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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 towards 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 interpath angle 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 interpath angle and FID was less clear. Marmots may not assess interpath angle in a continuous fashion; but we found that binning angle into four 45° bins explained a similar amount of variation as models that analyzed angle continuously. Future studies of interpath angle, especially those that focus on how different species perceive relative orientation, will likely enhance our understanding of its importance in flight decisions.

Key words: escape behavior, escape trajectory, escape theory, antipredator behavior, 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, b), 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 predicts 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 while 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 Bonefant 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 flight initiation distance. 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 towards 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 two sides of the triangle that meet at the refuge are the distance of the prey from refuge (DR_{prey}) and the predator's distance from refuge (DR_{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:

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

The model's predictions are based, in part, on the relationships between interpath angle, Φ, and FID. At its essence is the expectation that as Φ increases, prey must flee more directly towards 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 interpath angle 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 to 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 interpath angle would result in refuging prey fleeing more directly 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 towards 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 interpath angle 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, two 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 non-agitated states, i.e., 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 5±5.7 SD m 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 towards a refuge when flight begins. Since marmots are usually near their burrows and flee directly towards their refuge, an approaching researcher's pursuit trajectory is effectively angled towards 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 flight initiation distance (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 predator's distance from refuge was the distance from the second marker to the burrow's entrance. The interpath angle (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). While we collected multiple observations on some subjects, we elected to use a single observation (the first) from each individual in the study. Since 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 v.3.6.0 with the RStudio v1.2.1335 interface. Prior to analysis involving FID predicted by the race for life model, we calculated predicted 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 three 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 seven 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. While 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), we fitted a series of general linear models (GLM). 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 cosine of Φ as independent variables. We included an interaction term between DR_{prey}, DR_{pred}, and cos(Φ) 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 two-tailed alpha was set at 0.05.

To assess the influence of interpath (φ) angle on observed FID when compared to extrinsic factors, we fitted a GLM to explain variation in FID. Our independent variables included: alert distance, disturbance level, and interpath angle. 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 general linear model. 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 general linear models 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 seven different colony locations. We collected observations with a variety of values of Φ, representing a wide range of escape scenarios, but with a bias towards low values of Φ (Figure 5).

Using the law of cosines, we calculated a predicted measure of FID from values of the cosine of Φ, 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 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, $P = 0.016$). Cos(Φ) however 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 towards 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 this reduced dataset, we again found a 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 3).

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

Discussion

While 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}, while consistent with Cooper's predictions, seems to reflect a bias in our data towards 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 interpath angle, but we did detect a significant effect of the interaction between DR_{prey} and cos(phi) (Table 2). This effect could indicate the potential of a contextual effect of interpath angle on FID. In biological terms, an animal further away from refuge may assess risk differently in fleeing towards 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 interpath angle than other factors when deciding when to initiate flight.

Our results demonstrated that when compared to other variables typically reported to explain variation in FID, such as alert distance and level of human disturbance, inter-path angle explained significant variation in FID. Our results are consistent with Kramer and Bonenfant's (1997) original findings, as well as those in Cooper's (2016) race for life model, and recent empirical findings reported by Eason et al. (2019). In all cases, as interpath angle decreased, FID decreased. However, we were unable to observe the corresponding relative increase in FID at larger interpath angle 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.

Cooper's race for life model hypothesizes that FID increases with interpath angle 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. While marmots may perceive running directly away from a predator to reach a refuge as reflecting relatively low risk, as interpath angle increases, perceptions of risk may not increase much as they flee towards 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 towards a predator may offer other benefits. Prey that flee towards approaching aerial predators are much more likely to survive than those that fled away from a predator (Shifferman and Eilan 2004; Ilany and Eilam 2007). By fleeing towards 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 grey 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 (Cooper 2015b; Samia et al. 2015). 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 while 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 Fredrick (2007, 2010) 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. While 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 2009). 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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Table 1. Number of individuals sampled at each colony location as part of this study. Colonies in areas of high human activity were categorized as "High Disturbance", while areas of low human activity were categorized as "Low Disturbance".

	High Disturbance				Low Disturbance		
	Gothic	Bench/River Town	Marmot	Picnic	Boulder Meadow	North Picnic	Stonefield
N	16	27	12	11	4	5	6

Table 2. 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**
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*

Table 3. Summary of results of linear models testing the statistical effect of the race for life model parameters on observed FID^2. The full model reports model results for the complete dataset, the reduced model reports results from a model where observations with a $DR_{prey} < 3$ m are excluded, but with the same parameters. Bold illustrates significant ($P < 0.05$) terms in the model .

	Variable	Estimate	*SE*	*Partial* R^2	*P*
Full Model	*Intercept*	1.751	0.094	0.850	**< 0.001**
(*N* = 81)	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} x DR_{pred} x $cos(\Phi)$	0.001	0.001	0.030	0.136
Reduced Model:	*Intercept*	2.420	0.166	0.894	**< 0.001**
DR_{prey} > 3m (*N* = 36)	DR_{prey}	-0.051	0.007	0.255	**< 0.01**
	DR_{pred}	0.019	0.003	0.482	**< 0.001**
	cos(Φ)	-0.215	0.282	0.021	0.451
	DR_{prey} x DR_{pred} x $cos(\Phi)$	-0.0004	0.001	0.014	0.529

Table 4. Results of linear models explaining variation in observed flight initiation distance. Each model treats interpath angle 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 interpath angle increases, prey must flee more directly towards an approaching predator, will assess a greater risk, and flee sooner (i.e., FID will increase

Model N = 81		Variable	Estimate	*SE*	Partial R^2	*P*
1.	**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**
2.	**0-45, 46-90, 91-**	*Intercept*	-0.398	0.151		**0.010**
	135, 163-180	*Alert Distance*	0.922	0.091	0.579	**<0.001**
	R^2 **= 0.97**	*Low Disturbance*	0.185	0.057	0.122	**0.002**
	Δ AIC = 1.116*	*46°- 90°*	0.174	0.074	0.105	**0.021**
		91° -135°	0.149	0.067		**0.027**
		136° -180°	0.240	0.104		**0.024**
3.	**0-60, 61-120, 121-**	*Intercept*	-0.369	0.152		**0.018**
	180	*Alert Distance*	0.932	0.092	0.577	**<0.001**
	R^2 **= 0.97**	*Low Disturbance*	0.179	0.058	0.112	**0.003**
	Δ AIC = 3.516	*61° - 120°*	-0.253	0.149		0.059
		121° - 180°	-0.236	0.157		**0.003**
4.	**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°	0.072	0.056	0.021	0.199

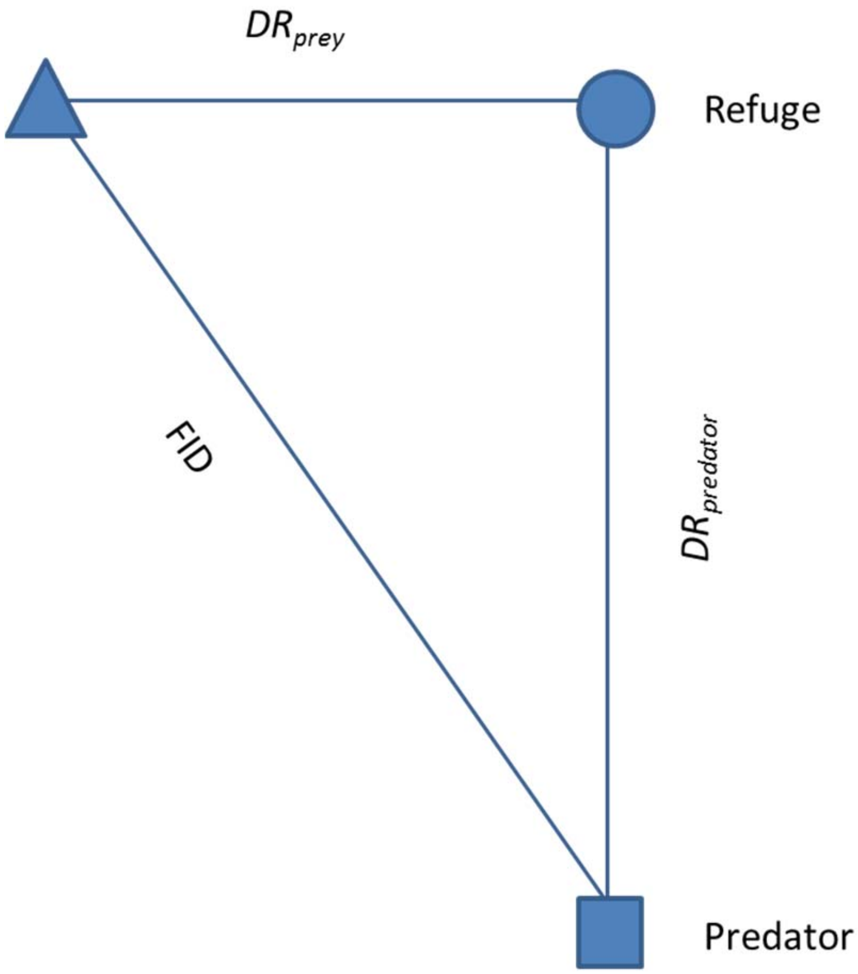

Figure 1. In the race for life model (Coper 2016) FID is identical to that predicted by Kramer and Bonenfant (1997) predictions are made for the general case in which the prey, predator and refuge are unaligned, permits the refuge to be located any direction from the prey. Except in the two linear cases 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 ($DR_{predator}$ and DR_{prey}) and are represented by the length of two sides, and the interpath angle to the refuge (Φ) lying between these two sides. FID is the length of the side opposite the interpath angle.

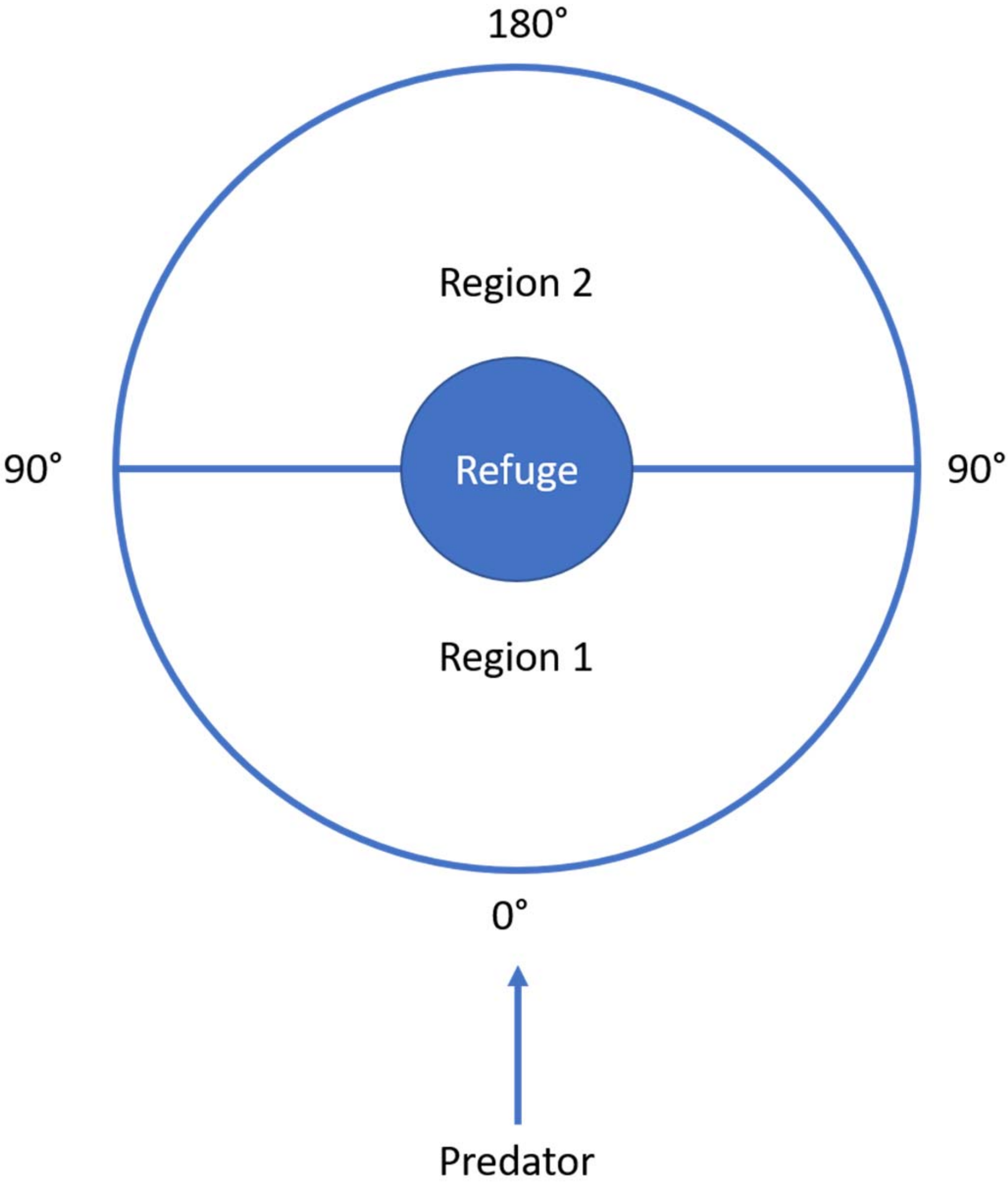

Figure 2. The race for life model predicts that flight initiation distance decreases as the interpath angle decreases, the interpath angle ranging from 0° (prey fleeing straight away for the predator to 180° (prey fleeing straight toward the predator. A simplified prediction of the race for life model 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.

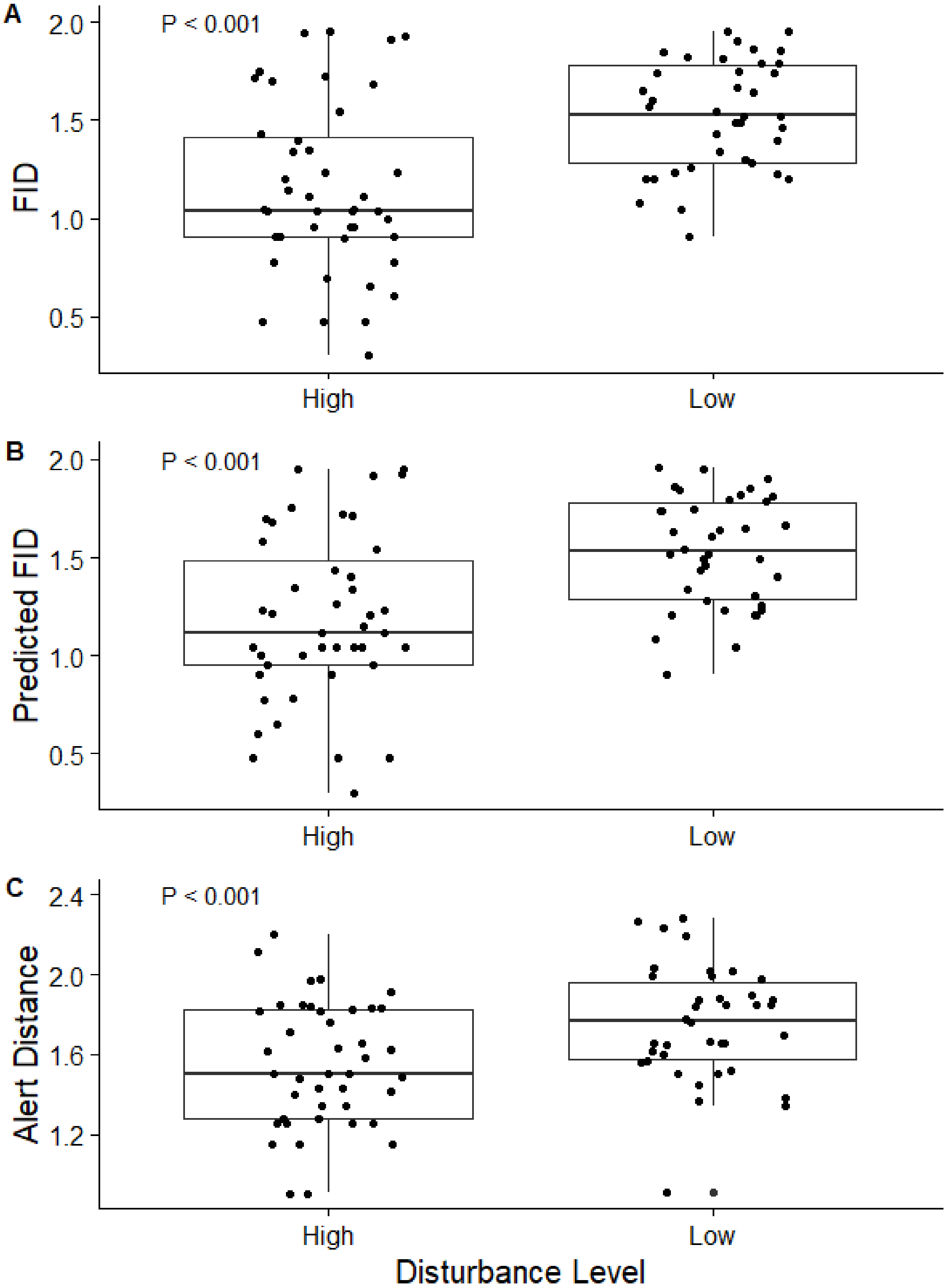

Figure 3. The $\log_{10}$-transformed alert distance, flight initiation distance (FID) and predicted FID all were longer in relatively isolated up valley locations (low disturbance) than in down valley locations where marmots are more frequently exposed to human presence (high disturbance). Mann Whitney 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.

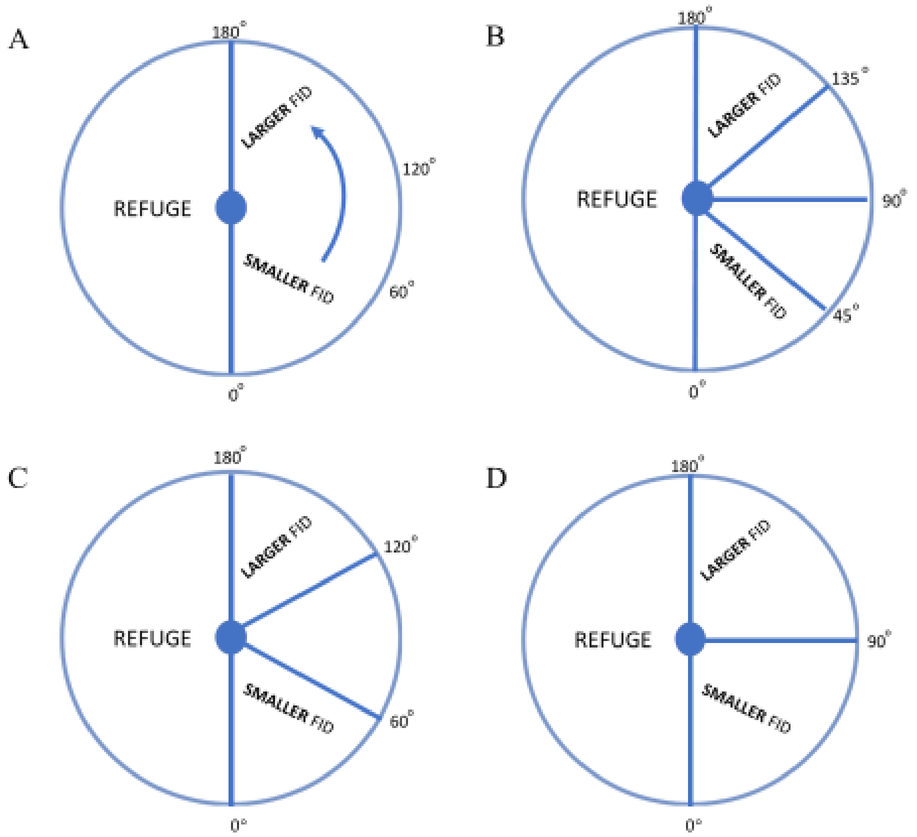

Figure 4. The four different schemes used to categorize angle in our linear model analyses. These figures represent a refuge as the small central circle, and a predator's potential relative path somewhere along the outer circle. **A.** Interpath angle is treated as a continuous variable. **B.** Interpath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

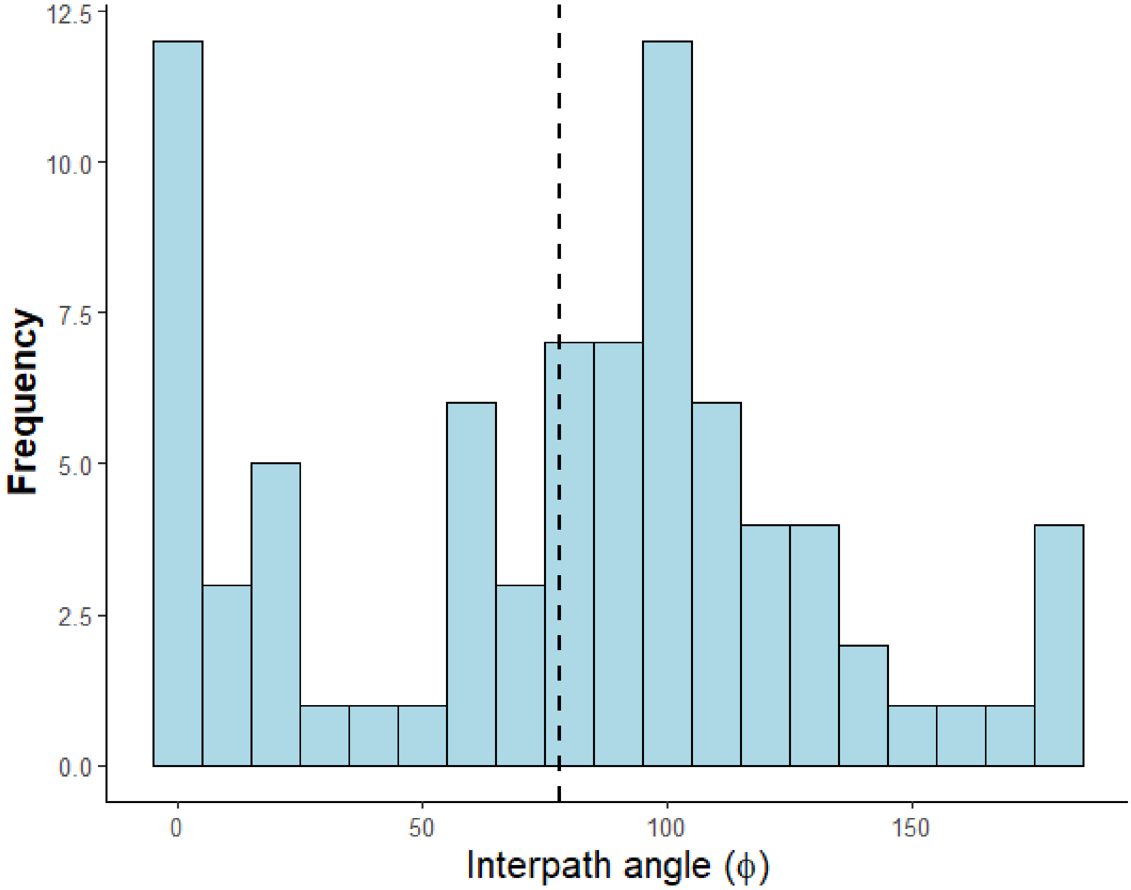

Figure 5. Frequency histogram of values of interpath angle (Φ) observed in the field.

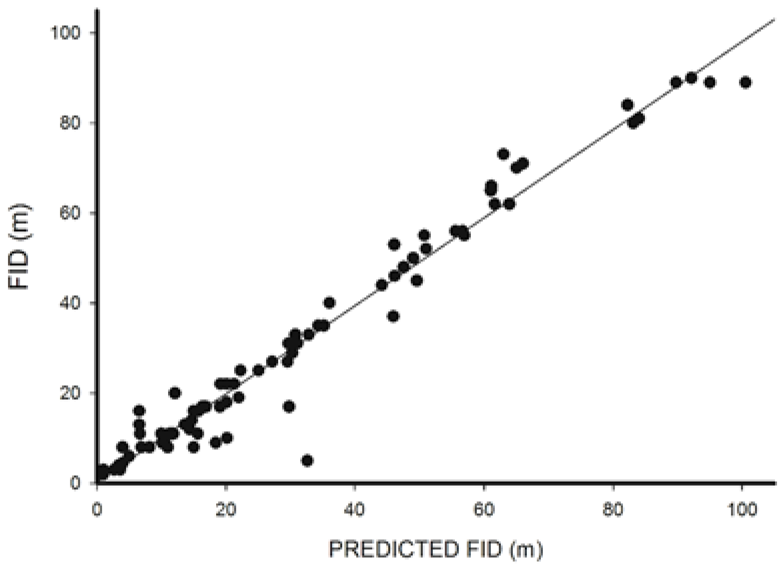

Figure 6. Observed FID is highly correlated with predicted FID. Although this simple correlation does not account for effects of alert distance or location on FID, the association remains very high when these factors are also considered.

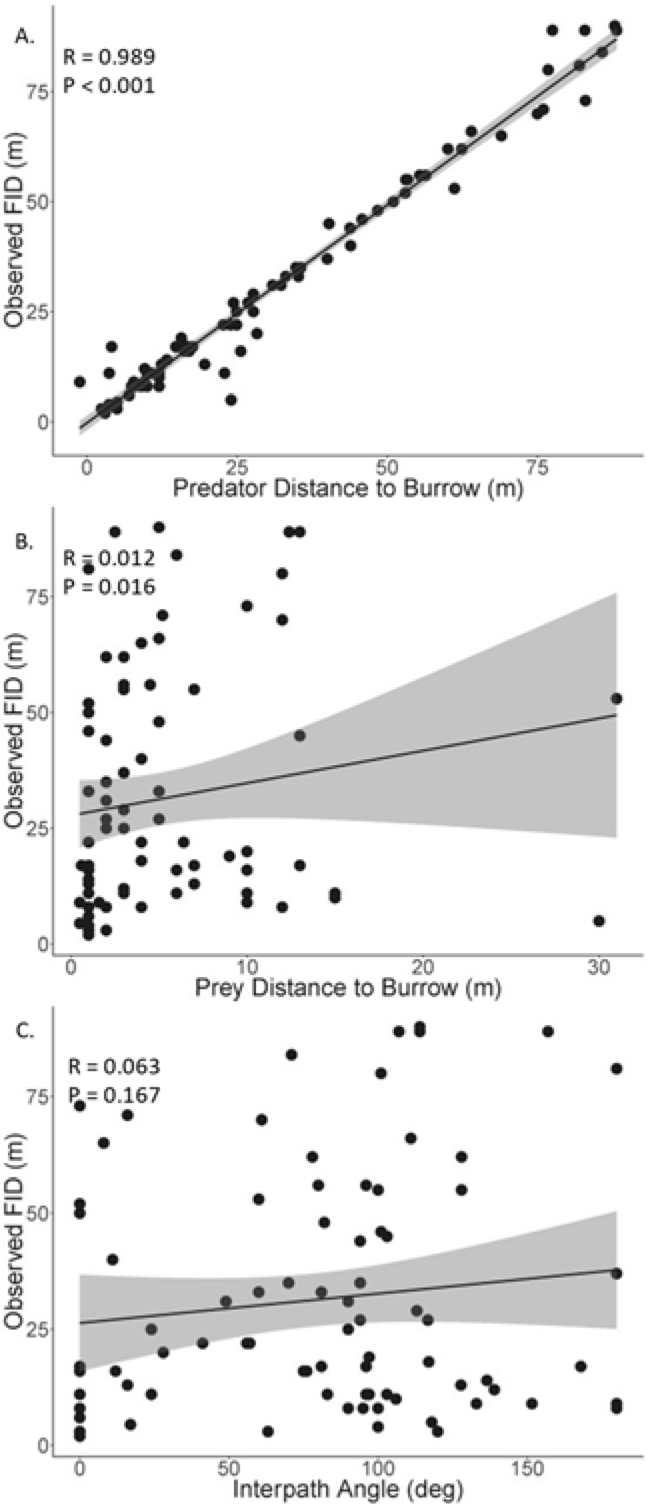

Figure 7. A. Predator distance to refuge (DR_{pred}) is highly correlated with FID, this relationship. **B.** DR_{prey} is significantly correlated with FID, with FID increasing as prey distance to refuge increases. This relationship is consistent with the central hypotheses in escape theory, that being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