Copeia, 2003(2), pp. 408–413

Changes in the Escape Responses of the Lizard *Acanthodactylus erythrurus* under Persistent Predatory Attacks

José Martín and Pilar López

We hypothesized that, through persistent predatory attacks, lizards should increase progressively the magnitude of their escape response. We simulated in the field a continuous attack by a persistent predator on *Acanthodactylus erythrurus* lizards and examined the characteristics of successive escape responses, microhabitats used for fleeing, and the refuges used. Lizards responded to the persistent attacks by increasing the distances they fled and the degree of cover in microhabitats into which they escaped. Lizards also changed their escape strategy from the first to the successive attacks. Initially, most individuals did not hide but stopped after running and remained vigilant, whereas almost all individuals hid subsequently. In addition, after successive predatory attacks, lizards used more structurally complex refuges (i.e., larger and with more obstructive cover). These refuges were probably safer although they may lower the lizard's capacity to observe the predator's subsequent behavior. These data suggest that lizards interpret persistent predatory attacks as an increase in predation risk and that lizards adjusted the magnitude of their escape and antipredatory responses to predation risk level.

An animal that detects an approaching predator needs to decide when and how to escape because fleeing may be costly (Ydenberg and Dill, 1986). Approaching predators do not always pose an immediate threat; thus, animals should tend to adjust their escape and antipredatory responses to save time and energy when risk is low. Many lizards escape from predators with a short flight to the nearest available refuge (Cooper, 1997a; Martín and López, 2000a). However, other species of lizards living in open habitats with sparse cover rely more on speed and running long distances to escape (Bulova, 1994). An intermediate case occurs when the predator can still locate and capture a concealed lizard (Martín and López, 2000b). In these latter two cases, a longer flight may be needed not only to reach a refuge but, more important, to avoid being located by the predator in the refuge. However, because fleeing may be costly, the escape response should balance the benefits of avoiding predators and saving energy of running sequences. Juveniles of the lizard *Psammodromus algirus* (Martín and López, 1995a, 1996) and a cichlid fish (Dill, 1990) adjusted their escape speed as a function of the speed of the predator, which may allow them to maintain a fixed margin of safety (Kramer and Bonenfant 1997).

Although, some predators may search elsewhere after having prey escape, others may remain in ambush outside a refuge or try to flush the prey from the refuge and launch a new attack. Such successive persistent attacks may be considered as an increase in the risk of predation (Cooper, 1997b; Martín and López, 2001). Each new repeated attack may indicate for the prey that the predator persists in attempting to capture that particular prey. Thus, through successive predatory attacks, lizards should increase progressively the magnitude of their escape response (e.g., by fleeing longer distances). Lizards may also adjust their successive escape responses to the microhabitat structure (Cooper, 1998a; Martín and López, 1998, 2000b). By increasing the cover of the microhabitats through which they run, lizards may have shorter and less costly repeated flight responses without incurring a higher risk of being captured.

However, hiding might be dangerous because the prey loses visual contact with the predator and, thus, become more susceptible to ambush. Prey should balance the partial protection provided by a refuge with the capacity to predict the predator's subsequent behavior. In successive attacks, prey should hide in increasingly more structurally complex refuges.

In this paper, we simulated a continuous attack by a persistent predator on *Acanthodactylus erythrurus* and examined the characteristics of successive escape responses, microhabitats used for fleeing, and refuges used.

Materials and Methods

Species and study site.—The common fringe-toad or spiny-footed lizard (*A. erythrurus*) is a medium-sized lacertid lizard (adult snout–vent length up to 82 mm). It is the only lizard of its genus present in Western Europe, where it oc-

cupies xeric, open, sandy areas with sparsely distributed vegetation (Arnold, 1987). This lizard feeds mainly on ants, which it captures in the open after short, rapid attacks launched from ambushing sites (Belliure et al., 1996).

The study was conducted in a siliceous and sandy area in southwestern Madrid (central Spain) at an average elevation of 600 m. The area was covered by an open ''dehesa'' woodland characterized by *Quercus ilex* forest with an understory of dispersed low shrub cover (mainly *Lavandula stoechas*, *Thymus mastichina*, and less frequently *Retama sphaerocarpa* and *Daphne gnidium*) and extensive areas of bare sand substrates between isolated bushes. We often observed in the area predators known to prey on this lizard, including several raptors, shrikes, and foxes (Martín and López, 1990).

Escape behavior.—We observed lizards in the field during July 2001. We haphazardly walked through the area between 0900 h and 1300 h GMT, when lizards were active. When a lizard on open ground was sighted with binoculars, we attempted to approach the lizard directly. The same person performed all approaches, walked at the same medium speed (about 40 m/min), and wore the same clothing, while another person recorded the lizard's behavior, to avoid confounding effects that may affect risk perception of lizards (e.g., Burger and Gochfeld, 1993; Cooper, 1997b). The usual response of the lizard was either to flee rapidly to the protective cover of a bush and hide in it or to run but then suddenly stop in the open without hiding (see below). We defined ''approach distance'' as the distance between the lizard and the observer when the lizard first moved (straight-line measured to the nearest 0.1 m). We characterized the escape response magnitude by measuring the total distance covered during active flight (''distance fled''; Bulova, 1994; Cooper, 1997a). Immediately after a lizard hid or stopped, we approached it, simulating a second predatory attack with the same characteristics. Thereafter, we simulated a third predatory attack. We measured distance fled for each attack. We did not note the approach distances in the repeated attacks, because lizards had often to be flushed from the bushes where they were hidden by slightly shaking the bush, simulating a search for the lizard by the predator. During attacks, we marked the refuges used by lizards with flags, and later we measured distances and recorded microhabitat characteristics.

To analyze whether the escape response of lizards was determined by the microhabitat and availability of refuges (Martín and López, 2000b; Cooper, 1997a), we measured the microhabitat along each of the three escape trajectories. We recorded contacts of foliage with a vertical stick at 25-cm intervals. Microhabitats could be classified according to the relative conspicuousness of a lizard (Martín and López, 2000b). Thus, fewer, lower contacts characterized microhabitats where lizards were more visible to potential predators (e.g., bare soil, short grass, leaf litter), and more numerous and higher contacts indicated microhabitats that provided visual cover and that might be used as refuges (e.g., bushy vegetation such as *Quercus*, *Lavandula*, *Thymus*, etc.). This procedure allowed us to calculate the proportion of sites along the escape trajectory where cover that might be used as a refuge was present (''trajectory cover'').

We also took four 20-cm transects, one at each of the four cardinal orientations radiating from the point where the individual stopped or hid in a refuge. We used a scored stick standing vertically at eight sample points (two points at 10-cm intervals in each of the four transects), and recorded the contacts with the stick at ground level of open microhabitats (i.e., grass, rocks or bare soil) or with bush vegetation cover. This procedure allowed us to calculate for each observation the percent cover values in the area surrounding the lizard's refuge (i.e., percent of contacts with bush cover; ''refuge cover''). The sampling of multiple points to characterize surfaces near the lizards rather than only measuring the particular point at the lizard's location allowed a better characterization of the microhabitat (for a similar sampling methodology see Martín and López, 1998). Because lizards often hid in bushes that were isolated between bare soil areas, we measured the ''refuge volume'' (i.e., the approximate volume, length $\times$ width $\times$ height, of the bush used) as an indication of the protective effectiveness of the refuge. We also measured the ''refuge height'' at the point where the lizard hid.

The escape response is influenced by temperature in some lizards (e.g., Hertz et al., 1982; Rocha and Bergallo, 1990; Smith, 1997). Lizards could not be captured immediately after they fled to measure their body temperatures. However, during sampling periods, average air temperatures were high (27.3 ± 0.5 C), and the analysis did not show any significant difference between periods ($P > 0.60$). Thus, we are confident that temperature did not influence the results of this experiment.

Data analysis.—We recorded the escape response of 43 lizards (three repeated continuous

TABLE 1. CHARACTERISTICS OF THREE SUCCESSIVE ESCAPE RESPONSES AND OF THE REFUGES USED BY *Acanthodactylus erythrurus* LIZARDS IN RESPONSE TO SIMULATED CONTINUOUS ATTACKS BY A PERSISTENT PREDATOR (SEE MATERIALS AND METHODS FOR THE MEANING OF VARIABLES). Small letters give the results of posthoc Tukey's HSD tests for differences between means for that variable; means with the same letter are not significantly different (P to reject = 0.05).

	First	Second	Third
Distance fled (cm)	143 ± 14 a	229 ± 20 b	243 ± 26 b
Trajectory cover (%)	32 ± 5 a	49 ± 4 b	66 ± 4 c
Refuge cover (%)	51 ± 6 a	79 ± 4 b	98 ± 1 c
Refuge height (cm)	31 ± 4 a	47 ± 4 b	65 ± 6 c
Refuge volume (m^3)	0.2 ± 0.1 a	0.4 ± 0.1 b	1.5 ± 0.7 c

attacks for each individual). Given the large size of the area surveyed (more than 5 km^2), the high lizard density (about 60 adults/ha; unpubl. data), and because we avoided walking routes taken previously, the probability of repeated sampling on the same individual was very low. We assessed the effects of repeated attack on the choice of an escape strategy (hiding vs stopping in the open) by comparing the frequencies observed to an expected binomial distribution assuming frequencies to be equiprobable. We employed McNemar χ^2-tests for the significance of changes to test whether the choice of escape strategy changed significantly from one response to the subsequent one (Siegel and Castellan, 1988).

Differences between successive escape responses and characteristics of the refuges used by each individual were evaluated by means of repeated measures analyses of variance (ANOVA) on data normalized by logarithmic transformation. Tests of homogeneity of variances (Levene's test) showed that in all cases variances were not significantly heterogeneous after transformation (Sokal and Rohlf, 1995). Pairwise comparisons were planned using Tukey's honestly significant difference (HSD) tests. Differences in the escape responses between individuals that used different escape strategies were evaluated using one-way ANOVAs or analyses of covariance (ANCOVA) to remove the effect of covariation between variables. To examine the relationship between escape behavior characteristics and microhabitat cover along the escape trajectory, we calculated Pearson's product moment correlation coefficients on log-transformed data (Sokal and Rohlf, 1995).

RESULTS

Escape strategies.—In the first attack, lizards did not show a preferred escape strategy (binomial test, $P = 0.36$) and either ran and then stopped in the open in an alert position, but without hiding (58.1%, 25 of 43), or hid in a refuge (41.9%, 18 of 43), usually a bush. In the second attack lizards changed their strategy significantly (McNemar test, $\chi^2 = 8.45$, $P = 0.004$) and preferentially hid in a refuge (74.4%; binomial test, $P = 0.002$), although some lizards still stopped in the open and did not hide (25.6%). In the third attack, all but one individual (97.7%) hid in a refuge ($P < 0.0001$), which meant a significant change in the strategy of lizards that had not hidden previously (McNemar test, $\chi^2 = 8.10$, $P = 0.004$).

Approach distance.—Approach distance and distance fled in the first attack were not significantly correlated for all data pooled ($r = 0.07$, $F = 0.19$, df = 1,38, $P = 0.66$). However, when we analyzed separately the two escape strategies, we found that when lizards hid in a refuge, the approach distance was significantly and positively correlated with distance to the refuge ($r = 0.64$, $F = 10.88$, df =1,16, $P = 0.004$). In contrast, when lizards did not hide but stopped in the open, the approach distance was significantly and negatively correlated with distance to the point where the lizard stopped ($r = -0.48$, $F = 6.06$, df =1,20, $P = 0.02$).

Distance fled.—Lizards responded to the continuous attacks by increasing the distance that they fled (one-way repeated measures ANOVA, $F = 11.57$, df = 2,82, $P < 0.0001$; Table 1). Lizards increased the distance fled significantly from the first to the second attack (Tukey test, $P = 0.0005$) but not from the second to the third attack ($P = 0.96$). Lizards that fled long distances in the first attack did not necessarily flee long distances in the second attack ($r = -0.17$, $F = 1.17$, $P = 0.29$). A similar lack of relationship was found between the second and the third flights ($r = 0.15$, $F = 0.91$, $P = 0.35$). However, lizards that increased the distance fled from the first to the second escape, thereafter showed a lower increase in the distance fled

from the second to the third escape ($r = -0.53$, $F = 15.7$, $P = 0.0003$).

Lizards increased the cover of the microhabitats to which they escaped (i.e., trajectory cover) through the successive sequences (one-way repeated measures ANOVA, $F = 22.02$, df = 2,82, $P < 0.0001$; Table 1). They increased cover both from the first to the second (Tukey test, $P = 0.0003$) and from the second to the third escape ($P = 0.012$). The distance fled varied with microhabitat cover. Lizards ran farther when they fled through microhabitats with less cover in the first ($r = -0.40$, $F = 7.64$, $P < 0.01$), second ($r = -0.36$, $F = 6.12$, $P = 0.018$), and third escapes ($r = -0.68$, $F = 34.57$, $P < 0.0001$).

In the first attack, lizards that did not hide fled significantly longer distances (166 ± 18 cm, $n = 25$) than lizards that hid (110 ± 21 cm, $n = 18$; $F = 8.96$, $P = 0.005$). This difference was, however, nonsignificant when the effect of covariation with microhabitat cover in the escape trajectory was removed (ANCOVA, $F = 1.08$, $P = 0.30$). Thus, differences observed in distance fled may be a result of the fact that lizards that did not hide ran through microhabitats with significantly less cover (20 ± 6% cover) than lizards that hid (48 ± 6%; $F = 12.68$, $P = 0.001$). In the second attack, differences in distance fled were not significant (one-way ANOVA, $F = 1.95$, $P = 0.17$), but lizards that did not hide still ran through microhabitats with less cover (37 ± 8%) than lizards that hid (53 ± 4%; $F = 6.51$, $P = 0.015$).

Use of refuges.—Through the successive attacks, lizards used refuges that each time had significantly more cover (one-way repeated measures ANOVA, $F = 29.33$, df = 2,82, $P < 0.0001$), significantly greater height ($F = 20.63$, $P < 0.0001$), and significantly more volume ($F = 26.36$, $P < 0.0001$) than the previous one used (Table 1). This trend was significant from the first to the second attack (Tukey tests, $P = 0.0001$ in all cases), and from the second to the third attack ($P < 0.01$ in all cases). Therefore, in successive continuous attacks lizards increased the potential safety and complexity of the refuge used.

Discussion

Lizards changed their escape strategy during successive continuous attacks. Initially, most individuals did not hide but stopped after running and remained vigilant. Because the lizard has the predator under surveillance, it can flee again if the predator continues to approach. In contrast, because most available refuges are not entirely safe, hiding might be dangerous because the prey may lose visual contact with the predator, thus increasing the probability of later being taken by surprise (Martín and López, 1999). Nevertheless, the choice of strategy was dependent on microhabitat cover. Lizards running through microhabitats with more obstructive visual cover where they were less conspicuous tended to hide and fled shorter distances. This indicates that differences in the escape responses of lizards may be partially explained by the differences in relative safety of the microhabitats that they occupy (Bulova, 1994; Martín and López, 1995b; Cooper, 1997a).

The differential use of refuges through successive attacks may be explained because, in addition to the lower opportunities to monitor the predator's subsequent behavior, refuges may be costly in terms of loss of time available for foraging or mate searching (Sih, 1997) or physiological costs (Martín and López, 2000a). However, when predation risk increases, the benefits of using refuges may outweigh their potential costs.

Theoretical studies and field experiments indicate that, 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 (e.g., Ydenberg and Dill, 1986; Cooper 1997a). We found this relationship in *A. erythrurus* but only when individuals actually ran to hide to a refuge. However, optimal escape theory applies only to prey that flee to refuges (Ydenberg and Dill, 1986). The relationship is the opposite when lizards stopped without hiding. In this case, lizards might be compensating for a shorter approach distance (i.e., a higher risk) with a longer distance fled. Because they did not hide in a refuge, lizards that have delayed the escape decision started to run when the predator was closer. To maintain a constant margin of safety, as do woodchucks, *Marmota monax*, (Kramer and Bonenfant, 1997), they should run further.

The observed increase in the magnitude of the successive escape responses suggests that continuous persistent predatory attacks were interpreted as an increase in predation risk. This result agrees with the general tendency of many animals, including lizards, to modify their microhabitat or refuge use according to the estimated levels of predation risk (Lima and Dill, 1990; Cooper, 1997b; Martín and López, 2001). These data may indicate that lizards perceived a higher predation risk because of persistence by an individual predator, although individual recognition of the predator may not be needed

if the assessment was based on attack rate (Cooper, 1998b).

Even if refuges were entirely safe, an increase in distance fled means an increase in the probability of eluding the predator. However, longer flights may be energetically more costly, increase oxygen debt, and/or require the use of anaerobic metabolism, which may affect short-term performance in subsequent escapes. In this context, the first escape response of *A. erythrurus* was shorter than the subsequent ones. This suggests that lizards adjust the magnitude of their escape response according to predation risk level. Alternatively, changes in other components of the escape response such as an increase in microhabitat cover or refuge safety may allow lizards to increase the magnitude of the antipredatory response without increasing costs of longer flights.

After continuous predatory attacks, lizards used more structurally complex refuges. For example, during their first escape lizards used the relatively abundant low and small bushes of *Lavandula* or *Thymus*, where they often hid just inside the margin of the bush. In subsequent responses, lizards sometimes used isolated rocky outcrops with large patches of thorny subarboreal vegetation or intricate underground galleries of rabbits under spiny bushes. However, these latter types of refuges are relatively scarce in the microhabitat occupied by *A. erythrurus*. This suggests that lizards may initially use any available refuge, but, if the risk persists, they might use previously known escape routes to refuges that provide a high degree of safety (e.g., Clarke et al., 1983). Anecdotal observations of marked individuals that on different days ran to the same specific large refuges from different locations also suggests this strategy (unpubl. data).

Acknowledgments

We thank two anonymous reviewers for helpful comments, Ana for field assistance, and ''El Ventorrillo'' MNCN Field Station for use of their facilities. The study and animal care protocol was approved by the Environmental Agency of the Madrid Local Government (''Agencia del Medio Ambiente de la Comunidad de Madrid''). Financial support was provided by the DGESIC project PB-98-0505, MCYT project BOS 2002-00547, and a ''Ramón y Cajal'' MCYT contract to PL.

Literature Cited

Arnold, E. N. 1987. Resource partitioning among lacertid lizards in Southern Europe. J. Zool. (suppl.) 1:739–782.

Belliure, J., L. M. Carrascal, and J. A. Díaz. 1996. Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. Ecology 77: 1163–1173.

Bulova, S. J. 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. Copeia 1994: 980–992.

Burger, J., and M. Gochfeld. 1993. The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. J. Herpetol. 27:426–430.

Clarke, M. F., K. Burke Da Silva, H. Lair, R. Pocklington, D. L. Kramer, and R. L. Mclaughlin. 1983. Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. Oikos 66:533–537.

Cooper, W. E., Jr. 1997a. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). Can. J. Zool. 75:943–947.

———. 1997b. Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. Copeia 1997:613–619.

———. 1998a. Effects of refuge and conspicuousness on escape behavior by the broad-headed skink (*Eumeces laticeps*). Amphib.-Reptilia 19:103–108.

———. 1998b. Risk factors and emergence from refuge in the lizard *Eumeces laticeps*. Behaviour 135: 1065–1076.

Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. Environ. Biol. Fish. 27:147–152.

Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. 30:676–679.

Kramer, D. L., and M. Bonenfant. 1997. Direction of predator approach and the decision to flee to a refuge. *Ibid.* 54:289–295.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640.

Martín, J., and P. López. 1990. Amphibians and reptiles as prey of birds in southwestern Europe. Smiths. Herpetol. Inf. Serv. 82:1–43.

———, and ———. 1995a. Escape behaviour of juvenile *Psammodromus algirus* lizards: constraint of or compensation for limitations in body size? Behaviour 132:181–192.

———, and ———. 1995b. Influence of habitat structure on escape tactics of *Psammodromus algirus* lizards. Can. J. Zool. 73:129–132.

———, and ———. 1996. The escape response of juvenile *Psammodromus algirus* lizards. J. Comp. Psychol. 110:187–192.

———, and ———. 1998. Shifts in microhabitat use by the lizard *Psammodromus algirus*: responses to seasonal changes in vegetation structure. Copeia 1998: 780–786.

———, and ———. 1999. When to come out from a refuge: risk-sensitive and state-dependent in an alpine lizard. Behav. Ecol. 10:487–492.

———, and ———. 2000a. Costs of refuge use affect escape decisions of iberian-rock lizards, *Lacerta monticola*. Ethology 106:483–492.

———, AND ———. 2000b. Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. Can. J. Zool. 78:265–270.

———, AND ———. 2001. Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. Behav. Ecol. 12:386–389.

ROCHA, C. F. D., AND H. G. BERGALLO. 1990. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. Ethol. Ecol. Evol. 2:263–268.

SIEGEL, S., AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. 2d ed. McGraw-Hill, New York.

SIH, A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. Trends Ecol. Evol. 12: 375–376.

SMITH, D. G. 1997. Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. Behav. Ecol. 8:622–629.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. 3d ed. W. H. Freeman, New York.

YDENBERG, R. C., AND L. M. DILL. 1986. The economics of fleeing from predators. Adv. Stud. Behav. 16: 229–249.

DEPARTAMENTO DE ECOLOGÍA EVOLUTIVA, MUSEO NACIONAL DE CIENCIAS NATURALES, CSIC, JOSÉ GUTIÉRREZ ABASCAL 2, 28006 MADRID, SPAIN. E-mail: (JM) jose.martin@mncn.csic.es. Send reprint requests to JM. Submitted: 7 May 2002. Accepted: 23 Oct. 2002. Section editor: M. E. Douglas.