



Development of boldness and docility in yellow-bellied marmots



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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

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