

**1Heritability and genetic correlations of personality traits in a wild population of
2yellow-bellied marmots (*Marmota flaviventris*)**

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18Running head: Genetic (co)variance of personality

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24 Abstract

25 Describing and quantifying animal personality is now an integral part of behavioural
26 studies because individually distinctive behaviours have ecological and evolutionary
27 consequences. Yet, to fully understand how personality traits may respond to selection,
28 one must understand the underlying heritability and genetic correlations between traits.
29 Previous studies have reported a moderate degree of heritability of personality traits but
30 few of these studies have either been conducted in the wild or estimated the genetic
31 correlations between personality traits. Estimating the additive genetic variance and
32 covariance in the wild is crucial to understand the evolutionary potential of behavioural
33 traits. Enhanced environmental variation could reduce heritability and genetic
34 correlations thus leading to different evolutionary predictions. We estimated the additive
35 genetic variance and covariance of docility in the trap, sociability (mirror image
36 stimulation), and exploration and activity in two different contexts (open-field and mirror
37 image simulation experiments) in a wild population of yellow-bellied marmots (*Marmota*
38 *flaviventris*). We estimated both heritability of behaviours and of personality traits and
39 found non-zero additive genetic variance in these traits. We also found non-zero maternal,
40 permanent environment, and year effects. Finally, we found phenotypic, genetic, and
41 permanent environment correlations between several, but not all, traits. Most notably, we
42 found a strong genetic correlation between activity in the open field test and sociability.
43 This is one of a handful of studies to adopt a quantitative genetic approach to explain
44 variation in personality traits in the wild, and thus, provides important insights into the
45 potential variance available for selection.

46

47 Keywords: personality, heritability, behavioral syndromes, quantitative genetics

48

49 **Introduction**

50 Individuals from many taxa have been shown to behave in consistent, individually
51 different ways (Gosling, 2001) – a phenomenon referred to as personality – which may
52 have important ecological and evolutionary consequences (Réale *et al.*, 2007). Within
53 personality research, the maintenance of personality variation is an important question in
54 behavioural ecology and evolution. This is because personality traits may be linked to life
55 history syndromes (Wolf *et al.*, 2007), can have fitness consequences (Smith &
56 Blumstein, 2008), and influence population demography (Armitage, 1986). Personality
57 variation may be maintained because there are multiple optima on a fitness landscape, or
58 because there is fluctuating selection over time or space (Boon *et al.*, 2007). However, in
59 each of these scenarios, personality traits must be heritable to evolve. To understand how
60 personality traits may evolve, it is important to understand the additive genetic variation
61 upon which selection may act. Additionally, many personality traits are phenotypically
62 correlated with each other and create what are referred to as behavioural syndromes (Sih
63 *et al.*, 2004). Such syndromes may constrain selection and prevent the erosion of genetic
64 variation under constant selection (Dochtermann & Dingemanse 2013). Therefore, to
65 understand the potential response to selection of a trait within a population, one must
66 know the heritability of that trait, as well as the constraints generated by genetic
67 correlations (Lande & Arnold, 1983).

68 Few studies have investigated the genetic and environmental sources of
69 (co)variances of behaviour and personality (Stirling *et al.*, 2002) despite the importance

70of these effects on evolution (Falconer & Mackay, 1996; Lynch & Walsh, 1998; Kruuk *et*
71*al.*, 2008). Even fewer studies have estimated the heritability of personality traits in the
72wild, thus we know little about how personality may respond to selection in nature. Lab-
73based estimates seemingly over-estimate heritabilities when compared to the low to
74moderate estimates reported in the wild (van Oers *et al.*, 2005; Sinn *et al.*, 2006; Lea *et*
75*al.*, 2010; Taylor *et al.*, 2012; Niemelä *et al.*, 2013), suggesting that the natural
76environment has a large effect on phenotypes and that phenotypic plasticity is the main
77driver of mean behavioural trait variation. A recent study by Dochtermann *et al.* (2014)
78shows that previous studies did not directly estimate heritability of personality, but rather
79estimated heritability of the behaviour. They suggest that one should estimate heritability
80of personality using the between individual variance (i.e. repeatability) as the
81“phenotypic” variance of the personality trait. Thus, heritability of personality, noted h^2P ,
82is the ratio of additive genetic variance over the variance attributed to the individual, and
83heritability of the behaviour, noted h^2B , is the classic heritability ratio of additive genetic
84variance over total phenotypic variance

85 The formation of phenotypic correlations between personality traits is an active
86area of evolutionary and behavioural ecology (Dochtermann & Roff, 2010; Dochtermann
87& Dingenmanse, 2013). Two hypotheses, constraint and adaptive, are used to explain the
88formation of these syndromes. The constraint hypothesis states that personality traits have
89an underlying genetic or physiological cause (Sih *et al.*, 2004) and that this correlation
90prevents traits from reaching their own independent optima (Dochtermann, 2010). The
91adaptive hypothesis states that natural selection forms these suites of behaviours to be
92adaptive in that population’s specific environment (Bell, 2005; Dingenmanse *et al.*, 2007;

93 Wilson, 1998). Thus, to determine the (co)variance structure of syndromes, we must also
94 understand the potential underlying genetic, maternal, and permanent environmental
95 variance. Detection of genetic correlations may support the constraint hypothesis (Sih *et*
96 *al.* 2004), but knowledge of fitness optima are necessary to determine whether
97 correlations act as constraints on evolution. The presence of maternal or permanent
98 environmental correlations suggests a potential adaptive link between behavioural traits.
99 This is because maternal effects and the environment individuals encounter can shape
100 correlations to have any potential advantage within that specific environment.

101 We quantified the additive genetic, maternal, and permanent environment
102 variances and covariances of four personality traits – docility, activity, sociability, and
103 exploration – in a wild population of yellow-bellied marmots (*Marmota flaviventris*-
104 hereafter referred to as marmots). Behavioural syndromes are hypothesized to have an
105 underlying genetic component (i.e. genetic correlation, Dochtermann *et al.*, 2013). Here
106 we calculate heritability using both the classic method of estimation (Falconer & Mackay,
107 1996), referred as heritability of the behaviour h^2B , as well as the newer method using the
108 ratio of additive genetic variance to repeatability, referred as heritability of personality
109 h^2P (Dochtermann *et al.*, 2014). It should be noted that all previous studies have only
110 estimated h^2B and not h^2P (except for Dochtermann *et al.*, 2014). Like other studies in the
111 wild (Taylor *et al.*, 2012), we expect heritability of the behaviour to be relatively small
112 because of high environmental variation. This estimate should increase when using the
113 newer method because only a subset of the original phenotypic variance is used to
114 calculate the heritability of personality. Although we expect phenotypic correlations

115among and within personality traits, we have no *a priori* hypotheses about the underlying
116architecture of those correlations.

117

118**Methods**

119*Study species and sites*

120Yellow-bellied marmots are large (3-5kg), semi-fossorial, sciurid rodents, native to North
121America, that live in colonies that consist of one or more matrilineal groups (Frase &
122Hoffmann, 1980; Armitage, 2014). Marmots are active from mid-April to mid-October
123and hibernate through the winter (Blumstein *et al.*, 2006). We differentiate three age
124categories: juveniles, which are young of the year; yearlings, individuals that have
125survived their first winter; and adults, individuals that have survived their second winter
126and are reproductively mature. Our study population is located in the upper East River
127Valley, Gunnison, Colorado, the site of Rocky Mountain Biological Laboratory (RMBL),
128Gothic, Colorado (38° 57' 29" N; 106° 59' 06" W). We regularly trap multiple colonies in
129and around the RMBL. This population has been followed since 1962 (Armitage, 2010),
130and the individual behaviour for some traits used in this study has been collected since
1312002 (Petelle *et al.*, 2013).

132

133*Pedigree*

134We assigned parentage using DNA collected from individuals studied from 2002-2012.
135Detailed methods are described in (Blumstein *et al.*, 2010; Olson & Blumstein, 2010).
136Briefly, we extracted DNA using Qiagen QIAamp DNA MINI kits and genotyped
137individuals at 12 microsatellites. Alleles were visualized and scored using

138 GENEMAPPER, and parentage was assigned using CERVUS 3.0 (Kalinowski *et al.*,
139 2007). Juveniles were trapped the first time they emerged out of the maternal burrow.
140 This allowed us to behaviourally match juveniles to mothers. We used CERVUS to
141 confirm maternity and to match paternity to juveniles using a maximum likelihood
142 method at 95% trio confidence. Most marmots were regularly trapped and observed
143 within the population; therefore we assumed a sampling proportion of 99% for candidate
144 mothers and 96% for candidate fathers. Proportion of loci typed was 0.948 and the
145 proportion mistyped was set at 0.01. Since many adult female marmots are philopatric,
146 and therefore potentially highly related, we set the proportion of female marmots related
147 at a level of $R > 0.4$ or higher each year. The differences between the expected
148 assignment rate and the observed assignment rate in CERVUS were never larger than 3%
149 for any cohorts. We also used the software COLONY 2.0 (Wang 2004) to confirm
150 assignments made with CERVUS (Olson & Blumstein, 2010). Since 2002, we have
151 genotyped 1432 individuals from 136 dams and 71 sires (see Supplementary Table 1 for
152 pedigree information).

153

154 *Quantifying Personality*

155 Docility is a commonly measured personality trait, and estimates how an individual
156 reacts to being trapped and handled (Réale *et al.*, 2000; Petelle *et al.*, 2013). We
157 quantified docility in 920 individuals with data collected during 7904 trapping events
158 from 2002 through 2012 (767 individuals had repeated measurements; mean = 4.07;
159 standard deviation = 3.22). At each trapping event we dichotomously (0/1) scored
160 whether individuals struggled in the trap, tooth chattered, alarm called, struggled in the

161 bag, and hesitated to walk into the handling bag. These were summed and subtracted
162 from the total potential score. Thus, an individual who scored 5 is considered docile
163 during that trapping event while an individual who scored 0 is considered non-docile.

164 During the 2010-2012 active seasons, we tested 183 individuals in 508 open-field
165 (OF) and mirror image stimulation (MIS) tests (108 individuals had repeated
166 measurements; mean = 1.97, standard deviation = 1.16). After individuals had been
167 regularly trap processed (weighed, left hind foot measured, sexed, ear tags checked and
168 replaced if required, feces collected if present), they were brought to a shaded arena for
169 testing. Thus, OF and MIS tests were done relatively soon after docility measurements.
170 Full methods for OF and MIS are published elsewhere (Petelle & Blumstein, 2014), but
171 briefly, during the OF test, individuals were placed in an opaque arena measuring 91.4
172 cm³ made of thick PVC sheeting. Individuals were allowed to explore the arena without
173 obstruction for three minutes. Immediately after the first three minutes, and while still in
174 the arena, individuals were presented with a mirror for the MIS test.

175 OF and MIS behaviour was scored using the event recorder JWatcher (Blumstein
176 & Daniel, 2007), which allowed us to quantify the duration and frequency of the
177 following behaviours; walk (quadrupedal and bipedal), look (quadrupedal and bipedal),
178 jump, alarm call, and sniffing/smelling. For MIS only, we also included
179 scratching/pawing at the mirror. We also quantified the number of squares each individual
180 entered and the proportion of squares entered (Petelle & Blumstein, 2014). OF tests are
181 often used to test activity and exploration in personality studies (Carter *et al.*, 2013), and
182 MIS has been used previously with this population to assess sociability (Armitage, 1986),
183 although our specific methods were different. It should be noted that while this is a wild

184 population, these tests are conducted in a non-natural setting (trapping and arena).
185 However, components of docility and the arena tests have been shown to be ecologically
186 relevant (Armitage, 1986; Fuong *et al.*, 2015).

187

188 *Statistical Analysis*

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

193 We estimated additive genetic, permanent environment, maternal, and year effects
194 for the resulting OF and MIS components and docility using an animal model with a
195 Bayesian approach (Wilson *et al.*, 2010; Hadfield, 2010). All traits were fitted with sex
196 and age class. Docility was also fitted with day of the year, days between trials, time (AM
197 or PM), pedestrian traffic, growth rate, and mass as fixed effects. Growth rate and mass
198 were individually centered. Activity (OF) was also fit with days between trials, trial
199 number, and predator presence. Exploration included day of the year and pedestrian
200 traffic. Activity (MIS) also included days between trials, pedestrian and predator
201 presence. These fixed effects had previously been shown to significantly influence
202 personality traits (Petelle *et al.*, in revision). The sociability component had previously
203 not been analyzed, so we included sex, age class, day of the year, pedestrian traffic,
204 predator presence, days between trial, and trial number as fixed effects (see Petelle *et al.*,
205 2013 for methods on the calculation of pedestrian traffic and predator pressure). We
206 estimated additive genetic (V_A , identity link to the pedigree), permanent environment

207(V_{PE} , identity), maternal environment (V_{ME} , mother id), and year (V_Y) variance
208parameters. Variance parameters were estimated as the posterior mode with 95% credible
209intervals based on the posterior distribution of the parameter. The posterior distribution of
210heritability of behaviour was estimated with the equation $h^2B = V_A/V_P$. In this equation V_P
211is the total phenotypic variance conditioned on the fixed effects. The heritability of
212personality (Dochtermann *et al.*, 2014) was estimated with the equation $h^2P = V_A/V_{ind}$.
213Where V_{ind} is the among-individual variation ($V_A + V_{PE} + V_{ME}$) used as the numerator
214when estimating repeatability, $r = V_{ind}/V_P$.a Since variance parameters are bounded above
215zero, we estimated importance of random effects by looking at the deviance information
216criteria (DIC) (Spiegelhalter *et al.*, 2002). DIC is analogous to the Bayesian version of
217Akaike information criterion (AIC). For this reason, we used a delta DIC value under 4
218(Burnham *et al.*, 2011) to identify important random effects. To do so, we removed
219random effects full model and estimated the DIC. Furthermore, to understand how these
220variance changed with the additional random effects, we fitted models with individual,
221maternal, and permanent environment effects removed consecutively (Kruuk *et al.*, 2008;
222Hadfield, 2010). We considered effects with 95% CI excluding zero to be significant.

223 To estimate pairwise correlations between traits, we fitted bivariate models for
224each pair of personality traits and estimated the covariance between traits for each
225random effect. We then rescaled the covariances into correlations.

226 Principle components were calculated in SPSS 18.0 (Chicago, IL). For all other
227analyses, we used the package MCMCglmm (Hadfield, 2010) in R v. 3.1.1 (R
228Development Core Team, 2014). For univariate models, the posterior distribution was
229sampled every 500 iterations with a burning of 30,000 for a total of 1,000 samples. The

230 bivariate models were sampled every 1000 iterations with a burning of 30,000 for a
231 sample of 1,000. We used non-informative inverse-Wishart priors for the (co)variances
232 for all models. For both \mathbf{G} and \mathbf{R} priors, we specified \mathbf{V} as the phenotypic variance
233 divided equally among the random terms and residuals ($\mathbf{V} = \mathbf{V}_p / (\text{number of random}$
234 $\text{effects} + 1)$) and we provided the lowest degree of belief possible while keeping proper
235 prior ($\nu = 0.002$ for univariate models and $\nu = 1.002$ for bivariate models). Mixing of
236 chain was assessed visually and the autocorrelation was < 0.05 for all parameters.

237

238 **Results**

239 *PCA of OF and MIS behaviours*

240 We extracted four and six principle components for OF and MIS tests, respectively
241 (Supplementary Table 2). After reviewing the component loadings, we identified two OF
242 and three MIS components that corresponded with personality traits. The first component
243 in each test was labeled activity, the second and third component of the OF and MIS test,
244 respectively, were identified as exploratory, and the second MIS component was labeled
245 sociability (Supplementary Table 1 for component loadings). The first OF and MIS
246 components, both labeled activity, were characterized by positive loadings of the percent
247 of the squares visited, the number of lines crossed, the total number of jumps, walks, and
248 looks, and the total proportion of time walking. The proportion of time looking was also
249 negative loaded onto the first OF component. The second OF and third MIS component,
250 labeled exploration, were described by positive loadings of number of sniffs/smells and
251 the proportion of time spent smelling. Finally, the second MIS component, labeled
252 sociability, was characterized by the positive loading of proportion of time spent at the

253 mirror, and negatively associated with latency to approach the mirror and proportion of
254 time looking. The two OF components explained approximately 52% of the variance
255 while the three MIS components explained 56%.

256

257 *Univariate decomposition of the variance*

258 All full models fell within a delta DIC of 4, and thus were equally plausible as the best
259 model (Burnham *et al.*, 2011) (Supplementary Table 3). We found non-zero heritability in
260 all of our traits (0.025 – 0.145) (see Figure 1; Table 1). Not surprisingly, our estimates of
261 heritability increased greatly when repeatability was used instead of phenotypic variance
262 to calculate heritability of personality (0.126 – 0.575), and in some cases increased an
263 order of magnitude (Table 1).

264 The variation attributed to the permanent environment, maternal, and year effects were
265 also small in most cases, but were non-zero for all traits (Figure 1; Table 1).

266

267 *Estimation and decomposition of covariances among personality traits*

268 We found a number of phenotypic correlations (i.e. behavioural syndromes) among
269 personality traits. As expected, we found a positive phenotypic correlation between
270 activity in the OF and MIS tests ($r_p = 0.571$; 95% CI = 0.303 to 0.741). We also found a
271 positive correlation between sociability and activity in both OF and MIS (OF
272 activity/sociability: $r_p = 0.483$; 95% CI = 0.107 to 0.708 and MIS activity/sociability: $r_p =$
273 0.392; 0.132 to 0.698). We found a positive correlation between docility and exploration
274 in the MIS context ($r_p = 0.348$; 95% CI = 0.069 to 0.624). Finally, we found one negative

275 correlation between activity in the OF test and docility ($r_P = -0.348$; 95% CI = -0.581 to
276 -0.028) (Table 2).

277 We then investigated the potential genetic, permanent environment, and maternal
278 correlations that may be the underlying cause of these phenotypic correlations. We found
279 only one significant genetic correlation – activity in the OF test and sociability ($r_G =$
280 0.673 ; 95% CI = 0.005 to 0.833) (Table 2). We did, however, find a number of near
281 significant correlations (asterisked in Table 2), which may indicate a power limitation of
282 our data. We also found a number of permanent environmental correlations between
283 activity in the OF and MIS tests ($r_{PE} = 0.641$; 95% CI = 0.095 to 0.862), and,
284 interestingly, between docility and exploration in the MIS test (0.521; 0.070 to 0.806)
285 (Table 2). We found no maternal correlations (Table 2). It should be noted that there are a
286 number of phenotypic, genetic, and permanent environment correlations that are
287 moderate to high but were not significant because of large 95% confidence intervals.
288 Variance and covariance estimates are given in the supplementary tables.

289

290 Discussion

291 We have five main results. First, all of the personality traits we investigated have low but
292 significant heritability indicating their evolutionary potential. Second, this heritability
293 increased greatly when using repeatability as the denominator so that we could estimate
294 the heritability of personality. Although this is not surprising, since the denominator is
295 much smaller, it does highlight that previous estimates of heritability of personality are
296 lower than their true value. Third, there are a number of distinct phenotypic correlations
297 indicating the existence of behavioural syndromes. Fourth, genetic correlations among

298 personality traits (Table 2) indicate the existence of potential genetic constraints on
299 adaptive evolution. Fifth, the existence of permanent environmental correlations indicates
300 that the environment marmots were reared in has coupled the traits together. Thus, these
301 traits in marmots could evolve further, but the underlying genetic and permanent-
302 environment correlations would constrain their evolutionary dynamics.

303 This is the first study of free-living animals, to our knowledge, that calculates
304 both heritability of a behaviour and heritability of personality. Our heritability of
305 behaviour estimates are qualitatively similar when compared with previous studies (Sinn
306 *et al.*, 2006; Taylor *et al.*, 2012). Moreover, while previous estimates of heritability of
307 behaviour varied widely, heritability estimates are generally smaller when estimated in
308 the wild than in captivity (Sinn *et al.*, 2006; Taylor *et al.*, 2012; Niemelä *et al.*, 2013). For
309 example, as in our study, Taylor *et al.* (2012) found low heritability in docility ($h^2 =$
310 0.09), aggression ($h^2 = 0.12$), and activity ($h^2 = 0.08$) in wild red squirrels (*Tamiasciurus*
311 *hudsonicus*). Low heritability might suggest that these traits are under stabilizing or
312 directional selection by being linked to fitness and that genetic variation has been eroded
313 (Falconer & Mackay, 1996; Kruuk *et al.*, 2000), an equally likely hypothesis is that
314 residual and phenotypic variances covary and this reduces heritability estimates (Stirling
315 *et al.*, 2002). When using the Dochtermann *et al.* (2014) approach to estimate heritability
316 of personality, our estimates of heritability increased. Our estimates of repeatability were
317 all moderate (Bell *et al.*, 2009) and significant, suggesting that among individual
318 variation is important in this population. Furthermore, this result underscores the fact that
319 genes have a moderate to large influence on personality.

320 Similarly to previous studies (Réale *et al.*, 2009; Taylor *et al.*, 2012), we found
321 that permanent-environment effects are present for these traits suggesting that the
322 consistent environment potentially plays a much larger role in accounting for phenotypic
323 variation than the underlying genes (see also Blumstein *et al.*, 2013). Female marmots are
324 philopatric (Armitage, 1984) and experience the same environment throughout life. The
325 overall quality of this habitat may have long-term consequences on these traits. We also
326 found small maternal effects in docility ($m^2 = 0.05$), exploration (0.04), and sociability
327 (0.05). Maternal effects can have long-term consequences on individuals (Reinhold,
328 2002; Weaver *et al.*, 2004; Räsänen & Kruuk, 2007). Activity, exploration, and sociability
329 are important parameters that may effect dispersal, and previous work in our system
330 found that more social or well-connected female marmots are more likely to remain in
331 their natal colony (Armitage, 1986; Blumstein *et al.*, 2009). The exact ecological function
332 of docility has yet to be tested in this species, however we, and others, have found that
333 maternal stress response influences offspring personality (Petelle *et al.*, *in prep.*; Hinde *et*
334 *al.*, 2012).

335 We found a number of traits correlated at the phenotypic level, with underlying
336 environmental or genetic correlations. Activity was correlated at both the phenotypic and
337 permanent environment level between the OF and MIS test as expected if tests are
338 measuring the same traits. The absence of significant genetic correlation might reflect the
339 sample size. Exploration however was not correlated between OF and MIS suggesting
340 that the tests might have measured different trait (Watanabe *et al.*, 2012; Carter *et al.*,
341 2013). Activity was also positively correlated at the phenotypic and the genetic level (OF
342 test) with sociability. This correlation could arise if more active individuals are coming

343 into contact with more individuals, or because there is a high degree of betweenness
344 among different social groups (Krause *et al.*, 2010). Betweenness is a social network
345 metric that measures the centrality of an individual based on the shortest paths between
346 pairs of individuals in that group. Thus, if an individual connects two groups and has
347 connections within each group, they have a high level of betweenness (Wey *et al.*, 2008).

348 Additionally, the phenotypic correlation between activity (OF) and sociability is
349 in the same direction and general magnitude as the genetic correlation (0.483 to 0.673
350 respectively) (Cheverud, 1988; Dochtermann, 2011). Although we cannot directly test the
351 phenotypic gambit (Hadfield *et al.*, 2007) due to our large credible intervals, it is
352 important to note that phenotypic correlations are not always good indicators of genetic
353 correlations because permanent environment and maternal effects may obscure such a
354 correlation.

355 We found a negative phenotypic correlation between activity in the OF test and
356 docility. This makes sense because docility is partly calculated from active behaviors
357 while in the trap and being handled (struggling in trap or bag). Thus, more active
358 individuals in the OF test may also be more active in the trap and therefore receive lower
359 docility scores. In contrast, docility and exploration in the MIS test were positively
360 correlated. Given that docility is the first behaviour scored and MIS the last test
361 performed, this correlation may indicate that docile individuals are more thoroughly
362 explorative given enough time passes, or vice versa, non-docile individuals become less
363 explorative as the tests transition from OF to MIS.

364 Although many of the phenotypically-correlated traits did not have an underlying
365 genetic correlations, we did find moderate, but non-significant genetic and permanent

366environment correlations. This suggests two possible explanations. First, that these traits
367are in fact correlated at the genetic or permanent environmental levels and we do not
368have sufficient power to estimate correlations or reduce confidence intervals. Or, second,
369these traits are in fact uncorrelated. This first explanation is more likely because we found
370large, but nevertheless non-significant genetic correlations. This was due, again, to our
371large credible intervals. This result, however, underscores the idea that most studies
372assume that the same trait is measured between contexts (Watanabe *et al.*, 2012; Carter *et*
373*al.*, 2013). However, if the same trait measured in two contexts is not genetically
374correlated, the traits are indeed different. Caution is thus necessary when personality
375traits are measured in different contexts because they may not have any underlying
376genetic correlation and selection may act independently on them.

377 Testing for underlying genetic, permanent environment, or maternal effects is
378important for understanding whether syndromes act as constraints on adaptive evolution.
379Few studies have done so, and those in the wild are even less common because of the
380sample size requirement (Bell, 2005; Dingemanse *et al.*, 2007). Our study had large
381confidence intervals suggesting that we did not have the power to detect many of the
382potential correlations that may be present. However, we did find one genetic correlation
383underlying our phenotypic correlations, and two were correlated at the environmental
384level. This finding is consistent with the adaptive hypothesis that the shared environment
385generates correlations between traits. Although our study does not directly study the
386adaptive significance of these traits, future studies should investigate how these traits
387influence fitness. Studies at the phenotypic level suggest an adaptive strategy for
388syndrome because differences in correlations were found in 12 populations of three-

389spined sticklebacks (*Gasterosteus aculeatus*) where predation differed between
390populations (Dingemanse *et al.*, 2007).

391 In conclusion, this study illustrates the large influence of the environment on
392behavioural trait variation. Indeed, the magnitude of environmentally-caused variation
393means that large sample sizes are needed to estimate genotypic/phenotypic correlations in
394wild populations (Kruuk, 2004). While our trap-related sample sizes were very large
395(>7000 trapping events), we conducted substantially fewer OF and MIS experiments,
396thus limiting our ability to estimate potentially small effects. Nonetheless, with those
397somewhat smaller samples sizes we were able to estimate other non-genetic effects in our
398mixed models, which further highlights the relatively small amount of genetic variation
399in these traits. The exact ecological consequences of the personality traits in this study are
400unknown at this time. Future work should focus on understanding the maintenance of
401variation in personality and identify their consequences on population dynamics.

402

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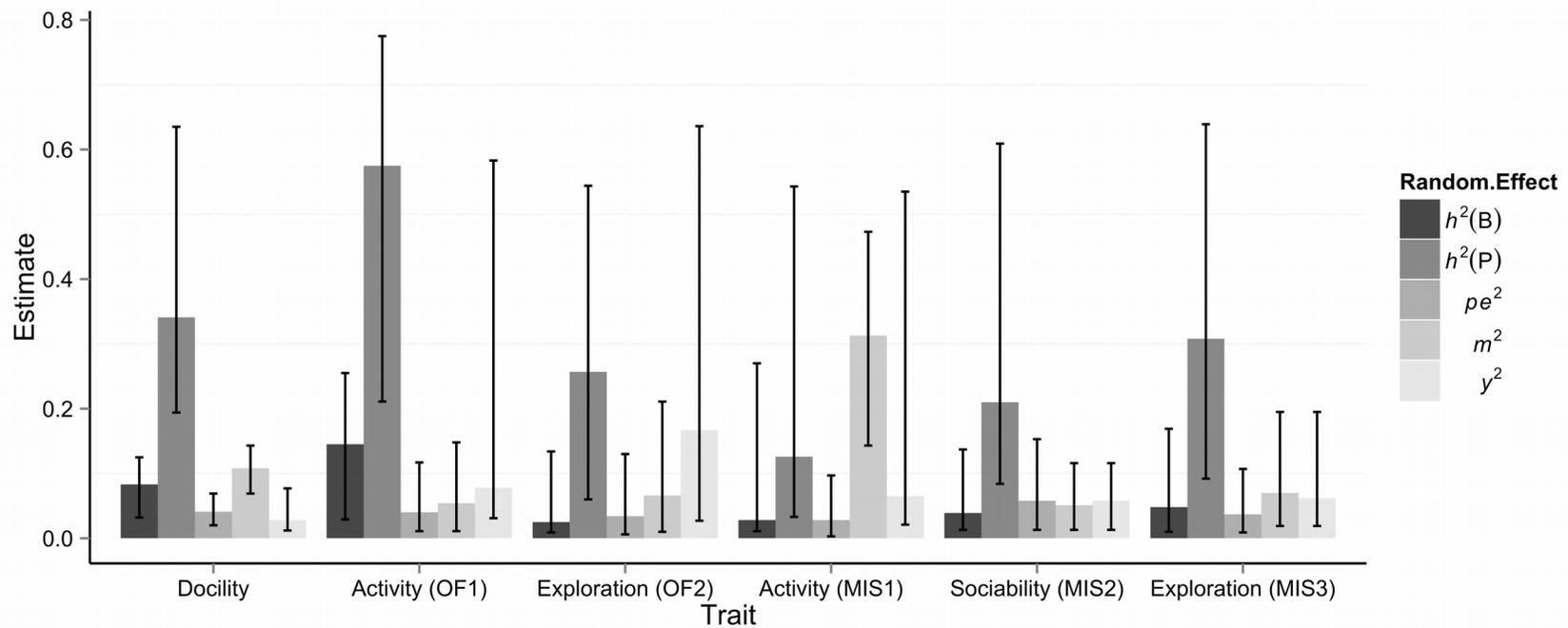
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568 Figure 1.

569 Proportion of variance explained by additive genetic variance of the behavior ($h^2(B) = V_A/V_P$) and personal-
570 ity ($h^2(P) = V_A/r$), permanent environment effects ($pe^2 = V_{PE}/V_P$), maternal effects ($m^2 = V_{ME}/V_P$), and year
571 effects ($y^2 = V_{YE}/V_P$) for each personality trait. The posterior mode is reported as the estimate and the
572 equivalent of the 95% confidence interval are illustrated.



573

574 **Table 1.**

575 Heritability of behaviour ($h^2 B = V_A/V_P$), heritability of personality ($h^2 P = V_A/r$), permanent environment effects ($pe^2 = V_{PE}/V_P$),

576 maternal effects ($m^2 = V_{ME}/V_P$), year effects ($y^2 = V_{YE}/V_P$), residual effects, and repeatability ($r = (V_A + V_D + V_{PE})/V_P$) for docility,

577 activity and exploration in both contexts, and sociability. All effects are estimated from the posterior mode in the univariate models

578 and are given with the equivalent of 95% credible intervals in parentheses.

Trait	$h^2 B$	$h^2 P$	pe^2	m^2	y^2	Residual	Repeatability
Docility	0.083 (0.032 to 0.125)	0.341 (0.194 to 0.635)	0.108 (0.069 to 0.143)	0.041 (0.020 to 0.069)	0.028 (0.012 to 0.077)	0.738 (0.685 to 0.777)	0.186 (to 0.221)
Activity (OF1)	0.145 (0.029 to 0.255)	0.575 (0.211 to 0.775)	0.054 (0.011 to 0.148)	0.040 (0.011 to 0.117)	0.078 (0.031 to 0.583)	0.567 (0.254 to 0.729)	0.241 (to 0.392)
Exploration (OF2)	0.025 (0.009 to 0.134)	0.257 (0.060 to 0.544)	0.066 (0.010 to 0.211)	0.034 (0.006 to 0.130)	0.167 (0.027 to 0.636)	0.574 (0.242 to 0.759)	0.186 (to 0.374)
Activity (MIS1)	0.028 (0.011 to 0.270)	0.126 (0.033 to 0.543)	0.313 (0.143 to 0.473)	0.028 (0.003 to 0.097)	0.065 (0.021 to 0.535)	0.404 (0.183 to 0.545)	0.481 (to 0.600)
Sociability (MIS2)	0.039 (0.013 to 0.137)	0.210 (0.084 to 0.609)	0.051 (0.013 to 0.116)	0.058 (0.013 to 0.153)	0.058 (0.013 to 0.116)	0.709 (0.436 to 0.823)	0.182 (to 0.323)
Exploration (MIS3)	0.048 (0.010 to 0.169)	0.308 (0.092 to 0.639)	0.070 (0.019 to 0.195)	0.037 (0.009 to 0.107)	0.062 (0.019 to 0.195)	0.628 (0.346 to 0.806)	0.239 (to 0.378)

579

580**Table 2.**

581Phenotypic, genetic, permanent environment, and maternal correlations between each pair of personality traits. All correlations are
 582given with 95% credible intervals. Significant correlations are in bold.

Personality Traits	Phenotypic Correlation	Genetic Correlation	Permanent Environment Correlation	Maternal Correlation
Docility/ Activity (OF1)	-0.348 (-0.581 to - 0.028)	-0.408 (-0.731 to 0.212)	-0.497 (-0.724 to 0.103)*	-0.351 (-0.673 to 0.232)
Docility/ Exploration (OF2)	0.112 (-0.233 to 0.403)	-0.023 (-0.632 to 0.488)	0.209 (-0.276 to 0.606)	-0.021 (-0.485 to 0.478)
Docility/ Activity (MIS1)	-0.179 (-0.447 to 0.075)	-0.064 (-0.688 to 0.457)	-0.104 (-0.571 to 0.260)	-0.329 (-0.688 to 0.207)
Docility/ Sociability (MIS2)	0.046 (-0.342 to 0.322)	-0.223 (-0.460 to 0.561)	-0.158 (-0.617 to 0.380)	-0.105 (-0.589 to 0.306)
Docility/ Exploration (MIS3)	0.348 (0.069 to 0.624)	0.191 (-0.383 to 0.653)	0.521 (0.070 to 0.806)	-0.247 (-0.620 to 0.271)
Activity (OF1)/ Explo- ration (OF2)	-0.330 (-0.584 to 0.051)	-0.139 (-0.736 to 0.377)	-0.493 (-0.752 to 0.104)	-0.028 (-0.585 to 0.486)
Activity (OF1)/ Activ- ity (MIS1)	0.571 (0.303 to 0.741)	0.660 (-0.134 to 0.890)	0.641 (0.095 to 0.862)	0.314 (-0.184 to 0.764)
Activity (OF1)/ Socia- bility (MIS2)	0.483 (0.107 to 0.708)	0.673 (0.005 to 0.833)	0.497 (-0.199 to 0.740)	0.126 (-0.275 to 0.754)
Activity (OF1)/ Explo- ration (MIS3)	0.049 (-0.367 to 0.359)	0.302 (-0.518 to 0.605)	-0.309 (-0.610 to 0.486)	0.039 (-0.427 to 0.590)
Exploration (OF2)/ Activity (MIS1)	-0.199 (-0.494 to 0.204)	-0.314 (-0.615 to 0.646)	-0.322 (-0.747 to 0.272)	0.044 (-0.573 to 0.555)

Exploration (OF2)/ Sociability (MIS2)	0.099 (-0.376 to 0.420)	-0.008 (-0.528 to 0.586)	-0.132 (-0.557 to 0.568)	0.342 (-0.529 to 0.647)
Exploration (OF2)/ Exploration (MIS3)	0.394 (-0.077 to 0.631)	0.271 (-0.377 to 0.720)	0.439 (-0.144 to 0.805)*	0.230 (-0.380 to 0.708)
Activity (MIS1)/ So- ciability (MIS2)	0.392 (0.132 to 0.698)	0.549 (-0.233 to 0.833)	0.539 (-0.057 to 0.820)*	0.200 (-0.406 to 0.741)
Activity (MIS1)/ Ex- ploration (MIS3)	-0.401 (-0.615 to 0.037)*	-0.276 (-0.838 to 0.342)	-0.624 (-0.799 to 0.196)	0.120 (-0.563 to 0.548)
Sociability (MIS2)/ Exploration (MIS3)	-0.079 (-0.384 to 0.380)	0.085 (-0.657 to 0.480)	-0.120 (-0.492 to 0.570)	-0.333 (-0.642 to 0.509)

583

584