

Development and structure of boldness and aggression in yellow-bellied marmots

Student: Vanessa Alejandro, Dakota McCoy

Mentor: Matt Petelle, Dan Blumstein

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ABSTRACT

The ontogeny of personality traits is crucial to understanding their ecological significance but has not yet been well-studied. We examined the development of two traits that are commonly correlated in a syndrome, boldness and aggression, in a long-term study of yellow-bellied marmots (*Marmot flaviventris*). Using data collected since 2002, we quantified the repeatability and syndrome structure of these two traits in two age groups (juveniles and yearlings/adults). We quantified boldness through Flight Initiation Distance (FID) tests and aggression through two methods: (i) summing scored behaviors of individuals during trapping to create an index of aggression, and (ii) examining each trapping behavior individually. We found that aggression is a repeatable personality trait in both age classes, but that boldness is only a repeatable personality trait in yearlings/adults. We found no correlation between boldness and aggression in either group. We found that variance in aggression decreased from pups to yearlings/adults, and variance in boldness tended to increase. This suggests that personality traits can develop at different times and that these two traits may be under different directional selection during our study.

Keywords: yellow-bellied marmot, boldness, aggression, docility, personality, syndrome

INTRODUCTION

Animal personality is defined as consistency in inter-individual differences in behavior across time or contexts (Sih et al. 2004; Herczeg & Garamszegi 2012). Réale et al. (2007) classified personality traits into five categories (shyness-boldness, exploration–avoidance, activity, sociability, and aggression). Each can be viewed as continuous traits with an individual falling somewhere along a given continuum. Personality traits can also be correlated across contexts in consistent individual differences to create a behavioral syndrome.

Personality traits, and syndromes have been shown to have major impacts on ecology and evolutionary dynamics (Sih et al. 2004). Personality may influence a variety of important

life history traits that may include: fitness (Gerald et al. 2001, Dingemanse et al. 2002, Réale and Festa-Bianchet 2003, Both et al. 2005, Dingemanse and Reale 2005, Camperio Ciani et al. 2007), the likelihood of natal dispersal (Dingemanse et al. 2002, Mehlman et al. 1995, Fraser et al. 2001), an individual's dominance (Dingemanse and de Goede 2004), and an individual's ability to acquire a high-quality territory (Both et al. 2005) Thus, personality may have profound effects on evolutionary and population dynamics (Reale et al. 2007).

Personality traits may also be correlated across contexts and create behavioral syndromes. The study of such syndromes has become increasingly important to understand the potential trade-offs and constraints to adaptive evolution (Sih et al. 2004). Thus, it is valuable to understand both the development of both consistent individual differences (personality or temperament), and the development of correlations across contexts (syndromes).

Previous ontogenetic research has focused on how personality traits develop over life-stages and whether the structure of behavioral syndromes is stable across ontogeny (Sinn et al. 2004, Bell and Stamps 2004, DiRienzo et al. 2012). For example, boldness, an individual's reaction to a non-novel, risky situation, was followed in dumpling squid (*Euprymna tasmanica*) (Réale et al. 2007, Pruitt and Riechert *in press*). These particular squid exhibit consistent behavior within a context from young adulthood to sexual maturation. At sexual maturity, shy individuals displayed more plasticity while feeding than their bold counterparts, and bold individuals were more plastic in a threat context (Sinn et al. 2004). However, to some extent, we expect ontogenetic trajectories to be influenced by context because different populations or years may select for different traits or syndromes (Réale and Festa-Bianchet 2003, Bell and Stamps 2004). For example, boldness and aggression in two populations of sticklebacks (*Gasterosteus aculeatus*) were inconsistent over ontogeny, but syndrome structure stayed stable (Bell and Stamps 2004). In one stickleback population, aggression, defined as the degree of aggressiveness towards mates, prey, and potential or actual predators (Reale et al. 2007, Pruitt and Riechert *in press*), was the only trait that remained consistent from juvenile to adult, but the correlation between boldness and aggression also remained. In a second population, no correlations remained stable, and aggression was the only trait to remain consistent across ontogeny (lasting until the individuals were sub-adults) (Bell and Stamps 2004).

Correlations between boldness and aggression have been seen in numerous taxa including fish (e.g., Bell 2004, Ruiz-Gomez & Huntingford 2012, Brick and Jakobsson 2001, Schjolden et al. 2005, Moretz et al. 2007, Bourne and Sammons 2008), spiders (for review, see Pruitt And Riechert 2012), in birds (Dingemansse et al. 2007), and in mammals (Benus et al. 1991). A recent review by Wiedenmayer (2009) showed that anti-predator behavior, and therefore aggression and boldness, developed sequentially through a reorganization of unlearned responses and behavioral modifications from repeated exposure to frightening

stimuli. Therefore, experience may play an integral role in the formation and structure of personality traits and syndrome structure. For example, fish raised in captivity had personalities similar to their parents, but increased their boldness when presented with a frightening stimuli. Early experience and the environment also may influence syndrome structure. Populations of stickleback fry exhibited the common aggression–activity–exploration syndrome only in environments with predators (Dingemanse et al. 2007)).

Recent research suggests that boldness and aggression (more so than other personality traits) may be correlated because both are modulated by the same hormones (Chang et al. 2012). Alternatively, there is some evidence that these traits are correlated due to common genetics and molecular pathways (Ketterson and Nolan 1999). If the two are genetically linked, a syndrome, strong selection on one, may “carry along” the other trait along a pathway of least resistance (Shluter 1996, Bell 2004). While this hypothesis assumes that there are evolutionary constraints, it is also possible that positive selection for combinations of behaviors could produce correlations between boldness and aggression (Cheverud 1996); this could be termed an “adaptive” hypothesis (Bell 2004). For example, it is possible that in certain environments, aggressive behavior could only be viable if balanced by shy behavior. Under the adaptive hypothesis, selection could also decouple pairings of aggression and boldness, should such a correlation prove maladaptive (Wilson 1998).

Understanding the development of boldness and aggression is important because we do not fully understand the adaptive reason for consistent behavior. Certainly, personality may be linked to different life-history strategies (Biro and Stamps 2008); for example, tradeoffs in fecundity (early versus late) and growth versus mortality have been proposed as reasons that individual variation in boldness and aggression are maintained (Stamps 2007). However, the consistency in individual expression of these traits is considered “puzzling,” since one would expect behavioral plasticity to be advantageous in many situations (Biro and Stamps 2008). Teasing apart aspects of the development of these personality traits along with the structure of the boldness-aggression syndrome throughout ontogeny will provide insights into the adaptive nature of personality traits.

Here we capitalize on a long-term ecological study of yellow-bellied marmots (*Marmota flaviventris*). Previous research shows that personality traits could have direct influence on reproduction rate in females. For instance, submissive females produced few offspring, social females about a third, and aggressive females a little more than half (Armitage 1986). In this study we investigate the development of boldness and aggression and the putative relationships between them. We categorized marmots into two age class categories—juveniles, and a combined group containing yearlings and adults. We justify this because in most respects,

yearlings behave in very adult-like ways and have similar mortality rates, while about 50% of pups die between birth and the end of their first hibernation (Armitage & Downhower 1974).

METHODS

Study Subject and Site

We studied yellow-bellied marmots at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38° 77'N, 106° 59'W) from 2002 to 2012. These facultatively social, sciurid rodents, weigh between 2 - 4 kg, live in kin groups based around matriline, and dwell in subalpine meadows, slopes, and clearings (Frase and Hoffman 1980). Marmots were trapped and individually marked with numbered ear tags (for permanent identification) and fur dye to facilitate identification from afar (e.g., Armitage 1982; Blumstein et al. 2009). We observed marmots from distances that did not disturb their normal behavior in the following seven colonies: Marmot Meadow, Boulder, Picnic, River, Bench, Avalanche, and the Gothic Townsite during the peak activity hours of 0630-1000 h and 1600-1900 h. We separated the colonies into two categories, up valley and down valley, because of differences in phenology (Blumstein 2009). Individuals from up-valley colonies (Picnic, Marmot Meadow, and Boulder) typically emerged 10-14 days after individuals in down-valley colonies (Van Vuren & Armitage 1991; Blumstein 2009).

To assess boldness, we conducted 892 Flight Initiation Distance (FID) experiments on 394 individuals (163 juveniles; 231 yearlings and adults) from 2003-2012. Docility was assessed with 9137 trapping events on 1668 individuals (1112 juveniles; 556 yearlings and adults) from 2002-2011. By quantifying boldness and docility in these two age categories, we examined the development of personality traits and syndromes.

Quantifying boldness with flight initiation distance

Flight initiation distance (FID), the distance an individual first flees an approaching threat (Ydenberg & Dill 1986; Blumstein 2003) is an anti-predator behavior that is commonly used as a metric for individual boldness (e.g., Cooper 2009, Wilson et al. 1994). In yellow-bellied marmots, FID has been shown to be both phenotypically (Blumstein et al. 2004) and genetically correlated (Blumstein et al. 2010) with maximum running speed, thus creating a locomotor-ability-boldness syndrome. Observers were trained until they consistently walked at a 0.5 m/s pace across a variety of terrains (Runyan and Blumstein 2004).

After arriving at a site, the researcher sat and quietly observed the marmots for at least 5 min, identifying any visible marmots by their fur marks. Once a marmot was selected as the test subject, the researcher stood and walked directly at the marmot at the constant pace. We recorded when marmots first became alert by raising their heads and looking toward the human (alert distance), when marmots first fled (flight initiation distance), the distance from marmot to researcher when the trial began (start distance), and the distance from the marmot to the burrow when it fled (burrow distance). After conducting a trial, the observer waited at least 10 min before conducting another trial. Additional experimental approaches were only conducted on different subjects, and individual marmots were tested no more than once per day (mean days between trials = 7.6, range = 1 – 57 days).

Personality traits are by definition, repeatable (Reale et al. 2007). To quantify repeatability of boldness, we fit linear mixed effects models to both age categories that included trial number, the distance from the marmot to the burrow, the distance from researcher to marmot at the start of the trial, alert distance, valley location, sex, time of day (AM or PM), and date as fixed effects. We included alert distance because previous research has shown it to have an effect on FID (Blumstein 2010). Furthermore, distance to burrow and distance from the researcher to marmot at the start of trial were included because we *a priori* suspected that these might affect FID (start distance: Cooper et al. 2008; distance to refuge: Dill and Houtman 1989; Blumstein 1994). In order to control for effects from the progression of the day and season we included time of day and the date. Our last fixed effect, trial number, was needed to control for habituation. We fitted marmot identity and year as random effects.

We calculated repeatability by dividing the amount of variance explained by marmot ID by the total amount of variance explained in the model. The resulting number represents the percent of variance explained by individual identity. We used a log-likelihood ratio test to determine whether marmot identity explained a significant amount of variation.

Quantifying aggression with trapping behavior

When trapped, marmots were transferred from the wire cage to a canvas handling bag for subsequent processing. At each trapping event, we recorded behaviors the marmot exhibited 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/or whether they failed to immediately walk into the handling bag. We studied the development of these traits individually, and we also created a docility index (Réale & Festa-Bianchet 2000). Following Réale & Festa-Bianchet (2000), we subtracted the sum of the dichotomously scored behaviors from 5 to create the index. A score of 5 thus indicates a non-

aggressive, docile individual, and inversely a low score indicates an aggressive, non-docile individual. For statistical analysis, we used both this summed aggression score and the individual scores from each trapping behavior.

To quantify repeatability of aggression, we fit linear mixed effect models for each age category with valley location, sex, time of day (AM or PM), and date. We included valley location to control for phenological differences between up and down valley. Time of day and date were included because of differences within day and throughout the active season. Sex was also included to control for potential differences between males and females. We included marmot identity and year as random effects. We extracted best linear unbiased predictors (BLUPS), which control for fixed effects to create individual docility scores for each marmot. Using BLUPS in this way has become common practice in quantifying personality traits (e.g., Schielzeth et al. 2008, Minderman et al. 2009). Repeatability was calculated as above.

We also fit general linear mixed-effects models for each individual trapping behavior with valley location, sex, time of day, and date as fixed effects. Individual and year were included as random effects. Log likelihood ratio tests were test significance of individual. Repeatability was not calculated for these models because generalized linear models do not provide residual variance.

Quantifying a Boldness-Aggression Syndrome

To test whether a boldness-aggression syndrome was present in this population of marmots, we took two approaches. First, we tested for a correlation between boldness and aggression for both age classes (juveniles and the combined yearling/adult class) by fitting linear mixed-effects models of FIDs that included docility BLUPS as an additional fixed effect. That is, we tested whether docility accounted for variation in FID, by including docility BLUPS as a fixed effect in our model. If a correlation existed between docility and boldness, the result of this model would indicate that marmot identity would not be significant because this variance would be explained by docility.

Second, we used a Principle Component Analysis (PCA) to understand the relationship between separate trapping behaviors and FID BLUPS. We calculated mean scores for each trapping behavior for each individual and included these values and FID BLUP in a PCA. This was done for each age group.

Statistical Details

All linear mixed-effects models were performed in R 2.14 (R Development Core Team 2011) with the lmer function in the lme4 package (Bates et al. 2011). We tested significance of random effects for the mixed effects models by performing log-likelihood ratio tests (Pinheiro & Bates 2000). Principle Components were extracted using SPSS 20 (IBM, New York). Throughout, we interpret $P < 0.05$ as significant, and $0.05 < P < 0.1$ as representing a non-significant trend. To estimate whether variance of each behavior differed from pups and adults, we used Levene's test (previously used for estimating change in behavioural variance in McPhee 2004). Analysis of changes in variance can indicate whether selection may be operating (e.g., Snell et al. 1988): for example, a decrease in variance may indicate that some sort of selection is present. Analyzing changes in variance during ontogeny informs our study of the development of these personality traits, because it reveals patterns that may be selection-driven

RESULTS

Is boldness repeatable?

We found that juvenile marmots were not consistently bold, but that yearlings and adults showed consistent individual differences in flight initiation distance (Table 1). For juveniles, females fled at significantly greater distances than males. As expected, alert distance also had a significant effect on FID both for juveniles and adults/yearlings; the sooner a marmot pup alerts to the researcher, the sooner the individual fled (Table 2). For yearling and adults, the farther the marmot was from its burrow, the greater the FID.

Is aggression repeatable?

Our aggression docility index (calculated from the sum of trapping behaviors) was a repeatable personality trait in juveniles, yearlings, and adults (Table 1). Juveniles became less aggressive as the active season progressed (Table 3). No such effect was seen in yearlings and adults (Table 3). However, time of day had a significant effect on aggression in yearlings and adults; marmots become more aggressive as the day progressed.

For juveniles, valley location was significant for each individual trapping behavior, with up valley marmots being significantly more likely to bite and struggle in the trap, while down valley marmots were significantly more likely to call, walk immediately into the bag, and tooth chatter (Table 4). Juveniles were significantly more likely to struggle in the trap in the morning rather than the afternoon. As the season progressed, juveniles were significantly more likely to

walk directly into the bag and tooth chatter, but were significantly less likely to call, struggle, or try to bite through the trap (Table 4).

For yearlings and adults, valley location was significant for all behaviors, with up-valley marmots performing all behaviors more frequently except tooth-chattering and calling, for which the opposite effect was observed (Table 5). Males were significantly more likely to tooth chatter than females. Marmots were more likely to struggle, tooth-chatter, and to not walk immediately into the bag as the day progressed. Date was significant in whether the marmot walked directly into the bag or struggled in the trap, with a later date indicating higher likelihood of the marmot remaining calm in the trap but not walking immediately into the bag (Table 5).

Is there a syndrome?

Both methods showed no evidence of a syndrome. The Boldness linear mixed effects model which incorporated aggression BLUPs as a fixed effect showed that the aggression BLUPs did not explain a significant amount of variation in FID. That is, there was no observable, significant correlation between quantified boldness and aggression.

In our second method, the Principle Component Analysis, we also found no evidence for a syndrome. For juveniles, we extracted two principle components. The first was defined by struggling, biting, and not walking into the bag. We interpret this as an aggressive response. The second was defined by tooth-chattering and the FID BLUP. We were unable to interpret this component, although we expect that this odd result was driven by the very low number of pups who tooth-chattered ($n=112$). For yearlings and adults, we extracted two principle components. The first was defined by tooth chattering and alarm calling. We interpret this as a fearful response. The second was defined by biting and walking into the bag. We interpret this as an aggressive response.

How does variation change over time?

Using Levenne's test, we found that variance in boldness did not significantly differ between pups and adults ($t = 3.022$, $p = 0.083$). Variance in aggression, however, was significantly reduced in adults ($t = 29.67$, $p < 0.0001$).

DISCUSSION

Boldness

Our results indicate that boldness is not a trait in pups, but is present in yearlings/adults. Although boldness was insignificant, certain factors affected pup FID: valley, alert distance, and sex. The two areas (up and down valley) contain different environmental factors like the amount of humans (personal observation). Long-term habituation could explain closer FIDs in down-valley individuals, as human disturbance is greater down-valley. Furthermore, alert distance also influences flight distance. The quicker a marmot becomes alert to the observer the quicker the marmot flees. This effect has been seen in previous studies on marmot FID using a subset of this data (Runyan and Blumstein 2004). In yearlings and adults two factors were significant: alert distance and burrow distance. Distance to burrow has been linked to minimizing overexposure to predators (Blumstein 1998).

We are not certain why boldness exists only in yearlings/adults, but we hypothesize that pups focus on foraging or play. The tradeoff between foraging and vigilance does not apply to pups because they are concerned with only increasing their fat percentage. Pups emerge significantly later than most adults and need to triple their weight in order to survive the winter, thus, the time constraint causes boldness to be an insignificant trait in pups. Also, pups had a lower mean FID and alert distance than adults/yearlings. This indicates that the observer is able to get closer to the pups, which supports our hypothesis that pups are preoccupied foraging or playing. On the other hand, yearlings/adults have developed distinct strategies through boldness that allows them to better balance the tradeoff, which explains why they have a higher FID. So, as marmots age, individual strategies emerge that lead to particular benefits. For instance, shy adult male marmots are more likely to be territorial-colonial and produce more offspring (Armitage 2003). Furthermore, bold females are better recruiters of yearlings than shy females. Shy females tend to recruit only a few shy females, while, bold females recruit many bold and shy females (Armitage 2003).

Many explanations can be proposed as to why the development of boldness occurs this way. We are not completely certain of a single explanation. A possible hypothesis could be that pups canalize later in age in order to better adapt to their surroundings. A tradeoff between foraging and exposure to predation is associated with boldness. A bolder individual will forage more than a shy individual, but the former individual risks overexposure to predators. The canalization of boldness could be a strategy each marmot utilizes to find a balance in the tradeoff.

Aggression

Aggression, however, is a highly repeatable personality trait both in juveniles and in adults/yearlings. Aggression may be responsible for later life behaviors, such as dominance; there is some support for the idea that marmots practicing dominant behaviors early in life—such as play, which would be affected by aggressive or docile tendencies—is highly important to their social interactions later in life (Nowicki and Armitage 2010). Thus, it would be crucial for

marmots to develop differing aggressive strategies early in life, to ensure success in future dominance hierarchies. In rhesus macaques serotonin levels modulate both aggression and social dominance (referred to as competent social behavior), resulting in a phenotypic correlation (Higley et al. 1992). In fact, many behaviors coded as “aggressive” are also coded as representing “social dominance,” further underscoring the relationship between the two. Thus, it is possible that aggression/docility develops early in a marmots life because of the need to practice and hone skills relating to social interactions.

It is also possible that competition for milk and other resources (e.g., warmth) in the burrow could select for marmots that instinctively adopt different aggressive strategies from birth. Some have suggested that juvenile rodents compete for milk in the burrow, and juvenile rabbits face severe competition for milk (Bautista et al. 2008). In marmots, juvenile weight is crucial in determining survivorship; marmots must reach a critical mass to survive hibernation (Woods and Armitage 2003). This suggests that there would be strong selection for behaviors, which directly increase marmot weight. For example, an aggressive pup may compete for milk with siblings, while a docile pup may wait until aggressive individuals leave and then obtain milk. Depending on the situation, either strategy may be more favorable.

Aggression is important in several other areas of fitness. It enhances dispersal of yearling males (Armitage 1974), and yearling females delay dispersal when local adults do not display aggressive tendencies (Downhower and Armitage 1974). In one study of marmots classifying behavior as “social,” aggressive,” or “submissive,” aggressive females produced over half of the pups. It is possible that these widespread fitness advantages of adopting clear strategies in the realm of docility/aggression create strong selection pressures for innate (or early-developing) aggression/docility.

Variance in aggression decreases from juveniles to yearlings/adults. This suggests that, although the trait is present from a young age, selective pressures lead to a narrowing of viable strategies as time goes on. This could be due to learning based on specific environmental conditions, practicing and honing skills, which are already present, or differentially mortality. As the year goes on, pups become significantly less aggressive; this indicates that some honing of skills and/or learning are present even in the first year. Additionally, whether the pup lives in up or down valley (farther or closer from human habitation, later or earlier emergence, respectively) has a significant effect on its individual trapping behaviors. This further suggests that environment plays a role in the development of the trait of aggression over time.

Behavioral Syndrome

We did not find a behavioral syndrome between the traits of boldness and aggression, a result contrary to many previous findings. This suggests that the traits are not connected by an

underlying genetic or molecular mechanism, an implication found also by a study of stickleback: Bell (2004) found this syndrome only in populations subject to high predation risk. They conclude that this implies that the syndrome evolves through selection on multiple aspects of boldness and aggression phenotypes. Other studies have shown that this syndrome is expressed because of selection on hormones modulating many behavior patterns (see Veenema et al. 2011).

Ultimately, boldness emerged as a trait in yearlings/adults and increased in variance as age progressed, while aggression existed as a trait throughout the marmot's life but decreased in variance. Boldness may not exist in pups because there is no benefit for a particular strategy since the pups are focusing on foraging to gain enough weight in order to survive the winter. Variance increases in boldness because boldness becomes canalized in the form of various strategies that are beneficial in a varying environment. On the other hand, the aggressive personality trait exists in pups because aggression influences play, which predicts future dominant roles. Furthermore, aggression may decrease in variance because a certain type of aggression strategy may be more favorable for adults.

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TABLE 1: Repeatability of personality traits- boldness and docility- and separate trapping behaviors (partial measures of docility) in adult/yearling and juvenile yellow-bellied marmots.

	JUVENILES			ADULTS AND YEARLINGS		
	r	lrt	p	r	lrt	p
Boldness	0.04057	0.06786	0.79447	0.10912	5.80564	0.01597
Docility	0.18327	159.315	< 0.0001	0.27187	763.251	< 0.0001
Bite		91.9	< 0.0001		180.908	< 0.0001
Called		178.0	< 0.0001		647.1	< 0.0001
Struggled		21.2	< 0.0001		255.73	< 0.0001
Tooth		109.5	< 0.0001		218.13	< 0.0001
Reluctance to Walk into Bag		76.0	< 0.0001		456.004	< 0.0001

TABLE 2: Fixed effects explaining variation in Flight Initiation Distance, a measure of boldness.

	JUVENILES		ADULTS AND YEARLINGS	
	Estimate	p-value	Estimate	p-value
Intercept	12.3731	0.3419	2.0926	0.9274
Sex (M)	-5.3166	0.0492	0.0249	0.8748
Trial	2.5396	0.4695	-0.2511	0.8081
Time (PM)	-0.9417	0.6945	-0.7968	0.3865
Date	-0.1045	0.1093	-0.0257	0.5575
Valley (Up)	6.4326	0.0276	1.2972	0.4657
Alert Distance	0.8173	< 0.0001	0.7507	< 0.0001
Burrow Distance	0.1405	0.1955	0.3385	< 0.0001

Female, AM, and down-valley are reference groups

TABLE 3: Fixed effects explaining variation in summed trapping behaviors, a measure of aggression.

	Juveniles		Adults/Yearlings	
	Estimate	p value	Estimate	p value
(Intercept)	2.0563	< 0.0001	4.2683	< 0.0001
Sex (M)	-0.0138	0.9487	-0.0471	0.1583
Valley (Up)	-0.1474	0.0643	0.0117	0.4225
Time (PM)	0.0216	0.587	-0.1206	< 0.0001
Date	0.0101	< 0.0001	0.0005	0.5273

Female, AM, and down-valley are reference groups

TABLE 4: Fixed effects explaining variation in juvenile trapping behaviors, a measure of aggression.

	Bite		Called		Walk_Bag		Tooth		Struggled	
	Estimate	P-Value	Estimate	P-value	Estimate	P-Value	Estimate	P-Value	Estimate	P-Value
(Intercept)	0.1348	0.0035	1.1003	< .0001	0.0384	0.8947	-0.0779	0.0095	0.813	< .0001
Sex (M)	0.0049	0.6159	0.0006	0.9127	0.0093	0.3832	0.0036	0.6386	0.0073	0.7826
Valley (Up)	0.0407	< .0001	-0.1041	< .0001	-0.0419	0.0141	-0.0174	0.0016	0.1171	< .0001
Time (PM)	0.0063	0.3089	-0.0121	0.5242	0.0026	0.8583	0.0134	0.0545	-0.026	0.0393
Date	0.0005	0.0271	-0.0038	< .0001	0.003	< .0001	0.0005	0.0001	-0.0033	< .0001

Female, AM, and down-valley are reference groups

TABLE 5: Fixed effects explaining variation in adult/yearling trapping behaviors, a measure of aggression.

	Bite		Called		Walk_Bag		Tooth		Struggled	
	Estimate	P-Value	Estimate	P-value	Estimate	P-Value	Estimate	P-Value	Estimate	P-Value
(Intercept)	0.0705	0.0084	0.2925	< 0.0001	0.8559	< 0.0001	0.0452	0.061	0.1614	0.0001
Sex (M)	0.0062	0.3961	0.0134	0.3278	0.0086	0.6047	0.0283	0.0013	0.01	0.1977
Valley (Up)	0.0523	< 0.0001	-0.1208	< 0.0001	0.0365	0.0353	-0.0186	0.0417	0.1006	< 0.0001
Time (PM)	0.0147	0.0529	0.0417	< 0.0001	-0.0258	0.0353	0.0284	< 0.0001	0.0107	0.2635
Date	0.0002	0.2064	-0.0004	0.0639	-0.0006	0.0024	0	0.9471	-0.0005	0.0092

Female, AM, and down-valley are reference groups

TABLE 6: Principal Component Analysis of mean individual trapping behaviors with the Best Linear Unbiased Prediction (BLUP) generation from the Linear Mixed-Effect Model of FID in Juveniles.

Component	Juveniles		Adults/Yearlings	
	1	2	1	2
Tooth	.035	.685	.677	.197
Called	.389	.463	.780	-.158
Struggled	.782	.114	.416	.471
Bite	.764	.187	.152	.748
Walk_Bag	-.685	.126	-.214	.690
FID BLUP	-.023	.715	.277	.011

Graph 1: Graph of aggression and boldness syndrome:

