

Escape and alerting responses by Balearic lizards (*Podarcis lilfordi*) to movement and turning direction by nearby predators

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Received: 19 September 2008 / Accepted: 8 March 2009 / Published online: 11 April 2009
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Abstract Escape theory predicts that prey monitoring an approaching predator delay escape until predation risk outweighs costs of fleeing. However, if a predator is not detected until it is closer than the optimal flight initiation distance (FID = distance between predator and prey when escape begins), escape should begin immediately. Similarly, if a change in a nearby predator's behavior indicates increased risk, the optimal FID increases, sometimes inducing immediate escape. If a predator that has been standing immobile near a prey suddenly turns toward the prey, greater risk is implied than if the predator turns away. If the immobile predator suddenly moves its foot without turning, it might be launching an attack. Therefore, we predicted that frequency of fleeing and preparation to flee are greater when a predator turns toward than away from prey and that frequency of fleeing when a predator suddenly moves decreases as distance between predator and prey increases. We verified these predictions in the Balearic lizard *Podarcis lilfordi* in field experiments in which an investigator simulated the predator. Lizards fled and performed alerting responses indicating readiness to flee more

frequently when the predator turned toward than away from them, and fled more frequently the nearer the predator.

Keywords Antipredatory behavior · Escape behavior · Predation risk · Turn direction · Squamata

Introduction

Escape theory predicts that when prey see approaching predators, their responses vary with risk of predation and cost of fleeing. If a predator is sighted at a distance for which cost of fleeing outweighs the expected cost of remaining (not fleeing), prey are expected to delay escape responses until the predator draws near enough for the cost of remaining to equal the cost of fleeing (Ydenberg and Dill 1986) or for expected fitness after the encounter to be maximized (Cooper and Frederick 2007). If a predator is sighted when already closer than the flight initiation distance (FID, the distance separating prey from predator when escape begins) predicted for an aware prey, a prey should begin its escape attempt immediately (Cooper 1998; Blumstein 2003; Stankowich and Coss 2006).

FID depends on the prey's evaluation of the probability that it has been detected and is being attacked because these considerations affect perceived risk (Cooper 1998). A predator that is stationary near a prey may pose a risk insufficient to elicit escape, but if the predator quickly turns toward the prey, the prey may assess an abrupt increase in probability that it is being attacked (Cooper 1998). If the predator is closer than the optimal FID for the new risk level, the prey should attempt to escape immediately. This prediction has been verified for three lizard species, the skink *Plestiodon laticeps*, the iguanid *Dipsosaurus dorsalis*, and the phrynosomatid *Holbrookia propinqua* (Cooper

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1997a, b, c, 1998, 2003). In all three species, the probability of fleeing was greater when an experimenter standing nearby turned toward than away from the prey.

The distance between a stationary predator and prey should strongly affect the difference in response by prey when the predator rapidly turns toward versus away from the predator. If a predator is very close, any movement may elicit escape because prey do not have the luxury of delaying escape attempts to evaluate the threat if they are to escape a real attack. At somewhat longer distances between predator and prey, turning toward the prey is expected to elicit escape more frequently than turning away due to assessment of greater risk that places the predator closer than the optimal FID only when turned toward. At still longer distances, the increase in risk due to turning may not be great enough for the predator to be closer than optimal FID regardless of turn direction. In that case, low frequency of escape and no difference between turn directions is predicted. All of these predictions have been verified in the only two studies of effects of turn direction over a range of distance (Cooper 1997a, 1998).

Any rapid movement by a potential predator is expected to elicit escape or preparation for escape more frequently at close range than when a predator is farther from the prey, but this effect has been examined only for movement involving changes in direction by predators. We predicted that movement parallel to the body of prey in the same direction as the prey's orientation (i.e., in the direction the prey would travel should it move straight ahead) would elicit escape movements more frequently at close range than when the predator was more distant.

Flight intention movements are in situ body movements that suggest readiness to escape. They have been reported in *D. dorsalis* and *H. propinqua*, but at frequencies too low for analysis (Cooper 1998, 2003). We predicted that the frequency of such movements would be greater in high-risk than low-risk situations for both turn direction and parallel movements by predators.

We conducted field experiments to examine effects of turning direction and parallel movements in relation to distance between predator and prey in the Balearic lizard, *Podarcis lilfordi*. We tested the hypothesis that lizards flee or exhibit alerting behavior more often when a nearby predator turns or moves suddenly if the predator is standing closer. We predicted that frequency of escape movement and/or alerting movements is greater when a nearby predator turns toward a prey or moves suddenly without turning than when it turns away from a prey. Because the immediate risk to a prey posed by predator movement decreases as distance between predator and prey increases, we predicted that the effect of sudden movement without turning on escape and alerting is largest when the predator is very close to the prey and declines to zero as distance increases.

Materials and methods

Animal and study site

Podarcis lilfordi is a medium-sized (ca. 80 mm maximum snout–vent length) lacertid that is an omnivorous active forager endemic to the Balearic islands (Barbadillo et al. 1999). We collected data on Aire, an islet off Menorca, Balearic Islands, Spain, between 28 April and 1 May 2005 on sunny days when lizards were fully active. The vegetation consisted of low bushes, some of which were dense enough to provide effective cover for the lizards, and several species of flowering plants used as food sources by *P. lilfordi* (Pérez-Mellado 1989). In most of the study area, plant cover was sparse, with patches of exposed rock and soil predominant.

Natural and simulated predators

We simulated predators by approaching lizards ourselves. Human beings are not natural predators of *P. lilfordi*. However, because biologists and other collectors removed many of these lizards from Aire before they were fully protected, it is possible that some natural selection has been exerted for escape from human beings. It remains possible that Balearic lizards responded to risk of being trampled rather than predation per se. If so, the predictions still apply based on risk assessment in relation to avoidance of injury or death. Birds are the major predators on Aire [kestrels (*Falco tinnunculus*) and possibly visiting species from Menorca (e.g., shrikes)]. Resident seagulls (*Larus cachinnans*) are potential predators (Cramp and Simmons 1982), but do not eat *P. lilfordi* on Cabrera (Araújo et al. 1977). Mammalian and ophidian predators are currently absent from Aire (Pérez-Mellado 1989).

People can approach easily on rough terrain that would block model predators, move realistically, and—barring accident—pose no actual threat of mortality. Possible disadvantages of using experimenters as predators include inability to detect predator-specific escape responses and experimenter bias. Predator-specific escape responses occur in chameleons (Stuart-Fox et al. 2006). They are unknown in *P. lilfordi* but may occur. Regardless of their existence, the escape responses measured are expected to conform to the prediction that the probability of fleeing increases with risk. Experimenter bias is possible whenever the experimenter knows the treatments and predicted outcomes, but can be reduced or eliminated by standardizing methods. To minimize any effects of bias, methods for each type of trial were practiced, and trial sequences were selected before collecting data.

Human simulation of predatory attack is an effective, frequently used method of studying escape behavior

(reviewed by Stankowich and Blumstein 2005) by diverse vertebrates (fish: Grant and Noakes 1987; frogs: Cooper et al. 2009a, b; lizards: e.g., Martín and López 1999; Martín et al. 2003; Cooper and Wilson 2007a, b; birds: Blumstein 2003; Cárdenas et al. 2005; mammals: Blumstein and Pelletier 2005; Stankowich and Coss 2006), insects (Cooper 2006a), and other taxa (e.g., Hemmi 2005). It works well for *P. lilfordi* (Cooper et al. 2006). Many studies of lizards using this method have verified predictions of escape theory about FID for factors affecting risk of predation (cost of not fleeing) and cost of fleeing (e.g., Heatwole 1968; Burger and Gochfeld 1990; Martín and López 1996; Cooper 1997a, b, c, 1999, 2000; Cooper et al. 2003, 2006; Cooper and Whiting 2007).

Data collection, designs, and analyses

We located large adult lizards (sexes undetermined) by visually searching while walking slowly through the study site. One experimenter (W.E.C.) conducted all approaches while wearing the same clothes. Before each trial, the experimenter moved to a location affording the lizard an unobstructed view of him. *Podarcis lilfordi* sometimes climb in plants or on piles of rocks, but all lizards tested were on the ground. We approached only lizards that were not engaged in feeding, foraging, or other activities that might distract their attention; only lizards that were motionless, but appeared to be alert were used. The experimenter moved very slowly to a preselected distance from the lizard, stopped for 5 s, and then executed movements appropriate to the particular experimental treatment. All tests (except two indicated as one-tailed based on directional prediction) were two-tailed with $\alpha = 0.05$.

In the study on the effect of direction of turning by the predator, the experimenter moved to a position 1.8–3.0 m from a lizard and oriented his body parallel to the lizard's body orientation, facing in the same direction as the lizard. In this position, neither the lizard nor the investigator faced the other. Instead, the investigator oriented his body so that a line through his shoulders was perpendicular to the lizard's longitudinal axis and, when facing straight ahead, his eyes were oriented in the same direction as a line passing along the lizard's longitudinal axis from the vent to the snout and projected forward. Then the experimenter turned rapidly toward or away from the lizard. Each lizard was tested in both conditions, the second trial following the first after approximately 10 s. No lizard hid. The experimenter recorded whether the lizard fled or performed an alerting response in each trial. Alerting lizards stood higher, leaned forward in a direction in which escape might begin, and sometimes turned away from the experimenter. We interpret alerting as implying response strength intermediate to fleeing and not moving.

Use of a counterbalanced repeated-measures design is a standard technique to statistically control for any sequential effects of testing, especially the possibility that response strength might increase in second trials. However, the magnitude of the effect of the first turn direction on response in second trials might be greater for one of the two initial turn directions. It seems extremely unlikely that turning away initially would cause a larger increase in perceived risk than turning toward lizards. If turning toward lizards initially were to increase the probability of escape or alerting in second trials more than turning away initially, it would be more difficult to detect the predicted effects of turn direction. Differences between conditions in frequency of fleeing, alerting, or either of these were analyzed using sign tests. Differences in numbers of lizards that fled or alerted during first and second trials were analyzed using two Fisher exact probability tests, one for each direction of turning. Effect sizes are reported as g (Cohen 1992).

In the study of effects of sudden movement on frequency of escape, the experimenter approached a lizard to a preselected distance and stopped while oriented as above. The experimenter stopped on exposed soil briefly, then made a sudden movement parallel to the lizard's longitudinal axis by moving his foot rapidly in contact with the ground in a backward direction (posteriad with respect to the lizard) while not changing his position. Fifteen lizards were tested with the experimenter standing at each of four ranges of distance from the lizard (0.9–1.7, 1.8–3.0, 3.1–4.5, 4.6–6.1 m). Each lizard was tested only once. This was ensured by moving through each area on the study site only once during the study, and by testing lizards in succession that could be distinguished by continuously monitored locations or obvious differences in appearance. Differences in frequency of escape movements between distances from the experimenter when movement occurred were tested for significance using Fisher exact probability tests. Effect sizes for Fisher exact tests are reported as $r_{\text{equivalent}}$ (Rosenthal and Rubin 2003).

Results

Effects of predator turning direction

When the investigator turned toward lizards ($n = 52$), over 60% of individuals moved away, about 10% adopted an "alert" stance with extended legs often used just prior to fleeing, and about 25% did not move (Fig. 1; Table 1). When the investigator turned away from the same lizards, a smaller proportion of individuals fled and a much higher proportion of lizards did not flee than when the investigator turned toward them (Fig. 1). Few (25%) moved away, only

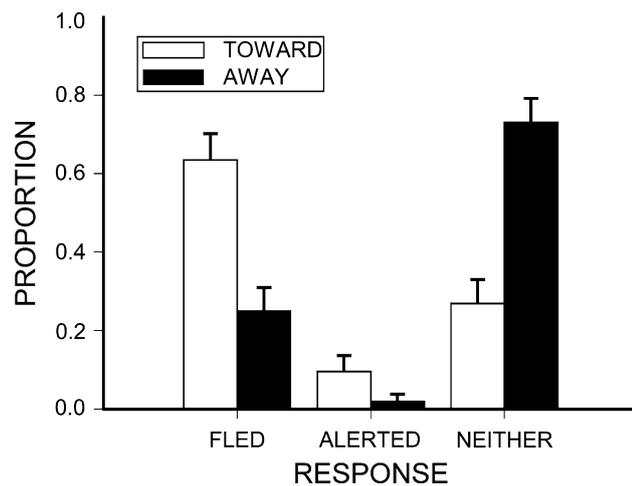


Fig. 1 Proportions of Balearic lizards (*Podarcis lilfordi*) that fled or performed alerting behavior indicating readiness to flee were greater when the experimental predator turned toward than away from lizards

Table 1 Frequencies of moving, alerting, and neither moving nor alerting in the two trials for each lizard, one in which the predator turned away from the lizard and the other in which the predator turned toward the lizard

Away	Toward		
	Move	Alert	Neither
Move	13	0	0
Alert	1	0	0
Neither	19	5	14

2% adopted the alert posture, and 73% did not move (Table 1). The proportion of individuals that alerted was low in both trials, especially when the investigator turned away from lizards (Fig. 1).

Large majorities of movement and alerting occurred in trials in which the investigator turned toward lizards (Table 1). Excluding lizards that did not react visibly in either trial or fled in both trials, all of the remaining individuals reacted more strongly when the investigator turned toward them (Table 1, sign test, $P = 6.0 \times 10^{-8}$; $g = 0.50$). Restricting the analysis to escape movements, 13 lizards moved in both trials, 14 moved in neither trial, and 20 lizards moved when the investigator turned toward, but not away, from them. Among lizards that moved in only one of the two trials, all moved only when the investigator turned toward them (Table 1, sign test, $P = 4.8 \times 10^{-7}$; $g = 0.50$).

The frequency of alerting was higher when the investigator turned toward a lizard than away from it (Table 1). The single lizard that alerted when the predator turned away fled when the predator turned toward it. Among the six individuals that alerted, alerting was the stronger

response for the five that alerted when turned toward and the weaker for the one that alerted when the predator turned away. Rank response was as predicted for all six individuals (sign test, $P = 0.032$; $g = 0.50$), i.e., response was stronger when the predator turned toward lizards.

No sequential effects were detected. During second trials in which the investigator turned away, 5 of 26 lizards moved and none alerted; whereas 8 of 26 fled and 1 alerted in second trials in which the investigator turned toward them. When the investigator turned toward lizards, 15 moved and 3 alerted in first trials, and 18 moved and 2 alerted during second trials. Numbers that fled or alerted did not differ significantly between first and second trials either when the investigator turned away from (Fisher exact test, $P = 0.35$) or toward lizards (Fisher exact test, $P = 0.76$).

Effect of sudden movement

Sudden backward foot movement by an investigator standing near a lizard elicited the same behaviors as turning near a lizard, i.e., movement away, alerting, or no detectable reaction. Frequencies of these behaviors varied with the distance between investigator and lizard. When the investigator was 0.9–1.7 m from the lizard, all but one lizard fled, none alerted, and only one did not flee. When the investigator was 1.8–3.0 m from the lizards, all but 2 of 15 moved, none alerted, and two did not move. When the investigator was 3.1–4.5 m from lizards, less than half of lizards fled, and only one alerted. For distances of 4.6–6.1 m, no lizard fled and only one alerted. In summary (Fig. 2), the proportion that fled was greatest at the shortest distance and declined to zero at the greatest distance range. Alerting was observed only at distances great enough that most lizards did not flee (Fig. 2).

Because results were nearly identical for distances <1.8 m (14 of 15 moved) and 1.8–3.0 (13 of 15 moved), data for these distances were pooled for analysis. The frequency of movement by lizards was significantly greater when the investigator stood ≤ 3.0 m from the lizard than at either of the longer distances and in the range 3.1–4.5 m than in the 4.6–6.1 m range (Table 2). The pattern of significance was identical for either moving or alerting to that for only moving (Table 2).

Comparisons of results for sudden foot movements with turns at distances of 1.8–3.0 m show that sudden movement elicited escape (13 of 15) significantly more frequently than turning away (13 of 52) from a lizard (Fisher exact test, $P = 2.5 \times 10^{-5}$, $r_{\text{equivalent}} = 0.47$). The frequencies of escape did not differ between foot movements and turns toward (33 of 52) lizards (Fisher exact test $P = 0.12$, $r_{\text{equivalent}} = 0.15$).

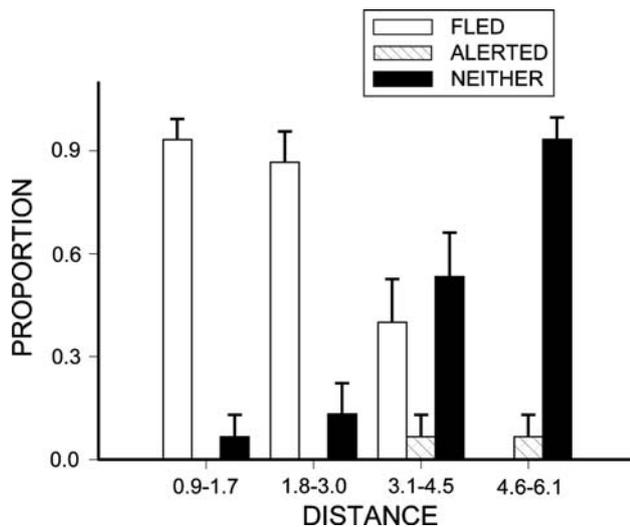


Fig. 2 The proportion of Balearic lizards (*Podarcis lilfordi*) that fled when a predator moved its foot decreased as distance (m) between lizard and predator increased. Few lizards performed alerting responses in this experiment, and none at the closer distances. Sample sizes for lizards that fled, alerted, or neither were 14, 0, and 1 for both the 0.9–1.7 m and 1.8–3.0 m distances; 6, 1, and 9 for 3.1–4.5 m distances; and 0, 1, and 14 for 4.6–6.1 m distances

Table 2 Lizards were more likely to move or alert when a predator suddenly moved if the predator was closer to them than standing farther away

Behavior	Distance (m)			
	3.1–4.5		4.6–6.1	
	<i>P</i>	<i>r</i> _{equivalent}	<i>P</i>	<i>r</i> _{equivalent}
Moved				
≤3.0 m	0.0002	0.60	<0.0001	0.78
3.1–4.5 m			0.017	0.39
Moved or alerted				
≤3.0 m	0.014	0.40	1.45 × 10 ⁻⁶	0.74
3.1–4.5 m			0.035	0.33

Data are given as probabilities (*P*) of no difference from Fisher exact tests and corresponding effect sizes (*r*_{equivalent})

Discussion

Direction of turning by a nearby predator strongly affected probability of fleeing, as indicated by the effect size, which had the maximum possible value. As predicted by assessment of greater risk by a prey when a predator turns toward it, lizards were more likely to flee when a predator turned toward than away from them. Of the 38% of lizards that fled in only one trial, all did so when the predator turned toward. Analyses in which response strength was ranked in the order fleeing > alerting > not moving produced results qualitatively identical to those for fleeing versus not fleeing, but with an even lower *P* and an identically high effect

size. These strikingly consistent findings suggest that *P. lilfordi* can rapidly and accurately assess differences in risk based on the direction of movements by simulated nearby predators.

Due to proximity, any movement made by a predator implies some risk that must be evaluated immediately (Cooper 1998). This accounts for the finding that 25% of lizards fled both when the predator turned toward them and turned away from them. In contrast to these shy individuals, bolder lizards, 37% of all lizards tested, did not flee when the predator turned in either direction.

We consider alerting behavior without fleeing to indicate assessment of risk intermediate to that requiring immediate escape and risk requiring no immediate response. Analysis of data for lizards for which alerting was the strongest response showed that turning toward a lizard is more likely than turning away to elicit alerting. The analysis of frequencies of predicted rank response supports our contention that alerting is a response of intermediate intensity that indicates readiness to flee. Despite the small sample sizes, the occurrence of maximum possible effect sizes supports both findings and emphasizes their consistency.

Effects of rapid backward movement of a foot by a nearby predator varied greatly with distance between predator and prey. As predicted by escape theory (Ydenberg and Dill 1986; Blumstein 2003; Stankowich and Coss 2006; Cooper and Frederick 2007), fleeing was most frequent when the predator was closest and decreased progressively as distance between predator and prey increased. These findings confirm the prediction that rapid movement close to prey can induce escape even if it is not directed toward the prey. Because the predator’s movement is fast, the assessed risk rises in a step function, suddenly placing the predator closer than the optimal approach distance given its current behavior, and prey flee immediately. When a predator is close enough, prey cannot afford the luxury of evaluating direction of movement precisely before fleeing.

The greater frequency of fleeing when a researcher rapidly moved his foot backward than when he turned away while standing at the same distance from the lizard suggests that lizards can discern the difference in movement and rapidly assess the lower risk posed by a predator turning away. Cues used to assess the difference in risk are unknown, but may include facial features, especially eyes. FID by black iguanas (*Ctenosaura similis*) is greater when predator eye size is artificially enlarged (Burger and Gochfeld 1992), and escape by broad-headed skinks (*P. laticeps*) on trees is often delayed until the lizard passes out of an indirectly approaching predator’s field of view (Cooper 1997a). Loss of eye contact may signal reduced risk for *P. lilfordi*. Other cues, such as exposure

of posterior versus anterior body parts, or direction of turning per se may be important, but have not been investigated.

For a predator standing at the same distance from prey, frequency of fleeing did not differ when the predator turned toward the prey or moved its foot backward. Although a somewhat higher frequency of escape was observed for backward foot movement, the difference was not significant and the effect size was not large. The lack of difference between turning toward prey and backward foot movement suggests that perceived risk is too great during backward foot movement to delay escape for further evaluation of risk. A predator facing in the same direction as the lizard and moving a foot backward may be interpreted as moving forward and possibly toward the lizard. The backward movement of the foot on the ground may have given the impression of a predator starting to accelerate, implying the need for rapid escape if an attack were initiated. The greater likelihood of escape for both trials in which the predator turned toward them and trials in which the predator moved his foot backward than for trials in which the predator turned away could have been a consequence of the prey's evaluation that risk increased when the predator turned toward the lizard or moved its foot backward, that risk decreased when the predator turned away, or both. Further study is needed to clarify this issue and identify the cues used by lizards to assess degree of risk implied by nearby movement.

All present results are consistent with the predictions of escape theory (Ydenberg and Dill 1986; Cooper and Frederick 2007) regarding FID provided that prey can quickly adjust their assessment of risk to ongoing changes in predator behavior. This interpretation was made for effects of predator turning direction in other lizard species (Cooper 1997a, 1998, 2003). Rapid response by *Anolis lineatopus* to acceleration by an approaching predator (Cooper 2006b) also shows that lizard prey can adjust their assessment of risk and escape accordingly in response to real-time changes in predator behavior.

When a predator's behavior is constant, cost of fleeing and predation risk curves relating expected fitness to distance between predator and prey are fixed for prey during its approach (Ydenberg and Dill 1986; Cooper and Vitt 2002; Cooper and Frederick 2007). Risk and cost change with distance, but the forms of the curves do not. However, if the predator changes its speed of approach or alters its path, the risk curve changes. When the experimental predator turned toward lizards, immediate escape presumably occurred in those individuals that evaluated their new position as being nearer to the predator than the optimal FID (Blumstein 2003; Stankowich and Coss 2006). Individual differences in risk assessment and, therefore, optimal FID, place individuals along a continuum from

shyness to boldness (López et al. 2005; Cooper 2009). A similar interpretation applies to responses to foot movements. Shy individuals fled when the predator turned toward them or moved its foot, but bolder individuals did not flee, presumably because the predator remained farther away than the optimal flight initiation specified by their assessment of risk.

Alerting behavior may indicate that assessed risk is nearly great enough to elicit escape and may reveal preparation for escape. Another possibility is that alerting signals predators that they have been detected, reducing the likelihood that the prey can be captured. Because several lizards are known to use pursuit-deterrent signals (e.g., tail and dewlap displays; Dial 1986; Hasson et al. 1989; Leal and Rodriguez-Robles 1997; Cooper 2001; Cooper et al. 2004), experimental tests of this possibility are needed. However, pursuit deterrence seems unlikely in the experiment on direction of turning because the predator was very close to the lizard. Typically, pursuit-deterrent signals are performed at a distance, not when the predator is very near (Woodland et al. 1980; Cooper 2001). That no lizards alerted at the closest distances in the study of foot movement, but two alerted at longer distances, is consistent with pursuit-deterrent signaling, but the sample is far too small to support pursuit-deterrence as a function of alerting behavior.

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