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# Heritability and genetic correlations of personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*)

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## Abstract

Describing and quantifying animal personality is now an integral part of behavioural studies because individually distinctive behaviours have ecological and evolutionary consequences. Yet, to fully understand how personality traits may respond to selection, one must understand the underlying heritability and genetic correlations between traits. Previous studies have reported a moderate degree of heritability of personality traits, but few of these studies have either been conducted in the wild or estimated the genetic correlations between personality traits. Estimating the additive genetic variance and covariance in the wild is crucial to understand the evolutionary potential of behavioural traits. Enhanced environmental variation could reduce heritability and genetic correlations, thus leading to different evolutionary predictions. We estimated the additive genetic variance and covariance of docility in the trap, sociability (mirror image stimulation), and exploration and activity in two different contexts (open-field and mirror image simulation experiments) in a wild population of yellow-bellied marmots (*Marmota flaviventris*). We estimated both heritability of behaviours and of personality traits and found nonzero additive genetic variance in these traits. We also found nonzero maternal, permanent environment and year effects. Finally, we found four phenotypic correlations between traits, and one positive genetic correlation between activity in the open-field test and sociability. We also found permanent environment correlations between activity in both tests and docility and exploration in the MIS test. This is one of a handful of studies to adopt a quantitative genetic approach to explain variation in personality traits in the wild and, thus, provides important insights into the potential variance available for selection.

## Introduction

Individuals from many taxa have been shown to behave in consistent, individually different ways (Gosling, 2001) – a phenomenon referred to as personality – which may have important ecological and evolutionary consequences (Réale *et al.*, 2007). Within personality research, the maintenance of personality variation is an important question in behavioural ecology and evolution. This is because personality traits may be linked to life history syndromes (Wolf *et al.*, 2007), can have fitness consequences (Smith & Blumstein, 2008) and influence population demography (Armitage, 1986). Personality variation may be maintained because there are multiple optima on a fitness landscape, or because there is fluctuating selection over time or space (Boon *et al.*, 2007). However, in each of these scenarios, personality traits must be heritable to evolve. To under-

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stand how personality traits may evolve, it is important to understand the additive genetic variation upon which selection may act. Additionally, many personality traits are phenotypically correlated with each other and create what are referred to as behavioural syndromes (Sih *et al.*, 2004). Such syndromes may constrain selection and prevent the erosion of genetic variation under constant selection (Dochtermann & Dingemanse, 2013). Therefore, to understand the potential response to selection of a trait within a population, one must know the heritability of that trait, as well as the constraints generated by genetic correlations (Lande & Arnold, 1983).

Few studies have investigated the genetic and environmental sources of (co)variances of behaviour and personality (Stirling *et al.*, 2002) despite the importance of these effects on evolution (Falconer & Mackay, 1996; Lynch & Walsh, 1998; Kruuk *et al.*, 2008). Even fewer studies have estimated the heritability of personality traits in the wild; thus, we know little about how personality may respond to selection in nature. Laboratory-based estimates seemingly overestimate heritabilities when compared to the low to moderate estimates reported in the wild (van Oers *et al.*, 2005; Sinn *et al.*, 2006; Lea *et al.*, 2010; Taylor *et al.*, 2012; Niemelä *et al.*, 2013), suggesting that the natural environment has a large effect on phenotypes and that phenotypic plasticity is the main driver of mean behavioural trait variation. A recent study by Dochtermann *et al.* (2014) shows that previous studies did not directly estimate heritability of personality, but rather estimated heritability of the behaviour. They suggest that one should estimate heritability of personality using the between-individual variance (i.e. repeatability) as the 'phenotypic' variance of the personality trait. Thus, heritability of personality, noted $h^2P$, is the ratio of additive genetic variance over the variance attributed to the individual, and heritability of the behaviour, noted $h^2B$, is the classic heritability ratio of additive genetic variance over total phenotypic variance.

The formation of phenotypic correlations between personality traits is an active area of evolutionary and behavioural ecology (Dochtermann & Roff, 2010; Dochtermann & Dingenmanse, 2013). Two hypotheses, constraint and adaptive, are used to explain the formation of these syndromes. The constraint hypothesis states that personality traits have an underlying genetic or physiological cause (Sih *et al.*, 2004) and that this correlation prevents traits from reaching their own independent optima (Dochtermann, 2010). The adaptive hypothesis states that natural selection forms these suites of behaviours to be adaptive in that population's specific environment (Wilson, 1998; Bell, 2005; Dingemanse *et al.*, 2007). Thus, to determine the (co)variance structure of syndromes, we must also understand the potential underlying genetic, maternal and permanent environmental variance. Detection of genetic correlations may support the constraint hypothesis (Sih *et al.*, 2004), but knowledge of fitness optima is necessary to determine whether correlations act as constraints on evolution. The presence of maternal or permanent environmental correlations suggests a potential adaptive link between behavioural traits. This is because maternal effects and the environment individuals encounter can shape correlations to have any potential advantage within that specific environment.

Furthermore, to understand how populations evolve, it is important to understand not only the covariance between traits, but the fitness consequences of these covariances. Previous studies in this population by Armitage (1986) show that affiliative behaviour, using mirror image stimulation (MIS) tests, was associated with recruitment of adult females to the natal colony. Recruitment of reproductive females can influence colony and metapopulation dynamics (Ozgul *et al.*, 2009). Furthermore, measurements of docility (which was based on how individuals responded to trapping) were associated with survival and reproductive success in bighorn sheep (*Ovis canadensis*) (Réale *et al.*, 2000, 2009), as well as dispersal tendency in roe deer (*Capreolus capreolus*) (Debeffe *et al.*, 2014). Activity has also been shown to influence offspring growth in red squirrels (*Tamiasciurus hudsonicus*) (Boon *et al.*, 2007). Although the tests here and in other studies were conducted in a non-natural setting, these traits have been shown to correlate with ecologically functional behaviours that influence fitness (Smith and Blumstein, 2008).

We quantified the additive genetic, maternal and permanent environment variances and covariances of four traits – docility, activity, sociability and exploration – in a wild population of yellow-bellied marmots (*Marmota flaviventris* hereafter referred to as marmots). Here, we calculate heritability using both the classic method of estimation (Falconer & Mackay, 1996), referred as heritability of the behaviour $h^2B$, and the newer method using the ratio of additive genetic variance to repeatability, referred as heritability of personality $h^2P$ (Dochtermann *et al.*, 2014). It should be noted that all previous studies have only estimated $h^2B$ and not $h^2P$ (except for Dochtermann *et al.*, 2014). Like other studies in the wild (Taylor *et al.*, 2012), we expect heritability of the behaviour to be relatively small because of high environmental variation. This estimate should increase when using the newer method because only a subset of the original phenotypic variance is used to calculate the heritability of personality. Behavioural syndromes are hypothesized to have an underlying genetic component (i.e. genetic correlation, Dochtermann & Dingemanse 2013). Although we expect phenotypic correlations among and within personality traits, we have no *a priori* hypotheses about the underlying architecture of those correlations.

## Materials and methods

### Study species and sites

Yellow-bellied marmots are large (3–5 kg), semi-fossorial, sciurid rodents, native to North America, which live in colonies that consist of one or more matrilineal groups (Frase & Hoffmann, 1980; Armitage, 2014). These colonies typically consist of one adult male, multiple adult females and their kin. The number of adult females from 2001 to 2012 varied between 1 and 23 (mean = 4.78; SD = 4.67). Marmots are active from mid-April to mid-October and hibernate through the winter (Blumstein *et al.*, 2006). We differentiate three age categories: juveniles, which are young of the year; yearlings, individuals that have survived their first winter; and adults, individuals that have survived their second winter and are reproductively mature. Our study population is located in the upper East River Valley, Gunnison, Colorado, the site of Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado (38° 57′ 29″N; 106° 59′ 06″W). We regularly trap multiple colonies in and around the RMBL. This population has been followed since 1962 (Armitage, 2010), and the individual behaviour for some traits used in this study has been collected since 2002 (Petelle *et al.*, 2013).

### Pedigree

We assigned parentage using DNA collected from individuals studied from 2002 to 2012. Detailed methods are described in Blumstein *et al.* (2010) and Olson & Blumstein (2012). Briefly, we extracted DNA using Qiagen QIAamp DNA Mini kits and genotyped individuals at 12 microsatellites. Alleles were visualized and scored using GENEMAPPER, and parentage was assigned using CERVUS 3.0 (Kalinowski *et al.*, 2007). Juveniles were trapped the first time they emerged out of the maternal burrow. This allowed us to behaviourally match juveniles to mothers. We used CERVUS to confirm maternity and to match paternity to juveniles using a maximum likelihood method at 95% trio confidence. 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. Proportion of loci typed was 0.948 and the proportion mistyped was set at 0.01. As many adult female marmots are philopatric, and therefore potentially highly related, 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 & Blumstein, 2012). The differences between the expected assignment rate and the observed assignment rate in CERVUS were never larger than 3% for any cohorts. Since 2002, we have genotyped 1432 individuals from 136 dams and 71 sires (see Table S1 for pedigree information).

### Quantifying personality

Docility is a commonly measured personality trait and estimates how an individual reacts to being trapped and handled (Réale *et al.*, 2000; Petelle *et al.*, 2013). We quantified docility in 920 individuals with data collected during 7904 trapping events from 2002 through 2012 (767 individuals had repeated measurements; mean = 4.07; standard deviation = 3.22). At each trapping event, we dichotomously (0/1) scored whether individuals struggled in the trap, tooth chattered, alarm called, struggled in the bag and hesitated to walk into the handling bag. These were summed and subtracted from the total potential score. Thus, an individual who scored 5 was considered docile during that trapping event, whereas an individual who scored 0 was considered nondocile.

During the 2010–2012 active seasons, we tested 183 individuals in 508 open-field (OF) and mirror image stimulation (MIS) tests (108 individuals had repeated measurements; mean = 1.97, SD = 1.16). After individuals had been regularly trap processed (weighed, left hind foot measured, sexed, ear tags checked and replaced if required, faeces collected if present), they were brought to a shaded arena for testing. Thus, OF and MIS tests were carried out relatively soon after docility measurements. Full methods for OF and MIS are published elsewhere (Petelle & Blumstein, 2014), but briefly, during the OF test, individuals were placed in an opaque arena measuring 91.4 $cm^3$ made of thick PVC sheeting. Individuals were allowed to explore the arena without obstruction for 3 min. Immediately after the first 3 min, and while still in the arena, individuals were presented with a mirror for the MIS test.

OF and MIS behaviour was scored using the event recorder JWATCHER (Blumstein & Daniel, 2007), which allowed us to quantify the duration and frequency of the following behaviours: walk (quadrupedal and bipedal), look (quadrupedal and bipedal), jump, alarm call and sniffing/smelling. For MIS only, we also included scratching/pawing at the mirror. We also quantified the number of squares each individual entered and the proportion of squares entered (Petelle & Blumstein, 2014). OF tests are often used to test activity and exploration in personality studies (Carter *et al.*, 2013), and MIS has been used previously with this population to assess sociability (Armitage, 1986), although our specific methods were different. Briefly, differences include the use of a longer acclimation period and trial duration. This study extracted activity and exploration components from the MIS tests (see below), whereas Armitage (1986) only extracted sociability components.

### Statistical analysis

Rather than analysing each OF/MIS behaviour separately, we chose to reduce the number of correlated traits using a principal components analysis with varimax rotation. OF and MIS behaviours were analysed separately. Components with eigenvalues greater than 1.0 were retained for further analysis.

We estimated additive genetic, permanent environment, maternal and year effects for the resulting OF and MIS components and docility using an animal model with a Bayesian approach (Hadfield, 2010; Wilson *et al.*, 2010). All traits were mean-centred and scaled to a variance of 1 prior to the analysis. All traits were fitted with sex and age class. Docility was also fitted with day of the year, days between trials, time (AM or PM), pedestrian traffic, growth rate and mass as fixed effects. Growth rate and mass were individually centred. Activity (OF) was also fit with days between trials, trial number and predator presence. Exploration included day of the year and pedestrian traffic. Activity (MIS) also included days between trials, pedestrian and predator presence. These fixed effects had previously been shown to significantly influence personality traits (M. B. Petelle J.G.A. Martin, & D.T. Blumstein in revision). The sociability component had previously not been analysed, so we included sex, age class, day of the year, pedestrian traffic, predator presence, days between trial and trial number as fixed effects (see Petelle *et al.*, 2013 for methods on the calculation of pedestrian traffic and predator pressure). We estimated additive genetic ($V_A$, identity link to the pedigree), permanent environment ($V_{PE}$, identity), maternal environment ($V_{ME}$, mother id) and year ($V_{YE}$) variance parameters. Variance parameters were estimated as the posterior mode with 95% credible intervals (CI) based on the posterior distribution of the parameter. All variance ratios and correlations were estimated based on (co)variance components at each MCMC iteration, thus providing a posterior distribution. The posterior distribution of heritability of behaviour was estimated with the equation $h^2B = V_A/V_P$. In this equation, $V_P$ is the total phenotypic variance conditioned on the fixed effects. The heritability of personality (Dochtermann *et al.*, 2014) was estimated with the equation $h^2P = V_A/V_{ind,}$ where $V_{ind}$ is the among-individual variation ($V_A + V_{PE} + V_{ME}$) used as the numerator when estimating repeatability, $r = V_{ind}/V_P$. As variance parameters are bounded above zero, we estimated importance of random effects by looking at the deviance information criteria (DIC) (Spiegelhalter *et al.*, 2002). DIC is analogous to the Bayesian version of Akaike information criterion (AIC). For this reason, we used a delta DIC value under 7 (Burnham *et al.*, 2011) to identify potentially important random effects. To understand how these trait variances changed with the additional random effects, we fitted models with individual, maternal and permanent environment effects removed consecutively (Kruuk *et al.*, 2008; Hadfield, 2010).

To estimate pairwise correlations between traits, we fitted bivariate models for each pair of personality traits and estimated the covariance between traits for each random effect. We then rescaled the covariances into correlations.

Principle components were calculated in SPSS 18.0 (Chicago, IL, USA). For all other analyses, we used the package MCMCGLMM (Hadfield, 2010) in R v. 3.1.1 (R Development Core Team, 2014). For univariate models, the posterior distribution was sampled every 500 iterations with a burn-in of 30 000 for a total of 1000 samples. The bivariate models were sampled every 1000 iterations with a burn-in of 30 000 for a sample of 1000. For both *G* (random effects) and *R* (residuals) priors, we specified $V = 1$ and $nu = 1$. For bivariate models, we used for both *G* and *R* priors $V = 0.5*I_2$ (2*2 diagonal matrix with 0.5 on the diagonal) and $nu = 1.002$. We used a Gaussian error distribution for all models and normality was checked visually. Mixing of chain was assessed visually, and the autocorrelation was <0.05 for all parameters.

## Results

### PCA of OF and MIS behaviours

We extracted four and six principle components for OF and MIS tests, respectively (Table S2). After reviewing the component loadings, we identified two OF and three MIS components that corresponded with personality traits. The first component in each test was labelled activity, the second and third components of the OF and MIS test, respectively, were identified as exploratory, and the second MIS component was labelled sociability (Table S1 for component loadings). The first OF and MIS components, both labelled activity, were characterized by positive loadings of the percentage of the squares visited, the number of lines crossed, the total number of jumps, walks and looks, and the total proportion of time walking. The proportion of time looking was also negative loaded onto the first OF component. The second OF and third MIS components, labelled exploration, were described by positive loadings of number of sniffs/smells and the proportion of time spent smelling. Finally, the second MIS component, labelled sociability, was characterized by the positive loading of proportion of time spent at the mirror, and negatively associated with latency to approach the mirror and proportion of time looking. The two OF components explained approximately 52% of the variance, whereas the three MIS components explained 56%.

### Univariate decomposition of the variance

All full models fell within a delta DIC of 7 and thus were equally plausible as the best model (Burnham

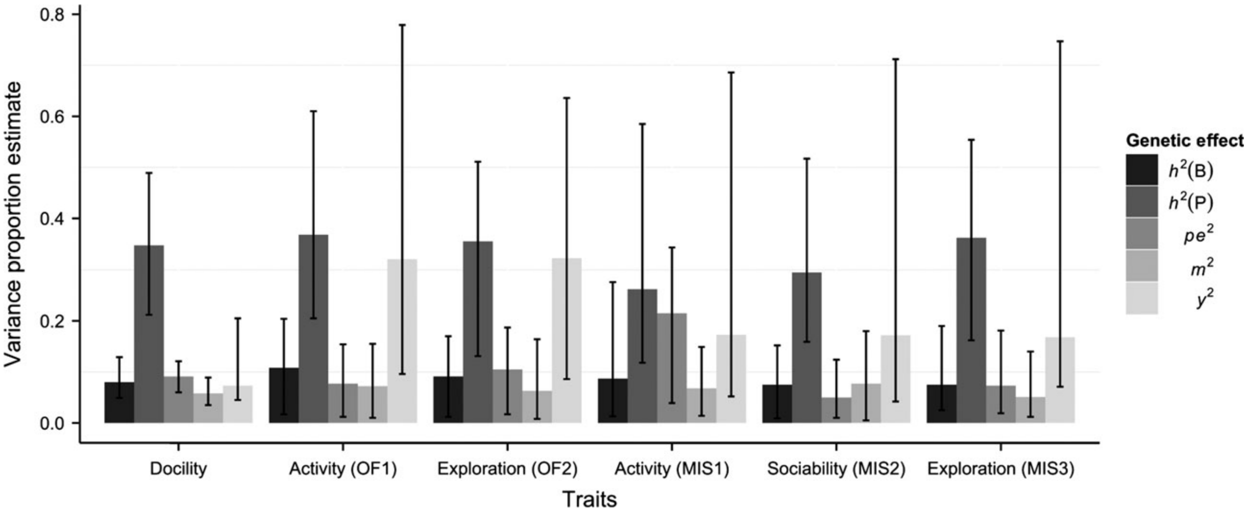

**Fig. 1** Proportion of variance explained by additive genetic variance of the behaviour ($h^2$ $(B) = V_A/V_P$) and personality ($h^2(P) = V_A/V_{\mathrm{ind}}$), permanent environment effects ($pe^2 = V_{PE}/V_P$), maternal effects ($m^2 = V_{ME}/V_P$) and year effects ($y^2 = V_{YE}/V_P$) for each personality trait. The posterior mode is reported as the estimate and the equivalent of the 95% credible interval are illustrated.

*et al.*, 2011) (Table S2). We found nonzero heritability in all of our traits (0.075–0.091) (see Fig. 1; Table S3). Not surprisingly, our estimates of heritability increased greatly when $V_{\mathrm{ind}}$ was used instead of phenotypic variance to calculate heritability of personality (0.262–0.362) (see Fig. 1; Table S3).

The variation attributed to the permanent environment, maternal and year effects was also nonzero for all traits (Fig. 1; Table S3).

### Estimation and decomposition of covariances among personality traits

We found four phenotypic correlations (i.e. behavioural syndromes) among personality traits. As expected, we found a positive phenotypic correlation between activity in the OF and MIS tests ($r_P = 0.444$; 95% CI = 0.239–0.644). We also found a positive correlation between activity in both OF and MIS tests and sociability ($r_{POF} = 0.428$; 95% CI = 0.072–0.603 and $r_{\mathrm{PMIS}} = 0.291$; 95% CI = 0.080–0.586). Docility was negatively correlated with activity in the OF test ($r_P = -0.241$; 95% CI = −0.471 to −0.026) (Table 1).

We then investigated the potential genetic, permanent environment and maternal correlations that may be the underlying cause of these phenotypic correlations. We found one significant genetic correlation between activity in the OF test and sociability ($r_G = 0.639$; 95% CI = 0.031–0.799). We also found two permanent environmental correlations: one between activity in the OF and MIS tests ($r_{PE} = 0.575$; 95% CI = 0.127–0.864) and one between docility and exploration in the OF test ($r_{PE} = 0.518$; 95% CI = 0.042–0.737). We found no maternal correlations (Table 1). It should be noted that there are a number of phenotypic, genetic and permanent environment correlations that are moderate but were not significant because of large 95% confidence intervals. Variance and covariance estimates are given in the supplementary tables.

## Discussion

We have five main results. First, all of the personality traits we investigated have low heritability indicating their evolutionary potential. Second, this heritability increased greatly when using repeatability as the denominator so that we could estimate the heritability of personality (Fig. 1; Table S3). Although this is not surprising, as the denominator is much smaller, it does highlight that previous estimates of heritability of personality are lower than their true value. Third, there are a number of distinct phenotypic correlations indicating the existence of behavioural syndromes. Fourth, one genetic correlation was detected among personality traits (Table 1) indicating the existence of potential genetic constraints on adaptive evolution. Fifth, the existence of permanent environmental correlations indicates that the environment has coupled the traits together. Thus, these traits in marmots could evolve further, but the underlying genetic and permanent environment correlations would constrain their evolutionary dynamics.

This is the first study of free-living animals, to our knowledge, that calculates both heritability of a behaviour and heritability of personality. Our estimates of heritability of behaviour are qualitatively similar when compared with previous studies (Sinn *et al.*, 2006; Taylor *et al.*, 2012). Moreover, although previous estimates of heritability of behaviour varied widely, heritability

**Table 1** Phenotypic, genetic, permanent environment and maternal correlations between each pair of personality traits. All correlations are given with 95% credible intervals. Significant correlations are in bold.

| Personality traits | Phenotypic correlation | Genetic correlation | Permanent environment correlation | Maternal correlation |
|---|---|---|---|---|
| Docility/ Activity (OF1) | **−0.241 (−0.471 to − 0.026)** | −0.256 (−0.664 to 0.246) | −0.317 (−0.687 to 0.088) | −0.249 (−0.663 to 0.184) |
| Docility/ Exploration (OF2) | 0.086 (−0.191 to 0.310) | 0.090 (−0.555 to 0.462) | 0.200 (−0.253 to 0.569) | −0.051 (−0.433 to 0.461) |
| Docility/ Activity (MIS1) | −0.143 (−0.399 to 0.078) | −0.006 (−0.637 to 0.382) | −0.156 (−0.593 to 0.241) | −0.225 (−0.633 to 0.263) |
| Docility/ Sociability (MIS2) | −0.100 (−0.299 to 0.218) | −0.077 (−0.491 to 0.486) | −0.131 (−0.538 to 0.411) | −0.173 (−0.580 to 0.310) |
| Docility/ Exploration (MIS3) | 0.192 (−0.078 to 0.406) | 0.084 (−0.336 to 0.642) | **0.518 (0.042 to 0.737)** | −0.260 (−0.577 to 0.320) |
| Activity (OF1)/ Exploration (OF2) | −0.343 (−0.497 to 0.040) | −0.185 (−0.667 to 0.366) | −0.451 (−0.794 to 0.037) | −0.196 (−0.560 to 0.447) |
| Activity (OF1)/ Activity (MIS1) | **0.444 (0.239 to 0.644)** | 0.643 (−0.086 to 0.842) | **0.575 (0.127 to 0.864)** | 0.527 (−0.192 to 0.755) |
| Activity (OF1)/ Sociability (MIS2) | **0.428 (0.072 to 0.603)** | **0.639 (0.031 to 0.799)** | 0.485 (−0.172 to 0.729) | 0.243 (−0.302 to 0.739) |
| Activity (OF1)/ Exploration (MIS3) | −0.016 (−0.276 to 0.304) | 0.159 (−0.499 to 0.588) | 0.014 (−0.515 to 0.479) | 0.113 (−0.498 to 0.542) |
| Exploration (OF2)/ Activity (MIS1) | −0.094 (−0.412 to 0.145) | 0.009 (−0.615 to 0.569) | −0.271 (−0.685 to 0.274) | 0.031 (−0.581 to 0.525) |
| Exploration (OF2)/ Sociability (MIS2) | 0.126 (−0.276 to 0.339) | −0.009 (−0.585 to 0.524) | 0.117 (−0.424 to 0.548) | 0.259 (−0.529 to 0.590) |
| Exploration (OF2)/ Exploration (MIS3) | 0.352 (−0.043 to 0.537) | 0.381 (−0.355 to 0.721) | 0.309 (−0.121 to 0.773) | 0.261 (−0.354 to 0.679) |
| Activity (MIS1)/ Sociability (MIS2) | **0.291 (0.080 to 0.586)** | 0.591 (−0.204 to 0.838) | 0.519 (−0.072 to 0.792) | 0.210 (−0.424 to 0.645) |
| Activity (MIS1)/ Exploration (MIS3) | −0.228 (−0.502 to 0.045) | −0.308 (−0.773 to 0.332) | −0.385 (−0.788 to 0.187) | −0.041 (−0.588 to 0.531) |
| Sociability (MIS2)/ Exploration (MIS3) | −0.045 (−0.380 to 0.266) | 0.025 (−0.650 to 0.456) | −0.114 (−0.460 to 0.559) | −0.100 (−0.579 to 0.517) |

estimates are generally smaller when estimated in the wild than in captivity (Sinn *et al.*, 2006; Taylor *et al.*, 2012; Niemelä *et al.*, 2013). For example, as in our study, Taylor *et al.* (2012) found low heritability in docility ($h^2 = 0.09$), aggression ($h^2 = 0.12$) and activity ($h^2 = 0.08$) in wild red squirrels (*Tamiasciurus hudsonicus*). Low heritability might suggest that these traits are under stabilizing or directional selection by being linked to fitness and that genetic variation has been eroded (Falconer & Mackay, 1996; Kruuk *et al.*, 2000), however an equally likely hypothesis is that residual and phenotypic variances covary and this reduces heritability estimates (Stirling *et al.*, 2002). When using the Dochtermann *et al.* (2014) approach to estimate heritability of personality, our estimates of heritability increased. Our estimates of repeatability were all moderate (Bell *et al.*, 2009) and significant, suggesting that among-individual variation is important in this population. Furthermore, this result underscores the fact that personality does have the ability to evolve in a wild population.

Similarly to previous studies (Réale *et al.*, 2009; Taylor *et al.*, 2012), we found that permanent environment effects are present for these traits suggesting that the consistent environment potentially plays an equally important role in accounting for phenotypic variation as the underlying genes (see also Blumstein *et al.*, 2013). Female marmots are philopatric (Armitage, 1984) and experience the same environment throughout life. The overall quality of this habitat may have long-term consequences on these traits. We also found nonzero maternal effects in all of our traits (0.051–0.077). Maternal effects can have long-term consequences on individuals (Reinhold, 2002; Weaver *et al.*, 2004; Räsänen & Kruuk, 2007). Activity, exploration and sociability are important parameters that may affect dispersal, and previous work in our system found that more social or well-connected female marmots are more likely to remain in their natal colony (Armitage, 1986; Blumstein *et al.*, 2009). The exact ecological and evolutionary function of docility has yet to be identified in this species; however, we, and others, have found that maternal stress response influences offspring personality (M. B. Petelle , B.N. Dang, & D.T. Blumstein in prep. ; Hinde *et al.*, 2015). Interestingly, year effects varied greatly (0.073–0.322). This result demonstrates that variation in the environment among years can explain a large amount of variation in behavioural traits.

We found four traits correlated at the phenotypic level, with all but one having underlying environmental or genetic correlations. Activity was correlated at both the phenotypic and permanent environment level between the OF and MIS test as expected if tests are measuring the same traits. The absence of significant genetic correlation might reflect the sample size in this case. However, exploration was not correlated between

OF and MIS suggesting that the tests we used here might have measured different trait (Watanabe *et al.*, 2012; Carter *et al.*, 2013).

Activity was also positively correlated at the phenotypic and the genetic level (OF test) with sociability. This correlation could arise if more active individuals are coming into contact with more individuals, or because there is a high degree of betweenness among different social groups (Krause *et al.*, 2010). Betweenness is a social network metric that measures the centrality of an individual based on the shortest paths between pairs of individuals in that group. Thus, if an individual connects two groups and has connections within each group, they have a high level of betweenness (Wey *et al.*, 2008).

Although not significant, the genetic correlation between activity in both tests was in the same direction and general magnitude as the phenotypic correlation (0.643–0.444, respectively) (Cheverud, 1988; Dochtermann, 2011). Although we cannot directly test the phenotypic gambit (Hadfield *et al.*, 2007) due to our large credible intervals, it is important to note that phenotypic correlations are not always good indicators of genetic correlations because permanent environment and maternal effects may obscure such a correlation.

We found a negative phenotypic correlation between activity in the OF test and docility. This makes sense because docility is partly calculated from active behaviours while in the trap and being handled (struggling in trap or bag). Thus, more active individuals in the OF test may also be more active in the trap and therefore receive lower docility scores.

Although many of the phenotypically correlated traits did not have underlying genetic correlations, we found moderate, but nonsignificant, genetic and permanent environment correlations. This suggests two possible explanations. First, that these traits are in fact correlated at the genetic or permanent environmental levels and we do not have sufficient power to estimate correlations or reduce credible intervals. Or, second, these traits are in fact uncorrelated. This result underscores the idea that most studies assume that the same trait is measured between contexts (Watanabe *et al.*, 2012; Carter *et al.*, 2013). However, if the same trait measured in two contexts is not genetically correlated, the traits are indeed different. Caution is thus necessary when personality traits are measured in different contexts because they may not have any underlying genetic correlation and selection may act independently on them.

Testing for underlying genetic, permanent environment or maternal effects is important for understanding whether syndromes act as constraints on adaptive evolution. Few studies have carried this out, and those in the wild are even less common because of the sample size requirements (Bell, 2005; Dingemanse *et al.*, 2007). Our study had large credible intervals suggesting that we did not have the power to detect many of the potential correlations that may be present. However, we did find one genetic correlation underlying our phenotypic correlations, and two were correlated at the environmental level. This finding is consistent with the adaptive hypothesis that the shared environment generates correlations between traits. Although our study does not directly study the adaptive significance of these traits, future studies should investigate how these traits influence fitness. Studies at the phenotypic level suggest an adaptive strategy for syndromes because differences in correlations were found in 12 populations of three-spined sticklebacks (*Gasterosteus aculeatus*) where predation differed between populations (Dingemanse *et al.*, 2007).

In conclusion, this study illustrates the large influence of the environment on behavioural trait variation. Indeed, the magnitude of environmentally caused variation and sometimes larger year effects means that large sample sizes are needed to estimate genotypic/phenotypic correlations in wild populations (Kruuk, 2004). Although our trap-related sample sizes were very large (>7000 trapping events for docility), we conducted substantially fewer OF and MIS experiments, thus limiting our ability to estimate potentially smaller effects and correlations. Nonetheless, with the somewhat smaller sample sizes, we were able to estimate other nongenetic effects in our mixed models. The exact ecological and evolutionary consequences of the personality traits in this study are unknown at this time; however, studies (Smith and Blumstein, 2008) suggest that personality variation has fitness consequences. Future work should focus on understanding the maintenance of variation in personality and identify their consequences on population dynamics.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Table S1** Summary statistics for the entire pedigree and pedigrees informative for docility and the OF/MIS tests.

**Table S2** Principle component analysis results from the open field (OF) and mirror image stimulation (MIS) tests.

**Table S3** Heritability of behaviour ($h^2\ B = V_A/V_P$), heritability of personality ($h^2\ P = V_A/V_{ind}$) where $V_{ind} = (V_A + V_{ME} + V_{PE})$, permanent environment effects ($pe^2 = V_{PE}/V_P$), maternal effects ($m^2 = V_{ME}/V_P$), year effects ($y^2 = V_{YE}/V_P$), residual effects, and repeatability ($r = V_{ind}/V_P$) for docility, activity and exploration in both contexts, and sociability.

**Table S4** Traits, random effects, deviance information criteria (DIC), and delta (Δ) DIC for docility, activity and exploration in OF and MIS tests, and sociability.

**Table S5** Phenotypic variance and covariances between each pair of traits.

**Table S6** Genetic variance and covariances between each pair of traits.

**Table S7** Permanent environment variance and covariances between each pair of traits.

**Table S8** Maternal variance and covariances between each pair of traits.

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