

Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards, *Podarcis lilfordi*

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During encounters with predators, prey must balance the degree of risk against the loss of fitness-enhancing benefits such as feeding and social activities. Most studies of tradeoffs between risk and cost of escaping have measured flight initiation distance and time to emerge from refuge, for which theory provides robustly supported predictions. Tradeoffs involving other aspects of encounters, including distance fled and time between escape and return to a food source, have received little theoretical or empirical attention. By adapting models of flight initiation distance and time between entry into refuge and emergence, we predict effects of predation risk and cost on distance fled and time to return to a source of benefit after fleeing. Acting as simulated predators that approached at a fixed speed, we conducted an experimental field study to test the hypotheses that flight initiation distance, distance fled, and time to return to food by Balearic lizards (*Podarcis lilfordi*) decrease with the presence and amount of insect food. Predictions of the models were strongly supported, including those for distance fled and return time, but predictions for other cost factors and predation risk factors remain to be tested. *Key words:* antipredatory behavior, approach distances, escape behavior, flight initiation distance, Squamata. [*Behav Ecol* 17:554–559 (2006)]

Prey confronted by predators that are approaching or stationary nearby must make tradeoffs between self-preservation and profitable activities such as foraging and reproduction. Because these fitness-enhancing behaviors often entail increased predation risk, greater risk is a cost of each of them (e.g., Lima and Dill 1990; Candolin 1997; Koga et al. 1998; Krupa and Sih 1998; Cooper and Vitt 2002). Prey can compensate for increased risk by altering aspects of behavior such as degree of activity, microhabitat use, or closeness to refuge (Cooper et al. 1990; Lima and Dill 1990) but may also alter their short-term decisions regarding antipredatory behaviors. Given the opportunity to forage or engage in agonistic or courtship behaviors that increase fitness, prey often accept greater predation risk than at other times, often by permitting predators to come closer before fleeing and by emerging from refuge sooner (Cooper 1999; Díaz-Uriarte 1999; Martín and López 1999a, 1999b; Hazlett and Rittschof 2000; Martín et al. 2003).

In a diversity of animals, predation risk affects diets, when and where foraging occurs, and prey handling (Lima and Dill 1990). When predators are nearby, prey may avoid encounters with them by altering diel activity and habitat use (Clarke 1983; Gilliam and Fraser 1987; Skutelsky 1996; Turner 1996; Cowlshaw 1997a). Other options are to choose foraging sites that minimize risk (Cerri and Fraser 1983; Holmes 1991; Hughes and Ward 1993; Suhonen 1993a, 1993b) and to increase vigilance, which may decrease the rate of energy gain from foraging (Krebs 1980; Lima 1987). Predation risk may cause predators to eat less profitable foods (Dill and Fraser 1984; Lima and Valone 1986; Phelan and Baker 1992) and to

alter handling of food to minimize exposure to risk (Lima et al. 1985; Lucas 1985; Cooper 2000a). Prey in refuges may forego or reduce the rates of foraging (Cowlshaw 1997b; Sih 1992; Cooper 1998a).

When food is available and a predator approaches, prey must decide how close to allow the predator to approach before fleeing and how far to flee. If the predator stops approaching when the prey flees, but remains nearby, the prey must decide whether to return to the food source and how long to delay the return. The decision about when to start fleeing is predicted by the escape theory (Ydenberg and Dill 1986), but little is known about decisions regarding how far to flee or about return to food sources after attack by a predator.

A model of escape decisions (Ydenberg and Dill 1986) predicts that prey should not flee immediately on detecting a predator but should continue their activities while monitoring the predator and initiate escape only when cost of remaining (predation risk) equals cost of escaping (Ydenberg and Dill 1986). The model predicts the distance between predator and prey when escape begins, which is called flight initiation distance or approach distance (also flush distance). If time spent in refuge before emerging is substituted for distance, the model describes the time to emerge from refuge (Martín and López 1999a).

The model cannot predict flight initiation distance quantitatively because fitness costs are unknown but makes many useful ordinal predictions. Escape theory predicts that for a given curve relating predation risk to distance between predator and prey, flight initiation distance should be shorter when cost of escaping is greater. It also predicts that for a given cost of escape curve, flight initiation distance is greater when risk due to remaining is greater. These qualitative predictions have been verified for many risks and costs (e.g., Lima and Dill 1990; Bonenfant and Kramer 1996; Cooper 1997a, 1997b, 1997c, 1998a, 1998b, 1999, 2000a, 2003a, 2003b; Cooper et al.

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2003; Martín et al. 2003). As magnitude of benefit that may be lost by fleeing increases, the model predicts that flight initiation distance decreases.

Distance fled should depend on many risk factors and on costs of fleeing too far, especially, costs due to opportunities lost. Distance fled can be modeled analogously to the model of approach distance of Ydenberg and Dill (1986), but with distance fled on the horizontal axis and fitness costs due to predation risk and escaping on vertical axes (Figure 1). Given a particular cost of escape curve, predicted distance fled is greater for the higher of two risk curves. For a given predation risk curve, predicted distance fled is shorter for the higher of two cost of escaping (benefit of staying) curves. An optimality model would permit the prey to maximize fitness, but the model suggested here is adequate to test many ordinal predictions about the effects of risk and cost of escape. If a prey must abandon food to flee, the food may escape or be eaten by a competitor. By remaining closer to the food, the prey may reduce the likelihood of losing benefits. Distance fled is predicted to be shorter when escape increases the chances of losing benefit than when no immediate benefit is obtainable. It is further predicted that distance fled should be decreased as the potential opportunity cost of fleeing increases.

Decisions regarding whether to return to the site of attack should be based on a tradeoff between predation risk and benefit of returning. Failing to return within a specified time is analogous to remaining in refuge that long. Returning to a source of food, a potential mate, or other attractive site near a predator is comparable to accepting greater risk by emerging from refuge. Economic decisions regarding time to emerge can be predicted by substituting time to return for time to emerge in the model of Martín and López (1999a) or William E. Cooper and William F. Frederick (unpublished data). The model is formally identical to that in Figure 1 with return time on the horizontal axis, cost of approaching the predator (risk) on the left vertical axis, and cost of not returning on the right vertical axis. When prey must leave a valuable food source to flee, the probability of returning to the site where escape began should be greater and time to return should be shorter than when no food is present. As the amount of food present increases, greater opportunity cost of fleeing and increasing likelihood of losing the food with greater time spent away from it suggest that the prey should return after briefer absence.

We conducted a field experiment to study the tradeoffs between predation risk and feeding opportunity by Balearic lizards (*Podarcis lilfordi*) presented 0, 1, 4, or 8 large maggots. We predicted that approach distance, distance fled, and return time would be shorter and probability of returning higher when food was present than absent. Because previous tests of effects of opportunity costs on approach distance contrasted behavior of prey having large opportunity costs or none, predictions about the effects of quantitative variation in escape cost remain untested. We predicted that approach distance, distance fled, and return time decrease as number of food items increases.

METHODS

The study site was conducted on Aire, an islet off the coast of Menorca, Balearic Islands, Spain in early May 2005 on sunny days between 8:45 AM and 3:50 PM when lizards were active and foraging. Aire is an ideal site for studies of tradeoffs between antipredatory behavior and foraging because the exceedingly high population density of the Aire population facilitates data collection. Due to high density, intense intraspecific competition for food items occurs, including kleptoparasitism (Cooper and Pérez-Mellado 2003). Potential loss of food items to competitors provides strong motivation for liz-

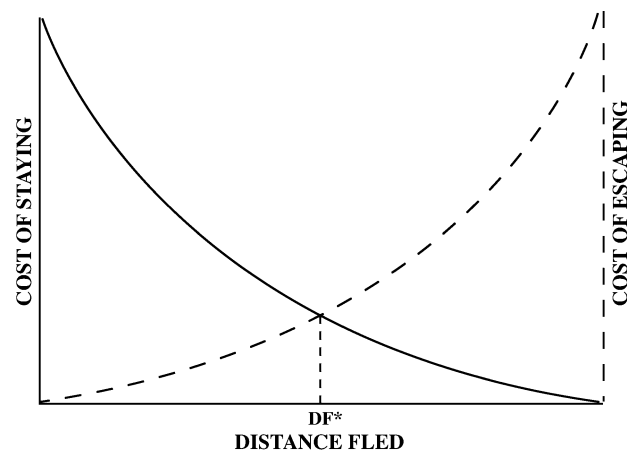


Figure 1

A simple model in which predicted distance fled occurs when the predation risk (cost of not fleeing) for a prey fleeing that distance equals the opportunity cost (cost of escape) of fleeing. Thus, the intersection of the risk and cost curves gives the predicted distance fled, DF^* .

ards to continue foraging while a predator approaches when prey are present and to return to prey after fleeing.

To assess effects of presence of prey and magnitude of potential energetic benefit on aspects of antipredatory behavior, we presented varying numbers of prey items in plastic petri dishes to lizards in the field. The dishes were transparent, allowing lizards to see the prey. A heated needle was used to make numerous holes in the sides and tops of petri dishes to allow lizards to detect chemical cues from prey. To prevent lizards from eating the prey, the upper and lower halves of each petri dish were taped together. The prey were maggots of a calliphorid fly which contaminated a culture of mealworms (*Tenebrio molitor*). These maggots are very attractive prey items for *P. lilfordi* due to its large size (17- to 20-mm total length, ca. 0.2 g) and high mobility.

To begin a trial, an investigator placed a petri dish on the ground, withdrew 6–8 m and stood motionless while waiting for a lizard to approach. When a lizard contacted a dish by tongue flicking, pushing, or walking on it, the investigator approached the dish directly at a practiced speed of 81 ± 1 m/min and stopped approaching when the lizard began to flee. The investigator recorded the approach distance and distance fled before the lizard stopped for the first time, both the nearest 0.1 m, and then withdrew to his initial position and stood immobile. The time in seconds between the escape and return to the petri dish was recorded up to a maximum of 120 s for lizards that did not return.

The 4 experimental treatments were 8, 4, 1, and 0 maggots per petri dish, which corresponded to decreasing magnitude of energetic benefit available, the zero group being the control for effects of investigation of a novel stimulus in the absence of food. Numbers of trials per treatment were evenly distributed over times of day. Tests were conducted in high-density sites. Each investigator conducted one or more trials per site, being careful not to test the same individual twice, and then moved to a new site. Because tested lizards were not marked, it is possible that one or more individuals were tested twice. However, the potential for pseudoreplication was minimized by use of multiple observation sites by each investigator and by the sheer density of the lizards, dozens of which could often be seen at once.

Parametric statistical analyses of approach distance, distance fled, and time to return to the petri dish were conducted using a single-factor analysis of variance for an independent groups

design (Zar 1996). We used Kolmogorov–Smirnov (KS) tests to ensure normality and Levene’s tests for homogeneity of variances. When necessary, data were logarithmically transformed to meet assumptions of normality and/or homogeneity of variance. When significant main effects were detected, multiple comparisons were performed using Tukey’s tests (Zar 1996). Because many individuals did not return to petri dishes containing no maggots, the distribution of return times was intractably nonnormal when the control group was included. Therefore, parametric analysis of return times was restricted to the 3 treatments in which maggots were present. A Kruskal–Wallis test (Zar 1996) was performed to permit multiple comparisons involving the control group. After detection of a significant main effect, nonparametric paired comparisons of return times for unequal sample sizes were conducted as in Zar (1996). Frequency of return within 120 s was compared between the control group and each experimental group using Fisher’s Exact probability tests. Raw probabilities are reported for these tests, but significance was assessed using sequential Bonferroni adjustment (Wright 1992). Significance tests were two-tailed with $\alpha = 0.05$ unless otherwise indicated.

RESULTS

Approach distance

The distribution of approach distance did not deviate significantly from normality (KS = 0.081, degrees of freedom [df] = 89, $P = 0.20$), and variances were not significantly heterogeneous ($F_{3,103} = 2.24$, $P > 0.08$). Approach distance differed significantly among treatments ($F_{3,103} = 3.50$, $P = 0.018$; Figure 2a). The only significant difference between pairs of treatments was a shorter approach distance when 8 prey were present than when none were present. Other differences between pairs of treatments were nonsignificant ($P > 0.19$ each) due to high variability within treatments (Figure 2a) due to some individuals in all groups having long approach distances.

Differences in approach distance between the control group were 15% for the 1-maggot, 19% for the 4-maggot, and 31% for the 8-maggot treatments. Approach distance was 19% shorter for 8 maggots than 1 maggot. For the control group, the range of approach distances was 0.8–2.2 cm, with only 2 of 18 individuals allowing approach closer than 1.0 m. Lizards investigating petri dishes containing 1 maggot had a 0.4–2.3 m range of approach distance with 9 of 24 individuals allowing approach closer than 1.0 m. When 4 maggots were present, the range of approach distances was 0.4–2.8 m, and 14 of 22 individuals permitted approach closer than 1.0 m. In the 8-maggot treatment, the range of approach distances was 0.4–1.8 m, with 11 of 17 allowing approach of ≤ 1.0 m. Fisher’s Exact tests show that significantly greater proportions of individuals allowed approach as close as 1 m in the 4- and 8-maggot treatments ($P = 0.001$ and 0.0016 , respectively) than when no maggots were present. The difference between the control and 1-maggot treatments was substantial but not significant after Bonferroni adjustment ($P = 0.038$, one-tailed). No other differences approached significance ($P > 0.10$ each).

Although the preceding tests reveal no effect of number of maggots between 1 and 8 on approach distance, the mean approach distance increased progressively with the number of prey (Figure 2a). The parametric correlation between mean approach distance and number of prey is $r_4 = -0.93$, $P < 0.036$, one-tailed, indicating that approach distance decreased as number of prey increased.

Distance fled

Raw data were nonnormal, but logarithmically transformed data did not exhibit significant departure from normality

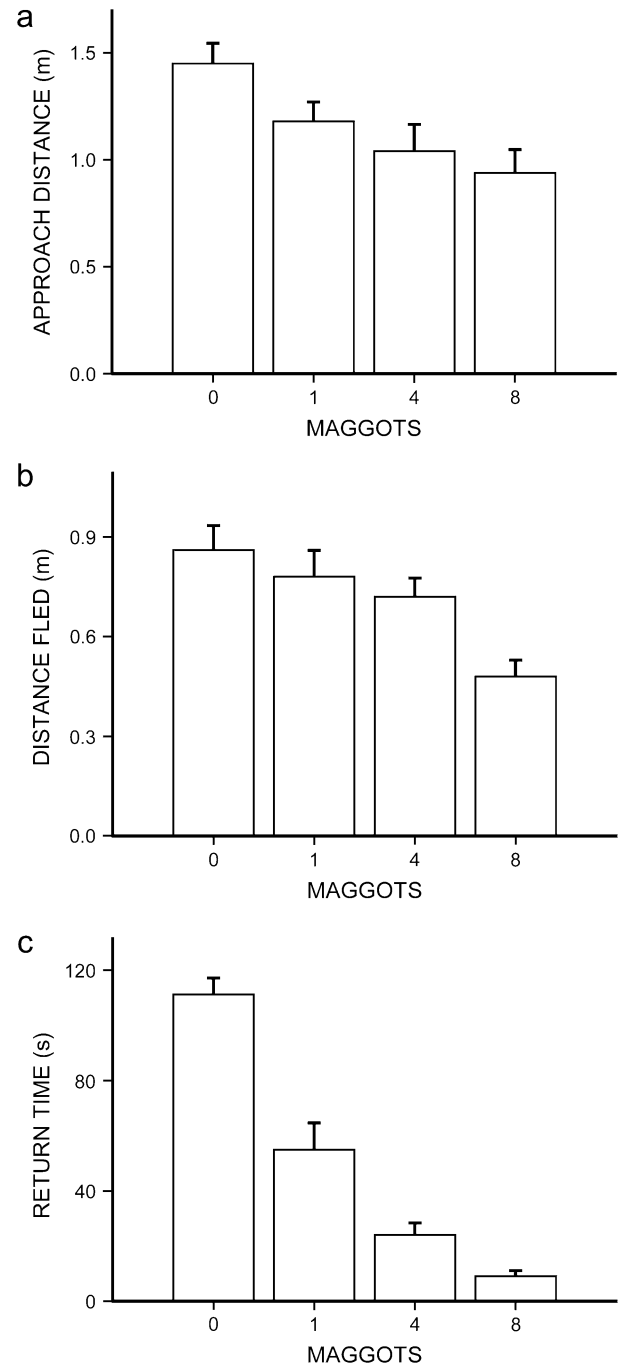


Figure 2

Escape and return to food source by *Podarcis lilfordi* when varying numbers of maggots were present. (a) Approach distance. (b) Distance fled. (c) Time to return. Main bars show means. Error bars represent 1.0 standard error.

(KS = 0.084, df = 107, $P = 0.059$), and variances were homogeneous ($F_{3,103} = 1.14$, $P > 0.10$). Approach distances varied significantly among treatments ($F_{3,103} = 4.27$, $P = 0.004$; Figure 2b). Lizards in the 8-maggot treatment fled significantly shorter distances than those in all other treatments ($P = 0.004$ for 8 vs. 0; $P = 0.025$ for 8 vs. 1; and $P < 0.049$, one-tailed for 8 vs. 4). No other differences between pairs of treatments closely approach significance ($P > 0.45$ each).

Approach distance declined as number of maggots increased, the 1-, 4-, and 8-maggot groups fleeing 8%, 15%,

and 31% shorter distances than the controls. The difference for 1 and 4 maggots was only 6%. The nonparametric correlation between distance fled and number of maggots was 1.0. The parametric correlation is $r_4 = -0.99$ ($P < 0.013$).

Return time

For treatments in which maggots were present, both the raw data and logarithmically transformed data were nonnormal. For data transformed logarithmically twice in succession, deviation from normality was nonsignificant although barely so ($KS = 0.094$, $df = 89$, $P = 0.05$), and variances were not significantly heterogeneous ($F_{2,86} = 1.96$, $P > 0.14$; Figure 2c). The main effect of maggot number was highly significant ($F_{2,86} = 20.20$, $P \ll 0.001$). Lizards in the 8-maggot treatment had significantly shorter return times than those in 1- and 4-maggot treatments ($P < 0.001$ each). The difference in return times between the 1- and 4-maggot treatments was not significant ($P > 0.36$). The standard error was highest in the 1-maggot treatment (Figure 2c) because one-fourth of individuals did not return, but others returned fairly quickly.

In the nonparametric analysis including all treatments, the main effect of treatment was highly significant ($\chi^2_3 = 57.29$, $P \ll 0.001$; Figure 2c). Nonparametric multiple comparisons for unequal sample sizes showed that return times were significantly longer when no maggots were present than when 1 ($P < 0.005$), 4 ($P < 0.001$), or 8 maggots ($P < 0.001$) were present. For similar comparisons, the results agreed with those of the parametric analysis but with higher P values: return times did not differ significantly for the 1- and 4-maggot treatments ($P > 0.10$) and were significantly longer for petri dishes containing 1 maggot ($P < 0.005$) and 4 maggots ($P < 0.05$, one-tailed) than for 8 maggots.

Ranges of return times were 38–120 s for the control group, 3–120 s for the 1-maggot group, 3–67 s for the 4-maggot group, and 1–38 s for the 8-maggot group. Lizards returned to the food source of 1 maggot in 49%, of 4 maggots in 18%, and of 8 maggots in 8% of the time to return to control dishes. Even among the 3 treatments in which food was present, differences in mean time to return were large: return times to 4 and 8 maggots were 45% and 15% of that to 1 maggot, and return to 8 maggots was 34% of that to 4 maggots.

Lizards returned to the food source of 1 maggot in 49%, of 4 in 18%, and of 8 in 8% of the time to return to control dishes. A significantly higher proportion of individuals failed to return within 120 s in the control treatment than in the 1-maggot ($P < 1.6 \times 10^{-4}$), 4-maggot ($P < 4.0 \times 10^{-9}$), and 8-maggot ($P < 7.6 \times 10^{-8}$) treatments.

DISCUSSION

Approach distance

Prey make tradeoffs in approach distance between risk and opportunity to feed. That approach distance is shorter when food is present is consistent with predictions by Ydenberg and Dill (1986) model and an optimality model (Cooper and Frederick, unpublished data) that approach distance is less when cost of escape is greater. The results extend previous findings for *P. lilfordi* with plant food (Cooper and Pérez-Mellado 2004) to prey and are comparable to those for broad-headed skinks, which permit closer approach when near the prey (Cooper 2000a).

Analysis of variance restricted to treatments including maggots did not verify the prediction that approach distance increases with magnitude of benefit. High variability prevented detection of differences among the 3 food treatments despite substantial percentage reductions in approach distance with

increasing numbers of prey that were consistent with the prediction. Nevertheless, the extremely high negative correlation between number of maggots and mean approach distances suggests that approach distance decreases as magnitude of benefit that might be lost increases.

Distance fled

Present findings suggest that prey decisions about how far to flee are based on economic decisions. The difference among treatments in combination with shorter distances fled in the 8-maggot treatment than in all others support the prediction that distance fled is determined by a balance between predation risk and opportunity costs. It is consistent with previous findings that Balearic lizards fled shorter distances when fruit was present than absent (Cooper and Pérez-Mellado 2004). The small percentage difference in distance fled in 1- and 4-maggot treatments suggests that large benefit is needed for substantial reduction in distance fled. All lizards had abundant plant food available. Smaller rewards in 1- and 4-maggot treatments may not have been sufficient to justify large decreases in approach distance, whereas the decrease was substantially greater for a larger reward of 8 maggots.

The high negative correlation between distance fled and number of maggots suggests that prey make graded adjustments of distance fled in relation to variation in benefit obtainable by returning to food or lost by fleeing too far. Feeding opportunities may be lost while a prey escapes because the food leaves the area or hides and because other predators may eat it. Due to high population density, Balearic lizards attempting to eat fruit or large insects are subject to intense kleptoparasitism by conspecifics (Cooper and Pérez-Mellado 2003). Thus, reduction in distance fled when insect food is present may be especially important in this species.

Data for several risk factors, including predation pressure, degree of cover available, the predator's approach speed, predator persistence, distance from refuge, and tail autotomy, as well as the escape cost of abandoning food, are consistent with the model's predictions. Lava lizards (*Microlophus* sp.) in the Galapagos flee greater distances on islands where they are exposed to greater predation threat (Stone et al. 1994). Lizards flee greater distances when vegetative cover is sparse than where it is dense (Snell et al. 1988; Martín and López 1995). Distance fled by the lacertid lizard *Psammotromus algirus* increases with the predator's approach speed (Martín and López 1996). In broad-headed skinks, distance fled on the ground was not affected by approach speed (Cooper 1997b). However, the total fled distance that lizards fled may have been greater during rapid approach because lizards that used trees as refuges were more likely to climb when approached rapidly (Cooper 1997b). That broad-headed skinks approached twice in succession were more likely to enter refuge during second than first approaches suggests that they fled greater distances when assessed risk was greater. In keeled earless lizards (*Holbrookia propinqua*), males with autotomized tails fled greater distances, presumably due to greater risk due to impaired running ability (Cooper 2003a). Distance fled was not affected by autotomy in females, which in some species appear to switch to a strategy of greater crypsis when slowed (Cooper et al. 1990; Cooper 2003c). In the same species, distance fled is greater when lizards are at greater risk due to being further from refuges (Cooper 2000b). The prediction that distance fled is shorter when escape may have a large opportunity cost is supported by 2 studies requiring Balearic lizards to flee from food sources (Cooper and Pérez-Mellado 2004; this study).

The only finding that seemingly contradicts the model's prediction is that distance fled by wall lizards (*Podarcis muralis*)

did not differ in populations believed to experience different predation pressure (Diego-Rasilla 2003). This finding is equivocal because frequency of broken tails was the index of predation pressure but is known to reflect efficiency of predation and not necessarily predation pressure. The limited data available support the model's predictions.

Return time

The prediction that probability of return to the food source would be greater when food was present than absent was verified by the significantly greater probability of return in all 3 treatments with maggots than in the control condition. Thus, prey trade greater risk entailed by approaching a predator for a chance to obtain a fitness-enhancing food reward. Previous evidence for similar tradeoffs includes return to females or sites where the females had been despite having to approach a predator by breeding male broad-headed skinks (*Eumeces laticeps*; Cooper 1999; Cooper and Vitt 2002) and to food near the predator by Balearic lizards (pieces of fruit, Cooper and Pérez-Mellado 2004) and broad-headed skinks (crickets, Cooper 2000a).

The hypothesis that time between fleeing and return decreases as food items increase was strongly supported. Prey accept greater risk by approaching a predator for greater benefit. The prediction that return time is shorter for higher cost of not returning is supported by return of male broad-headed skinks to females (Cooper 1999) and or Balearic lizards to plant food (Cooper and Pérez-Mellado 2004).

Predation risk, escape, and foraging

All aspects of escape discussed here are adjusted to the degree of opportunity cost. However, approach distance and distance fled were less sensitive than return time to differences in amount of benefit. A possible reason is that the reward was small relative to risk while a predator approached. Because predators stopped moving when prey began to flee, distance fled presumably was determined by risk and opportunity cost when flight was initiated. Accordingly, percentage differences between pairs of treatments were similar for flight initiation distance and distance fled. Once a lizard fled, assessed risk presumably decreased greatly when the predator became immobile. We suggest that with lower risk posed by a stationary predator, difference in return time could be greater for a given difference in cost than the differences for approach distance and distance fled. During brief approaches and fleeing, threat of losing the food by kleptoparasitism is reduced because any other individuals close to the food flee. On the other hand, failure to return rapidly may lead to kleptoparasitic losses, promoting greater risk taking for larger food benefits.

Partly due to availability of predictive models (Ydenberg and Dill 1986; Martín and López 1999a), studies of tradeoffs between costs associated with predation risk and lost opportunities have focused on approach distance and time to emergence. Our data suggest that two other aspects of prey behavior, distance fled and return time, can be predicted using similar reasoning. Fuller understanding of escape will require development of models to explain escape speeds, angles, and trajectories, as well as decisions to select and enter refuges. Ultimately, such models should be linked with studies of longer term aspects of prey behavior such as habitat selection (e.g., Gilliam and Fraser 1987; Sih 1992).

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