Behavioral correlations across multiple stages of the antipredator response: do animals that escape more readily also hide longer?

Chelsea Ortiz-Jimenez[1], Marcus Michelangeli[2], Erika Pendleton[3], Andrew Sih[4], and Jennifer Smith[3]

[1]University of California Davis
[2]Monash University
[3]Mills College
[4]University of California

March 07, 2024

Abstract

While numerous studies have examined either initial prey responses to an approaching predator (flight initiation distance, FID), or subsequent hiding behavior (e.g. latency to resume activity), to our knowledge, no previous studies have repeatedly tested multiple individuals in nature, to quantify whether both FIDs and latencies to resume activity are repeatable, and whether these two stages of the antipredator response are positively correlated. This correlation is ecologically important in that opportunity costs of predator avoidance are particularly large if the same individuals tend to both escape more readily and hide longer. Here, we examined California ground squirrels' (Otospermophilus beecheyi) responses to human approach, and provided the first example showing that, as predicted: FIDs, latencies to resume activity, and other aspects of prey responses post-FID were repeatable and positively correlated. Interestingly, we also found that across a gradient of human activity, squirrels in areas with higher human activity were generally bolder.

Introduction

To understand predator impacts on prey and, in particular, non-consumptive effects of predators on prey (Preisser et al. 2005; Peacor et al. 2020), a key issue is to elucidate factors that explain variation in prey responses to perceived predation risk (Lima 1998; Brown & Kotler 2004; Creel & Christianson 2008; Wirsing et al. 2020). The overall prey response is commonly split into two main stages: escape when an attack occurs or appears imminent, and subsequent avoidance often by staying in or near refuge (Lima & Dill 1990; Heithaus et al. 2009). Although this basic framework has long been part of standard predator-prey behavioral ecology, most studies have either quantified escape responses (e.g., flight initiation distances (FIDs); e.g., Stankowich & Blumstein 2005; Moller et al. 2016), or refuge use (e.g., time spent in refuge; Cooper & Sherbrooke 2015). Surprisingly, few have examined both for the same individuals, particularly in the field. Here, we repeatedly quantified the responses of individually marked, free-ranging animals to the approach of a potentially threatening human. We present what we believe is the first study to test for consistent individual differences in multiple stages of the overall prey response to risk: in initial escape tendencies, in behavior during the escape, and in latency to resume activity after spending time in refuge. In particular, our study is, to our knowledge, the first to examine the fundamental point of individual-level correlations among these aspects of the antipredator response. Under field conditions, even with natural variation in context (e.g., distance to refuge, vegetation height, presence of conspecifics), are the same individuals that are more fearful than others in the sense of fleeing more readily also more fearful in the sense of staying longer in refuge before resuming activity? This correlation across stages of the prey response, if it exists, provides an underlying mechanism for a tradeoff involving not just the cost versus benefit of early versus late escape, or early versus late emergence from refuge, but for a tradeoff based on variation in fearfulness expressed across stages. Before describing our field study on ground squirrel antipredator responses, we next provide a bit more detail on the general conceptual overview.

When prey first detect a potential predator, they can, but often do not, immediately initiate an escape attempt. Instead, prey often monitor the predator's behavior, and only initiate escape when the predator approaches more closely. A standard metric for assessing fear is thus an animal's flight initiation distance (FID), the distance at which an individual flees from an approaching intruder. Theory predicts that because active escape from predators has costs (e.g., energy and lost opportunities), prey should typically not initiate escape as soon as they detect predators but should instead optimize their FID by fleeing only when predators have come close enough that the costs of not fleeing are higher than the costs of escaping (Ydenberg & Dill 1986). A large literature (e.g., Stankowich & Blumstein 2005; Moller et al. 2016; Morelli et al. 2019) shows that FIDs can depend on characteristics of the predator (e.g., greater FID if predators are perceived to be more dangerous), the prey (e.g., the prey's state, escape ability, or behavioral type), the social context (e.g., presence of conspecifics), and the ecological context (e.g., availability and distance of refuge). With regard to prey traits, the current interest in animal personalities (Sih et al. 2004a,b; Reale et al. 2007) suggests a need to measure consistent individual differences in FIDs; however, to date, relatively few studies have quantified the repeatability of FIDs in nature (but see Carette et al. 2009; Moller & Tryjanowski 2014; Cabrera et al. 2017).

After animals flee from a predator, they have further decisions to make including whether to run into shelter and if so, when to emerge. Rather than run all the way to shelter, animals sometimes flee and then 'stop and look' to apparently re-assess the danger. The distance that they flee before they 'stop and look' can be used as an additional measure of fearfulness (i.e., more fearful animals likely have a larger 'stop and look' distance). If prey flee to shelter, then a key decision is when to emerge to resume activity (Sih 1992; Cooper & Frederick 2007). More fearful animals likely have a longer latency to resume activity. While FIDs have been measured in many species (Bonenfont & Kramer 1996; Stankowich & Blumstein 2005; Engelhardt & Weladji 2011; Petelle et al. 2013; Moller & Tryjanowski 2014; Uchida et al. 2015), fewer studies have explored post-FID responses (but see Bonenefont & Kramer 1996; Cooper & Sherbrooke 2015; Tätte et al. 2018; Breck et al. 2019) and, to our knowledge, no studies have quantified consistent individual differences (repeatability) of post-FID responses – either in isolation or in relation to other components of the antipredator response.

If FIDs, 'stop and look' distances, and latency to resume activity all reflect differences among individuals in underlying fear, then consistent individual differences in these should be positively correlated. These correlations are ecologically important; for example, the core idea that more fearful animals suffer greater opportunity costs (e.g., greater reductions in feeding rate) from avoiding predators hinges not just on them escaping more readily to shelter, but crucially, on them hiding, often for long periods, before resuming activity. It is thus striking that, to our knowledge, no previous studies have tested the hypothesis that larger FIDs are positively correlated with longer latencies to resume activity. Ideally, analyses of multi-stage prey responses to predators should test for effects of both individual differences in behavioral tendencies and multiple aspects of the context (ecological and social) on each stage of the overall response; however, as far as we know, no previous studies have attempted to do that.

We studied the responses of focal animals to approaching humans. With the global expansion of human presence, animal responses to human activity can have important effects on individual and species success (Strasser and Heath 2013; Arroyo et al. 2017). How well animals cope may depend on a variety of factors including their behavior and/or their past experience with human disturbance (Sih et al. 2011, 2012; Lapiedra et al. 2017). In many cases, animals respond to humans as predators, actively avoiding areas of human activity (Oriol-Cotterill et al. 2015; Clinchy et al. 2016; Suraci et al. 2019). In other cases, however, repeated exposure to humans leads to habituation (Stankowich & Blumstein 2005; Geffroy et al. 2015; Blumstein 2016; Uchida & Blumstein 2021). The reduced fear of humans can be associated with a general increase in boldness, exploration or aggressiveness as often seen in animals in urban environments (Moller 2008; Rodriquez-Prieto et al. 2008; Miranda et al. 2013; Uchida et al. 2015; Breck et al. 2019). However, whilst behavioral adjustments in animals inhabiting urban environments are well-documented, less is known about how human activities shape behavior or behavioral variation in animals residing in natural areas, such as reserves or parks that are comparatively insulated from urban disturbance (Gonson et al. 2016; Watson et al. 2016; Corisini et al. 2019).

Here, we examined how variation in rates of human activity shape risk-sensitive behavior throughout multiple steps of the antipredator response in a free-living mammal, the California ground squirrel (*Otospermophilus beecheyi*). Ground squirrels are ecosystem engineers, a major prey species in the California grasslands (Smith et al. 2016) and display a suite of behavioral responses to threats (Owings & Ledger 1980; Hanson et al. 1997; Putman et al 2015; Ayon et al. 2017) including human approach (Hammond et al. 2019). While ground squirrels are often deemed pests by humans, they are generally not directly killed by humans. This species therefore offers an interesting opportunity to examine how animals exposed to varying levels of human activity adapt their behavior in the presence of humans. Specifically, we repeatedly recorded both the squirrels' flight initiation distances (Ydenberg & Dill 1986, Bjorvik et al 2014; Uchida et al. 2015), and their post-FID behaviors as discussed above (Fig. 1). Thus, our study is unique in allowing us to both (1) explore how human activity influences each decision of a squirrel's antipredator response (i.e., when to flee and whether and how long to shelter) and (2) examine the covariation between different components of the antipredator response. We predicted that human activity would influence multiple components of a squirrel's risk-sensitivity and anti-predator response. We further predicted that if aspects of the antipredator response are correlated, then an individual's FID response should also correspond to their risk-sensitivity across other contexts, such as their willingness to enter a trap across multiple potential trapping sessions. Finally, we also examined other factors that might contribute to risk-sensitive decision-making including age and sex of the focal individual, the surrounding microhabitat features, and conspecific presence.

Materials & Methods

Study site and subjects

We studied free-ranging ground squirrels at Briones Regional Park in Contra Costa County, California, USA (Latitude: 37.93 North, Longitude: 122.13 West, Elevation: 319 m above mean sea level). For this study, we focused on a 0.96-hectare site that is a well-known picnic and resting area near a main entrance to the otherwise less human-disturbed 6117-acre Briones Regional park (Fig. S1). Since 2013, we live trapped, marked, and released individuals of known age, sex, reproductive state, and mass (see Smith et al. 2018 for details). Further, we recorded the proportion of days an individual was trapped on available trapping days (henceforth 'trappability'). Squirrels were individually fur marked, and on non-trapping days, we identified individuals from a distance using binoculars to record spatial locations and, in 2018 and 2019, their flight initiation distances (FIDs, see below). We combined all spatial data from May to July of these two years to determine each squirrel's home site, or the locations each individual squirrel spent the majority of their time. Locations of trapped and free-living squirrels were noted daily based on a standard set of natural (e.g., burrows, trees) and artificial (e.g., picnic tables, outhouse) landmarks at the study site. We quantified human activity by counting the number of humans present within 15 m of each landmark (Hammond et al. 2019). Following van der Marel et al. (2019), we calculated human activity at each location by dividing the number of humans at a location by its total observation time each summer (henceforth 'home site human activity score'). Within our site, human activity ranged over a spatial gradient going eastward from moderately high to low.

Flight initiation distance trials

Between the hours of 0900-1400, we selected subjects for FID trials using a regular sampling regime to increase the evenness of sampling across subjects (Altmann 1974). Focal squirrels were only chosen while foraging and not moving (e.g., walking or socializing) to isolate responses to human approach.

Prior to each assay, the walker noted the location, date, time of day, number of conspecifics within 5 m, and vegetation cover. We considered conspecifics to be present when they were within 5 m of the focal individual; this is the distance this species is most sensitive to environmental changes (Leger et al. 1983;

Ortiz et al. 2019). We categorized vegetative cover as high when it effectively covered the body of adults foraging quadrupedally and low when it did not (low = 0-10 cm; high >10 cm) (Owings & Coss 1977; Ortiz et al. 2019).

The walker approached the focal subject at a speed of 0.5-m/sec (Runyan & Blumstein 2004). All walkers were trained to ensure consistent speed and posture. Each walker dropped one marker at their departure location and a second marker at the exact moment the squirrel fled. The distance between the focal squirrel and the flight marker was then measured (± 0.1 m). We also noted the distance between the focal squirrel and (i) the walker's starting location (henceforth 'starting distance') and (ii) the subject's nearest burrow since these influence FIDs in other species (henceforth 'distance from shelter'; Bonenfant & Kramer 1995; Engelhardt & Weladji 2011).

After the initial flee response, observers continued to watch the focal squirrel to record its behavior. Squirrels typically took one of two options as their post-FID response: (1) fled into shelter and re-emerged over some period of time or (2) fled and stopped to watch at a distance. If a squirrel ran into shelter, we then recorded how long it took to re-emerge from shelter (henceforth 'shelter emergence time'). If a squirrel did not run into shelter, we recorded the total distance it fled from the walker (henceforth 'stop look distance').

Statistical analysis

Analysis was conducted in R version 3.6.2 using the Bayesian package*brms* (Bürkner 2017) an interface to Stan (Stan Development Team 2015) for linear mixed-effects models (see Supplement). FIDs were square-root transformed prior to analysis to meet model assumptions of normality of residuals. We report posterior means for all estimated parameter with 95% credibility intervals (CIs).

Flight initiation distance analysis

We first examined the effects of social and environmental factors on FIDs. Specifically, we ran a univariate mixed model with the following predictors: year, life-stage (juvenile or adult), sex, individual trappability, trial number, number of conspecific present, vegetation cover, starting distance, home site human activity score, and distance to shelter. We included home site identity, walker identity, and squirrel identity nested within home site identity as random intercepts. Home site identity was included as a random intercept because multiple squirrels were tested from the same home site and thus would more likely be similar to each other. Walker identity was included to control for potential experimental variation arising from differences among walkers. Finally, we recognized that in scenarios where individuals were tested in the presence of other conspecifics simultaneously, the FID of these individuals were not independent. Thus, we re-ran our model after filtering the data to only include the FID of the first individual to flee within these group testing situations but found that the same predictor effects remained as in our full dataset model (Table S1).

Individual FID repeatability ($\mathrm{R}_{\mathrm{FID}}$) was calculated by extracting the variance components from our full FID model and using the following formula:

$$R_{\mathrm{FID}} = \frac{V_{\mathrm{ind}}}{(V_{\mathrm{ind}} + V_{\mathrm{home}} + V_{\mathrm{obs}} + \ V_{\mathrm{res}})}$$

Where $\mathrm{V}_{\mathrm{ind}}$ is the among-individual variance, $\mathrm{V}_{\mathrm{home}}$ is the among-home site variance, $\mathrm{V}_{\mathrm{obs}}$ is the among-observer variance, and $\mathrm{V}_{\mathrm{res}}$ is the residual variance.

Post-flight initiation distance response and correlation analysis

Given that squirrels could only take one of two escape options, we first ran a binomial model exploring the factors that influenced whether a squirrel sheltered or not (Table S2) and then we ran separate bivariate models to analyze these disparate post-FID responses and their among-individual correlations with FID. Specifically, one model contained FID and shelter emergence time as response variables, and the second model contained FID and stop look distance as response variables. Shelter emergence time and stop look distance were both modelled using a Gamma distribution and log-link function. Both bivariate models contained the same set of predictors (year, sex, life stage, trial number, home site activity score and trappability). Walker identity and squirrel identity were included as random intercepts. To estimate the correlation between an individual's FID and post-FID response, we extracted the posterior mean among-individual random intercept correlation from each model respectively. We also estimated the repeatability (R) of each post-FID response by extracting the variance components from their respective models and using the following formula for Gamma distributed variables (Nakagawa et al. 2017):

$$R = \frac{V_{\text{ind}}}{V_{\text{ind}} + V_{\text{obs}} + ln(1 + \frac{1}{\upsilon})}$$

where V_{ind} is the among-individual variance, V_{obs} is the among-observer variance, and υ is the shape parameter of the gamma distribution.

Results

Flight initiation distance

We found FIDs were repeatable (R = 0.29; 95% CI [0.172, 0.409]). Human activity within an individual's home site predicted its FID; squirrels experiencing greater human activity had shorter FIDs; i.e., were bolder (Table 1; Fig. 2A). Highly trappable individuals also had shorter FIDs than less trappable individuals (Table 1; Fig. 2B). Females had shorter FIDs than males (Table 1). FIDs increased with group size (Table 1; Fig. 2C) suggesting squirrels were quicker to flee from an approaching human when more conspecifics were present. We also found that squirrels had longer FIDs with longer starting distances (Table 1).

Post-flight initiation distance response and correlation

Squirrels ran into shelter in 30% of trials. Juveniles sheltered (as opposed to 'stop and look') more frequently than adults (Table S2). Squirrels tested near a burrow were more likely to run into shelter (Table S2), but no other factor significantly explained variation in likelihood of running to shelter. Notably, the decision to run into shelter was not repeatable (R = 0.038 [0, 0.119]), but time to emerge from shelter was repeatable (R = 0.39 [0.191, 0.59]). Individuals from home sites that experience greater human activity emerged from shelter more quickly than squirrels from home sites with lower human activity levels (-2.336 [-4.413, -0.431]; Table S3; Fig. 3A). Furthermore, more trappable individuals had shorter shelter emergence times than less trappable individuals (-1.359 [-2.456, -0.359]; Table S3; Fig. 3B). We also found a high positive among-individual correlation between emergence time from shelter and FID (0.57 [0.139, 0.967]; Fig. 4A), indicating that individuals that allowed walkers to approach more closely before fleeing were also faster to re-emerge from shelter. Time to emerge from shelter decreased with trial number (0.137 [0.030, 0.241]; Table S4).

The response to stop and look from a distance occurred in 70% of trials (stop look distance mean: 5.1 ± 0.3 S.E. m; range: 0.2 m to 27.7m). Stop and look distances were only weakly repeatable (R = 0.216 [0.073, 0.370]) and we found no significant predictors for stop look distance (Table S4). However, we did find a high positive among-individual correlation between stop look distance and FID, suggesting that individuals that allowed walkers to approach more closely before fleeing also fled shorter distances from the walker following their FID response (0.736 [0.428, 0.988]; Fig. 4B).

Discussion

Our study shows that variation in human activity can profoundly affect multiple aspects of risk-sensitivity and antipredator responses in wildlife even over relatively small spatial scales. Specifically, ground squirrels residing in areas of greater human activity consistently had shorter FIDs than squirrels residing in adjacent, nearby areas of lower human activity. Importantly, repeated exposure to human activity also influenced the post-FID response, as squirrels from high human disturbance areas also fled shorter distances before stopping to observe a potential threat following their flight response, and if they fled into shelter, were consistently faster to emerge from shelter. Squirrels from high activity sites have likely habituated to high human activity, thus responding less to an approaching human compared to individuals that have less experience with humans. While many other studies have observed animal habituation to non-dangerous humans (Petelle et al. 2013; Vincze et al. 2016; Uchida et al. 2019; Uchida & Blumstein 2021), it is striking that variation in the degree of habituation emerged over a small spatial scale (i.e., within a 1-hectare area). Beyond the strong effects of relative human activity on multiple antipredator behaviors, we also documented consistent individual differences in the suite of repeatable behaviors along a general, shy-bold continuum (Wilson et al. 1994) including high among-individual correlations between FID and post-FID responses for the first time.

Having a highly correlated suite of behaviors may be adaptive or maladaptive, depending on the situation and environment in which the animal resides (Trouilloud et al. 2004; Geffroy et al. 2015; Wilson et al. 2020). In this case, having correlated behaviors throughout the antipredator response may be beneficial when it comes to predators (e.g., when real danger is present, animals should both flee readily and hide for a relatively long time before resuming activity). However, the correlation may exacerbate unnecessary over-avoidance of humans that can be a substantial problem in human disturbed environments (Trimmer et al. 2017; Guiden et al. 2019). Unhabituated animals might both flee too readily from humans (that are not actually dangerous), but also wait too long to emerge from shelter which may mean a lost opportunity in foraging time. On the other hand, getting habituated in terms of both reduced tendency to flee and reduced time spent inactive can be beneficial. However, if getting bolder (here, when habituating to humans) carries over to other situations, this can be ecologically relevant. For example, we know that bolder squirrels pick-up more fleas (Smith et al. 2021) and have increased venom resistance (Holding et al. 2020). Perhaps most notably, it has been suggested that boldness associated with habituation to humans can make animals less wary when encountering actual, dangerous predators, which can obviously be very costly (Lowry et al. 2012; Geffroy et al. 2015). Thus, anthropogenic influences on boldness could influence disease transmission and predator-prey dynamics.

Here, we found that animals that were bolder, apparently due to being habituated to human activity, were also more readily trapped. Other studies have found mixed evidence for an association between boldness and trappability (Biro 2012; Michelangeli et al. 2015; Brehm & Mortelliti 2018). The observation that trappability predicts antipredator behavior can have important implications as a systematic bias when trapping for monitoring, ecological research or pest control (Biro & Dingemanse 2009; Garvey et al. 2020).

Besides strong effects of human activity and individual differences, the three main antipredator responses were largely either unaffected or only weakly affected by the social (presence and number of conspecifics) and environmental contexts (distance to shelter, vegetation cover) that we considered. We predicted that animals that are closer to shelter would exhibit shorter FIDs and that vegetation cover would affect FIDs, but these factors did not significantly affect FIDs. FIDs were, however, affected by the social context (group size). In theory, this effect could have gone either way. If larger groups with “many eyes” (Pulliam 1973) should detect predators sooner, animals in larger groups should flee sooner (i.e., have larger FIDs). On the other hand, the dilution or confusion effects (Bertram 1978) can make animals in larger groups safer in which case, FIDs should be smaller. In fact, FIDs increased with group size, consistent with the former mechanism. This finding is particularly interesting given that California ground squirrels are less vigilant when foraging in groups (Ortiz et al. 2019). Taken together, this suggests that, on average, individuals foraging in groups may benefit from both increased energy intake and earlier detection of threats. However, humans are not a direct threat to this species and consistently fleeing early due to human disturbance can lead to decreased energy intake in the long run. Thus, the social information provided from group foraging may only be beneficial when confronted with an actual predator.

We also found evidence for more subtle context-dependence in these antipredator behaviors. In particular, after fleeing (post-FID response), the decision to ‘stop and look’ versus flee all the way to shelter was largely environmentally context dependent. Animals showed no consistent individual differences in this decision. Instead, they were more likely to flee to shelter if available shelter was closer. Interestingly, juveniles were generally more likely to flee to shelter rather than ‘stop and look’; this presumably reflects their greater vulnerability to predators and, thus, greater fear (Putman et al. 2015).

We believe our findings of high individual-level correlation among multiple stages of the antipredator response are consistent with our general conceptual framework, contributing new insights and opportunities for the study of animal personalities. Future research should continue to investigate these correlations throughout the overall antipredator response in other species and the trade-offs animals face across all stages of prey's response to risk and not just their initial flight response. Doing so can also provide more insights on the impacts of human activity on wildlife behavior, predator-prey dynamics and ecosystem function.

Ethics

All methods used were approved by the Animal Care and Use Committee at Mills College and UC Davis and is consistent with guidelines of the American Society of Mammologists for the use of wild mammals in research.

Acknowledgements

We are grateful to the numerous members of Team Squirrel for contributing to data collection for this study. We thank the staff of the East Bay Regional Park District, especially to J. Miller and D. Bell, and to the California Department of Fish and Wildlife for their cooperation. This work was supported by a National Science Foundation Graduate Research Fellowship for Ortiz-Jimenez and a National Science Foundation ROA supplement (DEB 1456730) awarded to Sih and Smith. Ortiz-Jimenez was further supported by Cota-Robles Fellowship and Jastro Shields Award from UC Davis. Smith was supported by the Letts-Villard Endowed Professorship in the Natural Sciences from Mills College and the Undergraduate Education Program of the W. M. Keck Foundation. Pendleton and Smith were supported by the Barrett Foundation through the Jill Barrett Undergraduate Program in Biology at Mills College. Lastly, we thank Mary Bowerman Research fund from Save Mount Diablo for supporting Ortiz-Jimenez, Pendleton and Smith.

References

Altmann J. (1974). Observational study of behavior: sampling methods.*Behav.* 49(3–4), 227–66.

Arroyo, B, Mougeot, F, & Bretagnolle, V. (2017). Individual variation in behavioural responsiveness to humans leads to differences in breeding success and long-term population phenotypic changes. *Eco Lett* , 20(3), 317-325.

Ayon RE, Putman BJ, Clark RW. (2017). Recent encounters with rattlesnakes enhance ground squirrel responsiveness to predator cues.*Behav Ecol Sociobiol* , 71(10), 1-10.

Bertram BCR. (1978). *Living in groups: predators and prey* . Krebs JR, Davies NB. Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford, pp 64–96

Biro PA. (2012). Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. *Oecologia* , 171(2), 339–45.

Biro PA, Dingemanse NJ. (2009). Sampling bias resulting from animal personality. *Trends Ecol Evol* , 24(2), 66–7.

Bjorvik LM, Dale S, Hermansen GH, Munishi PKT, Moe SR. (2014). Bird flight initiation distances in relation to distance from human settlements in a Tanzanian floodplain habitat. *J Ornithol* , 156(1), 239–46.

Blumstein DT. (2016). Habituation and sensitization: new thoughts about old ideas. *Anim Behav* , 120, 255–62.

Bonenfant M, Kramer DL. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax* .*Behav Ecol* , 7(3), 299–303.

Breck SW, Poessel SA, Mahoney P, Young JK. (2019). The intrepid urban coyote: a comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Sci Rep* . 9(1), 1-11.

Brehm AM, Mortelliti A. (2018). Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality.*Anim Behav* , 142, 101–12.

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Eco lett* , 7(10), 999-1014.

Burkner P-C. (2017). brms: an R package for bayesian multilevel models using stan. *J Stat Soft.* 80(1), 1-28.

Cabrera D, Andres D, McLoughlin PD, Debeffe L, Medill SA, Wilson AJ, et al. (2017). Island tameness and the repeatability of flight initiation distance in a large herbivore. *Can J Zool* , 95(10), 771–8.

Carrete M, Tella JL. (2009). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol Lett.* 6(2), 167–70.

Clinchy M, Zanette LY, Roberts D, Suraci JP, Buesching CD, Newman C, et al. (2016). Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. *Behav Ecol* , 27(6), 1826-1832.

Cooper WE JR, Frederick WG. (2007). Optimal time to emerge from refuge.*Biol J Linn Soc* , 91(3), 375–82.

Cooper, WE, & Sherbrooke, WC. (2015). FEAR and DREAD: starting distance, escape decisions and time hiding in refuge. *Behaviour* , 152(10), 1371-1389.

Corsini M, Marrot P, Szulkin M. (2019). Quantifying human presence in a heterogeneous urban landscape. *Behav Ecol* , 30(6), 1632–41.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol Evol* , 23(4), 194-201.

Engelhardt SC, Weladji RB. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can J Zool* , 89(9), 823–30.

Garvey PM, Banks PB, Suraci JP, Bodey TW, Glen AS, Jones CJ, et al. (2020). Leveraging motivations, personality, and sensory cues for vertebrate pest management. *Trends Ecol Evol* , 35(11), 990–1000.

Geffroy B, Samia DSM, Bessa E, Blumstein DT. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol Evol,* 30(12), 755–65.

Gonson C, Pelletier D, Gamp E, Preuss B, Jollit I, Ferraris J. (2016). Decadal increase in the number of recreational users is concentrated in no-take marine reserves. *Mar Pollut Bull* , 107(1), 144–54.

Guiden PW, Bartel SL, Byer NW, Shipley AA, Orrock JL. (2019). Predator–prey interactions in the Anthropocene: reconciling multiple aspects of novelty. *Trends Ecol Evol* , 34(7), 616–27.

Hammond TT, Vo M, Burton CT, Surber LL, Lacey EA, Smith JE. (2019). Physiological and behavioral responses to anthropogenic stressors in a human-tolerant mammal. *J Mammal* , 100(6), 1928–40.

Hanson MT, Coss RG. (1997). Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to avian and mammalian predators. *J Comp Psychol* , 111(2), 174–84.

Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., & Dill, L. M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J Anim Eco* , 78(3), 556-562.

Holding ML, Putman BJ, Kong LM, Smith JE, Clark RW. 2020. Physiological stress integrates resistance to rattlesnake venom and the onset of risky foraging in California ground squirrels. *Toxins* , 12(10), 617.

Lapiedra O, Chejanovski Z, Kolbe JJ. (2016). Urbanization and biological invasion shape animal personalities. *Glob Change Biol* , 23(2), 592–603.

Leger DW, Owings DH, Coss RG. (1983). Behavioral ecology of time allocation in California ground squirrels (*Spermophilus beecheyi):* microhabitat effects. *J Comp Psychol* , 97(4), 283–91.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions.

Bioscience, 48(1), 25-34.

Lima SL, Dill LM. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool,* 68, 619–640.

Lowry H, Lill A, Wong BBM. (2012). Behavioural responses of wildlife to urban environments. *Biol Rev* , 88(3), 537–49.

Michelangeli M, Wong BBM, Chapple DG. (2015). It's a trap: sampling bias due to animal personality is not always inevitable. *Behav Ecol* , 27(1), 62–7.

Miranda AC, Schielzeth H, Sonntag T, Partecke J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Glob Change Biol* , 19(9), 2634–44.

Morelli F, Benedetti Y, Diaz M, Grim T, Ibanez-Alamo JD, Jokimaki J, et al. (2019). Contagious fear: escape behavior increases with flock size in European gregarious birds. *Ecol Evol* , 9(10), 6096–104.

Moller AP, Rubolini D, Lehikoinen E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *PNAS* , 105(42), 16195–200.

Moller AP, Tryjanowski P. (2014). Direction of approach by predators and flight initiation distance of urban and rural populations of birds.*Behav Ecol* , 25(4), 960–6.

Moller AndersP, Kwiecinski Z, Tryjanowski P. (2016). Prey reduce risk-taking and abundance in the proximity of predators. *Curr Zool* , 63(6), 591-598.

Nakagawa S, Johnson PCD, Schielzeth H. (2017). The coefficient of determination R 2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J R Soc Interface* , 14(134), 20170213.

Oriol-Cotterill A, Valeix M, Frank LG, Riginos C, Macdonald DW. (2015). Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* , 124(10), 1263–73.

Ortiz CA, Pendleton EL, Newcomb KL, Smith JE. (2019). Conspecific presence and microhabitat features influence foraging decisions across ontogeny in a facultatively social mammal. *Behav Ecol Sociobiol* , 73(4), 1-14.

Owings DH, Coss RG. (1977). Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behav* , 62(1–2), 50–68.

Owings DH, Leger DW. (2010). Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *Zeitschrift fur Tierpsychologie* , 54(2), 163–84.

Peacor, S. D., Barton, B. T., Kimbro, D. L., Sih, A., & Sheriff, M. J. (2020). A framework and standardized terminology to facilitate the study of predation-risk effects.

Ecology, 101(12), e03152.

Petelle MB, McCoy DE, Alejandro V, Martin JGA, Blumstein DT. (2013). Development of boldness and docility in yellow-bellied marmots.*Anim Behav* , 86(6), 1147–54.

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecolog* y, 86(2), 501-509.

Pulliam HR. (1973). On the advantages of flocking. *J Theor Biol* , 38(2), 419–22.

Putman, B. J., Coss, R. G., & Clark, R. W. (2015). The ontogeny of antipredator behavior: age differences in California ground squirrels (*Otospermophilus beecheyi*) at multiple stages of rattlesnake encounters. *Behav Ecol and Sociobiol* , 69(9), 1447-1457.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation\ for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. (2007). Integrating animal temperament within ecology and evolution. *Biol Rev* , 82(2), 291–318.

Rodriguez-Prieto I, Fernandez-Juricic E, Martin J, Regis Y. (2008). Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav Ecol* , 20(2), 371–7.

Runyan AM, Blumstein DT. (2004). Do individual differences influence flight initiation distance? *J Wildl Manage* , 68(4), 1124–9.

Sih A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *Am Nat* , 139(5), 1052–69.

Sih A, Bell AM, Johnson JC, Ziemba RE. (2004). Behavioral syndromes: an integrative overview. *Q Rev Biol* , 79(3), 241–77.

Sih A, Bell A, Johnson JC. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* , 19(7), 372–8.

Sih A, Ferrari MCO, Harris DJ. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evol Appl* , 4(2), 367–87.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J. (2012). Ecological implications of behavioural syndromes. *Eco Lett* ,15(3), 278–89.

Smith JE, Long DJ, Russell ID, Newcomb KL, Munoz VD. (2016).*Otospermophilus beecheyi* (Rodentia: Sciuridae). *Mammal Species* , 48(939), 91–108.

Smith, JE, Gamboa, DA, Spencer, JM, Travenick, SJ, Ortiz, CA, Hunter, RD, & Sih, A. (2018). Split between two worlds: automated sensing reveals links between above-and belowground social networks in a free-living mammal. *Proc R Soc B* , 373(1753), 20170249.

Smith JE, Smith IB, Working CL, Russell ID, Krout SA, Singh KS, et al. (2021). Host traits, identity, and ecological conditions predict consistent flea abundance and prevalence on free-living California ground squirrels. *Int J Parasitol* .

Stan Development Team. (2015). “RStan: the R interface to Stan.” R package version 2.21. 2, http://mc-stan.org/

Stankowich T, Blumstein DT. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proc R Soc B* , 272(1581), 2627–34.

Strasser EH, Heath JA. (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *J Appl Ecol* , 50(4), 912–9.

Suraci JP, Clinchy M, Zanette LY, Wilmers CC. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice.*Ecol Lett* , 22(10), 1578–86.

Tatte K, Moller AP, Mand R. (2018). Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Anim Behav* , 136, 75–86.

Trimmer PC, Ehlman SM, Sih A. (2017). Predicting behavioural responses to novel organisms: state-dependent detection theory. *Proc R Soc B* , 284(1847), 20162108.

Trouilloud, W, Delisle, A, & Kramer, DL. (2004). Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmunks. *Anim Behav* , 67(4), 789-797.

Uchida, K., & Blumstein, D. T. (2021). Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behav Ecol.*

Uchida K, Suzuki K, Shimamoto T, Yanagawa H, Koizumi I. (2015). Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. *J Zool* , 298(3), 225–31.

Uchida K, Suzuki KK, Shimamoto T, Yanagawa H, Koizumi I. (2019). Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behav Ecol* , 30(6), 1583–90.

van der Marel A, Lopez-Darias M, Waterman JM. (2019). Group-enhanced predator detection and quality of vigilance in a social ground squirrel.*Anim Behav* , 151, 43–52.

Vincze E, Papp S, Preiszner B, Seress G, Bokony V, Liker A. (2016). Habituation to human disturbance is faster in urban than rural house sparrows. *Behav Ecol* , 27(5), 1304–13.

Watson JEM, Shanahan DF, Di Marco M, Allan J, Laurance WF, Sanderson EW, et al. (2016). Catastrophic declines in wilderness areas undermine global environment targets. *Curr Biol* , 26(21), 2929–34.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol Evol* , 9(11), 442-446.

Wilson MW, Ridlon AD, Gaynor KM, Gaines SD, Stier AC, Halpern BS. (2020). Ecological impacts of human-induced animal behaviour change.*Ecol Lett* , 23(10), 1522–36.

Wirsing, AJ, Heithaus, MR, Brown, JS, Kotler, BP, & Schmitz, OJ. (2021). The context dependence of non-consumptive predator effects. *Eco Lett* , 24(1), 113-129.

Ydenberg RC, Dill LM. (1986). The economics of fleeing from predators.*Adv Study Behav* , 16, 229–49.

Table 1. Predictor effects on squirrel flight initiation distance (FID). Values include posterior mean estimates +- standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

Figure 1. Graphic depicting multiple components of the antipredator response.

Figure 2. Model predicted relationship between FID and**A)** average level of human activity at home site, **B)**trappability, and **C)** foraging group size. Shaded regions in A and B represent 95% credible intervals. For panel **C** , the middle quartile (dark line) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median, and the closed circles correspond to the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper—lower quantile).

Figure 3. Model predicted relationship between emergence time and **A**) human activity and **B**) trappability. Shaded regions represent 95% credible intervals.

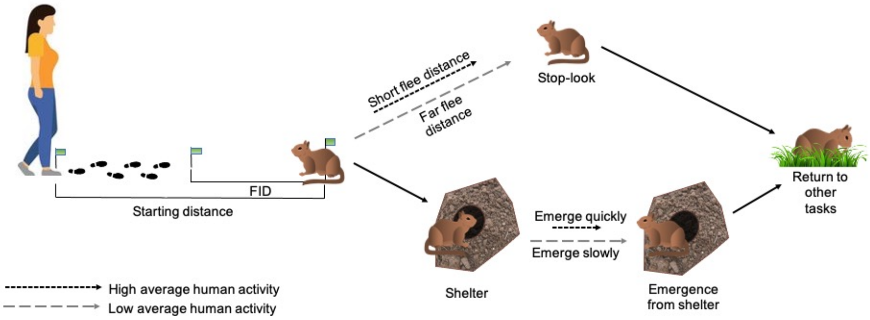
Figure 4. Among-individual correlation between FID and**A**) emergence time and **B**) stop look distance. BLUPs (best linear unbiased predictors) represent posterior means of individual random intercepts extracted from the multivariate models.

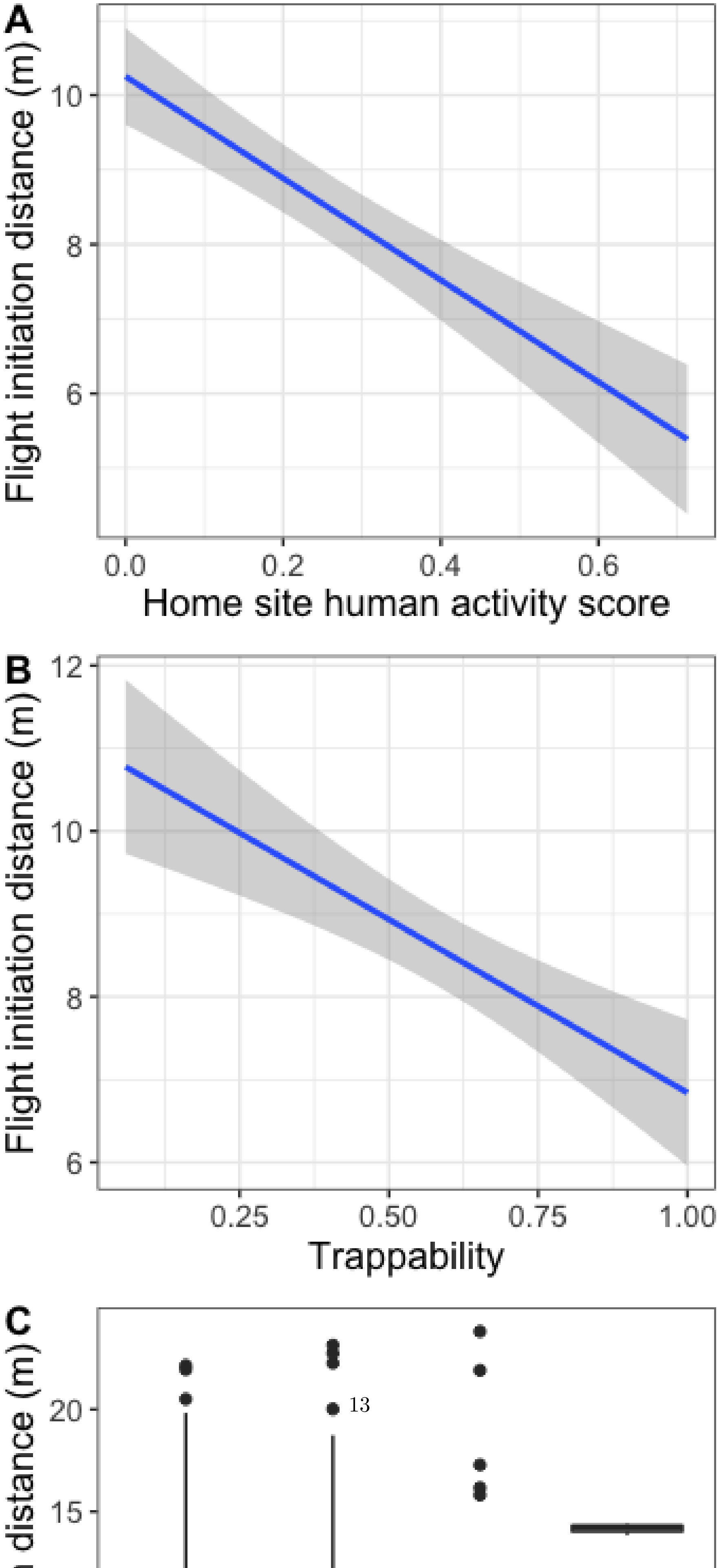
Table 1. Predictor effects on squirrel flight initiation distance (FID). Values include posterior mean estimates +- standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

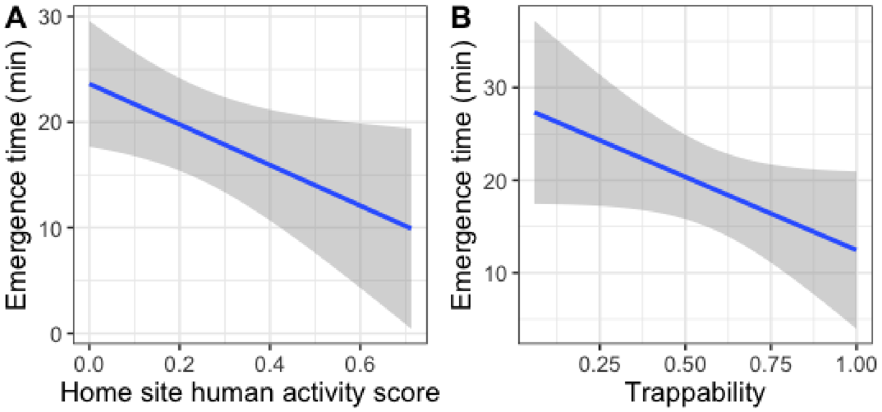
term	estimate ± SE	95 % CI
(Intercept)	3.053 ± 0.230	(2.611, 3.506)
Year	**-0.347 ± 0.095**	**(-0.534, -0.163)**
Sex (1)	**-0.242 ± 0.113**	**(-0.466, -0.020)**
Life-stage (1)	0.042 ± 0.095	(-0.142, 0.228)
Trial Number	0.011 ± 0.016	(-0.020, 0.042)

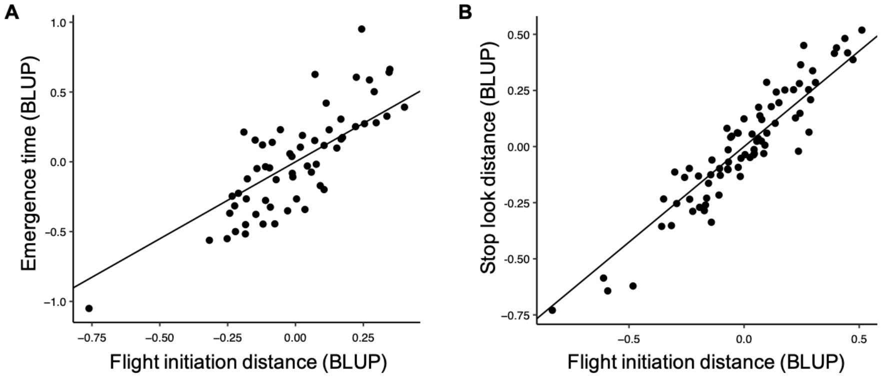
Number of conspecifics present	**-0.148 ± 0.048**	**(0.053, 0.243)**
Vegetation cover (1)	0.013 ± 0.081	(-0.148, 0.171)
Distance to nearest shelter (m)	0.012 ± 0.011	(-0.100, 0.034)
Starting distance (m)	**0.028 ± 0.006**	**(0.017, 0.039)**
Home site human activity	**-1.184 ± 0.356**	**(-1.909, -0.497)**
Trappability	**-0.452 ± 0.187**	**(-0.820, -0.086)**

Life stage: juvenile = 0, adult = 1; Sex: male = 0, female = 1; random intercepts: focal animal, home site and walker identity




A
Flight initiation distance (m)
10
8
6
0.0
0.2
0.4
0.6
Home site human activity score
B
Flight initiation distance (m)
12
10
8
6
0.25
0.50
0.75
1.00
Trappability
C
distance (m)
20
15


A
Emergence time (min)
0
10
20
30
0.0
0.2
0.4
0.6
Home site human activity score
B
Emergence time (min)
10
20
30
0.25
0.50
0.75
1.00
Trappability


A
Emergence time (BLUP)
1.0
0.5
0.0
-0.5
−1.0
−0.75
−0.50
−0.25
0.00
0.25
Flight initiation distance (BLUP)
B
Stop look distance (BLUP)
0.50
0.25
0.00
-0.25
-0.50
−0.75
−0.5
0.0
0.5
Flight initiation distance (BLUP)