



Development of boldness and docility in yellow-bellied marmots



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ARTICLE INFO

Article history:

Received 29 January 2013

Initial acceptance 15 March 2013

Final acceptance 3 September 2013

Available online 18 October 2013

MS. number: A13-00087R

Keywords:

behavioural syndrome

boldness

docility

Marmota flaviventris

ontogeny

personality

yellow-bellied marmot

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

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

Previous studies on the development of personality have focused primarily on quantifying repeatability with maternal effects (Groothuis et al. 2008; Rödel & Meyer 2011), early experience (DiRienzo et al. 2012), or across life stages (Bell & Stamps 2004; Sinn et al. 2008; Gyuris et al. 2012; Wilson & Krause 2012). For example, threespine sticklebacks, *Gasterosteus aculeatus*, were

tested for stability in multiple personality traits across life stages (Bell & Stamps 2004). The authors found little stability in single personality traits across life stages, but that a syndrome, boldness and aggression, was consistently detected across ontogeny (Bell & Stamps 2004). In that study, stability was inferred from a positive correlation between juvenile and adult personality traits. Thus, individuals with stable personality traits maintained the same level of aggression or boldness relative to others across ontogeny. Studies that focused on repeatability within life stages showed mixed results. Individual dumpling squid, *Euprymna tasmanica*, were repeatable in their level of boldness as juveniles, but this repeatability disappeared for a period upon sexual maturation and reappeared in adulthood (Sinn et al. 2008). During the period of sexual maturity, and depending on their behavioural type, squid were more plastic in certain ecologically relevant contexts. For example, shyer individuals were more plastic in a feeding context than bolder individuals. Conversely, repeatability was present within life stages in both firebugs, *Pyrrhocoris apterus* (Gyuris et al. 2012) and lake frogs, *Rana ridibunda* (Wilson & Krause 2012).

These studies suggest that personality traits, in some species, are plastic within or between life stages. Thus, juvenile personality may not always predict adult personality, and plasticity may

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increase within a life stage whereby individuals may change their level of a particular personality trait. This low repeatability might be seen in certain life stages because individuals may experience differential selection over time, selection may favour plasticity (opportunity for multiple alternative strategies), or there may be a single best strategy for a given a set of environmental conditions (Fox & Westneat 2010). Thus, it is important to understand the development of personality and how these traits interact within and between life stages.

Here we capitalize on a long-term ecological study of yellow-bellied marmots, *Marmota flaviventris*, to investigate repeatability and the stability (i.e. correlation at the individual level) within and across three life stages for boldness and docility traits. Previous research on yellow-bellied marmots has shown that personality traits exist in both yearling and adult individuals and can influence fitness (Svendson & Armitage 1973; Svendsen 1974; Armitage 1986; Armitage & Van Vuren 2003). Thus, we hypothesize that all three age categories will exhibit these two personality traits. We do not have a priori hypotheses about the stability of these traits across ontogeny or whether there is a behavioural syndrome between the two. Additionally, our new and extensive data set allows us to understand how environmental variables affect personality at different life stages. Thus, our first aim was to understand how repeatability varies between life stages. Our second aim was to investigate whether juvenile personality levels predict yearling and adult personality levels (that is, the longitudinal stability of these personality traits). Our third aim was to describe whether a behavioural syndrome exists and is stable between boldness and docility across these same life stages. Our last aim was to explore how an individual's current state and environment affect personality within life stages (Brydges et al. 2008; Luttbeg & Sih 2010).

METHODS

Study Subjects and Site

Between 2002 and 2011, we studied yellow-bellied marmots in the Upper East River Valley, in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. (38°77'N, 106°59'W). Yellow-bellied marmots are facultatively social, sciurid rodents, which weigh 2–6 kg, live in matrilineal groups and dwell in subalpine meadows, slopes and clearings (Frase & Hoffmann 1980). The Upper East River valley is divided in two parts, up- and down-valley, that differ in elevation, phenology and human disturbance. Three of the colonies were located up-valley while four were down-valley. Marmots were trapped on a regular basis using Tomahawk live traps and individually marked with numbered eartags for permanent identification and fur dye to facilitate identification from afar (Armitage 1982; Blumstein et al. 2009). Almost all of the individuals were trapped for the first time as juveniles and thus were of known age. Juveniles are individuals in their first summer of life; yearlings, or 1-year-olds, are in their second summer of life; adults are 2 years or older (Armitage & Downhower 1974).

Quantifying Environmental Factors

Marmots are seasonally active and we study them in a valley that is used for summer tourism. We quantified human presence for 12 days during the peak summer months of 2010 by continuously recording pedestrian activity within 300 m of six colonies (Li et al. 2011). Human traffic was not quantified in some colonies where personality data were collected, but our previous study showed that more humans were present at our down-valley sites (including those sites where impact was not specifically quantified)

than our up-valley sites. Thus, we averaged human visits in two down-valley colonies and four up-valley colonies, and used these average values for unquantified colonies (down valley: Bench, Avalanche and River); we believe that these averages provide a good approximation of human disturbance in unstudied colonies. We used these averages for all years because, while not precisely quantified, human disturbance seemed not to change much between years (hiking and biking trails remained the same throughout the duration of data collection for this study; tourism was steady).

Predator presence was quantified from 2002 to 2011 by dividing the number of predators seen during observations at a colony by the total number of observation sessions at that colony. We used predator sightings only during the early season (mid-April through June) because predators become harder to view as vegetation grows during the active season. We also quantified the number of predators seen per hour of observation to test whether there were any differences between indexes. The indexes were highly correlated (Pearson correlation: $r_{95} = 0.961$, $P < 0.001$), indicating no bias in the number of predators seen per observation session. A total of 203 aerial predators and 292 terrestrial predators were seen during this time.

Quantifying Boldness with Flight Initiation Distance

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

After arriving at a site, the researcher sat and quietly observed and identified subjects for at least 5 min. Once a target subject was identified, the observer walked directly towards the marmot at a constant pace. Observers were trained until they consistently walked at a 0.5 m/s pace across a variety of terrains (Runyan & Blumstein 2004). We recorded when an individual first raised its head and looked towards the researcher (alert distance), when it first fled (FID), its distance from the researcher when the trial began (start distance), its distance from a burrow when it fled (burrow distance) and its initial behaviour (forage, look, other; 'look' implies that the marmot was looking at the researcher). All distances were first marked with flags dropped during the trial and calculated afterwards by pacing. Individual pace length was calculated during training. The researcher waited at least 10 min before conducting another trial on a different subject. Individual marmots were tested no more than once per observation session (morning/afternoon sessions).

Quantifying Docility with Trapping Behaviour

Docility was assessed during 8217 trapping events for 861 juveniles, 445 yearlings and 266 adults from 2002 to 2011. We use the description of docility set forth by Réale et al. (2000). Docility here is defined as an individual's reaction to being trapped and handled. Docility is a commonly used metric of personality and is often used as a measure of risky behaviour (Réale et al. 2007, 2009; Careau et al. 2010). When trapped, marmots were transferred to a cloth handling bag for subsequent processing. At each trapping event, we recorded each marmot's behaviour while in the trap prior to being put in the trap bag. We dichotomously (i.e. 0/1) scored whether or

not individuals emitted alarm calls, tooth chattered, struggled in the trap, bit the cage, and whether they failed to walk immediately into the handling bag. Following Réale et al. (2000), we summed the dichotomously scored behaviours and subtracted this from the total potential score. A score of 0 thus indicates a nondocile individual, and inversely a score of 5 indicates a docile individual.

Statistical Analyses

Age-specific repeatability and environmental effects

We first analysed each life stage separately to estimate age-specific repeatability of the behaviours and to determine the environmental effects specific at each age class. We fitted univariate linear mixed-effects models (i.e. one dependent variable with multiple fixed and random effects; Dingemanse & Dochtermann 2013) for both behaviours (boldness and docility) for each age class (juvenile, yearling, adult). For all models, individual identity and year were fitted as random effects to assess both personality and yearly environmental variation, respectively. Repeatability was estimated as the ratio of the variance associated with the individual identity effect divided by the total phenotypic variance (i.e. sum of individual, yearly and residual variances), a significant repeatability indicating personality. Additional fixed effects were fitted and are described below.

Fixed effects of flight initiation distance (boldness) included trial number per individual, trials done each day at the colony level, time (days) between trials, start and alert distances, the distance from the marmot to the burrow, sex, time of day (morning or afternoon), pedestrian traffic, predator presence, estimated mass on 15 August, estimated mass gain from 1 June to 15 August, initial behaviour and date. Trial number and the number of trials conducted at a colony per day were included to control for potential habituation effects. Time between trials was included to control for potential biases in repeatability (Bell et al. 2009). We included start distance and alert distance and the initial distance to a burrow because previous research has shown that they affect FID (start and alert: Blumstein 2010; distance to refuge: Dill & Houtman 1989). We included mass at 15 August and mass gain as proxies for body condition and growth rate, respectively. Both measures have theoretically been shown to influence personality (Stamps 2007; Biro & Stamps 2008; Luttbeg & Sih 2010). We used mass at capture as a measure of body condition. We included initial behaviour because it could influence when individuals become alert to possible predators. To control for effects from the progression of the day and season, we included time of day and the date. Flight initiation distance was square-root transformed prior to analyses to conform to the normality of residuals assumption of linear models. Fixed effects of docility were time (in days) between trapping, sex, time of day (morning or afternoon), date, pedestrian traffic, predator presence, mass gain and mass at capture. Sex was included to control for potential differences between males and females. Time of day and date were included because of differences within day and throughout the active season.

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

Correlation between life stages and between behaviours

To estimate the correlations, or stability, between juvenile, yearling and adult behaviours at the individual level, we fitted trivariate mixed models (i.e. three dependent variables with multiple fixed and random effects; Dingemanse & Dochtermann 2013) for each behaviour, considering each age class as a different trait. Individual identity and year were fitted as random effects with an unstructured 3×3 (co)variance matrix estimating three variance components (one for each trait) and their three pairwise covariances. Correlations were then calculated from the (co)variance matrix as the rescaled covariances (i.e. covariance between two traits divided by the square root of the product of the variances of the two traits). The residual matrix was constrained to be a 3×3 diagonal matrix because of the structure of our data. To test whether variance components differed between the three age classes, we used an LRT between models with and without constraints of equality of variance components for the three age classes. We used a similar test for pairwise comparison of variance components but constraining only two age classes at a time to be equivalent. Significance of behavioural correlations at the individual level between age classes was estimated using an LRT between models with and without a covariance parameter constrained to zero.

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

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

Ethical Note

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

Table 1
Fixed effects explaining variation in the univariate model of boldness (quantified as the negative of flight initiation distance) for three age classes of yellow-bellied marmots

	Juveniles		Yearlings		Adults	
	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
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 (male)	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 (afternoon)	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	2.62e-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 behaviour (look)	0.302 (0.328)	0.704	0.041 (0.194)	0.881	-0.048 (0.230)	0.772

Significant effects are in bold.

RESULTS

Environmental Factors

Environmental factors affected boldness of juveniles, yearlings and adults differently. For juveniles, boldness increased with predator pressure and as the day progressed. As expected, juveniles fled sooner if they alerted sooner (Table 1). Yearling boldness increased with predator pressure. Yearlings also became bolder as the number of trials and pedestrian traffic increased. Males were bolder than females, and individuals that gained mass quicker were also bolder. Individuals in better body condition were less bold. Again, individuals fled sooner if they alerted to the observer sooner. Adult boldness increased as trial number, pedestrian traffic and predator presence increased. Adult males were less bold than females. Furthermore, both alert distance and distance to burrow affected boldness: individuals that alerted sooner and that were farther from a burrow were less bold (Table 1).

We found that juveniles became more docile as the active season progressed (Table 2), while no such effect was seen in yearlings or adults (Table 2). Additionally, faster-growing yearlings were more docile, and yearlings in better body condition were less docile in the afternoon. Adults were more docile as the time between trials (days) increased. Males were less docile than females, and individuals were less docile in the afternoon and in areas with higher pedestrian traffic. Date and mass at capture were highly correlated for both juveniles and adults (Pearson correlation: juvenile: $r_{4006} = -0.884$; yearling: $r_{2292} = -0.894$), which created a multicollinearity issue, and therefore reduced our ability to isolate their independent effects.

Table 2
Fixed effects explaining variation in the univariate model of trapping behaviours, a measure of docility, for three age classes of yellow-bellied marmots

	Juveniles		Yearlings		Adults	
	Estimate (SE)	P	Estimate (SE)	P	Estimate (SE)	P
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)	0.950	0.004 (0.001)	0.005
Sex (male)	0.022 (0.043)	0.352	-0.010 (0.063)	0.409	-0.238 (0.086)	0.001
Time (afternoon)	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)	0.820	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)	0.680	0.001 (0.001)	0.566

Significant effects are in bold.

Repeatability within and Correlation between Life Stages

The repeatability estimates for boldness differed significantly between the three age classes ($\chi^2_2 = 6.01, P = 0.049$). Juvenile and adult marmots were not differentially consistent in their boldness (repeatability: $r = 0.037$ and $r = 0.048$, respectively), but yearlings ($r = 0.402$) showed consistent individual differences in boldness (Table 3). The individual variance component for yearlings did not differ significantly from that for juveniles ($\chi^2_1 = 2.237, P = 0.134$), but was significantly higher than that for adults ($\chi^2_1 = 4.431, P = 0.035$), and juvenile and adult variance components did not differ significantly from one another ($\chi^2_1 = 0.001, P = 0.966$; Table 4). We found no significant correlations between age classes in boldness (juvenile–yearling: $\chi^2_1 = 0.12, P = 0.728, N = 24$ individuals; juvenile–adult: $\chi^2_1 = 0.12, P = 0.727, N = 2$ individuals; yearling–adult: $\chi^2_1 = 0.055, P = 0.814, N = 13$ individuals; Table 4, Fig. 1). The few individuals measured at different ages, however, limited our ability to correctly estimate these correlations.

Docility was repeatable in juveniles ($r = 0.168$), yearlings ($r = 0.262$) and adults ($r = 0.272$) (Table 3). The individual variance component estimates for docility differed significantly between the three age classes ($\chi^2_2 = 8.57, P = 0.013$). The individual variance component for adults was significantly higher than that for juveniles ($\chi^2_1 = 8.48, P = 0.003$), whereas the yearling component did not differ statistically from that of juveniles ($\chi^2_1 = 2.11, P = 0.137$) or adults ($\chi^2_1 = 2.43, P = 0.113$) (Table 4). Docility was significantly correlated across all life stages (juvenile–yearling: $\chi^2_1 = 64.49, N = 401$ individuals, $P < 0.001$; juvenile–adult: $\chi^2_1 = 13.04, N = 146$ individuals, $P = 0.001$; yearling–adult: $\chi^2_1 = 37.81, N = 158$ individuals, $P < 0.001$) with correlation coefficients higher than 0.6 (Table 4, Fig. 1).

Table 3

Variance, ratio and significance of random effects using log-likelihood ratio tests (LRT) for both docility and boldness univariate calculated from models for juvenile, yearling and adult yellow-bellied marmots

Trait	Number of observations, individuals	Mean (SD) traits	Variance			Ratio		LRT (<i>df</i> =1)		<i>P</i>	
			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	119.498	37.212	<0.001	<0.001
Yearlings	2294, 445	4.384 (0.870)	0.208	0.027	0.792	0.262	0.034	185.344	10.368	<0.001	0.001
Adults	2607, 266	4.294 (0.989)	0.254	0.005	0.932	0.272	0.005	421.061	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	17.416	0.238	<0.001
Yearlings	204, 81	-43.268 (32.793)	0.617	0.082	1.536	0.402	0.053	13.907	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

Note that repeatability estimates from trivariate (Table 4) and univariate (Table 3) models differed slightly because only significant fixed effects from the univariate models were included in the trivariate analyses.

Behavioural Syndrome

Using a bivariate model for each age class, we found that the correlation between boldness and docility was not significant for any age class (repeatability \pm SE: juveniles: $r = 0.582 \pm 0.352$, LRT = 2.28, $N = 96$ individuals, $P = 0.131$; yearlings: $r = 0.186 \pm 0.193$, $\chi^2_2 = 0.829$, $N = 99$ individuals, $P = 0.362$; adults: $r = 0.587 \pm 0.936$, $\chi^2_2 = 1.608$, $N = 80$ individuals, $P = 0.204$).

DISCUSSION

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

Environmental Effects

Environmental factors that correlated with personality traits changed over developmental stages, suggesting that the environment influences age-specific personality (Stamps & Groothuis 2010). We saw boldness increase (in juveniles) and docility decrease (in yearlings and adults) as the day progressed. Although the exact reason for the within-day change is unknown, similar within-day changes in personality have also been seen in two species of coral reef fish due to temperature changes (Biro et al.

2010). Daily temperature changes may influence metabolic rate (Armitage 1991), which could influence personality traits (Biro et al. 2010). Body condition decreased boldness and docility in yearlings. These results are inconsistent with theoretical work suggesting that individuals in better body condition take more risks but incur fewer costs because they are better able to hold resources and escape predators (Luttbegg & Sih 2010).

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

Marmot interaction with humans seemed to have variable effects. Boldness increased with trial number and pedestrian traffic in yearlings and adults. Together, these factors suggest that marmots habituate to human disturbance over the summer (Li et al. 2011). Additionally, past research on eastern chipmunks, *Tamias striatus* (Martin & Réale 2008) and burrowing owls, *Athene cunicularia* (Carrete & Tella 2010) found a correlation between human disturbance and personality, suggesting habituation or habitat selection based on personality. In contrast, docility decreased in adults as pedestrian traffic increased. This coupled with an increase in docility as the days between capture increased suggest that marmots may become more sensitive to human interaction when trapped.

Yearlings that grew faster were more docile but also bolder. These are not consistent with the predictions made by Biro & Stamps (2008), who predicted that individuals that grow faster should engage in more risky behaviour to maintain that growth rate. Individual marmots do not have to protect or actively look for food patches (i.e. vegetation is abundant at our study site), thus decoupling the predicted link between risky behaviour and growth

Table 4

Repeatability (on diagonal), correlations (below diagonal) and pairwise comparison of repeatability (above diagonal) for docility and boldness for the different age classes (juvenile, yearling, adult) of yellow-bellied marmots

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

Estimates were obtained from trivariate models for each behaviour, considering each age class as a different trait. Estimates of repeatability are slightly different from univariate models (Table 1) because only significant fixed effects were used in these models to avoid overparametrization.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; see text for exact P values (parameter bounded to zero).

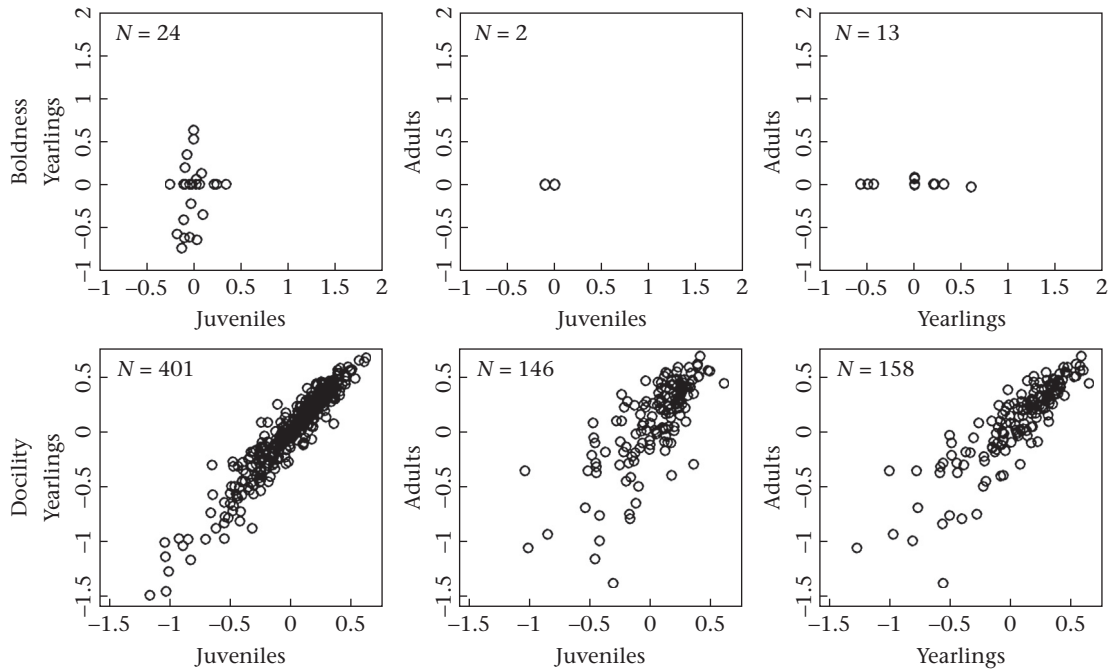


Figure 1. Relationships between juvenile–yearling, juvenile–adult and yearling–adult personality in yellow-bellied marmots. The top panel represents boldness (negative FID). The bottom panel represents docility (trapping behaviours). Best linear unbiased predictors (BLUPs) from trivariate models of boldness and docility are used for illustration purposes only. *N* represents the number of individuals for which data were available for both traits.

rate. In addition, faster-growing individuals might benefit from docility simply by not investing in more active and energetically costly nondocile behaviours.

Sex differences were found in yearling and adult boldness. Yearling males were bolder than females. All yearling males disperse, and this difference in boldness may be a method for individual males to prepare for dispersal. Alternatively, adult males were less bold than adult females. There is no apparent reason for this, but females have the added cost of gestation and lactation, and therefore need to be bolder to forage and survive hibernation (Andersen et al. 1976). Sex differences were also found in adult docility, with males being less docile than females. This result is inconsistent with the findings of a study of alpine marmots, *Marmota marmota*, where sexes did not differ in docility (Ferrari et al. 2013). However, Ferrari et al.'s (2013) study did not account for potential differences within each age group as our study did.

Repeatability within Life Stages

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

Future research should focus on the potential reasons for a lack of boldness in juveniles and adults. Juveniles may lack individual differences because they have not yet undergone experiences that lead to differentiation (Freund et al. 2013). Alternatively, lack of a boldness personality trait might be due to differences in life-history strategy between each life stage. Body mass strongly affects overwinter survival in juveniles but does so to a lesser degree in adults (Lenihan & Vuren 1996). Juveniles triple their body mass in the 3

months from first emergence to hibernation. Thus, juveniles should prioritize foraging by adopting a single consistent strategy, while yearlings may adopt multiple strategies to cope with certain life stage events such as dispersal. Juveniles have also been found to be less vigilant than yearlings and adults in general, supporting the hypothesis that they prioritize foraging (Li et al. 2011). Juvenile, or smaller, poeciliid fish (*Brachyraphis episcopi*) were also found to be bolder than larger individuals, suggesting there is a trade-off between growth and potential mortality (Brown & Braithwaite 2004). Adults, however, must cope with a highly variable, harsh environment and must therefore be plastic (Armitage 1991).

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

Stability within and between Traits across Time

We found differences between personality traits in stability across development. Boldness was not stable across development but docility was. Individuals' levels of boldness varied across all three life stages. However, the small sample of individuals with boldness data in multiple age classes limits conclusions from this data. We found no correlation between any age group. This result is consistent with the idea that behaviour is plastic and should change depending on the environment (Fox & Westneat 2010). Although the exact cause of the plasticity in personality is unknown, repeatability in boldness may be due to life stage events. For example, almost all yearling males and about half the yearling females disperse, and therefore, individuals exhibit different behavioural strategies to cope with dispersal or staying at the natal

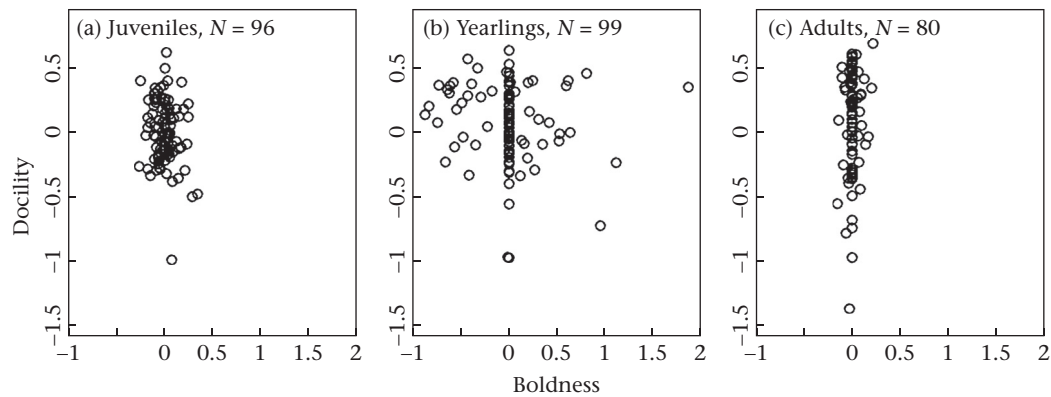


Figure 2. Relationship between docility and boldness in yellow-bellied marmot (a) juveniles, (b) yearlings and (c) adults. Best linear unbiased predictors (BLUPs) from bivariate models of docility and boldness are used for illustration purposes only. *N* represents the number of individual for which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

colony. Again, adults have settled at a location and must cope with the changing yearly environment (Armitage 1991). Individuals are therefore changing their behavioural plasticity depending upon age-specific life-history events.

In contrast to boldness, docility appears to be stable throughout an individual's lifetime, given the strong positive correlations between the three age classes in the present study. This suggests that docility is established at birth or early in life and is stable throughout an individual's lifetime. Adult docility may result from previous environmental constraints and selection during development (Sinn et al. 2008).

Behavioural Syndrome

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

Conclusion

In conclusion, we found that boldness and docility developed differently across life stages. This has major implications for our understanding of personality and raises a large number of questions about what might explain that difference. Juveniles grow rapidly and do not mate, yearlings disperse, and adults reproduce. Specific constraints and life histories of each age class are likely the basis for the observed differences in the ontogeny of personality. Selection can vary across life stages (Schluter et al. 1991; McNamara et al. 2009) and, therefore, different behavioural traits may be differentially important in those stages. Although we did not test for selection in this study, future research should focus on quantifying these different selection pressures throughout development and the potential adaptive reasons for the differences in the development of personality traits.

Acknowledgments

M.B.P. was supported by a GAANN fellowship, a GK-12 fellowship, and the UCLA Department of Ecology and Evolutionary Biology. D.M. was a National Science Foundation (NSF) REU fellow supported by DBI 0731346. V.A. was partially supported by a RMBL scholarship. J.G.A.M. was supported by a FQRNT fellowship and by the NSF. D.T.B. was supported by the National Geographic Society,

UCLA (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the NSF (IDBR-0754247 and DEB-1119660 to D.T.B., as well as DBI 0242960 and 0731346 to the Rocky Mountain Biological Laboratory). We thank all the marmoteers over the past decade for help collecting the data, and the Blumstein lab for comments on previous versions of the manuscript. We also thank Lynn Fairbanks, Peter Nonacs, and three anonymous referees for their constructive feedback on previous versions of the manuscript.

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