

Article

Predator–prey distance and latency to flee from an immobile predator: functional relationship and importance

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Abstract

When an immobile prey has detected an immobile predator nearby, predation risk is greater when the predator is closer. Consequently, prey flee with shorter latency as standing distance (predator–prey distance when both are still) decreases. Since it was first reported in 2009, this relationship has been confirmed in the few species studied. However, little is known about the functional relationship between standing distance and latency to flee (LF). We hypothesized that LF increases as standing distance increases at short distances, but reaches a plateau at longer distances where prey can escape reliably if attacked. We simulated immobile predators by moving slowly into positions near striped plateau lizards *Sceloporus virgatus*, stopping and then remaining immobile, and recording LF from the stopping time. LF increased from shorter to longer standing distances in a decelerating manner. The relationship was concave downward, and LF was indistinguishable among the longer standing distance groups. Latency to flee appears to reach a plateau or approach an asymptotic value as standing distance increases. The effect size of standing distance was large, indicating that *S. virgatus* sensitively adjusts LF to the level of risk associated with standing distance. Relationships between risk assessment and theoretical zones associated with risk, its assessment by prey, and escape decisions are discussed. Effect sizes of standing distance were substantial to large in all studies to date, indicating that standing distance is an important predation risk factor when both predator and prey are immobile.

Key words: antipredatory behavior, escape behavior, latency to flee, squamata, standing distance.

For prey exposed to predators, the ability to make escape decisions that maximize their chances of survival is essential (Lima 1998; Lima and Dill 1990). Studies of escape have focused on escape decisions by an immobile prey that monitors an approaching predator and decides how close to let the predator approach before fleeing (Ydenberg and Dill 1986; Cooper and Frederick 2007, 2010; Cooper 2015a). When the prey detects an approaching predator, it should monitor its position and motion to assess risk (Ydenberg and Dill 1986; Cooper 2008a). Other escape scenarios exist, but their associated prey decisions have received scant attention (Cooper 2015a). Monitoring predators is assumed to occur in cost-benefit models in all scenarios (Ydenberg and Dill 1986; Martín et al. 2009;

Cooper 2015a,b). We focus on the scenario in which an immobile prey detects an immobile predator nearby and decides when to flee.

In recent models in which prey and predator are immobile, the prey's latency to flee (LF) is determined by a trade-off between cost of immobility, which increases over time because the predator is increasingly likely to detect and attack, and cost of fleeing, which is primarily loss of opportunities at the prey's location (Cooper et al. 2012; Martín et al. 2009). If no attack occurs, the prey is predicted to base its decision about how long to remain immobile before fleeing in part on the distance separating predator and prey (Martín et al. 2009; Cooper et al. 2012; Cooper and Sherbrooke 2013a).

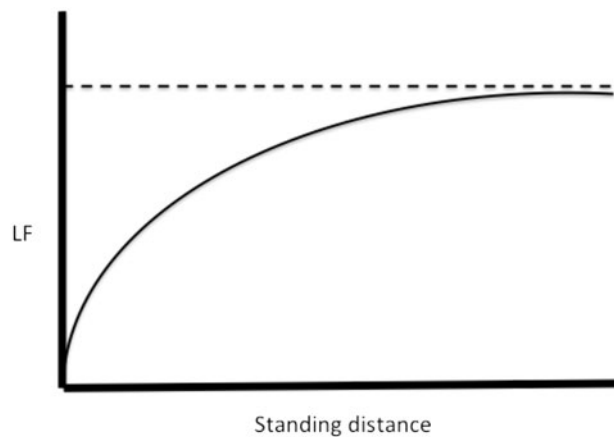


Figure 1. Latency to flee is predicted to increase to an asymptote (dashed line) as standing distance increases. Alternatively, it might increase linearly or by some other function to a fixed maximum and remain constant at longer standing distances.

Standing distance (D) is the distance between immobile predator and prey. Models predict that LF decreases as D decreases because probability of being detected and attacked is greater at a given latency and risk of being captured is greater when a predator is closer (Martín et al. 2009; Cooper et al. 2012; Cooper 2015a). These models are similar to escape models predicting flight initiation distance (FID = predator–prey distance when prey flee from approaching predators; Ydenberg and Dill (1986); Cooper and Frederick, (2007)) Ydenberg and Dill, 1986). The prediction for D has been strongly supported (Martín et al. 2009; Cooper et al. 2012; Cooper and Sherbrooke 2013a), as have prediction that LF decreases as risk from other factors, including speed and directness of approach, repeated approach, and eye contact, increases (Cooper et al. 2012). Nevertheless, our knowledge is limited due to recency of the models. Even the functional relationship between LF and D is unknown.

Unless escape ability changes if detected by the predator or a predator's ability to detect or capture prey changes at certain distances, assessed risk should decrease continuously as D increases. Existing models predict that LF increases monotonically as D increases (Martín et al. 2009; Cooper et al. 2012). Beyond some distance, though, assessed risk is too small for LF to increase further; at sufficiently long distances, prey may not detect or monitor predators. Our new prediction is that LF reaches a maximum or an asymptote at long D s (Figure 1).

This can be understood in light of a modified Ydenberg and Dill (1986) escape model. Blumstein (2003) and Stankowich and Coss (2006) defined d_{\max} as the predator–prey distance beyond which prey do not continuously monitor a predator and may not detect it. At distances closer than d_{\max} , prey monitor approaching predators and assess risk and cost of fleeing (lost opportunities to engage in fitness-enhancing activities). If a predator continues to approach, prey flee at an FID predicted by a criterion that differs between Ydenberg and Dill's (1986) and Cooper and Frederick's (2007, 2010) models.

If a predator is detected closer than a minimum distance, d_{\min} , prey flee immediately (Blumstein 2003; Cooper 2008b). Distance shorter than d_{\min} form zone I, the interval from d_{\min} to d_{\max} is zone II, and $d > d_{\max}$ is zone III (Blumstein 2003; Stankowich and Coss 2006; Cooper 2015a). In zone I, FID increases with d at slope 1.0 (Cooper 2008b); in zone II, prey assess risk and FID is longer for greater risk (Blumstein 2003; Stankowich and Coss 2006; Cooper 2015a). Monotonic increase of FID is predicted in zones I and II by

all models (Ydenberg and Dill 1986; Cooper and Vitt 2002; Cooper and Frederick, 2007), but beyond prey do not flee in zone III.

Similar effects of distance on assessed risk are expected by in LF and FID models (Ydenberg and Dill(1986) for FID, Cooper et al.(2012) for LF). Based on the assumption that prey employ qualitatively similar assessment mechanisms for deciding LF and FID, we predicted that LF increases monotonically to a maximum as D increases, but reaches a maximum and does not increase further at longer distances. The shortest distance at which LF is maximal is analogous to d_{\max} for FID. Because it is uncertain whether a nonzero D exists below which LF is zero, which would correspond to d_{\min} , it is unclear whether distinct zones I and II occur for LF.

For the lizard *Sceloporus virgatus*, we examine the hypothesis that the relationship between D and LF is concave downward and reaches an asymptote or plateau where D is too long for the predator to pose a grave threat should it attack. We review all reported effect sizes of D on LF and augmented the review by calculating an effect size for the lizard *Iberolacerta cyreni* using data from the adults from a previously published study (Martín et al. 2009).

Materials and Methods

Animals, field site, and conditions

S. virgatus is a small (maximum snout-vent length = 71 mm) phrynosomatid lizard (Cooper et al. 2001; Stebbins 2003; Watters 2009, 2010). Like other ambush foraging insectivores, these lizards remain motionless most of the time. Because they are immobile while foraging, moving primarily to capture prey or move between ambush posts, they move infrequently (Cooper et al. 2001). They spend only 0.80 percentage of the time moving (Cooper et al. 2001). Because motion may allow the predator to detect them, lizards may remain immobile to avoid being detected and attacked. These features make *S. virgatus* an excellent species for studies requiring immobility by prey near an immobile predator.

The study of *S. virgatus* was conducted on the east slope of the Chiricahua Mountains in Cochise County, Arizona, USA at elevation 1,700–1,800 m in the Coronado National Forest. Lizards were observed in open areas along creeks and in open woods nearby. At this locality, *S. virgatus* usually occurs on fairly level ground, rocks, logs, and trees, but sometimes occupies other microhabitats such as steep slopes and clumps of grass. We restricted observations to lizards on fairly level ground or flat rocks.

Observations were made in May to early June of 2013 on warm, sunny days at 09:00–15:30 Mountain Standard Time). Lizards had finished post-emergence basking and were active near preferred body temperature. We made focal observations of adults, excluding juveniles. We did not record sex because FID does not differ between sexes of *S. virgatus* (Smith 1996), suggesting that monitoring of predators and risk assessment may be similar in the sexes of this species.

Data collection, design and analysis

A researcher walked slowly until he sighted a lizard, and then moved very slowly (ca. 0.3 m/s) to the desired position at a predetermined D from the lizard specified below, and stopped moving while facing the lizard while in the lizard's field of view. The D s were estimated visually while moving into position, and then were measured at the conclusion of the each trial. To be clearly visible to these lizards, it is important to be to their right or left, not directly in front of or behind them (Cooper 2008b). The investigator remained immobile

until the lizard fled and then recorded LF in seconds. If a lizard did not flee within 600 s after the experimenter stopped, its LF was recorded as 600 s.

Researchers are used widely to simulate predators in studies of economic escape behavior. Predictions of economic escape models (Ydenberg and Dill 1986; Cooper and Frederick 2007) and of latency to emerge from refuge (hiding time) have been confirmed consistently by many studies, showing that prey assess people as posing predation threat (Cooper 2009a). Using a human surrogate predator permits data to be collected rapidly in rough terrain that impedes artificial predator models and avoids the ethical issue of actual predation that might occur using natural predators.

After a focal observation was completed, WEC moved along a transect searching for another lizard. Pseudoreplication was avoided in this way and by observing where the lizard in the previous observation fled. After completion of a transect, the researcher moved to a new location in another part of the study site and began another transect. No transects overlapped, and each transect was traversed only once.

A single factor experiment was used to examine the relationship between D and LF. The experiment had an independent group design in which each lizard was tested only once. Because the form of the relationship between D and LF, not merely detection of an effect of D, was the focus of this study, more and smaller intervals of D were used than in previous studies. The 7 starting distance groups were 1–1.9 m ($n = 11$); 2.0–2.9 m ($n = 10$); 3.0–3.9 m ($n = 10$); 4.0–4.9 m ($n = 10$), 5.0–6.9 m ($n = 9$), 7.0–8.9 m ($n = 9$), and 9.0–15.9 m ($n = 7$). Starting distance, the predator–prey distance when approach begins, does not affect FID at slow approach speed (Cooper and Sherbrooke 2013b; Samia and Blumstein 2013). Because the speed at which the investigator moved to a given D was slower than in studies that found no effect of starting distance on FID in *S. virgatus*, different distances moved to reach Ds presumably did not affect assessed risk once a trial began (Cooper 2005b; Cooper and Sherbrooke 2013a).

We considered using ANOVA with D as the independent variable to analyze the LF data, but the distribution of both raw and logarithmically transformed escape latencies violated the assumption of normality required for parametric ANOVA (Kolmogorov–Smirnov $d = 0.21$, $P < 0.01$ for raw data and $d = 0.19$, $P < 0.05$ for log data). Furthermore, because the data were censored at 600 s, survival analysis is the appropriate statistical approach (Klein and

Moeschberger 2005). The test for a main effect of D on LF was a generalization of Gehan’s generalized Wilcoxon test. Comparisons between pairs of D groups were made using Cox-Mantel tests. The test statistic reported for the Cox-Mantel tests is a z score. Because 21 paired comparisons were possible for the 7 groups, we conducted sequential Bonferroni tests (Wright 1992) to assess significance of the comparisons. Besides tests for grouped Ds, we ran regressions of LF on D using 3 models for censored data: exponential, lognormal, and normal. For each we allowed a maximum of 50 iterations for the estimate to converge within 0.001, but only 14–15 iterations were needed. We also calculated a Spearman rank correlation between LF and D. In studies relating FID to starting distance, a constraint that $FID \leq \text{starting distance}$ causes a small positive correlation between the variables even if starting distance has no biological effect on FID (Dumont et al. 2012). This constraint does not apply to this study because D and LF have different units.

Differences in proportions of prey that did not flee within 600 s among D groups were tested for significance using Fisher exact tests. Because sample sizes for each group were small and 21 paired comparisons between D groups would severely limit the power of the tests, we made selected comparisons using pooled groups of Ds. Raw P values are reported, but significance is based on sequential Bonferroni adjustment (Wright 1992).

Statistical tests were 2-tailed (except χ^2) with $\alpha = 0.05$. Effect sizes are reported as $r_{\text{equivalent}}$ for survival analyses and Fisher exact tests (Rosenthal and Rubin 2003), and ρ for Spearman rank correlation. To obtain an effect size for adult *I. cyreni*, Jose Martín conducted an ANOVA with juveniles excluded from a previously published data set (Martín et al. 2009) and calculated η^2 as the effect size (Cohen 1973).

Results

The LF differed significantly among D groups (Figure 1; $\chi^2 = 43.04$, $df = 6$, $P = 1.1 \times 10^{-7}$) with large effect size ($r_{\text{equivalent}} = 0.59$). Paired comparisons using Cox-Mantel tests revealed many significant differences between D groups (Table 1). The LF was significantly shorter for the 1.0–1.9 m D group than all other groups except the 2.0–2.9 m group and was marginally shorter than for that group (Table 1). The LF was significantly shorter in the 2.0–2.9 m

Table 1. Pattern of significance of differences in latency to flee among pairs of standing distance groups based on Cox-Mantel tests for survival analysis

	2.0–2.9	3.0–3.9	4.0–4.9	5.0–6.9	7.0–8.9	9.0–15
1.0–1.9	3.02 0.0044	4.59 < 1.0×10^{-5} *	4.74 < 1.0×10^{-5} *	4.53 0.00001*	4.53 0.00001*	4.07 0.00005*
2.0–2.9		1.41 0.16	3.23 0.0012*	2.87 0.0041	2.84 0.0046	2.99 0.0028*
3.0–3.9			3.06 0.0022*	2.34 0.019	2.49 0.013	2.66 0.0077
4.0–4.9				0.99 0.32	0.57 0.57	0.12 0.91
5.0–6.9					0.32 0.75	0.89 0.38
7.0–8.9						0.60 0.55

Values shown are z scores in the first line for each comparison and P in the second line. Asterisks indicate p values that are significant using sequential Bonferroni adjustment for the number of tests.

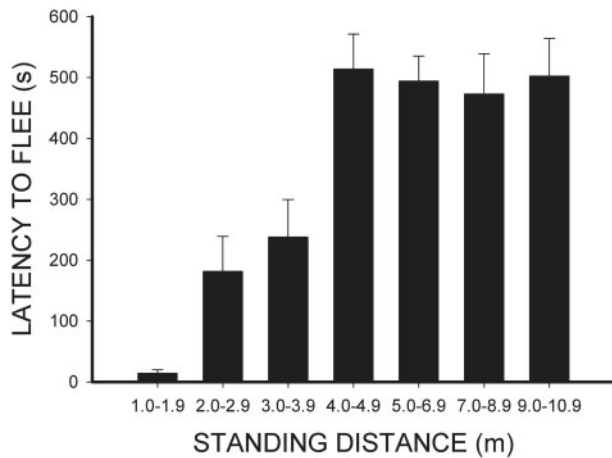


Figure 2. Latency to flee by an immobile *Sceloporus virgatus* increases over a range of standing distances and then reaches a maximum value or approaches an asymptotic value. Error bars represent 1.0 SE.

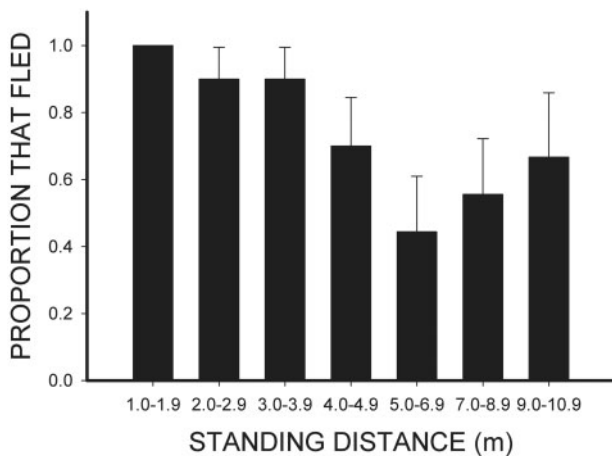


Figure 3. Proportions of individuals of *Sceloporus virgatus* that flee within 600 s. Error bars indicate 1.0 standard error of a proportion.

group than in the 4.0–4.9 m and 9.0–15.9 m groups and marginally shorter than in the 5.6–6.9 m and 7.8–8.9 m groups (Table 1). The LF was significantly shorter in the 3.0–3.9 m than the 4.0–4.9 m group (Table 1). Examination of Table 1 reveals that $P < 0.01$ for several other pairs of groups. Because the sequential Bonferroni test is excessively stringent, the low P values suggest that LF was shorter for the 3.0–3.9 m group than for all longer D groups. None of the differences in LF between pairs of groups from 4.0–4.9 m and longer approached significance.

LF decreased significantly as D decreased (exponential regression: $\chi^2 = 51.18$, $df = 6$, $P < 1.0 \times 10^{-8}$). The effect size was large ($r_{\text{equivalent}} = 0.63$). The regression equation was $LF = -0.18SD + 3.26s$, where SD is D. Lognormal and normal regressions produced identical values of β , similar intercepts (2.73 and 3.26 s), and high levels of significance ($P = 2.6 \times 10^{-7}$ and $P = 1.8 \times 10^{-5}$). LF was positively and significantly correlated with D (Spearman $\rho = 0.76$, $n = 66$, $P < 1.0 \times 10^{-6}$).

The proportion of individuals that fled within 600 s increased as D decreased from 1.00 at the shortest Ds to a mean of 0.59 for the 4 longest D groups (Figure 2). The proportion of individuals that fled was: 1) significantly smaller for the 4 longest D groups pooled

than the 3 shortest groups pooled (Fisher exact test: $P < 0.001$; $r_{\text{equivalent}} = 0.49$) and 2) significantly smaller for the 4.0–4.9 m group than the 3 shortest groups pooled ($P = 0.0002$; $r_{\text{equivalent}} = 0.45$). The proportion that fled in the 4.0–4.9 m D group was marginally greater than in all longer groups pooled ($P = 0.07$, $r_{\text{equivalent}} = 0.25$).

Without Bonferroni adjustment, the proportion of lizards that fled in the shortest D group was significantly greater than in D groups of 4.0–4.9 m or longer (4.0–4.9 m, $P = 0.0010$; 5.0–6.9 m, $P = 0.026$; 7.0–8.9 m, $P = 0.0081$; 9.0–10.9 m, $P = 0.0063$). The proportion that fled in the shortest group did not differ significantly from that of the 2.0–2.9 m or 3.0–3.9 m D group ($P = 1.0$ each). The 2.0–2.9 m and 3.0–3.9 m D groups had significantly larger proportions that fled than the 3.9–4.0 m D group ($P = 0.011$ each).

Discussion

Relationship between D and LF

As predicted, LF increased as D increased and the relationship was concave downward with an apparently decelerating increase in LF as D increased. That LF increased as D increased from 1 to 5 m, but no differences occurred among the 4 longest D groups verifies the hypothesis that LF reaches a plateau or gradually approaches an asymptote at longer Ds where risk is lower. This implies that assessed predation risk decreases rapidly between 1.0 and 4.9 m and then becomes stable. Theory predicts that assessed risk increases as D decreases, which occurs because by a given latency, the predator is more likely to have detected the prey and because when D is shorter, the prey is more likely to be captured when attacked. Nevertheless, some decrease in LF might occur at longer D if prey suppresses movements when predators are nearby. It is assumed that these factors affect assessed risk, but experimental proof that the probability of being captured if attacked increases as D decreases is unavailable.

At shorter Ds than used in this study, assessed risk is expected to increase as D decreases, reaching a maximum when prey and predator are in contact. At $D = 0$ even highly cryptic prey are expected to flee as soon as they come into contact (Broom and Ruxton 2005). This corresponds to a zero intercept of the relationship between LF and D. At 0.5 m/s approach speed, FID for *S. virgatus* is 0.8–1.5 m (Cooper 2009a,b), close to the shortest Ds used in the present study. The LF continues to increase as D increases to about 5 m, then reaches a maximum or approaches an asymptote. This suggests that a predator that remains immobile nearby can induce escape at distances longer than FID for a predator that is approaching slowly. The cumulative effect over time must occur in zone II (Blumstein 2003), that range of distances in which prey assess risk before fleeing. If risk assessment mechanisms are similar for approaching and immobile predators, the maximum distance for which LF increases as D increases might correspond to d_{max} (Blumstein 2003; Stankowich and Coss 2006). Therefore, the distance where LF stops increasing as D increases may be the longest distance at which risk is assessed, which lies at the boundary of zones II and III for approaching predators (Blumstein 2003).

Previous studies of D and FID in *S. virgatus* and *Callisaurus draconoides* did not show that LF increases over a wide range of D. For *S. virgatus* only 2D groups were used (Cooper and Sherbrooke 2013a), making it impossible to tell if LF would approach a plateau. In *C. draconoides*, LF was shorter in the shortest of 4D groups, but did not differ among the other (Cooper and Sherbrooke 2013a). A study of *C. draconoides* using narrower D groups with small gaps

between adjacent groups could establish whether or not LF increases over a range of short Ds and then reaches a plateau.

That proportions of lizards that fled were greatest at the shortest Ds corroborates the finding for LF and shows that mean LF was underestimated. The estimate is accurate for the shortest D group because all individuals fled. The degree of underestimation increases until about 5 m. Because high proportions of individuals did not flee in the longer D groups, LF might continue to increase at longer Ds. This should be examined for trials longer than 600 s. Because similar proportions of individuals fled in the longer D groups, it is unlikely that LF continues to increase at Ds longer than 5 m.

The results support our prediction, but LF might be quadratically related to D, increasing to a maximum and then declining somewhat at longer (unexamined) Ds, as proposed by Stankowich and Coss (2006) for the relationship between FID and starting distance. This seems unlikely given the similar LF values at longer Ds.

At long Ds sufficiently long for risk to be assessed as very low or for a predator to be ignored, movements may occur for foraging or other reason unrelated to the predator. In our study, the proportion that moved at the longest distances may have been more related to foraging or other activities than antipredatory behavior. Effects of D on LF while a predator remains immobile and proportion of individuals are similar. Shorter LF and greater likelihood of fleeing occur at shorter D (Cooper 2010), underscoring the importance of an immobile predator's proximity as a cue to risk.

Importance of D

D had a large effect on LF in *S. virgatus*, larger than those of some major risk factors on FID (Stankowich and Blumstein 2005). The effect size of D on LF ($r_{\text{equivalent}} = 0.59$ for grouped data and $r_{\text{equivalent}} = 0.63$ and $\rho = 0.83$ for ungrouped data using exponential regression and Spearman rank correlation, respectively) was larger for *S. virgatus* than that of some of the most important predation risk factors on FID (directness of approach, distance to refuge) and nearly as large or larger than for others (perch height, habituation to human presence, repeated approach and approach speed) depending on which of the 3 effect sizes reported here is used for comparison (Cooper 2009a,b; Cooper and Avalos 2010).

Large effect suggests that *S. virgatus* adjusts LF precisely over D between 1.0 and 4.9 m, fleeing sooner when greater risk is implied by shorter D. In another study of *S. virgatus* effect size was $\eta^2 = 0.60$ ($r \approx 0.77$; Cooper and Sherbrooke 2013a), slightly larger than that from the survival analysis, but very close to that in our nonparametric correlation. A likely reason for this pattern is that the present study included more starting distance groups, and no difference occurred among the longest groups.

Effect sizes of D are substantial to large (η^2 was 0.46–0.78) in other phrynosomatids (*C. draconoides*, *S. jarrovi* and *Urosaurus ornatus*; Cooper and Sherbrooke 2013a) and in lacertids were $\eta^2 = 0.60$ for *Podarcis lilfordi* (Cooper et al. 2012) and $\eta^2 = 0.33$ in our new analysis for adults only for *I. cyreni* (Martín et al. 2009). Findings suggest that D strongly affects LF in most lizards, and is somewhat important in all species studied. Further study is needed to assess the validity of the D model (Cooper et al. 2012) for taxa other than lizards and to examine reasons for variation in effect sizes among lizard taxa.

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