential mechanisms underlying consistent individual differences has become of great importance as these can help explain the cause and maintenance of personality (Réale et al., 2007; Sih et al., 2004; Stamps and Groothuis, 2010). Maternal effects are one potential mechanism that underlies these differences. Maternal effects are well known to influence offspring phenotypes through their effects on growth and metabolism, immune function, and behavior (Groothuis and Schwabl, 2008; Hayward and Wingfield, 2004; Mousseau and Fox, 1998). These phenotypic changes are modulated by the maternal ecology that reflects life history tradeoffs, maternal characteristics, and the maternal environment. The consequences of these maternal effects are still debated, but they may permit calibration of maternal resources or reflect an adaptive strategy to prepare offspring for their adult environment (Mousseau and Fox, 1998). For example, mothers use cues in their environment, including information on conspecific density (Dantzer et al., 2013), resources (Kapheim et al., 2011), and predators (Storm and Lima, 2010), to alter their offspring's phenotypes so as to prepare them for that particular environment. The prenatal period is crucial for many of these maternal effects (Boersma and Tamashiro, 2015; Hayward and Wingfield, 2004; Mousseau and Fox, 1998) but the postnatal lactation period in mammals can also profoundly influence offspring behavior (Hinde et al., 2015).

This postnatal period may be a potential driver of consistent individual differences in behavior. Hormones delivered through milk may have profound impacts on offspring behavior (Duckworth et al., 2015; Hinde et al., 2015; Kapoor et al., 2006). Glucocorticoids (GCs) are a class of steroid hormones that help mobilize energy under stressful situations (Sapolsky et al., 2000), and have been shown to correlate with personality or coping styles (Carere et al., 2005; Costantini et al., 2012; Koolhaas et al., 1999). In a variety of mammals, an unstable environment that induces stress in pregnant or lactating females can have large effects on offspring's social and sexual behavior (Kaiser and Sachser, 2005). Mother rats (*Rattus norvegicus*), for example, with chronic stress and higher circulating levels of GCs during pregnancy, bear offspring with increased anxiety in novel situations, reduced inclination for social interaction, and behavior that resembles depression in humans (Weinstock, 2001). However, mothers with increased GC levels during lactation produce offspring with a decreased stress response, improved conditional learning, and a weakened fear-related behavioral response (Catalani et al., 2000). Recent research by Hinde et al. (2015)

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also indicates that GCs delivered through milk predicted temperament in rhesus macaques (*Macaca mulatta*): females with higher GC levels had offspring with higher nervousness and lower confidence scores. Female social rank and parity were also associated with GC levels; thus, stress or life history strategy is also associated with offspring personality.

It is important to note that glucocorticoids are not exclusively associated with stress, but are also important regulators of metabolism of carbohydrates, proteins, and fats (Sapolsky et al., 2000). The amount of GCs transferred to the offspring during lactation can influence that offspring's metabolism and growth. Individual differences in growth and metabolism are thought to create a syndrome with personality differences (Réale et al., 2010; Stamps, 2007). Thus, maternal GCs delivered through lactation can interact to cause differences in offspring personality in multiple ways; by inducing neural differences between individuals to increase risk-taking behavior, or by increasing metabolism or growth, which in-turn influence individual differences in behavior. Although previous research has shown that maternal life history and GC levels may be associated with offspring personality (Hinde et al., 2015), there are few studies on free-living mammals. Since personality type may have important ecological and evolutionary consequences (for review see Réale et al., 2007), understanding the causes of personality variation is a fundamental question in ecology.

In addition to directly testing for maternal effects associated with GC levels, another important method to identify how indirect genetic effects may influence traits employs a quantitative genetic approach. Quantitative genetics partitions trait variance into additive genetic variance as well as other indirect genetic effects such as maternal, litter or cohort, and permanent environment effects (Falconer and Mackay, 1996; McAdam et al., 2014). Previous research on yellow-bellied marmots (*Marmota flaviventris*) identified maternal effects in docility (Petelle et al., 2015). In contrast to the previous study, we now specifically test for direct maternal effects in juveniles. We expect that variance which was once attributed to nonspecific maternal effects would decrease as direct effects of maternal glucocorticoid levels are accounted for by including this variable in the quantitative genetic model.

We used data from a long-term study on a population of yellow-bellied marmots to study the relationship between potential maternal effects and offspring docility. This population is located in and around the Rocky Mountain Biological Laboratory (Colorado, USA) and has been continually studied since 1962 (Armitage, 2014; Blumstein, 2013). Previous research has shown that individuals in this population have a variety of consistent individual differences (Armitage, 1986; Petelle et al., 2013). For this study, we collected fecal samples from lactating mothers, and thus obtained baseline GC levels that may serve as a proxy for hormones passed to offspring during lactation (Sheriff et al., 2011; Smith et al., 2012; Verkerk et al., 1998). We then used a quantitative genetic approach to partition phenotypic variance to understand both general maternal effects as well as the effects of maternal GC levels on juvenile docility.

2. Material and methods

2.1. Study species and site

From 2002 to 2012, we studied marmots in and around the Rocky Mountain Biological Laboratory (RMBL), located in the Upper East River Valley in Gothic, Colorado (38 77′N, 106 59′W). Marmots are large (2–6 kg), semi-fossorial, sciurid rodents that live in colonies with one or more matrilines (Frase and Hoffmann, 1980). We trapped marmots by placing Tomahawk-live traps near burrow entrances. After capture, the marmots were transferred to cloth handling bags to have their weight, sex, and reproductive status checked (Blumstein et al., 2006). Each marmot was given a set of unique ear-tag numbers and their dorsal pelage marked with Nyanzol fur dye for identification from afar.

2.2. Quantifying docility

We use the personality trait – docility – because juvenile docility has previously been shown to be repeatable, and docility is stable over life stages (Petelle et al., 2013). Juveniles are defined as individuals in their first summer of life (Armitage and Downhower, 1974) and docility is an individual's reaction to being trapped and handled (Petelle et al., 2013; Réale et al., 2000). To assess docility, we quantified how individuals responded to being trapped and handled for 645 juveniles in 3120 trapping events conducted between 2002 and 2012. We recorded trap behavior of the marmots before they were placed in the handling bag. Specifically, we dichotomously (0/1) scored whether an individual bit the trap, struggled in the trap, tooth-chattered, alarm called, and whether they walked into the handling bag immediately. Scores were summed and subtracted from the total potential score to yield a docility index for that trapping event. A score of 0 denotes a non-docile individual while a score of 5 denotes a docile individual.

2.3. Pedigree

We assigned parentage of newly emerged pups using hair samples collected on the first trapping event for each individual. All samples were collected from 2002 to 2012. Full methods for pedigree construction can be found in Olson et al. (2012), but briefly, we extracted DNA using Qiagen DNA kits and amplified sequences using polymerase chain reaction. We used *GeneMapper* (Applied Biosystems) to score alleles, and *CERVUS 3.0* (Kalinowski et al., 2007) to construct the pedigree. *CERVUS 3.0* assigns parentage by accounting for all possible mother/father/offspring allele combinations and calculating the probability of each combination. The likelihood score, in turn, is compared to a critical value generated by simulation to complete the parentage assignment at a given confidence level (See Supplemental Information Table 1 for pedigree information). We trapped juveniles upon first emergence from the burrow, which allows us to behaviorally assign juveniles to mothers if there is ambiguity in maternal assignment. Most marmots were regularly trapped and observed within the population; therefore we assumed a sampling proportion of 99% for candidate mothers and 96% for candidate fathers. Female marmots are philopatric, and therefore have high potential relatedness. Thus, we set the proportion of female marmots related at a level of $R > 0.4$ or higher each year (Blumstein et al., 2010; Lea et al., 2010; Olson et al., 2012). The dataset we used for these analyses contained genotypes from 1432 individuals from 136 dams and 71 sires (see Supplementary Table 1 for pedigree information).

2.4. Maternal glucocorticoids

To calculate fecal corticosterone metabolite levels (we refer to this as GC levels), we collected fecal samples from individuals or traps during trapping events. Individuals were in traps typically less than two hours. Fecal samples were collected directly from individuals during handling or were freshly collected from the trap. Hardened fecal samples were not collected. After collection, the feces were stored at −20 °C and shipped on dry ice to our lab at the University of California, Los Angeles for extraction. We first homogenized and sorted the feces to remove solids such as rocks, grass, and seed shells. For the extraction process, the feces were then apportioned into 0.2 g samples, suspended in 90% aqueous ethanol, and boiled for 20 min. Next the samples were cooled to room temperature and centrifuged for 20 min. The resulting supernatant was poured into 16 × 100 mm tubes and the process was repeated. Afterwards, the combined supernatants were dried in a vacuum centrifuge for 17 h. The purified samples were then submerged in Absolute ethanol, stored at −20 °C. Finally, the samples were assayed with a radioimmunoassay to determine GC levels. Full method for GC extraction can be found in Smith et al. (2012).

Although not directly measured, we assume that maternal GC levels during lactation are good proxies for the hormone amount transferred to offspring. Fecal glucocorticoid levels have been shown to be good indicators of free glucocorticoid plasma levels (Sheriff et al., 2011), and plasma levels are correlated with glucocorticoid levels in milk in other species (Catalani et al., 2011; Verkerk et al., 1998). Juvenile emergence from the natal burrow signals the end of lactation, and we witnessed the first incidence of emergence in most cases. Marmots lactate for about 30 days (Nee, 1969). Thus, an average maternal GC level (basal level) during lactation was calculated using GC samples measured within the 30 days prior to juvenile emergence ($\bar{x} = 1.310$; stdev = 0.559). By averaging maternal GC levels over these 30 days we calculate a basal level of stress in the maternal environment over that time period. To eliminate any potential stress associated with trapping, we only used GC levels from samples collected by ≥2 days from a previous trapping event because of a slow gut passage time (Smith et al., 2012).

2.5. Statistical analysis

We fitted an animal model to explain variation in juvenile docility as a function of date, time (AM/PM), mass at emergence, sex, trial, litter size, dam age, and maternal GC levels. We also included interactions between sex, litter size, mass at emergence, and dam age with maternal GC levels. An animal model is a linear mixed effects model connected to a pedigree that partitions variance components (Kruuk, 2004). These effects were included because they have been previously shown to have a relationship with marmot personality or because they may influence the transmission of maternal hormones. Date was included to control for potential seasonal variation in docility (Petelle et al., 2013). We did not include mass at time of the docility trial because date and mass are correlated ($r = 0.696$; $p < 0.0001$). Time of day was included to control for potential within-day changes in hormone levels (Armitage et al., 1996). The juvenile's mass at emergence is a proxy for how much milk, and therefore maternal hormones, were transmitted to that individual (Catalani et al., 2000; Monclús et al., 2011). Sex was included to control for sex-dependent effects (Monclús and Blumstein, 2012). We included trial number to control for potential habituation effects of trapping on individual docility levels (Martin and Réale, 2008). Litter size was incorporated to serve as a proxy for maternal body condition and because it is associated with environmental conditions (Blueweiss et al., 1978; Tafani et al., 2013). Dam age was included in our analysis because it is an important covariate in mediating the effect of GC in offspring behavior and can give us an indication of (potential) maternal life history strategy (Monclús et al., 2011). We also included a number of two-way interactions in our model. Mass upon emergence might be dependent upon the number of siblings so we fit an interaction between emergence mass and litter size. Furthermore, the effect of maternal GC may be mediated by the amount of milk ingested during lactation and so we included a two-way interaction between emergence mass (a proxy for milk intake) and maternal GC level. Finally, past work has shown that a dam's age and offspring sex interact with maternal GC level to influence personality (Hinde et al., 2015).

We included juvenile identity, maternal identity, litter, and year as random effects. By using an animal model with these random effects, we are able to partition the variance into additive genetic effects, permanent environmental effects, and indirect genetic effects including litter, maternal, and year effects. Permanent environment is the environmental effect that is constant across an individual's repeated measures (Kruuk and Hadfield, 2007). We did not include colony since most individuals are from their natal colony and this was already included in the permanent environment effect. We estimated additive genetic (V_A, identity link to the pedigree), maternal environment (V_{ME}, mother id), litter (V_L, litter id), permanent environment (V_{PE}, identity of individual), and year (V_{YE}) variance parameters. Following Wilson et al. (2010), variance parameters were estimated as the posterior mode with 95% credible intervals (CI) based on the posterior distribution of the parameter. We estimated heritability, maternal, litter, permanent environment, and year effect by dividing the corresponding variance parameter by the total phenotypic variance. Repeatability was calculated as the sum of both additive genetic, maternal, and permanent environmental variance divided by total phenotypic variance (Wilson et al., 2010).

To understand how variance changes with addition of random effects, we used a nested model approach and removed a single random effect at a time (Kruuk, 2004). We removed in order; maternal, individual, litter, and finally permanent environment effects because these are associated with variance at the among-individual level (Supplemental Table 1).

All analyses were conducted in R v. 3.1.1 (Team, 2015) using the package MCMCglmm (Hadfield, 2010). The posterior distribution was sampled every 500 iterations with a burn in of 10,000 for a total of 1000 samples. We set our **G** (random) and **R** (residual) priors as V = 1 and nu = 1 (Petelle et al., 2015). We used a Gaussian error distribution (Petelle et al., 2013; Réale et al., 2000). Trace plots were visually checked and autocorrelation was <0.05.

2.6. Animal welfare

This experiment was carried out under protocols approved by the Animal Use and Care Committees of the University of California Los Angeles and the RMBL (UCLA protocol No. 2001-191-01 renewed annually), and under permits from the Colorado Division of Wildlife (TR917 issued annually). We took all precautions to reduce any undue stress to marmots. Individuals were returned immediately to the original trap location, and were in the traps no longer than 2–3 h. Marmots were not injured handling, and all individuals were handled while inside a cloth handling bag to reduce stress.

3. Results

The final analysis consisted of 2483 docility measurements from 645 juveniles from 82 dams collected over a span of 10 years. We found that individuals were more docile later in the year (Table 1). Marmots were more docile later in the day, and as the number of trials increased (Table 1). We also found an interaction between maternal GC level and dam age; older mothers with higher GC levels have less docile juvenile offspring (Table 1; Fig. 1). We found no effect of sex, emergence mass, or litter size on juvenile docility (Table 1).

Docility was previously reported to be repeatable in juvenile marmots (Petelle et al., 2013), and, as expected, individual's docility scores

Table 1
Fixed effects explaining variation in the univariate animal model of docility for juvenile yellow-bellied marmots. Significant effects are in bold.

Effect	Coefficient	Lower 95% CI	u-95% CI	*p*-Value
Intercept				
−2.22E + 00				
−3.21E + 00				
−1.20E + 00	**<0.001**			
Date	**7.81E-03**	**5.00E-03**	**1.10E-02**	**<0.001**
Time (afternoon)	**8.62E-02**	**1.09E-02**	**1.75E-01**	**0.05**
Sex (male)	−5.03E-02	−2.51E-01	1.47E-01	0.652
Maternal GC (ng)	8.44E-04	−1.95E-03	3.75E-03	0.548
Mass at emergence	4.34E-04	−4.70E-03	5.94E-03	0.880
Litter size	9.51E-03	−6.08E-02	7.96E-02	0.772
Maternal age	**8.73E-02**	**2.62E-02**	**1.38E-01**	**0.002**
Trial	**4.67E-02**	**2.53E-02**	**6.97E-02**	**<0.001**
Sex (male) * maternal GC	4.41E-04	−4.82E-04	1.32E-03	0.322
Mass at emergence * maternal GC	9.10E-06	−1.46E-05	3.50E-05	0.518
Litter size * maternal GC	5.14E-05	−2.41E-04	4.10E-04	0.742
Maternal age * maternal GC	**−4.83E-04**	**−7.77E-04**	**−2.18E-04**	**<0.001**

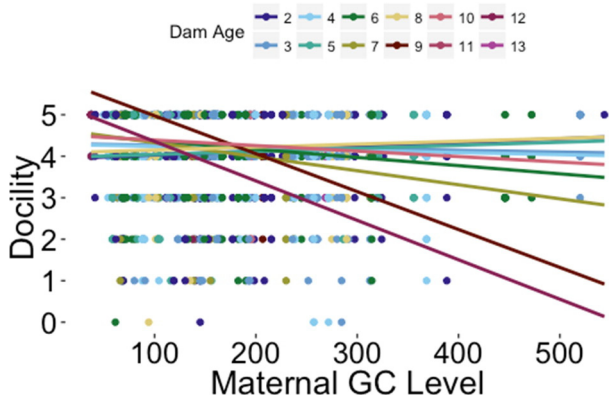

Fig. 1. Relationship of the interaction between maternal GC level and damage on docility level. Slopes for the represented lines are estimated from predicted values. Figure in color in on-line version.

were repeatable in this smaller data set ($r = 0.195$; 95% C.I. = 0.145 to 0.246). We found small, non-zero heritability ($h^2 = 0.060$; 95% C.I. = 0.034 to 0.099), as well as effects of mother ($m^2 = 0.067$; 95% C.I. = 0.033 to 0.102), litter ($l^2 = 0.055$; 95% C.I. = 0.034 to 0.087), permanent environment ($pe^2 = 0.053$; 95% C.I. = 0.034 to 0.088), and year ($y^2 = 0.090$; 95% C.I. = 0.050 to 0.267) (Fig. 2).

4. Discussion

Maternal effects can have large and immediate behavioral consequences for offspring. Our study of free-living yellow-bellied marmots reveals that maternal GC levels during lactation are significantly and negatively associated with juvenile docility, and this effect is mediated through maternal age. Older mothers with higher GC levels had offspring with lower docility scores compared to younger mothers with higher GC levels. This result suggests that maternal age has an important influence on how GCs are passed on to offspring. This finding supports prior studies that show mothers with high GC levels during postnatal periods had offspring with weaker fear-related responses (Catalani et al., 2000), and exhibited higher nervousness and lower confidence scores (Hinde et al., 2015)

The interaction between age and GC level is especially interesting, and may be adaptive. Previous research in this system shows that mothers with high GC levels, which were attributed to experiencing higher predator pressure, produced sons that were more likely to disperse than mothers with lower GC levels (Monclús et al., 2011). That study, however, found no main effect of age. Individual differences in exposure to predation risk can create a dispersal syndrome; bold and less docile individuals are more likely to disperse in roe deer (*Capreolus capreolus*) (Debeffe et al., 2014). Thus, females may be engaged in an adaptive strategy that uses current and future reproduction to increase their own potential inclusive fitness.

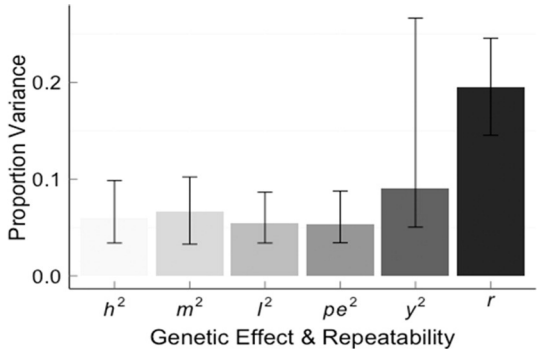

Fig. 2. Proportion of variance explained by additive genetic ($h^2 = V_A/V_P$), maternal ($m^2 = V_M/V_P$), litter ($l^2 = V_l/V_P$), permanent environment ($pe^2 = V_{PE}/V_P$), year ($y^2 = V_Y/V_P$), and repeatability ($r = (V_A + V_M + V_{PE})/V_P$) with 95% credible intervals. Estimates are calculated from the posterior mode of the full model.

Mothers make "decisions" about current and future reproductive tradeoffs and, as they age, they may be more likely to invest energy in their offspring as a form of terminal investment (Fisher and Blomberg, 2011; Hoffman et al., 2010). In other words, resource allocation to offspring tends to increase with age since older mothers invest more in current reproductive success than in future reproductive success. We may expect older females that are investing more energy in offspring to pass on more GCs to their offspring through greater milk production (Lee and Kim, 2006). Our results do not support this hypothesis of greater terminal investment by mothers as they age, because we found no interaction between offspring mass and maternal GC level. We would expect improved body condition of offspring of older mothers if this hypothesis were true, as well as lower docility levels for those individuals.

Another potential adaptive hypothesis is that females may use offspring dispersal to increase their fitness. Approximately 50% of female marmots disperse from their natal colony (Armitage, 1991). Yearling females can therefore choose whether to disperse. Past research has tried to identify factors that may influence dispersal (Armitage et al., 2011; Blumstein et al., 2009), but maternal age has yet to be shown to significantly influence yearling dispersal. However, younger adult females may benefit from having female offspring stay in their natal colony to enhance their fitness through colony growth, while older females may have already reached a potential fitness peak in their own colony's growth (sensu Armitage and Schwartz, 2000). Thus, to increase potential fitness, older females transmit GCs to female offspring and force those females out of the natal colony and seeding new colonies while young mothers try to keep more docile offspring in the natal colony.

One potential, non-adaptive, mechanistic hypothesis for the significant interaction between mother's age and GC levels is that older mothers require more time to return to baseline GC levels after exposure to a chronic stressor. As individuals age their pituitary adrenal response to chronic stress attenuates. For example, after a stressful encounter, older rats take significantly longer for their GC levels to return to normal (Odio and Brodish, 1989). Therefore, older mothers are physiologically limited in their ability to control their adrenal cortex. Offspring of older mothers may experience prolonged exposure to GCs, explaining their lower docility levels through direct exposure to GCs or through maternal behavior (Champagne and Meaney, 2006). Previous research in rats demonstrated that high-grooming mothers that were stressed altered their maternal care and had levels of offspring grooming that compared to lines bred for low-grooming phenotypes (Champagne and Meaney, 2006). This reduction in grooming behavior has long-lasting consequences in offspring behavior (Liu et al., 1997).

Interestingly, we identified additional specific maternal effects by decomposing variances using a quantitative genetic approach despite the fact that we included a direct maternal effect in the model. We expected lower maternal effects with the inclusion of maternal glucocorticoid levels because the inclusion of maternal glucocorticoids should erode the variance attributed to maternal effects in the quantitative genetic analysis. This finding is notable because few previous studies have detected significant maternal effects on personality (Freund et al., 2013; Petelle et al., 2015; Taylor et al., 2012). The presence of litter, or even cohort, effects highlights the potential influence of social effects on phenotypes (Taylor et al., 2012; Wolf et al., 1998). A juvenile's social environment and behavior influences future social dominance (Blumstein et al., 2013) and personality traits (Bends and Henkelmann, 1998). These early social interactions can thus set personality trajectories and be responsible for the maintenance of personality traits via social niche specialization (Bergmüller and Taborsky, 2010). The permanent environment with year effects suggests that the environment has a profound role in explaining variation in behavioral phenotypes. Although the exact nature of these effects are unknown at this

time, pre- and post-natal environments–including the nature and amount of social interactions as well as other (a)biotic factors–may have important consequences on resulting behavior.

We also found significant effects of date, time of day, and trial. Date has already been found to be associated with docility in a previous study, but strangely, time of day seemingly does not influence docility in juveniles (Petelle et al., 2013). However, that study had a much larger sample size and included different fixed effects (this current study was limited by GC samples). Trial number was also associated with docility levels; individuals were more docile the more trials they had. This suggests a habituation effect that is commonly seen in personality studies (Martin and Réale, 2008).

5. Conclusions

Overall, our study found that juvenile docility was associated with maternal GC levels, but this effect was mediated by maternal age. This could be a byproduct of older mothers unable to respond appropriately after an acute stressor, or could reflect a potential adaptive strategy. Because docility is stable across life (Petelle et al., 2013), this result shows that stressors can have long lasting phenotypic effects on individuals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yhbeh.2016.12.014.

References

Armitage, K.B., 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. Ecology 67, 1186–1193.
Armitage, K.B., 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu. Rev. Ecol. Syst. 22, 379–407.
Armitage, K.B., 2014. Marmot Biology: Sociality, Individual Fitness, and Population Dynamics. Cambridge University Press, Cambridge.
Armitage, K.B., Downhower, J.F., 1974. Demography of yellow-bellied marmot populations. Ecology 55, 1233–1245.
Armitage, K.B., Schwartz, O.A., 2000. Social enhancement of fitness in yellow-bellied marmots. Proc. Natl. Acad. Sci. 97, 12149–12152.
Armitage, K.B., Salsbury, C.M., Barthelmess, E.L., Gray, R.C., Kovach, A., 1996. Population time budget for the yellow-bellied marmot. Ethol. Ecol. Evol. 8, 67–95.
Armitage, K.B., Vuren, D.H.V., Ozgul, A., Oli, M.K., 2011. Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. Ecology 92, 218–227.
Bends, R.F., Henkelmann, C., 1998. Litter composition influences the development of aggression and behavioural strategy in male *Mus domesticus*. Behaviour 135, 1229–1249.
Bergmüller, R., Taborsky, M., 2010. Animal personality due to social niche specialisation. Trends Ecol. Evol. 25, 504–511.
Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., Sams, S., 1978. Relationships between body size and some life history parameters. Oecologia 37, 257–272.
Blumstein, D.T., 2013. Yellow-bellied marmots: insights from an emergent view of sociality. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 368, 20120349.
Blumstein, D.T., Chung, L.K., Smith, J.E., 2013. Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). Proc. R. Soc. B Biol. Sci. 280, 20130485.
Blumstein, D.T., Lea, A.J., Olson, L.E., Martin, J.G.A., 2010. Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. J. Evol. Biol. 23, 879–887.
Blumstein, D.T., Ozgul, A., Yovovich, V., Van Vuren, D.H., Armitage, K.B., 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. J. Zool. 270, 132–138.
Blumstein, D.T., Wey, T.W., Tang, K., 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc. R. Soc. B Biol. Sci. 276, 3007–3012.
Boersma, G.J., Tamashiro, K.L., 2015. Individual differences in the effects of prenatal stress exposure in rodents. Neurobiol. Stress 1, 100–108.
Carere, C., Drent, P.J., Privitera, L., Koolhaas, J.M., Groothuis, T.G., 2005. Personalities in great tits, *Parus major*: stability and consistency. Anim. Behav. 70, 795–805.
Catalani, A., Alemà, G.S., Cinque, C., Zuena, A.R., Casolini, P., 2011. Maternal corticosterone effects on hypothalamus–pituitary–adrenal axis regulation and behavior of the offspring in rodents. Neurosci. Biobehav. Rev. 35, 1502–1517.
Catalani, A., Casolini, P., Scaccianoce, S., Patacchioli, F.R., Spinozzi, P., Angelucci, L., 2000. Maternal corticosterone during lactation permanently affects brain corticosteroid receptors, stress response and behaviour in rat progeny. Neuroscience 100, 319–325.
Champagne, F.A., Meaney, M.J., 2006. Stress during gestation alters postpartum maternal care and the development of the offspring in a rodent model. Biol. Psychiatry 59, 1227–1235.
Costantini, D., Ferrari, C., Pasquaretta, C., Cavallone, E., Carere, C., von Hardenberg, A., Réale, D., 2012. Interplay between plasma oxidative status, cortisol and coping styles in wild alpine marmots, *Marmota marmota*. J. Exp. Biol. 215, 374–383.
Dantzer, B., Newman, A.E.M., Boonstra, R., Palme, R., Boutin, S., Humphries, M.M., McAdam, A.G., 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science 340, 1215–1217.
Debeffe, L., Morellet, N., Bonnot, N., Gaillard, J.M., Cargnelutti, B., Verheyden-Tixier, H., Vanpé, C., Coulon, A., Clobert, J., Bon, R., et al., 2014. The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. Proc. R. Soc. Lond. B Biol. Sci. 281, 20140873.
Duckworth, R.A., Belloni, V., Anderson, S.R., 2015. Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. Science 347, 875–877.
Falconer, D.S., Mackay, T.F.C., 1996. In: Cummings, B. (Ed.), Introduction to Quantitative Genetics, fourth ed. England, Essex.
Fisher, D.O., Blomberg, S.P., 2011. Costs of reproduction and terminal investment by females in a semelparous marsupial. PLoS One 6 e15226-e15226.
Frase, B.A., Hoffmann, R.S., 1980. Marmota flaviventris. Mamm. Species 1–8.
Freund, J., Brandmaier, A.M., Lewejohann, L., Kirste, I., Kritzler, M., Krüger, A., Sachser, N., Lindenberger, U., Kempermann, G., 2013. Emergence of individuality in genetically identical mice. Science 340, 756–759.
Groothuis, T.G.G., Schwabl, H., 2008. Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 363, 1647–1661.
Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.
Hayward, L.S., Wingfield, J.C., 2004. Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. Gen. Comp. Endocrinol. 135, 365–371.
Hinde, K., Skibiel, A.L., Foster, A.B., Del Rosso, L., Mendoza, S.P., Capitanio, J.P., 2015. Cortisol in mother's milk across lactation reflects maternal life history and predicts infant temperament. Behav. Ecol. 26, 269–281.
Hoffman, C.L., Higham, J.P., Mas-Rivera, A., Ayala, J.E., Maestripieri, D., 2010. Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. Behav. Ecol. 21, 972–978.
Kaiser, S., Sachser, N., 2005. The effects of prenatal social stress on behaviour: mechanisms and function. Neurosci. Biobehav. Rev. 29, 283–294.
Kalinowski, S.T., Taper, M.L., Marshall, T.C., 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. 16, 1099–1106.
Kapheim, K.M., Bernal, S.P., Smith, A.R., Nonacs, P., Wcislo, W.T., 2011. Support for maternal manipulation of developmental nutrition in a facultatively eusocial bee, *Megalopta genalis* (Halictidae). Behav. Ecol. Sociobiol. 65, 1179–1190.
Kapoor, A., Dunn, E., Kostaki, A., Andrews, M.H., Matthews, S.G., 2006. Fetal programming of hypothalamo-pituitary-adrenal function: prenatal stress and glucocorticoids. J. Physiol. 572, 31–44.
Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokhuis, H.J., 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23, 925–935.
Kruuk, L.E.B., 2004. Estimating genetic parameters in natural populations using the "animal model.". Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 359, 873–890.
Kruuk, L.E.B., Hadfield, J.D., 2007. How to separate genetic and environmental causes of similarity between relatives. J. Evol. Biol. 20, 1890–1903.
Lea, A.J., Blumstein, D.T., Wey, T.W., Martin, J.G., 2010. Heritable victimization and the benefits of agonistic relationships. Proc. Natl. Acad. Sci. 107, 21587–21592.
Lee, J.-Y., Kim, I.-H., 2006. Advancing parity is associated with high milk production at the cost of body condition and increased periparturient disorders in dairy herds. J. Vet. Sci. 7, 161–166.
Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., Sharma, S., Pearson, D., Plotsky, P.M., Meaney, M.J., 1997. Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. Science 277, 1659–1662.
Martin, J.G., Réale, D., 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Anim. Behav. 75, 309–318.
McAdam, A.G., Garant, D., Wilson, A.J., 2014. The effects of others' genes: maternal and other indirect genetic effects. Quantitative Genetics in the Wild. Oxford University Press, pp. 84–103.
Monclús, R., Blumstein, D.T., 2012. Litter sex composition affects life-history traits in yellow-bellied marmots. J. Anim. Ecol. 81, 80–86.

Monclús, R., Tiulim, J., Blumstein, D.T., 2011. Older mothers follow conservative strategies under predator pressure: the adaptive role of maternal glucocorticoids in yellow-bellied marmots. Horm. Behav. 60, 660–665.
Mousseau, T.A., Fox, C.W., 1998. The adaptive significance of maternal effects. Trends Ecol. Evol. 13, 403–407.
Nee, J.A., 1969. Reproduction in a population of yellow-bellied marmots (*Marmota flaviventris*). J. Mammal. 50, 756–765.
Odio, M., Brodish, A., 1989. Age-related adaptation of pituitary-adrenocortical responses to stress. Neuroendocrinology 49, 382–388.
Olson, L.E., Blumstein, D.T., Pollinger, J.R., Wayne, R.K., 2012. No evidence of inbreeding avoidance despite demonstrated survival costs in a polygynous rodent. Mol. Ecol. 21, 562–571.
Petelle, M.B., Martin, J.G., Blumstein, D.T., 2015. Heritability and genetic correlations of personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*). J. Evol. Biol. 28, 1840–1848.
Petelle, M.B., McCoy, D.E., Alejandro, V., Martin, J.G., Blumstein, D.T., 2013. Development of boldness and docility in yellow-bellied marmots. Anim. Behav. 86, 1147–1154.
Réale, D., Gallant, B.Y., Leblanc, M., Festa-Bianchet, M., 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim. Behav. 60, 589–597.
Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.-O., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos. Trans. R. Soc. B 365, 4051–4063.
Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318.
Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 21, 55–89.
Sheriff, M.J., Dantzer, B., Delehanty, B., Palme, R., Boonstra, R., 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecologia 166, 869–887.
Sih, A., Bell, A.M., Johnson, J.C., Ziemba, R.E., 2004. Behavioral syndromes: an integrative overview. Q. Rev. Biol. 79, 241–277.
Smith, J.E., Monclús, R., Wantuck, D., Florant, G.L., Blumstein, D.T., 2012. Fecal glucocorticoid metabolites in wild yellow-bellied marmots: experimental validation, individual differences and ecological correlates. Gen. Comp. Endocrinol. 178, 417–426.
Stamps, J., Groothuis, T.G., 2010. The development of animal personality: relevance, concepts and perspectives. Biol. Rev. 85, 301–325.
Stamps, J.A., 2007. Growth-mortality tradeoffs and "personality traits" in animals. Ecol. Lett. 10, 355–363.
Storm, J.J., Lima, S.L., 2010. Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. Am. Nat. 175, 382–390.
Tafani, M., Cohas, A., Bonenfant, C., Gaillard, J.-M., Allainé, D., 2013. Decreasing litter size of marmots over time: a life history response to climate change? Ecology 94, 580–586.
Taylor, R.W., Boon, A.K., Dantzer, B., Reale, D., Humphries, M.M., Boutin, S., Gorrell, J.C., Coltman, D.W., McAdam, A.G., 2012. Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. J. Evol. Biol. 25, 614–624.
Team, R.C., 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria; 2014.
Verkerk, G.A., Phipps, A.M., Carragher, J.F., Matthews, L.R., Stelwagen, K., 1998. Characterization of milk cortisol concentrations as a measure of short-term stress responses in lactating dairy cows. Anim. Welf. 7, 77–86.
Weinstock, M., 2001. Alterations induced by gestational stress in brain morphology and behaviour of the offspring. Prog. Neurobiol. 65, 427–451.
Wilson, A.J., Reale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A., Kruuk, L.E., Nussey, D.H., 2010. An ecologist's guide to the animal model. J. Anim. Ecol. 79, 13–26.
Wolf, J.B., Brodie III, E.D., Cheverud, J.M., Moore, A.J., Wade, M.J., 1998. Evolutionary consequences of indirect genetic effects. Trends Ecol. Evol. 13, 64–69.