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Original Article

Latency to flee from an immobile predator: effects of predation risk and cost of immobility for the prey

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When a predator is immobile near an immobile prey, the probability that the predator will detect and attack increases over time. The prey's cost of moving, thereby abandoning crypsis due to immobility, therefore decreases. Cost of not moving increases over time if movement is required for prey to conduct fitness-enhancing activities. We tested a cost-benefit model that predicts effects of factors that affect predation risk and cost of not moving on a prey's latency to flee. Acting as simulated predators, we conducted experiments on the lizards *Iberolacerta cyreni* and *Podarcis lilfordi*. All predictions for 5 risk factors and a cost of moving factor were verified. Lizards fled sooner when the predator stood closer, approached rapidly rather than slowly before stopping, approached directly rather than indirectly, and gazed at the lizard rather than away from it, and after the second of 2 successive approaches. Latency to move was shorter in the presence than absence of a mealworm, suggesting the importance of opportunity cost of immobility. The effect of standing distance has 2 components, greater rate of detection by the predator and greater risk of being captured if detected at shorter distances. Escape theory has been highly successful in predicting how close a prey allows a predator to approach before fleeing. Our model extends an economic approach to study of escape decisions in response to an immobile predator that may be an ambush forager or an active forager that has stopped moving nearby. *Key words*: ambush, escape, latency to flee, opportunity cost, predation risk, standing distance. [*Behav Ecol*]

INTRODUCTION

During encounters with predators, prey must assess the degree of predation risk and cost of antipredatory behaviors and use the assessments to make crucial escape decisions. Several models of escape behavior (Ydenberg and Dill 1986; Stankowich and Blumstein 2005; Cooper and Frederick 2007) apply when a prey that has detected an approaching predator monitors the predator's approach prior to reaching a decision to flee (Blumstein 2003; Stankowich and Coss 2006; Cooper 2010). Such models do not apply when an immobile prey detects an immobile predator. However, this must occur frequently, either when a prey moves toward the predator and stops before detecting it or on detecting it or when an approaching predator stops moving before coming close enough to elicit escape.

When a prey has detected an immobile predator, the prey may remain immobile or move away from the predator. By remaining immobile, the prey may reduce the likelihood of being detected at a given instant, but the longer it remains immobile, the greater is the likelihood that the predator will detect it. Martín et al. (2009) presented a graphical model of this scenario that predicts that fleeing time (= latency to flee,

Table 1) decreases as the probability that the predator will detect and attack the prey increases. In their model, the cost of fleeing is represented by an increase in the probability of being attacked after being detected as a consequence of moving. Because the probability that the predator will detect an immobile prey increases as time increases, this cost of fleeing decreases over time. The model predicts that latency to flee is shorter when the probability of being detected at a given moment is greater. As predicted, latency to flee was shorter when risk was greater, as implied by fast, direct previous approach as opposed to slow, indirect previous approach (Martín et al. 2009). Because the high- and low-risk situations differed in several respects (i.e., in the high-risk situation, the predator moved before the lizard fled and chased the lizard into refuge, and the lizard entered refuge and emerged before its latency to flee was measured (Martín et al. 2009), the effects of individual risk factors remain uninvestigated.

A graphical model by Ydenberg and Dill (1986) and an optimality model by Cooper and Frederick (2007, 2010) predict that flight initiation distance (distance between predator and prey when the prey begins to flee), increases as predation risk increases and decreases as cost of fleeing, primarily cost of opportunity lost by escaping, increases. Predictions of these cost-benefit models of escape behavior are strongly supported by a large body of research conducted in the past 25 years.

Here, we develop and test a model of latency to flee or otherwise abandon immobile crypsis that is restricted to intervals during which neither prey nor predator moves and which

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Received 13 September 2011; revised 15 February 2012; accepted 17 February 2012.

Table 1
Terms for model and empirical variables used in this study

Cost of fleeing	expected loss of fitness incurred by escape movement that attract a predator's attention. The longer the time since predator and prey became immobile, the greater is the likelihood that the predator will detect the prey. Therefore, the cost of fleeing decreases as time increases.
Cost of immobility	expected loss of fitness due to loss of opportunity to engage in fitness-enhancing activities while remaining immobile.
Cost of moving	expected loss of fitness incurred by nonescape movements that attract a predator's attention.
Latency to flee (move)	time elapsed after a predator is detected immobile near the prey before the prey flees (moves).
Latency to hide	time elapsed between adoption of immobility by a predator and refuge entry by a prey.
Opportunity cost of immobility	fitness lost to prey by failing to engage in a fitness-enhancing activity.
Predation risk factor	in this study, a variable factor whose level affects risk of being detected, attacked, and captured for a prey that is immobile near an immobile predator.
Predator persistence	the degree to which a predator continues to hunt the prey as indicated in this case by a first or second attack in a sequence of 2. Prey may assess that a predator that attacks a second time poses a greater threat than implied by the first attack and may adjust antipredatory responses accordingly.
Standing distance	distance between and immobile prey and an immobile predator.

incorporates opportunity cost of not moving as well as cost associated with factors affecting predation risk. As stated by [Martín et al. \(2009\)](#), risk of being detected increases as time increases while the prey and a nearby predator stay immobile. At a given detection rate, the cumulative probability of being detected while remaining immobile increases over time. Therefore, the cost of moving (i.e., the remaining benefit of immobility) decreases as time spent immobile increases. After a given duration of immobility, cost of moving is lower when predation risk is higher because the increase in risk attributable to motion is lower than when risk of being detected is lower prior to movement. Flight initiation distance decreases as cost of fleeing increases due to loss of feeding ([Cooper 1999](#); [Cooper et al. 2003, 2006](#); [Cooper and Pérez-Mellado 2004](#)) or social opportunities ([Cooper 2000a, 2009a](#); [Cooper and Wilson 2007a](#)). When an immobile prey must forgo feeding, courtship or other profitable activity to remain cryptic, cost of remaining immobile increases as time spent motionless increases because the prey's food becomes more likely to escape and social opportunities may become unavailable. Therefore, latency to flee, thereby abandoning crypsis due to immobility, is predicted to decrease as cost of remaining immobile increases.

The relationships among risks, costs, and latency to flee or move can be portrayed in a graphical model (Figure 1) similar to that of [Ydenberg and Dill \(1986\)](#) for flight initiation distance. The horizontal axis is time elapsed since immobility has begun. The cost of fleeing (moving) due to increased probability of being detected, attacked, and killed due to moving decreases as latency to flee increases. The cost of remaining immobile increases as time increases. The prey is predicted to remain immobile as long as cost of moving is greater than cost of remaining immobile. The prey should flee (move) when cost of remaining immobile becomes greater than cost of moving. When the costs are equal, a brief unstable equilibrium occurs. The predicted latency to flee occurs at the la-

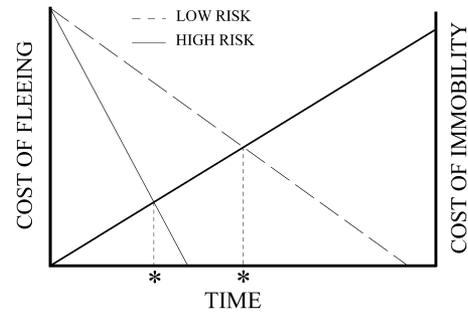


Figure 1

The predicted latency to flee is the time when cost of fleeing (narrower lines) and cost of remaining immobile (thicker line) are equal, that is, the time since immobility of predator and prey began when the cost lines intersect. A higher risk curve intersects the cost of immobility curve after a shorter time than does a lower risk curve. Therefore, the model predicts shorter latency to flee (or abandon crypsis by moving) when risk is greater. Similarly, the higher of 2 cost of immobility lines intersects a single cost of fleeing line after a shorter time, predicting shorter latency to flee or move.

tency corresponding to the intersection of cost of moving and cost of remaining immobile curves (Figure 1).

Our model differs from that of [Ydenberg and Dill \(1986\)](#) in that it predicts latency to flee rather than flight initiation distance and that higher risk corresponds to shorter latency to flee rather than longer flight initiation distance. The vertical axes of our model, which portray cost of fleeing and cost of immobility, are shown on opposite sides from related axes in the [Ydenberg and Dill](#) model. However, the models are structurally similar and both assume that the predicted behavior occurs when the cost of fleeing is equal to the cost of not fleeing. Both models assume that the prey monitors the predator throughout the encounter. Our model, if successful, will have similar advantages and drawbacks to the [Ydenberg and Dill](#) model, but only our model predicts the optimal flight initiation distance, that is, the flight initiation distance at which fitness is maximized. In the [Ydenberg and Dill](#) model, the prey can do not better than break even, that is, not gain or lose fitness. In the optimality model, prey can often increase their fitness. The main advantage of both models is the ability to make accurate qualitative predictions about the relative magnitudes of flight initiation distance under different levels of risk and cost factors. The main flaws of the [Ydenberg and Dill \(1986\)](#) model are that escape decisions are suboptimal even if qualitatively correct and may be qualitatively incorrect, especially if fitness gained from a current opportunity is larger than the cost of being killed ([Cooper and Frederick 2007, 2010](#)).

Many factors that affect the prey's assessment of risk alter the slopes of the cost of moving curve. For example, prey may assess greater risk when a predator stands closer to than farther from the prey. Due to the greater probability of being detected, the cost of moving curve will be lower at any given time when the predator stands closer. Furthermore, the risk of being captured if attacked will be greater when the predator stands closer. Therefore, the cost of moving curve will intersect the cost of immobility curve at a shorter time than when the predator stands farther from the prey (Figure 1). Similarly, if food is present, the cost of immobility will be higher at any time than when food is absent, and the cost of remaining immobile curve will intersect the cost of moving curve sooner than when food is absent. Similar considerations apply to various risk factors and costs of immobility. In general, latency to flee (move) is predicted to be longer when cost of moving is higher than when it is lower and shorter when cost of remaining immobile is higher than when it is lower.

We conducted field experiments in which human investigators simulated predators of 2 species of lacertid lizards, *Iberolacerta cyreni* and *Podarcis lilfordi*, to test predictions of the economic model of latency to flee. Cost of moving decreases as degree of predation risk increases because the probability of being detected and attacked is increased less by moving when risk already high. Therefore, we predicted that latency to flee decreases as predation risk increases for the risk factors standing distance, predator approach speed, directness of approach, predator persistence (first vs. second attacks), and eye contact. Previous studies of flight initiation distance show that assessed risk is greater for faster than slower approaches, direct than indirect approaches, and the second of 2 successive approaches (reviewed by Stankowich and Blumstein (2005)). We also predicted shorter latency to flee when the predator's gaze is directed toward rather than away from the prey because risk of being detected and attacked is greater then, reducing cost of moving. We also predicted that latency to move decreases as the cost of remaining immobile, as represented by forgoing a feeding opportunity, increases.

MATERIALS AND METHODS

Study site and predators

The study of *P. lilfordi* was conducted on the islet of Aire off the coast of Menorca, Balearic Islands, Spain in late June 2010 in sunny conditions when lizards were fully active. Patches of open ground were interspersed with sparse vegetation. Low bushes, rocks, and holes at the base of a stone fence provided refuges. Data collection was facilitated by the very high population density of *P. lilfordi* (Pérez-Mellado and Corti 1993). Although Aire has had no permanent residents since 1930s, biologists, lighthouse personnel, and boaters visit it. Mammalian and ophidian predators are absent from Aire (Pérez-Mellado 1989), where birds are the main predators. Kestrels (*Falco tinnunculus*) are predators of lizards in southern Europe (Cramp and Simmons 1980). On some Menorcan islets, especially where they breed, kestrels are major predators on *P. lilfordi*. Kestrels frequently visit Aire but have not bred there in recent years. Seagulls (*Larus cachinnans*) are present on Aire, but seagulls rarely eat lizards (Cramp and Simmons 1983). *Larus cachinnans* is not known to eat *P. lilfordi* in Cabrera (Araújo et al. 1977) or *P. atrata* in the Columbretes Islands (Catalá et al. 1990; Gomez 1991). Shrikes (*Lanius* spp.), which are important predators of lizards, occur on Menorca and some of its islets. They may occasionally visit Aire.

The experiments on *I. cyreni* were conducted in early mid-July 2010 in the Guadarrama Mountains, Madrid Province, Spain at Alto de Telegrafo at an elevation of 1900 m. At the study site, granitic rocks and shrubs (*Juniperus communis* and *Cytisus oromediterraneus*) on otherwise open ground or grassy meadows provided refuges for lizards. Data were collected on sunny days between 0900 and 1300 h, times when lizards are fully active. Snakes, birds, and mammals are the major predators of *I. cyreni*. Two snakes occur at the study site, *Vipera latastei* and *Coronella austriaca*, the latter a specialist on lizard prey (Rugiero et al. 1995). Avian predators of lizards at the site include several raptors (booted eagles, *Hieraaetus pennatus*; buzzards; *Buteo buteo*; kestrels, *F. tinnunculus*), shrikes (*Lanius meridionalis*), crows (*Corvus corax*), and rock thrushes (*Monticola saxatilis*) (Martín 1990; Salvador and Veiga 2003). Mammalian predators include weasels (*Mustela nivalis*), snow voles (*Chionomys nivalis*), and perhaps foxes (*Vulpes vulpes*) (López et al. 2003).

Data collection, design, and analysis

We served as simulated predators in all the studies by moving toward a lizard, stopping, and then standing still until the lizard

moved. Human beings are not natural predators of *P. lilfordi* or *I. cyreni*, but biologists and amateur collectors have captured and removed many lizards from their natural habitats. Using human researchers as simulated, predators has been very effective in studies of escape behavior in diverse prey (reviewed by Stankowich and Blumstein 2005), including fish (Grant and Noakes 1987), frogs (Cooper et al. 2009a, 2009b), lizards (e.g., Cooper 2000b; Martín et al. 2003; Cooper and Wilson 2007b), birds (Blumstein 2003; Cárdenas et al. 2005), mammals (Blumstein and Pelletier 2005; Stankowich and Coss 2006), and arthropods (Hemmi 2005; Cooper 2006).

Data can be collected efficiently because humans can traverse rough terrain much better than inanimate predator models can. Another advantage is that actual predation can be avoided more easily than in studies using natural predators. A possible disadvantage is that responses to people might not have antipredatory motivation. However, many studies of lizards, most using human beings as model predators, have validated predictions of escape theory about flight initiation distance for various predation risk (cost of not fleeing) factors and cost of fleeing (e.g., reviewed by Stankowich and Blumstein 2005; Cooper et al. 2006; Cooper and Whiting 2007). Predator-specific responses might occur in *P. lilfordi* and *I. cyreni*, as they do in chameleons (Stuart-Fox et al. 2006). However, recent tests of *Sceloporus virgatus*, a lizard similar to our study species in being largely terrestrial, revealed no qualitative differences in responses to approaching people and models of snakes and birds (Cooper 2008).

Experimenter bias is a potential problem whenever an experimenter is aware of hypotheses being tested and experimental designs. To reduce or eliminate experimenter bias, we used standardized methods. We practiced approach speeds to maintain consistency among trials and attempted to use the same gait in all approaches. For each experiment, the treatment or condition order was chosen before any data were collected to preclude any unconscious selection of treatments to favor predicted outcomes.

Except as noted below, the investigator approached a lizard directly (on a straight line) using a slow practiced approach speed (0.5–0.6 m/s). Before beginning to approach, the investigator moved very slowly. After detecting a lizard, he moved to a position directly facing the lizard and stopped moving briefly before beginning to approach. Starting distance, the distance between predator and prey when the approach begins, affects flight initiation distance in *P. lilfordi* during fast, but not slow, approaches (Cooper et al. 2009c). Pseudoreplication was avoided by moving to a new location after testing an individual and not returning to the same area during the course of a particular experiment.

For each trial, the investigator recorded the latency to flee (s) (or move it toward a mealworm), beginning as soon as the investigator became immobile after approaching to the standing distance and ending when the lizard moved. Movements unrelated to escape were excluded from analyses, with the exception of movements to attack mealworms or control stimuli in the experiment on cost of immobility. Postural adjustments and short (<0.1 m) and very slow movements toward mealworms or prior to clear cut escape were excluded. The latter occurred in 2 trials immediately before more rapid escape movements. Only movements toward or into refuges were included. In a study of the effect of standing distance in *P. lilfordi*, the investigator stopped at 1 of 3 distances from the lizard: 1–3 m, 4–6 m, or 8–10 m. Each lizard was tested once in an independent groups design.

Iberolacerta cyreni was tested in the remaining studies. A factorial design with independent groups for both factors was used to investigate effects of predator approach speed and standing distance. Approach speeds were slow (0.5–0.6 m/s) and fast

(1.7–1.9 m/s); standing distances were 2 m and 3.5–4.0 m). Starting distance was 7–10 m, eliminating starting distance as a likely source of variation in latency to flee (Cooper et al. 2009c). Approach speeds were alternated, but standing distances were selected haphazardly, resulting in sample sizes of 10 for each speed at the shorter standing distance and of 13 for each speed at the longer standing distance. When a standing distance had been selected, data for both approach speeds were collected at that distance before the next standing distance was selected.

In the study of the effect of directness of approach by the predator on latency to flee, an independent groups design was used. The investigator approached slowly and stopped moving 2 m from the lizard. To approach indirectly, the investigator walked on a straight line that came no closer than 2 m from the lizard and then stopped moving when closest to the lizard. While approaching and after stopping, the investigator looked directly at the lizard.

To study the effect of predator persistence on latency to flee, we used slow, direct approaches, and stopped moving 2.5–3.5 m from the lizard. After the first latency to flee was recorded, the experimenter withdrew to permit approach from the same starting distance used in the previous trial. Then the investigator approached the same lizard a second time in the same way.

In the study of the effect of eye contact by an immobile predator on latency to flee, the investigator gazed directly at the lizard while approaching slowly and directly and stopped 2 m from the lizard. While standing still, the investigator gazed directly at the lizard in the eye contact group or looked above and approximately 30° to the right of the lizard in the no eye contact group. Trials were alternated between groups using an independent groups design.

The effect of presence of food on latency to move was studied for 31 individuals; in additional trials the investigators also recorded 2 other variables for 15 other lizards, the latency to hide (s), that is, the time between the predator's stopping and refuge entry and whether or not the lizard attacked the stimulus presented by the investigator. Approaches were slow and direct, standing distance was 1.5–2.5 m. Upon stopping, the investigator introduced a mealworm (larva of *Tenebrio molitor*) or a similarly sized stick tethered by a 0.5-m string of number 1 cotton suture to a 1.5-m rod. The mealworm was slowly moved to a position 0.5 m from a lizard to its right or left side in clear view on the rock or ground substrate. Distance between the investigator and the mealworm was the same as the standing distance. After placing the mealworm, the investigator stood motionless. Mealworms moved very little but did make some small movements. Some lizards bit mealworms, but no lizard was able to eat one due to interference by the tether. A trial was terminated after 120 s or when a lizard entered refuge. If a lizard failed to move in 120 s following introduction of the mealworm and adoption of immobility by the investigator, the trial was terminated and latency was recorded as 120 s. Each lizard was tested twice, once in the mealworm condition and once in the control condition. The order of conditions was counterbalanced among lizards.

Analyses for latency to flee and latency to hide were performed using analysis of variance (ANOVA) for a single-factor experiment with an independent groups design for the studies of effects of standing distance in *P. lilfordi* and of directness of approach and eye contact in *I. cyreni*. ANOVA for a factorial design with independent groups for both factors was used in the study of joint effects of approach speed and standing distance. Repeated measures ANOVAs were used to study the effects of repeated approaches and presence/absence of mealworms. The raw data of some data sets failed to meet the assumption of homogeneity of variance using Levene's tests. When this occurred, the analyses were performed using

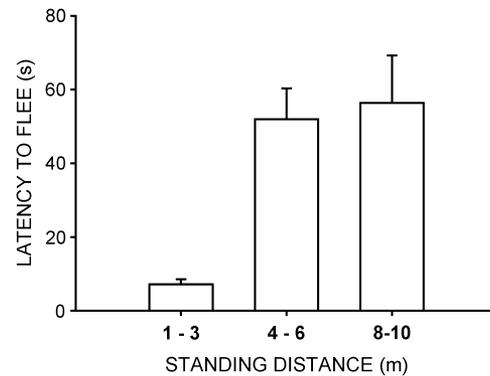


Figure 2

Latency to flee by *Podarcis lilfordi* for 3 standing distances ($n = 18$ each). Error bars represent 1.0 standard error.

transformations that removed heterogeneity of variance. These transformations were logarithmic for the study of effects standing distance, of standing distance and approach speed, and of directness of approach. Because logarithmic transformation failed to remove heterogeneity for the data on effect of eye contact, rank data were analyzed. Raw data met the assumption of homogeneity of variance in studies of effects of repeated approach and presence of food. Multiple comparisons in the study of effects of standing distance were made using Tukey's tests. The difference in frequency of attack between mealworm and control conditions was tested for significance using a Fisher exact probability test. Effect sizes are presented as η^2 for analyses of variance (Cohen 1992). Significance tests are two-tailed, with $\alpha = 0.05$.

RESULTS

Podarcis lilfordi

Latency to flee differed significantly among standing distances (Figure 2, logarithmically transformed data; $F_{2,34} = 29.28$; $P < 1.0 \times 10^{-6}$). The effect size was large ($\eta^2 = 0.63$). Latency to flee was significantly shorter at the 1–3 m standing distance than at either the 4–6 m or 8–10 m standing distance (Tukey's tests; $P < 0.001$ each). The mean difference in latency to flee did not differ significantly between the 2 longer standing distances ($P > 0.10$).

Iberolacerta cyreni

Risk factors

The experimenter's approach speed prior to standing still significantly affected latency to flee (logarithmically transformed data; $F_{1,42} = 43.55$; $P < 1.0 \times 10^{-6}$, Figure 3), latency being shorter at the faster approach speed. Latency to flee was significantly shorter at the closer than longer standing distance ($F_{1,42} = 26.06$; $P = 8.0 \times 10^{-6}$, Figure 3). The interaction between approach speed and standing distance was not significant ($F_{1,42} = 2.02$; $P = 0.162$, Figure 3). Effect sizes were $\eta^2 = 0.39$ for approach speed and $\eta^2 = 0.23$ for standing distance.

Latency to flee was significantly shorter when the experimenter approached directly (22.1 ± 2.8 s) rather than indirectly (105.4 ± 25.2 s) before standing still 2 m from a lizard (logarithmically transformed data; $F_{1,48} = 34.31$; $P < 1.0 \times 10^{-6}$). The effect size was intermediate ($\eta^2 = 0.43$).

When the experimenter stopped moving 2.5–3.5 m from the lizard, latency was significantly shorter after the second (41.7 ± 13.7 s) than after the first (69.0 ± 11.2) of 2 successive approaches ($F_{1,22} = 8.20$; $P = 0.009$). The effect size was $\eta^2 = 0.27$.

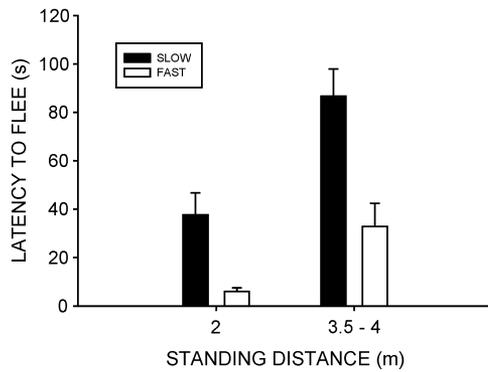


Figure 3

Latency to flee by *Iberolacerta cyreni* varied with standing distance and approach speed. Sample sizes were 10 at each approach speed at the shorter standing distance and 13 at each approach speed at the longer standing distance. Error bars represent 1.0 standard error.

When an experimenter stood still 2 m from a lizard, latency to flee was significantly shorter when the predator maintained eye contact with the lizard (79.2 ± 6.6 s) than when the experimenter did not maintain eye contact (138.6 ± 16.4 s) (rank data; $F_{1,42} = 5.56$; $P = 0.023$). The effect size was small ($\eta^2 = 0.12$). An alternative nonparametric analysis yielded similar results (Kruskal–Wallis ANOVA, $X^2_1 = 5.82$; $P = 0.016$).

Cost of remaining still

Lizards moved before 120 s had elapsed in all but one trial in the control (stick) condition. In some trials, a lizard fled toward or directly into refuge, whereas in others it attacked the mealworm or stick. The attention of lizards was attracted by movement of both the stick and the mealworm during placement and occasionally by small movements of mealworms after placement. It appeared that lizards were more persistent in attacks on mealworms than sticks; attacks on sticks were terminated very quickly upon contact. Lizards moved significantly sooner when a mealworm was present than in the control condition (logarithmically transformed data; $F_{1,30} = 14.90$; $P = 0.0056$; Figure 4). The effect size was $\eta^2 = 0.27$. In addition, latency to hide was significantly longer in the mealworm condition than in the control condition ($F_{1,14} = 30.69$; $P = 0.000073$; Figure 4). The effect size for latency to hide was large ($\eta^2 = 0.69$). The frequency of attack did not differ significantly between the mealworm (9 of 15) and control (6 of 15) conditions (Fisher $P = 0.45$).

DISCUSSION

All findings conform to the model's predictions, including effects of 5 factors that affect cost of fleeing on latency to flee and of the cost of remaining immobile during a foraging opportunity on latency to abandon crypsis by moving. The model's success shows that cost-benefit considerations affect decisions to remain immobile, implying tradeoffs between risk and benefits. It extends the utility of economic analysis of escape behavior, which has been used to explain variation in responses while a prey monitors an approaching predator, to the decision by an immobile prey to flee from a predator that is immobile nearby. Economic risk assessment and tradeoffs apply to a wide range of escape decisions, having been demonstrated extensively for flight initiation distance and time spent hiding in refuge before emerging, to a lesser extent for distance fled and probability of entering a refuge, and now for latency to flee (fleeing time).

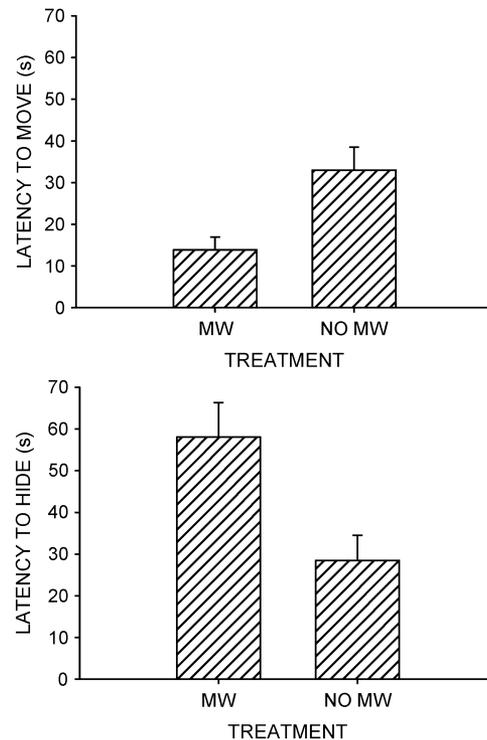


Figure 4

Latencies to move (upper) and hide (lower) by *Iberolacerta cyreni* in the presence and absence of a mealworm ($n = 31$ each for movement, 15 each for hiding). Error bars represent 1.0 standard error.

Standing distance

In both *P. lilfordi* and *I. cyreni*, latency to flee increased as the distance between the immobile prey and predator increased. Latency to flee was much longer at the longer standing distances (7–8 times for *P. lilfordi*, 2–5 times for *I. cyreni*) than when the predator stood very close to the lizard, suggesting that the joint risk of being detected after a given period of immobility and risk of being captured if attacked increase sharply at short standing distances. Alternatively stated, the value of crypsis due to immobility decreases more rapidly at shorter than longer standing distance. Prey are expected to flee immediately upon detecting an approaching predator closer than the optimal flight initiation distance (Blumstein 2003; Stankowich and Coss 2006; Cooper and Frederick 2010), but the relationship between optimal flight initiation distance and effects of standing distance is unknown. When an immobile predator is nearby, it is increasingly likely to detect and attack the prey as time passes. The closer it stands, the more likely is the prey to be detected and the greater its risk of being captured if attacked. The shortest standing distance in the present study is shorter than the actual flight initiation distance of *P. lilfordi* on Aire in many circumstances, especially those implying high risk (Cooper et al. 2009d, 2009e).

The finding that latency to flee in *P. lilfordi* did not differ between the 2 longer standing distances agrees with data for an ambush-foraging lizard, *S. virgatus*, in which no difference in latency to flee occurred at standing distances of 4–12 m (Cooper 2011), much longer than the typical flight initiation distance (Smith 1996; Cooper 2009b; Cooper and Avalos 2010). Latency to flee increased rapidly from the shortest to the intermediate standing distance but increased much less and nonsignificantly from the intermediate to the longest standing distance, suggesting that latency to flee increases at

a decreasing rate as standing distance increases. This applies only at distances short enough for prey to react by immobility and later by fleeing. Based on a projection from 3 standing distances, little increase in latency to flee may occur at standing distances not much longer than typical flight initiation distance.

When an immobile predator is beyond the optimal flight initiation distance for a moving predator, it is possible that standing distance does not affect or has a small effect on latency to flee in ambush foragers, which move infrequently. However, active foragers, including the 2 lacertids that we studied, spend a larger proportion of the time moving and move more frequently than ambush foragers (Perry 1999; Cooper 2005, 2007). For such species, cost of not moving may be greater than for ambush foragers, which can continue to search for prey visually while remaining immobile. We predict that latency to move is shorter for active foragers.

The effects of standing distance were as anticipated in the present study, but latency to flee need not always be shorter when predators stand closer. For closer predators, the probability of detecting the prey is greater at a given time, but so is the probability of capturing the prey once it has been detected. If the probability of capture upon being detected is sufficiently larger for a closer predator, prey might maintain crypsis longer. The latter effect would reduce the difference in latency to flee between shorter and longer standing distances. If sufficiently large, it might outweigh the other effects, reversing the prediction based on them.

Other predation risk factors

The shorter latency to flee by *I. cyreni* after fast than slow approaches supports the prediction that latency to flee decreases as cost of moving decreases (predation risk increases). Predator approach speed is a major risk factor that strongly affects flight initiation distance in diverse prey (Stankowich and Blumstein 2005), including lizards (Burger and Gochfeld 1990; Cooper 2003a, 2003b). Many of these factors have been studied and have the predicted effects in *P. lilfordi* (Cooper 2003a, 2003b; Cooper et al. 2009d, 2009e). The findings for *I. cyreni* show that assessment of risk associated with a predator's initial approach speed affects escape decisions even after the predator has stopped moving. The substantial effect size of approach speed and 2- to 6-fold decrease in latency to flee between slow and fast approaches show that approach speed is an important cue to risk when both prey and predator are subsequently immobile.

Higher probability of being captured if attacked by a faster than slower predator is expected to decrease latency to flee for a faster predator if risk of being detected is identical for fast and slow predators. Other factors associated with rapid approach may affect the rate of detection of immobile prey. If a faster predator searches more intently, latency to flee is predicted to be shorter because the probability of being detected after any time immobile is greater for the faster than slower predator. This may occur if a predator that approaches rapidly is more likely than one that approaches slowly to be hunting or to have detected the prey before or during the approach but does not know its exact position when it stops approaching. Any or all these relationships may account for the observed effect of approach speed.

The directness of approach by a predator and predator persistence also affected latency to flee, which was about 5 times longer for indirect than direct approaches and nearly twice as long for the first than for the second of 2 consecutive approaches. Risk associated with these variables also affects flight initiation distance, which increases as risk increases (Burger and Gochfeld 1990; Cooper 1997, 2003a, 2003b, 2009b).

Directness of approach and predator persistence may affect assessment of the probability that the predator has or will detect the prey during the period of immobility by the predator.

Eye contact with the predator while the predator was immobile induced a shortened latency to flee, which was about 1.75 times longer when the predator did not look directly at the prey. Despite the substantial mean reduction in latency to flee, the effect size was small due to greater variability in the group without eye contact than with eye contact. In numerous studies of effects of directness of approach on flight initiation distance in lizards and perhaps other taxa, effects of directness of approach and directness of gaze are confounded because gaze is direct during direct approaches and indirect during indirect approaches. Thus, reported effects of directness of approach on flight initiation distance and latency to flee may in part be consequences of differences in directness of the predator's gaze. However, directness of approach consistently affects flight initiation distance, whereas directness of gaze does not, suggesting that directness of approach per se is an important factor used to assess risk. In the current study, the effect size of directness of approach was 3.6 times larger than that of eye contact. Nevertheless, some prey respond to features of predator's eyes, and this effect is not dependent on directness of gaze during approach (Burger and Gochfeld 1981).

Effects of gaze were variable in previous studies. Predator orientation did not affect flight initiation distance of bicolor damselfish, *Pomacentrus partitus* (Helfman and Winkelman 1997). In Columbian black-tailed deer, *Odocoileus hemionus columbianus*, the main effect of predator gaze was not significant, but the effect of an investigator's gaze differed between sexes (Stankowich and Coss 2006). Given the very long starting distances, it may have been difficult for deer to distinguish between direct and indirect gazes. In the lizard *S. virgatus*, directness of predator gaze did not affect flight initiation distance when the predator approached indirectly, that is, on a straight path that came no closer than 1 m from the lizard at its closest point (tangent) to the lizard. The variability of effects of eye contact/directness of gaze on aspects of escape indicate that some prey assess risk as being greater when the predator stares at them than when the predator looks elsewhere. More detailed studies are needed to evaluate circumstances in which directness of gaze is used as a cue to risk.

Opportunity cost and latencies to move and hide

In the study of effect of mealworm presence, we refer to latency to move rather than latency to flee because lizards in the mealworm condition did not flee from the investigator but instead abandoned crypsis associated with immobility to approach mealworms. Latency to move when a mealworm was present was less than half that in the absence of a mealworm, verifying the prediction that latency until abandonment of crypsis decreases when immobility is costly. That 40% of individuals in the control condition attacked sticks suggests that visual cues to potential prey in the control condition may have reduced the effect size of food presence. This interpretation is consistent with the larger effect size of presence of food on latency to hide because lizards in the mealworm condition handled the prey before entering refuge, whereas those in the control condition did not handle sticks or spent less time handling them. Latency to refuge entry after contact with a mealworm or stick was not measured but was undoubtedly longer after contact with a mealworm.

The shorter latency to move when a mealworm was present than absent confirms the prediction that latency to move decreases as foraging cost of remaining immobile increases. The model of Martín et al. (2009) successfully predicted the

decrease in latency to move as predation risk increased but was not designed to predict effects of opportunity costs. Our new model, which is formally equivalent to Ydenberg and Dill (1986) model for flight initiation distance, provides a basis for predicting effects of both predation risk and cost of not moving.

Range of applicability of escape theory and future directions

Optimal escape theory and related models that predict flight initiation distance apply to latency to flee or latency to move when a prey has detected a predator moving toward it. This scenario matches approach of an immobile prey by an actively foraging predator. The prey may be an ambush forager, a resting active forager and, regardless of its foraging mode, may have stopped moving upon detecting the predator, thereby increasing the likelihood of avoiding detection by the predator. Our model that predicts latency to flee applies when both predator and prey are immobile. This may occur when an ambush predator moves to a new ambush post near an immobile prey. It can also occur when an actively foraging predator stops moving near an immobile prey, either to rest or to search for a prey that has stopped moving. Escape theory has been very successful in predicting effects of numerous predation risk factors and factors that affect costs of fleeing on flight initiation distance. Testing of the model of latency to flee has only begun, but all its predictions that have been tested have been supported. Tests of additional cost of moving and cost of not moving factors should be examined in diverse prey to establish the breadth of applicability of the model.

FUNDING

The research on Aire was funded by the research project: CGL2009-12926-C02-02 from the Spanish Ministry of Science and Innovation. The research on *I. cyreni* was supported by the research project MCI-CGL2008-02119/BOS from the Spanish Ministry of Science and Innovation.

We thank Mario Garrido and Ana Pérez-Cembranos for logistical help in Aire. We are grateful to El Venterillo MNCN Field Station for providing use of facilities in the Guadarrama Mountains. We are also thankful for scientific permits issued by the Conselleria de Medi Ambient of Balearic Government and the "Comunidad de Madrid" Environmental Agency.

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