

# Interactive effect of starting distance and approach speed on escape behavior challenges theory

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Escape theory predicts flight initiation distance (FID, predator-to-prey distance when escape begins) based on fixed functions relating costs and benefits of fleeing to distance between a prey and an approaching predator. Theory accurately predicts effects of costs for fixed functions and changes in functions due to changes in predator behavior approach. Less obvious is how the effect of starting distance (predator-to-prey distance when approach begins) on FID can be explained when predator behavior does not change during approach. We simulated predators to study effects of starting distance on FID in Balearic lizards (*Podarcis lilfordi*). Starting distance and approach speed affected FID interactively. It increased as starting distance increased during faster, but not slower, approaches. Because risk functions are considered fixed for a given approach speed, we must explain why FID varies with starting distance, why only for rapid approach, and how risk is assessed. Because prey approached slowly assess risk as small until the predator is very close, approach from greater distance has little effect on risk curves. Because continued rapid approach suggests that the predator has detected the prey and is attacking, not merely approaching, risk varies with starting distance. Theoretical difficulty in explaining the effect of starting distance on FID disappears if risk curves vary among starting distances at faster approach speeds, but each curve is fixed. This might occur if prey use a temporal rule of thumb assigning increasing risk as duration of rapid approach increases. *Key words*: antipredatory behavior, approach distance, escape, flight initiation distance, flush distance, starting distance. [*Behav Ecol*]

Escape theory was developed to predict how close a prey allows a predator to approach before starting its escape attempt (FID = flight initiation distance). In the scenario of 2 cost-benefit models, a prey that detects a predator at a distance does not flee immediately but monitors the approach until some criterion for fleeing is met. The criterion for one model is that costs of not fleeing (due to predation risk) and costs of fleeing are equal (Ydenberg and Dill 1986); for the other model, the criterion is maximization of expected fitness after the encounter (Cooper and Frederick 2007a). In both models, the predator's approach is treated implicitly as having a fixed trajectory and speed. It is assumed that curves relating distance between predator and prey to costs of not fleeing and of fleeing do not change during approach, that is, predation risk (cost of not fleeing) and benefit (cost of fleeing) curves retain their forms throughout approach. The cost-benefit models do not address methods by which prey assess risk, but both spatial and temporal aspects of approach may be important (Stankowich and Coss 2006). Prey unable to precisely calculate risk may employ simple rules of thumb to assess risk (Bouskila and Blumstein 1992), which might be based on cues such as distance, duration, and speeds.

Escape theory is strongly supported by verification of its predictions for numerous risk factors in diverse prey (reviewed by Stankowich and Blumstein 2005). However, a static view of risk curves has been a source of concern for some specialists in antipredatory defenses. To maximize probability of surviving a

predator-prey encounter, prey should be responsive to changes in predator behavior that imply changing risk (Blumstein 2003; Stankowich and Coss 2006; Lima S, personal communication). Two findings indicate that prey assess risk dynamically during encounters to select FID. Lizards are much more likely to flee immediately when a nearby predator turns toward than away from them (Cooper 1997b, 1998). In the lizard *Anolis lineatopus*, FID increases when the predator accelerates during its approach and decreases when the predator decelerates (Cooper 2006a). Such cases are compatible with existing theory if prey rapidly assess changes in risk, switching from one risk curve to another.

A possible sort of dynamic risk assessment that has been ignored is that the form of the predation risk curve may be altered during an encounter even if features of the approach such as speed and trajectory remain constant. The first hint of such an effect was that FID increased with increase in starting distance (distance between predator and prey when the predator begins to approach) in many species of birds that were approached at constant speed (Blumstein 2003). This finding has been extended to a mammal (Stankowich and Coss 2006) and a lizard (Cooper 2005), suggesting that starting distance may affect escape decisions in diverse taxa. Implications of the relationship for escape theory have not been addressed but challenge the static view that risk curves have fixed shapes during approaches at constant speed on unchanging trajectories.

The effect of starting distance on FID varies among species. FID increased with starting distance in 64 of 68 Australian bird species (Blumstein 2003). To account for these findings, Blumstein modified model of Ydenberg and Dill (1986). In his model, a prey that detects a predator closer than some minimum distance (zone 1) should flee immediately. This is

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consistent with the interpretation of effects of sudden turning or movement by a nearby predator, which is that a prey that detects an approaching predator closer than the FID predicted by costs and benefits should flee immediately; closer than some minimum distance, predators will almost always be closer than the predicted FID (Cooper 1997b, 1998). An exception may occur when a prey's lifetime fitness may be increased by not fleeing at all (Cooper and Frederick 2007a).

In zone 2 of Blumstein's (2003) model, FID is predicted by cost and benefit as in the model of Ydenberg and Dill (1986). In zone 3, prey do not respond to predators. Blumstein (2003) found that FID increased with increases in starting distance in zone 2. In the Columbian black-tailed deer (*Odocoileus hemionus columbianus*), the sole mammal studied, FID increased with starting distance up to a maximum distance, that is, in zone 2 (Stankowich and Coss 2006).

In previous studies of lizards, starting distance had no effect in *Urosaurus ornatus*, but FID increased slightly as starting distance increased in *Sceloporus virgatus* but only at the faster of 2 approach speeds (Cooper 2005). At slow approach speeds, starting distance did not affect FID in 3 species of ambush foragers (Cooper 2005, 2007) or in the active forager *Aspidoscelis exsanguis* (Cooper 2008a). FID increased as starting distance increased in *A. exsanguis*, but this was interpreted as an artifact of foraging movements (Cooper 2008a).

We studied effects of starting distance on FID in the Balearic lizard (*Podarcis lilfordi*) to examine the potentially graded effect of predator approach speed on the FID  $\times$  starting distance relationship. We predicted that starting distance and approach speed interact to determine FID. For slow approaches, starting distance is predicted not to affect FID because risk is very low until a predator is very close. In contrast, the longer a predator approaches rapidly, the more likely it is to have detected the prey already and be attacking or to continue approaching until it detects the prey. Such a finding would challenge escape theory by suggesting that risk curves might change continuously during approach, a hitherto unsuspected form of dynamic risk assessment. We incorporate the effect of starting distance on FID into existing theory and suggest that prey may use a temporal rule of thumb to assess risk during approach at a given speed.

## METHODS

The study was conducted in the islet of Aire, which is located offshore from Menorca, Balearic Islands, Spain, between 26 April and 10 May 2005 on sunny days when lizards were fully active. The study site was sparsely vegetated, having patches of open ground between plants, which included low bushes and flowering plants that are food sources for the omnivorous *P. lilfordi* (Barbadillo et al. 1999). Rocks and holes at the base of a stone fence and some larger bushes served as refuges. Aire has had no permanent residents since the 1930s, but the island is visited often by biologists and visitors to a lighthouse (Pérez-Mellado 1989).

The main predators in Aire are birds, especially kestrels (*Falco tinnunculus*). Kestrels frequently eat lizards (Cramp and Simmons 1980) and are important predators on *P. lilfordi* in some Menorcan islets. No kestrels nested in Aire in 2005, but they often visited. Seagulls are abundant in Aire but infrequently eat lizards (Cramp and Simmons 1982). The species that breeds in Aire, *Larus cachinnans*, is not known to eat *P. lilfordi* (Araújo et al. 1977). Shrikes (*Lanius* spp.) are major predators of lizards that occur in Menorca and may occasionally visit Aire. No mammalian or ophidian predators occur in Aire (Pérez-Mellado 1989).

We approached lizards to simulate predatory attacks. This method has been justified extensively elsewhere and is a com-

monly used, effective method for studying escape in various prey taxa (justification: Cooper and Wilson 2007a; Cooper 2008a; taxa: insects [Cooper 2006b], crabs [Hemmi 2005], fish [Grant and Noakes 1987], frogs [Martín et al. 2005; Cooper et al. 2009a, 2009b], lizards [e.g., Cooper 1997a, 2000; Martín and López 1999; Martín et al. 2003; Cooper and Wilson 2007a, 2007b], birds [Blumstein 2003; Cárdenas et al. 2005], and mammals [Blumstein and Pelletier 2005, Stankowich and Coss 2006, 2007]; review for diverse taxa [Stankowich and Blumstein 2005]).

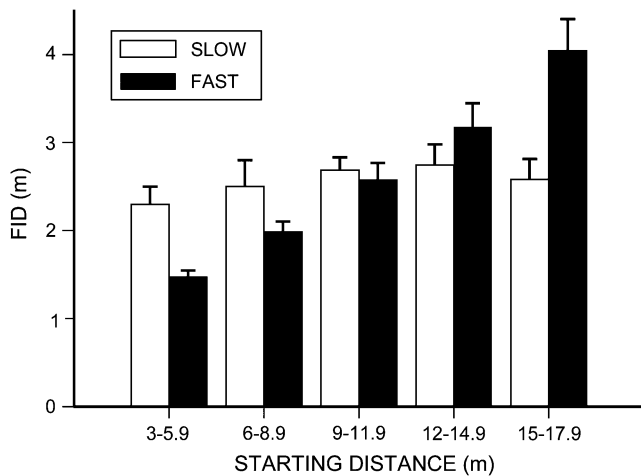
Care must be taken to reduce or eliminate possible experimenter bias due to knowledge of hypotheses and treatments. To reduce the possibility of bias, we standardized methods of approach by practicing approach speeds to make them consistent. We predetermined the sequence of trials to avoid unconscious selection of lizards in particular settings that might affect escape. Some deviation from the predetermined sequence occurred due to differences in frequency of our ability to move to the desired starting distances.

To locate lizards, we searched visually while walking slowly through the study site. An experimenter moved very slowly to a location that afforded the lizard a clear view of him and was in the desired interval of starting distance. Lizards were approached from either side but not from behind or in front because detection may be impaired from these directions, affecting escape behavior (Cooper 2008b). The experimenter stopped briefly and oriented directly toward the lizard, marked the starting point to permit later measurement of starting distance, and approached directly at 1 of 2 speeds. Approach speeds were slower ( $80.8 \pm 0.8$  m/min,  $n = 10$ ) and faster ( $115.8 \pm 3.5$  m/min,  $n = 10$ ). When the lizard fled, the experimenter stopped and recorded FID and starting distance to the nearest 0.1 m. We avoided pseudoreplication by moving through a particular area only once. At the conclusion of the test for one lizard, other individuals were usually in sight and could be distinguished readily from the lizard that had just fled based on differences in size and location relative to the escape path of the previously tested lizard. When any confusion might exist, the experimenter moved to a new location.

To study the effect of starting distance on FID, we used a  $2 \times 5$  factorial independent groups design with 2 approach speeds and 5 intervals of starting distance (3.0–5.9, 6.0–8.9, 9–11.9, 12–14.9, and 15.0–17.9 m). Sample sizes for slower approaches were 20 for each starting distance category. For fast approaches, sample sizes were 28 for 3.0–5.9 m, 31 for 6.0–8.9 m, 30 for 9.0–11.9 m, 27 for 12.0–14.9 m, and 28 for 15.0–17.9 m. Factorial analysis of variance (ANOVA) including the interaction term was used to examine effects of approach speed and distance. The assumption of homogeneity of variance was examined using Levene's test; that of normality was assessed using Kolmogorov–Smirnov tests. Data that did not meet the assumptions were logarithmically transformed prior to analysis. After detecting a significant interaction, we conducted least significant difference (LSD) test to examine differences between pairs of means for starting distance intervals. Using the same data set, we conducted a regression analysis allowing slopes to differ between approach speeds as well as separate regression analyses for each approach speed. Analyses were conducted using Statistica. Significance tests were 2 tailed at  $\alpha = 0.05$ . Effect sizes are presented as  $\eta^2$  for ANOVA and  $r$  or  $R^2$  for regression (Cohen 1992).

## RESULTS

Variances of FID were significantly heterogeneous among intervals of starting distance using the raw data (Levene's  $F_{9,234} = 6.59$ ,  $P < 0.0001$ ). After logarithmic transformation,



**Figure 1**  
FID by *Podarcis lilfordi* approached either slowly or rapidly from 5 intervals of starting distance. Error bars represent 1.0 standard error.

variances were homogeneous (Levene's  $F_{9,234} = 1.92$ ,  $P = 0.05$ ). Using transformed data, ANOVA statistics for the main effects of starting distance and approach speed were  $F_{4,234} = 13.43$ ,  $P < 0.001$ , and  $F_{1,234} = 0.24$ ,  $P > 0.10$ , respectively. These effects cannot be interpreted separately because the interaction between starting distance and approach speed was significant ( $F_{4,234} = 6.74$ ,  $P < 0.0001$ ;  $\eta^2 = 0.08$ ). LSD tests showed that no significant difference in FID occurred among distance intervals at the slower approach speed (Figure 1) but that at the faster approach speed FID was significantly shorter for the shortest distance intervals (Table 1).

Similar results were obtained in a regression analysis conducted using a general linear model that allowed different slopes for each approach speed. In this model, actual starting distance rather than starting distance interval was used as a continuous predictor and approach speed as a categorical predictor. The interaction was stronger than in the previous analysis (starting distance  $\times$  approach speed interaction:  $F_{2,230} = 49.48$ ,  $P < 1.0 \times 10^{-6}$ ; approach speed:  $F_{1,230} = 22.49$ ,  $P = 4.0 \times 10^{-5}$ ; whole-model  $R^2 = 0.51$ ). Addition of a starting distance squared term to the model did not contribute any additional explanatory power ( $R^2 = 0.52$ ). The starting distance  $\times$  approach speed interaction was significant ( $F_{2,228} = 3.66$ ,  $P = 0.027$ ) in the latter analysis. Other terms from the analysis with the squared term were approach speed  $\times$  starting distance squared ( $F_{2,228} = 0.85$ ,  $P = 0.43$ ) and approach

speed ( $F_{1,228} = 1.41$ ,  $P = 0.24$ ). At the slow approach speed, the regression of FID on starting distance was not significant ( $F_{1,98} = 3.15$ ,  $P = 0.08$ ,  $r = 0.20$ ). At the faster speed, the regression was significant ( $F_{1,132} = 97.9$ ,  $P < 1.0 \times 10^{-6}$ ,  $r = 0.65$ ). The relationship was  $FID = 0.085SD + 0.004$ , where SD = starting distance. The intercept did not differ from zero ( $t_{132} = 0.04$ ;  $P = 0.96$ ).

## DISCUSSION

### Effect of starting distance on FID

FID increased as starting distance increased during fast, but not slow, approaches. That addition of a starting distance squared term to the regression added no explanatory power suggests that FID increases linearly with starting distance during rapid approaches. Our findings agree qualitatively with those for *S. virgatus* (Cooper 2005), but the effect of starting distance during fast approach on FID was somewhat stronger in *P. lilfordi*. For *P. lilfordi*, FID for the longest starting distance was 2.75 times that for the shortest starting distance interval, whereas the comparable figure calculated from the regression equation for *S. virgatus* ( $FID = 0.15SD + 1.70$  m, where SD = starting distance, Cooper 2005) was 1.76.

The only other lizards for which the relationship has been studied are *U. ornatus* (Cooper 2005), *Leiocephalus carinatus* (Cooper 2007), and *A. exsanguis* (Cooper 2008a). At slow approach speeds, FID was unrelated to starting distance in all 3 species. FID appeared to increase with increase in starting distance in *A. exsanguis* when all movements initiated during approach were considered to be escape, but the lizards frequently resumed foraging during approaches. Because starting distance was unrelated to FID when apparent foraging movements were excluded, the relationship was considered an artifact of spontaneous foraging movements (Cooper 2008a). That interpretation may have not been entirely justified because some teiids (Anderson 1993), including *A. exsanguis* (Cooper W, personal observation), often move away from slowly approaching observers, starting and stopping repeatedly while maintaining a distance of several meters rather than fleeing rapidly.

No such movements occurred in *P. lilfordi*, which moved during approaches only to escape. Although *P. lilfordi*, like *A. exsanguis*, is an active forager, its percent time moving (PTM) of 35.5 is much lower than that of *A. exsanguis* (PTM = 82.4; W.E.C., unpublished data). Artifactual relationships between starting distance and FID may be largely limited to very active foragers in conditions that favor short pauses between movements and species that forage as they move slowly away from predators. Artifacts may be more likely during slower approaches because the greater duration and shorter FID of slow approaches allow more time for spontaneous movement than is available during fast approaches. High PTM, brief pauses, and slow withdrawal rather than rapid escape by *A. exsanguis* presumably account for the relationship between starting distance and FID detected during slow approaches (Cooper 2008a).

Increase in FID with increase in starting distance has been detected with certainty in only 2 lizards, but they are very distantly related and differ ecologically, one being an ambusher and the other an active forager. Because foraging mode affects defensive behavior in lizards (Vitt and Congdon 1978; Vitt and Price 1982), the relationship may be widespread in lizards. The sole obvious commonality between studies of the 2 species is that the FID  $\times$  starting distance relationship occurred only during fast approaches. No relationship between starting distance and FID has been demonstrated for any lizard species at slow approach speed.

**Table 1**  
FID increased as starting distance increased during rapid approach

	Starting distance (m)			
	6.0–8.9	9.0–11.9	12.0–14.9	15.0–17.9
3.0–5.9 m	0.0075	$2.0 \times 10^{-6}$	$<1.0 \times 10^{-6}$	$<1.0 \times 10^{-6}$
6.0–8.9 m		0.026	$8.9 \times 10^{-5}$	$<1.0 \times 10^{-6}$
9.0–11.9 m			0.072 <sup>a</sup>	$9.7 \times 10^{-5}$
12.0–14.9 m				0.037

*P* values from LSD tests are shown for each pair of starting distance intervals.

<sup>a</sup> Although this 2-tailed *P* value is marginal, the difference in FID between the 9.0–11.9 m and 12.0–14.9 m starting distance intervals is significant using a 1-tailed test that is justified by the directional prediction that FID increases as starting distance increases.

## Dynamic risk assessment

### Starting distance

Relationships between starting distance and FID are more likely to be positive during rapid than slow approach for at least 2 reasons. First, approaches that begin at less than the optimal FID elicit immediate escape (Cooper 2008a), as predicted by the Ydenberg and Dill (1986) model in Blumstein's (2003) zone 1 and by the optimal escape model (Cooper and Frederick 2007a). A prediction (Stankowich T, personal communication) that the slope of FID on starting distance equals 1.0 at such close distances was verified for *A. exsanguis* (Cooper 2008a). Because FID increase with approach speed, the range of distances in which FID increases at a slope of 1.0 with starting distance (zone 1) must be greater for fast approaches.

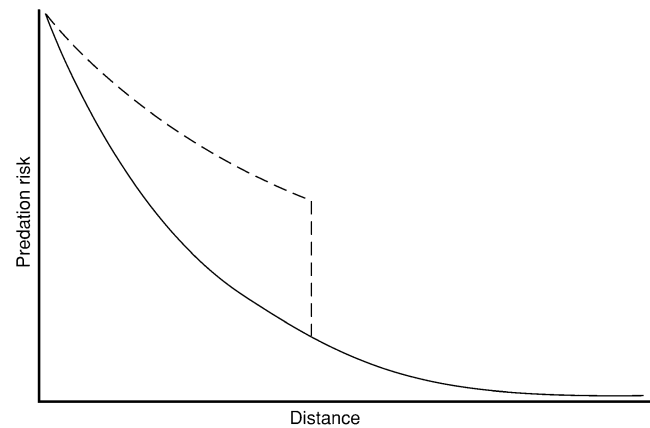
Second, at distances greater than the optimal FID for a given risk curve, prey may interpret continued approach beginning at greater starting distances as evidence that the predator has detected it or is more likely to detect it and attack. Prey may treat prolonged approach as an indicator that a predator is attacking rather than simply moving toward the prey. These interpretations may be more accurate and urgent if the approach is rapid (Cooper 2005; Stankowich and Coss 2006). Such change in assessment or risk during approach would lead to an altered, elevated risk curve and greater optimal FID, causing FID to be greater for approaches begun at greater starting distances. This effect should be greater for fast than slow approaches because FID increases with approach speed, less time being available before a prey is overtaken.

Beyond the findings discussed above for 2 lizards, nothing is known about graded effects of approach speed on the FID  $\times$  starting distance relationship. Additional studies are needed to ascertain if the relationship between FID and starting distance strengthens, as we predict, over a range of approach speeds. Some prey maintain spatial or temporal margins of safety to ensure their ability to escape (Bonenfant and Kramer 1996; Cárdenas et al. 2005; Stankowich and Coss 2006). Such margins should not affect the relationship between FID and starting distance because the margins are fixed for each speed.

### Implications for escape theory

Increase in FID as starting distance increases has important implications for escape theory if the increase indicates continuous change in risk curves during approaches. Theoretical predictions have been confirmed for many risk and cost factors, but current theory was not intended to apply to risk and/or cost curves that change continuously. Because changes in a predator's trajectory toward or away from a prey (Cooper 1997b) and increase in duration of approach (starting distance; Blumstein 2003; Cooper 2005; Stankowich and Coss 2006) affect risk, prey should maximize fitness by updating risk assessment during approaches to account for such changes. Consequently, a single risk curve may not apply throughout the approach as originally portrayed by current models of FID (Ydenberg and Dill 1986; Cooper and Frederick 2007a) and their counterparts for hiding time in refuge (Martín and López 1999; Cooper and Frederick 2007b). Existing models were not intended to exclude the possibility that prey respond to changes in risk during approaches. Escape models can accommodate changes in risk curves and associated FIDs if it is assumed that prey monitoring approaching predators assess changes that alter the relationship between distance from the predator and risk, that is, risk curves (Figure 2).

Current theory is adequate for risk and cost curves that are static during approach. It can also allow shifts among risk and cost curves when warranted by changes in cues to risk occur



**Figure 2**

A fixed curve (solid) relates predation risk to distance between predator and prey as a predator approaches at constant speed and does not otherwise alter its behavior in ways affecting risk. If the approaching predator suddenly accelerates or alters its path to directly approach a prey that it might have passed by, risk increases suddenly, which can be represented by a step-like shift to a higher risk curve (dashed). Because the curve reflecting benefits of not fleeing does not change, optimal FID is greater for the higher risk curve.

during approaches. Much remains to be learned about what features lead to changes in risk and cost curves during approaches and the relevant functional relationships. Cues that may change risk during approaches include change in approach speed, trajectory, and eye contact, all of which involve changes in predator behavior. Associated changes in FID are readily interpreted as switches between risk curves based on rapid change in risk assessment. Rapid changes in environmental conditions affecting detectability and probability of escape might also cause changes between risk curves, and arrival or departure of the prey's prey or conspecifics might alter benefit curves. Such changes may be abrupt, causing rapid shifts between risk curves that could cause relationships between distance and risk or cost to appear to be step functions.

The unusual feature of starting distance is that duration (distance) of approach affects risk assessment without change in predator behavior. Not only does risk increase as a predator approaches but also the level of the entire risk curve is affected by the starting point. Although the relationship between starting distance and FID has been discovered only recently, its occurrence in 3 major vertebrate taxa (Blumstein 2003; Cooper 2005, 2008a; Stankowich and Coss 2006) suggests that it is widespread. Existing theory can explain the relationship if a separate risk curve is associated with each combination of starting distance and speed.

Omniscient prey select a risk curve by noting starting distance and approach speed and calculating the risk relationship. Expecting real prey to do so is unrealistic. The model of Cooper and Frederick (2007a) does not specify how prey assess risk curves and, as an optimality model, is subject to the criticism that prey cannot make the calculations required for optimal decisions. Instead, they may use simple rules of thumb to approximate optimal decisions (Bouskila and Blumstein 1992). For starting distance, prey might use rules of thumb relating approach speed to duration of approach. This view is consistent with findings of studies that emphasize temporal aspects of approach (Cárdenas et al. 2005; Stankowich and Coss 2006).

When FID covaries with starting distance, assessed risk plausibly changes continuously during approach even though the

predator's behavior does not. This contrasts with cases in which changes in predator behavior may lead to at most a few changes between risk curves. Optimal escape theory, with its infinite number of possible risk curves, can account for the relationships among starting distance, approach speed, and FID. However, a model based on actual methods of risk assessment would be more satisfying. In the absence of adequate knowledge of assessment mechanisms, an optimality model suffices to interpret and successfully predict effects of a wide range of risk factors and costs of escape.

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