



Conditional syndromes: Effect of human disturbance and age on the correlation between flight initiation distance and vigilance in marmots

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Abstract

Behavioral syndromes—suits of correlated behaviors across different situations and contexts—are widespread and can have important ecological consequences because correlations between distinct behaviors shape how animals respond to changing environmental conditions and can limit behavioral plasticity. Behaviors such as vigilance, foraging, and exploration are correlated in many species and thus constitute a syndrome. Studying the structure of such syndromes is important to understand potential constraints on an animal's behavioral response to the environment. Importantly, we know relatively little about antipredator behavioral syndromes and how their structure is associated with environmental conditions. Here, we estimated the correlation between two antipredator behaviors in yellow-bellied marmots (*Marmota flaviventer*): flight initiation distance (FID), which quantifies the flightiness of an animal in response to a potential predator and time allocation to vigilance while foraging, which represents an individual's baseline level of wariness. We also examined the correlation between these traits under two different human disturbance levels by fitting a bivariate model on data collected over 18 years from 739 individuals. We found a modest positive among-individual correlation between FID and vigilance in adults, but no correlation between those variables in the much larger yearling cohort, nor when datasets for yearlings and adults were combined. We found no support for the hypothesis that human disturbance changed the structure of the syndrome (when present). Our study suggests that antipredator syndromes may be age-specific, and thus constraints on the independent expression of the behaviors underlying those are age-specific as well.

Significance statement

Understanding the structure of antipredator behavioral syndromes is important to better predict how animals behave in response to environmental changes, including anthropogenic disturbance. This study examined the correlation between flight initiation distance (FID), which quantifies flightiness of individuals to an approaching predator, and time allocation to vigilance while foraging, which represents an individual's baseline level of wariness in yellow-bellied marmots. We also compared the syndrome structure in two different anthropogenically disturbed environments (highly- vs. less- disturbed). We found a positive correlation between FID and vigilance in adult marmots, but no correlation in yearlings. Anthropogenic disturbance did not modify the correlation structure between FID and vigilance. Overall, antipredator syndromes appear to be age-specific, and human disturbance, as quantified in the present study, does not influence the structure of antipredator syndromes. Our results suggest that flexible behavior plays a key role in allowing marmots to cope with human disturbance.

Keywords Anthropogenic disturbance · Behavioral syndrome · Ecotourism · Flight initiation distance · *Marmota flaviventer* · Personality

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Introduction

Recent anthropogenic environmental disturbances have driven global biodiversity loss (Dirzo et al. 2014). Human activities impose novel challenges on a wide range of species, which can negatively influence individuals, populations, and communities as well as ecosystems. To cope with human disturbance, wildlife may modify a variety of behaviors including antipredator, foraging, social, and movement (Lowry et al. 2013). Since behavioral modification is one of the mechanisms of rapid ecological responses to anthropogenic environmental change, it may have wider effects on individual fitness and population demography as well as ecosystem functioning (Smith et al. 2024; Uchida et al. 2024). Thus, understanding how wildlife respond behaviorally to human activities is important for conservation.

A growing literature shows how animals living around humans modify their anti-predator behaviors, including changes in antipredator vigilance and behavioral tolerance to humans (Geffroy et al. 2015; Samia et al. 2015; Bar-Ziv et al. 2023). For example, while humans impose threats to many species in natural environments, some wildlife in human-dominated environments exhibit relaxed antipredator behaviors and increased tolerance to humans (Møller et al. 2015; Uchida et al. 2019). Such tolerance modification plays an important role in wildlife's coexistence with humans by reducing the cost of responding to humans and increasing the probability of resource acquisition. At the same time, increased tolerance to humans, accompanied by reduced vigilance, can make prey species vulnerable to actual predators and novel threats such as pets and cars, leading to negative ecological consequences (Geffroy et al. 2015). Therefore, wildlife may engage in a range of anti-predator behaviors in response to complex threatening situations in anthropogenic environments. By studying this, we develop a better understanding of how wildlife behaviorally adjusts to human disturbance.

Flight initiation distance (FID) and vigilance during foraging are two antipredator behaviors commonly used to examine wildlife's behavioral response to anthropogenic disturbance (Blumstein 2016; Uchida and Blumstein 2021). FID measures the distance at which an individual initiates moving away from approaching humans, reflecting risk assessment to exposed urgent risk (Ydenberg and Dill 1986). In addition, given that FID measures responsiveness to particular threats posed by humans, it can also measure tolerance to humans (Blumstein 2006). In urban areas and where there is nature-based tourism, humans generally have neutral or positive interactions with animals and wildlife tolerate closer human approaches than in areas with less anthropogenic activity (Carrete and Tella 2017; Samia et al. 2017). Vigilance during foraging, on the other hand,

can measure how individuals allocate their energy and time to detecting perceived threats, which is typically traded-off against time and energy allocated to foraging (Lima 1987). Although observing these two behaviors may enable us to understand how wildlife behaviorally manages the cost of responding to threats and foraging opportunities, most prior studies have examined these behaviors independently.

Behavioral syndromes are found when distinct behavioral traits are correlated either within a behavioral context (e.g., correlation between antipredator behaviors in different environmental conditions) or across different contexts/situations (e.g., correlation between foraging, antipredator, and mating behaviors) (Sih et al. 2004; Dingemanse et al. 2012). The emergence of syndromes indicates that different situations act as a set of selective drivers on multiple behaviors. Current studies have revealed that human-induced environmental change is one of the factors that alter the structure of behavioral syndromes such as the breakdown of boldness-aggressiveness syndrome in urban song sparrows *Melospiza melodia* (Scales et al. 2011). Since behavioral syndromes are associated with limited behavioral plasticity (Sih et al. 2004), the new conditions found in anthropogenic environments may select against existing syndromes, resulting in a breakdown of correlations. Although FID and vigilance during foraging are broadly categorized as antipredator behaviors and may be correlated, very few studies have rigorously investigated the potential syndrome involving these two behaviors, particularly in environments heavily disturbed by humans. In natural environments, individuals that tend to spend more time scanning for threats would presumably detect human approaches and then escape at a greater distance. Thus, FID and vigilance may be positively correlated. However, if individuals have become highly tolerant of humans through habituation, their response to humans, as measured by FID, may be independent of their vigilance during foraging. A human detected from far away might not trigger an immediate escape and be tolerated to approach much nearer, thus removing the correlation between FID and vigilance.

Here we used the yellow-bellied marmots (*Marmota flaviventris*) in and around Rocky Mountain Biological Laboratory (RMBL), Gothic, CO, USA, as a mammalian model to study the structure of a putative antipredator behavioral syndrome. These marmots have been under continuous study for over six decades (Blumstein 2013, 2025; Armitage 2014), and we have quantified both vigilance and FID at the individual level since 2002. Furthermore, since the area is popular for outdoor recreation, including hiking and biking, marmot colonies vary in terms of their exposure to humans, which enables us to examine human impact on their behaviors and syndromes (Runyan and Blumstein 2004; Li et al. 2011; Morgan et al. 2021; Uchida and Blumstein 2021). We

aimed to determine whether there was a syndrome between FID and vigilance while foraging and, if so, how it was influenced by human disturbance. A prior study, with a limited sample size ($n=21$) of marmots, found no correlation between FID and vigilance at the individual level (Blumstein et al. 2004), while a relationship between the two behaviors was reported in Eastern grey kangaroos (*Macropus giganteus*; Edwards et al. 2013). Given these mixed results, we have a limited understanding of the nature of the behavioral syndrome between FID and vigilance.

Prior analyses of both marmot FID and vigilance have shown that increasing human visitation significantly altered these behaviors (Li et al. 2011; Morgan et al. 2021). In areas with higher human disturbance, marmots decreased FID but allocated more time to vigilance (Uchida and Blumstein 2021). Furthermore, FID decreased with repeated human approaches (Uchida and Blumstein 2021), indicating habituation to humans. Therefore, we predicted that the FID-vigilance correlation would disappear for marmots in areas that were highly disturbed by humans. Additionally, previous studies in other species have found that structure of behavioral syndrome varied by age class (Sweeney et al. 2013). Therefore, we predicted that age is also an important factor in shaping syndromes, though we did not have any specific prediction as to how this syndrome varied with age, because there is no general hypothesis pertaining to that.

Overall, if FID and vigilance are 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. However, if FID and vigilance are not correlated, animals may assess risk differently when they escape from approaching threats and forage. Animals may be better able to cope with variable human disturbances by flexibly managing these two antipredator behaviors.

Methods

Study sites and species

We studied marmots in the Upper East River Valley in and around the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA ($38^{\circ}57'$, $-106^{\circ}59'$). Marmots were observed during their 5-month active season (mid-April through mid-September) from 2002 to 2020. We studied marmots at 11 geographically-separated colony sites (Gothic town, River Annex, River, Bench, Horse Mound, Avalanche, Marmot Meadow, Picnic, North Picnic, Boulder, Stonefield). Some colonies were located near cabins (those in Avalanche, Bench and Gothic town), others were adjacent

to highly used hiking trails and roads (Horse Mound, Marmot Meadow, Picnic, River Annex). Following previous study (Uchida and Blumstein 2021), we categorized colonies that were closer than 250 m from hiking trails, roads and residential cabins as highly-disturbed areas (Gothic town, River Annex, Bench, Horse Mound, Avalanche, Marmot Meadow, Picnic). The distance 250 m was selected because it is beyond the distance at which most marmots begin to be alert to the presence of humans. Colonies with main burrows farther than 250 m from trails, roads, and cabins are categorized as less-disturbed areas (River, Boulder, North Picnic, Stonefield; details in Uchida and Blumstein 2021). Potential predators include red-tailed hawks (*Buteo jamaicensis*), red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) which are potentially present in all colony areas; golden eagles (*Aquila chrysaetos*) and American badgers (*Taxidea taxus*) are occasionally seen. All marmots are regularly live-trapped and marked using numbered ear tags and given unique fur marks for individual identification from afar (Blumstein 2013). Behavioral observations were conducted in the morning (07:00–12:00 h) and evening (16:00–19:30 h). We did not observe animals when it was raining, snowing, or when the wind was >3 on the Beaufort scale. It was not possible to collected data blinded to individual identity because our study involved focal animals in the field.

Measuring FID

Flight initiation distance was collected from 2002 to 2020. FID was measured by walking directly towards an identified marmot at a constant speed of 0.5 m/s. We targeted individuals that were relaxed (i.e., foraging or resting). By following Blumstein et al. (2015), the distance between the human and marmot at which the marmot first looked at the researcher was defined as the alert distance (hereafter; AD), and the distance at which the marmot fled was defined as flight initiation distance. We also measured the distance from the initial position where observer started approaching the subject as start distance (SD). Each distance was measured by laser rangefinder (Yardagepro 400, Bushnell Performance Optics), carefully calibrated paces, or a measuring tape. We also recorded the incline of the initial approach and the marmot's escape (measured in degrees with a clinometer), distance from nearest burrow, number of individuals within 10 m, as well as the substrate characteristics (high vegetation, low vegetation, dirt, talus, stone) of the marmot's initial location and escape. We classified vegetation above a quadrupedal marmot's shoulder/head (i.e., $>\text{ca. } 12 \text{ cm}$) as "high", while vegetation below their shoulder along with dirt, talus, and stone, were categorized as "low". Each individual was identified by its fur mark before

initiating an experiment. Over the years, multiple observers were trained to collect data consistently using these standardized protocols. In most cases, a FID was collected by a single observer. In some cases, a second 'spotter' helped identify marmots from afar. Each individual was measured an average of 2.24 times (range 1–9) throughout their lives.

Measuring vigilance

Vigilance data were collected from 2002 to 2020. The amount of time individually-identified marmots allocated to vigilance while foraging was measured by observing an individual for 2 min and quietly dictating behavioral transitions into an audio recorder. The ethogram included: stand forage, rear forage, stand look, rear look, walk, run, other, and out of sight (Chmura et al. 2016). Observer's dictated behavior in real time; the audio was later transcribed using JWatcher (Blumstein and Daniel 2007) to calculate the proportion of time in sight allocated to vigilance (sum of stand look and rear look) during the focal observation. We also recorded environmental factors that were previously shown to influence the vigilance levels in marmots (Chmura et al. 2016). These included the number of individuals within 10 m, the distance from the burrow and the substrate characteristic where marmots were initially located. Each individual was measured an average of 3.15 times (range 1–19) throughout their lives.

Statistical analysis

We fitted a bivariate mixed model (Gao et al. 2017) to estimate the among-individual correlation between FID and vigilance using all data collected from 2002 to 2020. In the analysis, we used adults and yearlings but not juveniles because our dataset of juvenile FID and vigilance was relatively small. In total, we collected behavioral data from 591 individuals: 227 individuals had both vigilance and FID data, 336 individuals only had vigilance data, and 28 individuals only had FID data. When separated by age class, data were collected from 282 adults (148 for vigilance only, 19 for FID only, and 115 for both) and 459 yearlings (291 for vigilance only, 33 for FID only, and 135 for both). We fitted FID and vigilance as dependent variables for each bivariate model with disturbance level (highly- and less-disturbed area) and age class (yearling and adult) as fixed effects. We also included valley position (up-valley sites are ca. 300 m higher than down-valley sites and this results in snowmelt and the start of the growing season being delayed by about two weeks—Blumstein 2009), sex, number of individuals within 10 m, substrate, and the number of observations for each individual within a year (trial number) as fixed effects to control for potential effect on FID and vigilance. For FID,

the AD, initial incline, and the distance from burrow where individuals were initially positioned were also included as fixed effects. We included year, colony and individual ID as random effects to account for the annual, colony, and individual variation. We \log_{10} -transformed all distance variables (FID, and distance to burrow).

The model was fitted with a Bayesian approach using MCMCglmm in R (Hadfield 2010), which allows us to estimate FID and vigilance of each individual and estimate the among-individual correlation between these two behaviors (Dingemanse and Wright 2020). Because FID and vigilance were sampled on different days, we employed a Bayesian MCMC framework to estimate among-individual correlations from non-simultaneous measurements. This statistical approach enables us to accommodate missing data and unequal numbers of observations across individuals. Moreover, the framework allows trait-specific predictors to be included, providing greater flexibility in modeling the processes underlying each behavior. The model was run for 5,100,000 iterations with a thinning of 5,000 iterations and a burn in of 100,000 iterations. Following fitting our planned initial model, we also fitted models on two human disturbance levels separately (high or low disturbance) to explore the effects of human disturbance on the structure of any identified behavioral syndromes. To do so, we separated the data based on disturbance level and fitted two separate bivariate models. FID and vigilance were included as dependent variables for each bivariate model and valley position, sex, age class, number of individuals within 10 m, substrate, and trial number were included as fixed effects. For FID, AD, initial incline, and distance from burrow were also included as fixed effects. Additionally, we also fitted the models on yearlings and adults separately to explore the age class-specific behavioral syndrome in response to human disturbance. We selected data based on the age class (yearling and adult) and created two different data to fit two bivariate models. Similar to the initial models and the disturbance-specific models, FID and vigilance were included as dependent variables for each bivariate model with valley position, disturbance level, sex, number of individuals within 10 m, substrate, and trial number within a year as fixed effects. The AD, initial incline, and distance from burrow were also included as fixed effects in the FID model. Year, colony and individual ID were included as random effects.

For all bivariate models, we used parameter expanded priors for all random effects in order to get flat priors on the correlations scale and weak priors on the variance parameters ($V = \text{diag}(2) * 0.02$, $\text{nu} = 3$, $\text{alpha.mu} = \text{rep}(0, 2)$, $\text{alpha.V} = \text{diag}(2) * 1000$). For all models, given that the two traits were not measured at the same time, it was not possible to estimate the correlation at the residual level between

the traits and thus we fixed it to zero by specifying an *idh* (banded main diagonal) prior for the residual variance-covariance matrix. This approach ensured that only the diagonal elements of the residual matrix were estimated, while the residual correlation was constrained to zero. Additionally, individuals with data on both traits were informative for the entire (co)variance matrix at the individual level including the covariance among traits, while individual with data on only one trait (either vigilance or FID) were informative for the variances only. For the residual variance, we used the following prior ($V = \text{diag}(2)$, $\text{nu}=0.002$). When the 95% highest posterior density intervals (HPDI) did not include 0, an estimate was considered statistically significant. For variance parameters that were constrained to be positive, statistical significance was considered when the lower limit of the 95% HPDI was higher than 0.001. For fixed effects, we also reported Bayesian p-values based on the proportion of counts of estimates in the posterior that were above or below zero, depending on the sign of the estimated posterior mode. We also estimated the within-individual repeatability of FID and vigilance over the individuals' life span using Bayesian posterior distributions of the variance components. More specifically, repeatability of each behavior was estimated as the proportion of variance attributable to among-individual differences, calculated from the posterior samples as $R = V_{\text{ind}}/(V_{\text{ind}} + V_{\text{res}})$. The V_{ind} represents the individual variance, and V_{res} is the residual variance. Since the fixed effects were included in the model, repeatability is adjusted.

All statistical analyses were conducted using software R, version 3.6.1 (R Development Core Team 2019).

Results

To fit our bivariate model, we used data from 739 individuals (adults: 281; yearlings: 458) that were collected from 2002 to 2020. The bivariate model that included all data showed that neither variation in vigilance nor FID were significantly explained by disturbance levels or sex (Table 1). Those individuals that lived in our up-valley sites allocated less time to vigilance than ones who lived in the lower part of the valley (posterior mean = -0.709 , 95%CI = $-1.28/-0.20$; Table 1), while valley position was not significant in the FID model (posterior mean = 0.427 , CI = $-0.45/-1.37$; Table 1). Yearlings were less vigilant while foraging compared to the adults (posterior mean = -0.11 , CI = $-0.20/-0.01$; Table 1), while age class did not explain variation in FID (posterior mean = -0.053 , CI = $-0.137/0.045$; Table 1). Marmots allocated less time to vigilance while foraging when conspecifics were around and the substrates were low (number of individuals within 10 m, posterior mean

= -0.072 , CI = $-0.099/-0.038$; substrate, posterior mean = -0.207 , CI = $-0.303/-0.100$; Table 1), but the number of trials did not explain significant variation in vigilance (posterior mean = 0.008 , CI = $-0.008/0.024$; Table 1). FID was positively associated with AD (posterior mean = 0.844 , CI = $0.775/0.920$; Table 1) and distance from burrow (posterior mean = 0.153 , CI = $0.100/0.199$; Table 1), while FID significantly decreased with initial slope (posterior mean = -0.002 , CI = $-0.004/-0.001$; Table 1) and trial number (posterior mean = -0.052 , CI = $-0.075/-0.029$; Table 1). FID was not strongly affected by substrate (posterior mean = -0.154 , CI = $-0.344/0.042$; Table 1).

In the entire data set, we found limited but significant repeatability of FID ($R=0.121$, CI = $0.212/0.046$; S1), and vigilance ($R=0.097$, CI = $0.140/0.060$; S1). The among-individual correlation between FID and vigilance was positive but it was not significantly different from zero (correlation of FID-vigilance, posterior mean = 0.283 , 95% HPDI = $-0.083/0.648$; Fig. 1, S2, Table 2). Similarly, when the models were fitted to highly- and less-disturbed

Table 1 The fixed effects fitted for FID (flight initiation distance) and vigilance while foraging in the bivariate model for the whole population dataset. Posterior mean, lower and upper 95% HPDI's and p-values extracted from MCMC are shown

| | Posterior mean (95% HPDI) | Effective sample size | p |
|--------------------------------|--|-----------------------|------------------|
| FID | | | |
| Intercept | $-3.416 (-3.875/-2.990)$ | 1000 | <0.001 |
| Disturbance level (low) | 0.011 ($-0.486/0.606$) | 1000 | 0.964 |
| Valley position (up) | 0.228 ($-0.338/0.756$) | 1000 | 0.398 |
| Sex (male) | -0.03 ($-0.118/0.078$) | 1000 | 0.528 |
| Age class (yearlings) | -0.015 ($-0.103/0.069$) | 863.3 | 0.738 |
| N individuals within 10 m | -0.004 ($-0.037/0.026$) | 1000 | 0.818 |
| Substrate (low) | -0.143 ($-0.318/0.009$) | 902 | 0.088 |
| Trial number | $-0.053 (-0.075/-0.030)$ | 1000 | <0.001 |
| Alert distance (AD) | $0.856 (0.791/0.920)$ | 1000 | <0.001 |
| Initial incline | $-0.002 (-0.004/0.0003)$ | 1000 | 0.018 |
| Disturbance from burrow | $0.159 (0.116/0.206)$ | 1000 | <0.001 |
| Vigilance | | | |
| Intercept | $0.503 (0.153/0.835)$ | 1036.6 | 0.01 |
| Disturbance level (low) | 0.010 ($-0.044/0.453$) | 1000 | 0.996 |
| Valley position (up) | $-4.474 (-0.935/-0.076)$ | 1000 | 0.04 |
| Sex (male) | 0.006 ($-0.081/0.091$) | 1131.1 | 0.928 |
| Age class (yearlings) | $-0.108 (-0.185/-0.030)$ | 1000 | 0.006 |
| N individuals within 10 m | $-0.083 (-0.115/-0.055)$ | 1000 | <0.001 |
| Substrate (low) | $-0.180 (-0.259/-0.093)$ | 1185 | <0.001 |
| Trial number | 0.003 ($-0.012/0.016$) | 1000 | 0.654 |

Significant fixed effects are in bold. The reference categories are shown in parentheses for each variable

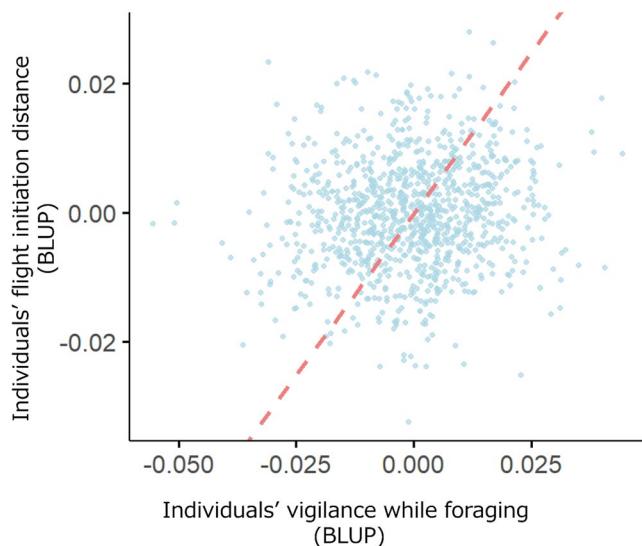


Fig. 1 The relationship between FID (flight initiation distance) and vigilance while foraging using “best linear unbiased predictions” (BLUP) extracted from Bayesian model for the full dataset. BLUPs were used only for illustration purposes. This plot illustrates the individual variation in FID and vigilance while foraging. The dashed line represents 1:1 relationship for comparison

Table 2 Results of bivariate model illustrating among-individual variance and correlation between FID (flight initiation distance) and vigilance while foraging for the whole population dataset. Posterior means of the correlation coefficient were not significantly different from zero where the 95% HPDI included zero

| | Posterior mean (95% HPDI) | Effective sample size |
|----------------------------|---------------------------|-----------------------|
| Variance of FID | 0.035 (0.015/0.058) | 1000.000 |
| Variance of vigilance | 0.078 (0.048/0.109) | 1162.813 |
| Covariance: FID-vigilance | 0.014 (-0.004/0.034) | 837.238 |
| Correlation: FID-vigilance | 0.283 (-0.083/0.648) | 1008.289 |

Fig. 2 The relationship between FID (flight initiation distance) and vigilance while foraging using “best linear unbiased predictions” (BLUP) extracted from Bayesian model for (a) the marmots in highly-disturbed areas and (b) the marmots in less-disturbed areas. The plots illustrate the individual variation in FID and vigilance while foraging. The dashed line represents 1:1 relationship for comparison. BLUPs were used only for illustration purposes

Table 3 Results of bivariate model illustrating among-individual variance and correlation between FID (flight initiation distance) and vigilance while foraging for highly-disturbed areas (a) and less-disturbed areas (b)

| | Posterior mean (95% HPDI) | Effective sample size |
|----------------------------------|---------------------------|-----------------------|
| (a) Highly-disturbed area | | |
| Variance of FID | 0.035 (0.010/0.059) | 1000.000 |
| Variance of vigilance | 0.083 (0.050/0.121) | 899.456 |
| Covariance: FID - vigilance | 0.007 (-0.015/0.030) | 792.902 |
| Correlation: FID - vigilance | 0.144 (-0.266/0.551) | 785.239 |
| (b) Less-disturbed area | | |
| Variance of FID | 0.075 (0.010/0.154) | 790.628 |
| Variance of vigilance | 0.101 (0.023/0.177) | 1000.000 |
| Covariance: FID - vigilance | 0.027 (-0.024/0.083) | 983.760 |
| Correlation: FID - vigilance | 0.341 (-0.258/0.876) | 1000.000 |

453 individuals and 182 individuals were used in highly- and less-disturbed areas respectively. Posterior means of the correlation coefficients were not significantly different from zero

areas separately, the estimated among-individual correlations between FID-vigilance in highly-disturbed areas and less-disturbed areas were not significantly different from zero (correlation of FID-vigilance of the highly-disturbed areas, posterior mean = 0.144, HPDI = -0.266/0.551; correlation of FID-vigilance in less-disturbed areas, posterior mean = 0.341, HPDI = -0.258/0.876; Fig. 2, S2, Table 3).

When adults and yearlings were analyzed separately, we identified a significant correlation between FID and vigilance while foraging in adults (correlation of FID-vigilance, posterior mean = 0.586, HPDI = 0.202/0.931; Fig. 3, S2, Table 4), indicating that more vigilant individuals escaped from a longer distance. Although yearling marmots that escaped at a greater distance spent less time vigilant while foraging, this negative relationship was not statistically significant (correlation of FID-vigilance, posterior mean = -0.239, HPDI = -0.849/0.454; Fig. 3, S2, Table 4).

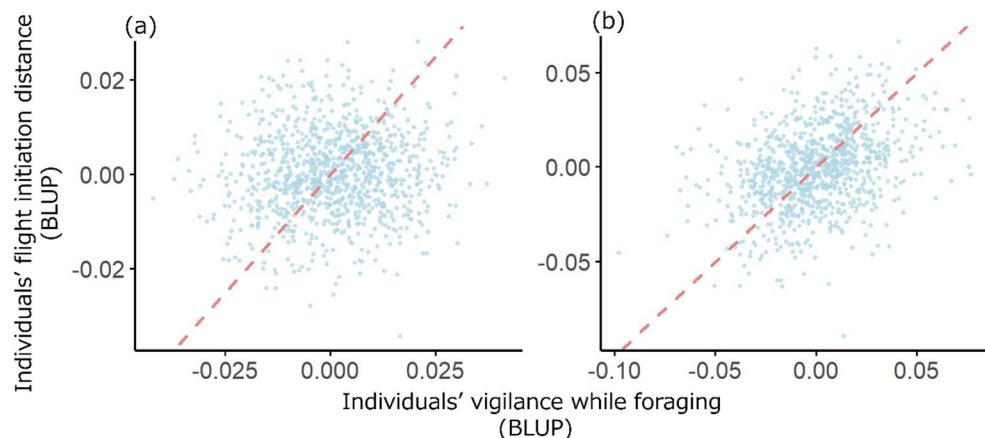


Fig. 3 The relationship between FID (flight initiation distance) and vigilance while foraging using “best linear unbiased predictions” (BLUP) extracted from Bayesian model for (a) yearlings and (b) adults. The plots illustrate the individual variation in FID and vigilance while foraging. The dashed line represents 1:1 relationship for comparison. BLUPs were used only for illustration purposes

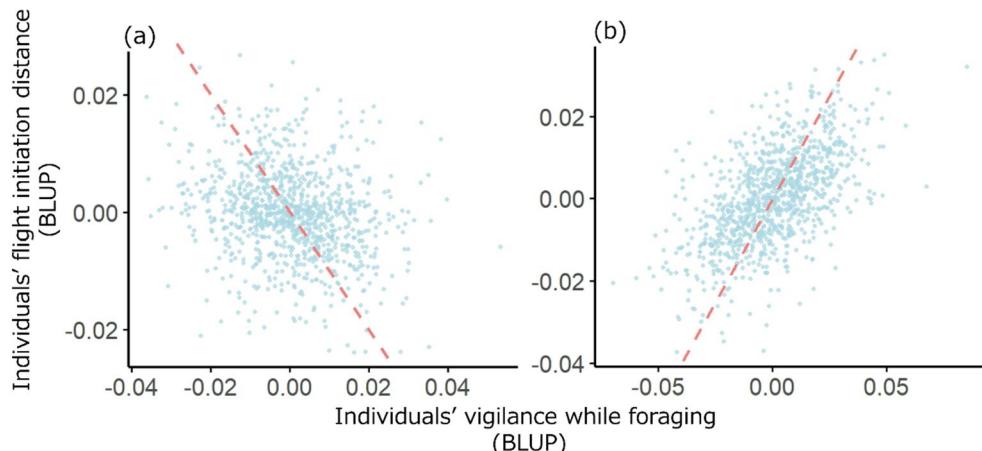


Table 4 Results of bivariate model illustrating among-individual variance and correlation between vigilance and FID (flight initiation distance) for yearlings (a) and adults (b)

| | Posterior mean (95% CI) | Effective sample size |
|-------------------------------------|----------------------------|-----------------------|
| (a) Yearling dataset | | |
| Variance of FID | 0.028 (0.00/0.067) | 1000.000 |
| Variance of vigilance | 0.078 (0.024/0.130) | 1000.000 |
| Covariance: FID - vigilance | -0.012 (-0.043/0.014) | 989.425 |
| Correlation: FID - vigilance | -0.239 (-0.849/0.434) | 1000.000 |
| (b) Adult dataset | | |
| Variance of FID | 0.034 (0.002/0.067) | 1113.872 |
| Variance of vigilance | 0.099 (0.060/0.149) | 773.129 |
| Covariance: FID - vigilance | 0.033 (0.004/0.065) | 1000.000 |
| Correlation: FID - vigilance | 0.586 (0.202/0.931) | 1000.000 |

458 individuals in yearling and 281 individuals in adult data set were used. Posterior means of the correlation coefficients that were significantly different from zero are in bold

Discussion

We estimated the among-individual correlation between FID and vigilance while foraging and examined the effect of anthropogenic disturbance on this antipredator behavioral syndrome in yellow-bellied marmots. No significant correlation was detected in the entire dataset of marmots and the expression of the syndrome was not associated with human disturbance levels. On the other hand, FID and vigilance were positively correlated in adult marmots, but not among yearling marmots, with no apparent effect of human disturbance in either age class. Taken together, our results suggest that the syndrome between these two antipredator behaviors does not become established until individuals have matured and it is not influenced by the magnitude of anthropogenic disturbances present in our study system, at least as we quantified them.

A correlation between FID and vigilance may reflect general wariness, and benefit individuals by enhancing

their ability to successfully detect and escape from danger. However, the lack of correlation between FID and vigilance while foraging indicates that these two antipredator behaviors may be the product of distinct underlying behavioral mechanisms. For example, FID may involve an immediate escape decision in response to an imminent threat, while time allocation to vigilance may reflect an ongoing cost-benefit tradeoff while foraging. FID often reflects fearfulness toward actual threats that individuals are exposed to. We found a positive correlation between FID and AD as commonly reported (e.g., Blumstein 2010; Dumont et al. 2012), suggesting that FID is correlated with alertness in situations where individuals are at risk. Additionally, FID was repeatable as found in other species (such as in burrowing owls *Athene cunicularia*; Carrete and Tella 2010; Eurasian red squirrels *Sciurus vulgaris*; Uchida et al. 2020). These results may imply that FID is a personality trait that permits animals to respond to immediate danger. On the other hand, individuals may allocate their time to either vigilance or foraging by balancing the benefits of gaining food and the cost of scanning for threats that individuals are not yet exposed to. Therefore, vigilance while foraging can be a more context-dependent antipredator behavior, influenced by various factors such as food availability, environmental conditions, and social factors. Indeed, time allocated to vigilance was associated with individuals' valley position, age class, number of individuals in their surroundings, and substrate in our statistical model (Table 1). Our result also revealed low repeatability in vigilance, implying that vigilance while foraging might be a more plastic antipredator behavior. Animals may flexibly manage their antipredator behaviors to effectively avoid threats while securing food resources, enabling them to behaviorally adjust to various risky situations.

The lack of correlation between FID and vigilance while foraging may be adaptive in some contexts, particularly in environments that are highly disturbed by humans. Human-dominated environments may amplify the decoupling of the

correlation between two antipredator behaviors because of the modified risk-landscape and habituation to humans. In human-dominated environments including urban areas and sites for ecotourism, wildlife are often exposed to novel challenges such as vehicles and introduced predators. These require individuals to be vigilant to unpredictable threats. At the same time, they are exposed to harmless humans repeatedly, which may habituate wildlife to humans (Čapkun-Huot et al. 2024). In such situations, decreasing FID while enhancing or sustaining general wariness may be adaptive. Alternatively, if the presence of humans decreased predation risk by creating a human-shield (Berger 2007; Scales et al. 2011), weakening selection pressure on fearfulness may decouple the antipredator syndrome. For example, while three-spined sticklebacks *Gasterosteus aculeatus* under strong predation pressure had a positive correlation between boldness and aggressiveness, there was no such correlation among individuals under low predation pressure (Bell and Sih 2007). Human-induced decreased predation pressure may allow contextual decision-making in individuals which may be more adaptive than having a consistent response. In our previous study in this system, FID tended to decrease over 15 years and this was enhanced in the areas with higher human visitation; a finding consistent with habituation to humans over time due to continuous human exposure (Uchida and Blumstein 2021). Interestingly, in contrast to the FID, we also found decreased time allocation to vigilance while foraging over time (Uchida and Blumstein 2021). Taken together, habituation to humans does not necessarily mean that overall fearfulness is modified, but may reflect an independent and adaptive response to benign exposure to humans. Indeed, habituated marmots that do not emit alarm calls in response to humans, respond with alarm calls and enhanced vigilance when a red fox walks by their burrows (KU and DTB personal observations). Additionally, although the area in which the RMBL is located is actively used by hikers, bikers and scientists during the summer season (Morgan et al. 2021), hawks and mid-sized predators, such as foxes, were found throughout the study site. This complex selection pressure established via human activity may render contextual decision-making in younger and less-experienced individuals beneficial.

Studying the correlation among behavioral traits may enable us to understand how different ecological contexts shape behavior. What is notable is that this correlation was only found in adults in our study. The 95% HPDI for the correlation in yearlings was wider ($-0.85/0.43$) than adult marmots ($0.202/0.931$). A wide HPDI for a correlation, as seen for the yearlings, is often observed when a flat prior is used to estimate a weak correlation or when power is low. The emergence of significant among-individual correlation in adult marmots with an absence of correlation in yearlings

indicates that behavioral syndromes or individual consistency in these behaviors strengthen with age.

There are at least four different processes that could explain the age-specific pattern of the responses. First, it could indicate that the structure of the syndrome changes based on the developmental stage, such that as yearlings mature the relationship between the behaviors strengthens. Second, the pattern may reflect differential dispersal, indicating that a particular phenotype is associated with individual dispersal tendency which is also age-dependent. Third, the pattern could reflect differential survival to adulthood based on the strength of an individual's syndrome. Fourth, the absence of the syndrome in yearlings could be a product of methodological limitations such as the sample size. However, because the number of yearlings (458) was much larger than the number of adults (281), sample sizes were large which strongly suggests that statistical power did not prevent us from detecting a correlation in yearlings.

The adaptive syndrome structure may change over the course of development, which has been seen in studies using captive animals that can control the environmental conditions. Behavioral syndromes, for example, did not appear until individuals matured (e.g., desert funnel-web spiders *Agelenopsis pennsylvanica*; Bosco et al. 2017). The inconsistencies in behavioral syndrome structure indicate that adaptive behavioral strategies may differ across developmental stages. For marmots, the rate of body mass gain during summer is a crucial factor for over-winter survival, and therefore yearlings are required to spend more time foraging during the active season compared to adults because they are still growing and must also store fat for their 7-month hibernation (Heissenberger et al. 2020). Higher energy requirements in yearlings compared to adults may weaken the syndrome, leading to the ontogenetic variation in syndrome structure. Alternatively, early-life experiences or environmental conditions may also shape different syndrome patterns across life stages. Younger individuals may still be adjusting their responses to threats, whereas adults have more stable behavioral strategies. Although it was not statistically significant, yearling marmots that exhibited higher vigilance tended to escape at shorter distances from humans. Since wildlife sometimes approach potential threats, such as predators, to assess and learn risks (i.e., predator inspection; Fitzgibbon 1994), younger marmots may similarly monitor humans at closer distances to learn the risk of humans. This could result in a negative relationship between FID and vigilance in yearling marmots, even though individuals had higher vigilance. These early-life experiences may lead to a differential form of antipredator behavioral syndrome across the life-stages.

A number of studies have identified personality-dependent dispersal or behavioral dispersal syndromes (Carrete

and Tella 2010; Cote et al. 2010). In general, bolder, more aggressive, and more exploratory individuals tend to be more likely to disperse and disperse farther than individuals that are shy, less aggressive, and less exploratory (e.g., as seen in great tits *Parus major*; Korsten et al. 2013). In marmots, virtually all yearling males and about half the females disperse (Armitage 2014). Thus, the differential dispersal of particular phenotypes may shape the age-dependent anti-predator syndrome in yellow-bellied marmots. Additionally, we know that the form of behavioral syndrome is associated with differential survival in other species (such as three-spined sticklebacks; Bell and Sih 2007) and it is possible that this explains the emergence of the syndrome in older animals. Future work is required to differentiate the mechanisms underlying possible personality-dependent dispersal and differential survival using a large sample size to explain the development of a syndrome in older animals.

We also found that FID and vigilance were explained by different factors. While FID was not associated with age class, the number of other individuals within 10 m and the position within the valley that individuals inhabited, time allocated to vigilance decreased when individuals were in the upper valley. Vigilance was also associated with age class and the number of individuals within 10 m. Marmots living up-valley have less time to gain body mass during the active season because spring snowmelt is delayed about 2 weeks compared to the down-valley part of our study site (Armitage 2014). Therefore, marmots living up-valley must spend more time foraging to prepare for hibernation rather than allocating time to vigilance compared to down-valley conspecifics. Further, marmots could reduce their vigilance cost and increase time allocated to foraging when other individuals are present because there are more eyes to detect potential predators. FID was associated with incline and distance from the burrow where the individuals were initially positioned. These factors influence the probability of a successful escape and thus influence perceptions of risk.

Management implications

Although increased tolerance to humans may play an important role in human-wildlife coexistence by reducing stress imposed by the presence of humans, it can also increase the vulnerability of wildlife to predators if tolerance to humans is accompanied by decreased vigilance (Geffroy et al. 2015). Our study found a lack of correlation between FID and vigilance in most cases, meaning that tolerance to humans is not necessarily associated with decreased vigilance. However, since we also found a significant and positive correlation in adults, wildlife managers should be aware that even benign human exposure may have age-specific effects on wildlife's vulnerability to the predators. For example, increasing

human tolerance in adult marmots may lead to negative ecological consequences, and therefore human-marmot interaction should be regulated. It is important to better study how animals respond to different types of threats to better understand antipredator syndromes across different stimuli (Sih et al., 2023).

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Author contributions KU, IJD, and DTB conceived and designed the study. KU, IJD, and JM performed the statistical analyses. All authors interpreted the concept and results.

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Data availability Data and R code used in this article are available at <https://osf.io/3jg6v/>.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval All applicable institutional guidelines for the use of animals were followed. Marmots are studied under permits issued annually by Colorado Parks and Wildlife (TR-917), UCLA (ARC Protocol # 2001–191), and permission of the Rocky Mountain Biological Laboratory. We set the traps under the shade and covered them with vegetation and rocks onward days. Each marmot was in the trap no longer than 2 h and released immediately at the place close to the burrow after the 5–15 min handling time. Marmots were handled in a cloth handling bag that covered their face to minimize stress. We used an alcohol swab before affixing ear tags. Vigilance observations were carried out at distances at which marmots were not obviously affected by the observer. We did not conduct focal observation on individuals that were obviously responding to the observer's presence. To reduce disturbance while measuring flight initiation distance, the observer approached at a constant speed and left the site soon after the data were collected (a brief disturbance that took only a couple of minutes).

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