

Are vigilance and flight initiation distance correlated in yellow-bellied marmots?

Abstract

Behavioral syndromes are widespread and can have important ecological consequences, since correlations between distinct behaviors shape how animals can respond to changing pressures and can limit behavioral plasticity. Various antipredator behaviors have been identified within behavioral syndromes in many species, and therefore studying the structure of potential behavioral syndromes is important for understanding an animal's overall behavioral response to predators. This study focused on two antipredator behaviors in yellow-bellied marmots (*Marmota flaviventer*): time allocation to vigilance during foraging, which represents an individual's baseline level of wariness, and flight initiation distance (FID), which quantifies the flightiness of an animal in response to a predator. We estimated the correlation between these traits by fitting bivariate model on data collected over 18 years and found a modest correlation between vigilance and FID at the individual level.

Introduction

Just as humans have unique personalities, non-humans also may behave in consistently different ways and this may have ecological consequences (Niemelä and Dingemanse 2014). If individually distinct behaviors are consistent throughout time, and therefore less likely a result of external factors, the behavior is repeatable, and variation in that behavior within a population can be explained by individual identity (Bell et al. 2009). Animal personalities are common in many species and are important to consider as a source of variation in a population.

When multiple repeatable, individually distinct behaviors are correlated, they form a behavioral syndrome (Sih et al. 2004). Behavioral syndromes involving many different traits have been identified in a wide variety of species. Examples of behavioral syndromes include startle latency and early exploratory behavior in great tits (van Oers et al. 2003) or aggression during hunting with sexual cannibalism in female fishing spiders (Arnqvist and Henriksson 1997). Behavioral syndromes result in individuals with distinct behavioral types that can be seen in a variety of situations (Sih et al. 2004). For example, territorial aggression is correlated with aggression in different contexts in syndromes identified in male fiddler crabs and blue tits, with more territorial individuals also exhibiting higher aggression in the presence of predators or human handling, respectively (Reaney and Backwell 2007) (Fresneau et al. 2014). Behaviors like aggression, risk-taking and boldness have been commonly identified in syndromes, and therefore behavioral syndromes likely play an important role in shaping overall antipredator behavior in many animals.

Flight initiation distance (FID), which is the distance at which an animal flees from an approaching person, and vigilance while foraging are two important antipredator behaviors that have been studied in many species, including yellow-bellied marmots (*Marmota flaviventer*). While previous studies of marmots with relatively small samples found that FID was not significantly explained by individual identity (Runyan and Blumstein 2004) (Blumstein et al. 2004), another found significant individual differences in yearling marmots (Petelle et al.

2013). However, FID was found to be repeatable in a number of studies of birds (Carrete and Tella 2009) (Evans et al. 2010) (Scales et al. 2011) (Carrete and Tella 2017). Vigilance was previously found to be repeatable within individual marmots (Blumstein et al. 2004).

FID has been identified in several other behavioral syndromes. Territorial aggression and FID were correlated in rural populations of song sparrows (Scales et al. 2011) (Evans et al. 2010), and similar syndromes were identified between FID, exploratory behavior towards new food sources, and aggression in response to predators in rural populations of burrowing owls (Carrete and Tella 2017). In female kangaroos, FID was correlated with time allocation to vigilance during foraging (Edwards et al. 2013). Variation in individual time allocation to vigilance may be explained by other antipredator behaviors. Vigilance is thought to be traded off against foraging, since animals that allocate more time to watching for predators limit their food intake (Lima and Dill 1989). This trade off allows for a range in vigilance to be selected for, and the relative boldness or wariness of individuals has been found to impact foraging strategies in other species. Greater boldness was associated with more time spent feeding in barnacle geese (Kruvers et al. 2009) and higher food intake in fallow deer (Bergvall et al. 2011), so a correlation between time allocation to vigilance during foraging and FID is likely.

Previous studies on vigilance in marmots have focused on how different social, environmental, and other factors influence the time marmots allocate to vigilance during foraging (Bednekoff and Blumstein 2009) (Mady and Blumstein 2017). Blumstein et al. (2004) used a relatively small data set and correlated residuals of vigilance and FID from general linear models; there is a need to reanalyze this relationship with a larger data set and using more contemporary statistics.

The structure of syndromes may be influenced by predation risk (Bell and Sih 2007), and many species view humans as predators (Frid and Dill 2002). Prior work has identified differences in personalities between populations with different levels of human impact (Lapiedra et al. 2017). Furthermore, there are several instances of behavioral syndromes that exist in rural populations breaking down in urban populations (Scales et al. 2011) (Carrete and Tella 2017) (Bókony et al. 2012). Since behavioral syndromes are often associated with limited behavioral plasticity (Sih et al. 2004), the new conditions found in urban environments may be selecting against existing syndromes. It is possible that this decoupling of correlated traits has occurred with marmots in more highly disturbed colonies, and in order to understand if human activity is influencing behavioral syndromes, it is necessary to analyze potential correlations in behaviors along with differences in the level of human disturbance to marmots' habitat.

Analysis of both vigilance and FID with respect to disturbance levels has already shown that increasing human impacts on habitat has the potential to significantly alter these behaviors. In colonies with higher levels of human disturbance, marmots allocated more time to vigilance, and potentially because of this increased vigilance, gained less body mass (Uchida and Blumstein 2021). FID is also impacted by disturbance level, with marmots in more disturbed areas generally fleeing at a shorter distance, but the study also found that at the individual level

FID decreases with repeated approaches, except in some higher FID marmots whose FIDs increased over multiple trials (Uchida and Blumstein 2021).

The variety of habituation and sensitization responses found in analyses of FID and vigilance indicates a complex antipredator response and shows the need for further study of how these two behaviors are related. If vigilance and FID are in fact correlated, it is necessary to consider them together to fully understand behavioral responses, especially when human activity has the potential to severely disturb wildlife and cause long term behavioral changes with potential fitness costs.

Methods

FID

Flight initiation distance is measured by walking directly towards an identified marmot at a speed of 0.5 meters per second and marking the spots at which the marmot first looked at the researcher and the spot at which the marmot fled. The distances from the marmot's original location to the start of the approach, the initial alert (AD) and the initial flight (FID) are measured, and the slopes of the initial approach and the marmot's escape, as well as the substrate of the marmot's initial location and escape, are noted.

Vigilance

The amount of time marmots allocate to vigilance while foraging is measured by observing an individual for 2 minutes and quietly dictating behavioral transitions into an audio recorder. The ethogram includes: stand forage, rear forage, stand look, rear look, walk, run, other, out of sight. Researchers classify behaviors in real time, and the audio is later transcribed using the software JWatcher to calculate the proportion of time allocated to vigilance during the focal observation.

Statistical analysis

We fitted a bivariate model to estimate the correlation between FID and vigilance using data collected from 2002 to 2020. Valley position, disturbance level, sex, age class, number of individuals within 10m and trial number were fitted as fixed effects for both vigilance and FID. For vigilance, substrate level (high/low) was also included as a fixed effect, and alert distance, initial slope, initial substrate level and distance to burrow were also fitted as fixed effects for FID. We included year, colony, and unique identification (UID) as random effects. The model was fitted with a Bayesian approach using MCMCglmm in R. The model was run for 5,100,000 iterations with a thinning of 5,000 iterations and a burn in of 100,000 iterations.

Table 1. Summary of FID and vigilance data used in model.

	vigilance	FID
individuals	563	254
years	19	12

colonies	15	11
observations	3157	919

Results

Some of the fixed effects included in the model were significant and can explain variation in the two traits. For vigilance, substrate level and the number of individuals within 10m were the most significant effects [table 2]. Alert distance was particularly important in explaining variation in FID, although the distance to burrow, trial number and initial slope were also significant [table 3]. This bivariate model included multiple random effects, and therefore correlation between vigilance and FID must be considered with respect to each individual random effect. There is some variance among year in both FID and vigilance, but no correlation between these two traits [table 4]. At the colony level there is a slightly higher variance in both traits and no correlation [table 4]. The variances for both FID and vigilance are lower for UID than for colony, so there is greater consistency in these traits at the individual level. The correlation with respect to UID was 0.29840 (-0.028208/0.67942), somewhat higher than the other random effects, and while the credible interval does include 0, the majority of the distribution is positive. This indicates a weak, positive correlation between vigilance and FID with respect to UID.

Table 2a. Fixed effects fitted in the bivariate model for vigilance.

	posterior mean	p	eff. sample
intercept	0.5069536 (0.1935845/0.7897653)	0.002 **	1145.6
valley position up	-0.4765681 (-0.9273851/-0.0476869)	0.046 *	1000
disturbance level low	0.0158079 (-0.4348735/0.4507410)	0.900	1000
sex male	0.0051091 (-0.0734677/0.1020248)	0.910	1263.3
age class yearling	-0.1087455 (-0.192014/-0.0346281)	0.016 *	1000
number w/in 10m	-0.0828702 (-0.112053/-0.0572413)	<0.001 ***	1000
substrate low	-0.1809831 (-0.2655344/-0.0984245)	<0.001 ***	1042.6
trial number	0.0037276 (-0.0102967/0.0168464)	0.614	1000

Table 2b. Fixed effects fitted in the bivariate model for flight initiation distance (FID).

	posterior mean	p	eff. sample
intercept	-3.4191924 (-3.8611203/-2.9489543)	<0.001 ***	1092.6
valley position up	0.2371121 (-0.3117809/0.8708510)	0.346	1000
disturbance level low	-0.0029691 (-0.6217588/0.5570655)	0.992	1161.5
sex male	-0.0307399 (-0.1243771/0.0565658)	0.508	1000
age class yearling	-0.0145748 (-0.0997385/0.0713817)	0.748	1000
number w/in 10m	-0.00453 (-0.0345077/0.0280439)	0.802	909.6
alert distance	0.8571531 (0.7848313/0.9265411)	<0.001 ***	1000
initial slope	-0.0022884 (-0.0042625/-0.0004837)	0.016 *	1000

initial substrate low	-0.1438379 (-0.3026133/0.0171571)	0.078	1000
distance to burrow	0.1583198 (0.1140592/0.2013427)	<0.001 ***	1000
trial number	-0.0533234 (-0.0747074/-0.0293294)	<0.001 ***	1000

Table 3a. (yearlings vigilance)

	posterior mean	p	eff. sample
intercept	0.4523362 (0.0626750/ 0.8673324)	0.036 *	1000.0
valley position up	-0.365275 (-0.8905315/ 0.1682358)	0.158	998.6
disturbance level low	-0.013249 (-0.5852924/ 0.5280192)	0.942	1000.0
sex male	-0.0441428 (-0.1546411/ 0.0679961)	0.428	1000.0
number w/in 10m	-0.0867064 (-0.1277374/-0.0422847)	<0.001 ***	948.4
substrate low	-0.1038803 (-0.2250407/ 0.0287004)	0.114	1000.0
trial number	0.0030887 (-0.0206356/ 0.0249133)	0.774	1000.0

Table 3b. (yearlings FID)

	posterior mean	p	eff. sample
intercept	-3.2778993 (-3.8332215/-2.7766305)	<0.001 ***	1000.0
valley position up	0.3484696 (-0.0537948/ 0.8960471)	0.096 .	1872.3
disturbance level low	0.1220569 (-0.3622102/ 0.6286063)	0.586	1101.8
sex male	-0.0660963 (-0.1961682/ 0.0629632)	0.330	1000.0
number w/in 10m	0.0489376 (-0.0022767/ 0.1029045)	0.068 .	883.9
alert distance	0.8139484 (0.6982650/ 0.9221256)	<0.001 ***	1000.0
initial slope	-0.0001263 (-0.0036399/ 0.0038586)	0.932	1000.0
initial substrate low	-0.4897441 (-0.8629633/-0.1458769)	0.010 **	611.9
distance to burrow	0.1711172 (0.1005807/ 0.2506437)	<0.001 ***	1000.0
trial number	-0.0924279 (-0.1380076/-0.0455646)	<0.001 ***	1000.0

Table 4a. (adults vigilance)

	posterior mean	p	eff. Sample
intercept	0.4965435 (0.1558014/ 0.8589864)	0.012 *	1000.0
valley position up	-0.5891925 (-1.0780379/-0.0946812)	0.020 *	1000.0

disturbance level low	0.0024397 (-0.4706373/ 0.5743499)	0.968	1229.9
sex male	0.0165891 (-0.1483591/ 0.1445100)	0.828	1000.0
number w/in 10m	-0.0728455 (-0.1112472/-0.0292585)	<0.001 ***	892.8
substrate low	-0.233088 (-0.342272/-0.1268142)	<0.001 ***	1000.0
trial number	0.0041438 (-0.0130583/ 0.0234243)	0.668	1000.0

Table 4b. (adults FID)

	posterior mean	p	eff. sample
intercept	-3.5753948 (-4.0573444/-3.0454499)	<0.001 ***	1000.0
valley position up	0.1858794 (-0.3950912/ 0.8501795)	0.496	1000.0
disturbance level low	-0.0748355 (-0.7044086/ 0.5516570)	0.794	1000.0
sex male	0.0112923 (-0.1233721/ 0.1321533)	0.856	1000.0
number w/in 10m	-0.0374166 (-0.0763523/ 0.0014343)	0.062	851.1
alert distance	0.8972605 (0.8114458/ 0.9879036)	<0.001 ***	1126.5
initial slope	-0.0027165 (-0.0049513/-0.0004408)	0.024 *	1000.0
initial substrate low	-0.0263759 (-0.2062861/ 0.1570976)	0.782	1154.2
distance to burrow	0.1481754 (0.0917257/ 0.2091503)	<0.001 ***	1000.0
trial number	-0.0308206 (-0.0562819/-0.0021156)	0.016 *	871.9

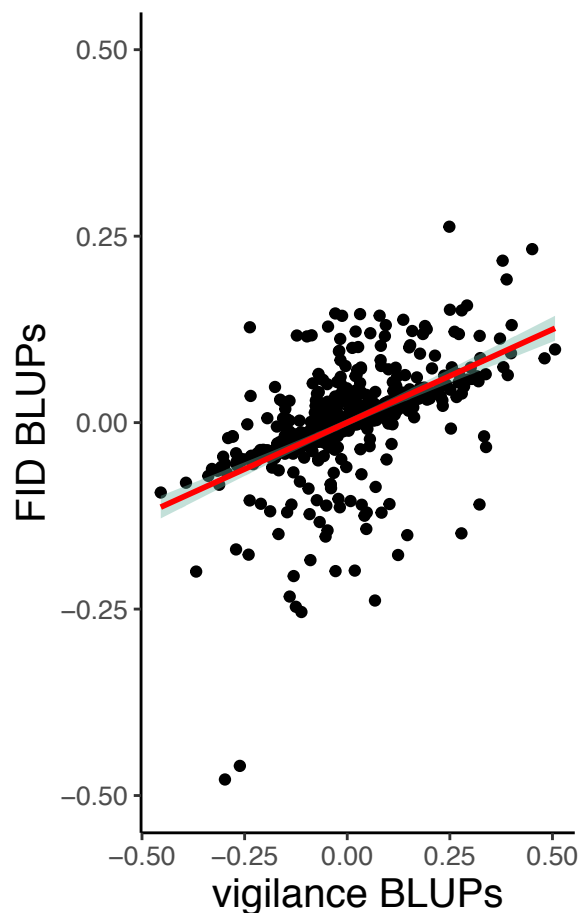


Figure 1. Correlation between vigilance and FID plotted using the posterior mean of the best linear unbiased predictors (BLUPs) for each UID. Dots represent individual UIDs, and the green shading shows the 95% confidence interval.

Table 4. Variances and correlation between vigilance and FID for each random effect. Estimates reported with 95% credible intervals.

effect	$V_{\text{vigilance}}$	V_{FID}	correlation
year	0.033158 (0.0091816/0.06808)	0.016120 (0.0001662/0.03870)	0.059579 (-0.5733171/0.69555)
colony	0.117926 (0.02301/0.2838)	0.162422 (0.02486/0.4180)	-0.045506 (-0.65197/0.6797)
UID	0.07801 (0.050008/0.11062)	0.03571 (0.016101/0.06059)	0.29840 (-0.028208/0.67942)

effect	$V_{\text{vigilance}}$	V_{FID}	correlation
all			
year	0.033158 (0.0091816/0.06808)	0.016120 (0.0001662/0.03870)	0.059579 (- 0.5733171/0.69555)
colony	0.117926 (0.02301/0.2838)	0.162422 (0.02486/0.4180)	-0.045506 (- 0.65197/ 0.6797)
individual	0.07801 (0.050008/0.11062)	0.03571 (0.016101/0.06059)	0.29840 (- 0.028208/0.67942)

yearlings			
year	0.0082249 (1.151e-08/0.03009)	0.0371781 (1.991e-06/0.10134)	-0.0380349 (-0.7874/ 0.75848)
colony	0.14412 (2.656e-02/0.35674)	0.10352 (4.727e-07/0.40920)	-0.24348 (-0.9585/0.48976)
individual	0.072955 (3.240e-02/0.12458)	0.024748 (2.800e-08/0.06412)	-0.239509 (-0.8586/ 0.43717)
adults			
year	0.045132 (1.306e-02/0.09215)	0.013613 (1.668e-06/0.03662)	0.129024 (-0.6009/0.77969)
colony	0.14000 (0.006525/0.3538)	0.21210 (0.022725/0.5350)	0.07005 (-0.550549/0.7462)
individual	0.10746 (0.062884/0.15669)	0.03720 (0.004135/0.07462)	0.57137 (0.181110/0.93668)

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23.

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