

Escaping predators on vertical surfaces: *Lacerta perspicillata* in limestone quarries of Lithaca

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Abstract: Escape behavior of the Mediterranean lizard *Lacerta perspicillata* was studied experimentally in a limestone quarry at Lithaca on the island of Menorca, Balearic Islands, Spain. These lizards are exposed to avian predators while active on vertical rock faces. Simulated kestrel attacks using a cardboard model elicited escape responses from nearly all lizards approached. Methods of escape included entering a crevice, retreating over or around an edge, running behind a shrub growing against the rock surface, running behind a shrub and dropping to the ground ("bush to ground"), and retreating under or behind a rock isolated from a rock face. Most lizards fled directly to the closest available refuge or to alternative refuges only slightly farther away. Nevertheless, lizards that initially perched near crevices more frequently fled to other types of refuge than lizards that were initially near other refuges. The latter usually fled to the closest refuge. Lizards predominantly fled parallel to the ground or directly toward it (down) into a refuge regardless of the direction of attack (above, below, straight on). Direction of attack affected the type of refuge used. Lizards approached from above were more likely to flee to bush-ground or crevices than those approached from below or the same height. Straight-line retreat directly to a refuge appears to be the most viable escape strategy for these lizards when faced with attacks by avian predators, but the direction of attack may influence decisions based on risk.

Résumé : Nous avons étudié expérimentalement le comportement du lézard méditerranéen *Lacerta perspicillata* lorsqu'il cherche à échapper à des prédateurs dans une carrière de pierre calcaire à Lithaca dans l'île de Minorque, Espagne. Les lézards ont été exposés à la présence d'oiseaux prédateurs durant leurs activités sur les parois rocheuses. Les attaques simulées de crécerelles au moyen de modèles de carton déclenchent des réactions chez presque tous les lézards qui cherchent à fuir en entrant dans une crevasse, en se sauvant derrière ou autour d'une crête, en courant derrière un buisson accolé au rocher, en se laissant tomber au sol ou en se réfugiant derrière ou sous une pierre isolée de la paroi. La plupart des lézards fuient vers le refuge disponible le plus proche ou vers un autre refuge situé tout près. Néanmoins, les lézards perchés près d'une crevasse au départ gagnent des refuges d'un autre type que les lézards perchés près de refuges autres que des crevasses; ces derniers s'orientent généralement vers le refuge le plus proche. Les lézards suivent surtout des parcours parallèles au sol, ou en direction du sol (vers le bas) pour atteindre un refuge, indépendamment de la direction de l'attaque (par dessus, par dessous ou en ligne droite). La direction de l'attaque affecte le type de refuge utilisé. Les lézards attaqués d'en haut sont plus enclins à se réfugier derrière des buissons au sol ou dans des crevasses que les lézards attaqués par dessous ou de front. Un parcours en ligne droite vers un refuge semble être la stratégie la plus sûre pour ces lézards en présence d'oiseaux prédateurs, mais la direction des attaques peut influencer les décisions en fonction du risque.

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Introduction

Animals approached by predators must make rapid escape decisions based on predator type, angle and velocity of predator approach, and physical structure of the habitat in which they live (e.g., Cooper 1977a, 1977b, 1998a, 1998b, 1998c). Responses to predators are likely among the most important decisions faced by animals because lack of success in response results in death and thus total loss of future reproductive success (Greene 1988). Predation can be avoided by potential prey at a number of points in the predation process.

For example, potential prey can signal to a predator at a distance that it is aware of the presence of the predator and thus prepared for escape (pursuit deterrence), enter a refuge when approached by a predator, thereby becoming unavailable, dodge a predator's attack, or employ defense mechanisms that allow escape once it is captured.

Pursuit deterrence can involve displays specific to predator approach, such as tail waving in earless lizards, zebra-tailed lizards, and curly-tailed lizards (Dial 1986; Hasson et al. 1989; Cooper 2000a, respectively; see also Cooper 1998d), as well as displays used for other purposes, such as

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dewlap extension or head bobbing in *Anolis* spp. (Leal and Rodriguez-Robles 1997). As Cooper (2000b) has pointed out, many more subtle behaviors may play roles in pursuit deterrence, including short-distance movements away from predators. Prey dodge predator attacks in many ways as well. Entering refuges such as crevices is so widespread that virtually all field naturalists have observed it in animals as diverse as marine crustaceans, moray eels, tailless whip scorpions, spiders, plethodontid salamanders, tropidurine lizards, and a nearly endless list of other animals (e.g., Gilliam and Fraser 1987; Pitcher et al. 1988; for lizards, reviewed by Greene 1988; Cooper 1998c, 1998d). Among lizards, not only do many enter crevices, but many also have morphological or behavioral traits that make extraction difficult (reviewed by Cooper et al. 1999, 2000). Alternative escape behaviors often occur when lizards' access to refuges is blocked (Cooper 1999a). Many lizards, such as whiptails (*Cnemidophorus*), simply maintain a safe distance from potential predators while continuing to forage, dodging to the side or moving farther forward if the predator advances (Vitt and Price 1982). Once captured, some lizards bite, scratch, or whip with their tail, whereas others, such as *Cordylus cataphractus*, bite their own tail so that predators like snakes can never get a grip on a swallowable end (Cogger and Zweifel 1998; Pianka and Vitt 2003).

Trade-offs are often made between predator-avoidance behaviors and other important behaviors, such as social behavior or territorial defense (Cooper 1999b). However, when a predator attack is imminent, escape from predators should have priority over other behaviors. Nevertheless, in some species, such as the broad-headed skink (*Eumeces laticeps*), males guarding females during the breeding season allow closer approach by predators, which suggests that the potential fitness payoff associated with mate guarding equals or exceeds the risk until the predator approaches closely (Cooper 1999b).

Lizards are ideal models for studies of predator escape because many are (i) small in body size and (ii) diurnal and easily observed, and (iii) their behaviors can easily be quantified. Moreover, in many instances their real or potential predators are well known. Birds, because of their high mobility and high energy requirements, are undoubtedly the most important diurnal predators of lizards. For example, roadrunners (*Geococcyx californianus*) capture large numbers of whiptail lizards (*Cnemidophorus*: Teiidae) (Echternacht 1967) and shrikes capture phrynosomatids, gekkonids, and other lizards (Pianka 1986). Based on cursory observations, lizards have been categorized as using "known escape routes" (e.g., Vitt and Congdon 1978; Vitt and Price 1982), but quantitative data demonstrating that lizards know where to go when attacked are lacking. An alternative hypothesis is that they simply go to the closest available refuge, making their escape decision at the time that they are attacked. Experiments in which the closest refuge was blocked revealed that lizards fled toward alternative refuges (Cooper 1999a). These hypotheses are not mutually exclusive; lizards may "know" the best escape route, use it when possible, and select other options based on immediate threats when their preferred option imposes high risk. They may also "know" which among several possible refuges offers the best protection from predators.

We designed a set of field experiments to determine responses of lizards to a model predator under natural field conditions. We selected a lizard species that can be easily detected by flying predators (birds) because of its use of vertical and horizontal rock surfaces with open exposure. The lizard *Lacerta perspicillata* (Lacertidae) inhabits vertical and horizontal surfaces on limestone quarries in the Balearic Islands of Spain that were excavated in the Middle Ages. The population dates back to the late 19th or early 20th century, when the lizards were introduced from North Africa (probably Algeria). *Lacerta perspicillata* occur at high density, are strictly diurnal, and are easily observable. Moreover, they can be approached to within 2 m with no apparent disturbance. Thick shrubs at edges of rock surfaces offer refuge; lizards can simply retreat on the rock surface behind the shrub. It is difficult to detect lizards and pinpoint their exact location behind bushes because the refuges have low light levels, and available light is broken up by shrub branches and leaves. Moreover, branches and leaves interfere directly with the flight path of an approaching bird. The limestone quarry contains few lizard predators, but there are several kestrel (*Falco tinnunculus*) nests near the study site. In addition, a migrant population of the lark *Lanius excubitor* is known to eat lizards in the area, and a wide variety of additional European birds are known predators of lizards (e.g., Martín and López 1990). We address the following questions: (i) do lizards use the shortest available escape route, select alternative routes, suggesting that some routes are better than others, or simply move away randomly? (ii) do lizards escape to the nearest refuge, the best refuge, or select a refuge randomly? Because kestrels and other predatory birds have direct-flight access to lizards exposed on rock surfaces, our expectation was that lizards would quickly and directly run to the nearest refuge when approached by such a predator.

Methods and materials

A large isolated population of *L. perspicillata* lives on surfaces of a limestone quarry located at Lithica on the island of Menorca in the Balearic Islands. A model was designed to mimic the shape and size of an attacking bird of prey (with a kestrel as a model) with the head bent downward to provide lizards with a view of the model with eyespots. Behavioral responses of lizards to the model (see below) indicate that it serves well as a proxy for a bird of prey. We constructed three identical models and attached them to wooden poles 2 cm in diameter \times 2.5 m in length (Fig. 1). Three investigators practiced approaches in order to standardize data collection. By selecting different pathways through the quarry we used different lizards for each test to ensure that all observations were independent. We searched the quarry for an undisturbed *L. perspicillata*, which was then tested. Each investigator slowly approached the focal lizard, stopping at a distance of approximately 2–3 m from it. If the lizard responded to the approach, it was not tested. Once the investigator was within range, the model was presented. Three protocols were used to present the model: (1) from above the lizard, (2) from below the lizard, and (3) from the same level as the lizard (direct approach). For the "above" approach, the model was raised approximately 2 m above the lizard and moved forward and down to it. For

Fig. 1. Model bird of prey used for predator escape trials with *Lacerta perspicillata*. The head was bent partially down to expose the eyespots to the lizard.

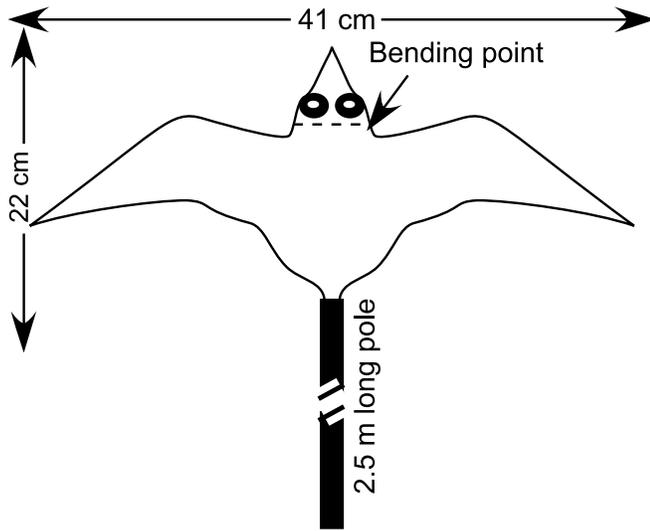
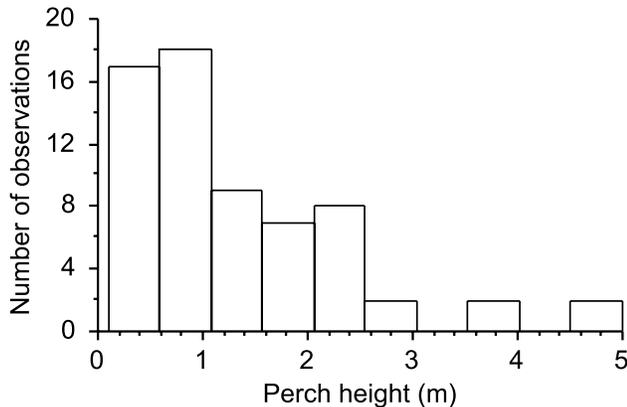


Fig. 2. Distribution of perch heights for *L. perspicillata* observed on vertical limestone surfaces.



the “below” approach, the model was held below the lizard and moved forward and up to it. Distance below varied depending on the height of the lizard’s perch, but in most trials exceeded 1 m. For the “same height” approach, the model was held at a height equal to that of the lizard and moved directly toward it. In all trials, models were presented at a moderately rapid rate and were stopped when they reached the initial position of the experimental lizard.

When approached by the model, lizards had the options of not responding, simply changing their position on the surface, or entering some kind of refuge. We defined a refuge as any place the lizards went that made them unavailable to an approaching predator (the model in this case). The following data were recorded for each trial: approach type (above, below, same height), lizard’s perch height, direction in which the lizard fled (measured as the angle, with 0° as straight up and 180° as straight down), distance the lizard fled (hereinafter lizard escape distance), whether or not the lizard entered a refuge, type of refuge, distance to the closest refuge, direction to the closest refuge, type of the nearest

Table 1. Summary of descriptive statistics for habitat variables, refuge location, and direction in which *L. perspicillata* fled ($N = 65$).

	Mean \pm SE	Range
Rock height	4.017 \pm 0.400	0.10–15.00
Perch height	1.340 \pm 0.141	0.10–5.00
Direction to nearest refuge	113.462 \pm 7.092	0.00–180.00
Direction to refuge used	120.308 \pm 7.215	0.00–180.00
Direction lizard fled	119.538 \pm 7.298	0.00–180.00

refuge, and distance and direction to the refuge used. The latter two measurements differed from the distance and direction that lizards actually moved in that they were fixed points in the habitat. Most lizards fled in a more or less straight line to a refuge, so the direction in which the lizard fled was accurate along the entire course. In instances when the flight course was not a straight line, we estimated a straight-line angle across a slightly curved trajectory. Lizards could go directly or indirectly to refuges and they might travel farther than the distance to the refuge by going behind or into it. We also recorded the height of the rock surface on which the lizard was observed. When the lizard’s perch height equals the height of the rock surface, the lizard was on top of the limestone surface. In most cases, lizards on top of rock surfaces were positioned at the edge so that they could see over it.

Because distributions of distances measured (lizard escape distance, distance to the nearest refuge, distance to the refuge used) were not normal, all distance measures were \log_{10} -transformed prior to the main statistical analyses. Analysis of covariance (ANCOVA) was used to test for differences among experimental groups when dependent variables were correlated with other relevant variables. Chi-square and Fisher’s exact probability tests were used to analyze frequency differences among approach and refuge types. Statistical analyses were performed with StatView 5® and Statistica 1999®.

Results

Lacerta perspicillata in this study typically positioned themselves on vertical rock faces from just above ground level to as high as the top of rock faces 5 m in height (Fig. 2). Thirty lizards were approached from above by the model predator, 20 times from below, and 26 times from the same height as the lizard, for a total of 76 predator escape trials. Although a marginally significant difference existed between investigators in escape distances used by lizards ($F_{[2,58]} = 2.9, P = 0.0617$), this difference disappeared when the effect of distance to the refuge was removed (data collector, $F_{[2,58]} = 0.8, P = 0.4940$; interaction between data collector and distance lizard fled, $F_{[2,58]} = 2.18, P = 0.1002$). The variation among investigators reflects variation in choice of lizards to test rather than variation in response to models associated with the investigator.

Sixty-five lizards (85.5%) entered refuges, 11 (14.5%) did not. Of those that sought refuge, 29 (44.6%) escaped by running behind a shrub growing against the rock surface, 7 (10.8%) went behind a shrub and dropped to the ground (“bush to ground”), 10 (15.4%) entered crevices, 18 (27.7%)

Fig. 3. Distribution of directions that *L. perspicillata* fled when approached by a model bird of prey; 0° indicates straight up and 180° indicates straight down.

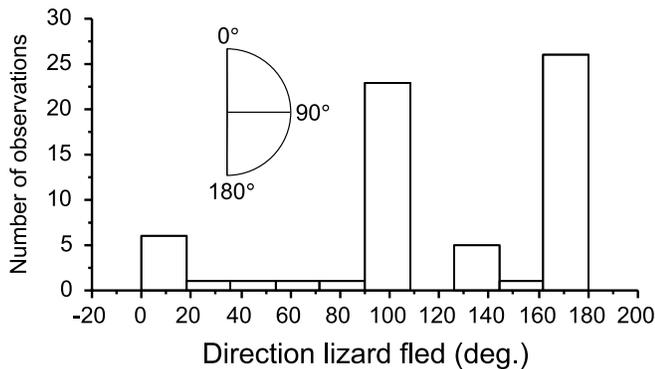
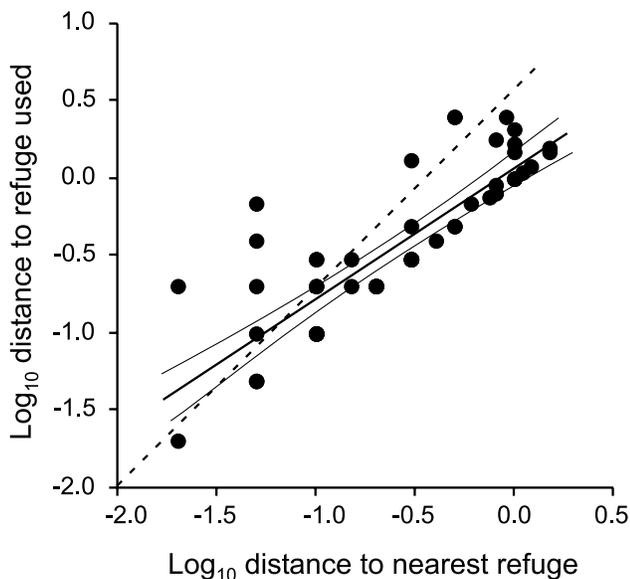


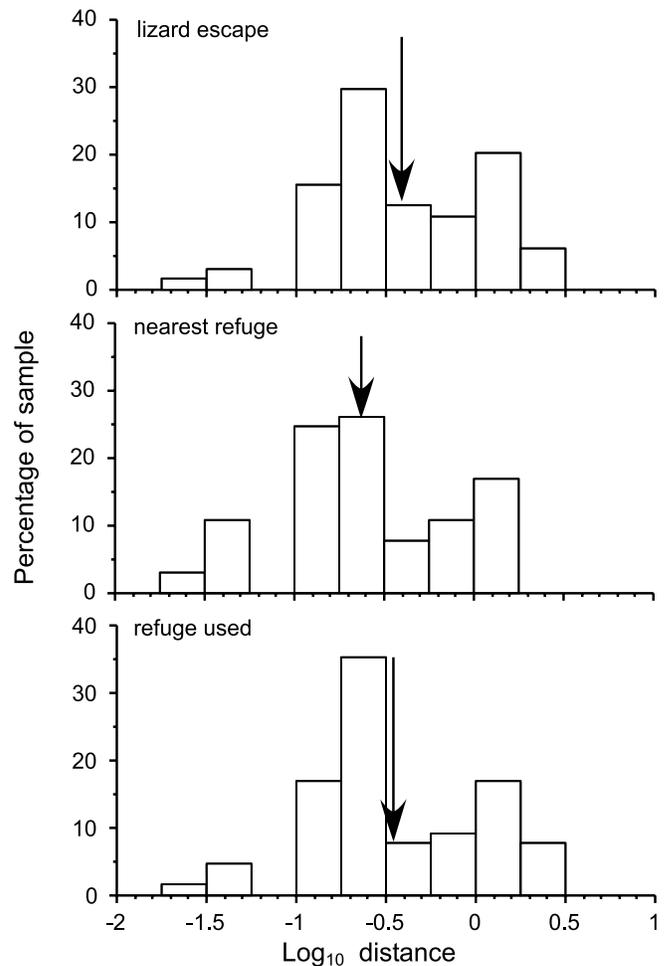
Fig. 4. Relationship between the distance to the nearest available refuge and the distance to the refuge used by *L. perspicillata*. Log distance to the refuge used = $0.058 + 0.849 \times \log$ distance to the nearest refuge; $R^2 = 0.709$. The broken line indicates equality between the distance the lizard fled and the distance to the nearest refuge.



escaped by running out of sight around or over a rock edge, and 1 (1.5%) went behind a small rock. For the most part, lizards occupied positions relatively low on the rock faces, fled directly to either the closest refuge or one only slightly farther away, and, on average, fled at an angle of about 120° down from vertical (Table 1). Close examination of flight-angle data reveals that most lizards fled either parallel to the ground or directly toward the ground when seeking refuge from the approaching model (Fig. 3).

Significant relationships existed between lizard escape distances and distances to both the nearest refuge ($R^2 = 0.496$, $F_{[1,62]} = 61.0$, $P < 0.0001$) and the refuge used ($R^2 = 0.571$, $F_{[1,62]} = 82.4$, $P < 0.0001$). The difference between distance the lizard fled and distance to refuge selected was small (0.028 ± 0.057 m; mean \pm SE), indicating that lizards tended to run almost directly to refuges. The difference between distance the lizard fled and distance to the nearest ref-

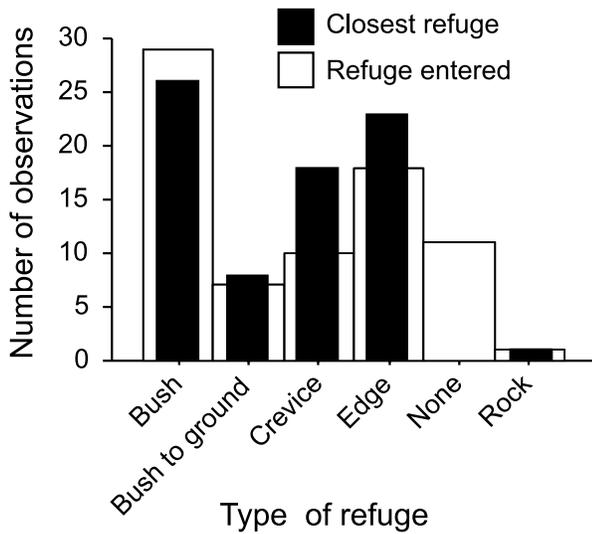
Fig. 5. Distances lizards fled (lizard escape distance), distances to the nearest refuge, and distances to the refuge used for *L. perspicillata* approached by a model bird of prey. The arrows indicate the mean.



uge (often not used) was much greater (0.225 ± 0.06 m), indicating that lizards ran farther than necessary to seek refuge (Mann–Whitney U test, $Z = -3.076$, $P = 0.0021$). Distance to the refuge used was also correlated with the distance to the closest refuge ($R^2 = 0.704$; $F_{[1,63]} = 153.4$, $P < 0.0001$; Fig. 4). Direction of approach by the model had no effect on escape distance (ANCOVA, $F_{[2,58]} = 0.98$, $P = 0.3798$); no effect of distance to the refuge used was detected (interaction term, $F_{[2,58]} = 1.2$, $P = 0.3229$). On average, direction in which lizards fled and direction to the refuge used differed by only $6.08 \pm 4.56^\circ$, indicating that lizards generally ran directly toward refuges. Refuges used were generally <1.0 m from lizards' initial positions on rock faces (Fig. 5).

Twenty-three of 65 lizards that fled (35.4%) entered refuges of a type that differed from that of the closest refuge (Fig. 6). When bush, bush to ground, or rock refuges were closest, lizards usually used them. However, lizards close to crevice or edge refuges often opted for alternative refuges. When data for lizards that did not enter refuges are excluded, individuals nearest crevices selected other refuge types significantly more frequently than did individuals nearest all other refuge types (Fisher's test, $P = 0.0156$). The probability of using refuge types other than the nearest refuge was signifi-

Fig. 6. Comparisons of closest refuge type and refuge type used for *L. perspicillata*.



cantly greater for lizards nearest crevices than nearest bushes, bush to ground, and rock pooled (Fisher’s test, $P = 0.0024$), but did not differ significantly between those nearest crevice and edge (Fisher’s test, $P = 0.283$) or between edge and bush, bush to ground, and rock pooled.

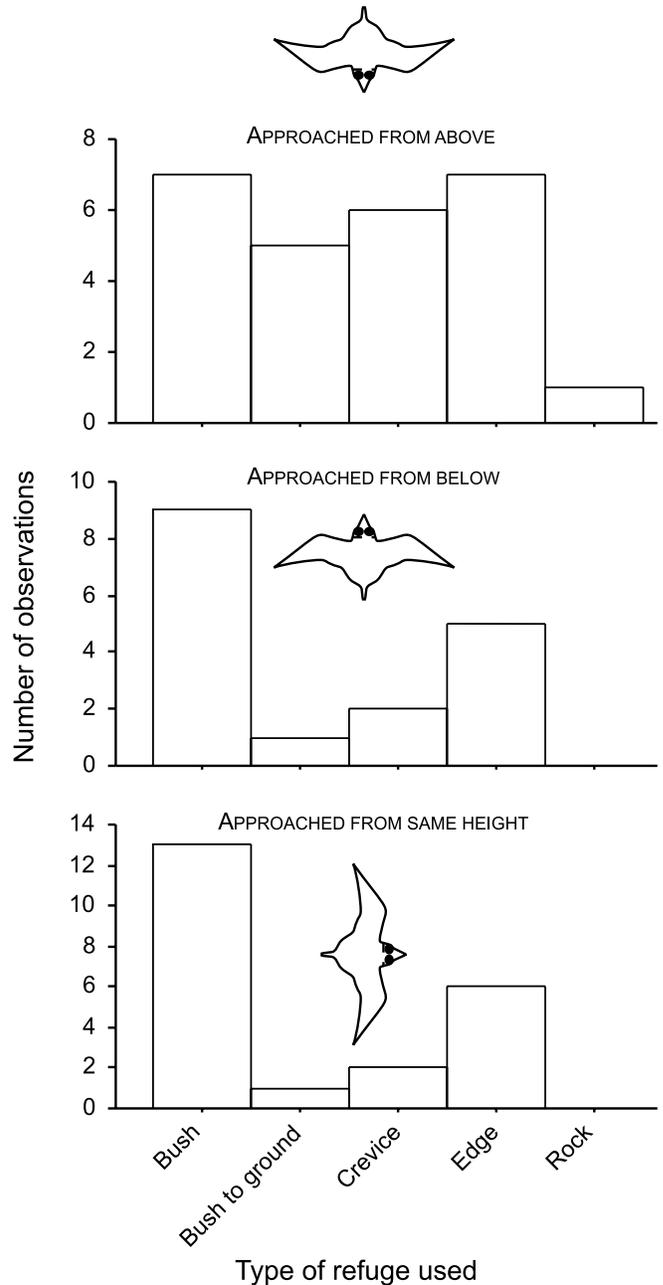
Approach direction affected the type of refuge selected ($\chi^2 = 8.38$, $P < 0.020$; Fig. 7). Approach direction did not affect the likelihood of entering a refuge ($\chi^2 = 0.056$, $P > 0.10$). When approached from above, lizards used bushes less frequently and used bush to ground and crevices as refuges more frequently than when approached from the same height or below. These differences were not attributable to relationships between perch height and types of refuge. Perch height did not differ significantly among types of refuges used ($F_{[5,70]} = 1.09$, $P < 0.376$).

Discussion

Optimal escape theory predicts distances between predators and prey at which an escape response will be initiated (Ydenberg and Dill 1986; Martín and López 1999; Cooper and Vitt 2002; Cooper et al. 2003). In its simplest form, optimal escape theory predicts that escape behaviors will be initiated when the risk of predation equals or exceeds the potential fitness gain associated with the status quo (the “cost” of escape). Risk factors vary enormously, and many remain poorly studied (e.g., Cooper 1998a). Among the most obvious are the predator’s speed relative to the prey’s, directness of approach, distance to and accessibility of refuges, predator persistence, and the predator’s ability to capture the prey.

Lizards living on vertical rock surfaces easily avoid predation by many potential predators because the predators (e.g., snakes, terrestrial lizards) cannot gain access to them. The cost of living on such surfaces is likely associated with reduced opportunities for capturing prey that live on the ground or in vegetation. Open rock surfaces do, however, provide direct access to avian predators. Lizards should minimize exposure by retreating rapidly from their perches when approached by flying predators.

Fig. 7. Variation in type of refuge used by *L. perspicillata* according to the direction of approach by a model bird of prey. Lizards approached from above more frequently chose bush to ground and crevice than those approached from the other directions.



Even though lizards did not always select the closest refuge, they selected refuges that were not much farther away than the closest refuge. Our results not only support the long-held notion that sit-and-wait foraging lizards use “known escape routes” (Vitt and Congdon 1978; Vitt and Price 1982), they also suggest that lizards recognize good refuges. Our results confirm that *L. perspicillata* opt for escape routes that provide them with easy access to refuges in a manner which suggests that they know exactly where to go. Nevertheless, attacks from above resulted in more lizards fleeing to crevices and bush to ground. This suggests that attacks from above might have a higher associated risk and

lizards may choose the closest rather than the “best” refuge or one with which they have had previous experience. The possibility exists, for example, that crevices have a degree of uncertainty with respect to safety which causes lizards to use them only when the risk of capture by avian predators is particularly high, and they are the closest refuges. The physical structure of crevices may be uncertain for lizards that do not use them often (e.g., the lizard may not be able to retreat far enough into the crevice to effect escape). Other potential predators (e.g., scorpions, snakes) may use the crevices, adding to their uncertainty as escape routes. In addition, even if crevices are safe havens for lizards being attacked by avian predators from above, emergence from crevices may pose a higher risk than selecting alternative refuges from which emergence has no added risk (see Cooper 1998e).

Even though several kinds of refuge are available to lizards on vertical limestone surfaces, 44.6% of lizards retreated behind shrubs growing against the limestone, with some jumping to the ground. This behavior allows easy escape from attacking birds because the distance to refuge is short, shrubs interfere with the predator’s line of sight toward the lizard, limbs and leaves break up light penetration, making the lizard more cryptic in the shade of the shrub, and leaves and branches physically isolate the lizards from approaching avian predators. Moreover, because the visual landscape experienced by the lizard changes as it moves, alternative escape routes and refuges can be assessed as lizards move toward the refuge selected from the initial perch.

Refuges used were frequently farther from the lizards than other available refuges even though the two are highly correlated. The reasons why lizards might select refuges that are farther away than necessary include a perceived certainty that doing so will not incur additional risk (e.g., enough time exists to get to the refuge), that refuges might vary in quality, or that the lizards have made successful escapes earlier when using the same refuge. Alternatively, if a lizard has not explored the area in which it lives, a familiar refuge might be a better choice than an unfamiliar one. Even when escaping toward a particular refuge, a lizard often did not enter the refuge at the closest point of access. Finally, our results indicate that decisions concerning refuge as a predation attempt unfolds may be complex. Even though *L. perspicillata* appeared to make good choices in seeking refuge from flying predators, the observation that lizards failed to enter a refuge at the closest point of access and their frequent use of alternative refuges suggest that predators attacking from the air may anticipate use of the closest refuge by an escaping lizard, and lizards may respond accordingly, either through behavioral adjustments or as a result of natural selection on escape behaviors. Alternatively, use of some crevices may carry additional risk. The false smooth snake (*Macroprotodon cucullatus*), for example, occurs in the quarries and is known to eat lizards. Lizards may avoid some crevices that are large enough to harbor snakes.

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References

- Cogger, H.G., and Zweifel, R.G. (Editors). 1998. Encyclopedia of reptiles and amphibians. Academic Press, San Diego.
- Cooper, W.E., Jr. 1997a. Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. *Herpetologica*, **53**: 464–474.
- Cooper, W.E., Jr. 1997b. Three factors affecting antipredatory behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator’s field of view. *Copeia*, 1997: 613–619.
- Cooper, W.E., Jr. 1998a. Conditions favoring anticipatory and reactive displays deflecting predatory attack. *Behav. Ecol.* **9**: 598–614.
- Cooper, W.E., Jr. 1998b. Direction of predator turning, a neglected cue to predation risk. *Behaviour*, **135**: 55–64.
- Cooper, W.E., Jr. 1998c. Effects of refuge and conspicuousness on escape behavior by the broad-headed skink (*Eumeces laticeps*). *Amphib.-Reptilia*, **19**: 103–108.
- Cooper, W.E., Jr. 1998d. Reactive and anticipatory display to deflect predatory attack to an autonomous lizard tail. *Can. J. Zool.* **76**: 1507–1510.
- Cooper, W.E., Jr. 1998e. Risk factors and emergence from refuge in the lizard *Eumeces laticeps*. *Behaviour*, **135**: 1065–1076.
- Cooper, W.E., Jr. 1999a. Escape behavior by prey blocked from entering the nearest refuge. *Can. J. Zool.* **77**: 671–674.
- Cooper, W.E., Jr. 1999b. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol.* **47**: 54–59.
- Cooper, W.E., Jr. 2000a. Multiple roles of tail display by the curly-tailed lizard, *Leiocephalus carinatus*: pursuit deterrent and deflective roles of a social signal. *Ethology*, **107**: 1137–1149.
- Cooper, W.E., Jr. 2000b. Pursuit deterrence in lizards. *Saudi J. Biosoc. Sci.* **7**: 15–28.
- Cooper, W.E., Jr., and Vitt, L.J. 2002. Optimal escape and emergence theories. *Comments Theor. Biol.* In press.
- Cooper, W.E., Jr., van Wyk, J.H., and Mouton, P.L.F.N. 1999. Incompletely protective refuges: selection and associated defences by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). *Ethology*, **105**: 687–700.
- Cooper, W.E., Jr., van Wyk, J.H., Mouton, P.L.F.N., Al-Johany, A.M., Lemos-Espinal, J.A., Paulissen, M.A., and Flowers, M. 2000. Lizard antipredator behaviors preventing extraction from crevices. *Herpetologica*, **56**: 394–401.
- Cooper, W.E., Jr., Pérez-Mellado, V., Baird, T., Baird, T.A., Caldwell, J.P., and Vitt, L.J. 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behav. Ecol.* In press.
- Dial, B.E. 1986. Tail display in two species of iguanid lizards: a test of the “predator signal” hypothesis. *Am. Nat.* **127**: 103–111.
- Echternacht, A.C. 1967. Ecological relationships of two species of the lizard genus *Cnemidophorus* in the Santa Rita Mountains in Arizona. *Am. Midl. Nat.* **78**: 348–359.
- Gilliam, J.F., and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.

- Greene, H.W. 1988. Antipredator mechanisms in reptiles. *In* *Biology of the Reptilia*. Vol. 16. Ecology B. Defense and life history. Edited by C. Gans and R.B. Huey. Alan R. Liss, Inc., New York. pp. 1–152.
- Hasson, O., Hibbard, R., and Ceballos, G. 1989. The pursuit deterrence function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.* **67**: 1203–1209.
- Leal, M., and Rodríguez-Robles, J.A. 1997. Signalling displays during predator–prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim. Behav.* **54**: 1147–1154.
- Martín, J., and López, P. 1990. Amphibians and reptiles as prey of birds in southwestern Europe. *Smithsonian Herpetological Information Service*, No. 82. pp. 1–43.
- Martín, J., and López, P. 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav. Ecol.* **10**: 487–492.
- Pianka, E.R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton University Press, Princeton, N.J.
- Pianka, E.R., and Vitt, L.J. 2003. Lizards: windows to the evolution of diversity. University of California Press, Berkeley. In press.
- Pitcher, T.J., Lang, S.H., and Turner, J.A. 1988. A risk-balancing tradeoff between foraging rewards and predation hazard in a shoaling fish. *Behav. Ecol. Sociobiol.* **22**: 225–228.
- Vitt, L.J., and Congdon, J.D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112**: 595–608.
- Vitt, L.J., and Price, H.J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica*, **38**: 237–255.
- Ydenberg, R.C., and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Stud. Behav.* **16**: 229–249.