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The Heritability of Fear: Decomposing Sources of Variation
in Marmot Flight Initiation Distance

A thesis submitted in partial satisfaction of the requirements
for the degree Master of Science in Biology

by

Mackenzie Anne Scurka

2023

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ABSTRACT OF THE THESIS

The Heritability of Fear: Decomposing Sources of Variation in Marmot Flight Initiation Distance

by

Mackenzie Anne Scurka

Master of Science in Biology

University of California, Los Angeles, 2023

Professor Daniel T. Blumstein, Chair

A variety of intrinsic and extrinsic factors shape an animal's antipredator behavior. Flight Initiation Distance (FID) is a common measurement for evaluating antipredator behavior and is used to assess an individual's shyness or boldness. Numerous Flight Initiation Distance studies, in a variety of taxa, have shown that FID is an economic decision that is sensitive to both the costs and benefits of flight. While there is some evidence that individuals may have repeatable FIDs, and there are several genes associated with FID (DRD4 and SERT), few studies have quantified the heritability of FID. Knowledge of heritability permits us to understand the evolutionary potential of a trait within a population, and heritable variation is yet another mechanism that enables animals to respond to a dynamically changing world. Here we conduct a variance decomposition analysis using the quantitative genetic mixed model (i.e., the "animal

model”) to identify the degree to which genetic and non-genetic factors explain variation in FID within a population of wild yellow-bellied marmots (*Marmota flaviventer*). Within our 18-year dataset of individually marked individuals, we found significant heritable variation for FID that we estimated at 0.16. These results demonstrate that genetics, in addition to environmental factors, influence an animal’s fear response. Understanding evolvability and plasticity of FID could have important implications for conservation.

The thesis of Mackenzie Anne Scurka is approved.

Thomas Bates Smith

James O. Lloyd-Smith

Daniel T. Blumstein, Committee Chair

University of California, Los Angeles

2023

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Introduction

As human-wildlife interactions change as a significant consequence of climate change and population growth, the ability to predict fear responses can be an important tool in wildlife conservation. A frequently used measurement among behavioral ecologists to assess fear response, or to determine how “shy” or “bold” an animal is, is Flight Initiation Distance (FID) (Ydenberg and Dill 1986). Flight Initiation Distance is the distance at which a prey will first flee from a potential threat. Many FID studies consist of cost-benefit analyses that analyze the economic tradeoffs associated with shyness and boldness (Blumstein 2003). While fleeing from threats early (resulting in larger FIDs) is an effective short-term defense mechanism, this flightiness is energetically costly and may lead to lower fitness (Dill and Houtman 1989). In addition to expending unnecessary energy, fleeing early may also force animals to abandon foraging or mating opportunities.

As animals navigate predator-filled landscapes, many different environmental variables explain variation in FID with varying relative effects across taxa (Møller et al. 2014; Nunes et al. 2018; Samia et al. 2016). Habitat and proximity to refuge have been demonstrated to impact risk assessment (Bonenfant and Kramer 1996). Many species, and most ungulates, have longer FIDs in open areas than wooded areas (Stankowich 2008). In human-dominated environments, urbanization leads to an overall reduction in FID in birds (Moller et al. 2015; Samia et al. 2015; Morelli et al. 2023). Temperature and seasonality can also be important predictors of FID. Despite variations in temperature collection methods, almost all lizard species have greater FIDs associated with lower temperatures, likely to compensate for the slowing of their biological processes (Blamires 2000; Cooper and Sherbrooke 2010; Rand 1964, Samia et al. 2016). Demographic variables are also important elements in shaping fear response. Sex and life history

traits such as age, size, and proximity to sexually receptive mates influence antipredator behavior in many species (Lima and Dill 1990). Differences in antipredator behavior throughout an animal's life could be explained by experience, reproductive status, or a variety of other factors. Additionally, while all animals are able to change their behavior when confronted with novel conditions or threats to some extent, the degree of this plasticity varies and needs to be further explored.

While meta-analyses across taxa have confirmed that environmental variables account for much of the variation in these dynamic escape decisions, very little is known about the degree to which genetic factors impact FID. Recent studies have found associations between different alleles of two genes and FID, suggesting that there is a heritable component to antipredator behavior (Holtmann et al. 2016; van Dongen et al. 2015; Garamszegi et al. 2014).

Polymorphisms in the dopamine receptor D4 (DRD4) and serotonin transport (SERT) genes have been linked to behaviors such as aggression, novelty seeking, anxiety, and most relevant to this study, fear (van Dongen et al. 2011). While these studies have only focused on FID correlating with DRD4 and SERT alleles in birds, other related research has shown that two specific DRD4 polymorphisms associated with personality variation in other related traits have been found in free-living bird species along with humans, vervet monkeys (*Chlorocebus pygerythrus*), and horses (*Equus caballus ferus*) (Ebstein 2006; Bailey et al. 2007; Momozowa et al. 2005). This evidence suggests that DRD4 variants and behavioral variation predates the divergence between avian and mammalian lineages, supporting the idea that these genes could be relevant for fear response across multiple classes in the animal kingdom (Fidler et al. 2007) and highlights the need to explore this connection in other taxa.

Only a handful of papers have monitored individuals and familial lineages over time to estimate the heritability of FID, and even fewer have sought to understand the evolutionary consequences of anthropogenic factors by examining the heritability of FID. A long-term study on barn swallows identified a U-shaped relationship between FID and age and estimated the heritability of FID as 0.48 (Møller 2014). Another study on burrowing owls (*Athene cunicularia*) calculated the heritability of the birds' FIDs in urban and rural settings. Heritability estimates ranged from 0.37 in urban settings to 0.80 in rural settings (Carrete et al. 2016). These high values and significant results provide strong evidence that there is a genetic component to fear response, and the difference between the two estimates merits further research to be done to explain how human disturbance acts as a selection pressure on animals' risk assessment. Additionally, since most FID research has been conducted in birds, we identified a need to examine FID heritability as a trait in more species across different taxa to better understand the evolution of risk assessment.

We studied FID inheritance in a population of wild and individually marked yellow-bellied marmots (*Marmota flaviventer*) that has been observed for over sixty years (Armitage 2014; Blumstein 2013). Since 2001, the project has also included a molecular genealogy and resulting pedigree. With over twenty years of FID observations and the molecular genealogy, this population is a valuable source of historical data and ideal for this study. To disentangle the genetic influences of FID from environmental factors, we used a type of mixed effects model called the "animal model" (Kruuk 2004). Using a pedigree, the model constructs a relatedness matrix to estimate how many genes are shared between each pair of individuals in a population. It then controls for fixed and random effects to estimate how much of the phenotypic variation

(V_p) in a trait is additive genetic variation (V_a). This calculation (V_a/V_p) results in a narrow-sense heritability (h^2) estimate.

Materials and Methods

Site and Trapping

The data were collected at the Rocky Mountain Biological Laboratory in Gothic, Colorado, where behavioral observations of this population of marmots began in 1962 (Armitage 1991; Blumstein 2013). However, the study began collecting DNA samples as well as FID data at the turn of the century, so the data used in this analysis consist of 1389 FID measurements taken from 2001-2019 with paired pedigree information. From late May to early September, marmots were caught using Tomahawk live traps at sites distributed along a five-kilometer longitudinal gradient that ranged in elevation from 2700 to 3100 meters above sea level (Edic 2022).

Captured animals were transferred into cloth handling bags where they were weighed and sexed. Marmots were tagged with numbered ear tags and marked with nontoxic Nyanzol fur dye so that they could be identified from a distance (Armitage and Johns 1982). Hair samples were also collected to extract DNA data to determine maternal and paternal relationships.

Flight Initiation Distance

To quantify FID, a researcher approached a group of marmots and waited quietly for five minutes so as not to further alarm the group. Marmots were identified by their unique fur dye symbol using binoculars and/or a 15-45X spotting scope and one individual was selected to approach. The researcher walked toward the marmot at a measured pace of 0.5-meter step/second and dropped flags at the researcher's starting point, the location when the marmot turned its head in response to the approach, and the location where the marmot fled (the

marmot's initial position). From these flag locations, starting distance (the distance between the marmot and researcher's initial position), alert distance (the distance between the marmot and the researcher when the marmot turned its head), and FID (the distance between the marmot and the researcher when the marmot fled) were determined using a meter tape or a Bushnell range finder. The distance between the marmot's initial position and the burrow it ran to was also measured. Substrate type, incline, the number of marmots in a ten-meter radius, and the distance between an animal's initial position and the burrow it escaped to were also recorded (Uchida and Blumstein 2021).

DNA Extraction and Molecular Genealogy

Hair samples were stored in envelopes and kept at -20°C. DNA was extracted using the QIAmp Mini Kit by Qiagen Inc and amplified via polymerase chain reaction (PCR.) We used microsatellite genotyping at twelve loci to match parents to offspring and analyzed allele frequencies using GENEMAPPER (Blumstein et al. 2010; Edic et al. 2020). Parentage was assigned by using CERVUS 3.0 with a 95% confidence interval. CERVUS 3.0 is a program that estimates mother-father relationships of offspring using pair-wise locus-by-locus likelihood scores (Kalinowski et al. 2007).

Statistical Analysis

We used the quantitative genetic mixed model (i.e., “animal model” (Kruuk, 2004)) to determine the degree to which environmental and genetic factors impact marmot FID. The random effects in our model included year, colony, and dam ID. Because FIDs also tend to be smaller in more disturbed colonies, controlling for colony location helped account for variation in environment and habituation (Uchida and Blumstein 2021). Including dam ID helped account for maternal effects. Both marmot ID and marmot ID linked to the pedigree were also included as random

effects, as marmot ID can help capture individual environmental variation not included in other measured variables. Sire ID was not included as a random effect since fathers are often less present than mothers around their pups. The fixed effects in our model included age, sex, distance from the marmot's initial position to the burrow it ran to, starting distance, incline of the marmot's initial position, substrate of the marmot's initial position, valley position, and number of marmots in a 10-meter radius (Li et al. 2004; Bonenfant and Kramer 1996; Monclús et al. 2015; Blumstein et al. 2004; Wey and Blumstein 2010). Because alert distance and starting distance are highly correlated ($r = 0.89$, $p = 2.2e-16$) we decided to use just one of these metrics. Starting distance was chosen over alert distance because it was the larger dataset (some animals had no recorded alert distance). Valley position includes up-valley and down-valley—two different clusters of colonies separated by less than three miles that vary slightly in elevation and human disturbance. To help account for habituation, we also included trial number, which is defined as the number of times a marmot has been flushed for FID measurements in a given year, as a fixed effect since recent research on this population has shown that FID decreases the more a marmot is approached within a year (Uchida and Blumstein 2021). The model was fitted in R version 4.1.2 (R Development Core Team 2021) using the package ASReml 4.1.0 (Butler et al. 2017).

The ASReml package animal model uses Restricted Maximum Likelihood to maximize the likelihood of observed data while accounting for random and fixed effects, updating iterations of the variance components until the changes in the component estimates become negligible (Butler et al. 2017). The model does this by generating a relatedness matrix from the provided pedigree and comparing the expected covariance structure based on the genetic relationships predicted by the matrix to the observed covariance among our random and fixed

effects. The outputs are variance component estimates which include colony (V_{colony}), year (V_{year}), maternal effects (V_{dam}), marmot ID capturing environmental variation (V_e), additive genetic effect (V_a), and residual variance (V_r). Total phenotypic variance (V_p) is calculated as the sum of these estimates.

We used two methods to assess the significance of the random effects in our model. We first reported the component estimate, standard error, and z-ratio (component estimate/standard error) for each effect using the summary function in the ASReml package. A z-ratio >2 is one metric for significance, although this metric is not as reliable as it is for fixed effects. To help determine significance for each effect, we also calculated a likelihood-ratio test (LRT) for the original model and another LRT on the model excluding the effect of interest. Twice the absolute difference between these two log-likelihoods is used as the test statistic for a chi-square test, with one degree of freedom. If the resulting p-value was less than 0.05, the effect was considered significant. Similarly, the solution, standard error, and z-ratio (solution/standard error) was reported for each fixed effect and a Wald test was conducted to determine the significance ($p < 0.05$) for each fixed effect. The marginal effects of each fixed effect were determined using the package lme4 1.1.32 (Bates et al. 2014) and then plotted using the package sjPlot 2.8.14 (Lüdtke et al. 2021).

Because heritability cannot exceed repeatability of a behavioral trait, repeatability was calculated as an upper limit estimate for heritability. Repeatability was estimated using ASReml 4.1.0 with linear mixed models and restricted maximum likelihood. Repeatability (R) was calculated as the proportion of V_p that can be explained by variation between individuals (V_{ind}), where V_p is partitioned into V_{ind} and variation within individuals (V_w).

$$R = V_{\text{ind}} / V_p = V_{\text{ind}} / (V_{\text{ind}} + V_w)$$

We generated an evolvability (E) estimate in addition to a heritability estimate to better understand the adaptive potential of FID in this population. While heritability refers to the amount of additive genetic variance that makes up total phenotypic variance, we define evolvability here as the ability of a population to generate new genetic material to respond to selective pressures over time (Houle 1992). We used ASReml 4.1.0 to estimate evolvability of FID using the vpredict function. This function interprets the ratio of V_a to the squared mean of FID in the population, which is indicative of how much genetic variation exists relative to the average FID value, as the potential for FID to respond to selection over time.

Ethical Note

The marmot study is conducted under the University of California, Los Angeles Institutional Animal Care and Use protocol (2001-191-01, renewed annually) and with permits from the Colorado Division of Wildlife (TR917, renewed annually). To facilitate observations, marmots were live trapped, marked, and released at the capture location within 15 minutes of handling. Trapping occurred in the morning and late afternoon under cool conditions, with traps checked within 2 hours of setting. Previous research has indicated that only a small number of marmots exhibited an increased glucocorticoid response when struggling in the trap (Smith et al. 2012), while the majority of trapping events involved calm individuals. No effects on population viability have been observed over the 61-year history of this study using these trapping methods. During flight initiation distance experiments, some marmots temporarily fled into their burrows. However, previous studies have shown that marmots can habituate to repeated experimental approaches without significant long-term fitness consequences (Uchida and Blumstein 2021). Observations were conducted at distances that did not visibly disrupt marmot behavior, which varied among different groups.

Results

Our final dataset included estimates for fixed effects, variance components, and conditioned variance. Repeatability, the upper limit estimate for heritability, was estimated as $R = 0.545$ (95% CI = 0.490-0.595). Heritability was estimated as $h^2 = 0.157$ (95% CI = 0.127 and 0.189) with the additive genetic effect being a highly significant variance component ($p = 6.752 \times 10^{-5}$). Colony was also a significant effect ($p = 0.042$). Year, maternal effects, and individual environmental effects did not explain significant variation in FID. Evolvability of FID was estimated as $E = 0.038$ (SE = 0.012).

There were several significant fixed effects (Table 1), including distance ran to burrow ($p < 1.0 \times 10^{-6}$), starting distance ($p < 1.0 \times 10^{-6}$), and trial number ($p = 0.012$). Though substrate overall was not a significant predictor of FID, FIDs of marmots on talus were significantly different from those on other substrates ($p = 0.012$). Age, sex, valley position, slope, substrate, and number of marmots within 10 m did not explain significant variation in FID. The residuals of the model followed a normal distribution.

The relationship between FID and the significant effects was further examined (Figure 1). Starting distance was strongly positively correlated with FID ($r = 0.78$, $p < 2.2 \times 10^{-16}$, 95% CI = 0.76-0.80). Trial number was slightly negatively correlated with FID ($r = -0.05$, $p = 0.065$, 95% CI = -0.102 -<0.01). Marmots in different colonies varied widely in their average FIDs, ranging from 12 m in the Gothic townsite and River Annex to 95 m at Stonefield. Mean FIDs on different substrates also varied, ranging from 25 m in high vegetation to 32 m on talus.

	Estimate	SE	Z Ratio	p
Fixed Effects				
Sex (Female Reference)				0.561
<i>Male</i>	-0.741	1.275	-0.582	
Age	-0.057	0.281	-0.202	0.842
Valley (Down-valley reference)				0.572
<i>Up-valley</i>	2.495	4.278	0.583	
Dist. to Burrow	0.594	0.084	7.070	< 0.001
Starting Distance	0.479	0.019	25.167	< 0.001
Slope	-0.033	0.027	-1.240	0.215
Substrate (Dirt Reference)				0.157
<i>HV</i>	1.064	2.120	0.502	0.962
<i>LV</i>	5.232	3.773	1.387	0.135
<i>S</i>	5.634	2.398	2.350	0.114
<i>T</i>	7.601	2.471	3.076	0.012
Number w/in 10 m	-0.249	0.363	-2.511	0.493
Trial Number	-0.881	0.351	-2.511	0.012
Variance Components				
V _{colony}	23.589	19.133	1.233	0.042
V _{year}	4.045	3.732	1.084	0.114
V _{dam}	11.332	8.655	1.309	0.141
V _e	7.47x10-05			1.000
V _a	45.921	13.982	3.284	6.752x10-5
V _r	205.843	10.200	20.181	
V _p	290.370			
Conditioned Variance Ratio				
h ²	0.158	0.045		
R	0.545	0.027		

Table 1: Solution and component estimates reported for fixed effects and random effects, respectively, are reported along with standard error (SE), z-ratio, and p-values (p). Heritability (h², measured as V_a / V_p) and Repeatability (R) are reported as well. Within the substrate effect, categories include high vegetation (HV), low vegetation (LV), stone (S), and talus (T).

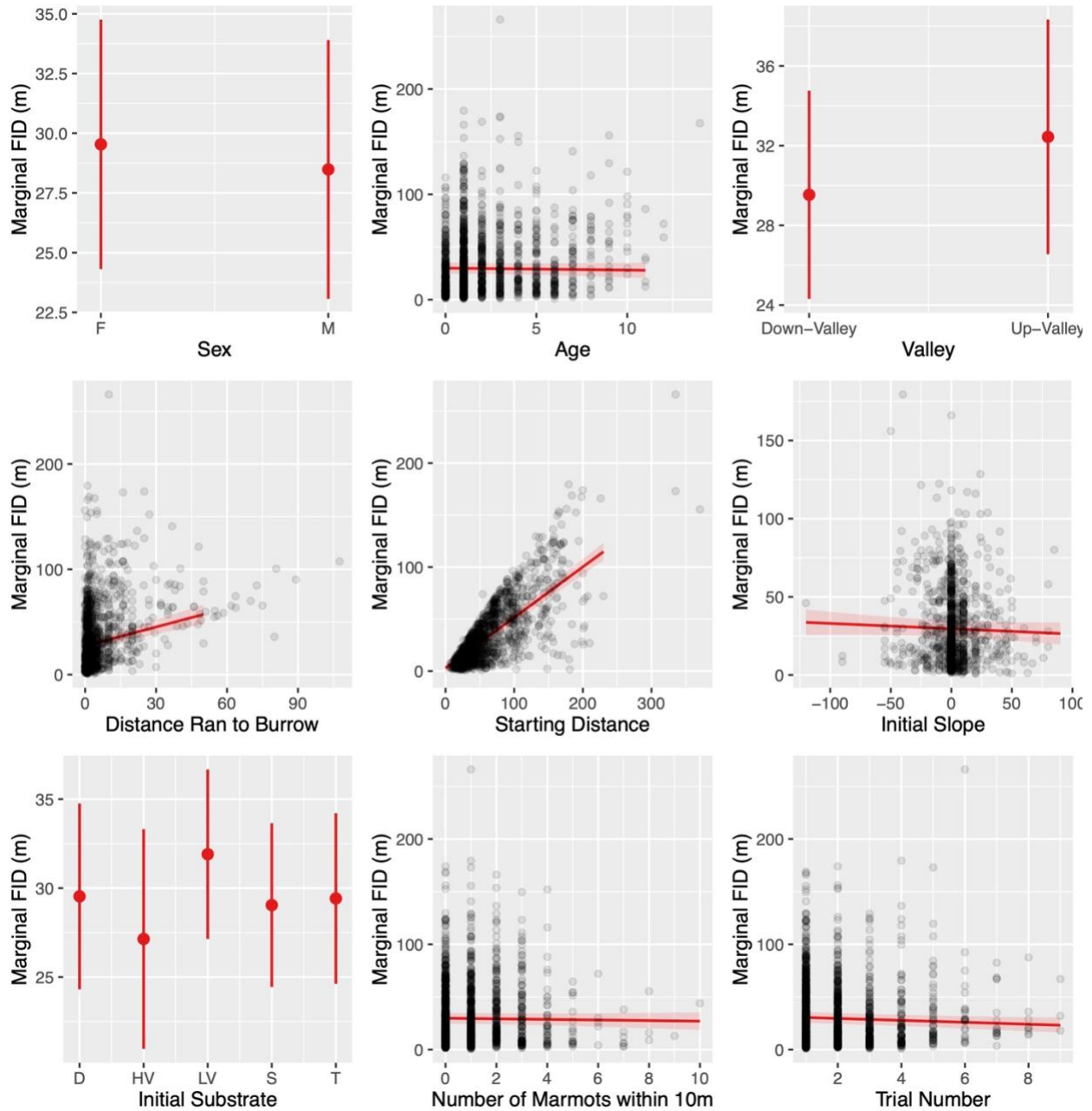


Figure 1: Marginal effects of fixed effects on FID. Age is measured in years. Distance Ran to Burrow and Starting Distance are measured in meters. Initial Substrate includes dirt (D), high vegetation (HV), low vegetation (LV), stone (S), and talus (T). Error bars represent a 95% confidence interval.

Discussion

As Human Induced Rapid Environmental Change (HIREC) influences animals in both rural and urban habitats, species must adapt either plastically or evolutionarily to survive in our changing world (Sih et al. 2011). After partitioning phenotypic variation in FID using the animal model, our evidence suggests that 16% of variation in FID is due to additive genetic effects. In the few other studies that measure the heritability of FID, h^2 estimates vary widely from 0.15-0.80. However, the higher estimates reported are from parent-offspring regressions, which tend to overestimate genetic contributions more than animal models due to their limitations in partitioning phenotypic variance (Carrete et al. 2016). Due to this difference, we feel confident that our design more accurately estimates h^2 than those that do not use the animal model.

Though our h^2 estimate is consistent with these few other existing estimates and is below our upper limit estimate of $R = 0.55$, a moderately high h^2 value may be surprising nonetheless. Behavior is often assumed to be highly plastic, and the extensive literature on FID has shown remarkably plastic responses. Nevertheless, behavioral traits have an average heritability of $h^2 = 0.24$ (Dochtermann et al. 2019). Considering that many of the heritability estimates factoring into this average have been estimated using parent-offspring regression or other quantitative genetics methods that might over-estimate additive genetic effects, we suspect that our h^2 estimate is, in reality, closer to this average.

Despite the support for our estimate, we have identified a few sources of potential error that may have contributed to inaccuracies in our analysis. Though we controlled for as many variables as we could in our model, we must acknowledge the possibility that there is a confounding variable we have not measured or included in this analysis which could lead to a possible overestimation of additive genetic effects. However, including too many variables in the

model can reduce the precision of variance component estimates (Wilson et al. 2009). Here we tried to strike a balance between these two common animal model pitfalls when estimating h^2 .

Evolvability was calculated as $E = 0.04$, suggesting that the potential for adaptive change of FID is low in this population of marmots despite moderately high heritability. This could be due to a variety of factors, such as limited allelic variation, or non-additive genetic effects, like gene-interactions, that limit a trait's ability to respond to selection (Hansen and Houle 2008; Carter et al. 2005).

As expected, a suite of environmental variables explain variation in FID. Although substrate overall did not significantly influence marmot FID in our variance decomposition analysis, FIDs conducted on marmots in talus field differed significantly than those in other forms of substrate. Marmots had longer FIDs, and were thus shyer, in talus field as opposed to high vegetation. This is consistent with prior studies done on this population (Blumstein et al. 2004) and is perhaps intuitive. Prey may be more likely to flee when they are more visible to potential predators. Also unsurprisingly, colony was a significant variable that explained variation in FID. Colonies vary in human exposure and relative tolerance to approaching humans (Uchida and Blumstein 2021). Colonies like Stonefield are not visited by people whereas some marmots living in the Gothic Town site live below cabins occupied by researchers and are substantially more tolerant than those in Stonefield and other similarly remote colonies.

Within a species, variation in boldness among and between individuals has meaningful effects on fitness. One meta-analysis on the fitness consequences of personality found that bolder individuals tend to have higher reproductive success while shyer individuals are more likely to live longer (Smith and Blumstein 2008). These formidable trade-offs likely maintain variation in boldness within a species, and as a result, are subject to fluctuate based on external factors.

Beyond species-specific consequences, shifts in average boldness of one species can have top-down effects that change the composition and spatial distribution of lower trophic levels. As a classic model, Laundré et al. (2001) reported that the 1995 wolf reintroduction in Yellowstone National Park triggered a behavioral cascade that deterred elk (*Cervus canadensis*) and bison (*Bison bison*) from browsing in more exposed areas, altering the park's vegetation. The landscape of fear can even be seen from space; Madin et al. (2011) found that the distribution of algae surrounding coral reefs was influenced by herbivorous fish, with the tallest algae canopies observed at greater distances from fish refugia.

From landscapes to seascapes, the degree to which genetic and environmental variables factor into fear responses could have significant implications for the overall behavioral response of a population (and consequently, the community), especially when challenged with new stressors. By understanding the extent that animals can alter their behavior over the course of a lifetime, or over generations, we can develop strategies to help protect them. Despite the limited application of animal personality in conservation science (MacKinlay and Shaw 2023), a number of studies have yielded promising findings that encourage further integration of both fields. For example, Martin-Wintle et al. (2017) found that certain combinations of personality types in captive giant pandas resulted in greater reproductive success, such as matching less aggressive females with more aggressive males. A recent review also found that boldness is one of the most variable traits within and across different species and conservation contexts, with no overarching unidirectional relationships to different ecological traits (e.g., survival or body condition) (MacKinlay and Shaw 2023). This suggests that boldness is a highly complex trait with population-specific nuances. Therefore, evolvability of FID, a key metric to quantify boldness, is

an important concept in our conservation toolbelt that can help us better understand animal populations' reactions to HIREC and shape management plans.

FID has been suggested to be a key metric for assessing the speed by which bird species can adapt to urbanization (Lin et al. 2012). Knowledge of a population's FID can be useful when creating buffer zones—the distance at which an animal is aware of human (or predator) presence but will not flee—in national parks, wildlife corridors, or any construction that involves potential contact between humans and wildlife (Lamichhane et al. 2019; Mwalyosi 1991). If carefully designed and derived from empirical evidence, buffer zones, also known as setback distances, can mitigate anthropogenic-induced impacts on wildlife (Fernández-Juricic et al. 2001; Rodgers and Smith 1997; Rodgers and Schwikert 2002; Weston et al. 2012). As an example, an Australian study on coastal birds demonstrated that implementing buffer zones of at least 25 meters between roads and beaches can significantly reduce vehicle-induced flushing (Schlacher et al. 2013). The observation that FID has both heritable and plastic components suggests some limitation on phenotypic plasticity and also suggests that populations may evolve and buffer zones may change over time because of evolutionary change. This suggests that management actions may have to be revisited periodically as the populations' response may evolve.

Finally, the evolvability of FID can serve as an indicator to assess the efficacy of conservation measures and to monitor the population trends of endangered species. The genetic basis of antipredator behavior varies among species, with some able to respond more plastically to environmental changes than others. Therefore, short-term conservation interventions may be necessary for species with a strong genetic component for antipredator behavior. Conversely, species with higher evolvability of escape behavior may have a better chance of long-term survival than those that must rely on modifying their antipredator strategies earlier in life.

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