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Empirical studies of escape behavior find mixed support for the race for life model

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Abstract

Escape theory has been exceptionally successful in conceptualizing and accurately predicting effects of numerous factors that affect predation risk and explaining variation in flight initiation distance (FID; predator–prey distance when escape begins). Less explored is the relative orientation of an approaching predator, prey, and its eventual refuge. The relationship between an approaching threat and its refuge can be expressed as an angle we call the “interpath angle” or “Φ,” which describes the angle between the paths of predator and prey to the prey’s refuge and thus expresses the degree to which prey must run toward an approaching predator. In general, we might expect that prey would escape at greater distances if they must flee toward a predator to reach its burrow. The “race for life” model makes formal predictions about how Φ should affect FID. We evaluated the model by studying escape decisions in yellow-bellied marmots *Marmota flaviventer*, a species which flees to burrows. We found support for some of the model’s predictions, yet the relationship between Φ and FID was less clear. Marmots may not assess Φ in a continuous fashion; but we found that binning angle into 4 45° bins explained a similar amount of variation as models that analyzed angle continuously. Future studies of Φ, especially those that focus on how different species perceive relative orientation, will likely enhance our understanding of its importance in flight decisions.

Key words: antipredator behavior, escape behavior, escape theory, escape trajectory, race for life model.

When a prey is confronted by an approaching predator, one of the most basic decisions it must make is how close to allow the predator to approach before beginning to flee (Ydenberg and Dill 1986). The distance between predator and prey when escape begins is referred to as the flight initiation distance (FID). Much of the increased interest in escape behavior results from theoretical models that permit predictions about the effects of many factors on FID (Stankowich and Blumstein 2005; Cooper and Blumstein 2015a, 2015b), and a variety of cost–benefit models have been extremely successful in predicting effects of single factors on FID (Cooper 2015; Samia et al. 2015; Blumstein et al. 2016).

All escape models assume that a prey detects a predator, monitors its approach, and then flees when some criterion is met. Economic models predict that FID is longer when the costs of remaining (not fleeing) are larger and is shorter when the costs of fleeing are greater. The major costs of fleeing include lost opportunities to feed, engage in social behavior, or conduct other activities that increase fitness. The Ydenberg and Dill (1986) model predict that prey initiate escape when the expected fitness costs of staying and fleeing are equal. If the prey were to allow the predators to approach closer, the risk would outweigh the lost opportunity costs. However, it is possible for a prey to increase its lifetime fitness after an encounter even if it allows the predator to kill it. This can happen, for example, if the prey can fertilize many eggs whereas the predator approaches. The Cooper and Frederick (2007) model, sometimes called optimal escape theory, addressed this issue by developing a formal optimality model that allows the prey to select the FID that maximizes its expected fitness after the encounter with the predator. These models have had great heuristic value, but make no predictions about the effects of multiple, simultaneously acting predation risk factors.

The first model to consider multiple risk factors was developed by Kramer and Bonenfant (1997). The model predicted FID when a prey was on a line between the predator and the prey's refuge and allowed the prey to flee straight away from the predator to its refuge. The model also predicted FID when the refuge was between the predator and the prey, assuming the prey would flee straight toward the predator to its refuge. Ultimately, the model predicted longer FIDs when the prey must flee toward the predator. The prediction was not explicitly economic but was based on the relative speeds of predator and prey, their distances from the refuge, and the locations of predator, prey and refuge when all were aligned. Field data for woodchucks *Marmota monax* strongly supported the model (Kramer and Bonenfant 1997), and has informed subsequent models of escape behavior that integrate multiple risk factors. Recent work by Eason et al. (2019) demonstrates the importance of relative orientation of predator, prey, and to a potential refuge on FID. When presented with multiple refuge options, Eastern grey squirrels *Sciuris carolinensis* choose the refuge option that optimized the tradeoff between distance fled to a burrow and how directly prey must run toward an approaching predator.

The "race for life model" (Cooper 2016) generalizes Kramer and Bonenfant's (1997) findings so that prey and predator can approach the refuge from any direction. The race for life model predicts FID based on the combined effects of predator and prey speeds, their distances and directions to refuge, and a margin of safety that ensures a prey's safe arrival at the refuge. When the prey decides to flee, its location and those of the predator and refuge form the vertices of a triangle (Figure 1). The lengths of the 2 sides of the triangle that meet at the refuge are the distance of the prey from refuge ($\mathrm{DR}_{\mathrm{prey}}$) and the predator's distance from refuge ($\mathrm{DR}_{\mathrm{pred}}$). The angle between these sides is the interpath angle (Φ) to refuge, and the side opposite Φ is the FID. The square of the predicted FID is given by the law of cosines:

$$\mathrm{FID}^2 = \mathrm{DR}_{\mathrm{prey}}{}^2 + \mathrm{DR}_{\mathrm{pred}}{}^2 - 2(\mathrm{DR}_{\mathrm{prey}} + \mathrm{DR}_{\mathrm{pred}}) \cos(\Phi).$$

The model's predictions are based, in part, on the relationships between Φ and FID. At its essence is the expectation that as Φ increases, prey must flee more directly toward an approaching predator. This scenario constitutes a higher perceived risk for the prey, causing it to flee sooner, leading to a longer FID (Figure 2). The relationship between Φ and an animal's choice FID is a critical assumption of these models, but until recently, little work has been done to empirically test this assumption.

We simulated predatory approaches with free-living yellow-bellied marmots *Marmota flaviventer* to evaluate the predictions of models of escape behavior in a natural system. We first asked if Cooper's race for life model could effectively predict FID in yellow-bellied marmots with parameters measured in the field. We then estimated the relative contribution of angle to explaining variation in FID when compared with other parameters in Cooper's race for life model, as well as explained by extrinsic environmental factors known to influence FID. If the predictions of the model were supported, simulated predatory approaches with a larger Φ would result in refuging prey fleeing more directly

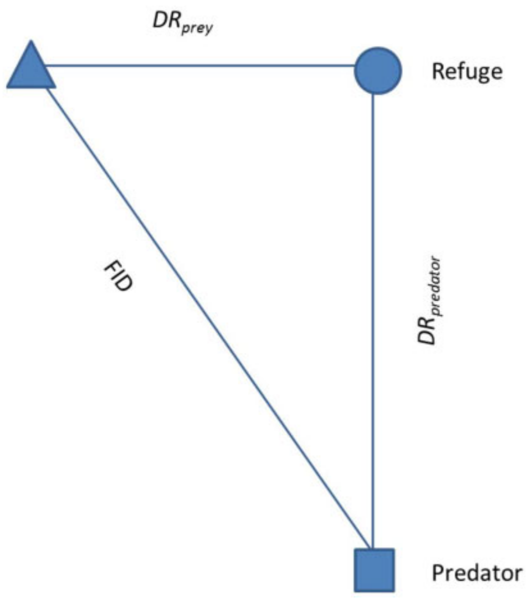

Figure 1. In the race for life model (Cooper 2016) FID is identical to that predicted by Kramer and Bonenfant (1997) predictions are made for the general case in which the prey, predator, and refuge are unaligned, permits the refuge to be located any direction from the prey. Except in the 2 linear cases of the Kramer and Bonenfant (1997) model, the locations of prey, predator, and refuge form the vertices of a triangle with distance or predator and prey to the refuge ($\mathrm{DR}_{\mathrm{predator}}$ and $\mathrm{DR}_{\mathrm{prey}}$) and are represented by the length of 2 sides, and the Φ lying between these 2 sides. FID is the length of the side opposite the Φ.

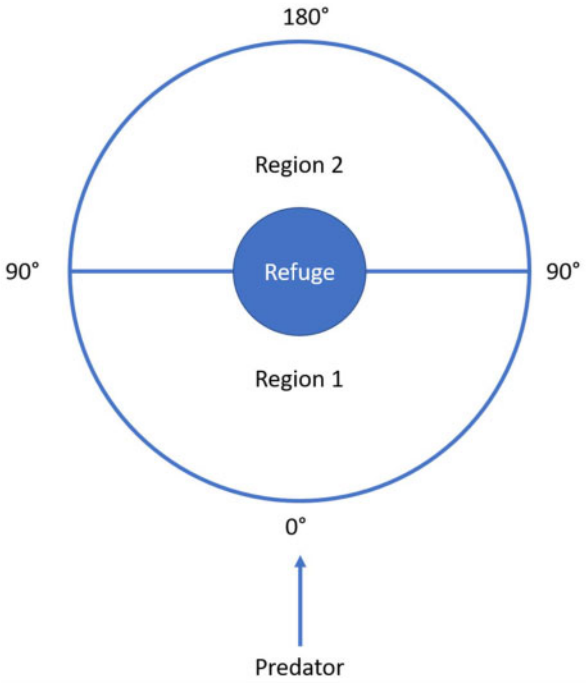

Figure 2. The race for life model predicts that FID decreases as the Φ decreases, the Φ ranging from 0° (prey fleeing straight away for the predator to 180°) prey fleeing straight toward the predator. A simplified prediction of the race for life model is that FID is shorter in Region 1 than Region 2 of the figure because the prey flees somewhat away from the predator at all angles in Region 1, but flees somewhat toward the predator at all directions in Region 2.

toward a predator, indicating a greater cost of fleeing, and thus leading to a larger FID.

Materials and Methods

Animals and study site

We studied yellow-bellied marmots, which use burrows constructed by themselves or conspecifics as refuges. The study was conducted in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic Colorado (38.96° N, 106.99° W). At this site, marmots are abundant and have been individually marked during the course of a long-term study of their behavior and ecology (Blumstein 2013; Armitage 2014). Animals live in discrete colony locations throughout the East River Valley where the RMBL is located. The colonies of River, Bench, and Gothic Town are located in the southern portion of the valley that encompasses the RMBL field station and seasonally used cabins which are subject to relatively heavier human use. The colonies Marmot Meadow, Picnic, Boulder, North Picnic, and Stonefield are in the northern portion of the valley and human use is limited to a mountain pass road, hikers, and cyclists, resulting in much comparatively less direct human disturbance. All subjects were live trapped and marked with numerically unique metal tags to their ears for permanent identification and their dorsal pelage was marked with black Nyanzol dye to permit identification from afar. Data were collected between June and August of 2015 and 2016.

Because yellow-bellied marmots have a readily detectable alerting response (they orient their heads toward an approaching human or predator), alert distance, the predator–prey distance when the alerting response is given, is easily measured. It is important to measure alert distance because FID generally increases as both starting distance (Blumstein 2003; Cooper 2005; Samia et al. 2013) and as alert distance increases (Blumstein 2010; Samia et al. 2013; Samia and Blumstein 2014, 2015). To explain the relationship between FID and alert distance or starting distance, Blumstein (2010) proposed the flush early and avoid the rush hypothesis, which predicts that FID increases as alert distance increases due to increased costs of monitoring the predator for a longer distance. Cooper and Blumstein (2014) identified several such costs. When alert distance is measured, its effect can be statistically accounted when determining the relationship of FID to other variables. We included alert distance in our analyses to avoid any false increases in apparent FID at long starting distances due to spontaneous movement by prey that have not detected the predator (but see Williams et al. 2014).

The race for life model includes a predator-to-prey speed ratio and a margin of safety that we did not measure. These variables help to determine the predator's distance from the refuge when flight begins, but do not appear in the final equation we used to calculate FID from the race for life model. We measured the distances to refuge of predator and prey and the Φ and used the law of cosines to calculate the predicted FID. Using this calculated value of FID, we can assess if our field-measured data support the race for life model.

Data collection

Prior to collecting data, 2 researchers practiced their walking pace used for approaches until they perfected a fixed approach speed of 0.5 m/s. We chose a slow, consistent approach speed to standardize the simulated predator stimulus, and to minimize eliciting variable stress responses. Practice continued during the study to ensure that approach speed did not drift. We located marmots with binoculars by scanning occupied colony sites and once sighted, we used its fur mark to identify the subject. We conducted experimental approaches only on individuals that were in nonagitated states, that is, those that were standing and looking at the surroundings, lying down and looking, or foraging. All subjects were within 31 m of their burrows, and on average stayed within mean (SD) 5 ± 5.7 of their burrows (range = 0.5–31 m).

Once we had an identified, relaxed subject, a solitary researcher approached the marmot directly at the practiced speed of 0.5 m/s. When the marmot turned its head toward him, the researcher dropped a marker. When the marmot began to flee, the researcher dropped another marker. The researcher continued to approach the marmot until it fled into its burrow and then walked to the marmot's initial location. A critical assumption of Cooper's model is that predators approach directly toward a refuge when flight begins. Because marmots are usually near their burrows and flee directly toward their refuge, an approaching researcher's pursuit trajectory is effectively angled toward its refuge. From this location, a laser rangefinder was used to measure alert distance (distance from the first marker to the point where the marmot began to flee), and FID (distance between the second marker and the marmot's initial location). The prey's distance to refuge was the distance from the point where escape was initiated and the burrow's entrance. The DR_{pred} was the distance from the second marker to the burrow's entrance. The Φ, measured with a compass was the angle between the lines leading from the burrow's entrance to the prey's location when it began to escape and the second marker (i.e., the researcher's position when escape began). Whereas we collected multiple observations on some subjects, we elected to use a single observation (the first) from each individual in the study. Because all marmots in this study population were individually marked, we knew each subject's age and sex. Individuals of different sexes and of different life stages can vary in their boldness, and hence FID (Petelle et al. 2013).

Analysis

All statistical analyses were performed using R version 3.6.0 with the RStudio version 1.2.1335 interface. Prior to analysis involving FID predicted by the race for life model, we calculated predicted flight initiation distance (FID) based on the measurements for each observation as the square root of the solution of the equation based on the law of cosines. In preliminary analyses, we established that FID did not substantially differ between the sexes (ANOVA using $\log_{10}$ (FID) as dependent variable: $F_{1,79} = 0.30$, $P = 0.58$). We recorded age in 3 categories, pups, yearlings, and adults. An ANOVA showed that $\log_{10}$ (FID) differed significantly among age groups ($F_{2,78} = 9.96$, $P < 0.001$, $\eta^2 = 0.20$; $\log_{10}$ (FID) ± 1 SE was 1.34 ± 0.22 for pups ($N = 38$), 1.42 ± 0.105 for yearlings ($N = 16$), and 1.54 ± 0.06 for adults ($N = 27$ for juveniles)). Variances were homogeneous (Levene's $F_{2,78} = 1.80$, $P = 0.17$). Using Tukey's HSD tests, FID was significantly shorter for pups than yearlings ($P = 0.034$) and adults ($P < 0.001$) but did not differ significantly between yearlings and adults ($P = 0.54$). We eliminated sex from the remaining analyses and included age.

Preliminary analyses also revealed highly significant effects of colony location and alert distance on FID. Alert distance explains considerable variation in FID (Blumstein et al. 2005; Samia et al. 2013; Samia and Blumstein 2014). Prior work has shown that marmots in our population that are differentially exposed to humans differ significantly in FID as well. By observing and quantifying the degree of human activity, Li et al. (2011) quantified the level of human disturbance for most colony sites in our study population. For our study, we used these scores to categorize each of our 7

Table 1. Number of individuals sampled at each colony location as part of this study

Number	High disturbance		Low disturbance				
	Gothic town	Bench/river	Marmot	Picnic	Boulder meadow	North picnic	Stonefield
N	16	27	12	11	4	5	6

Colonies in areas of high human activity were categorized as "high disturbance," whereas areas of low human activity were categorized as "low disturbance."

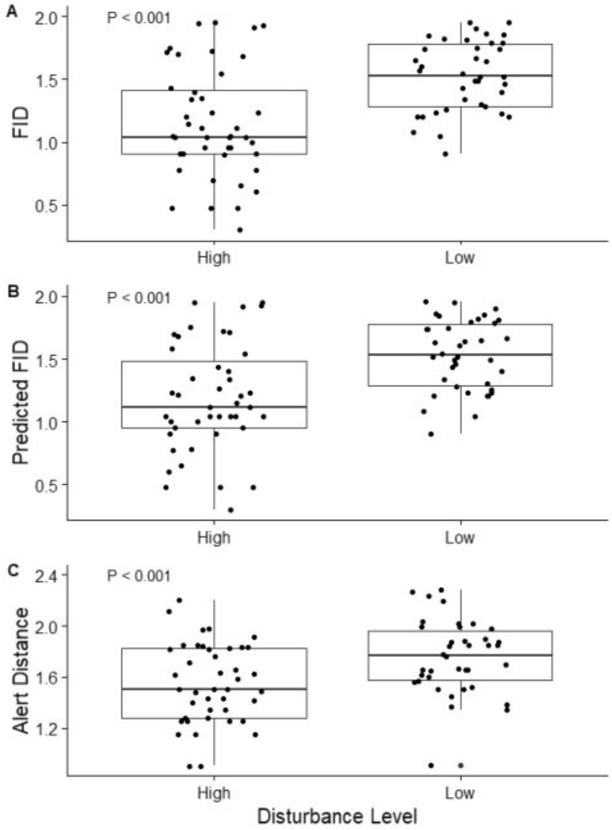

Figure 3. The $\log_{10}$-transformed alert distance, FID, and predicted FID all were longer in relatively isolated up valley locations (low disturbance) than in down valley locations where marmots are more frequently exposed to human presence (high disturbance). Mann–Whitney U-tests reveal that there are significant differences in the mean of each of these variables for low and high disturbance areas. Sample sizes were 39 at up valley locations and 42 at down valley locations.

colony sites into either a "high disturbance" or "low disturbance" category (Table 1). After finding a significant effect of location on FID (Figure 3), we fitted a multiple regression to analyze the effect of alert distance and disturbance on FID. Whereas mean FID was smaller in more disturbed locations, the directionality of statistical effects, and the degree of support for model predictions remained consistent. The significant effects of disturbance level ($P = 0.013$), and a marginally significant interaction between disturbance level and alert distance ($P = 0.050$) led us to include disturbance level, as well as alert distance in subsequent analyses.

To examine the predictive ability of the race for life model and that of the primary variables of that model (DR_{prey}, DR_{pred}, and the cosine of Φ; $\cos(\Phi)$), we fitted a series of general linear models (GLMs). We first conducted simple correlation tests to determine the relationship between individual model variables and observed FID.[2] The primary test of model predictions was a GLM with FID[2] as the dependent variable and DR_{prey}, DR_{pred}, and the $\cos(\Phi)$ as independent variables. We included an interaction term between DR_{prey}, DR_{pred}, and $\cos(\Phi)$ to test for interactive effects on a marmot's escape decision between escape trajectory and a marmot's proximity to its eventual refuge.

Variables with non-normal distributions were $\log_{10}$ transformed prior to analysis to improve distributions. Despite recent recommendation that regressions of FID on alert distance should be forced through the origin (Blumstein et al. 2015) because an alert distance of zero cannot have an FID longer than zero, we included intercepts in our statistical models. We did this because alert distance must be longer than FID to be meaningful, and because the relationship between FID and alert distance occurs in a range of distances at which the prey can detect the approaching predator and dynamically assess risk prior to fleeing and presumably optimize escape decisions (this is referred to as Zone II in Blumstein 2003; Cooper 2015). Predators first detected closer than Zone II should lead to immediate flight. The regression line of FID on alert distances in Zone II may have a positive or negative intercept depending on the prey's risk assessment process. Including the intercept in analyses permits the confirmation of a zero intercept. Effect sizes are reported as partial R^2 for the GLMs. Our 2-tailed alpha was set at 0.05.

To assess the influence of Φ on observed FID when compared with extrinsic factors, we fitted a GLM to explain variation in FID. Our independent variables included: alert distance, disturbance level, and Φ. Alert distance, FID, and DR_{prey} were $\log_{10}$ transformed before analysis.

The race for life model implies that FID will vary continuously with angle, and therefore we treated angle as a continuous variable in our GLM. However, animals may not make as fine distinctions in angle when making escape decisions, and may use coarser assessments of predator risk due to orientation. Therefore, we parameterized a series of GLMs in which we binned our data into different categories comprising different angles (Figure 4) which were based on the predictions of the models of Kramer and Bonenfant (1997), and Cooper (2016) and empirical results reported by Eason et al. (2019). Using AIC to compare model fits, we then assessed which angle categorization scheme most effectively explained variation in our data.

Results

We conducted trials on 81 unique marmots from 7 different colony locations. We collected observations with a variety of values of Φ, representing a wide range of escape scenarios, but with a bias toward low values of Φ (Figure 5). Using the law of cosines, we calculated a predicted measure of FID from values of the $\cos(\Phi)$, DR_{Prey}, and DR_{Pred} to verify that our field-measured data met the assumptions of Cooper's race for life model. In a simple regression analysis, nearly all of the variation in observed FID was explained by predicted FID (Figure 6; $F_{1,79} = 589.88$, $P = 0.001$, $R^2 = 0.94$). The statistical relationships between our measured independent

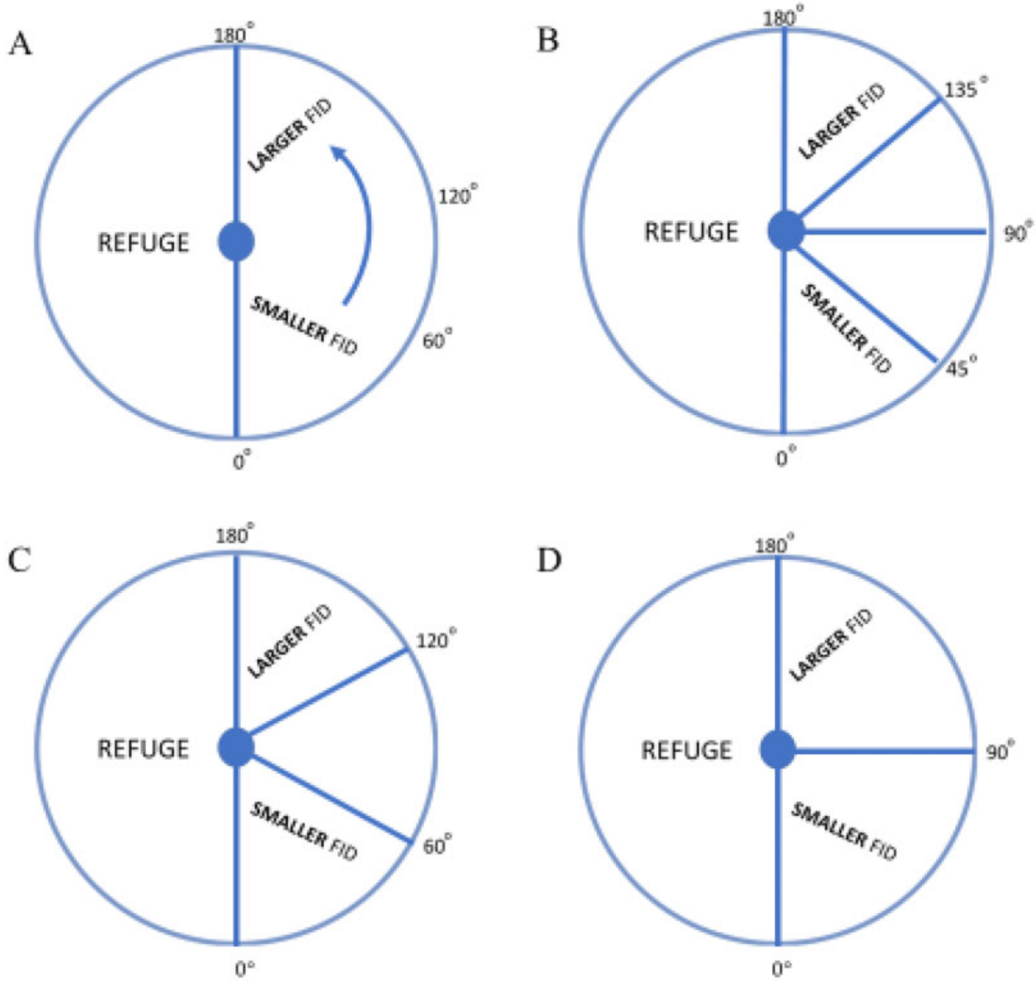

Figure 4. The 4 different schemes used to categorize angle in our linear model analyses. These figures represent a refuge as the small central circle, and a predator's potential relative path somewhere along the outer circle. (**A**) Interpath angle (Φ) is treated as a continuous variable. (**B**) Interpath angle (Φ) is binned into 4 categories (0–45, 45–90, 91–135, and 136–180). (**C**) Interpath angle (Φ) is binned into 3 categories (0–60, 60–120, and 121–180). (**D**) Interpathangle is binned into 2 categories (0–90 and 91–180).

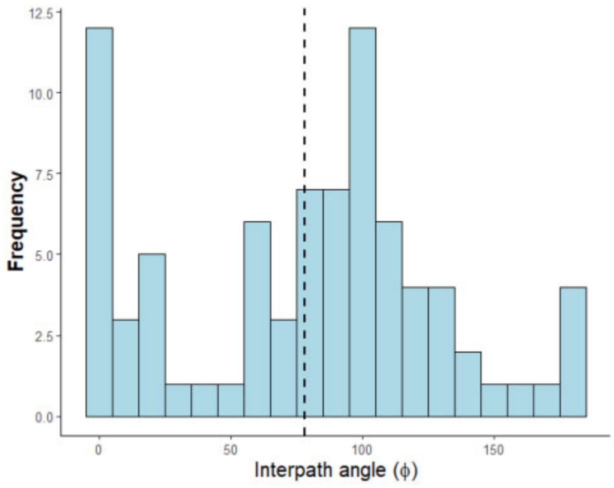

Figure 5. Frequency histogram of values of Φ observed in the field.

variables were much less definitive. In simple correlation tests, DR_{pred} had a highly significant positive relationship with observed FID^2 ($R = 0.989$, $P < 0.001$), and DR_{prey} also had a significant positive effect ($R = 0.698$, $P = 0.016$). However, Cos(Φ) had no significant statistical relationship with FID^2 ($R = 0.063$, $P = 0.167$) (Figure 7). When all variables are compared in a linear model, DR_{pred} explained a significant portion of the variation ($R^2 = 0.709$, $P < 0.001$), as well as a significant effect of cos(Φ) (Partial $R^2 = 0.002$, $P = 0.011$). However, there was little effect of DR_{prey} (Partial $R^2 = 0.030$, $P = 0.680$) or the interaction between DR_{prey}, DR_{pred}, and cos(Φ) (Partial $R^2 = 0.002$, $P = 0.136$) on explaining variation in FID.

We suspected the disproportionate effect of DR_{pred} may be due to a bias in our data toward small values of DR_{prey}. This bias may be due to marmots' tendency to forage quite close to their burrows, which would mathematically result in very similar values for FID and DR_{pred}, regardless of Φ. We then analyzed a smaller subset of the data, where observations with a $DR_{prey} < 3$ m were excluded. When analyzing the effect of our independent variables on FID in

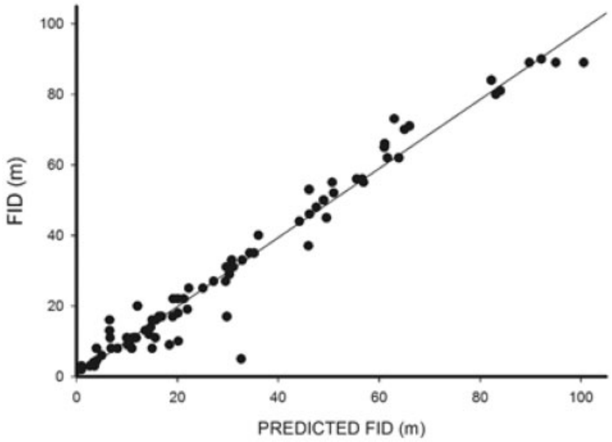

Figure 6. Observed FID is highly correlated with predicted FID. Although this simple correlation does not account for effects of alert distance or location on FID, the association remains very high when these factors are also considered.

this reduced dataset, we again found highly significant effects of DR_{pred} ($P < 0.001$) as well as DR_{prey} ($P < 0.001$), but no significant effect of cos(Φ) ($P = 0.451$) or the interaction term ($P = 0.529$) (Table 2).

Φ, consistently explained significant variation in observed FID when compared with external variables such as alert distance and disturbance level (Table 3). By comparing AIC values for each of our models, we found that the linear model in which Φ was continuous, and when binned into 4 categories of 0–45°, 46–90°, 91–135°, and 136–180° had greater predictive ability relative to the other 2 models tested. In our best categorical model, Φ explained significant variation ($P = 0.039$) after controlling for variation explained by alert distance ($P < 0.001$) and disturbance level ($P < 0.001$).

Discussion

Whereas we were able to use Cooper's model (Cooper 2016) to effectively predict FID, we did not observe the hypothesized statistical relationships between all model parameters and observed FID. The tight relationship between FID and DR_{pred}, whereas consistent with Cooper's predictions, seems to reflect a bias in our data toward smaller values of DR_{prey}. However, when excluding observations with small values of DR_{prey}, there is a marginal effect of DR_{prey} and no effect of Φ, but we did detect a significant effect of the interaction between DR_{prey} and cos(Φ) (Table 4) . This effect could indicate the potential of a contextual effect of Φ on FID. In biological terms, an animal further away from refuge may assess risk differently in fleeing toward an approaching predator than if it were closer to its burrow. Our analyses imply that animals farther away from their eventual refuge may place less importance on Φ than other factors when deciding when to initiate flight.

Our results demonstrated that when compared with other variables typically reported to explain variation in FID, such as alert distance and level of human disturbance, Φ explained significant variation in FID. Our results are consistent with Kramer and Bonenfant's (1997) original findings, as well as those in Cooper Jr.'s (2016) race for life model, and recent empirical findings reported by Eason et al. (2019). In all cases, as Φ decreased, FID decreased. However, we were unable to observe the corresponding relative increase in FID at larger Φ bins that approached 180°. This may suggest that marmots may not be assessing escape trajectories uniformly, but rather bin them into higher-level categories with varying levels of risk assigned to them.

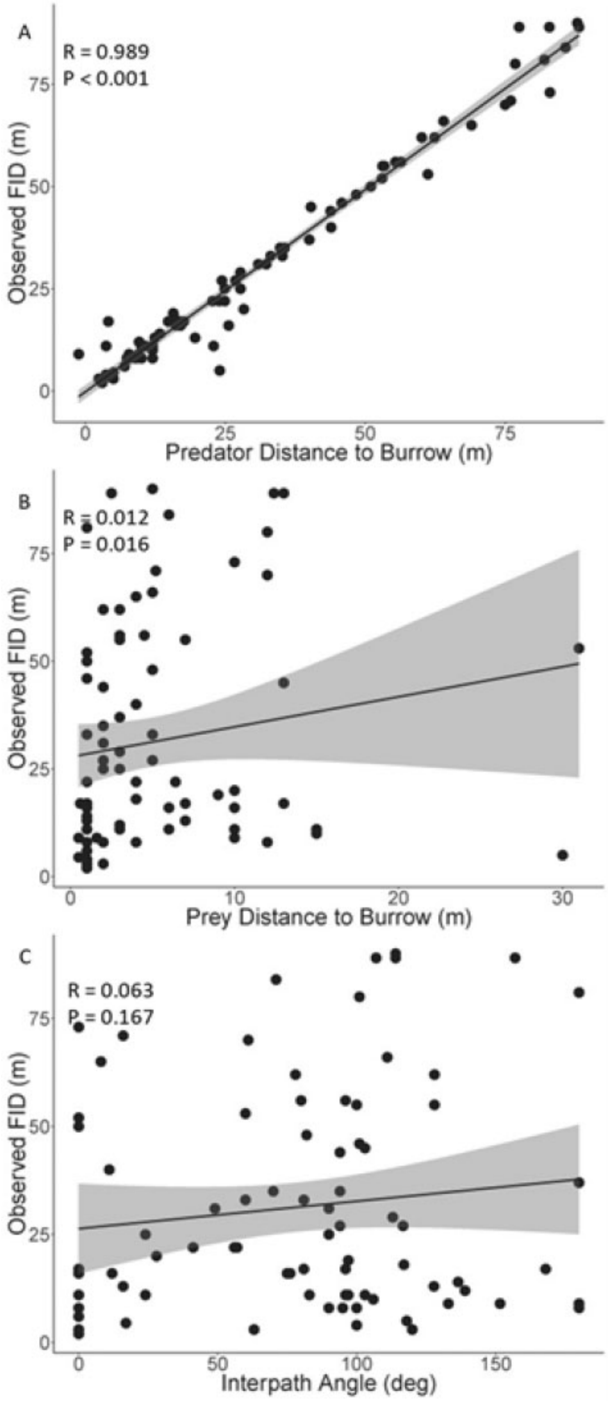

Figure 7. (**A**) DR_{pred} is highly correlated with FID, this relationship. (**B**) DR_{prey} is significantly correlated with FID, with FID increasing as prey distance to refuge increases. This relationship is consistent with the central hypotheses in escape theory, that being farther away from potential refuge constitutes a greater risk and should result in larger FID. (**C**) However, there is no significant relationship between Φ and FID.

Table 2. Summary of results of linear models testing the statistical effect of the race for life model parameters on observed FID^2

	Variable	Estimate	SE	Partial R^2	*P*-value
Full model ($N = 81$)	*Intercept*	1.751	0.094	0.850	**<0.001**
	DR_{prey}	0.005	0.013	0.002	0.6795
	DR_{pred}	0.032	0.002	0.709	**<0.001**
	$cos(\Phi)$	−0.326	0.125	0.085	0.011
	$DR_{prey} \times DR_{pred} \times cos(\Phi)$	0.001	0.001	0.030	0.136
Reduced model:	*Intercept*	2.420	0.166	0.894	**<0.001**
$\mathrm{DR}_{\mathrm{prey}}$	$\mathrm{DR}_{\mathrm{prey}}$	−0.051	0.007	0.255	**<0.01**
>3 m ($N = 36$)	$\mathrm{DR}_{\mathrm{pred}}$	0.019	0.003	0.482	**<0.001**
	$\cos(\Phi)$	−0.215	0.282	0.021	0.451
	$DR_{prey} \times DR_{pred} \times cos(\Phi)$	−0.0004	0.001	0.014	0.529

The full model reports model results for the complete dataset, the reduced model reports result from a model where observations with a $\mathrm{DR}_{\mathrm{prey}} < 3$ m are excluded, but with the same parameters. Bold illustrates significant ($P < 0.05$) terms in the model. Significant p-values ($P < 0.05$) are highlighted in bold.

Table 3. Results of linear models explaining variation in observed FID

Model $N = 81$	Variable	Estimate	*SE*	Partial R^2	*P*-value
Continuous	*Intercept*	−0.397	0.151		**0.011**
$R^2 = 0.97$	*Alert distance*	0.936	0.090	0.583	**<0.001**
Δ AIC = 0*	*Low disturbance*	0.181	0.057	0.207	**0.002**
	Φ	0.001	0.001	0.073	**0.016**
0–45, 46–90, 91–135, 163–180	*Intercept*	−0.398	0.151		**0.010**
$R^2 = 0.97$	*Alert distance*	0.922	0.091	0.579	**<0.001**
Δ AIC = 1.116*	*Low disturbance*	0.185	0.057	0.122	**0.002**
	46–90^{o}	0.174	0.074	0.105	**0.021**
	91–135^{o}	0.149	0.067		**0.027**
	136–180^{o}	0.240	0.104		**0.024**
0–60, 61–120, 121–180	*Intercept*	−0.369	0.152		**0.018**
$R^2 = 0.97$	*Alert distance*	0.932	0.092	0.577	**<0.001**
Δ AIC = 3.516	*Low disturbance*	0.179	0.058	0.112	**0.003**
	61–120^{o}	−0.253	0.149		**0.059**
	121–180^{o}	−0.236	0.157		**0.003**
0–90, 91–180	*Intercept*	−0.327	0.152		**0.035**
$R^2 = 0.97$	*Alert distance*	0.936	0.093	0.569	**<0.001**
Δ AIC = 4.354	*Low disturbance*	0.173	0.059	0.101	**0.004**
	91–180^{o}	0.072	0.056	0.021	**0.199**

Each model treats Φ as a different class of variable, either as a continuous numeric variable, or as a factor where angle is binned into categories. Categories were determined based on the predictions of Kramer and Bonenfant, namely that as the Φ increases, prey must flee more directly toward an approaching predator, will assess a greater risk, and flee sooner (i.e., FID will increase).

Table 4. Results of simple linear regressions explaining variation in FID as a function of alert distance and disturbance level, as well as the interaction between alert distance and disturbance level

Variable	Estimate	SE	*P*-value
Intercept	−0.532	0.190	**0.007**
Alert distance	1.083	0.121	**<0.001**
Low disturbance	0.793	0.312	**0.013**
*Alert distance * disturbance*	−0.367	0.184	*0.050*

Significant p-values ($p < 0.05$) are highlighted in bold. *P*-values between 0.05 and 0.1 are italicized; * indicates best supported models.

Cooper's race for life model hypothesizes that FID increases with Φ in a sigmoid fashion, rather than linearly. However, models that treated angle as a binary variable by binning angle into categories of 0–90° and 90–180°, did not outperform models that treated angle as having multiple states. Whereas marmots may perceive running directly away from a predator to reach a refuge as reflecting relatively low risk, as Φ increases, perceptions of risk may not increase much as they flee toward a predator. For instance, in fish and lizards, the most common escapes are often very close to straight away from the predator, but sometimes individuals escape at angles that are somewhat less directly away from the predator or even at right angles to the predator's path. Such an escape trajectory permits the prey to monitor the predator while fleeing (Domenici and Ruxton 2015; Cooper 2016; Cooper and Sherbrooke 2016). Fleeing toward a predator may offer other benefits. Preys that flee toward approaching aerial predators are much more likely to survive than those that fled away from a predator (Shifferman and Eilam 2004; Ilanay and Eilam, 2008). By fleeing toward a predator, the relative speeds of the predator and prey are increased, decreasing the window of opportunity for a successful capture (Howland 1974).

Far less is known about the effect of direction of escape on FID, although Kramer and Bonenfant (1997) showed FID is longer in woodchucks fleeing straight toward than straight away from a predator. In broad-headed skinks *Plestiodon laticeps*, FID increased as the escape direction was directed more toward a predator (Cooper 1997). In eastern gray squirrels, escape trajectory significantly influences their choice of refuge, with squirrels more likely to select a refuge further away if the relative angle of escape was more obtuse than a closer refuge, which would result in fleeing more away from a predator (Eason et al. 2019). Our results add to this accumulated knowledge and show that the direction marmots escape to a refuge with respect to the predator's path strongly affects FID.

Variation in land use, and in turn, degree of human disturbance had significant impacts on resulting FID in our study. Our results are consistent with previous findings for yellow-bellied marmots (Li et al. 2011; Petelle et al. 2013), and other species that reported smaller FIDs at sites where prey have frequent benign contacts with humans (Samia et al. 2015; Cooper and Blumstein 2015b). However, despite this variation in magnitude of FID across sites, the direction of relationship between angle and FID remains constant between levels of human disturbance.

Taken together, we found some support for the assumptions of Cooper's race for life model. More work remains to be conducted to evaluate the model. For instance, we did not vary predator approach velocity or quantify prey escape velocity. Studies have found that prey can dynamically alter their FID in response to variation in predator approach speed (Cooper 2006). Environmental structure and topography may also interact with an animal's orientation to a potential refuge, affecting escape speed and probability of evading capture. Not all escape routes are equal in a realistic, complex environment, and future studies must take this into account. And whereas Cooper's race for life model provides a mechanistic framework for how the effect of angle may change with predator approach speed, a comprehensive empirical test of this relationship remains to be done. Our findings suggest that it may be worthwhile to develop new theoretical models predicting how other combinations of risk factors, cost of fleeing factors, or both may affect escape decisions.

Although the race for life model is mechanistic rather than economic, future studies should consider how it might be incorporated into cost–benefit models. The currency of the Ydenberg and Dill (1986) and Cooper and Frederick (2007) models is expected fitness at the end of the predator–prey encounter. A link between these models and the race for life model is the probability of being killed and losing all fitness if the predator captures the prey before it reaches refuge. The question is how this relates to predator–prey distance before the prey flees.

Our results raise important questions regarding how prey use information in the environment to assess risk, and in turn to make escape decisions. Whereas contemporary models of escape behavior seek to capture the continuous variation in quantitative risk factors influencing FID, prey animals themselves may not perceive these risk factors in a continuous way. To that end, there is extensive research into the cognitive mechanisms by which animals categorize complex information to enhance memory and make more efficient decisions. Much of this work has focused on animal's ability to generalize stimuli in regards to predator recognition (Ferrari et al. 2016), as well as the mechanisms underlying spatial reasoning (Shettleworth 2010). Studies of escape behavior at the individual level must reconcile risk assessment and spatial reasoning to determine how animals assess complex and competing stimuli to determine optimal escape strategies. Much remains to be learned about decision-making processes by prey even for the relatively simple decision about when to flee, much less during the more complex interactions between predators and their fleeing prey that occur in nature.

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Conflict of interest

We declare we have no competing interests.

References

Armitage KB, 2014. *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. Cambridge (MA): Cambridge University Press.

Blumstein DT, 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J Wildlife Manage* **67**:852–857.

Blumstein DT, Fernandez-Jurcic E, Zollner PA, Garity SC, 2005. Inter-specific variation in avian responses to human disturbance. *J Appl Ecol* **42** 943–953.

Blumstein DT, 2010. Flush early and avoid the rush: a general rule of antipredator behavior? *Behav Ecol* **21**:440–442.

Blumstein DT, 2013. Yellow-bellied marmots: insights from an emergent view of sociality. *Philos. Trans. Royal Soc B* **368**:20120349.

Blumstein DT, Flores G, Munoz NE, 2015. Does locomotor ability influence flight initiation distance in yellow-bellied marmots? *Ethology* **121**:434–441.

Blumstein DT, Samia DS, Cooper WE, Jr, 2016. Escape behavior: dynamic decisions and a growing consensus. *Curr Opin Behav Sci* **12**:24–29.

Cooper WE, Jr, 1997. Factors affecting risk and cost of escape by the broad-headed skink *Eumeces laticeps*: predator speed, directness of approach, and female presence. *Herpetologica* **53**:464–474.

Cooper WE, Jr, 2005. When and how do predator starting distances affect flight initiation distances? *Can J Zool* **83**:1045–1050.

Cooper WE, Jr, 2006. Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology* **112**:858–864.

Cooper WE, Frederick WG, 2007. Optimal flight initiation distance. *J Theor Biol* **244**:59–67.

Cooper WE, Jr, 2009. Escape tactics and effects of perch height and habituation on flight initiation distance in two Jamaican anoles (Squamata: polychrotidae). *Int J Trop Biol Conserv* **58**:1199–1209.

Cooper WE, Jr, Blumstein DT, 2014. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behav Ecol* **25**:44–52.

Cooper WE, Jr, 2015. Reptiles. In: Cooper WE, JrBlumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge: Cambridge University Press. 113–151.

Cooper WE, Jr, Blumstein DT, 2015a. *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge: Cambridge University Press.

Cooper WE, Jr, Blumstein DT, 2015b. Escape behaviour: importance, scope, and variables. In: Cooper WE, JrBlumstein DT, editors. *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge: Cambridge University Press. 3–14.

Cooper WE, 2016. Fleeing to refuge: escape decisions in the race for life. *J Theor Biol* **406**:129–136.

Cooper WE, Sherbrooke WC, 2016. Strategic escape direction: orientation, turning, and escape trajectories of zebra-tailed lizards *Callisaurus draconoides*. *Ethology* **122**:542–551.

Domenici P, Blagburn JM, Bacon JP, 2011. Animal escapology I: theoretical issues and emerging trends in escape trajectories. *J Exp Biol* **214**:2463–2473.

Domenici P, Ruxton GD, 2015. Prey behaviors during fleeing: escape trajectories, signaling and sensory defenses. In: Cooper WE, Jr, Blumstein DT editors. *Escaping from Predators: An Integrative View of Escape Decisions by Prey*. Cambridge: Cambridge University Press. 199–224.

Eason PK, Nason LD, Je A, Jr, 2019. Squirrels do the math: flight trajectories in eastern gray squirrels *Sciurus carolinensis*. *Ecol Evol* **7**:66.

Ferrari MC, Crane AL, Chivers DP, 2016. Certainty and the cognitive ecology of generalization of predator recognition. *Anim Behav* **111**:207–211.

Frederick WG, Cooper WE, Jr, 2010. Predator lethality, optimal escape behavior, and autotomy. *Behav Ecol* **21**:91–96.

Howland HC, 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J Exp Biol* **47**:333–350.

Ilanay A, Eilam D, 2008. Wait before running for your life: Defensive tactics of spiny mice (Acomys cahirinus) in evading barn owl (Tyto alba) attack. Behavioral Ecology and Sociobiology **62**: 923–933.

Kramer DL, Bonenfant M, 1997. Direction of predator approach and the decision to flee to a refuge. *Anim Behav* **54**:289–295.

Li C, MonclÇs R, Maul TL, Jiang Z, Blumstein DT, 2011. Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Appl Anim Behav Sci* **129**:146–152.

Petelle MB, McCoy DE, Alejandro V, Martin JG, Blumstein DT, 2013. Development of boldness and docility in yellow-bellied marmots. *Anim Behav* **86**:1147–1154.

Samia DS, Nomura F, Blumstein DT, 2013. Do animals generally flush early and avoid the rush? A meta-analysis. *Biol Lett* **9**:20130016.

Samia DS, Blumstein DT, 2014. Phi index: a new metric to test the flush early and avoid the rush hypothesis. *PLoS ONE* **9**:e113134.

Samia DS, Blumstein DT, 2015. Birds flush early and avoid the rush: an interspecific study. *PLoS ONE* **10**:e0119906.

Samia DS, Blumstein DT, Stankowich T, Cooper WE, 2015. Fifty years of chasing lizards: new insights advance optimal escape theory. *Biol Rev* **91**:349–366.

Shettleworth SJ, 2010. *Cognition, Evolution and Behavior*. New York (NY): Oxford University Press.

Stankowich T, Blumstein DT, 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc Biol Sci* **272**:2627–2634.

Shifferman E, Eilam D, 2004. Movement and direction of movement of a simulated prey affect the success rate in barn owl *Tyto alba* attack. *J Avian Biol* **35**:111–116.

Williams DM, Samia DS, Cooper WE, Blumstein DT, 2014. The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. *Behav Ecol* **25**:1136–1147.

Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. *Adv Study Behav* **16**:229–249.