TRADEOFFS BETWEEN ESCAPE BEHAVIOR AND FORAGING OPPORTUNITY BY THE BALEARIC LIZARD (*PODARCIS LILFORDI*)

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ABSTRACT: Optimal escape theory predicts that prey permit closer approach by predators when fleeing is more costly, but does not predict other aspects of escape such as distance fled or the likelihood of returning to the initial site in the presence or absence of a resource such as food. Because a lizard preparing to feed may lose the feeding opportunity, optimal escape theory predicts that the lizard should allow a predator to approach closer before fleeing when a stationary food source is present than in its absence. In addition, we predicted that when a predator was nearby, lizards would flee a shorter distance and return more often when food was present than absent. We presented adult males of the omnivorous Balearic lizard, *Podarcis lilfordi*, with a tethered piece of pear or a pebble of similar size and shape. One of us approached a lizard in a standardized manner, stopping and remaining still when the lizard fled. The other investigator recorded escape and return behaviors. Lizards in the presence of food permitted closer approach before fleeing, fled a substantially shorter distance, and were far more likely to return to the site of stimulus presentation than when a pebble was presented. These findings suggest that prey may alter several aspects of escape behavior to reduce costs due to lost opportunities, and present a likelihood that interspecific variation exists in the combination of aspects of antipredatory behavior that are modified.

Key words: Escape behavior; Optimal escape theory; *Podarcis lilfordi*; Squamata; Trade-offs

OPTIMAL escape theory predicts that prey will begin escape attempts when a predator approaches to a point, the optimal approach distance, at which risk of predation equals the cost of escape (Ydenberg and Dill, 1986). This simple hypothesis makes numerous predictions about effects of various risk and cost factors. As risk increases for a constant cost, the distance between predator and prey when an escape attempt begins, the approach distance (= flight initiation distance), is predicted to increase. This has been confirmed in numerous studies of diverse taxa, including lizards (e.g., Bonenfant and Kramer, 1996; Bulova, 1994; Cooper, 1997*a,b,c*; reviewed by Lima and Dill, 1990). As cost of escape increases for a fixed degree of risk, approach distance is predicted to decrease (Cooper and Vitt, 2002; Ydenberg and Dill, 1986). Several predictions based on costs also have been confirmed (e.g., Cooper, 1999, 2000, 2003; Lima and Valone, 1986; Magnhagen, 1991; Martín et al., in press), but effects of costs on escape have been studied far less than those of risk of predation.

One important cost of fleeing that has received little attention despite its potentially widespread importance is forgoing feeding opportunities. The insectivorous scincid lizard *Eumeces laticeps* permits closer approach by a predator before fleeing when near an experimentally introduced cricket than in the absence of food (Cooper, 2000). After fleeing, the insectivorous lacertid lizard *Lacerta monticola* comes out of refuge sooner when experimentally introduced prey (mealworms) are visible from the refuge, indicating that loss of feeding opportunities is a cost of refuge use that influences time spent in refuge (Martín et al., 2003). This finding is relevant to optimal escape theory because it indicates that loss of feeding opportunity is an economic factor in refuge use, which is closely related to escape. If one replaces distance between predator and prey by time spent in refuge, optimal escape theory is transformed to predict optimal duration of stay in refuge before emerging.

We present the findings of a simple experimental field study designed to test the hypothesis that loss of opportunity to eat fruit due to fleeing is a cost of escape that results in decreased approach distance in the Balearic lizard (*Podarcis lilfordi*). Optimal escape theory as initially presented applied to prey that flee to refuges when approached by a predator detected beyond the optimal approach distance, but was intended to apply also to prey

that do not flee to refuges (Cooper and Vitt, 2002; Ydenberg and Dill, 1986). Its predictions appear to apply to nonrefuging lizards (Cooper et al., 2003). Individuals of *Podarcis lilfordi* often escape into refuges such as bushes and crevices beneath rocks (personal observations), but we used locations in which lizards were on bare soil or isolated rocks away from nearby bushes or piles of rocks (further than 15 m) that offered extensive crevices suitable as refuges. Lizards near refuges either run away on the surface or enter refuge, but lizards in open areas typically did not run to refuges, instead stopping in the open after fleeing. This behavior permitted us to examine the effect of presence of plant food on distance fled and return to the food despite the presence of a predator nearby.

In addition to the prediction about approach distance based on optimal escape theory, we made two other predictions not covered by the theory. Due to the nutritive value of the food presented, we predicted that lizards would flee farther in the absence of food than in its presence, accepting the greater risk of closer final proximity to the predator to enhance the opportunity to secure the food and possibly to reduce the cost of obtaining the food after fleeing. We also predicted that lizards would be more likely to return to an experimental site from which they had fled if food was present, thereby reducing the likelihood of loss of the food due to fleeing. These are novel predictions about tradeoffs between antipredatory and foraging behaviors although approaching a predator to feed has been reported previously in a lizard (Cooper, 2000).

MATERIAL AND METHODS

Balearic lizards are small, omnivorous lacertids (maximum SVL 81 mm) that reach extremely high density, up to 20,000 per hectare) on Aire, an islet off the coast of Menorca, Balearic Islands, Spain (Pérez-Mellado, 1998). Natural predators of *P. lilfordi* include mammals and birds, especially kestrels (*Falco tinnunculus*). We studied adult male *P. lilfordi* in June 2000 in warm, sunny conditions on Aire. To determine whether the cost of leaving food affects escape behavior by Balearic lizards, we approached lizards after introducing either a freshly cut piece of pear or a pebble of similar size (both about four cm in diameter).

Using human investigators to simulate predators has advantages and disadvantages. The primary advantage is ease of data collection. Once a lizard to be tested has been sighted, it is simple for the investigator to move into position for a trial and to move through variable terrain that might make approach by robotic predator models difficult or impossible. Data can be collected rapidly and efficiently. The two major potential difficulties are that the lizards may not perceive researchers as predators and that the investigator knows which trials are being conducted and might bias the results unconsciously. Many predictions of optimal escape theory have been confirmed in tests with human simulated predators (e.g., Cooper, 1997a–c, 1999, 2000; Cooper et al., 2003; Martín and López, 2003), and lizards are difficult to capture by hand. This suggests that although human beings differ in appearance from typical predators of *P. lilfordi*, these and other lizards respond to human investigators as to predators. We attempted to eliminate or minimize potential biases by practicing the method of approach so that lizards were approached in a consistent manner in all trials. Differences in responses of the animals tested in the presence and absence of food were too great to be attributed to any minor, unconscious differences in our approaches.

To start a trial, we located a lizard and placed the pear or pebble in an open site where it would attract the lizard's attention. The stimuli were tied by a 1-m string to a 1.5-m rod to permit us to place them on the ground without closely approaching lizards. The investigator slowly approached a lizard to avoid eliciting escape. When approached slowly *P. lilfordi* on Aire permit very close approach, perhaps due to reduced predation pressure on the islet. The investigator used the extended rod and string to position the pear or pebble in the lizard's view, thereby attracting its attention. When a stimulus had been put in place, the experimenter who placed it withdrew five meters. He waited until the lizard approached and investigated the stimulus and then approached the lizard directly at a speed of approximately 80 m/min. This investigator stopped approaching as soon as the lizard fled. The other investigator recorded approach distance (= flight initiation

distance, the distance from the approaching predator when the prey begins to flee), distance fled before stopping, and whether or not the lizard returned to the stimulus within two minutes. Distances were measured using a metric rule. We ensured that each individual was tested only once by moving to different locations between trials.

Sample sizes for approach distance and distance fled were 20 in the pear group and 19 in the pebble group, but return to the stimulus was not recorded for one member of each group. Data for approach distance and distance fled were tested for significance using analysis of variance for a single-factor experiment using an independent groups design (Zar, 1996). When the assumptions for analysis of variance were violated for approach distance data, the data were logarithmically transformed to obtain homogeneous variances and normality. Hartley's F_{max} tests were used to detect heterogeneity of variance (Winer, 1962). A Fisher exact probability test (Zar, 1996) was conducted to detect any difference between stimulus groups in proportion of individuals that returned to the stimulus after fleeing. Data are presented as means ± 1.0 SD. Alpha was 0.05, two-tailed.

RESULTS

Lizards readily approached and tongue-flicked tethered pear slices and pebbles. The major difference in escape behavior was a much shorter approach distance for lizards tested with pieces of pear than pebbles (pear: 0.35 ± 0.04 m; pebble: 1.08 ± 0.10 m). Variances of approach distance were significantly heterogeneous for the raw data (F_{max} = 4.93; df = 2, 37; $P < 0.02$). For logarithmically transformed data, differences among variances were marginally significant F_{max} = 2.60; df = 2, 37; $P = 0.05$, but did not reflect a serious violation of homogeneity. As predicted, approach distance was significantly shorter in the presence of pieces of pear than pebbles (F = 43.80; df = 1, 37; $P < 1 \times 10^{-6}$).

Distance fled was 28% greater for lizards tested with pebbles (0.77 ± 0.06 m) than pear (0.60 ± 0.05 m). Data on distance fled did not require transformation (F_{max} = 1.43; df = 2, 37; $P > 0.10$). The difference in distance fled between groups was significant (F = 4.19;

df = 1, 37; $P < 0.05$). Although the difference in distance is slight, it confirms the economically based prediction for distance fled.

Lizards were significantly more likely to return to pears than pebbles (Fisher $P <$ 0.0001). In the pear group 16 of 19 lizards returned to the pear after fleeing despite having to approach the experimenter. In the pebble group only one of the 18 individuals returned to the pebble after fleeing.

DISCUSSION

Based on costs of lost opportunity to feed entailed by fleeing, optimal escape theory predicts that prey permit closer approach by predators before fleeing when food is present due to loss of opportunity to feed. Our results confirm the prediction. This finding agrees with that for the insectivorous broad-headed skink, *Eumeces laticeps*, which allows closer approach by a predator while eating crickets than when not eating (Cooper, 2000). Limited data on foraging costs (this paper, Cooper, 2000) and social costs (Cooper, 1999) strongly support the basic premise of optimal escape theory that approach distance is determined by a balance between costs of escape and risk of predation. These results are consistent with findings that Iberian rock lizards, *L. monticola*, trade time spent in refuge against feeding and social opportunity costs (Martín et al., 2003, in press).

Two other aspects of antipredatory behavior not incorporated in optimal escape theory, distance fled and likelihood of returning to the initial site, were also affected by the presence of food. The distance that *P. lilfordi* fled was substantially shorter when food was present, suggesting that distance fled may be determined by a balance between risk of predation and cost of leaving a resource that is likely to be depleted rapidly. Competition for food may be intense in the Aire population of *P. lilfordi* due to the extremely high lizard density (Pérez-Mellado, 1998). Competiton for food is manifested by frequent attempts at kleptoparasitism in the Aire population (Cooper and Pérez-Mellado, 2003). Exposed food is likely to be discovered by other individuals quickly, placing a premium on the lizard remaining nearby. Therefore, lizards tested with pear pieces fled far enough to increase their safety, but not as far as when no

food was present that could be lost to competitors. This finding is analogous to the shorter latency to emerge from refuge in the presence of prey by the lacertid lizard *Lacerta monticola* (Martín et al., 2003) in that both indicate tradeoffs between food and predation risk. However, the finding that distance fled is traded off against the possible loss of a feeding opportunity is unique for *P. lilfordi*. Further study is needed of potential effects of tradeoffs between predation risk on the one hand and feeding and social opportunities on the other, on distance fled. For lizards that do not enter refuges, risk may be reduced by fleeing further and/or fleeing at greater approach distances. Some species may adjust either approach distance or distance fled, but not both, whereas others, such as *P. lilfordi*, might adjust both approach distance and distance fled to risk and cost levels. Theoretical attention to these issues is desirable.

The finding that, once the lizards stopped fleeing, they were far more likely to return to food than to a pebble near a stationary predator, dramatically indicates that the lizards trade off risk of predation against feeding opportunities. They accept the increased risk of approaching a predator to feed. Broad-headed skinks exhibit similar tradeoffs between increasing predation risk by approaching a predator and the magnitude of foraging and social opportunities to be gained (Cooper, 1999, 2000). Broad-headed skinks that had to approach a predator to feed attacked larger prey more frequently and with shorter latency than smaller prey (Cooper, 2000). Male *E. laticeps* also trade off risk of predation against social opportunities, not only permitting closer approach when in the presence of potential mates or rival males, but also frequently returning to experimentally introduced females despite the continued presence of the predator (Cooper, 1999).

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