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The heritability of fear: decomposing sources of variation in marmot flight initiation distance

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A variety of intrinsic and extrinsic factors shape an animal's antipredator behaviour. Flight initiation distance (FID) is a common way to evaluate antipredator behaviour and is used to assess an individual's shyness or boldness. Numerous FID studies, in a variety of taxa, have shown that FID is a 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 genetic variance of FID. Knowledge of genetic basis 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 conducted a variance decomposition analysis using the quantitative genetic mixed model (i.e. the 'animal model') to identify the degree to which genetic and nongenetic factors explained variation in FID within a population of wild yellow-bellied marmots, *Marmota flaviventer*. Within our 18-year data set of individually marked individuals, we found significant heritable variation for FID that we estimated at 0.15. 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.

Keywords:
antipredator behaviour
evolvability
conservation management plan
flight initiation distance
behavioural trait heritability

Human–wildlife interactions are changing due to climate change, habitat destruction, the spread of invasive species and population growth, to name a few drivers of conflict (Nyhus, 2016). With these changes, the ability to predict fearful responses can be an important tool in wildlife conservation because how individuals perceive safety may influence habitat use as well as population sustainability (Gaynor et al., 2021). A frequently used measurement among behavioural ecologists to assess fear response, or to determine how 'shy' or 'bold' an animal is, is flight initiation distance (FID) (Ydenberg & Dill, 1986). FID is the distance at which a prey will first flee from a potential threat. Many FID studies consist of cost–benefit analyses that estimate the economic trade-offs associated with shyness and boldness (Blumstein, 2003). While fleeing from threats early (resulting in larger FIDs) is an effective short-term defence mechanism, this flightiness is energetically costly and may lead to lower fitness (Cooper, 2015). In addition to expending unnecessary energy, fleeing early may also force animals to abandon foraging or mating opportunities (Lima & Dill, 1990).

As animals navigate predator-filled landscapes, many environmental variables explain variation in FID across taxa (Møller, 2014; Nunes et al., 2018; Samia et al., 2016). Habitat and proximity to refuge have been demonstrated to impact risk assessment (Bonenfant & Kramer, 1996). Many species, and most ungulates, have longer FIDs in open areas than in wooded areas (Stankowich, 2008). In human-dominated environments, urbanization leads to an overall reduction in FID in birds (Møller, 2014; Morelli et al., 2023; Samia et al., 2015). 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 & Sherbrooke, 2010; Rand, 1964, Samia et al., 2016). Demographic variables are also

important elements in shaping the fear response. Sex and life history traits such as age and size influence antipredator behaviour in many species (Lima & Dill, 1990). Differences in antipredator behaviour throughout an animal's life could be explained by experience, reproductive status or a variety of other factors. For example, parrotfish (family Scaridae) FID increases with size, likely due to higher reproductive value (Gotanda et al., 2009). Additionally, while many animals are able to change their behaviour when confronted with novel conditions or threats to some extent, the degree of this plasticity varies and must be further explored.

While meta-analyses across taxa have confirmed that environmental variables account for much of the variation in these dynamic escape decisions, 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 behaviour (Garamszegi et al., 2014; Holtmann et al., 2016; van Dongen et al., 2015). However, little is known about the genetic basis of FID, including its heritability and evolvability in natural populations. 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, *Hirundo rustica*, 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 some aspects of the fear response, and the difference between the two estimates warrants further research to explain how human disturbance acts as a selection pressure on

animals' risk assessment. Moreover, while most FID research has been conducted in birds, the heritability of FID may differ in other taxa, such as mammals, due to varying evolutionary pressures, ecological niches and behavioural adaptations. This indicates a broader need to assess FID heritability across diverse taxa to fully understand the evolution of risk assessment behaviours.

We studied FID inheritance in a population of wild and individually marked yellow-bellied marmots, *Marmota flaviventer*, that has been observed for over 60 years (Armitage, 2014; Blumstein, 2013). Since 2001, the project has also included a molecular genealogy and resulting pedigree. With over 20 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) that allows us to partition the phenotypic variance into its additive genetic and environmental components.

<H1>METHODS

<H2>Site and Trapping

Data were collected at the Rocky Mountain Biological Laboratory in Gothic, Colorado, U.S.A., where behavioural 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, resulting in 1389 FID measurements taken from 2001 to 2019 with paired pedigree information that were used for this study. From late May to early September,

marmots were caught using Tomahawk live traps at sites distributed along a 5 km altitudinal gradient that ranged in elevation from 2800 to 3100 m above sea level. Captured animals were transferred into cloth handling bags where they were weighed and their sex was determined. Marmots were tagged with numbered eartags and marked with nontoxic Nyanzol fur dye so that they could be identified from a distance (Armitage, 1982). Hair samples were also collected to extract DNA data to determine maternal and paternal relationships. Marmots in the study were spread across six lower-elevation sites referred to as 'down valley' as well as six higher-elevation sites referred to as 'up valley' (Fig. 1). Habitat varied between and within sites, including subalpine meadows, forest clearings and steep talus slopes (Armitage, 1982).

<H2>Flight Initiation Distance

To quantify FID, a researcher approached a group of marmots and waited quietly for 5 min so as not to further alarm them. In this context, a 'group of marmots' is defined as two or more marmots visible at a colony. Marmots were identified by their unique fur dye symbol using binoculars and/or a 15–45× spotting scope and one individual was selected to approach. The researcher walked towards the marmot at a measured pace of 0.5 m/s 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 metre tape or a Bushnell range finder.

To account for social interactions among marmots, which can influence their FID, a 10 m radius around the marmots was observed. Marmots are moderately social animals that often rely on alarm calling to alert group members of potential threats, and their group dynamics can affect their alertness and flight responses (Lea & Blumstein, 2011). Therefore, the number of marmots within this 10 m radius was recorded, along with substrate type, incline and the distance between an animal's initial position and the burrow it escaped to (Uchida & Blumstein, 2021). Substrate type included stone, talus, dirt, low vegetation (short grasses <10 cm) and high vegetation (dense shrubbery and tall grasses or wildflowers >10 cm) (Armitage, 1982). FIDs were conducted during mornings (0700–1100 hours) and late afternoons (1600–1800 hours) in warm summer months in clear weather.

<H2>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. (Valencia, CA, U.S.A.) and amplified via polymerase chain reaction (PCR.) We used microsatellite genotyping at 12 loci to match parents to offspring and analysed allele frequencies using GENEMAPPER (Blumstein et al., 2010; Edic et al., 2020). Parentage was assigned by using CERVUS 3.0 (Kalinowski et al., 2007), resulting in samples having a 95% confidence in parental assignment.

<H2>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 additive genetic and permanent environment effects, as well as year, colony and dam identity (ID). Because FIDs tend to be shorter in colonies with greater amounts of human disturbance, controlling for colony location helped account for variation in environment and habituation (Uchida & Blumstein, 2021). Including dam ID allowed us to account for maternal effects, including learning by offspring, as it allows us to separate additive genetic variation from maternal effects associated with maternal care and maternal environment effects.

Additive genetic effects were estimated by fitting marmot ID as a random effect linked to a genetic relatedness matrix derived from the pedigree (Kruuk, 2004). Permanent environmental effects were estimated by fitting marmot ID assuming individuals were not related (Kruuk & Hadfield, 2007). The fixed effects in our model included age and sex of focal marmots, distance from the marmot's initial position to the burrow it ran to, starting distance of the observer, incline of the marmot's initial position, substrate of the marmot's initial position, valley position (up valley versus down valley) and number of marmots in a 10 m radius (Blumstein et al., 2004; Bonenfant & Kramer, 1996; Monclús et al., 2015; Wey & Blumstein, 2010). Because alert distance and starting distance were highly correlated (r = 0.89, P = 2.2e-16), we elected to use starting distance because it was always recorded (alert distance was not recorded for all trials) and hence created a slightly larger data set. Valley position includes 'up valley' and 'down valley', two different clusters of colonies separated by less than 5 km 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 had 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 & Blumstein, 2021). The model was fitted in R version 4.1.2 (R Core Team, 2021) using the function 'asreml()' from the package 'ASReml' version 4.1.0 (Butler et al., 2017).

Statistical significance was assessed using likelihood ratio tests (LRT) comparing models with and without the random effects of interest (Pinheiro & Bates, 2000, pp. 57–96). For fixed effects, we used a Wald test with a Kenward–Rogers approximation for the number of degrees of freedom (Butler et al., 2017). Model assumptions were visually inspected and all were verified. For plotting only, marginal effects of each fixed effect were estimated using the package 'lme4' version 1.1.32 (Bates et al., 2015) and then plotted using the package 'sjPlot' version 2.8.14 (Lüdecke, 2024).

The random effect structure of the model estimated colony (V_{colony}), year (V_{year}), maternal effects (V_{dam}), permanent environment (V_{pe}), additive genetic effect (V_a) and residual variance (V_r). Total phenotypic variance (V_p) conditioned on the fixed effects was calculated as the sum of all the variance components. Narrow-sense heritability (h^2) was calculated as the proportion of the phenotypic variance that can be explained by additive genetic variance as $h^2 = V_a/V_p$.

Evolvability (E) was also estimated as the ratio of genetic variance to the squared mean of the trait ($E = V_a/\text{FID}^2$) (Houle, 1992). Evolvability 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. We also estimated unadjusted repeatability by fitting a model of FID including only individual identity as a random effect and without any fixed effects.

Ethical Note

The marmot study was 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, typically within 15 min of reaching a trap. Trapping occurred in the morning and late afternoon under cool conditions, with traps checked within 2 h of setting. Previous research has indicated that relatively few marmots exhibit an increased glucocorticoid response associated with struggling in a trap (Smith et al., 2012), and 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 FID 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 & Blumstein, 2021). Initial start distances were set at distances that did not visibly disrupt marmot behaviour, which varied among different groups.

<H1>RESULTS

Unadjusted mean (± SE) repeatability (R) was estimated as 0.539 ± 0.025. Mean (± SE) heritability (h^2) was estimated as 0.147 ± 0.045, with the additive genetic variance being significantly different from zero (Table 1). Colony was also significantly different from zero (Table 1). Year, maternal effects and individual environmental effects did not explain significant variation in FID. Mean (± SE) evolvability (E) of FID was estimated 0.037 ± 0.011.

There were several significant fixed effects (Table 1, Fig 2). Starting distance and distance to

burrow were strongly positively correlated with FID. Trial number was slightly negatively correlated with FID. Age, sex, valley position, slope, substrate and number of marmots within 10 m did not explain significant variation in FID. Marmots in different colonies varied widely in their average FIDs, ranging from 12 m in the highly human-disturbed Gothic townsite and low-disturbance River Annex (down valley) to 95 m at low-disturbance Stonefield (up valley). Mean FIDs on different substrates also varied, ranging from 25 m in high vegetation to 32 m on talus.

<H1>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 15% of variation in FID is due to additive genetic effects. Our estimate is in the low range of previously reported estimates of heritability of FID that vary widely from 0.15 to 0.80. However, the higher estimates reported are from parent–offspring regressions, which tend to overestimate genetic contributions more than animal models (Carrete et al., 2016). Furthermore, considering the high plasticity of behavioural traits, they often exhibit a lower heritability, with an estimated average of 0.24 (Dochtermann et al., 2019).

Moreover, heritability estimates are contingent on the structure of the fixed effects, and thus, the precise value of heritability can be significantly influenced by the fitted effects (Wilson et al., 2010). While we controlled for a limited number of variables with known effects, we acknowledge the potential presence of unmeasured confounding variables (e.g. injury or illness, social rank, hunger level, size of researcher conducting the FID), which could contribute to a

potential overestimation of additive genetic effects. Nevertheless, the incorporation of fixed effects primarily resulted in a reduction of residual variance, consequently leading to an increase in heritability estimates. It is also noteworthy that the excessive inclusion of variables in the model can lead to overfitting, collinearity and increased noise, which may diminish the precision and reliability of variance component estimates, making it difficult to accurately partition genetic and environmental contributions to the trait of interest (Wilson et al., 2010). Additionally, despite the moderate heritability observed for FID, the estimated evolvability stood at 0.04, suggesting a relatively low potential for adaptive changes in FID within this population.

As expected, a suite of environmental variables explained variation in FID. Although substrate overall did not significantly influence marmot FID in our variance decomposition analysis, FIDs conducted on marmots in high vegetation were the shortest and FIDs in low vegetation were the shortest compared to all other substrates. This is consistent with prior studies 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, but predators may also be easier to see in open habitats, potentially increasing FID as marmots can detect threats from further away. Also unsurprisingly, colony was a significant variable that explained variation in FID. Colonies vary in human exposure and relative tolerance to approaching humans (Uchida & 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 & Blumstein, 2008). These 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 effects that change the composition and spatial distribution of lower trophic levels. For instance, Laundré et al. (2001) reported that wolf reintroduction in Yellowstone National Park in 1995 triggered a behavioural 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 is influenced by herbivorous fish, with the tallest algae canopies observed at greater distances from fish refuges.

From landscapes to seascapes, the degree to which genetic and environmental variables factor into fear responses could have significant implications for the overall behavioural response of a population (and consequently, the community), especially when challenged with new stressors. By understanding the extent that animals can alter their behaviour 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 & 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, *Ailuropoda malanolecua*, 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 & 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 (Rodgers & Smith, 1997; Weston et al., 2012). As an example, an Australian study on coastal birds demonstrated that implementing buffer zones of at least 25 m between roads and beaches could significantly reduce vehicle-induced flushing (Schlacher et al., 2013). FID's heritable and plastic components indicate limits to phenotypic plasticity and suggest that populations may evolve, potentially altering the effectiveness of buffer zones over time. Thus, management actions may need periodic review to adapt to these changes.

Finally, the evolvability of FID can inform management options for endangered species and serve as an indicator to assess the efficacy of conservation measures. The genetic basis of antipredator behaviour 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 behaviour. Conversely, species with higher evolvability of escape behaviour may have a better chance of long-term survival than those that must rely on modifying their antipredator strategies earlier in life.

Author Contributions

Data Availability

Code and data to reproduce these analyses are available through the Open Science Framework (OSF) project: https://osf.io/j3vs2/

Declaration of Interest

The authors declare no conflicts of interest.

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Table 1

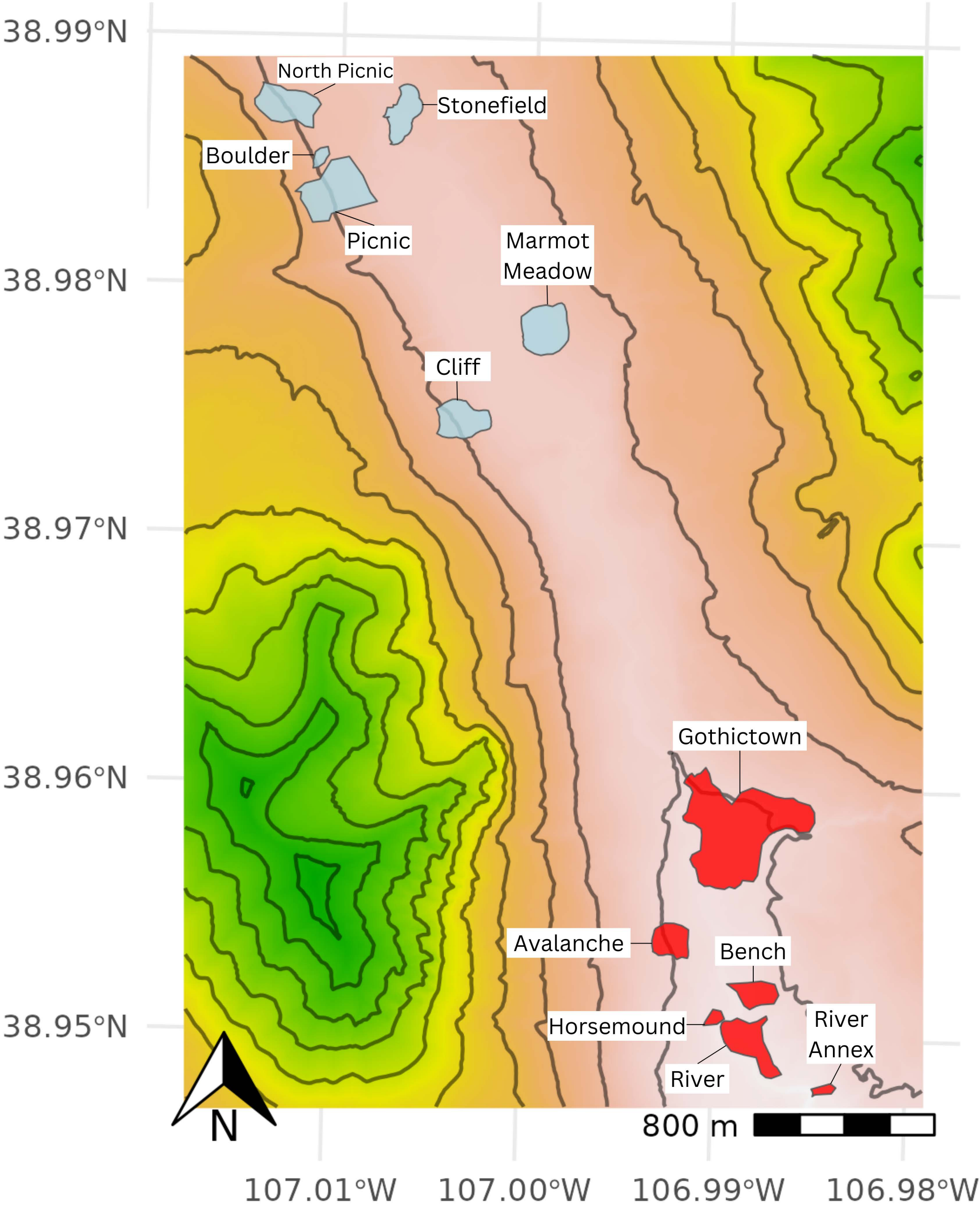
Parameter estimates from an animal model of flight initiation distance in yellow-bellied marmots

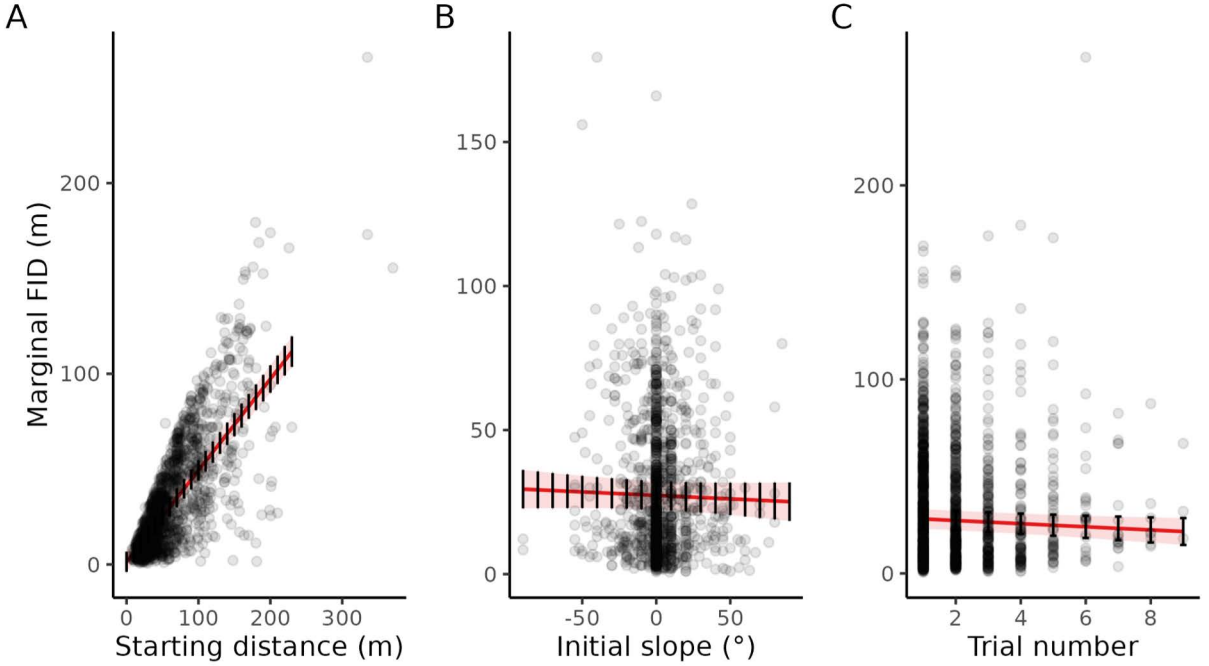
	Estimate	SE	*F*/LRT (*df*)	*P*
Fixed effects				
Intercept	1.41	3.44	3.06 (1, 13)	0.103
Sex (Male)	-0.48	1.16	0.17 (1, 491)	0.678
Age	-0.14	0.25	0.29 (1, 316.6)	0.587
Valley (Up valley)	4.38	4.27	1.05 (1, 10.2)	0.329
Distance to burrow	**0.61**	**0.08**	**57.77 (1, 1194)**	**<0.001**
Starting distance	**0.47**	**0.02**	**706.6 (1, 800)**	**<0.001**
Slope	-0.02	0.03	0.94 (1, 954.2)	0.332
Substrate			1.77 (4, 807.4)	0.132
HV	0.56	2.47		
LV	3.54	1.62		
S	0.75	1.55		
T	1	1.7		
Number within 10 m	-0.31	0.32	0.98 (1, 1204)	0.322
Trial number	**-0.74**	**0.34**	**4.76 (1, 1171)**	**0.029**
Variance components				
$\boldsymbol{V_{colony}}$	**27.349**	**20.218**	**6.585 (1)**	**0.010**
V_{year}	3.257	3.067	2.004 (1)	0.156
V_{dam}	8.804	6.865	2.204 (1)	0.137
V_{pe}	5.23×10-6	<0.001	<0.001 (1)	1.000
$\boldsymbol{V_a}$	**41.834**	**12.003**	**18.897 (1)**	**<0.001**
V_r	203.068	9.331		

Solution and component estimates (*F* tests for fixed effects, LRT for random effects) are reported along with SE and *P* values. HV: high vegetation; LV: low vegetation; S: stone; T: talus. V_a: additive genetic component; V_{pe}: permanent environment component; V_r: residual variance component. Significant outcomes are shown in bold.

Figure 1. Map of the study site and the colonies. Lines and colour gradient represent variation in elevation from 2800 to 3849 m. Red and blue polygons denote down valley and up valley colonies, respectively.

Figure 2. Marginal effects of (a) starting distance, (b) initial slope and (c) trial number on flight initiation distance (FID) in yellow-bellied marmots at Rocky Mountain Biological Laboratory. Open circles represent the data; lines, error bars and ribbon represent the model predictions with 95% confidence intervals.


38.99°N
38.98°N
38.97°N
38.96°N
38.95°N
North Picnic
Stonefield
Boulder
Picnic
Marmot
Meadow
Cliff
Gothictown
Avalanche
Bench
Horsemound
River
River
Annex
N
800 m
107.01°W
107.00°W
106.99°W
106.98°W


A
B
C
Marginal FID (m)
0
100
200
0
100
200
300
Starting distance (m)
150
100
50
0
-50
0
50
Initial slope (°)
200
100
0
2
4
6
8
Trial number