

1 **Development of boldness and docility in yellow-bellied marmots**

2 **Matthew B. Petelle^a, Dakota E. McCoy^{b,c}, Vanessa Alejandro^c, Julien G. A.**

3 **Martin^{a,d}, Daniel T. Blumstein^{a,c}**

4

5 *^aDepartment of Ecology & Evolutionary Biology, University of California Los Angeles,*
6 *CA USA*

7 *^bDepartment of Ecology & Evolutionary Biology, Yale University, New Haven, CT USA*

8 *^cThe Rocky Mountain Biological Laboratory, Crested Butte, CO USA*

9 *^dSchool of Biological Sciences, University of Aberdeen, Aberdeen, UK*

10

11 ^aCorrespondence: M Petelle, Department of Ecology & Evolutionary Biology, University
12 of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA

13 Tel: +1-310-267-4630

14 Fax: +1-310-206-3987

15 E-mail: mpetelle@ucla.edu

16

17 Word Count: 6703

18

19 Running head: Personality development

20 Personality traits are important because they can affect individual survival as well as how
21 a population may respond to environmental change. How these traits arise, whether they
22 are maintained throughout ontogeny, and how environmental factors differentially affect
23 them throughout life is poorly understood. Understanding these pathways is important for
24 determining the function and evolution of animal personality. We examined the
25 development of two commonly studied personality traits—boldness and docility—in a
26 long-term study of yellow-bellied marmots (*Marmota flaviventris*). Using data collected
27 between 2002 and 2011, we quantified the repeatability within three age groups
28 (juveniles, yearlings, and adults), the correlation between age-classes, and the
29 behavioural syndromes of these two traits within the three life stages. We quantified
30 boldness through Flight Initiation Distance (FID) tests, and we quantified docility
31 through marmots' response to being trapped. We found that boldness is repeatable only in
32 yearlings, but docility is repeatable in all age classes. We also found that juvenile docility
33 predicted later docility. We also found no behavioural syndrome between boldness and
34 docility in any life stage. This suggests an adaptive hypothesis: that these personality
35 traits develop independently and at potentially age-appropriate times. Thus, the
36 development of personality traits may facilitate animal's coping with age-dependent
37 requirements and constraints.

38

39 *Keywords:* ontogeny of personality, yellow-bellied marmots, boldness, docility,
40 behavioural syndrome

41

42 Personality, which is inferred from consistent individual differences in behaviour, can
43 have a profound effect on a population's evolutionary and ecological dynamics
44 (Dingemanse et al. 2004; Réale et al. 2007; Pruitt et al. 2012). Most studies of animal
45 personality, however, focus on short time periods or one life stage. This focus provides a
46 limited view of how personality interacts with physiology, life stage, experience, and the
47 environment (Stamps & Groothuis 2010). Indeed, an ontogenetic perspective provides a
48 more comprehensive understanding of the function and evolution of personality (Stamps
49 & Groothuis 2010).

50 Previous studies on the development of personality have focused primarily on
51 quantifying repeatability with maternal effects (Groothuis et al. 2008; Rödel & Meyer
52 2011), early experience (DiRienzo et al. 2012), or across life stages (Bell & Stamps 2004;
53 Sinn et al. 2008; Gyuris et al. 2012; Wilson & Krause 2012). For example, three-spined
54 sticklebacks (*Gasterosteus aculeatus*) were tested for stability in multiple personality
55 traits across life stages (Bell & Stamps 2004). The authors found little stability in single
56 personality traits across life stages, but that a syndrome, boldness and aggression, was
57 consistently detected across ontogeny (Bell & Stamps 2004). In that study, stability was
58 inferred from a positive correlation between juvenile and adult personality traits. Thus,
59 individuals with stable personality traits maintained the same level of aggression or
60 boldness relative to others across ontogeny. Studies that focused on repeatability within
61 life stages showed mixed results. Individual dumpling squid (*Euprymna tasmanica*) were
62 repeatable in their level of boldness as juveniles, but this repeatability disappeared for a
63 period upon sexual maturation and reappeared in adulthood (Sinn et al. 2008). During the
64 period of sexual maturity, and depending on their behavioural type, squid were more

65 plastic in certain ecologically relevant contexts. For example, shy individuals were
66 more plastic in a feeding context than bolder individuals. Conversely, repeatability was
67 present within life stages in both firebugs (*Pyrrhocoris apterus*) (Gyuris et al. 2012) and
68 lake frogs (*Rana ridibunda*) (Wilson & Krause 2012).

69 These studies suggest that personality traits, in some species, are plastic within or
70 between life stages. Thus, juvenile personality may not always predict adult personality
71 and plasticity may increase within a life stage whereby individuals may change their level
72 of a particular personality trait. This low repeatability might be seen in certain life stages
73 because individuals may experience differential selection over time, selection may favor
74 plasticity (opportunity for multiple alternative strategies), or there may be a single best
75 strategy for a given a set of environmental conditions (Fox & Westneat 2010). Thus, it is
76 important to understand the development of personality and how these traits interact
77 within and between life stages.

78 Here we capitalize on a long-term ecological study of yellow-bellied marmots
79 (*Marmota flaviventris*) to investigate repeatability and the stability (i.e. correlation at the
80 individual level) within and across three life stages for boldness and docility traits.
81 Previous research on yellow-bellied marmots shows that personality traits exist in both
82 yearling and adult individuals and can influence fitness (Svendson & Armitage 1973;
83 Svendson 1974; Armitage 1986; Armitage & Van Vuren 2003). Thus, we hypothesise
84 that all three age categories will exhibit these two personality traits. We do not have *a*
85 *priori* hypotheses about the stability of these traits across ontogeny or whether there is a
86 behavioural syndrome between the two. Additionally, our new and extensive data set
87 allows us to understand how environmental variables affect personality at different life

88 stages. Thus, our first aim was to understand how repeatability varies between life stages.
89 Our second aim was to investigate whether juvenile personality levels predict yearling
90 and adult personality levels (that is, the longitudinal stability of these personality traits).
91 Our third aim was to describe whether a behavioural syndrome exists and is stable
92 between boldness and docility across these same life stages. Our last aim was to explore
93 how an individual's current state and environment affect personality within life stages
94 (Brydges et al. 2008; Luttbeg & Sih 2010).

95

96 **METHODS**

97 *Study Subjects and Site*

98 Between 2002 and 2011, we studied yellow-bellied marmots in the Upper East
99 River Valley, in and around the Rocky Mountain Biological Laboratory in Gothic,
100 Colorado, USA (38 77'N, 106 59'W). Yellow-bellied marmots are facultatively social,
101 sciurid rodents, which weigh between 2-6 kg, live in matrilineal groups and dwell in
102 subalpine meadows, slopes, and clearings (Frase & Hoffmann 1980). The Upper East
103 River valley is divided in two parts, up- and down-valley, that differ in elevation,
104 phenology, and human disturbance. Three of the colonies were located up-valley while
105 four were down-valley. Marmots were trapped on a regular basis using Tomahawk live
106 traps and individually marked with numbered ear tags for permanent identification and
107 fur dye to facilitate identification from afar (Armitage 1982; Blumstein et al. 2009).
108 Almost all of the individuals were trapped for the first time as juveniles and thus were of
109 known age. Juveniles are individuals in their first summer of life; yearlings, or one year

110 olds, are in their second summer of life; adults are two years or older (Armitage &
111 Downhower 1974).

112

113 *Quantifying Environmental Factors*

114 Marmots are seasonally active and we study them in a valley that is used for
115 summer tourism. We quantified human presence for 12 days during the peak summer
116 months of 2010 by continuously recording pedestrian activity within 300 m of six
117 colonies (Li et al. 2011). Human traffic was not quantified in some colonies where
118 personality data were collected, but our previous study showed that more humans were
119 present at our down-valley sites (including those sites where impact was not specifically
120 quantified) than our up-valley sites. Thus, we averaged human visitation in two down
121 valley colonies and four up valley colonies, and used these average values for
122 unquantified colonies (down valley-Bench, Avalanche, and River); we believe that these
123 averages provide a good approximation of human disturbance in unstudied colonies. We
124 used these averages for all years because, while not precisely quantified, human
125 disturbance seemed not to change much between years (hiking and biking trails remained
126 the same throughout the duration of data collection for this study; tourism was steady).

127 Predator presence was quantified from 2002-2011 by dividing the number of
128 predators seen during observations at a colony by the total number of observation
129 sessions at that colony. We used predator sightings only during early season (mid-April
130 through June) because predators become harder to view as vegetation grows during the
131 active season. We also quantified the number of predators seen per hour of observation to
132 test whether there were any differences between indexes. The indexes were highly

133 correlated ($r_p = 0.961$; $P < 0.001$) indicating no bias in the number of predators seen per
134 observation session. A total of 203 aerial predators and 292 terrestrial predators were
135 seen during this time.

136

137 *Quantifying Boldness With Flight Initiation Distance*

138 To assess boldness, we conducted 563 Flight Initiation Distance (FID)
139 experiments on 237 individuals (86 juveniles; 81 yearlings; 70 adults) from 2003-2011.
140 FID is the distance at which an individual first flees from an approaching human
141 (Ydenberg & Dill 1986; Blumstein 2003), and is an antipredator behaviour that is
142 commonly used as a metric for individual boldness (Cooper 2009). It should be noted that
143 FID is inversely related to boldness; bold individuals have short FIDs whereas shy ones
144 have large FIDs. Thus we used the opposite (i.e. we made the values negative) of the FID
145 to obtain an index positively related to boldness.

146 After arriving at a site, the researcher sat, quietly observed, and identified
147 subjects for ≥ 5 min. Once a target subject was identified, the observer walked directly
148 towards the marmot at a constant pace. Observers were trained until they consistently
149 walked at a 0.5 m/s pace across a variety of terrains (Runyan & Blumstein 2004). We
150 recorded when an individual first raised its head and looked toward the researcher (alert
151 distance), when the marmot first fled (FID), the distance from marmot to researcher when
152 the trial began (start distance), the distance from the marmot to the burrow when it fled
153 (burrow distance), and the individual's initial behaviour (forage, look, other; "look"
154 implies that the marmot was looking at the researcher). All distances were first marked
155 with flags dropped during the trial and calculated afterwards by pacing. Individual pace

156 length was calculated during training. The researcher waited at least 10 min before
157 conducting another trial on a different subject. Individual marmots were tested no more
158 than once per observation session (AM/PM sessions).

159

160 *Quantifying Docility With Trapping Behaviour*

161 Docility was assessed during 8217 trapping events for 861 juveniles, 445
162 yearlings, and 266 adults from 2002-2011. We use the description of docility set forth by
163 Réale et al. (2000). Docility here is defined as an individual's reaction to being trapped
164 and handled. Docility is a commonly used metric of personality and is often used as a
165 measure of risky behaviour (Réale et al. 2007; Réale et al. 2009; Careau et al. 2010).

166 When trapped, marmots were transferred to a cloth, handling bag for subsequent
167 processing. At each trapping event, we recorded behaviours the marmot exhibited in the
168 trap prior to being put in the trap bag. We dichotomously (i.e. 0/1) scored whether or not
169 individuals: emitted alarm calls, tooth chattered, struggled in the trap, bit the cage, and
170 whether they failed to immediately walk into the handling bag. Following Réale et al.
171 (2000), we summed the dichotomously scored behaviours and subtracted this from the
172 total potential score. A score of 0 thus indicates a non-docile individual, and inversely a
173 score of 5 indicates a docile individual.

174

175 *Statistical Analyses*

176 *Age-specific repeatability and environmental effects*

177 We first analyzed each life stage separately to estimate the age specific
178 repeatability of the behaviours and to determine the environmental effects specific at each

179 age class. We fitted univariate linear mixed effects models (i.e. one dependent variable
180 with multiple fixed and random effects; Dingemanse & Dochtermann 2013) for both
181 behaviours (boldness and docility) for each age class (juvenile, yearling, and adult). For
182 all models, individual identity and year were fitted as random effects to assess both
183 personality and yearly environmental variation, respectively. Repeatability was estimated
184 as the ratio of the variance associated with the individual identity effect divided by the
185 total phenotypic variance (i.e. sum of individual, yearly and residual variances), a
186 significant repeatability indicating personality. Additional fixed effects were fitted and
187 are described below.

188 Fixed effects of flight initiation distance (boldness) included trial number per
189 individual, trials done each day at the colony level, time (days) between trials, start and
190 alert distances, the distance from the marmot to the burrow, sex, time of day (AM or
191 PM), pedestrian traffic, predator presence, estimated mass on 15 August, estimated mass
192 gain from 1 June to 15 August, initial behaviour, and date. Trial number and the number
193 of trials conducted at a colony per day were included to control for potential habituation
194 effects. Time between trials was included to control for potential biases in repeatability
195 (Bell et al. 2009). We included start distance and alert distance and the initial distance to
196 a burrow because previous research has shown it has an effect on FID (start and alert:
197 Blumstein 2010; distance to refuge: Dill & Houtman 1989). We included mass at 15
198 August and mass gain as proxies for body condition and growth rate, respectively. Both
199 measures have theoretically been shown to influence personality (Stamps 2007; Biro &
200 Stamps 2008; Luttbeg & Sih 2010). We used mass at capture as a measure of body
201 condition. We included initial behaviour because it could influence when individuals

202 become alert to possible predators. To control for effects from the progression of the day
203 and season we included time of day and the date. Flight initiation distance was square
204 root transformed prior to analyses to conform to the normality of residuals assumption of
205 linear models. Fixed effects of docility were time (days) between trapping, sex, time of
206 day (AM or PM), date, pedestrian traffic, predator presence, mass gain, and mass at
207 capture. Sex was included to control for potential differences between males and females.
208 Time of day and date were included because of differences within day and throughout the
209 active season.

210 We used a log-likelihood ratio test (LRT, estimated as minus twice the difference
211 in the likelihood of the nested models) to determine the significance of random effects
212 between models with and without a given random effect (Pinheiro & Bates 2000). The
213 LRT statistic follow a χ^2 distribution with difference in number of parameters between
214 the two models as degree of freedom (Pinheiro & Bates 2000). Univariate linear mixed-
215 effects models were fitted in R 2.14 (R Development Core Team 2011) with the lmer
216 function in the lme4 package (Bates et al. 2012). We reported full models after extracting
217 parameter estimates and MCMC *P*-values using the pvals.fnc function in the package
218 languageR (Baayen et al. 2008) based on a Markov chain Monte Carlo sampling with
219 30,000 simulations.

220

221 *Correlation between life stages and between behaviours*

222 To estimate the correlations, or stability, between juvenile, yearling, and adult
223 behaviours at the individual level, we fitted trivariate mixed models (i.e. 3 dependent
224 variables with multiple fixed and random effects; Dingemanse & Dochtermann 2013) for

225 each behaviour considering each age class as a different trait. Individual identity and year
226 were fitted as random effects with an unstructured 3x3 (co)variance matrix estimating
227 three variance components (one for each trait) and their three pairwise covariances.
228 Correlations were then calculated from the (co)variance matrix as the rescaled covariances
229 (i.e. covariance between two traits divided by the square-root of the product of the
230 variances of the two traits). The residual matrix was constrained to be a 3x3 diagonal
231 matrix because of the structure of our data. To test if variance components were different
232 between the three age classes, a LRT between models with and without constraints of
233 equality of variance components for the three age-classes was used. We used a similar
234 test for pairwise comparison of variance components but constraining only two age-
235 classes at a time to be equivalent. Significance of behavioural correlations at the
236 individual level between age-classes was estimated using a LRT between models with
237 and without a covariance parameter constrained to zero.

238 To identify the presence of age-specific behavioural syndromes, we estimated the
239 correlation between both behaviours at the individual level using bivariate mixed models
240 of boldness and docility for each age category. Individual identity and year were fitted as
241 random effects. Each random effect was specified with an unstructured 2x2 (co)variance
242 matrix thus estimating two variances (one for each behaviour) and their covariance. The
243 residual variance matrix was fitted as a diagonal matrix (i.e. covariance fixed to zero)
244 because of the structure of our data. The significance of the behavioural syndrome was
245 estimated using a LRT between models with and without the covariance between docility
246 and boldness fixed to zero.

247 Only fixed effects that were significant in univariate analyses were included in
248 multivariate analyses to avoid overparametrisation of models and facilitate convergence.
249 The sample size for multivariate models is a combination of the sample size reported in
250 Table 1 for univariate analysis (i.e. sample size for trivariate analysis of boldness is the
251 sum of the three sample size for age-specific models of boldness). Correlations estimated
252 in multivariate analysis, however, were estimated at the individual level meaning that
253 only individuals with data for both traits provided information for the correlation. We
254 thus reported the number of individuals as the sample size for correlation estimates.
255 Multivariate analyses were fitted using ASREML-R 3.0 (Gilmour et al. 2009).

256

257 **Ethical Note**

258 Marmots were studied under protocols approved by the UCLA and the RMBL
259 Animal Use and Care Committees (UCLA #2001-191-01 renewed annually) and under
260 permits issued annually by the Colorado Division of Wildlife (TR917 issued annually).
261 After trapping, individuals were released immediately at the trap location. Marmots were
262 in traps no longer than 2-3 hours, and typically much less time. Traps were shaded with
263 vegetation on warm days. Marmot handling was brief (typically between 5-15 min
264 depending upon what data needed to be collected) and marmots were not injured during
265 this handling. All marmots were handled while inside of a cone cloth-handling bag to
266 reduce stress. We swabbed ears before tagging individuals to reduce the chance of
267 infection. FID trials are a widely used measure of risk assessment that causes only a
268 transient change in behaviour.

269

270 **RESULTS**

271 *Environmental factors*

272 In boldness, we found that environmental factors affected juveniles, yearlings,
273 and adults differently. For juveniles, boldness increased as predator pressure increased.
274 Additionally, juvenile boldness increased in the afternoon. As expected, juveniles fled
275 sooner if they alerted sooner (Table 1).

276 Yearling boldness increased as predator pressure increased. Yearlings also
277 became bolder as the number of trials and pedestrian traffic increased. Males were bolder
278 than females, and individuals that gained mass quicker were also bolder. Individuals in
279 better body condition were less bold. Again, individuals fled sooner if they alerted to the
280 observer sooner. Adult boldness increased as trial number, pedestrian traffic, and predator
281 presence increased. Adult males were less bold than females. Furthermore, both alert
282 distance and distance to burrow affected boldness; individuals were less bold the sooner a
283 marmot alerted and the farther an individual was from its burrow (Table 1).

284 We found that juveniles became more docile as the active season progressed
285 (Table 2), while no such effect was seen in yearlings or adults (Table 2). Additionally,
286 faster growing yearlings were more docile, and yearlings in better body condition were
287 less docile in the afternoon. Adults were more docile as the time between trials (days)
288 increased. Males were less docile than females, and individuals were less docile in the
289 afternoon and in areas with higher pedestrian traffic. Date and mass at capture were
290 highly correlated for both juveniles and adults ($r_{Juvenile} = -0.884$; $r_{Adult} = -0.894$), which
291 creates a multicollinearity issue, and therefore reduces our ability to isolate their
292 independent effects.

293

294 *Repeatability within and correlation between life stages*

295 We found that juvenile and adult marmots were not differentially consistent in
296 their boldness (repeatability: $r_{Juvenile} = 0.037$; $r_{Adult} = 0.048$), but that yearlings ($r_{Yearling} =$
297 0.402) have consistent individual differences in boldness (Table 3). The repeatability
298 estimates for boldness were statistically different between the three age-classes ($\chi^2_2 =$
299 6.01 ; $P = 0.049$). The yearling individual variance component was not significantly
300 higher than juvenile ($\chi^2_1 = 2.237$; $P = 0.134$), but was for adults ($\chi^2_1 = 4.431$; $P = 0.035$).
301 Juvenile and adult variance components were not significantly different from one another
302 ($\chi^2_1 = 0.001$; $P = 0.966$; Table 4). We found no significant correlations between age-
303 classes in boldness (juvenile-yearling: $\chi^2_1 = 0.12$, $P = 0.728$, $N = 24$ individuals; juvenile-
304 adult: $\chi^2_1 = 0.12$, $P = 0.727$, $N = 2$ individuals; yearling-adult: $\chi^2_1 = 0.055$, $P = 0.814$, $N =$
305 13 individuals; Table 4, Fig. 1). The small number of individuals measured at different
306 ages, however, limits our ability to correctly estimate those correlations.

307 Docility was repeatable in juveniles ($r_{Juvenile} = 0.168$), yearlings ($r_{Yearling} = 0.262$),
308 and adults ($r_{Adult} = 0.272$) (Table 3). The individual variance component estimates for
309 docility were statistically different between the three age-classes ($\chi^2_2 = 8.57$; $P = 0.013$).
310 Adult individual variance component was significantly higher than the juvenile
311 component ($\chi^2_1 = 8.48$; $P = 0.003$) and the yearling component was not statistically
312 different from either the juvenile ($\chi^2_1 = 2.11$; $P = 0.137$) or adult ($\chi^2_1 = 2.43$; $P = 0.113$)
313 ones (Table 4). We found that docility was significantly correlated across all life stages
314 (juvenile-yearling: $\chi^2_1 = 64.49$, $P < 0.001$, $N = 401$ individuals; juvenile-adult: $\chi^2_1 =$

315 13.04, $P = 0.001$, $N = 146$ individuals; yearling-adult: $\chi^2_1 = 37.81$, $P < 0.001$, $N = 158$
316 individuals) with correlation coefficients higher than 0.6 (Table 4, Fig. 1).

317 It should be noted that repeatability estimates from trivariate models (Table 4)
318 differed slightly from univariate models (Table 3). The difference results from the fact
319 that only significant fixed effects from the univariate models were included in the
320 trivariate analyses.

321

322 *Behavioural syndrome*

323 Using a bivariate model for each age-class, we found that the correlation between
324 boldness and docility was not significant in any of the age-classes. For juveniles the
325 boldness-docility correlation was $r = 0.582 \pm 0.352$ SE (LRT = 2.28, $P = 0.131$; $N = 96$
326 individuals). Yearling boldness-docility correlation was $r = 0.186 \pm 0.193$ SE ($\chi^2_2 =$
327 0.829, $P = 0.362$; $N = 99$ individuals). Adult boldness-docility correlation was $r = 0.587$
328 ± 0.936 SE ($\chi^2_2 = 1.608$, $P = 0.204$; $N = 80$ individuals).

329

330 **DISCUSSION**

331 Our examination of the ontogeny of two personality traits, boldness and docility,
332 in yellow-bellied marmots found four main results that have general implications for our
333 understanding of the development of personality. First, environmental effects differed for
334 each age-class. Second, personality emerged in different age-classes. Third, personality in
335 one age-class is not necessarily correlated with personality in another. Fourth, a
336 behavioural syndrome was not present in any age-class.

337

338 *Environmental Effects*

339 Environmental factors that correlated with personality traits changed over
340 developmental stages suggesting that the environment influences age-specific personality
341 (Stamps & Groothuis 2010). We saw boldness increase (in juveniles) and docility
342 decrease (in yearlings and adults) as the day progressed. Although the exact reason for
343 the within-day change is unknown, similar within-day changes in personality have also
344 been seen in two species of coral reef fish due to temperature changes (Biro et al. 2010).
345 Daily temperature changes may influence metabolic rate (Armitage 1991), which could
346 influence personality traits (Biro et al. 2010). Body condition decreased boldness and
347 docility in yearlings. These results are inconsistent with theoretical work that suggests
348 that individuals in better body condition take more risks while incurring fewer costs
349 because they are better able to hold resources and escape predators (Luttbeg & Sih 2010).

350 In the three age-classes, we found that predator presence increased boldness as
351 previously reported in fish (Brown et al. 2005). This intuitively makes sense, since
352 individuals must strike a balance between being cautious in the presence of predators and
353 maintaining potential foraging and reproductive opportunities (Cooper & Pérez-Mellado
354 2004). Individuals that are more cautious may therefore lose these opportunities in
355 comparison to bolder individuals. Thus, we might expect bolder individuals in predator-
356 rich areas despite the high risk.

357 Marmot interaction with humans seemed to have variable effects. Boldness
358 increased with trial number and pedestrian traffic in yearlings and adults. Together, these
359 factors suggest that marmots habituate to human disturbance over the summer (Li et al.
360 2011). Additionally, past research on Eastern chipmunks (*Tamias striatus*; Martin &

361 Réale 2008) and burrowing owls (*Athene cunicularia*; Carrete & Tella 2010) found a
362 correlation between human disturbance and personality suggesting habituation or habitat
363 selection based on personality. In contrast, docility decreased in adults as pedestrian
364 traffic increased. This coupled with an increase in docility as the days between capture
365 increased suggest that marmots may become more sensitive to human interaction when
366 trapped.

367 Yearlings that grew faster were also more docile but also bolder. These are not
368 consistent with the predictions made by Biro and Stamps (2008) who predicted that
369 individuals that grow faster should engage in more risky behaviour to maintain that
370 growth rate. Individual marmots do not have to protect or actively look for food patches
371 (i.e. vegetation is abundant at our study site), thus decoupling the predicted link between
372 risky behaviour and growth rate. In addition, faster growing individuals might benefit
373 from docility simply by not investing in more active and energetically costly non-docile
374 behaviours.

375 Sex differences were found in yearling and adult boldness. Yearling males were
376 bolder than females. All yearling males disperse, and this difference in boldness may be a
377 method for individual males to prepare for dispersal. Alternatively, adult males were
378 found to be less bold than females. There is no apparent reason for this, but females have
379 the added cost of gestation and lactation, and therefore need to be bolder to forage and
380 survive hibernation (Andersen et al. 1976). Sex differences were also found in adult
381 docility with males being less docile than females. This difference in sex is inconsistent
382 with a study of alpine marmot (*Marmota marmota*) docility where no differences were

383 found between sexes (Ferrari et al. 2013). However, Ferrari et al. (2013) did not account
384 for potential differences within each age group as our study did.

385

386 *Repeatability within life stages*

387 We found that boldness and docility developed differently. Juvenile and adult
388 marmot boldness was not repeatable; thus it was not considered a personality trait in
389 juveniles or adults. However, yearling marmots had significantly repeatable boldness
390 levels. Interestingly, yearlings had a higher repeatability compared to adults suggesting
391 that behaviour is not developmentally constrained. Docility, however, was repeatable in
392 all age classes. These results suggest that these differences in personality development
393 may allow for individuals to act adaptively at age-appropriate times.

394 Future research should focus on the potential reasons for a lack of boldness in
395 juveniles and adults. Juveniles may lack individual differences because they have not yet
396 undergone experiences that lead to differentiation (Freund et al. 2013). Alternatively, lack
397 of a boldness personality trait might be due to differences in life-history strategy between
398 each life stage. Body mass strongly affects over-winter survival in juveniles but does so
399 to a lesser degree in adults (Lenihan & Vuren 1996). Juveniles triple their body mass in
400 three months from first emergence to hibernation. Thus, juveniles should prioritize
401 foraging by adopting a single consistent strategy, while yearlings may adopt multiple
402 strategies to cope with certain life stage events such as dispersal. Juveniles have also been
403 found to be less vigilant than yearlings and adults in general, supporting the hypothesis
404 that they prioritize foraging (Li et al. 2011). Juvenile, or smaller, poeciliid fish
405 (*Brachyrhaphis episcopi*) were also found to be bolder than larger individuals suggesting

406 there is a trade-off between growth and potential mortality (Brown & Braithwaite 2004).
407 Adults, however, must cope with a highly variable, harsh environment and must therefore
408 be plastic (Armitage 1991).

409 Alternatively, docility was repeatable in all age classes, indicating that this
410 personality trait develops early in life and canalizes with age. Individual differences in
411 docility may therefore be linked to positive feedback loops with the environment. This
412 result is supported by other studies that show adults are less plastic than juveniles (Sinn et
413 al. 2008; Gyuris et al. 2012). These differences in the development of personality traits
414 are consistent with the hypothesis that consistent individual differences in behaviour can
415 be adaptive and linked to life-history strategies (Wolf et al. 2007).

416

417 *Stability within and between traits across time*

418 We found differences between personality traits in stability across development.
419 Boldness was not stable across development but docility was. Individuals differently
420 changed in levels of boldness across all three life stages. However, the small number of
421 individuals with boldness data in multiple age-classes limits conclusions from this data.
422 We found no correlation between any age group. This result is consistent with the idea
423 that behaviour is plastic and should change depending on the environment (Fox &
424 Westneat 2010). Although the exact cause of the plasticity in personality is unknown,
425 repeatability in boldness may be due to life stage events. For example, almost all yearling
426 males and about half the yearling females disperse, and therefore, individuals exhibit
427 different behavioral strategies to cope with dispersal or staying at the natal colony.
428 Again, adults have settled at a location and must cope with the changing yearly

429 environment (Armitage 1991). Individuals are therefore changing their behavioral
430 plasticity depending upon the age-specific life-history events.

431 In contrast to boldness, docility is stable throughout the individual's life with
432 strong positive correlations between the three age-classes. This suggests that docility is
433 established at birth or early in life and is stable during the whole life of an individual.
434 Adult docility may result from previous environmental constraints and selection during
435 development (Sinn et al. 2008).

436

437 *Behavioural syndrome*

438 Boldness and docility have previously been shown to form a behavioural
439 syndrome (Réale et al. 2009), however, we found no correlation between boldness and
440 docility in any life stage (Figure 2). This is intuitive for juveniles and adults that do not
441 show consistent individual differences in boldness, but do show consistency in docility.
442 Although a syndrome could form later in life, the manner in which each personality trait
443 develops might preclude such a formation.

444

445 *Conclusion*

446 In conclusion, we found that boldness and docility developed differently across
447 life stages. This has major implications for our understanding of personality and raises a
448 large number of questions about what might explain that difference. Juveniles grow
449 rapidly and do not mate, yearlings disperse, and adults reproduce. Specific constraints
450 and life-histories of each age-class are likely the basis for the observed differences in the
451 ontogeny of personality. Selection can vary across life stages (Schluter et al. 1991;

452 McNamara et al. 2009) and, therefore, different behavioural traits may be differentially
453 important in those stages. Although we did not test for selection in this study, future
454 research should focus on quantifying these different selection pressures throughout
455 development and the potential adaptive reasons for the differences in the development of
456 personality traits.

457

458 **Acknowledgments**

459 M.B.P. was supported by a GAANN fellowship, a GK-12 fellowship, and the UCLA
460 Department of Ecology and Evolutionary Biology. D.M. was an NSF REU fellow
461 supported by DBI 0731346. V.A. was partially supported by a RMBL scholarship.
462 J.G.AM was supported by a FQRNT fellowship and by the NSF. D.T.B was supported by
463 the National Geographic Society, UCLA (Faculty Senate and the Division of Life
464 Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the NSF
465 (IDBR-0754247 and DEB-1119660 to D.T.B., as well as DBI 0242960 and 0731346 to
466 the Rocky Mountain Biological Laboratory). We thank all the marmoteers over the past
467 decade for help collecting the data, and the Blumstein lab for comments on previous
468 versions of the MS. We also thank Lynn Fairbanks, Peter Nonacs, and three anonymous
469 reviewers for their constructive feedback on previous versions of the MS.

470

471 **References**

472 **Andersen, D. C., Armitage, K. B. & Hoffmann, R. S.** 1976. Socioecology of marmots:
473 female reproductive strategies. *Ecology*, 57, 552-560.

474 **Armitage, K. B.** 1982. Yellow-bellied marmot. In: *CRC handbook of census methods for*
475 *terrestrial vertebrates* (Ed. by D. E. Davis), pp. 148-149: CRC Press Boca Raton,
476 Florida.

477 **Armitage, K. B.** 1986. Individual differences in the behavior of juvenile yellow-bellied
478 marmots. *Behavioral Ecology and Sociobiology*, 18, 419-424.

479 **Armitage, K. B.** 1991. Social and population dynamics of yellow-bellied marmots:
480 results from long-term research. *Annual Review of Ecology and Systematics*, 22,
481 379-407.

482 **Armitage, K. B. & Downhower, J. F.** 1974. Demography of yellow-bellied marmont
483 populations. *Ecology*, 55, 1233-1245.

484 **Armitage, K. B. & Van Vuren, D. H.** 2003. Individual differences and reproductive
485 success in yellow-bellied marmots. *Ethology Ecology & Evolution*, 15, 207-233.

486 **Baayen, R. H., Davidson, D. J. & Bates, D. M.** 2008. Mixed-effects modeling with
487 crossed random effects for subjects and items. *Journal of Memory and Language*,
488 59, 390-412.

489 **Bates, D., Maechler, M. & Bolker, B.** 2012. lme4: Linear mixed-effects models using
490 S4 classes, 2011. URL <http://CRAN.R-project.org/package=lme4>. R package
491 version 0.999375-42.

492 **Bell, A. M. & Sih, A.** 2007. Exposure to predation generates personality in threespined
493 sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10, 828-834.

494 **Bell, A. M. & Stamps, J. A.** 2004. Development of behavioural differences between
495 individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal*
496 *Behaviour*, 68, 1339-1348.

497 **Bell, A. M., Hankison, S. J., Laskowski, K. L.** 2009. The repeatability of behaviour: a
498 meta-analysis. *Animal Behaviour*, 77, 771-783.

499 **Biro, P. A., Beckmann, C. & Stamps, J. A.** 2010. Small within-day increases in
500 temperature affects boldness and alters personality in coral reef fish. *Proceedings*
501 *of the Royal Society B: Biological Sciences*, 277, 71-77.

502 **Biro, P. A. & Stamps, J. A.** 2008. Are animal personality traits linked to life-history
503 productivity? *Trends in Ecology & Evolution*, 23, 361-368.

504 **Blumstein, D. T.** 2003. Flight-initiation distance in birds is dependent on intruder
505 starting distance. *The Journal of wildlife management*, 852-857.

506 **Blumstein, D. T.** 2010. Flush early and avoid the rush: a general rule of antipredator
507 behavior? *Behavioral Ecology*, 21, 440-442.

508 **Blumstein, D. T., Petelle, M. P., & Wey, T. W.** 2012. Defensive and social aggression:
509 repeatable but independent. *Behavioral Ecology*. doi:10.1093/beheco/ars183

510 **Blumstein, D. T., Wey, T. W. & Tang, K.** 2009. A test of the social cohesion
511 hypothesis: interactive female marmots remain at home. *Proceedings of the Royal*
512 *Society B: Biological Sciences*, 276, 3007-3012.

513 **Brown, C. & Braithwaite, V.A.** 2004. Size matters: a test of boldness in eight
514 population of the poeciliid *Brachyraphis episcopi*. *Animal Behaviour*, 68, 1325-
515 1329.

516 **Brown, C., Jones, F. & Braithwaite, V.** 2005. In situ examination of boldness–shyness
517 traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, 70,
518 1003-1009.

519 **Brydges, N. M. C., N., Heathcote, J. P. & Braithwaite, V. A.** 2008. Habitat stability
520 and predation pressure affect temperament behaviours in populations of three-
521 spined sticklebacks. *Journal of Animal Ecology*, 77, 229-235.

522 **Careau, V., Réale D., Humphries, M. M. & Thomas, D. W.** 2010. The pace of life
523 under artificial selection: personality, energy expenditure, and longevity are
524 correlated in domestic dogs. *The American Naturalist*, 175, 753-758.

525 **Carrete, M. & Tella, J. L.** 2010. Individual consistency in flight initiation distances in
526 burrowing owls: a new hypothesis on disturbance-induced habitat selection.
527 *Biology Letters*, 6, 167-170.

528 **Cooper Jr., W. E.** 2009. Variation in escape behavior among individuals of the striped
529 plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *Journal of*
530 *Herpetology*, 43, 495-502.

531 **Cooper Jr., W. E. & Pérez-Mellado, V.** 2004. Tradeoffs between escape behavior and
532 foraging opportunity by the Balearic lizard (*Podarcis lilfordi*). *Herpetologica*, 60,
533 321-324.

534 **Dill, L. M. & Houtman, R.** 1989. The influence of distance to refuge on flight initiation
535 distance in the gray squirrel (*Sciurus carolinensis*). *Canadian Journal of Zoology*,
536 67, 233-235.

537 **Dingemans, N. J., Both, C., Drent, P. J. & Tinbergen, J. M.** 2004. Fitness
538 consequences of avian personalities in a fluctuating environment. *Proceedings of*
539 *the Royal Society B-Biological Sciences*, 271, 847-852.

540 **Dingemanse, N. J. & Dochtermann, N. A.** 2013. Quantifying individual variation in
541 behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, 82,
542 39-54.

543 **DiRienzo, N., Pruitt, J. N. & Hedrick, A. V.** 2012. Juvenile exposure to acoustic
544 sexual signals from conspecifics alters growth trajectory and an adult personality
545 trait. *Animal Behaviour*, 84, 861-868.

546 **Ferrari, C., Pasquaretta, C., Carere, C., Cavallone, E., von Hardenberg, A., Réale,**
547 **D.** 2013. Testing for the presence of coping styles in a wild mammal. *Animal*
548 *Behaviour*, doi.org/10.1016/j.anbehav.2013.03.030.

549 **Fox, C. W. & Westneat, D. F.** 2010. Adaptation. In: *Evolutionary Behavioral Ecology*
550 (Ed. by D. F. Westneat & C. W. Fox), pp. 16-31. New York: Oxford University
551 Press.

552 **Frase, B. A. & Hoffmann, R. S.** 1980. *Marmota flaviventris*. *Mammalian Species*, 1-8.

553 **Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Küger, A.,**
554 **Sachser, N., Lindenberger, U. & Kempermann, G.** 2013. Emergence of
555 individuality in genetically identical mice. *Science*, 340, 756-759.

556 **Gilmour, A. R., Gogel, B., Cullis, B., Thompson, R., Butler, D., Cherry, M., Collins,**
557 **D., Dutkowski, G., Harding, S. & Haskard, K.** 2009. ASReml user guide
558 release 3.0. VSN International Ltd, Hemel Hempstead, UK.

559 **Groothuis, T. G. G., Carere, C., Lipar, J., Drent, P. J. & Schwabl, H.** 2008. Selection
560 on personality in a songbird affects maternal hormone levels tuned to its effect on
561 timing of reproduction. *Biology Letters*, 4, 465-467.

562 **Gyuris, E., Feró, O. & Barta, Z.** 2012. Personality traits across ontogeny in firebugs,
563 *Pyrrhocoris apterus*. *Animal Behaviour*, 84, 103-109.

564 **Lenihan, C. & Vuren, D. V.** 1996. Growth and survival of juvenile yellow-bellied
565 marmots (*Marmota flaviventris*). *Canadian Journal of Zoology*, 74, 297-302.

566 **Li, C., Monclús, R., Maul, T. L., Jiang, Z. & Blumstein, D. T.** 2011. Quantifying
567 human disturbance on antipredator behavior and flush initiation distance in
568 yellow-bellied marmots. *Applied Animal Behaviour Science*, 129, 146-152.

569 **Luttbeg, B. & Sih, A.** 2010. Risk, resources and state-dependent adaptive behavioural
570 syndromes. *Philosophical Transactions of the Royal Society B-Biological*
571 *Sciences*, 365, 3977-3990.

572 **Martin, J. G. & Réale, D.** 2008. Animal temperament and human disturbance:
573 implications for the response of wildlife to tourism. *Behavioural Processes*, 77,
574 66-72.

575 **McNamara, J. M., Houston, A. I., Barta, Z., Scheuerlein, A. & Fromhage, L.** 2009.
576 Deterioration, death and the evolution of reproductive restraint in late life.
577 *Proceedings of the Royal Society B: Biological Sciences*, 276, 4061-4066.

578 **Pinheiro, J. C. & Bates, D. M.** 2000. Mixed-effects models in S and S-Plus. Springer
579 Verlag New York.

580 **Pruitt, J. N., Cote, J. & Ferrari, M. C. O.** 2012. Behavioural trait variants in a habitat-
581 forming species dictate the nature of its interactions with and among
582 heterospecifics. *Functional Ecology*, 26, 29-36.

583 **R Development Team.** 2011. R: A language and environment for statistical computing.
584 R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,
585 URL <http://www.R-project.org/>.

586 **Réale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M.** 2000. Consistency of
587 temperament in bighorn ewes and correlates with behaviour and life history.
588 *Animal Behaviour*, 60, 589-597.

589 **Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J.** 2007.
590 Integrating animal temperament within ecology and evolution. *Biological*
591 *Reviews*, 82, 291-318.

592 **Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M.** 2009. Male
593 personality, life-history strategies and reproductive success in a promiscuous
594 mammal. *Journal of Evolutionary Biology*, 22, 1599-1607.

595 **Rödel, H. G. & Meyer, S.** 2011. Early development influences ontogeny of personality
596 types in young laboratory rats. *Developmental Psychobiology*, 53, 601-613.

597 **Runyan, A. M. & Blumstein, D. T.** 2004. Do individual differences influence flight
598 initiation distance? *Journal of Wildlife Management*, 68, 1124-1129.

599 **Schluter, D., Price, T. D. & Rowe, L.** 1991. Conflicting selection pressures and life
600 history trade-offs. *Proceedings of the Royal Society of London. Series B:*
601 *Biological Sciences*, 246, 11-17.

602 **Sinn, D. L., Gosling, S. D. & Moltischniowskyj, N. A.** 2008. Development of shy/bold
603 behaviour in squid: context-specific phenotypes associated with developmental
604 plasticity. *Animal Behaviour*, 75, 433-442.

605 **Stamps, J.** 2007. Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecology*
606 *Letters*, 10, 355-363.

607 **Stamps, J. & Groothuis, T. G. G.** 2010. The development of animal personality:
608 relevance, concepts and perspectives. *Biological Reviews*, 85, 301-325.

609 **Svendson, G. E. & Armitage, K. B.** 1973. Mirror-image stimulation applied to field
610 behavioral studies. *Ecology*, 54, 623-627.

611 **Svendson, G.E.** 1974. Behavioral and environmental factors in the spatial distribution
612 and population dynamics of a yellow-bellied marmot population. *Ecology*, 55,
613 760-771.

614 **Wilson, A. D. M. & Krause, J.** 2012. Personality and metamorphosis: is behavioral
615 variation consistent across ontogenetic niche shifts? *Behavioral Ecology*, 23,
616 1316-1323.

617 **Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J.** 2007. Life-history trade-offs
618 favour the evolution of animal personalities. *Nature*, 447, 581-584.

619 **Ydenberg, R. & Dill, L.** 1986. The economics of fleeing from predators. *Advances in the*
620 *Study of Behavior*, 16, 229-249.

621

622 **Table 1.**

623 Fixed effects explaining variation in the univariate model of boldness (quantified as the

624 negative of flight initiation distance) for three age-classes in yellow-bellied marmots.

625 Significant effects are in bold.

	Juveniles		Yearlings		Adults	
	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>
(Intercept)	-1.192 (2.544)	0.238	-7.328 (1.628)	<0.001	-6.237 (1.394)	<0.001
Time between trials (days)	-0.003 (0.012)	0.595	-0.022 (0.012)	0.168	0.017 (0.011)	0.151
Trial at colony (per day)	-0.035 (0.041)	0.718	-0.060 (0.045)	0.322	0.054 (0.064)	0.388
Sex (M)	0.201 (0.208)	0.442	0.200 (0.275)	0.047	-0.849 (0.336)	0.01
Trial per individual	0.032 (0.132)	0.853	0.120 (0.052)	0.005	0.255 (0.058)	<0.001
Time (PM)	0.442 (0.227)	0.035	-0.089 (0.169)	0.626	0.017 (0.190)	0.915
Pedestrian	0.021 (0.017)	0.118	0.048 (0.019)	0.001	0.031 (0.011)	0.003
Mass gain	0.002 (0.001)	0.367	0.001 (0.001)	0.022	4.332e-04 (0.000)	0.16
Mass in August	-0.002 (0.001)	0.295	-0.001 (0.000)	0.01	2.62 e-04 (0.000)	0.224
Predator Presence	3.614 (1.562)	0.005	6.917 (1.328)	<0.001	2.824 (0.976)	<0.002
Date	-0.002 (0.010)	0.936	0.015 (0.007)	0.065	-0.002 (0.007)	0.683
Alert distance	-0.061 (0.006)	<0.001	-0.043 (0.003)	<0.001	-0.035 (0.002)	<0.001
Distance to burrow	-0.001 (0.022)	0.655	-0.014 (0.008)	0.212	-0.044 (0.012)	<0.001
Initial behavior (Look)	0.302 (0.328)	0.704	0.041 (0.194)	0.881	-0.048 (0.230)	0.772

626

627

628 **Table 2.**

629 Fixed effects explaining variation in the univariate model of trapping behaviors, a
 630 measure of docility, for three age-classes in yellow-bellied marmots. Significant effects
 631 are in bold.

	Juveniles		Yearlings		Adults	
	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>	Estimate (SE)	<i>P</i>
(Intercept)	1.206 (0.399)	<0.001	3.851 (0.271)	<0.001	4.205 (0.155)	<0.001
Time between trials (days)	-0.002 (0.002)	0.206	-1.42e-04 (0.002)	0.95	0.004 (0.001)	0.005
Sex (M)	0.022 (0.043)	0.352	-0.010 (0.063)	0.409	-0.238 (0.086)	0.001
Time (PM)	0.043 (0.035)	0.342	-0.085 (0.035)	0.014	-0.137 (0.036)	<0.001
Date	0.015 (0.002)	<0.001	0.003 (0.002)	0.179	1.76e-04 (0.001)	0.973
Mass gain	-1.57e-05 (3.74e-05)	0.82	2.45e-04 (1.52e-04)	0.037	4.30e-05 (3.72e-05)	0.176
Mass at capture	-1.35e-04 (8.60e-05)	0.282	-1.43e04 (6.18e-05)	0.042	3.82e-05 (4.05e-05)	0.301
Pedestrians	0.003 (0.002)	0.213	0.005 (0.004)	0.165	-0.007 (0.004)	0.009
Predator Presence	4.00e-04 (0.001)	0.822	-5.03e-04 (0.001)	0.68	0.001 (0.001)	0.566

632

633 **Table 3**

634 Variance, ratio, and significance of random effects using log-likelihood ratio tests (LRT)
635 for both docility and boldness univariate calculated from models for juvenile, yearling,
636 and adult yellow-bellied marmots. Total number of observations, number of individuals
637 and mean of the traits are also reported. All the LRTs have only 1 degree of freedom.
638

Trait	Age	N obs- ind	Mean (SD)	Variance			Ratio		LRT		P-value	
				Identity	Year	Phenotypic	Identity	Year	Identity	Year	Identity	Year
Docility	Juveniles	3316- 861	4.183 (0.967)	0.151	0.029	0.895	0.168	0.032	119.5	37.21	<0.001	<0.001
	Yearlings	2294- 445	4.384 (0.870)	0.208	0.027	0.792	0.262	0.034	185.3	10.37	<0.001	0.001
	Adults	2607- 266	4.294 (0.989)	0.254	0.005	0.932	0.272	0.005	421.1	5.15	<0.001	0.023
Boldness	Juveniles	126- 86	-27.854 (24.396)	0.261	6.164	7.075	0.037	0.871	1.392	17.42	0.238	<0.001
	Yearlings	204- 81	-43.268 (32.793)	0.617	0.082	1.536	0.402	0.053	13.91	0.691	<0.001	0.406
	Adults	233- 70	-46.999 (38.654)	0.083	0.114	1.703	0.048	0.067	0.941	4.246	0.332	0.039

640 **Table 4.**
641
642 Repeatability (on diagonal), correlations (below diagonal), and pairwise comparison of
643 repeatability (above diagonal) for docility and boldness for the different age classes
644 (juvenile, yearling, adult) in yellow-bellied marmots. Estimates were obtained from
645 trivariate models for each behaviour considering each age class as a different trait.
646 Estimates of repeatability are slightly different from univariate models (Table 1) because
647 only significant fixed effects were used in these models to avoid overparametrization.

	Docility			Boldness		
	Juveniles	Yearlings	Adults	Juveniles	Yearlings	Adults
	0.190			0.019		
Juveniles	(0.021)***	NS	**	(0.027)	NS	NS
	0.857	0.268		0.379	0.373	
Yearlings	(0.159)***	(0.033)***	NS	(0.843)	(0.146)***	*
	0.624	0.782	0.293	-0.167	0.446	0.053
Adults	(0.161)***	(0.169)***	(0.039)***	(-8.861)	(1.432)	(0.057)
	0.921	0.819	0.969	6.988	1.451	1.746
Phenotypic	(0.029)	(0.038)	(0.041)	(4.665)	(0.235)	(0.228)

648

649

650 *:<0.05; **:<0.01; ***:<0.001, see text for exact p-values -:parameter bounded to zero

651

Figure legends

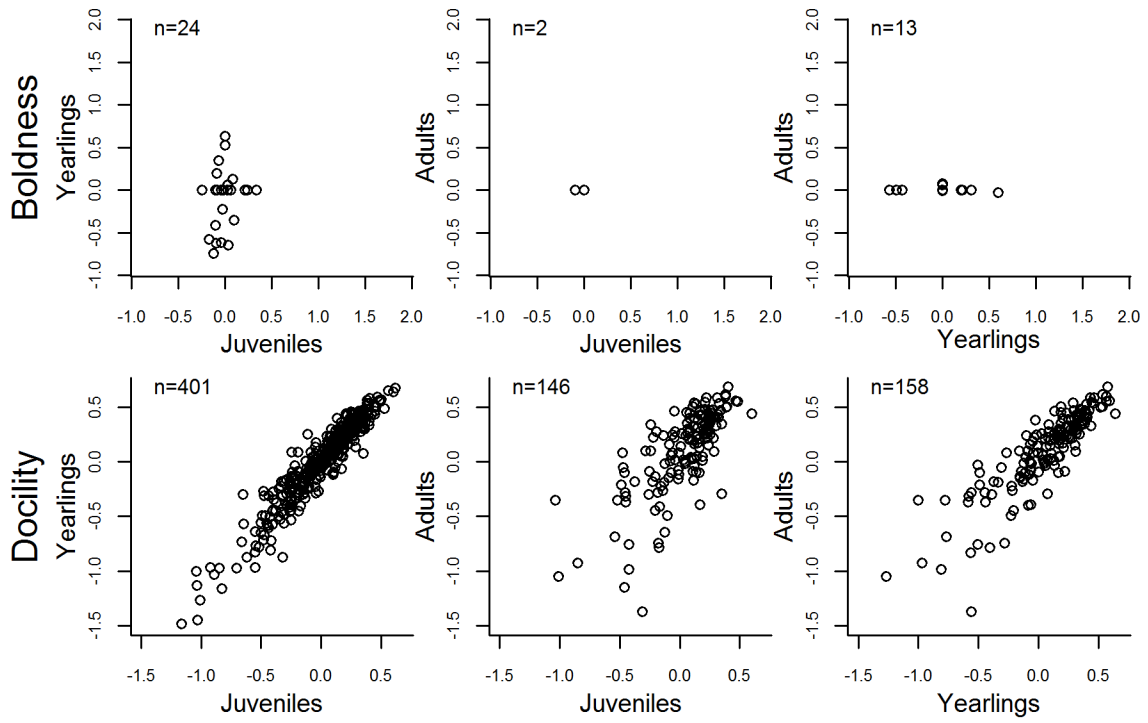
652 **Figure 1.** Relationship between juvenile/yearling, juvenile/adult, and yearling/adult
653 personality. The top panel represents boldness (negative FID). The bottom panel
654 represents docility (trapping behaviours). Best linear unbiased predictors (BLUPs) from
655 trivariate models of boldness and docility were used for illustration purposes only. N
656 represents the number of individuals for which data were available for both traits.

657

658 **Figure 2.** Relationship between docility and boldness for a) juveniles, b) yearlings, and c)
659 adults. Best linear unbiased predictors (BLUPs) from bivariate models of docility and
660 boldness were used for illustration purposes only. N represents the number of individual
661 for which data were available for both traits.

662

663 **Figure 1.**



664
665

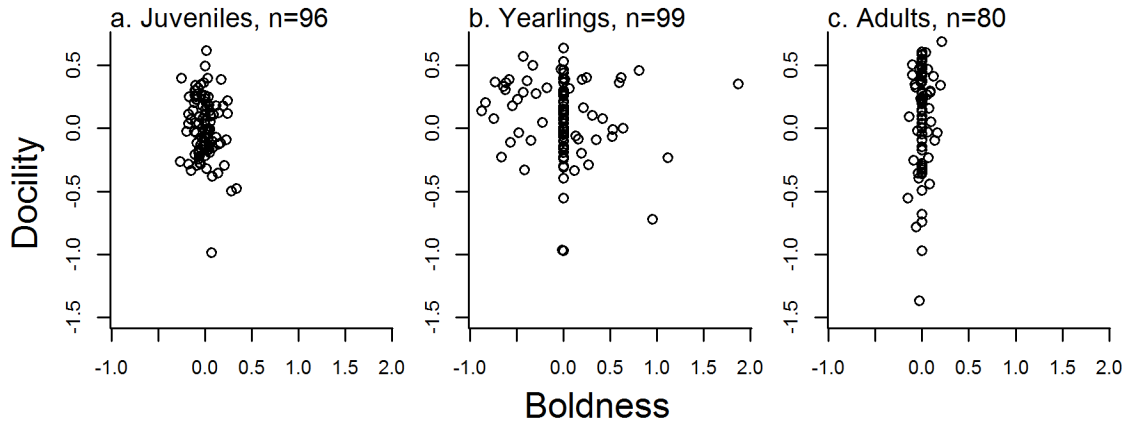
666

667

668 **Figure 2.**

669

670



671

672