

Behavioral syndromes in yellow-bellied marmots, *Marmota flaviventris*: Is there a correlation between boldness and exploration?

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Title

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Abstract

Animal personality typically refers to a behavioral manifestations stable across time and contexts (Sih *et al.* 2004, Réale *et al.* 2007). Personality has been shown to shape fitness and may therefore shape population dynamics through such traits as dominance, response to stress, and reproductive performance. Within the personality framework, behavioral syndromes refer to personality traits expressed population-wide that are consistent over a variety of contexts (e.g., an individual might be aggressive in mating, feeding, parental care), or correlations between different traits (e.g. aggression and boldness) (Réale *et al.* 2007). Using flight-initiation distance and open-field trials, respectively, we searched for correlations between boldness and exploration in 42 yellow-bellied marmots (*Marmota flaviventris*) from the area around the Rocky Mountain Biological Laboratory in Gothic, Colorado. We did not find a behavioral syndrome linking boldness and exploration in the marmots of RMBL.

Introduction

Animal personality typically refers to a behavioral manifestations stable across time and contexts (Sih *et al.* 2004, Réale *et al.* 2007). Personality has been shown to shape fitness and may therefore shape population dynamics through such traits as dominance, response to stress, and reproductive performance. For instance, individual variations in aggression - a state of great interest to ecologists - are capable of influencing mating, antipredator behavior, and dispersal - essential components of population birth, death, and migration (Sih *et al.* 2004). Dispersal from natal environments is responsible for the maintenance of genetic variation, and was found by Dingemanse *et al.* (2003) to be correlated with exploration of novel space in great tits (*Parus major*). In a meta-analysis of personality studies published on a variety of species, bold individuals were also found to incur greater reproductive success (Smith and Blumstein 2008).

Within the personality framework, behavioral syndromes refer to personality traits expressed population-wide that are consistent over a variety of contexts (e.g., an individual might be aggressive in mating, feeding, parental care), or correlations between different traits (e.g. aggression and boldness) (Réale *et al.* 2007). Behavioral syndromes can shape the coevolution of traits in a population, explaining potentially non-adaptive behavior when traits cross situations and contexts to cause less than optimum behavioral plasticity (Sih *et al.* 2004). For example, bold individuals who are inappropriately bold in situations in which they should be shy or *advantageously* aggressive mothers who are *overly* aggressive in parental contexts. Linked traits might also explain why populations do not always demonstrate adaptive behavior that we might expect to observe.

An example of such trait coevolution is discussed in Huntingford's paper demonstrating a behavioral syndrome of positively correlated anti-predator and conspecific breeding aggression in three-spine sticklebacks (Huntingford 1976). Huntingford posited that situations of high-predation might select against individuals who express heavy levels of breeding aggression that

is conspicuous to predators. Since the two traits were shown to be positively correlated, the selective pressure exerted on conspecific aggression might thus result in lower and higher anti-predator aggression in situations of high and low predation, respectively.

Yellow-bellied marmots (*Marmota flaviventris*) offer an ideal opportunity to study behavioral syndromes; they are large, diurnal, and – as burrow-dwelling animals – are reliably found in the same place. The marmots of the Rocky Mountain Biological Laboratory (RMBL) are particularly well-suited to study due to the long-term data on the population in and around the field station. Conducting individual-based studies at the RMBL is also relatively simple; Nyanzol fur marks and unique ears tags facilitate differentiation during social observation and trapping sessions, helping to ensure repeatable observations and avoid inadvertent pseudoreplication.

Additionally, Armitage and Van Vuren (2003) demonstrated that yellow-bellied marmots vary along a shy-bold continuum and that these behavioral phenotypes correlate with dispersal, play behaviors, and recruitment success. It remains uninvestigated, however, whether there exists in yellow-bellied marmots a correlation between boldness and exploration. Behavioral syndromes linking these two traits have been demonstrated in great tits (*Parus major*) (Dingemanse *et al.* 2003) and blue-gill sunfish (*Lepomus macrochirus*), among others (Wilson and Goden 2009).

I investigated behavioral syndromes positively linking boldness and exploration in yellow-bellied marmots using flight-initiation distance and open-field testing, respectively.

Methods

We conducted our study on the marmots of the Rocky Mountain Biological Laboratory in Gothic, Colorado. Due to the logistical constraints of scoring open-field trials and small sample size for data collected during the summer of 2011, I worked with archived data from 2009 and 2010; the experiments remain essentially identical to those I performed as described in the methods section below.

Boldness is “an individual’s reaction to any risky situation, but not new situations” (Réale *et al.* 2007). Human presence, which presents risk without novelty, can be used to quantify individuals’ boldness through flight-initiation distance - the distance from an advancing threats at which an individual flees (Ydenberg and Dill 1986). Upon arriving at a colony, experimenters wait 10-15 minutes to allow marmots to habituate to human presence. After this period, we identify an individual and approach a trained pace of 0.5m/s, dropping flags to note when subjects alert to our approach and flee. We used a laser rangefinder (Bushnell, Kansas) or pacing to measure starting distance, flight initiation distance, and the distance from an individual to its burrow. Data on date, time, age, sex, initial behavior, the number of marmots within 10 meters (as judged by observer) initial substrate, escape substrate, the gait of the fleeing marmot, and slope (using a clinometer) were also gathered. Experimenters also recorded whether the marmot was at a site up valley (north of Gothic) or down valley (south of or in Gothic).

The mixed-effects model on FID data, run in R (R Development Team, 2011), included: trial number, Julian date, age class, sex, valley, initial substrate, escape slope, and distance to burrow. All variables were fixed except for unique ID (UID), which refers to an individuals’ ear tags. Results were then analyzed using a Monte Carlo Markov Chain (MCMC) with 30,000

simulations, providing p values and estimates used to evaluate significance and the directionality of influence on FID. A BLUP was then used to extract a behavioral profile for each individual. A best linear unbiased predictor (BLUP) was extracted for the random effects (Kruuk 2004). BLUPs have often been used to provide better estimates of a behavioral trait than just using the mean of repeated measures.

Exploration was quantified by recording an individual's behavior in an open-field test, commonly used to measure exploratory behavior and locomotive activity in rodents. Our open-field consisted of a 36" cubic box with a grid drawn upon the floor. A camcorder was mounted above the box to record the animals' behavior. Individuals were placed, one at a time, in the box for six minutes, and after three were exposed to a mirror (part of a different test called mirror-image stimulation); we only utilized the first three minutes of the trial. Based on their time in the box, the marmots were subjectively rated from 1-7 on a number of adjectives: active, aggressive, apprehensive, cautious, confident, curious, excitable, fearful, irritable, oppositional, playful, protective, deliberate, solitary, and strong.

A Principle Component Analysis performed in SPSS was used to reduce these adjectives into three factors. One of which was identified as an active/explorative axis. Factor scores for the activity axis were extracted from each open-field trial. They were analyzed with a linear mixed model along with trial, sex, age class, season (wherein 'early' is April, May; 'middle' is June, July; and 'late' is August, September), valley (wherein 'up valley' was north of Gothic and 'down valley' was in or south of Gothic), time between handling and trial (TBT), date between trials (DBT), and time of day as fixed effects and identity as a random effect. Individual BLUPs were then extracted for this personality trait.

A Pearson's correlation analysis was performed using BLUPs obtained on 42 individuals who had both an exploration and boldness score.

Results

The FID mixed-effects model included the variables: trial number, Julian data, age class, sex, valley, initial substrate, escape slope, and distance to burrow (Table 1). Using values obtained from the MCMC analysis, we found age (adult vs. pup), valley (up vs. down), distance to burrow, and alert distance to explain significant variance in FID scores. The mean generated by the MCMC indicates in what direction the variable affected flight-initiation distance. Negative values indicate that an increase in the value of the particular variable decreased flight initiation distance. All significant factors in the FID model had positive coefficient values except for age – an increase in age *decreased* the distance at which an animal fled by an average of 4.5 meters.

For open-field tests, only trial number (how many times an individual had previously been in the box) and valley (up vs. down) proved significant using MCMC scores, with p values of 0.000 and 0.0001, respectively

Forty two individuals had both an boldness and exploration value. A Pearson's correlation gave an $r^2 = -0.1707$ (t-value=-1.0816, d.f.=39, p-value =0.2861).

Discussion

We failed to find a significant correlation between boldness and exploration in the population of yellow-bellied marmots surrounded the Rocky Mountain Biological Laboratory. We thus infer that there was no boldness/exploration syndrome. While they may persist or be favored in certain conditions, behavioral syndromes represent a potentially maladaptive limit to behavioral plasticity. As aforementioned, behavioral spillover may results in situations in which animal are inappropriately bold or aggressive, for example. Thus, natural selection might select against persistent individual variations in personality traits and towards an optimum degree of expression between boldness and exploration. It is possible that the environment inhabited by the RMBL marmots favored severing a behavioral syndrome linking between the shy-bold and exploration-avoidance continuums seen in other species. Another possibility is that a behavioral syndrome between boldness and exploration never existed, and that selection always favored independent evolution of the two traits.

While we cannot be sure as to which description is more accurate, or the exact causes for decoupling, one can speculate as to various pressure that might favor independent evolution of boldness and exploration. Predation might serve to select against bold individuals who are inappropriately exploratory; an individual who allows predators to get close before fleeing *and* explores far from burrows into exposed areas is more likely to be caught than bold individuals who stay relatively close to burrows. Reproductive success might also be compromised in individuals for whom boldness and exploration are correlated; shy individuals, while perhaps avoiding predators more successfully, might be too shy to incur good mating success, especially given a propensity not to disperse and find mates.

It is interesting that we found no positive correlation between boldness and exploration given both that boldness has been linked to dispersal in RMBL's marmots and tests of exploration have been linked to dispersal in other species, such as *Parus major* (Dingemanse 2003). Perhaps the particular tests we employed as measures of exploration fail to capture the particular exploratory characteristics of the bold marmots inclined towards dispersal.

Exploratory behavior may also be subject to greater positive selective pressure in *Parus major* due to a difference in reproductive strategies. *Marmota flaviventris* have a generally polygynous system in which several females share one male. *Parus major*, though engaging in extra-pair copulations, are socially monogamous; when a pair divorces, it is the female that disperses farther to find new territory and mate (Harvey et al 1979). Approximately 50% of RMBL's females marmots disperse from their natal colonies. In males, dispersal is nearly 100% (Armitage and Downhower 1981). We might thus expect to females to show more variance in levels of exploration, while males would be subject to stronger selection toward boldness - particularly as yearlings when dispersal is most common.

It may be possible the RMBL marmots are in the process of developing a behavioral syndrome involving *negative* correlation between boldness and exploration (indeed, we did find a slight negative correlation between boldness and exploration, though it was not statistically significant). Hedrick (2000) showed this kind of compensatory negative correlation in male crickets, who compensate for risky calling by being more cautious in novel situations and displaying a greater latency to approach after being given a predator cue. In marmots, a negative correlation between boldness and exploration might facilitate a similarly adaptive compensation; individuals who are bolder towards predators might stay closer to burrows and those who venture further might flee from predator sooner upon alerting to them.

Using FIDs and open-field trials as measures of boldness and exploration, we did not find a behavioral syndrome linking the two personality traits in RMBL's population of yellow-bellied

marmots. It is possible that these two traits were never linked or that they were decoupled through natural selection; positive correlations between boldness and exploration could be selected against by reproductive and predation pressures. It is also *possible* that RMBL's marmots could be evolving a negative behavioral syndrome in which bold marmots tend to be less exploratory and vice versa. Future research might investigate the fitness consequences of boldness and exploration or correlations between these traits and other aspects of personality.

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	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	Pr(> t)
Intercept	-5.1130	-4.2785	-25.8174	16.0833	0.6910	0.6312
Trial	-0.4469	-0.3398	-1.2744	0.5563	0.4709	0.3220
Julian date	-0.0084	-0.0179	-0.1035	0.0675	0.6800	0.8477
Age Class (Yearling) §	-1.7547	-2.9393	-7.4610	1.6990	0.2085	0.4653
Age Class (Adult) § (*)	-4.5097	-6.0053	-10.5575	-1.3866	0.0096	0.0708
Sex (M) †	0.1909	-0.2598	-2.8367	2.2154	0.8371	0.9002
Valley (Down Valley)‡ (*)	7.1222	5.2795	2.0476	8.7259	0.0021	0.0005
Time (PM) α	1.6936	1.6314	-1.5047	4.9778	0.3203	0.2999
Initial Behavior (Look) •	0.5328	0.7191	-5.0330	6.1906	0.7987	0.8503
Initial Behavior (Social) •	10.0633	10.3434	-3.0479	22.6784	0.1145	0.1313
Initial Behavior (Walk) •	5.0210	4.7061	-13.2155	22.2713	0.6055	0.5862
# of Marmots within 10m	0.1377	0.0057	-1.1332	1.1077	0.9879	0.8048
Start Distance (°)	0.0774	0.0962	-0.0054	0.1952	0.0592	0.1272
Alert Distance (*)	0.7115	0.7273	0.6144	0.8357	0.0000	0.0000
Initial Substrate (High Vegetation) ∞	10.4570	11.7976	-6.0880	29.8417	0.1963	0.2625
Initial Substrate (Low Vegetation) ∞ (°)	7.0497	7.2685	-1.1020	15.9658	0.0938	0.1018
Initial Substrate (Stone) ∞	5.6767	6.5363	-1.5280	14.2416	0.1041	0.1483
Initial Substrate (Experimental) ∞	2.8362	4.0649	-4.7868	12.9078	0.3717	0.5233
Slope of Escape	0.0229	0.0284	-0.0289	0.0883	0.3403	0.4483
Distance to Burrow (*)	0.3898	0.3331	0.1129	0.5654	0.0045	0.0004

Table 1: Flight-initiation Distance Results from Monte Carlo Markov Chain with 30,000 simulations. (*) Indicates significance), (°) Indicates trending toward significance, § Juvenile as reference, †Female as reference, ‡Up valley as reference, α AM as reference, •Forage as reference, ∞ Dirt as reference

Table 2: Open-Field Tests Results from Results from Monte Carlo Markov Chain with 30,000 simulations. (*) Indicates significance) § Juvenile as reference, †Female as reference, ® Early Season as reference, ‡ Up valley as reference,

	Estimate	MCMC Mean	HPD 95 Lower	HDP95Upper	pMCMC	Pr (< t)
Intercept	1.0912	1.2056	0.4509	1.9223	0.0011	0.0039
Trial (*)	-0.9049	-0.8650	-1.1920	-0.5317	0.0000	0.0000
Sex (Male) †	-0.2846	-0.2596	-0.5828	0.0657	0.1107	0.1055
Age (2) §	0.1849	0.1189	-0.3526	0.5824	0.6177	0.4535
Age (3) §	0.0447	-0.0199	-0.5766	0.5105	0.9444	0.8768
Season (Middle)®	0.0996	-0.0581	-0.6187	0.5131	0.8443	0.7285
Season (Late)®	0.1859	-0.0483	-0.8420	0.7509	0.9027	0.6480
Valley (Down) ‡ (*)	0.7851	0.7726	0.4213	1.1376	0.0001	0.0001
Time Between Trial	-0.0051	-0.0049	-0.0135	0.0039	0.2629	0.2422
Date Between Trial	0.2233	0.2295	0.2688	0.2688	0.2688	0.2688

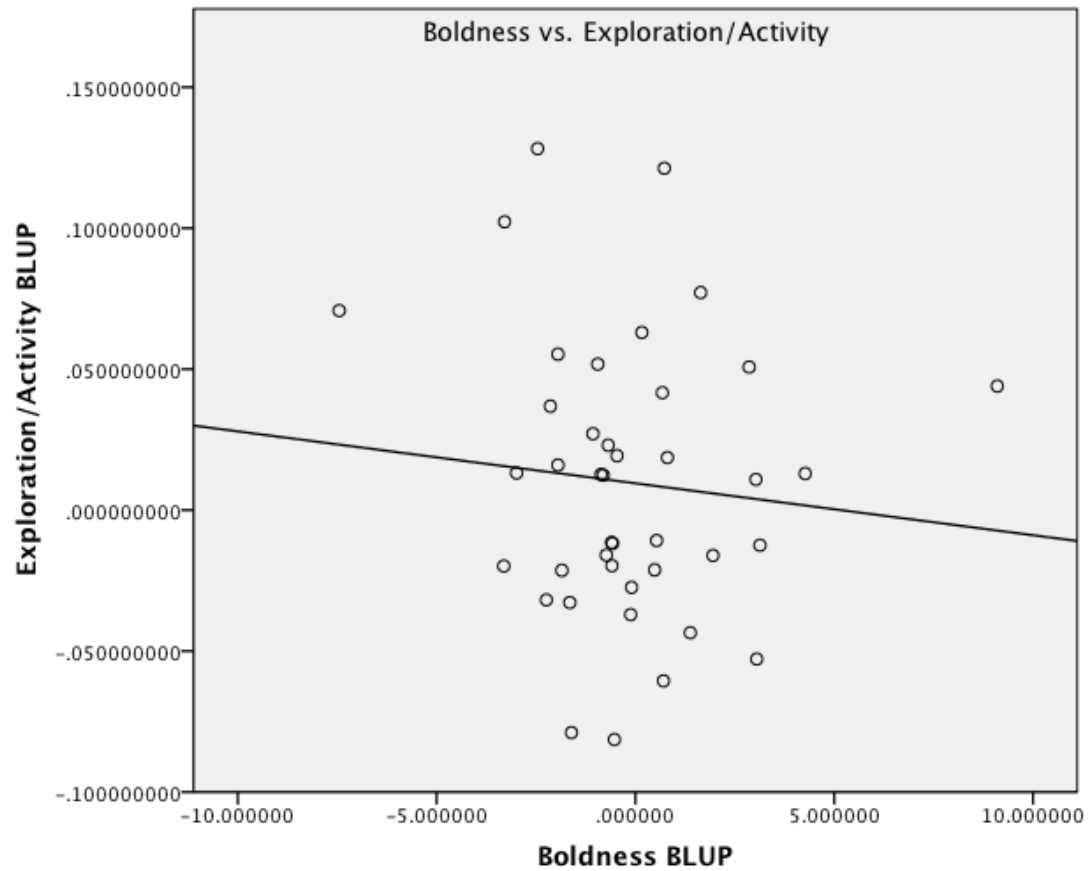


Figure 1: Individual Boldness scores plotted against Exploration/Activity scores. Results from Best Linear Unbiased Predictor Analysis for 42 individual.