

Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammotromus algirus*

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Abstract: Theoretical models of escape behavior suggest that the optimal distance at which an animal starts to flee (approach distance) increases with distance to the refuge. However, the extent of reliance on refuges may strongly affect this relationship. The lizard *Psammotromus algirus* escapes a predator by fleeing into leaf litter, which is very abundant but not a safe refuge because the predator could still locate and capture a concealed lizard. We test the hypothesis that escape decisions of this lizard species are based on the conspicuousness of individuals and the type of refuge used, rather than on the distance to cover per se. A field study showed that approach distance was not significantly correlated with distance to available refuges or distance actually fled. However, the type of microhabitat and the type of refuge used influenced the approach distance. Lizards started to flee earlier in microhabitats where they were presumably more visible to potential predators. Lizards ran to refuges that were similar in quality to, but farther from, the nearest available one. A longer flight may be needed to mislead the predator. However, because fleeing may be costly, the flight distance should be optimized. Thus, lizards ran farther and faster when they fled through unsafe microhabitats. Lizards with a low body temperature have lower escape performance and their approach distances should be greater. However, although air temperature affected escape speed, it was not significantly correlated with approach distance or flight distance. The relatively low reliance on refuges by *P. algirus* indicated that the expected relationship between escape decision and distance to the refuge did not exist. However, the results indicate that *P. algirus* optimizes its escape decisions according to the costs of fleeing and the costs of remaining.

Résumé : Les modèles théoriques du comportement de fuite indiquent que la distance optimale à laquelle un animal doit amorcer sa fuite (distance d'approche) devrait augmenter en fonction de la distance du refuge à atteindre. Cependant, la dépendance à l'égard des refuges peut fortement affecter cette relation. Le lézard *Psammotromus algirus* se sauve en fuyant vers la litière de feuilles, un refuge abondant mais pas très sûr car le prédateur peut facilement y localiser et capturer un lézard qui s'y est enfoui. Nous éprouvons ici l'hypothèse selon laquelle les décisions de fuite que prend ce lézard sont basées sur la visibilité des individus et le type de refuge utilisé, plutôt que sur la distance à parcourir jusqu'au couvert. Les résultats d'une étude sur le terrain ont démontré que la distance d'approche n'est pas en corrélation significative avec la distance jusqu'aux refuges disponibles ou avec la distance réellement parcourue. Cependant, le microhabitat et le type de refuge utilisé influencent la distance d'approche. Les lézards amorcent leur fuite plus tôt dans les microhabitats où ils sont plus visibles aux yeux de prédateurs éventuels. Les lézards courent vers des refuges de qualité équivalente à celle du refuge le plus proche, mais situés plus loin. Une fuite sur une plus grande distance peut s'avérer nécessaire pour mystifier le prédateur. Cependant, comme la fuite est un comportement coûteux, la distance parcourue doit être optimisée. De cette façon, les lézards courent plus loin et plus vite lorsqu'ils traversent des microhabitats incertains. Les lézards à température corporelle basse ont une performance de fuite moins bonne et doivent se ménager une plus grande distance d'approche. Cependant, bien que la température de l'air affecte la vitesse de fuite, elle n'est pas en corrélation significative avec la distance d'approche ou la distance de fuite. La dépendance relativement faible à l'égard des refuges chez *P. algirus* fait qu'aucune relation entre les décisions de fuir et la distance du refuge n'a été observée. Cependant, les résultats indiquent que *P. algirus* optimise ses décisions de fuir en fonction de ce que coûterait la fuite et de ce qu'il en coûterait de rester.

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Introduction

Theoretical models of escape behavior suggest that prey adjust their escape response so that the optimal distance at which they start to flee (approach distance) is the point

where the costs of staying exceed the costs of fleeing (Ydenberg and Dill 1986). Thus, because the risk of capture is higher for prey that are farther from a refuge, the approach distance should increase with the distance to the refuge (Dill and Houtman 1989; Dill 1990; Bonenfant and

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Kramer 1996). However, the extent of reliance on refuges for avoiding predators, and other components of predation risk such as the probability of detection by the predator (Lima and Dill 1990), may strongly affect the relationship between approach distance and distance to cover.

Many lizards escape from predators by running to hide in the nearest available refuge and, as predicted, their approach distance increases with the distance to the refuge (Cooper 1997a). However, other species of lizards living in open habitats with sparse cover rely more on speed and running long distances than on using refuges (Bulova 1994). An intermediate situation occurs when cover and refuges are readily available but not entirely effective for eluding predators. For example, the lacertid lizard *Psammodromus algirus* usually escapes by fleeing into patches of leaf litter under cover of shrubs that are similar in quality to, but farther from, the nearest available one (Martín and López 1995a). Leaf litter is very abundant in its habitat (Martín and López 1998), but does not provide a safe refuge because a predator could still locate the refuge and capture the concealed lizard. A longer flight may be needed not only to reach a refuge, but more importantly, to mislead the predator. However, because fleeing may be costly, the distance covered during active flight should be optimized by balancing the fitness effects of misleading predators and saving energy during running sequences.

We previously examined the flexibility in approach and flight distances of *P. algirus* in relation to seasonal variation in the habitat caused by the presence or absence of leaves on deciduous shrubs under which the lizards seek refuge (Martín and López 1995a). Lizards allowed a closer approach and fled for shorter distances during summer, when shrub cover was available. In this new experiment we examined in more detail the characteristics of the escape response within a season in relation to the microhabitats where lizards were located initially and along the escape trajectory, and to the types of refuge used. We aimed to test the hypotheses that, rather than being determined by distance to available refuges, the escape decisions of these lizards might be determined by (i) the conspicuousness of the lizards in the microhabitats where they are located initially (Heatwole 1968; Johnson 1970; Cooper 1998), which affects the probability of detection by a predator, and (ii) the safety of the type of refuge used, which affects the probability of capture. We also examined whether temperature affects the escape decisions of *P. algirus* and the characteristics of its escape response.

Methods

Species and study area

Psammodromus algirus is a medium-sized lizard inhabiting Mediterranean forests of the Iberian Peninsula and Northwest Africa. These lizards are important prey for many predators that rely on acoustic and visual cues, such as some raptorial birds (e.g., *Buteo buteo*, *Falco tinnunculus*, *Tyto alba*, *Athene noctua*), shrikes (*Lanius excubitor*; Martín and López 1990), and some mammals, such as weasels (*Mustela nivalis*) or foxes (*Vulpes vulpes*). Observations were made during April and May 1996 in an oak forest near Cercedilla (40°44'N, 4°02'W), Madrid Province, Spain. Vegetation included primarily trees and small saplings of a deciduous oak, *Quercus pyrenaica*, as well as two less abundant and dispersed

perennial shrubs, *Cistus laurifolius* and *Rosa* sp. Oak-leaf litter is very abundant on the ground year-round (Martín and López 1998).

Escape behavior

We walked through the area until a lizard was sighted with binoculars, whereupon we attempted to approach it directly. One person performed all approaches, walking at the same moderate speed (about 40 m/min) and wearing the same clothing, while another person recorded the lizard's behavior, to avoid confounding effects that may have affected lizards' risk perception (e.g., Burger and Gochfeld 1993; Cooper 1997b). The usual response of the lizards was to flee rapidly to the protective cover of a shrub and hide in the leaf litter under it (Martín and López 1995a), although they also used other type of refuge (see below). We defined the approach distance as the distance between the lizard and the observer when the lizard first moved (a straight line measured to the nearest 0.1 m). We determined the magnitude of the response by measuring the total distance covered during active flight ("escape-trajectory distance") (Bulova 1994; Cooper 1997a). "Escape duration" was the duration of active flight, measured with a stopwatch during the escape response. Thereafter, we could also calculate the "escape speed" (escape-trajectory distance divided by the time taken).

The "escape angle" was considered a circular variable (Domenici and Blake 1993), and was defined as the angle between the direction of the observer and the lizard's running path, estimated visually to the nearest 10°. Because responses from the left and right were pooled as if the observer was always on the right side of the animal, escape angles ranged between 0° and 180°. Thus, a lizard fleeing at an angle of 0° was running directly toward the observer. We considered an "away response" to occur when the lizard ran away from the observer (escape angle 91°–180°) and a "toward response" when it ran toward the observer (0°–90°).

Characteristics of the microhabitat

To analyze whether the escape response of a lizard was determined by the microhabitat and the availability of refuges (Martín and López 1995a; Cooper 1997a), we measured to the nearest 0.1 m the "distance to the nearest refuge" (a patch of abundant leaf litter under either low shrubs, like those in which the lizards actually hide, or rock crevices). Because the presence of the observer might constrain the lizards in terms of their direction of escape, we also measured the "distance to the nearest available refuge in the direction of the escape trajectory." The microhabitat locations of lizards before they fled and where they sought refuge were also recorded. Initial microhabitats were classified according to the relative conspicuousness of a lizard in them. Thus, there were some microhabitats where lizards were presumably more visible to potential predators, such as bare soil, patches of leaf litter far from shrub cover, or leaf litter under *C. laurifolius* (whose leaves are tiny and dispersed), and some microhabitats that provided visual cover such as grass, patches of leaf litter accumulated in or close to rock crevices, and patches of leaf litter under *Q. pyrenaica* or *Rosa* spp. Refuges were classified according to the level of safety they provided. Thus, leaf litter under *C. laurifolius* was considered unsafe because the leaves are tiny and form a thin layer (less than 1 cm deep) on the ground, so they offer less effective cover for a concealed lizard than *Q. pyrenaica* or *Rosa* sp. leaves, whereas rock crevices are the safest of the available refuges because predators cannot reach lizards within them. Occasionally a lizard climbed a tree trunk to escape, although this was an unusual strategy.

To analyze the microhabitat along the escape trajectory, we used a scored stick held vertically to record, at 50-cm intervals, the substrate in contact with it, i.e., grass, leaf litter, bare soil, or rocks, and, when present, the type of shrub cover (*Q. pyrenaica*, *C. laurifolius*, or *Rosa* sp.). We also noted whether the location could be

used as a refuge by lizards. This procedure allowed us to calculate the value of eight habitat variables: the number of contacts (i.e., cover) with each substrate and vegetation type and the number of potential refuges along the escape trajectory (Martín and López 1998).

The escape response of some lizards is influenced by temperature (Rand 1964; Hertz et al. 1982; Rocha and Bergallo 1990; Smith 1997). Lizards could not be captured immediately after they fled in order to measure their body temperature. However, air temperature is a relevant environmental variable influencing thermoregulation in *P. algirus* (Carrascal and Díaz 1989). Thus, to control for the effect of temperature in our results, we measured air temperature with a digital thermometer to the nearest 0.1°C (a shaded bulb 2 cm above the point where the lizard was initially sighted before it fled) immediately after each escape sequence.

Data analysis

We collected and analyzed information on 150 escape sequences of adult lizards. Given the large size of the area surveyed (more than 5 km²) and the high lizard density (about 60 adults/ha; unpublished data), and because we avoided walking routes taken previously, the probability of repeated sampling of the same individual was very low. We therefore treated all measurements as independent. Differences between escape responses were evaluated by analyses of variance on data normalized by logarithmic transformation when required. Tests of homogeneity of variances (Hartley's F_{\max} test) showed that in all cases variances were not significantly heterogeneous (Sokal and Rohlf 1995). To examine the relationship between escape-behavior characteristics and proportion of each microhabitat along the escape trajectory, temperature, or distance to refuge, we calculated Pearson's product moment correlation coefficients (Sokal and Rohlf 1995). We employed circular statistics to analyze escape angles (Batschelet 1981).

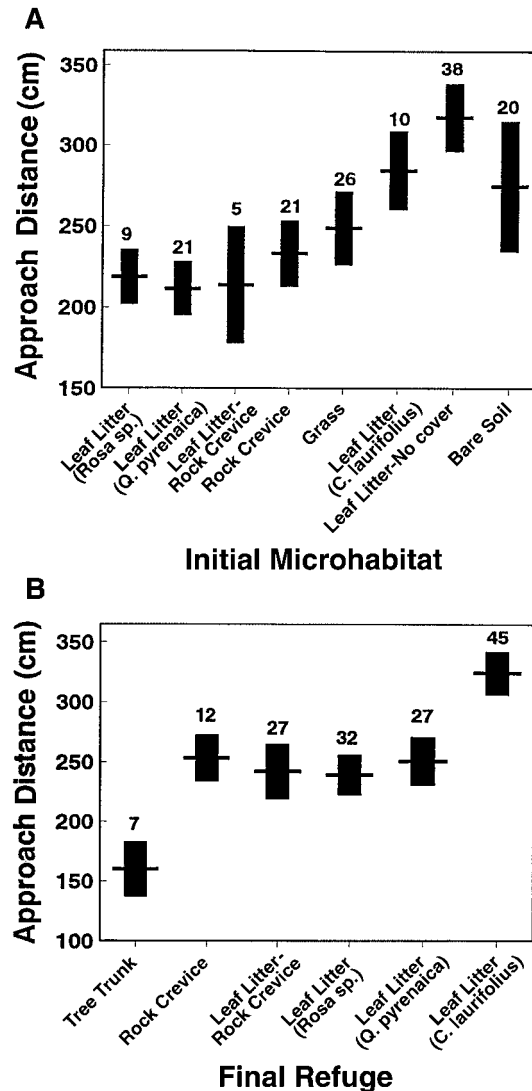
Results

Approach distance

Approach distance of lizards was not significantly correlated with either distance to the nearest available refuge ($r = 0.005$, $n = 150$, $P = 0.95$), distance to the nearest refuge in the direction of escape ($r = 0.03$, $P = 0.67$), escape-trajectory distance ($r = 0.03$, $P = 0.74$), or air temperature ($r = 0.07$, $P = 0.67$). However, the microhabitat at the initial location of lizards significantly influenced the approach distance ($F_{[7,142]} = 2.77$, $P = 0.01$) (Fig. 1A). This suggests that lizards started to flee earlier in microhabitats where they were presumably more visible to potential predators, such as patches of leaf litter without shrub cover, bare soil, or *C. laurifolius* leaf litter. Air temperature did not significantly affect the microhabitat where lizards were initially ($F_{[7,142]} = 1.33$, $P = 0.24$), and did not significantly correlate with either the distance to the nearest available refuge ($r = -0.06$, $n = 150$, $P = 0.45$) or the distance to the nearest refuge in the direction of escape ($r = -0.03$, $P = 0.68$).

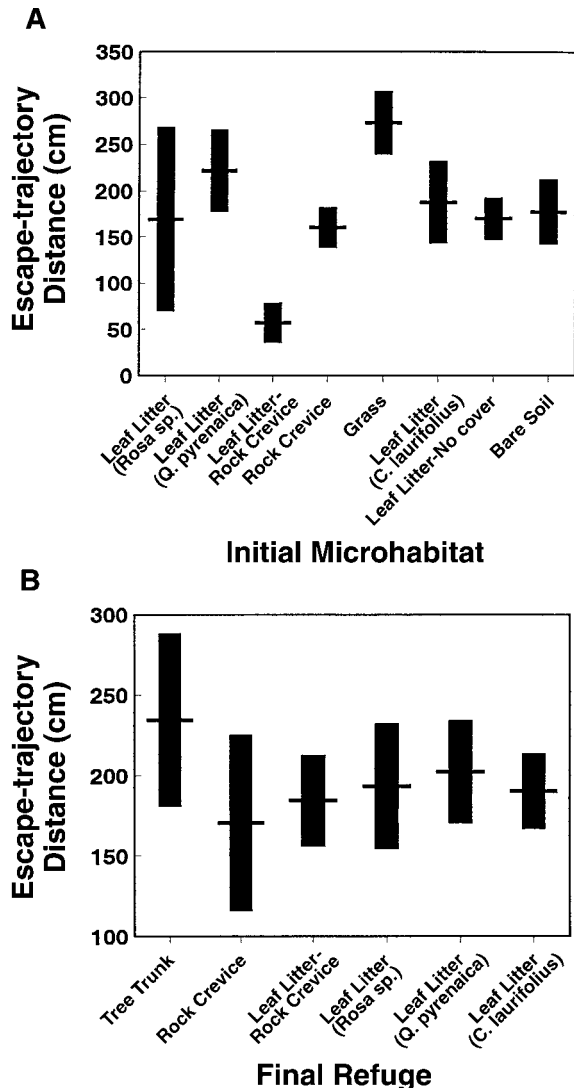
Differences in approach distance might have been due to significant differences between microhabitats in terms of distance to the nearest available refuge ($F_{[7,142]} = 7.09$, $P < 0.0001$) and distance to the nearest refuge in the direction of escape ($F_{[7,142]} = 5.48$, $P < 0.0001$). However, the expected relationship between distance to refuge and approach distance was not found for two microhabitat types, leaf litter without cover and *C. laurifolius* leaf litter, where lizards started to flee earlier even when available refuges were

Fig. 1. Approach distances of lizards (*Psammodromus algirus*) in relation to the microhabitat where they were initially located before fleeing (A) and to the type of refuge used after fleeing (B). Microhabitats are arranged according to the potential conspicuousness of a lizard standing there, and refuges are arranged according to their relative safety they provide from a predator. Numbers above the bars are sample sizes.



closer. This observation and analysis of the data further suggested that approach distance was affected by the type of refuge used ($F_{[5,144]} = 4.90$, $P < 0.0001$) (Fig. 1b). Thus, lizards that fled to hide in *C. laurifolius* leaf litter, which offered less effective cover, started to flee earlier than those in the other microhabitats. Lizards that climbed a tree trunk to escape, where terrestrial predators might not be able to pursue them, had shorter approach distances. In addition, the significant variation in air temperature according to the type of refuge used ($F_{[5,144]} = 5.68$, $P = 0.0001$) suggested that when the air temperature was high ($22.8 \pm 1.0^\circ\text{C}$; mean \pm SE), lizards had a high body temperature and were able to climb a tree, whereas when it was low ($15.6 \pm 1.1^\circ\text{C}$), they hid in the safer rock crevices or leaf litter close to rock crev-

Fig. 2. Escape-trajectory distances of *P. algirus* in relation to the microhabitat where lizards were initially located before fleeing (A) and to the type of refuge used after fleeing (B).



ices. Other refuges were used when the air temperature was moderate (on average, between 17.7 and 20.9°C).

Flight behavior

Neither the microhabitat where the lizard was located at the onset of flight ($F_{[7,142]} = 1.67$, $P = 0.12$) (Fig. 2A) nor the type of refuge used ($F_{[5,144]} = 0.13$, $P = 0.99$) (Fig. 2B) significantly affected the escape-trajectory distance. However, the escape-trajectory distance was positively correlated with the distance to the nearest available refuge ($r = 0.45$, $n = 150$, $P < 0.0001$) and the distance to the nearest refuge in the direction of escape ($r = 0.55$, $P < 0.0001$), and negatively correlated with the proportion of refuges along the escape trajectory ($r = -0.43$, $P < 0.0001$). Lizards ran to refuges that were similar in quality to, but farther from, the nearest available ones (the escape-trajectory distance minus the distance to the nearest refuge in the direction of escape was 1.4 ± 0.1 m (mean \pm SE), range 0–9.5 m). This trend did not vary significantly with the initial microhabitat

($F_{[7,142]} = 1.58$, $P = 0.14$) or the type of refuge ($F_{[5,144]} = 0.62$, $P = 0.68$). Lizards ran farther when they fled through unsafe microhabitats (i.e., with a low availability of refuges), such as those with a high proportion of grass ($r = 0.29$, $P < 0.0001$) or bare soil ($r = 0.29$, $P = 0.0003$), whereas lizards fleeing through safer microhabitats, such as those with a high proportion of leaf litter ($r = -0.29$, $P = 0.0006$), shrub cover (*Q. pyrenaica* + *C. laurifolius* + *Rosa* sp.; $r = -0.35$, $P < 0.0001$), or rocks ($r = -0.18$, $P = 0.03$), ran for shorter distances.

Lizards that ran farther also had significantly higher escape speeds ($r = 0.42$, $n = 150$, $P < 0.0001$). Neither the microhabitat on which the lizard was located before fleeing ($F_{[7,142]} = 1.16$, $P = 0.33$) nor the type of refuge used ($F_{[5,144]} = 0.64$, $P = 0.72$) significantly affected escape speed. However, lizards ran faster when they fled through microhabitats with a high proportion of grass ($r = 0.35$, $P < 0.0001$) or bare soil ($r = 0.29$, $P < 0.001$), and ran more slowly when they fled through microhabitats with a high proportion of leaf litter ($r = -0.26$, $P = 0.004$). The presence of other microhabitats did not affect speed ($P > 0.30$ in all cases). Air temperature was positively correlated with escape speed ($r = 0.31$, $n = 150$, $P < 0.001$), but not with escape-trajectory distance ($r = 0.04$, $P = 0.64$) or escape duration ($r = -0.13$, $P = 0.14$).

The orientation of lizards' flight paths relative to the observer's direction (escape angle) was random ($\chi^2 = 21.84$, $df = 17$, $P = 0.19$). The average angle ($\Phi \pm s$) of escape trajectories was $134.4 \pm 23.8^\circ$ (mean \pm SE) in the "away" responses and $58.1 \pm 24.1^\circ$ in the "toward" responses. "Away" responses did not occur significantly more often than "toward" responses (76 vs. 74 responses, respectively; binomial test, $P = 0.93$). This was true independently of the initial microhabitat type (binomial test, $P > 0.50$ in all cases). However, when the final refuge was the leaf litter under *Q. pyrenaica* shrubs, lizards ran preferentially away from us (20 vs. 7; binomial test, $P = 0.02$), whereas when the final refuge was a rock crevice or leaf litter close to rock crevices, lizards ran preferentially toward us (10 vs. 28; binomial test, $P = 0.006$). There were no significant differences for the other types of refuge ($P > 0.40$ in all cases).

Discussion

Approach distances for *P. algirus* were not dependent on the distance to available refuges or on the distance actually fled to a refuge. This result is apparently contrary to the models of escape behavior (Ydenberg and Dill 1986), which predict that approach distance should increase with distance to the refuge. It can, however, be explained by the fact that *P. algirus* does not rely on reaching an absolutely safe refuge, but on using abundant but relatively unsafe refuges that reduce but do not preclude its location and capture by the predator. To mislead the predator may be the more important goal of the escape strategy of this lizard. The conspicuousness of lizards to potential predators in different microhabitats may determine when to flee. Also, in other lizards, approach distance is correlated with degree of cryptic coloration (Heatwole 1968; Johnson 1970) or conspicuousness (Cooper 1998). Because predators sometimes need the stimulus of a moving prey for detection or attack, it would be

advantageous for prey to wait as long as possible before responding to a predator (Burger and Gochfeld 1990). Lizards may assess the probability of being detected (i.e., predation risk) differently in different microhabitats and adjust their approach distance accordingly. However, the results also suggest that the relative safety of nearby refuges also influenced escape decisions. Thus, when lizards were close to safe rock crevices, their approach distances were shorter, whereas when they had to hide in *C. laurifolius* leaf litter, their approach distances were longer. Because lizards concealed in *C. laurifolius* leaf litter may be more easily detected, only those that are far away from predators should rely on this type of refuge for concealment.

In contrast to the typical flight to leaf-litter refuges, some lizards climbed up a tree trunk to a height of 1–2 m. Trees are not used by *P. algirus* during its normal activities (Martín and López 1998), and lizards that climbed trees had shorter approach distances, which suggests that this unusual evasive strategy may reflect an alternative to eluding a nearby predator that might not have been detected in time to employ normal evasive action. A very close predator may otherwise easily locate and capture a lizard after it had fled to an unsafe leaf-litter patch. Also, differences in escape strategy may relate to different predator species. Thus, hiding in leaf litter may be effective against raptorial birds or shrikes, while climbing trees may be effective against some mammals (e.g., weasels or foxes). However, our data suggest that only lizards with a high body temperature are able to climb trees.

The variation in flight distance with the type of microhabitat along the escape trajectory suggests that lizards are optimizing the escape distance while they run. Because fleeing may be energetically costly, lizards should adjust the duration of flight according to microhabitat characteristics in order to maximize the probability of misleading predators while saving energy by avoiding unnecessarily long running sequences. Thus, lizards running through microhabitats with more potential refuges or more visual cover, where they were less conspicuous (i.e., the predator was less certain which refuge had been actually used), had shorter flight distances. Similarly, the variation in escape speed might also indicate that speed is not always maximized. The microhabitat itself might affect the speed of the lizards. Bare ground is easier to run on than leaf litter. Leaves and grass might impede the movement of lizards by providing a physical barrier to running. However, lizards also ran faster when grass was abundant, and in the laboratory, lizards induced to flee were able to attain similar maximal speeds on bare soil and in leaf litter (P. López and J. Martín, unpublished data). In other experiments, juvenile *P. algirus* (Martín and López 1995b, 1996) and a cichlid fish (*Melanochromis chipokae*; Dill 1990) adjusted their escape speed as a function of the predator's speed, which may have assured them of a fixed margin of safety. Therefore, animals may optimize the magnitude of their escape responses in order to save energy.

Lizards fled in random directions in relation to the observer. This suggests that when fleeing, lizards are not always maximizing the final distance between themselves and the predator, which they would do if they fled away from the predator. Alternatively, fleeing to an area where the predator

might be more easily misled, or to a previously known safe refuge (Clarke et al. 1983), may be more important in determining escape direction.

Lizards with a low body temperature are more vulnerable to predation (Christian and Tracy 1981), owing to their lower burst speed and escape performance (e.g., Hertz et al. 1982; Bauwens et al. 1995), and thus, they generally have greater approach distances (Rand 1964; Rocha and Bergallo 1990; Smith 1997). This may reflect behavioral decision-making to allow enough time to reach a refuge, taking into account the limitation of lower flight speeds. However, although temperature affected escape speed of *P. algirus*, it did not affect approach distance. Because refuges are abundant, the longer time needed to reach a particular refuge when flight speed is low might be unimportant. However, the choice of refuge type seemed to be influenced by temperature. Lizards with a low body temperature might prefer to hide in safer rock crevices because, if they used a less safe refuge such as leaf litter, they might be unable to run again if discovered by the predator. Variations in optimal antipredator strategy as a function of body temperature have been described in other lizard species (Hertz et al. 1982).

In conclusion, our experiment showed that in lizards which have a relatively low reliance on refuges, approach distance does not depend on distance to the refuge. However, the results also indicate that *P. algirus* optimizes its escape decisions according to the costs of fleeing and the costs of remaining (i.e., the probability of being detected in different microhabitat). Therefore, even when predator attack is imminent, lizards seem to be able to adjust their escape response to minimize the costs of flight (Ydenberg and Dill 1986).

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