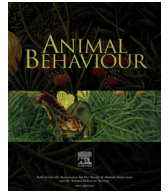




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## Behavioural correlations across multiple stages of the antipredator response: do animals that escape sooner hide longer?

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A fundamental assumption in predator–prey ecology is that prey responses comprise two main stages: escape when attack occurs or appears imminent and avoid the threat by seeking refuge until it has passed. While numerous studies have examined either initial prey responses to an approaching predator (flight initiation distance, FID), or subsequent hiding behaviour (e.g. latency to resume activity), to our knowledge, no previous studies have repeatedly tested multiple individuals in nature to quantify whether initial escape tendencies, behaviour during the escape and latency to resume activity are repeatable, and whether these stages of the antipredator response are correlated. The goal of this study was to explore how consistent spatial differences in rates of human activity shape risk-sensitive behaviour throughout multiple steps of the antipredator response (to humans) in California ground squirrels, *Otospermophilus beecheyi*, tested in various group sizes and environmental contexts across time. Our study provides the first example showing that, as predicted: FIDs, latencies to resume activity and other post-FID aspects of prey responses were repeatable and positively correlated at the among-individual level. This correlation is ecologically important in that it provides an underlying mechanism for a trade-off involving not only the cost versus benefit of early versus late escape, or early versus late emergence from refuge, but for a trade-off based on variation in fearfulness expressed across stages. Furthermore, we found that human activity influenced some, but not all, stages of the antipredator response.

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To understand predator impacts on prey and, in particular, nonconsumptive effects of predators on prey (Peacor et al., 2020; Preisser et al., 2005), a key issue is to elucidate factors that explain variation in prey responses to perceived predation risk (Brown & Kotler, 2004; Creel & Christianson, 2008; Lima, 1998; Wirsing et al., 2021). The overall prey response is commonly split into two main stages: escape when an attack occurs or appears imminent and avoid the threat often by staying in or near refuge (Heithaus et al., 2009; Lima & Dill, 1990). Although this basic framework has long been part of standard predator–prey behavioural ecology, most studies have either quantified escape responses (e.g. flight

initiation distances (FIDs); e.g. Møller et al., 2016; Stankowich & Blumstein, 2005), 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 human. Specifically, we tested for consistent individual differences in multiple stages of the overall prey response to risk (i.e. initial escape tendencies, behaviour during the escape and latency to resume activity after spending time in refuge).

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 behaviour 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

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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). The literature (e.g. Dill & Frid, 2020; Møller et al., 2016; Morelli et al., 2019; Stankowich & Blumstein, 2005) show 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 behavioural 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 (Réale et al., 2007; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) 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 Cabrera et al., 2017; Carrete and Tella, 2009; Møller & Tryjanowski, 2014).

Upon fleeing from predators, animals have subsequent decisions to make, including whether to run into shelter and, if so, when to emerge. Rather than running to shelter, animals sometimes flee and then 'stop and look', apparently to reassess 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 (Cooper & Frederick, 2007; Sih, 1992). More fearful animals likely have a longer latency to resume activity (Bókony et al., 2012; Cooper & Sherbrooke, 2015). While FIDs have been measured in many species (Bonenfant & Kramer, 1996; Engelhardt & Weladji, 2011; Møller & Tryjanowski, 2014; Petelle et al., 2013; Stankowich & Blumstein, 2005; Uchida et al., 2015), fewer studies have explored post-FID responses (but see Bonenfant & Kramer, 1996; Breck et al., 2019; Cooper & Sherbrooke, 2015; Tätte et al., 2018) 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. However, animals may compensate for the cost of escaping early by having shorter hiding times before resuming activity; in that case, we would expect a negative correlation between FID and post-FID behaviour. It is thus striking that, to our knowledge, no previous studies have tested the hypothesis that larger FIDs are positively or negatively correlated with longer or shorter latencies to resume activity. Ideally, analyses of multi-stage prey responses to predators should test for effects of both individual differences in behavioural 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 test this.

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 (Arroyo et al., 2017; Strasser & Heath, 2013). How well animals cope may depend on a variety of factors, including their behaviour and/or their past experience with human disturbance (Lapiedra et al., 2017; Sih et al., 2011, 2012). In many cases, animals respond to humans as predators, actively avoiding areas of human activity (Clinchy et al., 2016; Oriol-Cotterill et al., 2015; Suraci et al., 2019). In other cases, however, repeated

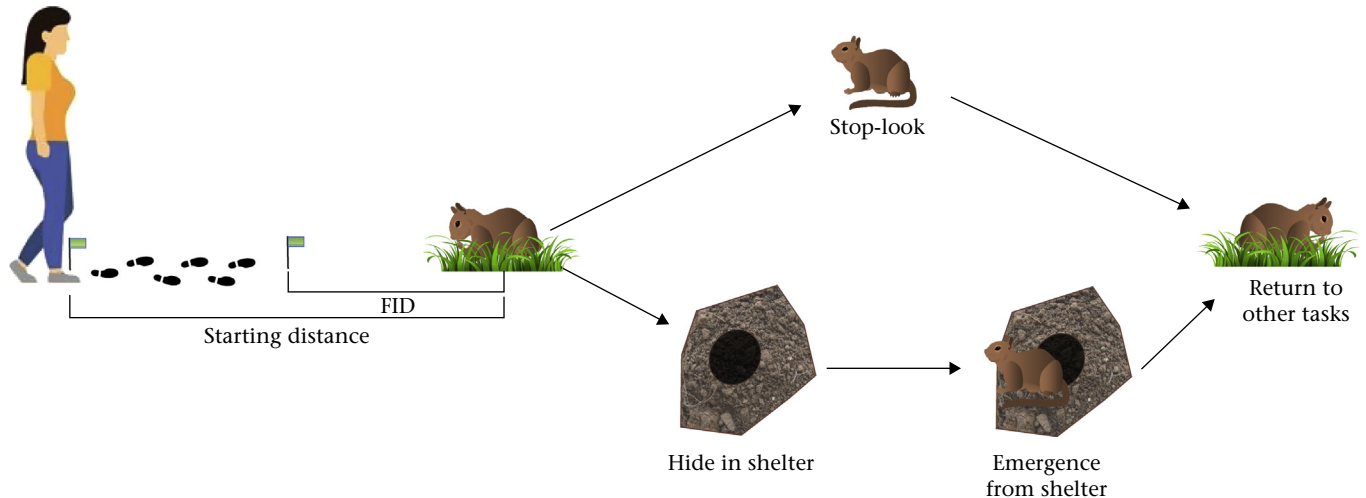
exposure to humans leads to habituation (Blumstein, 2016; Geffroy et al., 2015; Uchida & Blumstein, 2021; Stankowich & Blumstein, 2005). The reduced fear of humans can be associated with a general increase in boldness, exploration or aggressiveness as often seen in animals in urban environments (Breck et al., 2019; Miranda et al., 2013; Møller, 2008; Rodríguez-Prieto et al., 2008; Uchida et al., 2015). However, whilst behavioural adjustments in animals inhabiting urban environments are well documented, less is known about how human activities shape behaviour or behavioural variation in animals residing in natural areas, such as reserves or parks that are comparatively insulated from urban disturbance (Corsini et al., 2019; Gonson et al., 2016; Watson et al., 2016).

Here, we examined how variation in rates of human activity shape risk-sensitive behaviour 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 behavioural responses to threats (Ayon et al., 2017; Hanson & Coss, 1997; bib\_Owings\_and\_Leger\_1980Owings & Leger, 1980; Putman et al., 2015), 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 behaviour in the presence of humans. Specifically, we repeatedly recorded both the squirrels' FIDs (Bjørvik et al., 2014; Uchida et al., 2015; Ydenberg & Dill, 1986) and their post-FID behaviours 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 antipredator response, in that, squirrels who experience high human activity have become habituated to nonthreatening human disturbance and, thus, allow humans to approach closer. If correlated, a decrease in risk sensitivity to human approach will carry over to other components in the antipredator response. We further predicted that if stages of the antipredator response are correlated, then an individual's FID response should also correspond to its 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.

## METHODS

### Study Site and Subjects

We studied free-ranging ground squirrels at Briones Regional Park in Contra Costa County, California, U.S.A. (37.93°N, 122.13°W, elevation: 319 m above mean sea level). For this study, we focused on a 0.96 ha site that is a well-known picnic and resting area near a main entrance to the otherwise less human-disturbed 2476 ha Briones Regional Park (Appendix, Fig. A1). Since 2013, we live-trapped, marked and released 868 individuals of known age, sex, reproductive state and mass on a biweekly schedule (see Smith et al., 2018 for details). We recorded the proportion of days an individual was trapped on available trapping days per season (henceforth 'trappability'). Squirrels were individually fur-marked, and on days when trapping did not occur, trained observers identified individuals from a distance using binoculars to record spatial locations (see Smith et al., 2018 for details). Owing to the landscape



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

at the site, observers were able to accurately identify individuals from greater than 30 m with binoculars and stood on higher ground to gain a better view of the unique markings when the focal individual was in tall vegetation. Identity was further confirmed by a second observer prior to the start of the trial. For the present study, we focused on the antipredator responses of 88 individuals tested in 2018 and 2019. We combined all spatial data from May to July of these 2 years to determine each squirrel's home site, or the locations where each individual squirrel spent the majority of its 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 (Appendix, Fig. A1).

#### Flight Initiation Distance Trials

Between the hours of 0900 and 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 present and vegetation cover. We considered conspecifics to be present when they were within 5 m of the focal individual; this is the distance over which 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 as low when it did not (low = 0–10 cm; high >10 cm) (Ortiz et al., 2019; Owings & Coss, 1977).

The walker approached the focal subject at a speed of 0.5 m/s (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 (Fig. 1). The distance between the focal squirrel and the flight marker was then measured ( $\pm 0.1$  m). We also noted the

distance between the focal squirrel and (1) the walker's starting location (henceforth 'starting distance') and (2) the subject's nearest burrow (henceforth 'distance from shelter') since these influence FIDs in other species (Bonenfant & Kramer, 1996; Engelhardt & Weladji, 2011).

After the initial flee response, observers continued to watch the focal squirrel to record its behaviour. Squirrels typically took one of two options as their post-FID response: (1) fled into shelter and re-emerged after 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 and look distance'). While squirrels could 'stop and look' at a burrow and then proceed into shelter, this rarely occurred. Thus, for our analysis, we only used the squirrel's initial and immediate response to human approach. Individuals were only tested once within a day and, on average ( $\pm$  SE), 5.5  $\pm$  5.2 days passed between trials within a year (range 1–28 days).

#### Statistical Analysis

Analysis was conducted in R v.3.6.2 (R Core Team, 2020) using the Bayesian package 'brms' (Bürkner, 2017), an interface to Stan (Stan Development Team, 2015) for generalized linear mixed-effects models. We used relatively uninformative priors and four chains and ran models for 10 000 iterations with 1000 warm-ups. We used posterior predictive checks and trace plots to check for adequate mixing and model fit. All models converged with low among-chain variability (Rhat = 1). FIDs were square-root transformed prior to analysis to meet model assumptions of normality of residuals. We report posterior means for all estimated parameters with 95% credible 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 conspecifics 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 reran 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 data set model (Appendix, Table A1).

Individual FID repeatability ( $R_{\text{FID}}$ ) was calculated by extracting the variance components from our full FID model and using the following standard formula (Nakagawa & Schielzeth, 2010; Stoffel et al., 2017):

$$R_{\text{FID}} = \frac{V_{\text{ind}}}{(V_{\text{ind}} + V_{\text{home}} + V_{\text{obs}} + V_{\text{res}})} \quad (1)$$

where  $V_{\text{ind}}$  is the among-individual variance,  $V_{\text{home}}$  is the among-home site variance,  $V_{\text{obs}}$  is the among-observer variance and  $V_{\text{res}}$  is the residual variance.

#### Post-flight initiation distance response and correlation analysis

Given that squirrels took only one of two escape options, we first ran a beta-binomial model exploring the factors that influenced whether a squirrel sheltered or not (Appendix, Table A2) and then we ran separate bivariate models to analyse 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 and look distance as response variables. Shelter emergence time and stop and 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):

$$R = \frac{V_{\text{ind}}}{V_{\text{ind}} + V_{\text{obs}} + \ln\left(1 + \frac{1}{v}\right)} \quad (2)$$

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

#### Ethical Note

All methods used were approved by the Animal Care and Use Committees of Mills College and the University of California Davis (No. 19853). Procedures used for this study are consistent with guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016). Research permits were obtained from the California Department of Fish and Wildlife, Sacramento, California, U.S.A. and the East Bay Regional Park District, Castro Valley, California, U.S.A. On trapping days, Tomahawk live traps were covered with cardboard to provide

shade and checked at 30 min intervals. Once trapped, squirrels were then placed in a cone-shaped, cloth handling bag to reduce stress of the animals (Koprowski, 2002; Hammond et al., 2019). Squirrels remained in the handling bag for processing (i.e. obtain mass and sex) and marking and then released at the exact location they were trapped.

## RESULTS

### Flight Initiation Distance

We conducted 384 FID trials on 88 unique ground squirrels over the 2 years (2018, 2019: juvenile females:  $N = 21, 16$ ; juvenile males:  $N = 11, 7$ ; adult females:  $N = 20, 23$ ; adult males:  $N = 6, 6$ ; 22 individuals were tested in both 2018 and 2019). A total of 10 walkers were trained and used in the analysis. The mean ( $\pm$  SE) FID for both years combined was  $8.6 \pm 4.8$  m (range 0.04–23.81 m). For individuals sampled more than once within a summer ( $N = 85$ ), there was a mean replication of six trials per individual in 2018 and four trials per individual in 2019. For FID trials conducted on groups ( $N = 35$ ), we sampled an average of  $2 \pm 0.06$  individuals from each group.

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). FIDs increased with group size (Table 1, Fig. 2c), suggesting squirrels were quicker to flee from an approaching human when more conspecifics were present. Females had shorter FIDs than males (Table 1, Fig. 2d). We also found that squirrels had longer FIDs with longer starting distances (Table 1). Lastly, we found year had a significant impact on FID, with squirrels having shorter FIDs in 2019 than in 2018 (Table 1).

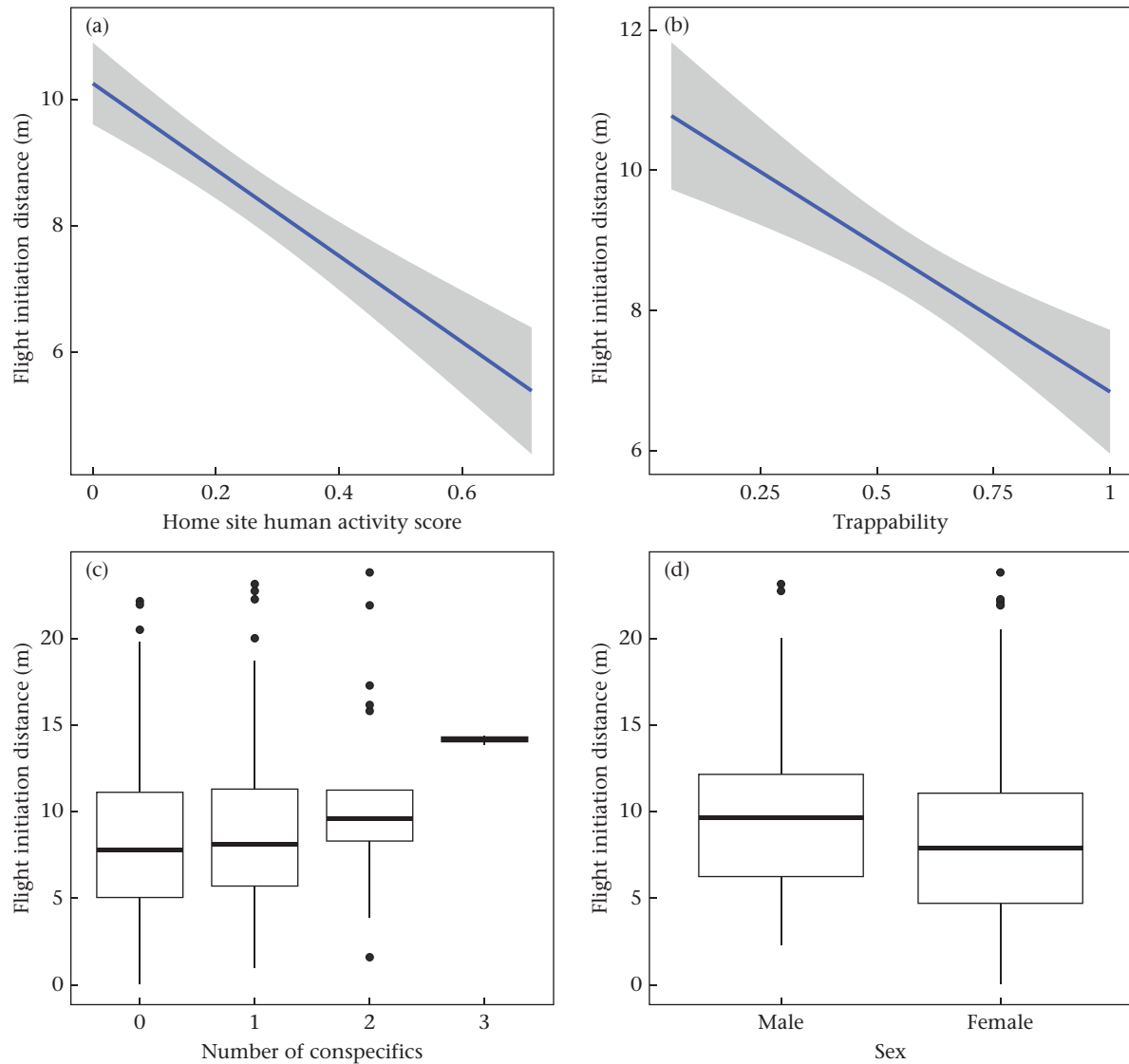
### Post-flight Initiation Distance Response and Correlation

Squirrels ran into shelter in 30% of trials. Juveniles sheltered (as opposed to 'stop and look') more frequently than adults (Appendix, Table A2). Squirrels tested near a burrow were more likely to run into shelter (Appendix, Table A2), 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 ( $R = 0.435$  [0.168, 0.676]). Individuals from home sites that experience greater human activity emerged from shelter more quickly than squirrels from home sites with lower human activity levels ( $-2.336$  [ $-4.413$ ,

**Table 1**  
Predictor effects on squirrel flight initiation distance (FID)

Term	Estimate $\pm$ SE	95% CI
(Intercept)	3.053 $\pm$ 0.230	(2.611, 3.506)
<b>Year</b>	<b>-0.347 <math>\pm</math> 0.095</b>	<b>(-0.534, -0.163)</b>
<b>Sex (1)</b>	<b>-0.242 <math>\pm</math> 0.113</b>	<b>(-0.466, -0.020)</b>
Life history stage (1)	0.042 $\pm$ 0.095	(-0.142, 0.228)
Trial Number	0.011 $\pm$ 0.016	(-0.020, 0.042)
<b>Number of conspecifics present</b>	<b>0.148 <math>\pm</math> 0.048</b>	<b>(0.053, 0.243)</b>
Vegetation cover (1)	0.013 $\pm$ 0.081	(-0.148, 0.171)
Distance to nearest shelter (m)	0.012 $\pm$ 0.011	(-0.010, 0.034)
<b>Starting distance (m)</b>	<b>0.028 <math>\pm</math> 0.006</b>	<b>(0.017, 0.039)</b>
<b>Home site human activity</b>	<b>-1.184 <math>\pm</math> 0.356</b>	<b>(-1.909, -0.497)</b>
<b>Trappability</b>	<b>-0.452 <math>\pm</math> 0.187</b>	<b>(-0.820, -0.086)</b>

Life history stage: juvenile = 0, adult = 1; sex: male = 0, female = 1; vegetation: low (0–10 cm) = 0, high (>10 cm) = 1; random intercepts: focal animal, home site and walker identity. Values include posterior mean estimates  $\pm$  standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.



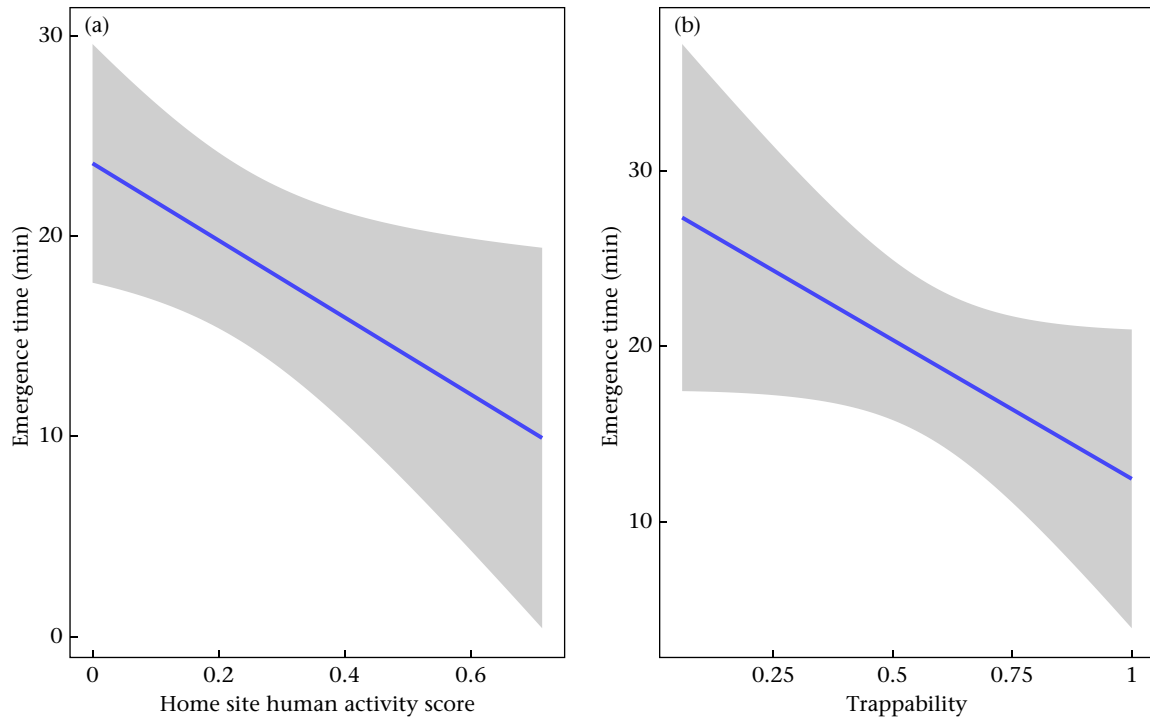
**Figure 2.** Model predicted relationship between flight initiation distance (FID) and (a) average level of human activity at home site, (b) trappability, (c) foraging group size and (d) sex. Shaded regions in (a) and (b) represent 95% credible intervals. For (c) and (d), the middle quartile (dark line) 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 quartile).

–0.431]; Fig. 3a, Appendix, Table A3). Furthermore, more trappable individuals had shorter shelter emergence times than less trappable individuals (–1.359 [–2.456, –0.359]; Fig. 3b, Appendix, Table A3). We also found a 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]; Appendix, Table A3).

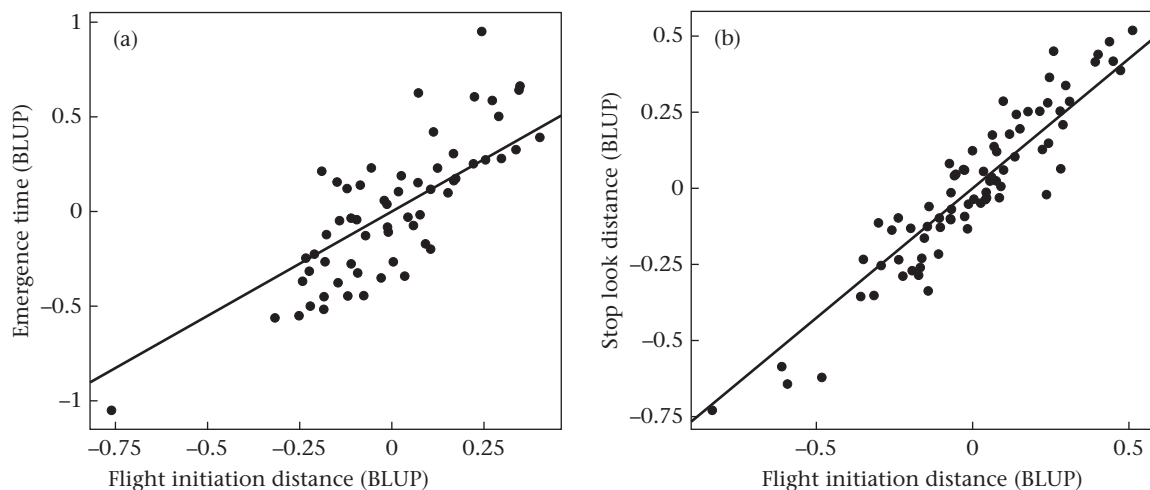
The response to stop and look from a distance occurred in 70% of trials (mean  $\pm$  SE stop and look distance: 5.1  $\pm$  0.3 m; range 0.2–27.7 m). Stop and look distances were only weakly repeatable ( $R = 0.216$  [0.073, 0.370]), and we found no significant predictors for stop and look distance (Appendix, Table A4). However, we did find a positive among-individual correlation between stop and 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 shelter response, as squirrels from high human disturbance areas were consistently faster to emerge from shelter. Furthermore, since FID and the post-FID responses were correlated, squirrels fled shorter distances before stopping to observe a potential threat following their flight response. 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 humans (Petelle et al., 2013; Uchida & Blumstein, 2021; Uchida et al., 2019; Vincze et al., 2016), it is



**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 correlations between flight initiation distance (FID) and (a) emergence time and (b) stop and look distance. BLUPs (best linear unbiased predictors, shown as black points) represent posterior means of individual random intercepts extracted from the multivariate models.

striking that variation in the degree of habituation emerged over a small spatial scale (i.e. within a 1 ha area). Beyond the strong effects of relative human activity on multiple antipredator behaviours, we also documented consistent individual differences in the suite of repeatable behaviours 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 behaviours may be adaptive or maladaptive, depending on the situation and environment in which the animal resides (Geffroy et al., 2015; Trouilloud et al., 2004; Wilson et al., 2020). In this case, having correlated behaviours throughout the antipredator response may be beneficial when encountering 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 (Guiden et al., 2019; Trimmer et al., 2017). Unhabituated animals might both flee too readily from nonthreatening humans but also wait too long to emerge from shelter, which may mean a lost foraging opportunity. On the other hand, getting habituated in terms of both reduced tendency to flee and reduced time spent inactive can be beneficial. However, if boldness (here, when habituating to humans) carries over to other situations, this can be ecologically relevant. For example, we know that bolder squirrels are prone to carrying 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 (Geffroy et al., 2015; Lowry et al., 2012). 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; Brehm & Mortelliti, 2018; Michelangeli et al., 2015). The observation that trappability predicts antipredator behaviour can have important implications as a systematic bias when trapping for monitoring, ecological research or pest control (Biro & Dingemans, 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 (distance to shelter, vegetation cover) contexts that we considered. We predicted that animals 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) 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 adult California ground squirrels are less vigilant when foraging in groups, and all animals – regardless of age or sex – decrease their intensity of vigilance as group size increases (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 behaviours. In particular, after fleeing (post-FID response), the decision to ‘stop and look’ versus flee 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 it was available nearby. 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 found that, on average, females had significantly shorter FIDs than males. We found this to be surprising as a large amount of literature have found either no sex differences in FID (Lemos-Espinal & Smith, 2021; Stankowich & Blumstein, 2005) or have found the opposite, with males having shorter FIDs than females (García-Arroyo & MacGregor-Fors, 2020; Guay et al., 2013). Often, sex differences that do occur are detected during the breeding season; however, our study was performed during the nonbreeding season and at a time where juveniles are weaned from their mothers. Previous studies have found that female California ground squirrels tend to have higher stress levels (Hammond et al., 2019) and larger home ranges (Boellstorff & Owings, 1995) than males. This may suggest that female ground squirrels encounter humans more frequently than males, due to their expansive home range, and thus have become more habituated to humans. More work is required to test this hypothesis. Lastly, we found FIDs in 2019 to be significantly shorter than FIDs in 2018. However, because the 2 years may have differed in many ways (e.g. environmental conditions, squirrel density, rates interactions with humans and predators), we cannot distinguish among these potential explanations for this result.

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. More broadly, such inquiries may reveal insights into how human-impacted behavioural syndromes affect population dynamics, community interactions and ecosystem functions, and provide more insights into the fundamental processes linking animal behaviour, humans and ecology.

### Data Availability

All data is available on Dryad (<https://doi.org/10.25338/B88P8W>; [https://datadryad.org/stash/share/IUALE8j\\_J6\\_GUzFkNjOeucO5cWl2RrDfcEojsO7-C0s](https://datadryad.org/stash/share/IUALE8j_J6_GUzFkNjOeucO5cWl2RrDfcEojsO7-C0s)).

### Author Contributions

C. A. Ortiz-Jimenez, E. Pendleton and J. E. Smith conducted field work to collect the data. M. Michelangeli and C. A. Ortiz-Jimenez analysed the data. A. Sih and J. E. Smith oversaw the project and advised C. A. Ortiz-Jimenez. All authors contributed to writing the manuscript and have approved the final manuscript.

### Declaration of Interest

None.

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### References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3–4), 227–266. <https://doi.org/10.1163/156853974X00534>
- 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. *Ecology Letters*, 20(3), 317–325. <https://doi.org/10.1111/ele.12729>
- Ayon, R. E., Putman, B. J., & Clark, R. W. (2017). Recent encounters with rattlesnakes enhance ground squirrel responsiveness to predator cues. *Behavioral Ecology and Sociobiology*, 71(10), 1–10. <https://doi.org/10.1007/s00265-017-2378-1>
- Bertram, B. C. R. (1978). Living in groups: Predators and prey. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 64–96). Oxford: Blackwell Scientific.
- Biro, P. A. (2012). Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. *Oecologia*, 171(2), 339–345. <https://doi.org/10.1007/s00442-012-2426-5>

- Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, 24(2), 66–67. <https://doi.org/10.1016/j.tree.2008.11.001>
- Björkvik, L. M., Dale, S., Hermansen, G. H., Munishi, P. K. T., & Moe, S. R. (2014). Bird flight initiation distances in relation to distance from human settlements in a Tanzanian floodplain habitat. *Journal of Ornithology*, 156(1), 239–246. <https://doi.org/10.1007/s10336-014-1121-1>
- Blumstein, D. T. (2016). Habituation and sensitization: New thoughts about old ideas. *Animal Behaviour*, 120, 255–262. <https://doi.org/10.1016/j.anbehav.2016.05.012>
- Boellstorff, D. E., & Owings, D. H. (1995). Home range, population structure, and spatial organization of California ground squirrels. *Journal of Mammalogy*, 76(2), 551–561. <https://doi.org/10.2307/1382363>
- Bókonyi, V., Kulcsár, A., Tóth, Z., & Líker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS One*, 7(5), Article e36639. <https://doi.org/10.1371/journal.pone.0036639>
- Bonenfant, M., & Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology*, 7(3), 299–303. <https://doi.org/10.1093/beheco/7.3.299>
- Breck, S. W., Poessel, S. A., Mahoney, P., & Young, J. K. (2019). The intrepid urban coyote: A comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Scientific Reports*, 9(1), 1–11. <https://doi.org/10.1038/s41598-019-38543-5>
- Brehm, A. M., & Mortelliti, A. (2018). Mind the trap: Large-scale field experiment shows that trappability is not a proxy for personality. *Animal Behaviour*, 142, 101–112. <https://doi.org/10.1016/j.anbehav.2018.06.009>
- Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7(10), 999–1014. <https://doi.org/10.1111/j.1461-0248.2004.00661.x>
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Cabrera, D., Andres, D., McLoughlin, P. D., Debeffe, L., Medill, S. A., Wilson, A. J., & Poissant, J. (2017). Island tameness and the repeatability of flight initiation distance in a large herbivore. *Canadian Journal of Zoology*, 95(10), 771–778. <https://doi.org/10.1139/cjz-2016-0305>
- Carrete, M., & Tella, J. L. (2009). Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biology Letters*, 6(2), 167–170. <https://doi.org/10.1098/rsbl.2009.0739>
- Clinchy, M., Zanette, L. Y., Roberts, D., Suraci, J. P., Buesching, C. D., Newman, C., & Macdonald, D. W. (2016). Fear of the human 'super predator' far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology*, 27(6), 1826–1832. <https://doi.org/10.1093/beheco/arw117>
- Cooper, W. E., Jr., & Frederick, W. G. (2007). Optimal time to emerge from refuge. *Biological Journal of the Linnean Society*, 91(3), 375–382. <https://doi.org/10.1111/j.1095-8312.2007.00802.x>
- Cooper, W. E., Jr., & Sherbrooke, W. C. (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. *Behavioral Ecology*, 30(6), 1632–1641. <https://doi.org/10.1093/beheco/arz128>
- Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23(4), 194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
- Dill, L. M., & Frid, A. (2020). Behaviourally mediated biases in transect surveys: A predation risk sensitivity approach. *Canadian Journal of Zoology*, 98(11), 697–704. <https://doi.org/10.1139/cjz-2020-0039>
- Engelhardt, S. C., & Weladji, R. B. (2011). Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Canadian Journal of Zoology*, 89(9), 823–830. <https://doi.org/10.1139/z11-054>
- García-Arroyo, M., & MacGregor-Fors, I. (2020). Tolerant to humans? Assessment of alert and flight initiation distances of two bird species in relation to sex, flock size, and environmental characteristics. *Ethology Ecology & Evolution*, 32(5), 445–456. <https://doi.org/10.1080/03949370.2020.1753115>
- Garvey, P. M., Banks, P. B., Suraci, J. P., Bodey, T. W., Glen, A. S., Jones, C. J., McArthur, C., Norbury, G. L., Price, C. J., Russel, J. C., & Sih, A. (2020). Leveraging motivations, personality, and sensory cues for vertebrate pest management. *Trends in Ecology & Evolution*, 35(11), 990–1000. <https://doi.org/10.1016/j.tree.2020.07.007>
- Geffroy, B., Samia, D. S. M., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, 30(12), 755–765. <https://doi.org/10.1016/j.tree.2015.09.010>
- 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. *Marine Pollution Bulletin*, 107(1), 144–154. <https://doi.org/10.1016/j.marpolbul.2016.04.007>
- Guay, P. J., Lorenz, R. D., Robinson, R. W., Symonds, M. R., & Weston, M. A. (2013). Distance from water, sex and approach direction influence flight distances among habituated black swans. *Ethology*, 119(7), 552–558. <https://doi.org/10.1111/eth.12094>
- Guiden, P. W., Bartel, S. L., Byer, N. W., Shipley, A. A., & Orrock, J. L. (2019). Predator-prey interactions in the Anthropocene: Reconciling multiple aspects of novelty. *Trends in Ecology & Evolution*, 34(7), 616–627. <https://doi.org/10.1016/j.tree.2019.02.017>
- Hammond, T. T., Vo, M., Burton, C. T., Surber, L. L., Lacey, E. A., & Smith, J. E. (2019). Physiological and behavioral responses to anthropogenic stressors in a human-tolerant mammal. *Journal of Mammalogy*, 100(6), 1928–1940. <https://doi.org/10.1093/jmammal/gyz134>
- Hanson, M. T., & Coss, R. G. (1997). Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to avian and mammalian predators. *Journal of Comparative Psychology*, 111(2), 174–184. <https://doi.org/10.1037/0735-7036.111.2.174>
- 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. *Journal of Animal Ecology*, 78(3), 556–562. <https://doi.org/10.1111/j.1365-2656.2008.01512.x>
- Holding, M. L., Putman, B. J., Kong, L. M., Smith, J. E., & Clark, R. W. (2020). Physiological stress integrates resistance to rattlesnake venom and the onset of risky foraging in California ground squirrels. *Toxins*, 12(10), 617. <https://doi.org/10.3390/toxins12100617>
- Koprowski, J. L. (2002). Handling tree squirrels with a safe and efficient restraint. *Wildlife Society Bulletin*, 30(1), 101–103. <https://doi.org/10.2307/3784642>. Retrieved from <http://www.jstor.org/stable/3784642>
- Lapiedra, O., Chejanovski, Z., & Kolbe, J. J. (2017). Urbanization and biological invasion shape animal personalities. *Global Change Biology*, 23(2), 592–603. <https://doi.org/10.1111/gcb.13395>
- Leger, D. W., Owings, D. H., & Coss, R. G. (1983). Behavioral ecology of time allocation in California ground squirrels (*Spermophilus beecheyi*): Microhabitat effects. *Journal of Comparative Psychology*, 97(4), 283–291. <https://doi.org/10.1037/0735-7036.97.4.283>
- Lemos-Espinal, J. A., & Smith, G. R. (2021). Flight initiation distance of *Urosaurus ornatus* from the Sierra de Samalayuca, Mexico. *Acta Herpetologica*, 16(1), 53–57. [https://doi.org/10.36253/a\\_b-9843](https://doi.org/10.36253/a_b-9843)
- Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, 48(1), 25–34. <https://doi.org/10.2307/1313225>
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640. <https://doi.org/10.1139/z90-092>
- Lowry, H., Lill, A., & Wong, B. B. M. (2012). Behavioural responses of wildlife to urban environments. *Biological Reviews of the Cambridge Philosophical Society*, 88(3), 537–549. <https://doi.org/10.1111/brv.12012>
- van der Marel, A., López-Darias, M., & Waterman, J. M. (2019). Group-enhanced predator detection and quality of vigilance in a social ground squirrel. *Animal Behaviour*, 151, 43–52. <https://doi.org/10.1016/j.anbehav.2019.02.017>
- Michelangeli, M., Wong, B. B. M., & Chapple, D. G. (2015). It's a trap: Sampling bias due to animal personality is not always inevitable. *Behavioral Ecology*, 27(1), 62–67. <https://doi.org/10.1093/beheco/arv123>
- Miranda, A. C., Schielzeth, H., Sonntag, T., & Pardecke, J. (2013). Urbanization and its effects on personality traits: A result of microevolution or phenotypic plasticity? *Global Change Biology*, 19(9), 2634–2644. <https://doi.org/10.1111/gcb.12258>
- Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, 63(1), 63–75. <https://doi.org/10.1007/s00265-008-0636-y>
- Møller, A. P., Kwieciniski, Z., & Tryjanowski, P. (2016). Prey reduce risk-taking and abundance in the proximity of predators. *Current Zoology*, 63(6), 591–598. <https://doi.org/10.1093/cz/zow114>
- Møller, A. P., & Tryjanowski, P. (2014). Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behavioral Ecology*, 25(4), 960–966. <https://doi.org/10.1111/beh.12399>
- Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Tätté, K., Markó, G., Jiang, Y., Tryjanowski, P., & Møller, A. P. (2019). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecology and Evolution*, 9(10), 6096–6104. <https://doi.org/10.1002/ece3.5193>
- Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination  $R^2$  and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface*, 14(134), 20170213. <https://doi.org/10.1098/rsif.2017.0213>
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society*, 85(4), 935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>
- Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C., & Macdonald, D. W. (2015). Landscapes of coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 124(10), 1263–1273. <https://doi.org/10.1111/oik.02224>
- Ortiz, C. A., Pendleton, E. L., Newcomb, K. L., & Smith, J. E. (2019). Conspecific presence and microhabitat features influence foraging decisions across ontogeny in a facultatively social mammal. *Behavioral Ecology and Sociobiology*, 73(4), 1–14. <https://doi.org/10.1007/s00265-019-2651-6>
- Owings, D. H., & Coss, R. G. (1977). Snake mobbing by California ground squirrels: Adaptive variation and ontogeny. *Behaviour*, 62(1–2), 50–68. <https://doi.org/10.1163/156853977X00045>
- Owings, D. H., & Leger, D. W. (1980). Chatter vocalizations of California ground squirrels: Predator- and social-role specificity. *Zeitschrift für Tierpsychologie*, 54(2), 163–184. <https://doi.org/10.1111/j.1439-0310.1980.tb01070.x>



- 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), Article e03152. <https://doi.org/10.1002/ecy.3152>
- Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, 86(6), 1147–1154. <https://doi.org/10.1016/j.anbehav.2013.09.016>
- Preisser, E. L., Bolnick, D. L., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 86(2), 501–509. <https://doi.org/10.1890/04-0719>
- Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, 38(2), 419–422. [https://doi.org/10.1016/0022-5193\(73\)90184-7](https://doi.org/10.1016/0022-5193(73)90184-7)
- 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. *Behavioral Ecology and Sociobiology*, 69(9), 1447–1457. <https://doi.org/10.1007/s00265-015-1957-2>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J., & Regis, Y. (2008). Antipredator behavior in blackbirds: Habituation complements risk allocation. *Behavioral Ecology*, 20(2), 371–377. <https://doi.org/10.1093/beheco/arn151>
- Runyan, A. M., & Blumstein, D. T. (2004). Do individual differences influence flight initiation distance? *Journal of Wildlife Management*, 68(4), 1124–1129. [https://doi.org/10.2193/0022-541X\(2004\)068\[1124:DIDIFI\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[1124:DIDIFI]2.0.CO;2)
- Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist*, 139(5), 1052–1069. <https://doi.org/10.1086/285372>
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79(3), 241–277. <https://doi.org/10.1086/422893>
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278–289. <https://doi.org/10.1111/j.14610248.2011.01731.x>
- Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), 367–387. <https://doi.org/10.1111/j.1752-4571.2010.00166.x>
- Sikes, R. S., & Animal Care and Use Committee of the American Society of Mammalogists. (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–668. <https://doi.org/10.1093/jmammal/gyw078>
- Smith, J. E., Gamboa, D. A., Spencer, J. M., Travenick, S. J., Ortiz, C. A., Hunter, R. D., & Sih, A. (2018). Split between two worlds: Automated sensing reveals links between above- and belowground social networks in a free-living mammal. *Proceedings of the Royal Society B: Biological Sciences*, 373(1753), 20170249. <https://doi.org/10.1098/rstb.2017.0249>
- Smith, J. E., Long, D. J., Russell, I. D., Newcomb, K. L., & Muñoz, V. D. (2016). *Otospermophilus beecheyi* (Rodentia: Scuriidae). *Mammalian Species*, 48(939), 91–108. <https://doi.org/10.1093/mspecies/sew010>
- Smith, J. E., Smith, I. B., Working, C. L., Russell, I. D., Krout, S. A., Singh, K. S., & Sih, A. (2021). Host traits, identity, and ecological conditions predict consistent flea abundance and prevalence on free-living California ground squirrels. *International Journal for Parasitology*, 51(7), 587–598. <https://doi.org/10.1016/j.ijpara.2020.12.001>
- Stan Development Team. (2015). *RStan: The R interface to Stan*. R package. version 2.21.2 <http://mc-stan.org/>.
- Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2627–2634. <https://doi.org/10.1098/rspb.2005.3251>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Strasser, E. H., & Heath, J. A. (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, 50(4), 912–919. <https://doi.org/10.1111/1365-2664.12103>
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22(10), 1578–1586. <https://doi.org/10.1111/ele.13344>
- Tätte, K., Möller, A. P., & Mänd, R. (2018). Towards an integrated view of escape decisions in birds: Relation between flight initiation distance and distance fled. *Animal Behaviour*, 136, 75–86. <https://doi.org/10.1016/j.anbehav.2017.12.008>
- Trimmer, P. C., Ehlman, S. M., & Sih, A. (2017). Predicting behavioural responses to novel organisms: State-dependent detection theory. *Proceedings of the Royal Society B: Biological Sciences*, 284(1847), 20162108. <https://doi.org/10.1098/rspb.2016.2108>
- Trouilloud, W., Delisle, A., & Kramer, D. L. (2004). Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmunks. *Animal Behaviour*, 67(4), 789–797. <https://doi.org/10.1016/j.anbehav.2003.04.013>
- Uchida, K., & Blumstein, D. T. (2021). Habituation or sensitization? Long-term responses of yellow-bellied marmots to human disturbance. *Behavioral Ecology*, 32(4), 668–678. <https://doi.org/10.1093/beheco/abab016>
- 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. *Journal of Zoology*, 298(3), 225–231. <https://doi.org/10.1111/jzo.12306>
- Uchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2019). Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology*, 30(6), 1583–1590. <https://doi.org/10.1093/beheco/arz117>
- Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V., & Liker, A. (2016). Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology*, 27(5), 1304–1313. <https://doi.org/10.1093/beheco/arw047>
- Watson, J. E. M., Shanahan, D. F., Di Marco, M., Allan, J., Laurance, W. F., Sanderson, E. W., Mackey, B., & Venter, O. (2016). Catastrophic declines in wilderness areas undermine global environment targets. *Current Biology*, 26(21), 2929–2934. <https://doi.org/10.1016/j.cub.2016.08.049>
- Wilson, D. S., Clark, A. B., Coleman, K., & Dearnstye, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9(11), 442–446.
- Wilson, M. W., Ridlon, A. D., Gaynor, K. M., Gaines, S. D., Stier, A. C., & Halpern, B. S. (2020). Ecological impacts of human-induced animal behaviour change. *Ecology Letters*, 23(10), 1522–1536. <https://doi.org/10.1111/ele.13571>
- Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., & Schmitz, O. J. (2021). The context dependence of non-consumptive predator effects. *Ecology Letters*, 24(1), 113–129. <https://doi.org/10.1111/ele.13614>
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229–249. [https://doi.org/10.1016/S0065-3454\(08\)60192-8](https://doi.org/10.1016/S0065-3454(08)60192-8)

## Appendix

**Table A1**

Predictor effects on squirrel flight initiation distance (FID) only including the first individual to flee in a group testing situation

Term	Estimate ± SE	95% CI
(Intercept)	2.995 ± 0.237	(2.527, 3.462)
<b>Year</b>	<b>−0.295 ± 0.102</b>	<b>(−0.495, −0.097)</b>
Sex (1)	−0.223 ± 0.119	(−0.456, 0.012)
Life history stage (1)	0.045 ± 0.101	(−0.152, 0.245)
Trial number	0.010 ± 0.017	(−0.024, 0.044)
<b>Number of conspecifics present</b>	<b>0.172 ± 0.061</b>	<b>(0.053, 0.292)</b>
Vegetation cover (1)	0.005 ± 0.086	(−0.163, 0.173)
Distance to nearest shelter (m)	0.015 ± 0.012	(−0.009, 0.038)
<b>Starting distance (m)</b>	<b>0.029 ± 0.006</b>	<b>(0.018, 0.041)</b>
<b>Home site human activity</b>	<b>−1.228 ± 0.376</b>	<b>(−1.994, −0.515)</b>
<b>Trappability</b>	<b>−0.472 ± 0.197</b>	<b>(−0.859, −0.085)</b>

Life stage: juvenile = 0, adult = 1; sex: male = 0, female = 1; vegetation: low (0–10 cm) = 0, high (>10 cm) = 1; random intercepts: focal animal, home site and walker identity. Values include posterior mean ± standard error (SE) with the 95% credible intervals (CIs). Significant outcomes are shown in bold.

**Table A2**

Predictor effects on a squirrel's decision to shelter for post-flight initiation distance response

Term	Estimate ± SE	95% confidence interval
(Intercept)	−1.150 ± 0.890	(−3.28, 0.210)
Year	−0.410 ± 0.390	(−1.200, 0.340)
Sex (1)	0.460 ± 0.360	(−0.230, 1.190)
<b>Life history stage (1)</b>	<b>−0.890 ± 0.320</b>	<b>(−1.550, −0.280)</b>
Number of conspecifics present	0.304 ± 0.211	(−0.100, 0.712)
Vegetation cover (1)	−0.190 ± 0.380	(−0.950, 0.540)
<b>Distance to nearest shelter (m)</b>	<b>−0.110 ± 0.054</b>	<b>(−0.220, −0.010)</b>
Starting distance (m)	0.029 ± 0.025	(−0.020, 0.079)
FID (m)	0.000 ± 0.038	(−0.076, 0.070)
Home site human activity	−0.680 ± 0.970	(−2.710, 1.170)
Trappability	0.780 ± 0.620	(−0.410, 2.060)

Life stage: juvenile = 0, adult = 1; sex: male = 0, female = 1; vegetation: low (0–10 cm) = 0, high (>10 cm) = 1; random intercepts: focal animal, home site and walker identity; FID: flight initiation distance. Values include posterior mean ± standard error (SE) with the 95% credible intervals (CIs). Significant outcomes are shown in bold.

**Table A3**

Predictor effects on shelter emergence time modelled with flight initiation distance (FID) in multivariate model

Term	Estimate $\pm$ SE	95% CI
Shelter emergence time		
(Intercept)	3.174 $\pm$ 0.511	(2.170, 4.181)
Year	-0.130 $\pm$ 0.289	(-0.704, 0.431)
Sex (1)	0.248 $\pm$ 0.319	(-0.380, 0.868)
Life history stage (1)	-0.026 $\pm$ 0.266	(-0.548, 0.494)
<b>Home site human activity</b>	<b>-2.336 <math>\pm</math> 1.022</b>	<b>(-4.413, -0.431)</b>
<b>Trial number</b>	<b>0.137 <math>\pm</math> 0.054</b>	<b>(0.030, 0.241)</b>
<b>Trappability</b>	<b>-1.359 <math>\pm</math> 0.532</b>	<b>(-2.456, -0.359)</b>
FID		
(Intercept)	3.149 $\pm$ 0.331	(2.485, 3.793)
Year	0.043 $\pm$ 0.160	(-0.266, 0.362)
Sex (1)	-0.181 $\pm$ 0.159	(-0.485, 0.140)
Trial Number	0.049 $\pm$ 0.028	(-0.004, 0.104)
Life history stage (1)	0.150 $\pm$ 0.133	(-0.112, 0.410)
Home site human activity	-0.627 $\pm$ 0.499	(-1.619, 0.362)
Starting distance (m)	0.010 $\pm$ 0.010	(-0.010, 0.028)
<b>Trappability</b>	<b>-0.661 <math>\pm</math> 0.262</b>	<b>(-1.182, -0.158)</b>
Number of conspecifics present	0.069 $\pm$ 0.075	(-0.080, 0.212)

Life stage: juvenile = 0, adult = 1; sex: male = 0, female = 1; random intercepts: focal animal, home site and walker identity. Values include posterior mean estimates  $\pm$  standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

**Table A4**

Predictor effects on stop look distance modeled with flight initiation distance (FID) in multivariate model

Term	Estimate $\pm$ SE	95% CI
Stop look distance		
(Intercept)	2.058 $\pm$ 0.284	(1.498, 2.612)
Year	0.080 $\pm$ 0.148	(-0.211, 0.372)
Sex (1)	-0.179 $\pm$ 0.175	(-0.522, 0.167)
Life history stage (1)	-0.194 $\pm$ 0.148	(-0.493, 0.0860)
Home site human activity	-0.278 $\pm$ 0.497	(-1.267, 0.709)
Trial number	-0.047 $\pm$ 0.028	(-0.103, 0.006)
Trappability	-0.147 $\pm$ 0.298	(-0.745, 0.431)
Number of conspecifics present	0.118 $\pm$ 0.098	(-0.073, 0.314)
FID		
(Intercept)	3.121 $\pm$ 0.270	(2.600, 3.660)
<b>Year</b>	<b>-0.517 <math>\pm</math> 0.111</b>	<b>(-0.736, -0.302)</b>
Sex (1)	-0.05 $\pm$ 0.128	(-0.306, 0.196)
Trial number	-0.009 $\pm$ 0.106	(-0.219, 0.193)
Life history stage (1)	-0.031 $\pm$ 0.017	(-0.066, 0.003)
<b>Home site human activity</b>	<b>-1.157 <math>\pm</math> 0.373</b>	<b>(-1.917, -0.453)</b>
<b>Starting distance (m)</b>	<b>0.035 <math>\pm</math> 0.006</b>	<b>(0.023, 0.047)</b>
<b>Trappability</b>	<b>-0.545 <math>\pm</math> 0.214</b>	<b>(-0.955, -0.119)</b>
<b>Number of conspecifics present</b>	<b>0.146 <math>\pm</math> 0.055</b>	<b>(0.039, 0.254)</b>

Life stage: juvenile = 0, adult = 1; sex: male = 0, female = 1; random intercepts: focal animal, home site and walker identity. Values include posterior mean estimates  $\pm$  standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.



High average  
human activity

Low average  
human activity

**Figure A1.** Aerial view of study site in Briones Regional Park, Contra Costa County, California, U.S.A. Human activity varies throughout the site, with high average human activity occurring to the left and gradually decreasing moving towards the right.