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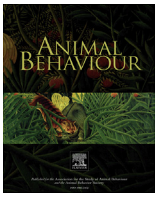

Mixed support for state maintaining risky personality traits in yellow-bellied marmots

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In a variety of taxa, individuals behave in consistently different ways. However, there are relatively few studies that empirically test the potential mechanisms underlying the causes and maintenance of these personality differences. Several hypotheses for the causes and maintenance of risky personality traits have been suggested but all have received mixed support. Both the pace-of-life hypothesis and state-dependent safety hypothesis propose that differences in internal state cause and maintain personality traits. Formally, the pace-of-life hypothesis states that differences in life-history traits including productivity (growth) and residual reproductive value (age) create initial differences in individual behaviour that is later maintained by positive feedback, while the state-dependent safety hypothesis suggests that body condition (mass) is responsible for causing and maintaining behavioural differences. We tested and evaluated whether either of these two hypotheses explained the causes or maintenance of variation in risk-related personality traits —defensive aggression, activity and exploration— in yellow-bellied marmots, *Marmota flaviventer*. We found little support overall for these hypotheses in explaining maintenance in activity or exploration. However, for defensive aggression, we found positive feedback for both mass and age.

Our understanding of animal personalities, or consistent individual differences in behaviour across time and context, has advanced greatly in recent years and has been repeatedly demonstrated to influence the ecology and evolution of populations and species (Pruitt & Ferrari, 2011; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, Johnson, & Ziemba, 2004; Smith & Blumstein, 2008). A number of theoretical explanations have been developed that link state and state-dependent behaviour to explain the causes and within-individual maintenance of consistent individual differences (Biro & Stamps, 2008; Dingemanse & Wolf, 2010; Luttbeg & Sih, 2010; Réale et al., 2010; Sih et al., 2015; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010). State can be defined as an intrinsic characteristic of an individual that is expressing a particular behaviour (Sih et al., 2015). Empirical support for these hypotheses is poor and there are relatively few studies testing them in wild systems. This lack of support emerges partly from the challenges of collecting adequate long-term individually based data.

The pace-of-life syndrome (POLS) hypothesis and the state-dependent safety (SDS) hypothesis are two of the main hypotheses explaining the maintenance of personality variation. The POLS hypothesis proposes that individuals vary in their life-history strategies and these strategies (co)vary with a suite of morphological, physiological and behavioural characteristics (Réale et al., 2010). For example, individuals that grow faster, reproduce earlier and have a higher metabolism would also be more proactive and engage in riskier behaviour (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007). We expect individuals to try to maintain their initial state because physiological and life-history trajectories are set early in life and it is costly to deviate from a given trajectory (Biro & Stamps, 2008). Furthermore, within the POLS, we would also expect differences in an individual's residual reproductive value and these differences to be coupled with state-dependent behaviour. Because individuals may make trade-offs between allocating energy to reproduction early or late in life, individuals with higher future reproductive value should take fewer risks so as to protect

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future assets (Clark, 1994). Empirical evidence for the POLS hypothesis is unclear with mixed support in different taxa (Biro & Post, 2008; Biro & Sampson, 2015; Careau, Bininda-Emonds, Thomas, Réale, & Humphries, 2009; Dammhahn, 2012; Edenbrow & Croft, 2011; Nicolaus et al., 2012; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004; Ward, Thomas, Hart, & Krause, 2004).

The state-dependent safety (SDS) hypothesis states that differences in body condition, size or energy reserves cause and maintain variation in personality (Luttbeg & Sih, 2010). Individuals in better condition are better able to avoid predators or fight conspecifics. Thus, body condition is maintained because individuals with higher body condition are better able to access or defend resources and escape predators, creating a positive feedback (i.e. state-dependent safety). Individuals with lower body condition are unable to take risks because they do not react accordingly (escape predators or fight effectively) and are incapable of increasing their condition (making the best of a bad job). However, empirical evidence for this hypothesis is equivocal (Martin & Réale, 2008).

Overall, both hypotheses predict the existence of covariance and positive feedback between a state (growth and age for POLS and mass for SDS) and behaviours leading to the maintenance of among-individual differences in both state and behaviour. To test these hypotheses, repeated observations of individuals must be collected on multiple behaviours and state variables over the life span of multiple individuals. We capitalized on a long-term study of yellow-bellied marmots, *Marmota flaviventer*, to evaluate these hypotheses explaining the maintenance of risk-related personality traits, defensive aggression, activity and exploration. This system offers a great opportunity to use a multiple-hypotheses testing approach since individuals not only differ in both their summer mass gain and their body condition, but they also live up to 16 years (Armitage & Downhower, 1974), which allows the study of the correlates of variation in potential future reproduction.

The POLS and SDS hypotheses each make specific predictions that can be used to assess whether one or all mechanisms are associated with the maintenance of personality variation. If risk-prone behavioural traits are maintained by POLS, we expect among-individual differences in summer growth (Biro & Stamps, 2008). Individuals that grow more over the summer need more energy and thus will take more risks to be able to sustain their growth trajectories. Summer growth should also be repeatable. We also expect there to be personality differences by age, a proxy of residual reproductive value (Stamps, 2007; Wolf et al., 2007) with older individuals taking more risks because they have lower residual reproductive value than younger individuals. By taking more risks, they could increase their remaining reproductive value (Pianka & Parker, 1975). Finally, if state-dependent safety maintains personality variation, we expect body mass, a proxy for body condition (Armitage, 2014), to be repeatable and to be positively correlated with risk-prone personality traits, where we expect to see heavier individuals taking more risks (Luttbeg & Sih, 2010). These predictions describe the maintenance of personality variation at the among-individual level, but these hypotheses can also explain within-individual variation in behaviour. As individuals deviate from their mean summer growth, age and mass, we expected them to also vary their risky behaviours accordingly by being more aggressive and explorative when above their mean and inversely by being less aggressive and less explorative when below their mean trait value.

To evaluate these hypotheses at both between-individual and within-individual levels we used an individual centering approach (Dingemanse & Dochtermann, 2013; van de Pol & Wright, 2009). Individual centering is a way to distinguish among- versus within-individual effects by fitting in the same model an individual mean state and its deviation from its mean for each observation. Combining an individual centering approach with a random regression analysis allowed us to test for a feedback mechanism that maintains personality and creates lasting among-individual differences over time (Sih et al., 2015). We thus expected a positive feedback loop between state and behaviour (Sih et al., 2015), measured as a positive correlation between the intercept and the slope with state at the individual level.

METHODS

Subjects

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Station, Gothic, Colorado, U.S.A. during 2002–2012. Marmots are large, facultatively social, semifossorial sciurid rodents that live in colonies (Frase & Hoffmann, 1980). Marmots at our study site were of known age because they are first trapped as juveniles soon after emergence from their natal burrows. We trapped individuals regularly between mid-May and mid-September using Tomahawk live-traps placed at burrow entrances. Individuals were transferred to a cloth handling bag, eartagged, weighed, sexed, their reproductive status was checked and they were given a unique fur mark (Blumstein, Wey, & Tang, 2009).

Quantifying Personality

We first quantified docility from 8990 trapping events on 1201 individuals (mean ± SD = 4.066 ± 3.217). Docility is defined here as an individual's reaction to being trapped and handled (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000) and is one way to evaluate risk-taking behaviour (Careau et al., 2009). At each trapping event, upon arrival at the trap, we noted whether individuals struggled in the trap, tooth-chattered, bit the cage, alarm-called or hesitated to walk into the handling bag. We dichotomously (0/1) scored these behaviours, summed them and subtracted this score from the total potential score to attain a docility index for that trapping event. To ease interpretability, we took the opposite of docility and labelled it defensive aggression (Blumstein, Petelle, & Wey, 2012). This allows us to ask whether there are the expected positive associations and feedback mechanisms between state and risky personality traits. We interpreted this behaviour as risky because it illustrates an aggressive response towards a potential predator (human) or aversive situation (being trapped and handled). Defensive aggression (opposite of docility) has previously been shown to have nonzero heritability (Petelle, Martin, & Blumstein, 2015), and individuals are consistent in their docility scores throughout development (Petelle et al., 2013).

Shortly after quantifying defensive aggression (typically within 1 h) we quantified exploration/activity using open field (OF) and mirror image stimulation (MIS) tests. Open field tests are a commonly used assay to assess fear-related traits and to estimate activity and exploration. Mirror image stimulation tests are used to quantify sociability, but may also be used to gather activity and exploration data. These two tests create two different contexts – one where individuals are unimpeded by obstacles, and another set in a social setting. OF and MIS tests are commonly used to assess risk-related personality in wild animals (Armitage, 1986; Boon, Réale, & Boutin, 2007; Royauté & Dochtermann, 2016). Activity and exploration are viewed as being risky activities because they may increase the possibility of encountering predators. These traits have also been shown to have nonzero heritability in yellow-bellied marmots (Petelle et al., 2015). During 2010–2012, we conducted 614 open field and mirror image stimulation trials on 226 individuals. Individuals were transferred from the trap to a cloth handling bag (see above) and transported to a square arena (91.4 × 91.4 × 91.4 cm) made of 0.47 cm thick, opaque PVC sheeting. Arenas were located less than 100 m away from colonies and were situated on flat ground. A mirror (30.5 × 61.0 cm) was placed at the base of one side of the arena and covered with an opaque sliding door. A door (61.0 cm^2) was cut out of the side opposite the mirror. Each trial consisted of a 3 min OF test where individuals could freely move and explore the arena. Immediately following the OF test, the sliding door was removed to expose the mirror for an additional 3 min. The MIS test was similar to the OF test with the addition of the mirror. Individuals were tested a maximum of once per day. Technical issues (e.g. camera failure) along with the inability to measure certain aspects of the individual – including predator pressure or mass at capture – restricted our OF analysis to 435 trials on 178 individuals (mean ± SD = 1.957 ± 1.154) and restricted our MIS analysis to 428 trials on 177 individuals (mean ± SD = 1.953 ± 1.152). For a full description of methods see Petelle et al. (2015).

All trials were scored with JWatcher 1.0 (Blumstein & Daniel, 2007). We calculated the number of events and the proportion of time spent alarm calling, jumping, looking, walking and sniffing the arena. In addition, we also counted the number of grid lines crossed and the proportion of squares visited for both OF and MIS, and for MIS, the proportion of time spent scratching or pawing the mirror, and the total proportion of time at the mirror. All scorers were trained to have >95% inter- and intraobserver agreement. Raw scores for both tests were subjected to a principal components analysis (PCA) and the resulting factor scores for each trial were used for further analysis. We used SPSS v.18.0 (Chicago, IL, U.S.A.) with varimax rotation to extract principal components. Principal component analysis of open field and mirror image stimulation data resulted in the extraction of four and six factors, respectively (Petelle et al., 2015). The first OF and MIS components were characterized by activity, while the second OF and third MIS component included exploratory activities. We thus limited our analyses to the first and second OF components and the first and third MIS factors (see Appendix Table A1 for PCA; Petelle et al., 2015).

Individuals are trapped consistently throughout the active season, and thus, we modelled individual summer growth and extracted best linear unbiased predictors (BLUPs) for specific dates (Martin & Pelletier, 2011). Using these BLUPs, we calculated summer growth by taking an individual's estimated mass on 1 September and subtracting their mass on 1 June. We use summer growth as a proxy metric for growth rate. We know the exact age of all natal individuals (the majority of our population). Individuals that immigrate into our colonies are all adults (≥2 years old), and thus we assumed that these individuals were least 2 years old. Mass, our estimate of body condition, was measured during capture.

Statistical Analysis

We first estimated the repeatability of different states (summer growth and mass) by fitting univariate linear mixed effects models (LMM) including individual and year as random effects and restricting the data to individuals for which we had a defensive aggression estimate. Repeatability of personality traits was similarly estimated with univariate mixed models including individual and year (defensive aggression) and individual only (OF and MIS tests) as random effects. Due to collinearity between summer growth, mass and age, and to avoid overparamaterization, we tested the POLS and SDS hypotheses for each behaviour by fitting three separate models, each of which tested the effect of only one state variable. We thus fitted 15 univariate mixed models using a Bayesian approach; three (summer growth, age, mass) for each of the five personality traits –defensive aggression, activity and exploration in both contexts (Table 1). Each model contained one of the individually centred state variables (summer growth, age or mass) and its deviation from individual mean. The centering approach permits us to estimate the between-individual (individual mean) and within-individual (deviation from individual mean) effects of state on behaviours and also assists with model convergence (Dingemanse & Dochtermann, 2013; van de Pol & Wright, 2009). To test for positive feedback loops, we also included a random regression term with a within-individual (deviation from the mean) state variable and individual identity. This in effect allows us to determine how within-individual behaviour changes as state (mass, growth or age) changes, and whether the nature of these changes varies across individuals. Random effects were similar to those used in univariate model testing.

All models were fitted in R v.3.3.1 (R Development Core Team, 2016) with either the package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015) for summer growth and mass and personality repeatability, or 'MCMCglmm' (Hadfield, 2010) for state-dependent random regressions models. Gaussian error distributions were used for all traits except for defensive aggression where we used an ordinal error distribution. All state-dependent random regression personality models had a relatively uninformative expanded prior with an R (residual) of $V = 1$, and nu = 1.002 and G (random effects) components had a $V = I_2$, nu = 2, alpha.mu = (0, 0) and alpha.V = $I_2 \times 1000$. Models were run for 7 500 000 iterations and sampled every 5000 iterations with a burn-in of 30 000 for a sample of 1490. We estimated 95% credible intervals from the posterior distribution and any interval not including 0 was considered significant. We checked trace plots for adequate mixing and all autocorrelations were < 0.1. Metadata are archived at https://sites.lifesci.ucla.edu/eeb-rmbl-marmots/. Data and R script are available at DOI 10.17605/OSF.IO/6HWBZ.

Ethical Note

Marmots were studied under protocols approved by the Animal Care and Use 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). Trapping was divided into morning and evening sessions and all traps were closed after each session to prevent animals from entering during the hot midday or at night. Individuals were typically in traps no longer than 3 h, and were often in traps for less than 2 h. Traps were provided shading when they were set on warm days. Once transported to the arena, individuals were placed in the shade until testing. Testing was usually completed within 1 h. After testing, all individuals were coaxed back into a trap and released at the point of capture. All animals were held for a minimal amount of time to conduct tests and were monitored during this time for any issues. No individuals were harmed during testing and no lasting issues with the testing protocol were observed.

RESULTS

Testing for Between-individual Variation

Mass and summer growth were both repeatable ($R_{mass} = 0.498$, LRT = 5725.2, $P < 0.001$; $R_{growth} = 0.077$, LRT = 13.987, $P < 0.001$). Defensive aggression, activity and exploration in both contexts were repeatable (Appendix Table A2). Repeatability of these traits has been shown previously (Petelle et al., 2015), but these models included different fixed effects and data structure. While these differences in fixed effects could potentially change a trait's

Table 1
Posterior mean estimate and 95% upper and lower credible intervals for individually centred growth, age and mass as well as their deviations from centre across all personality traits

State	Def. Agg.	Activity (OF1)	Exploration (OF2)	Activity (MIS1)	Exploration (MIS3)
Growth:					
Individual mean	**−2.87E-04 (−4.56E-04, −1.23E-04)**	**−4.25E-04 (−6.28E-04, −1.65E-04)**	1.26E-04 (−1.01E-04, 4.17E-04)	−2.66E-4 (−5.805E-04, 6.081E-06)	−8.084E-05 (−3.284E-04, 1.588E-04)
Deviation	**−2.47E-04 (−3.73E-04, −1.35E-04)**	**−6.45E-04 (−0.001, −3.68E-04)**	−1.49E-04 (−3.00E-04, 1.31E-04)	**−2.37E-4 (−5.42E-04, -3.90E-05)**	−2.054E-04 (−4.980E-04, 8.906E-05)
r Intercept/slope	0.129 (−0.418, 0.124)	**−0.907 (−0.997, −0.384)**	−0.791 (−0.938, 0.840)	−0.897 (−0.992, 0.637)	−0.779 (−0.986, 0.429)
Age:					
Individual mean	**−0.134 (−0.190, −0.082)**	**−0.124 (−0.184, −0.063)**	0.028 (−0.062, 0.062)	−0.060 (−0.124, 0.024)	**0.079 (0.008, 0.127)**
Deviation	**−0.158 (−0.225, −0.092)**	**−0.681 (−0.967, −0.412)**	**−0.564 (−0.766, −0.296)**	**−0.397 (−0.588, −0.107)**	**−0.346 (−0.555, −0.072)**
r Intercept/slope	**0.348 (0.011, 0.511)**	−0.535 (−0.946, 0.671)	**−0.958 (−.0.998, −0.413)**	−0.891 (−0.983, 0.378)	**−0.970 (−0.991, −0.366)**
Mass:					
Individual mean	**−2.81E-04 (−3.74E-04, −2.01E-04)**	**−2.69E-04 (−3.82E-04, −1.87E-04)**	3.76E-05 (−5.25E-05, 1.59E-04)	−1.59E-04 (−2.23E-04, 4.49E-06)	9.71E-06 (−6.19E-05, 1.44E-04)
Deviation	**−3.57E-04 (−4.39E-04, -2.81E-04)**	**−8.45E-04 (−0.001, −6.01E-04)**	**−2.89E-04 (−4.67E-04, −1.51E-04)**	**−4.82E-04 (−7.08E-04, −2.97E-04)**	**−1.20E-04 (−3.35E-04, −1.54E-05)**
r Intercept/slope	**0.290 (0.037, 0.417)**	**−0.742 (−0.960, −0.328)**	**−0.947 (−0.998, −0.386)**	**−0.985 (−0.999, −0.854)**	**−0.977 (−0.998, −0.639)**

Def. Agg.: defensive aggression; OF: open field; MIS: mirror image stimulation. Correlations between the intercept and slopes are also given. Estimates with credible intervals not including zero are considered significant and are shown in bold.

adjusted repeatability (Nakagawa & Schielzeth, 2010), repeatability was qualitatively similar.

Explaining Maintenance of Individual Variation

We found a small negative effect of individual mean (between-individual) summer growth rate on defensive aggression (Table 1, Appendix Fig. A1) and on activity in the OF context (Table 1, Appendix Fig. A2). Importantly, deviation from the individual mean (within-individual) in summer growth rate was negatively associated with defensive aggression and activity in both OF and MIS (Table 1, Figs. 1 and 2, respectively). We also found a negative correlation between the intercepts and the slopes, suggesting that faster-growing individuals were less active (in the OF) as they positively deviated from mean summer growth rates (Table 1).

We found a negative effect of age on between-individual differences in defensive aggression and activity in the OF test (Table 1, Appendix Fig. A2) and a small positive effect on exploration in the MIS (Table 1, Appendix Fig. A5). Within-individual variation was negatively associated with defensive aggression (Fig. 3), activity in both contexts (Figs. 1 and 2, respectively), and exploration (MIS) (Fig. 4). We also found a strong negative feedback between age and exploration. Relatively more exploratory individuals engaged in less exploration as they aged (Table 1). We also found a positive feedback between defensive aggression and age, suggesting that individuals that were initially more aggressive became even more aggressive as they aged.

Between-individual differences (mean individual effects) in mass were negatively associated with defensive aggression and activity in the OF test (Table 1, Appendix Fig. A2). Within-individual effects (deviation in mass from the individual mean) was significantly negative for defensive aggression (Fig. 3), activity in both contexts (Figs. 1 and 2, respectively), and exploration in the OF test (Table 1, Fig. 5). We found negative feedback for activity and exploration in both contexts (Table 1). We also found a positive feedback between defensive aggression and mass (Table 1).

DISCUSSION

Despite having relatively large sample sizes, our study of the maintenance of risky personality in marmots found no strong support for either the POLS or SDS hypothesis. Indeed, we consistently found negative relationships between state and behaviour that contradict the predictions from these hypotheses. We also found negative feedback mechanisms in almost all instances and these feedbacks potentially reduce variation in personality. Moreover, and again, in contrast to the expectations from the hypotheses, the mean and the deviation from the mean for both mass and age were negatively associated with defensive aggression. However, individuals that were initially more defensively aggressive became increasingly so as they aged and increased in mass, which resulted in a positive feedback.

Interestingly, for defensive aggression we found a negative effect of age and mass —which contradicted expectations from the hypotheses— but we also found positive feedback. Specifically, both the mean and the deviation from the mean for both mass and age were overall negatively associated with defensive aggression, but individuals that were initially more defensively aggressive became increasingly so as they aged and increased in mass. In other words, as marmots increased in mass and aged, individuals with higher mean scores of defensive aggression had steeper positive slopes (they became more defensively aggressive over time and as they gained mass than individuals with lower mean scores of defensive aggression).

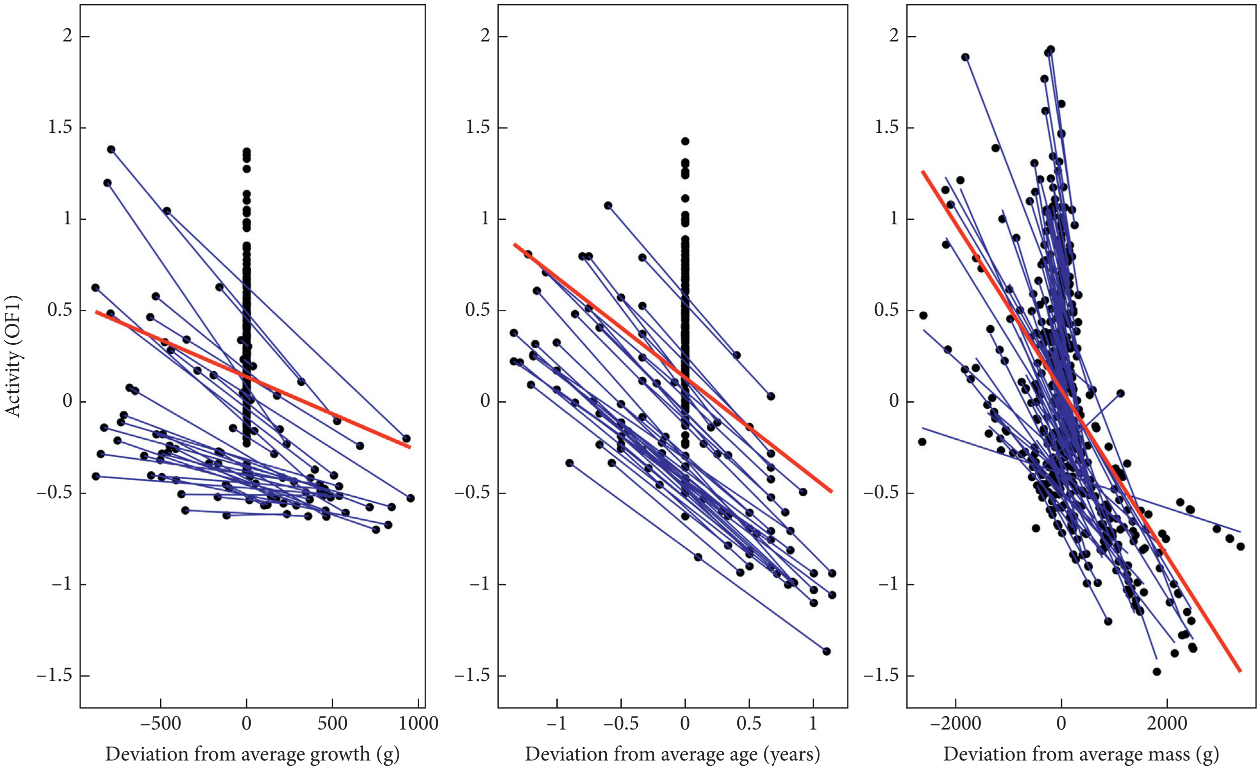

Figure 1. Relationship between activity in the open field (OF1) and deviation in mean state (growth, age, mass). Plots show predicted data from models.

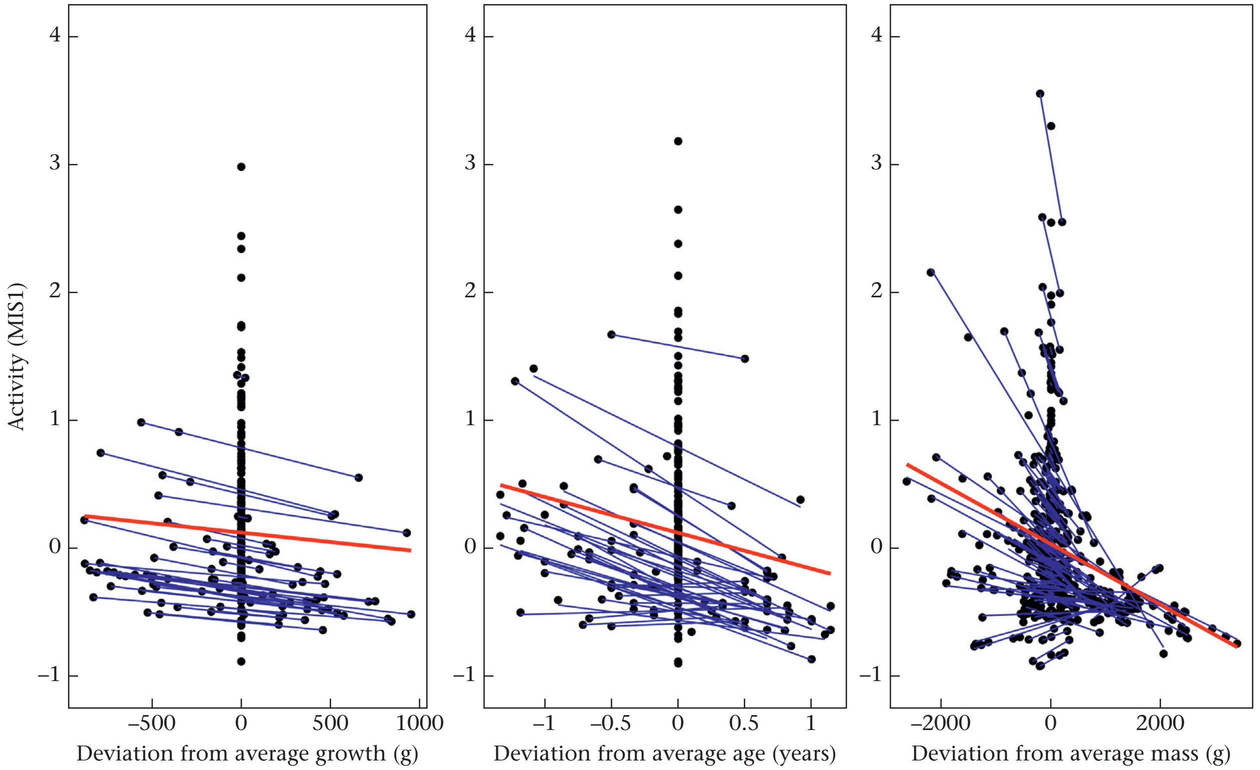

Figure 2. Relationship between activity in the mirror image stimulation (MIS1) and deviation in mean state (growth, age, mass). Plots show predicted data from models.

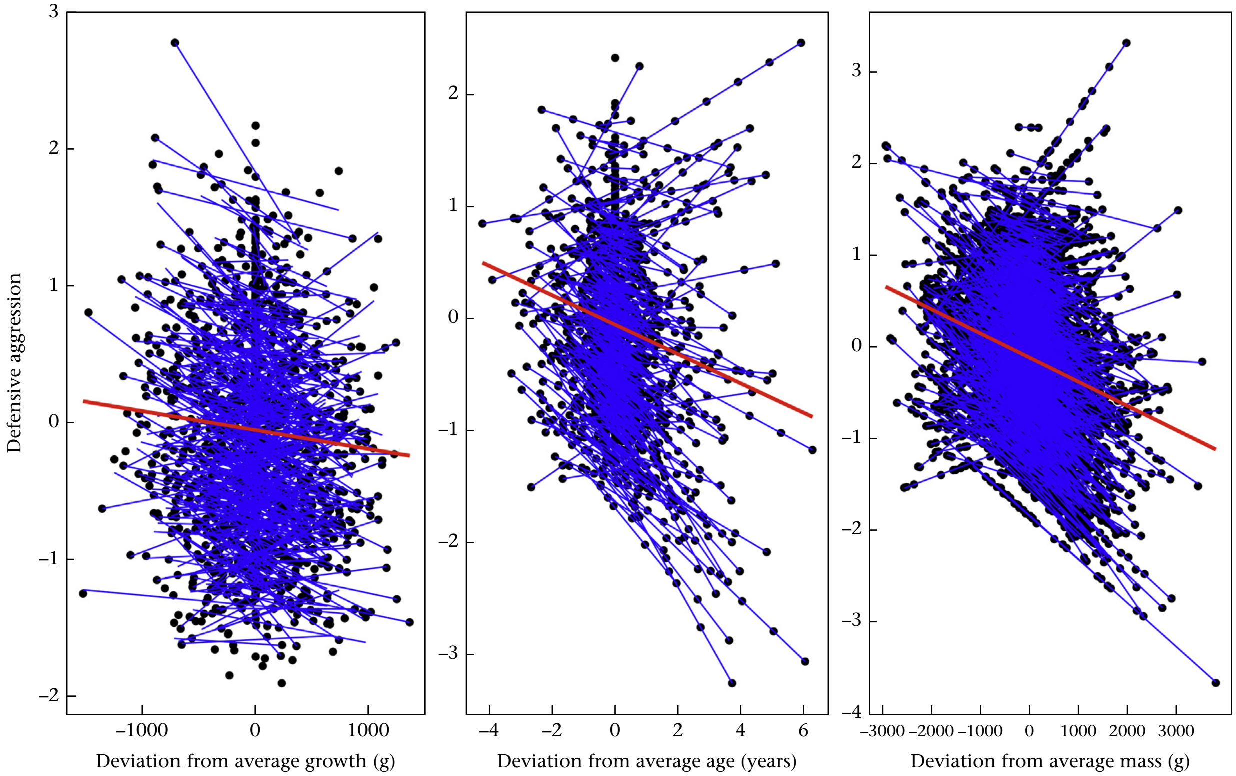

Figure 3. Relationship between defensive aggression and deviation from mean state (growth, age, mass). Plots show predicted values on the latent scale from models.

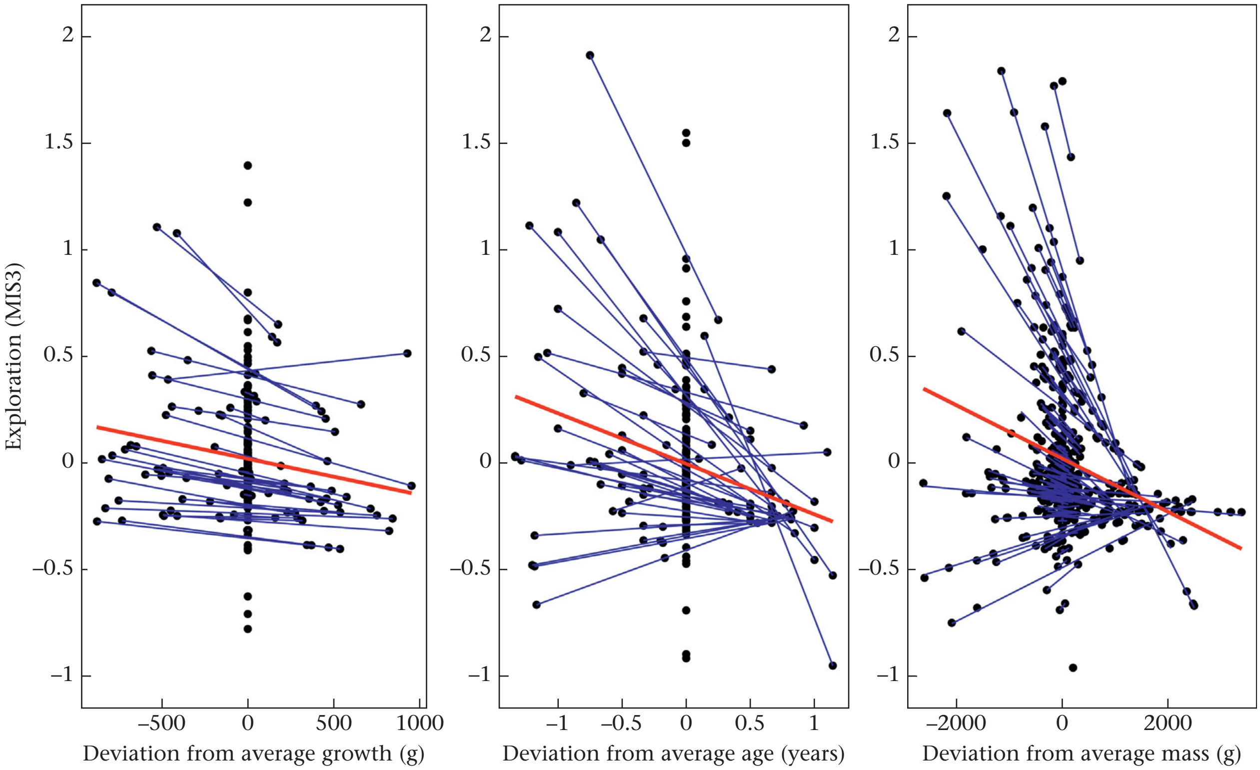

Figure 4. Relationship between exploration in the mirror image stimulation (MIS3) and deviation from the mean state (growth, age, mass). Plots show predicted data from models.

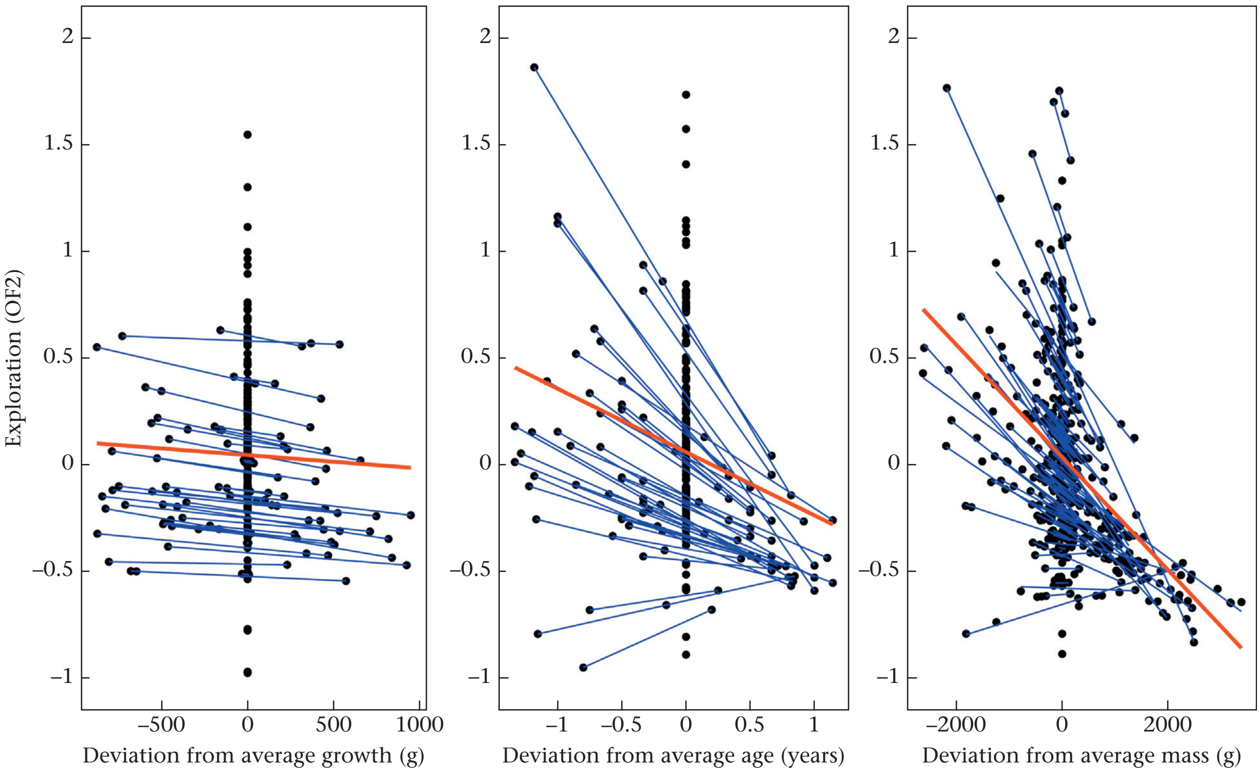

Figure 5. Relationship between exploration in the open field (OF2) and deviation in mean state (growth, age, mass). Plots show predicted data from models.

If the POLS (in our study, estimated by quantifying summer growth and residual reproductive value) explained variation in risk taking, then we would expect individuals that grow faster or are older (i.e. those with reduced residual reproductive value) to take more risks (Réale et al., 2010). However, we found that the mean and the difference from mean in summer growth and age were negatively associated with defensive aggression and activity in the OF context. Furthermore, we found a negative correlation between intercepts and slopes for activity. A number of previous studies have found a positive link between summer growth and risk taking (Careau, Thomas, Humphries, & Réale, 2008; Clobert et al., 2000; Pottinger, 2006; Ward et al., 2004). However, in one of the largest studies of a free-living population, Bouwhuis, Quinn, Sheldon, and Verhulst (2014) found a weak negative correlation between basal metabolic rate and personality in great tits, *Parus major*. This is consistent with our results that POLS does not cause and maintain variation in marmot personality traits. Our result is also consistent with a recent meta-analysis of state and personality variation that found little evidence for a relationship between state and personality (Niemela & Dingemanse, 2018).

It is unclear why summer growth is negatively associated with risky behaviours in marmots. Marmots must put on considerable mass to survive overwinter hibernation (Armitage, 2014) and are thus expected to maximize their summer growth. However, in recent years, earlier snowmelt has extended the plant-growing period, which has indirectly released marmots from this growth limitation (Ozgul et al., 2010). This extended plant-growing period, combined with many burrows into which marmots can escape to safety, means that individuals can grow with minimal risk by foraging relatively close to safety.

If residual reproductive value explains variation in risk taking, we should see older individuals taking more risks. We found some evidence that age is positively related to differences in exploration in the MIS test. Thus, lower residual reproductive value explains at least some of the between-individual differences in exploration in a social setting. Yet we also found a negative association between age and defensive aggression as measured in the OF, and a deviation from individual mean and risk taking in defensive aggression as measured in both the OF and MIS. Furthermore, the negative correlation between the intercept and the slope in both OF and MIS suggests that as individuals age, they become more similar in their exploration. This finding is consistent with Luttbeg and Sih's (2010) prediction that, as residual reproductive value decreases, individual differences should be eliminated. Conversely, we found a positive feedback mechanism between age and defensive aggression. Thus, our current results are mixed and inconsistent with the clear expectations from both the SDS and POLS hypotheses.

The state-dependent safety hypothesis predicts that individuals in better condition should take more risks. Previous work also has provided mixed support for the hypothesis. No association between body mass and docility was observed in bighorn ewes, *Ovis canadensis*, (Réale et al., 2000), and a previous review of muroid rodent personality found no association between open field exploration and body mass (Careau et al., 2009). However, heavier eastern chipmunks, *Tamius striatus*, were found to be less docile (and hence took more risks) (Martin & Réale, 2008). In yellow-bellied marmots, previous work found that heavier marmot yearlings were less docile (which is the inverse of defensive aggression) (Petelle et al., 2013), but this effect disappeared when we expanded our analysis to include all ages. In this study, we found a negative association between differences in mass and defensive aggression measured in the open field test. Our results are not only inconsistent with, but also reversed with, what is expected with the state-dependent body condition hypothesis.

Interestingly, individuals that deviated from their mean body mass varied in their defensive aggression, activity and exploration levels. Individuals were less defensively aggressive and active when heavier. This makes intuitive sense; individuals may take more risks to attempt to gain more mass (i.e. they may be more active or exploratory to find food). Mass compensation is also influenced by activity and exploratory behaviour in zebra finches, *Taeniopygia guttata* (Krause & Naguib, 2011). Additionally, we found negative correlations between the intercept and the slope of body mass, a finding that suggests negative feedback between mass and activity and exploration. Thus, individuals may be viewing their relatively good body condition as an asset worthy of protection (Clark, 1994) and to do so, they may reduce the risks that they take. Conversely, the positive feedback between mass and defensive aggression suggests that mass may maintain defensive aggression despite the negative between-individual and within-individual association between the two variables.

Among-individual state covariates explained some variation in personality traits, suggesting that state does explain some variation in personality. However, the within-individual results imply that individuals decrease their risk as they grow faster, age and weigh more, contrary to our predictions. Furthermore, we found mainly negative state-dependent feedback mechanisms between risk and state that reduced behavioural variation, rather than the positive state-dependent mechanisms that would be predicted to explain personality variation. Our study suggests that individuals follow an asset protection principle in line with a recent study on personality variation in the house cricket, *Acheta domesticus* (Royauté & Dochtermann, 2016). The among-individual association with state, with no corresponding risky behaviour/state positive feedback mechanisms, suggests that state and individual behavioural divergence may have occurred over evolutionary time and plateaued in our population (Sih et al., 2015). Thus, within-individual variation in state is no longer associated with behavioural divergence at the among-individual level. It is not clear why different feedback mechanisms are seen for different risky personality traits, but we do know that defensive aggression (docility) is not genetically correlated with activity or exploration (Petelle et al., 2015). Thus, these personality traits can evolve independently and different mechanisms may underlie their maintenance, or indeed, state and behavioural trait may not be genetically linked (Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018). Determining the fitness consequences of these traits would also help us understand the potential link between state and behaviour.

Given the complex results presented here, we cannot conclusively exclude state (summer growth, age, mass) as an underlying mechanism for the maintenance of personality variation in marmots. Yet there are other potential adaptive mechanisms that may explain personality variation including other physiological traits or social niche specialization (Bergmüller & Taborsky, 2010; Montiglio, Ferrari, & Réale, 2013). And, variation could be explained by more complex feedback interactions between intrinsic state characteristics and spatiotemporal differences in ecology (Montiglio et al., 2018). However, we are unable to model these complex interactions with our current data set. For example, activity and exploration are thought to influence an individual's ability to hold and retain food resources but may increase the probability of being discovered by predators. In our system, predation pressure differs by life stage as well as temporally and spatially throughout our colonies. Thus, the correlation between state and behaviour may be masked, if our trait measurements failed to capture this life-history trade-off. Future studies are required to identify the maintenance of individually distinctive risk taking in yellow-bellied marmots.

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Appendix

Table A1

Principal component analysis results from the open field (OF) and mirror image stimulation (MIS) tests (reproduced from Petelle et al., 2015)

Behaviour/trait	Open field				Mirror image stimulation					
	Activity 1	Exploration 2	3	4	Activity 1	Sociability 2	Exploration 3	4	5	6
No. of heart beats/15 s	0.136	−0.139	**0.601**	−0.519	0.131	−0.18	−0.057	**0.732**	−0.186	−0.258
Defecate	0.021	−0.162	0.404	**0.66**	0.123	−0.036	−0.05	0.041	−0.074	**0.868**
Urinate	0.073	0.128	−0.077	**0.594**	−0.107	−0.023	0.276	−0.086	0.476	0.323
Immediately out	0.008	0.053	**0.713**	0.088	−0.103	0.076	0.054	**0.801**	0.106	0.252
% Squares visited	**0.754**	0.34	0.11	0.062	**0.705**	0.263	0.443	0.011	0.092	0.105
No. of lines crossed	**0.908**	0.199	0.043	0.084	**0.755**	0.299	0.335	−0.044	0.034	0.046
No. of alarm calls	−0.112	−0.071	−0.385	−0.01	0.087	0.031	−0.158	0	**0.841**	−0.183
No. of jumps	**0.615**	−0.384	−0.214	0.152	**0.692**	0.14	−0.177	−0.116	−0.08	0.078
No. of sniffs	0.44	**0.82**	0.042	0.081	0.372	0.208	**0.827**	0.022	−0.023	−0.016
No. of walks	**0.889**	0.225	0.124	−0.011	**0.822**	0.289	0.314	0.066	−0.034	−0.008
No. of total looks	**0.793**	0.173	0.138	0.029	**0.728**	0.268	0.212	0.045	0.361	−0.017
Proportion of sniffs	0.335	**0.876**	0.048	0.085	0.264	0.16	**0.874**	−0.01	0.001	−0.017
Proportion of walks	**0.914**	0.126	0.158	−0.063	**0.808**	0.187	0.327	0.127	−0.089	−0.026
Proportion of looks	−**0.849**	−0.43	−0.146	0.015	−0.49	−**0.625**	−0.391	−0.017	0.123	0.048
Latency to approach mirror (s)	–	–	–	–	−0.327	−**0.608**	−0.197	−0.066	−0.171	−0.082
Proportion of time spent at mirror	–	–	–	–	0.14	**0.841**	−0.06	−0.064	0.155	−0.018
No. of scratch mirrors	–	–	–	–	0.426	**0.763**	0.206	−0.08	−0.097	−0.029
Proportion of scratch mirrors	–	–	–	–	0.169	**0.877**	0.168	−0.032	−0.11	−0.039
% Variance explained	42.518	9.896	8.867	7.563	40.351	9.178	6.963	6.555	6.178	5.715
Total variance	42.518	52.413	61.28	68.843	40.351	49.528	56.491	63.047	69.224	74.939

Component scores were varimax rotated. Variance for each component and total variance explained are also shown. We considered any variable > |0.500| as being significantly loaded onto that component. Significant loadings are bolded.

Table A2
Reported individual, year and residual (within-individual) variance

Personality trait	State	Individual	Year	Residual	Repeatability	*P*
Def. Agg.	Growth	0.192	0.012	0.682	0.216	<0.0001
	Age	0.189	0.011	0.683	0.214	<0.0001
	Mass	0.188	0.012	0.675	0.215	<0.0001
OF1 (Activity)	Growth	0.276	–	0.708	0.281	<0.0001
	Age	0.288	–	0.630	0.314	<0.0001
	Mass	0.231	–	0.600	0.278	<0.0001
OF2 (Exploration)	Growth	0.330	–	0.768	0.301	<0.0001
	Age	0.359	–	0.730	0.329	<0.0001
	Mass	0.328	–	0.737	0.308	<0.0001
MIS1 (Activity)	Growth	0.672	–	0.573	0.540	<0.0001
	Age	0.701	–	0.549	0.561	<0.0001
	Mass	0.658	–	0.557	0.542	<0.0001
MIS3 (Exploration)	Growth	0.211	–	0.853	0.199	<0.0001
	Age	0.213	–	0.839	0.202	<0.0001
	Mass	0.200	–	0.851	0.190	<0.0001

Def. Agg.: defensive aggression; OF: open field; MIS: mirror image stimulation. Repeatability is the proportion of variance attributed to among-individual variation and is the individual variance divided by total phenotypic variance. *P* values are calculated by log-likelihood ratio tests between models that include individual as a random effect and models that do not.

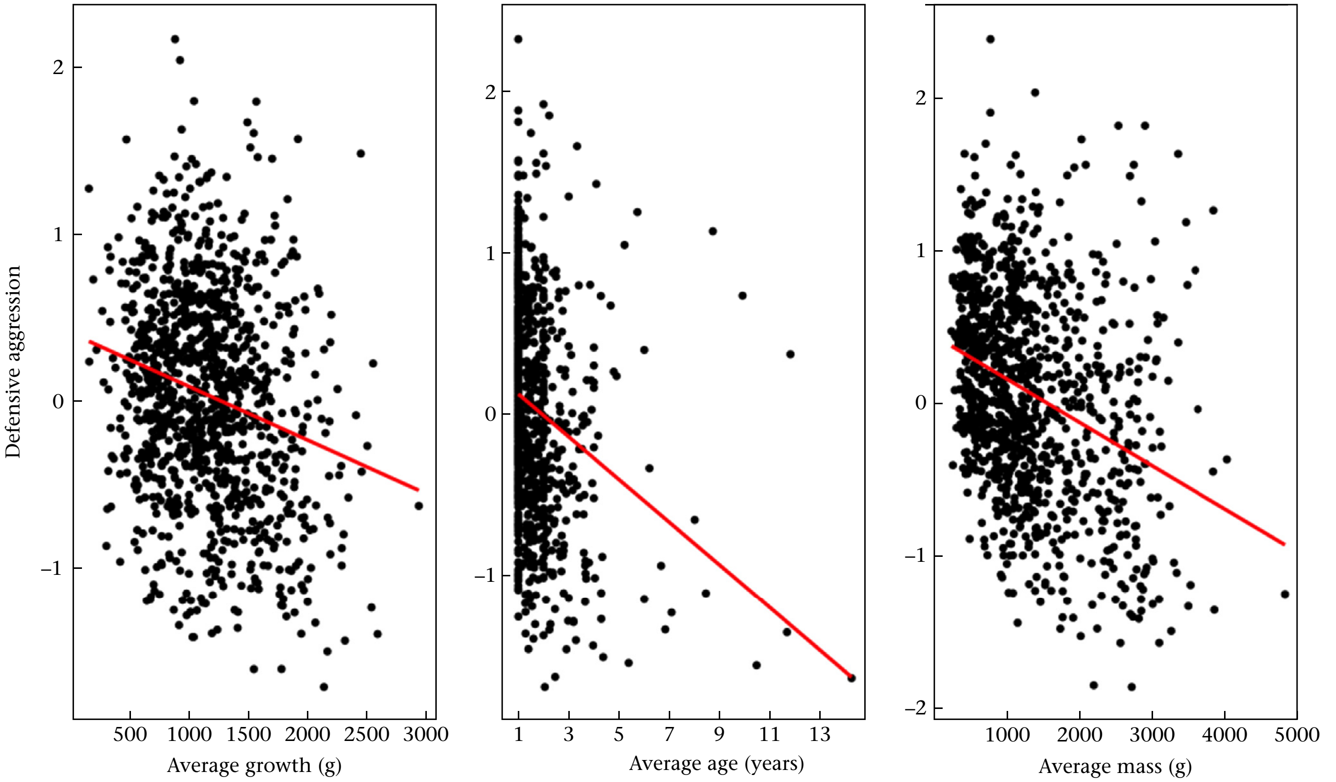

Figure A1. Relationship between defensive aggression and mean individual state (growth, age, mass). Scatterplots are made with predicted data. Predicted data were estimated on the latent scale, and can have values greater than the original ordinal data.

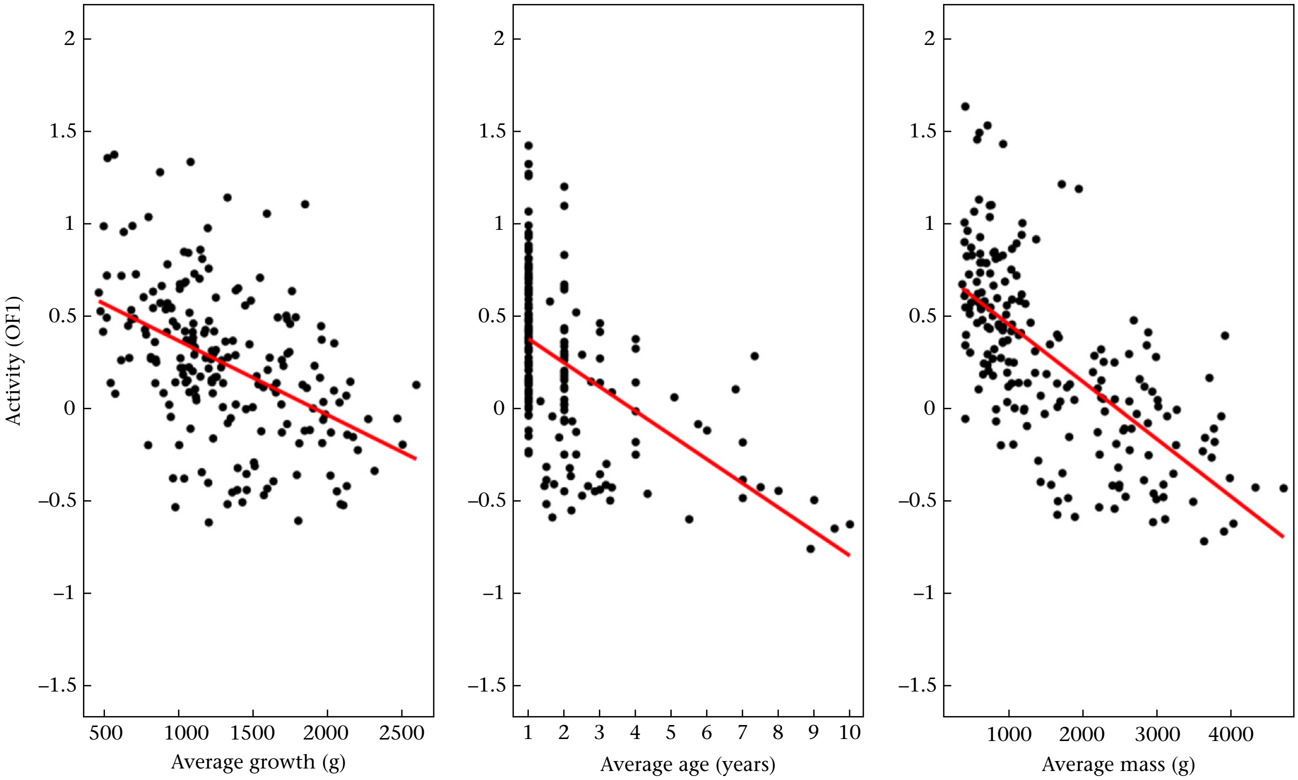

Figure A2. Relationship between activity in the open field (OF1) and mean individual state (growth, age, mass). Scatterplots are made with predicted data.

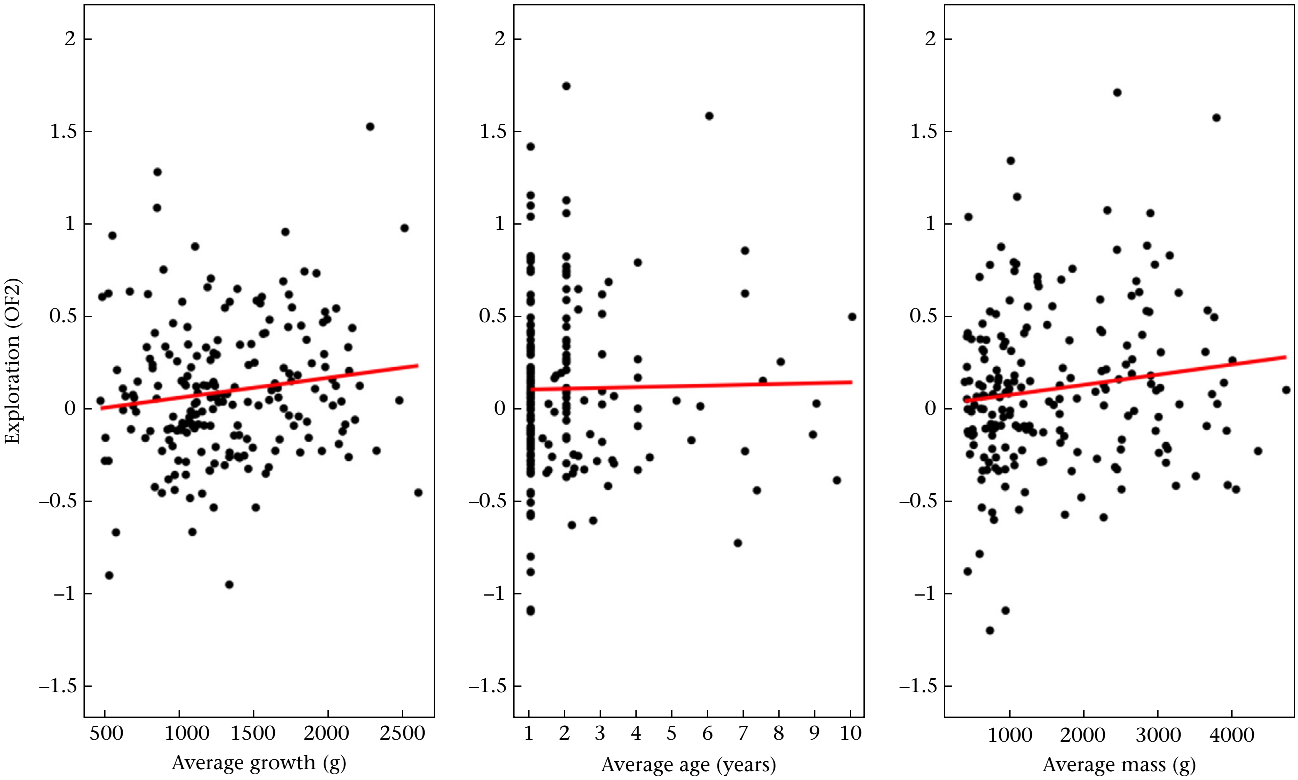

Figure A3. Relationship between exploration in the open field (OF2) and mean individual state (growth, age, mass). Scatterplots are made with predicted data.

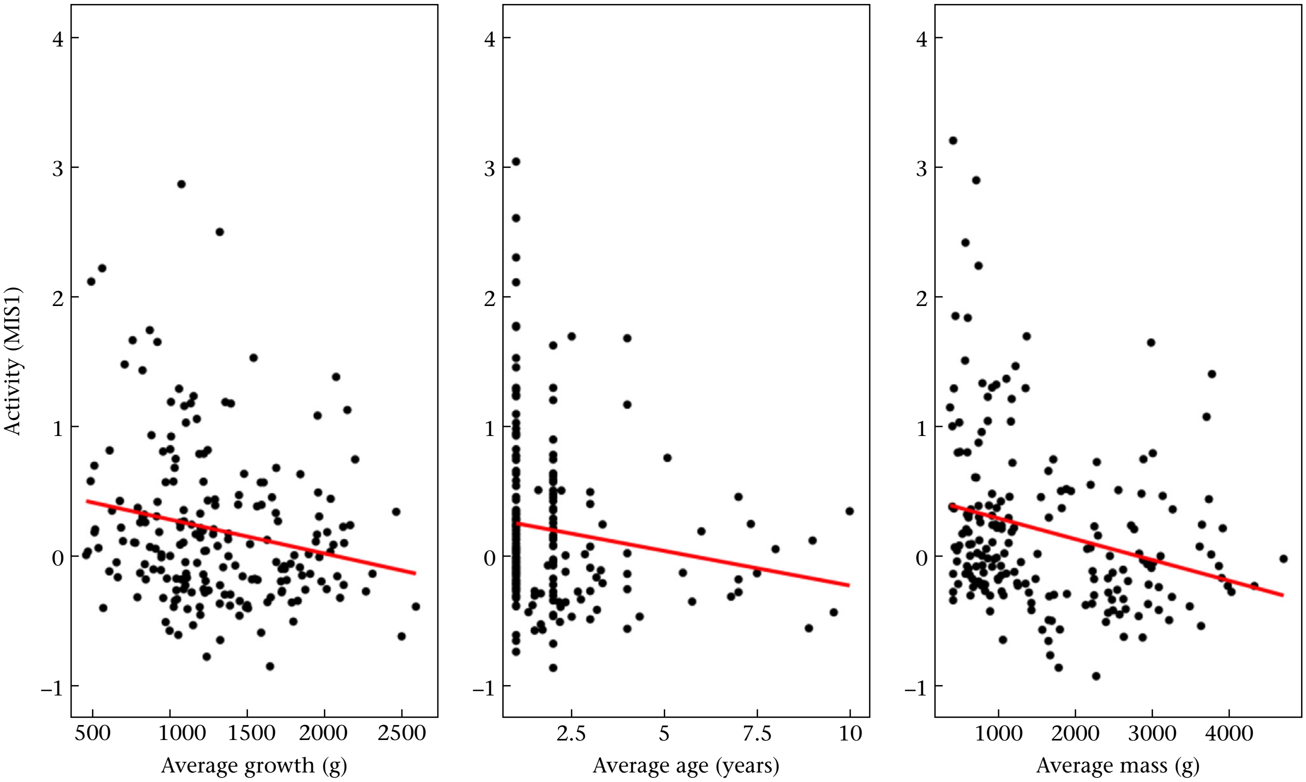

Figure A4. Relationship between activity in the mirror image stimulation (MIS1) and mean individual state (growth, age, mass). Scatterplots are made with predicted data.

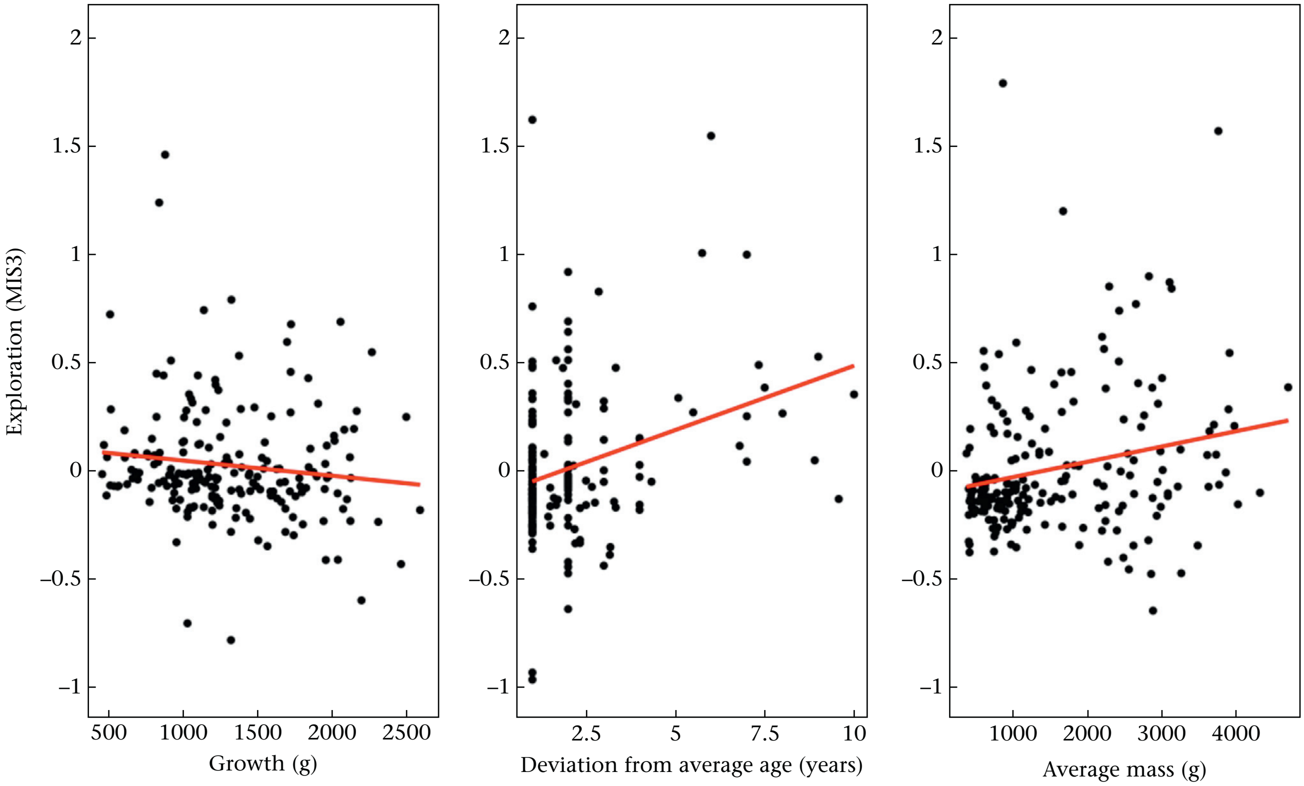

Figure A5. Relationship between exploration in the mirror image stimulation (MIS3) and mean individual state (growth, age, mass). Scatterplots are made with predicted data.