Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory

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Abstract. Escape theory predicts that flight initiation distance (FID = predator-prey distance when escape begins) increases as predation risk increases. We tested effects of variation of approach speed and directness, predator persistence, concealment, and weather conditions on FID in the Balearic lizard (*Podarcis lilfordi*) by ourselves simulating predators. We examined effects of directness of approach on probability of fleeing and of repeated approach on entering refuge and distance fled. As predicted, FID was greater for faster approach speed, more direct approach, during second than first approaches, and when lizards were exposed than partially concealed. Other effects of directness of approach and repeated approach also were as predicted by greater assessed risk by the lizards. The proportion of individuals that fled was greater for direct than indirect approaches. The proportion of lizards that entered refuges and distance fled were greater during the second of two successive approaches. Effects of weather on FID were complex. FID was shortest in the warmest conditions with no noticeable wind, when lizards were active. Lizards were inactive and basked in the other conditions. FID was longest at 20°C without wind, and intermediate FID occurred at 18°C in windy conditions. We present hypotheses for weather effects. Tests are needed to unravel effects of temperature and wind speed. All predictions of escape theory for simple risk factors, i.e., all except than weather conditions, were confirmed. Escape theory successfully predicts FID for these risks in *P. lilfordi*, other lacertids, and more broadly, in ecologically and taxonomically diverse lizards.

Keywords: antipredatory behavior, escape, flight initiation distance, predation risk, refuge, Squamata.

Introduction

Cost-benefit hypotheses about escape behavior emphasize that when a predator approaches, prey balance gains that may be obtained if they do not flee (escape costs) against the cost of not fleeing (expected fitness loss due to predation risk). A prey that detects a predator while it is still far away should delay escape attempts until some criterion relating escape costs to cost of not fleeing is met. The first economic escape model predicted that prey should delay fleeing until the predator draws near enough for costs of fleeing and not fleeing to be equal (Ydenberg and Dill, 1986). A more recent optimality model suggests that prey should begin to escape when the predator approaches to the distance at which expected fitness of the prey after the encounter is maximized (Cooper and Frederick, 2007). Both models predict flight initiation distance (FID = the distance between predator and prey when the prey begins to flee). Predictions of the two models differ quantitatively, but are qualitatively identical for many factors affecting predation risk and escape cost. Because risk and cost curves relating expected fitness to FID are unavailable, the models are currently equally useful for making predictions. Effects of a variety of risk and cost factors have been tested extensively in numerous taxa (reviewed by Stankowich and Blumstein, 2005); the findings indicate that both models are highly successful at predicting relative magnitude of FID for higher and lower levels of cost of fleeing and not fleeing. Our studies evaluate the validity of several predictions shared by the two escape models.

Predictions of escape theory have been tested most extensively for lizards (e.g., Agamidae – Cooper and Whiting, 2007a; Iguanidae – Burger and Gochfeld, 1990; Blázquez, Rodriguez-Estrella and Delibes, 1997; Cooper, 2003a; Cro-

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taphytidae – Husak and Rouse, 2006; Poly-chrotidae – Rand, 1964; Heatwole, 1968; Cooper, 2006a, 2006b; Phrynosomatidae – Johnson, 1970; Bulova, 1994; Smith, 1996; Cooper, 2000a, 2003; Cooper and Wilson, 2007a, 2007b; Tropiduridae – Marcellini and Jenssen, 1991; Stone, Snell and Snell, 1994; Labra and Leonard, 1999; Cooper, 2007; Gekkonidae – Cooper and Whiting, 2007a; Scincidae – Formanowicz, Brodie and Bradley, 1990; Cooper, 1997a, 1998a, 1998b, 1999, 2000b; Smith, 1997; Eifler, 2001; Cooper and Whiting, 2007a; Cordylidae – Whiting, 2002; Cooper and Whiting, 2007b). Escape by these lizards conforms very well to predictions of escape theory.

In European lacertid lizards several factors affecting FID have been examined for one or more species, but effects of numerous risk and/or cost factors have not been examined within a single species. In populations exposed to higher predation pressure *Podarcis muralis* have longer FID than in populations at less risk (Diego-Rasilla, 2003). *Psammodromus algirus* fled further when vegetative cover was sparse than when more cover was present (Martín and López, 1995). Risk increases as predator approach speed increases. As predicted, FID increases as approach speed increases in juvenile *P. algirus* (Martín and López, 1996). Of two species that differ in detectability due to difference in background (*Lacerta vivipara* on ground and *Iberolacerta horvathi* on rocks), the more detectable species has longer FID (Capizzi, Luiselli and Vignoli, 2007). However, because these species differ in many ways, it is uncertain whether the difference in visibility accounts for the difference in FID. Effects of escape costs have been detected in *Podarcis lilfordi*: FID is shorter in the presence of food that might be lost by escaping than in the absence of food (Cooper and Pérez-Mellado, 2004) and decreases with the amount of food present (Cooper, Pérez-Mellado and Hawlena, 2006).

One finding for a lacertid appears to contradict the prediction that FID increases as risk increases. Gravid female *L. vivipara*, which cannot run as rapidly as nongravid females and are therefore at greater risk, have shorter FID than nongravid females (Bauwens and Thoen, 1981). However, gravid females shift their escape strategy from fleeing to greater reliance on crypsis due to immobility; consequently, FID is shorter for gravid than nongravid females (Bauwens and Thoen, 1981). The prediction of escape theory does not apply when alternate strategies are used.

Because effects of few risk factors on escape behavior are known for lacertids, we conducted field experiments for several risk factors using the Balearic lizard, *P. lilfordi*, an actively foraging, omnivorous lacertid of medium size (80 mm maximum snout-vent-length) to test the prediction of escape theory that FID increases with risk associated with each factor. We predicted that FID would increase as predator approach speed increased, as directness of approach increased, when lizards were more exposed to view, and when the predator approached repeatedly. We compared FID in response to similar approaches in differing weather condition. We also tested associated predictions. Because lizards are predicted to be more likely to flee, to flee further, and be more likely to enter refuge when risk is greater, we tested the predictions that the proportion of lizards that flee increases with directness of approaches, and both distance fled and proportion of lizards that enter refuges are greater during second than first approaches.

Materials and methods

Study site and predators

The study was conducted on Aire, an islet off the coast of Menorca, Balearic Islands, Spain between 26 April and 10 May 2005 on sunny days when lizards were active (with the exception of the study of effects of weather conditions described below). The vegetation in much of our study area was sparse, with patches of open ground between plants. Most of the plants were low bushes, some of which provided cover for the lizards, and flowering species that provide food for the omnivorous *P. lilfordi* (Barbadillo et al., 1999). Rocks and holes at the base of a

stone fence provided additional refuges. A single human couple resided on Aire before the 1930s (Pérez-Mellado, 1989). Aire has had no permanent residents since the 1930s, but has not been entirely uninhabited due to visits by biologists, personnel who maintain a lighthouse, and boaters attracted by the lighthouse. No mammalian or ophidian predators are currently present (Pérez-Mellado, 1989).

The main predators on Aire are birds. Kestrels (*Falco tinnunculus*) are predators of lizards in southern Europe (Cramp and Simmons, 1980), and are important predators on *P. lilfordi* on some Menorcan Islets, especially where they breed. Kestrels do not currently nest, but frequently visit Aire. A colony of seagulls (*Larus cachinnans*) occurs on Aire, but seagulls only infrequently eat lizards (Cramp and Simmons, 1983) and *L. cachinnans* is not known to predate either *P. atrata* in the Columbretes Islands (Gomez, 1991; Catalá, Verdu and Garcia y Gans, 1990) or *P. lilfordi* in Cabrera (Araújo, Muñoz-Cobo and Purroy, 1977). Presumably due to the low abundance of predators, lizard densities are very high on Aire (Pérez-Mellado and Corti, 1993), which facilitated data collection. Shrikes (*Larus* spp.) present on Menorca and other islets may also be occasional visitors to Aire.

Method of approach

To study escape responses, we simulated predatory attacks by ourselves approaching lizards. Although human beings are not normally predators of *P. lilfordi*, biologists and amateur collectors have removed many from their natural habitats. Human simulation of predators has been very effective in studies of escape behavior (reviewed by Stankowich and Blumstein, 2005) by fish (Grant and Noakes, 1987), frogs (Cooper, Caldwell and Vitt, in press, in review), lizards (e.g., Cooper, 1997a, 2000a; Martín and López, 1999a; Martín, López and Cooper, 2003; Cooper and Wilson, 2007a, 2007b), birds (Blumstein, 2003; Cárdenas et al., 2005), mammals (Blumstein and Pelletier, 2005; Stankowich and Coss, 2006), insects (Cooper, 2006c) and other taxa (e.g., Hemmi, 2005).

The main advantages of having a researcher simulate a predator in lizard studies are that data collection can be done flexibly and efficiently: Human beings can negotiate uneven terrain much more easily and realistically than inanimate models of predators. An advantage over studies using natural predators is that actual predation cannot occur accidentally.

Potential disadvantages of simulating attacks using human predators are possible motivation of prey responses by something other than antipredatory escape behavior, inability to detect predator-specific response, and experimenter bias. Nonpredatory motivation might occur because experimenters differ in size, shape, and behavior from typical predators of lizards. This plausible concern is unfounded: many studies have confirmed predictions of escape theory about FID for numerous factors that affect risk of predation (cost of not fleeing) and cost of fleeing in lizards (e.g., Heatwole, 1964; Burger and Gochfeld, 1990; Martín and López, 1996; Cooper, 1997a, 1997b, 1997c, 1999, 2000b; Cooper

et al., 2003a; Cooper, Hawlena and Pérez-Mellado, 2006; Cooper and Whiting, 2007a).

We cannot dismiss the possibility that predator-specific responses occur in *P. lilfordi* because they occur in some contexts in chameleons (Stuart-Fox, Whiting and Mousalli, 2006). However, in recent tests of another lizards species, *Sceloporus virgatus*, which is similar to *P. lilfordi*, in being largely terrestrial, no qualitative differences to approach occurred between researchers and models of snakes and birds (Cooper, 2008b). In the present studies *P. lilfordi* exhibited typical escape behavior for terrestrial lizards.

The possibility of experimenter bias cannot be eliminated entirely when the experimenter is aware of the hypotheses being tested and the experimental design, but the likelihood of bias can be minimized by using standardized methods. We practiced approach speeds to maintain consistency among trials. We also attempted to approach using the same gait. For each experiment the treatment order was selected prior to any data collection to avoid unconscious selection of treatments to match lizards or circumstances.

Data collection, designs and analyses

We walked slowly through the study site searching visually for lizards. All lizards that we approached were adults. We did not determine sex, but any differences between sexes in escape behavior would be randomly distributed among treatments, increasing experimental error, but not biasing findings. Before beginning to approach, an experimenter moved to a location affording the lizard an unobstructed view of him. After stopping briefly and orienting toward the lizard, the experimenter began to approach using a preselected speed and directness appropriate for the particular experiment and treatment. Approach speeds ($n = 10$ each) were slow (51.0 ± 1.4 m/min), intermediate (80.8 ± 0.8 m/min), and fast (115.8 ± 3.5 m/min). Only the intermediate approach speed was used for all experiments except that on effects of approach speed. Starting distance, the distance between predator and prey when the predator begins to approach, affects FID in some birds, mammals, and lizards (Blumstein, 2003; Cooper, 2005, 2008a; Stankowich and Coss, 2006). Starting distance does not affect FID in *P. lilfordi* at the intermediate approach speed (our unpublished data). Based on findings for another lizard, *Sceloporus virgatus*, starting distance is likely to affect FID only during rapid approaches (Cooper, 2005). In the experiment on effects of approach speed, starting distances were 6-12 m. In this range starting distance might increase by at most one half meter during fast approach (our unpublished data).

The experimenter continued to approach until the lizard fled or the experimenter had reached the nearest point to the lizard on an indirect approach path. The experimenter recorded whether the lizard fled or not. If it fled the experimenter stopped moving immediately to record FID to the nearest 0.1 m. We avoided pseudoreplication by moving through an area only once during a given experiment and then collecting data in other locations. After one lizard was tested, others usually were immediately in sight. We noted the appearance and escape path of each tested lizard before

selecting the next lizard to be tested from those that were not near the escape path and appeared to be undisturbed. Because we returned to the same areas for different experiments, it is likely that some individuals were tested in more than one experiment.

The effect of approach speed on FID was tested using the slow, intermediate, and fast speeds and two observers (VPM and WEC) using a 2×3 factorial design. Data were analyzed using analysis of variance for an independent groups design with approach speed and observer as factors. Sample sizes were 10 for each group. To eliminate possible effects of starting distance on FID, an additional 2×2 analysis was conducted for the two slower approach speeds.

In the experiment on effects of directness of approach, lizards were approached directly or indirectly on paths bypassing them by a minimum of 1.0-1.5 m, 2.0-2.5 m or 3.0-3.5 m. Sample size was 16 for each group. Differences in frequency of fleeing among pairs of groups were examined using Fisher exact tests. Significance was established using sequential Bonferroni adjustment for the number of tests (Wright, 1992). The difference in FID between direct approaches and 1.0-1.5 m bypasses was assessed using a Mann-Whitney U test.

Effects of repeated approach were studied by directly approaching 20 lizards. Following the first approach, the experimenter recorded FID, distance fled, and whether the lizard entered a refuge (i.e., hid under a rock or bush) for the first approach. The experimenter then withdrew from the lizard's current position to the initial starting distance, approached again immediately or as soon as the lizard emerged fully from the refuge, and recorded the same variables. An additional eight lizards were tested to determine distance fled by lizards that did not enter refuge during either trial, bringing the sample size for distance fled without refuge entry in either trial to 18. The frequency of distance fled being greater after second than first approaches was examined using a sign test under the assumption equal frequencies. The difference in frequency of entering refuge in first and second trials was analyzed using a McNemar's test.

Effects of partial concealment on FID were examined for lizards that were fully exposed or partially concealed by plants, and could see the experimenter ($n = 19$ each). All approaches were direct. The influence of weather conditions on FID was studied by approaching slowly and directly under sunny conditions differing in wind speed, air temperature, and basking behavior. Weather conditions were: calm with air temperature $\geqslant 22°C$, lizards active without basking ($n = 10$); calm with lizards basking at 20.0-20.2°C ($n = 15$); and windy with air temperature 18.0-18.1°C ($n = 24$).

Analysis of variance was used for the remaining significance tests. Prior to each of these, the assumptions of homogeneity of variance and normality were examined using Levene's and Kolgomorov-Smirnov tests, respectively. Data that did not meet the assumptions were logarithmically transformed prior to analysis. Effects of approach speed, directness of approach, partial concealment, and weather conditions were examined by ANOVAs for independent groups designs, including interaction terms where appropriate. Tests of the effects of repeated approaches were conducted using randomized blocks (repeated measures) ANOVAs. After significant interactions were detected, we examined simple effects to detect sources of interaction. Tests of differences between pairs of means for weather conditions were conducted using Tukey's tests. All tests were two-tailed with $\alpha = 0.05$. Effect sizes are reported as η^2 for analysis of variance (Cohen, 1992); $r_{equivalent}$ for Fisher exact, Mann-Whitney U and McNemar's tests (Rosenthal and Rubin, 2003); and g for sign tests (Cohen, 1992).

Results

Approach speed

Variances of FID were homogeneous (Levene's $F_{5,52} = 1.02$, $P > 0.10$), but the distribution was significantly nonnormal (Kolmogorov-Smirnov $d = 0.125$, $P = 0.02$). For logarithmically transformed data, variances were homogeneous (Levene's $F_{5,52} = 2.03$, $P = 0.09$) and the distribution did not depart significantly from normality (Kolmogorov-Smirnov $d = 0.125$, $P = 0.20$). The main effect of speed was significant ($F_{2,52} = 34.14$, $P < 1 \times 10^{-6}$), but the main observer effect was not ($F_{1,52} = 1.32$, $P > 0.10$). However, the interaction between approach speed and observer was significant ($F_{2,52} = 7.47$, $P < 0.0014$, $\eta^2 = 0.11$). FID increased as approach speed increased for both observers (observer 1: $F_{2,25} = 6.14$, $P = 0.0068$, $\eta^2 = 0.33$; observer 2: $F_{2,27} = 32.10$, $P < 1.0 \times 10^{-6}$, $\eta^2 = 0.70$). However, FID increased by greater distances between pairs of approach speeds for approaches by observer 2 than for observer 1, especially between the intermediate and fast approach speeds (fig. 1). At the slow and intermediate approach speeds, FID did not differ significantly between observers (slow: $F_{1,17} = 2.70$, $P = 0.12$, $\eta^2 = 0.14$; intermediate: $F_{1,17} = 0.21$, $P > 0.10$, $\eta^2 = 0.01$). FID was significantly greater during approaches by observer 2 than observer 1 at the fastest approach speed ($F_{1,18} = 15.02$, $P < 0.0012$, $\eta^2 = 0.45$).

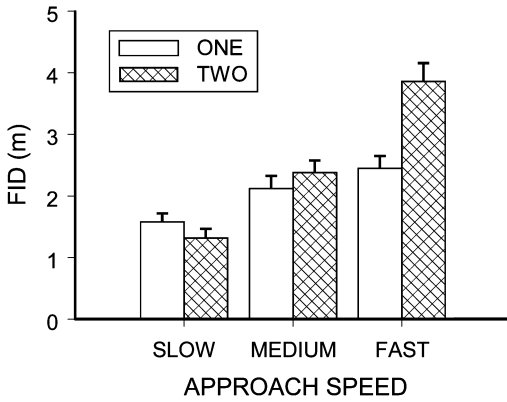At the two slower approach speeds, FID did not differ between observers ($F_{1,34} = 1.03$,

Figure 1. Effects of three approach speeds by two investigators on flight initiation distance (FID) by *Podarcis lilfordi*. Error bars show 1.0 SE.
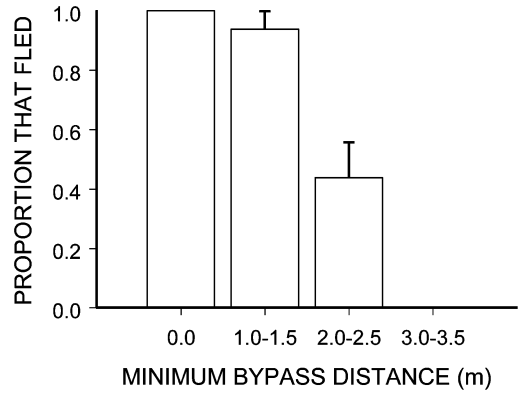

Figure 2. The proportion of individuals of *Podarcis lilfordi* that fled increased as the investigator approached more directly. Error bars show 1.0 SE.
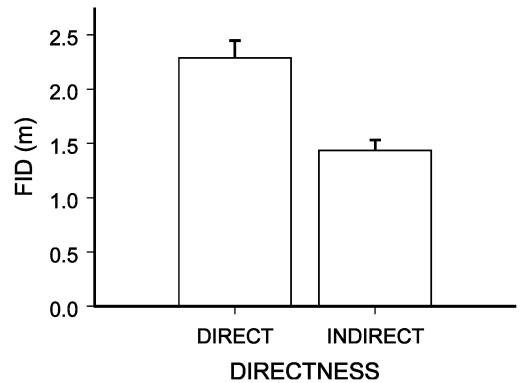
$P = 0.32$, $\eta^2 = 0.04$), but was significantly greater for intermediate than slow approach speed ($F_{1,34} = 23.41$, $P = 2.8 \times 10^{-5}$, $\eta^2 = 0.87$) in a range of approach speeds in which starting distance does not affect FID. The interaction between observer and the two slower approach speeds was not significant ($F_{1,34} = 2.48$, $P = 0.12$, $\eta^2 = 0.09$).

Directness of approach

Frequency of fleeing was greatest during direct approaches and decreased as approaches became less direct, especially for minimum bypass distances of at least two meters (fig. 2). The frequency of fleeing did not differ significantly between direct approach and approaches with 1-1.5 m minimum bypass distances (Fisher exact test, $P = 0.50$, $r_{equivalent} = 0.00$). Significantly higher proportions of individuals (Fisher tests) fled during direct approaches than 2.0-2.5 m bypasses ($P = 0.0004$, $r_{equivalent} = 0.56$) and 3.0-3.5 m bypasses ($P = 7.95 \times 10^{-23}$, $r_{equivalent} > 0.379$, the effect size calculator failed at powers lower than 10^{-19}), during 1.0-1.5 m than 2.0-2.5 m ($P < 0.0030$, $r_{equivalent} = 0.48$) and 3.0-3.5 m ($P = 2.8 \times 10^{-8}$, $r_{equivalent} = 0.79$) bypasses; and during 2.0-2.5 m than 3.0-3.5 m bypasses ($P < 0.0034$, $r_{equivalent} = 0.47$).

Figure 3. Flight initiation distance by *Podarcis lilfordi* was greater for direct approach than for indirect approach with a minimum bypass distance of 1.0-1.5 m. Error bars show 1.0 SE.

Differences in FID were examined for the two most direct approach categories, during which all but one individual fled. FID was significantly greater during direct approaches than 1.0-1.5 m bypasses (Mann-Whitney $U = 12.0$, $n = 15, 16$, $P = 2.0 \times 10^{-5}$, $r_{equivalent} = 0.67$; fig. 3).

Repeated approach

Only one of 29 lizards entered a refuge in the first trial, but 11 of 29 entered refuges during second approaches. One individual entered refuge in both trials; 10 entered refuge only during the second trial. Lizards were significantly more likely to enter refuge during second than
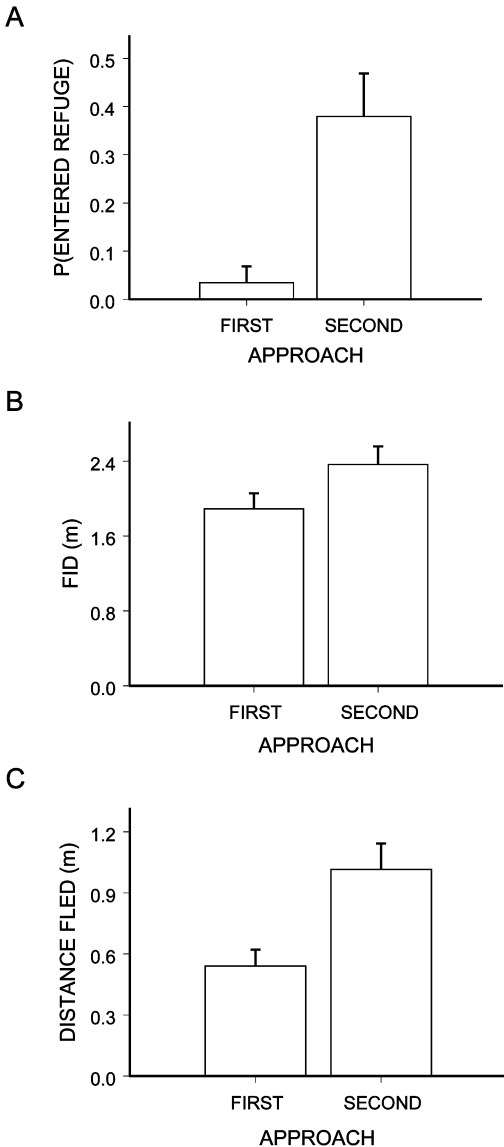
Figure 4. Effects of two successive approaches by an investigator on a) proportion of individuals that entered refuges, b) flight initiation distance (FID), and c) distance fled by *Podarcis lilfordi*. Error bars show 1.0 SE.

first approaches (McNemar's test, $\chi^2_1 = 8.10$, $P = 0.0044$; $r_{equivalent} = 0.48$; fig. 4a).

Variances of FID were homogeneous (Hartley's $F\max_{2,19} = 1.38$, $P > 0.10$), and distributions were normal during both approaches (Kolmogorov-Smirnov $d = 0.15$ and 0.21, respectively, $P > 0.05$ each). FID was significantly greater during second than first ap-

proaches (fig. 4b; $F_{1,19} = 10.65$, $P = 0.0041$, $\eta^2 = 0.36$).

Variances of distance fled were homogeneous (Hartley's $F\max_{2,17} = 2.52$, $P > 0.05$), and distributions were normal during both approaches (Kolmogorov-Smirnov $d = 0.15$ and 0.12, respectively, $P > 0.05$ each). Lizards fled significantly longer distances after second than first approaches (fig. 4c; $F_{1,28} = 7.92$, $P = 0.0088$, $\eta^2 = 0.22$). Furthermore, among lizards that did not enter refuge on either trial, 15 of 18 fled further on the second approach than the first (sign test, $P = 0.008$; $g = 0.33$). Distance fled was not significantly related to FID during first ($F_{1,18} = 2.18$, $P = 0.16$) or second ($F_{1,18} = 0.09$, $P = 0.77$) approaches.

Partial concealment

For lizards in the open, FID was 2.49 ± 0.12 m (range 2.25-2.74 m); for lizards partially concealed by vegetation, FID was 0.85 ± 0.12 m (range 0.61-1.09 m). The distribution of FID did not depart significantly from normality (Kolmogorov-Smirnov $d = 0.20$). Variances were homogeneous (Levene's $F_{1,36} = 0.83$, $P > 0.10$). FID was significantly longer for fully exposed than partially concealed lizards ($F_{1,36} = 93.32$, $P < 1.0 \times 10^{-6}$, $\eta^2 = 0.73$).

Effects of weather conditions on FID

Variances of raw data were significantly heterogeneous (Levene's $F_{2,46} = 4.83$, $P = 0.012$); those of logarithmically transformed FID were homogeneous (Levene's $F_{2,46} = 0.33$, $P > 0.10$). The distribution of the transformed data did not depart significantly from normality (Kolmogorov-Smirnov $d = 0.10$, $P > 0.05$). Transformed FID differed significantly among weather conditions/days ($F_{2,46} = 9.67$, $P < 0.001$, $\eta^2 = 0.30$; fig. 5). FID was significantly longer when lizards basked at 20°C in calm conditions than at 18°C in windy conditions and when lizards were active at greater than 22°C in sunny, calm conditions (Tukey's tests: $P = 0.048$ and $P < 0.001$, respectively).
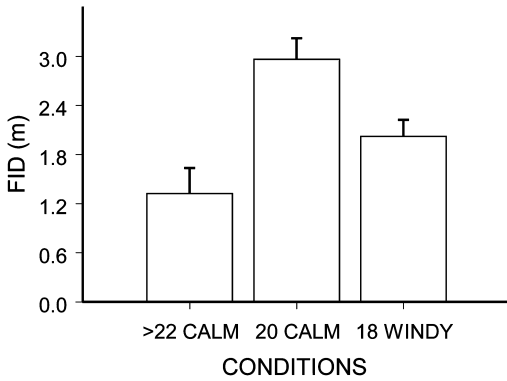
Figure 5. Flight initiation distance (FID) by *Podarcis lilfordi* was strongly affected by weather conditions (>22 CALM – above 22°C, little wind; 20 CALM – 22°C, little wind, 18 windy – 18°C, strong wind). Error bars show 1.0 SE.

FID was significantly longer when lizards were in sunny, windy conditions at 18°C than when active at temperatures warmer than 22.0°C in sunny, calm conditions.

Discussion

Risk factors and escape by Podarcis lilfordi

The broadest finding is that flight initiation distance by Balearic lizards conforms to predictions of escape theory (Ydenberg and Dill, 1986; Cooper and Frederick, 2007) for all four risk factors to which theory unequivocally applies: approach speed, directness of approach, partial concealment (conspicuousness), and repeated approach (predator persistence). For each of these factors FID was longer when predation risk was greater. The effects weather conditions are more complex, as discussed below, but also are consistent with predictions about FID.

Predator approach speed strongly affected FID, which was longer for faster than slower approaches. Although the main effect of speed was large, it cannot be interpreted simply because the interaction between observer and approach speed was significant. Interestingly, lizards responded similarly to the two observers at slow and intermediate approach speeds, but FID differed substantially between observers during fast approaches. In a study of effects of approach speed, directness of approach, and differences among individual predators on time spent hiding in refuges by Iberian rock lizards, *Iberolacerta cyreni*, no interaction was detected between approach speed and observer (Cooper, Martín and López, 2003b). However, observer and directness of approach interacted: responses by lizards to two observers were similar during indirect approach, but hiding times were longer after direct approaches by one of two observers (Cooper Martín and López, 2003b). The common thread may be that interaction was observed only at high risk levels. This does not explain why effects of approach speed and observer interacted in the present study, but not in the study of *I. cyreni*. One possibility is that despite efforts to standardize approaches, methods of approach differed somewhat between observers in one study at the higher approach speed and in the other during direct approaches. The relationship between FID and approach speed is strong, and was detected at approach speeds for which starting distance does not affect FID.

Directness of approach strongly affected FID, which was shorter for indirect approaches that bypassed lizards by 1.0-1.5 m than for direct approaches. No tests were conducted for indirect approaches at longer bypass distances because their minimum bypass distances were greater than the FID for direct approach, making the differences in FID irrelevant for testing the hypothesis that indirect approaches are assessed as implying less risk. Another indication that directness of approach affects risk assessment is that the proportion of lizards that fled decreased progressively as approaches became less direct. The proportion of lizards that fled during indirect approaches with minimum bypass distance of 1.0-1.5 m did not differ from that for direct approaches because the predator came close enough to elicit escape consistently. For less direct approaches, large effect sizes and significance of differences for all paired comparisons

between themselves and more direct approaches indicate that lizards evaluated progressively less direct approaches as implying less risk. In terms of escape theory, escape by a greater proportion of individuals implies that the optimal FID was reached by the predator for a greater proportion of individuals when approach was more direct.

Predator persistence as reflected by repeated approach affected all three escape variables as predicted: FID and distance fled were greater and a higher proportion of individuals entered refuges during second than first approaches. The effect size was largest for refuge entry; it was moderate for FID and distance fled. The smaller effect sizes for FID and distance fled may be related to uncontrolled, unmeasured differences in distance to the nearest refuge because FID increases as distance to refuge increases in some lizards (Cooper, 1997a, 2000a). Because all lizards were close to potential refuges such as bushes, holes, and rocks, effects of differences in distance to refuge presumably were not large, but may have increased error terms in the analyses, reducing effect sizes. That this occurred for distance fled is indicated by the larger effect size for lizards that did not enter refuges than for all lizards. Availability of multiple nearby refuges may account for the lack of relationship between FID and distance fled.

Conspicuousness, due to greater probability of being detected, is expected to increase assessed risk. The shorter FID of Balearic lizards partially concealed by vegetation than those fully exposed to view supports this view. Because only lizards facing in directions affording full, unobstructed views of the predator were approached, the difference in FID must be attributed to differential risk assessment rather than differences in ability to detect the predator.

FID varied among weather conditions, which differed in air temperature and wind speed. FID was shortest in the only conditions permitting full activity, i.e., in calm conditions at temperatures above 22.0°C, as predicted by the relationship between predation risk and FID because warm, active lizards can run faster

(Huey, 1982). The interpretation of the finding that FID was longer for lizards basking in calm weather at 20°C than in windy weather at 18.0°C is uncertain because both temperature and wind presumably affected thermoregulation (Huey, 1982). FID might increase at lower body temperature due to impaired escape ability (Rand, 1964). Alternatively, FID might decrease due to a shift in strategy toward greater reliance on crypsis due to immobility at temperatures greater than the maximum temperature at with lizards shift from escape to standing their ground and fighting (Hertz, Huey and Nevo, 1982). Wind and lower temperature combined may have lowered body temperature enough for lizards to begin a shift toward immobility, resulting in shorter FID. Cost of fleeing may have been a factor for lizards at 18.0°C, but not in warmer conditions. At 18.0°C in wind, but not in the other conditions, the lizards pressed their bodies flat on relatively warm rocks. Fleeing required them to temporarily lose any heat transfer from rock and to expose their bodies more fully to wind. These suggestions are clearly tentative hypotheses. Our findings about weather conditions must be interpreted with caution because multiple aspects of weather varied simultaneously, including differences in preceding weather. Controlled laboratory experiments are needed to isolate effects of weather variables.

Generality of risk × FID relationships in lizards

Approach speed strongly affects FID in all lizards tested. FID increases as approach speed increases in the iguanian families Agamidae (Cooper, 2003a; Cooper and Whiting, 2007a), Gekkonidae (Cooper and Whiting, 2007a), Iguanidae, Phrynosomatidae (Cooper, 2003b, in review), Polychrotidae (Cooper, 2006b), and the scleroglossan families Gekkonidae (Cooper and Whiting, 2007a), Lacertidae (Martín and López, 1996; this study), Scincidae (Cooper, 1997b; Cooper and Whiting, 2007a, 2007b), and Teiidae (Cooper et al., 2003).

Directness of approach affects FID in most species. FID increases with directness of approach in the iguanian families Agamidae (Cooper and Whiting, 2007a), Iguanidae (Burger and Gochfeld, 1990, 1992; Cooper, 1997b), and Phrynosomatidae (Bulova, 1994; Cooper, 2003b, in review), and in the scleroglossan families Gekkonidae (Cooper and Whiting, 2007a), Lacertidae (this study), Scincidae (Cooper, 1997b), and Teiidae (Cooper et al., 2003). No effect of directness on FID was observed in a skink *Mabuya acutilabris*, for which the sample size was too small for adequate statistical power, or in the cordylid *Cordylus niger*, for which the effect was marginal (Cooper and Whiting, 2007b).

Few studies have examined effects of repeated approach or conspicuousness, but in all cases FID was greater during second than first approaches and when lizards were partially concealed or otherwise less conspicuous than when more readily detectable. FID was greater for the second of two approaches in succession in two phrynosomatids (Cooper, 2003b, in review), a lacertid (Martín and López, 2003) and a skink (Cooper, 1997c). FID was greater for more than less conspicuous lizards in an iguanid (Cooper, 2003a), phrynosomatids (Johnson, 1970; Cooper, 2003b), polychrotids (Heatwole, 1968; Cooper, 2006a) and a skink (Cooper, 1998a).

Effects of weather on FID presumably reflect effects of weather on ability to thermoregulate and consequent differences in body temperature and escape ability (Huey, 1982). Effects of refuge temperature on hiding time have been studied more thoroughly than effects of temperature on FID (e.g., Martín and López, 1999a, 1999b; Polo, López and Martín, 2005; Cooper and Wilson, in press). In all of the cited studies, hiding time was shorter when occupation of cool refuges caused body temperature to decrease in refuges than when refuge and outside temperatures were similar. Ambient temperature affects escape ability and probability of fleeing (Christian and Tracy, 1981; Hertz, Huey

and Nevo, 1982), as well as probability of entering refuge (Cooper, 2000a, 2003a).

Findings for the relationship between FID and air temperature are mixed. In two phrynosomatids and an agamid, FID increased as air temperature increased, but the correlations were weak (Bulova, 1994; Blamires, 1999). A stronger positive correlation ($r = 0.52$) was found between FID and substrate temperature in the phrynosomatid *Holbrookia propinqua* (Cooper, 2000a). In the polychrotid *Anolis lineatopus*, the skink *Scincella lateralis* and the colubrid snake *Thamnophis sirtalis*, FID was greater for individuals with cooler body temperatures (Rand, 1964; Smith, 1997; Shine, O'Connor and Mason, 2000). Longer FIDs are predicted by escape theory at cooler body temperatures when decreased locomotor speed accompanies lower temperature, as it does in squamates (Huey, 1982).

An alternative strategy to fleeing when maximum speed cannot be attained is to remain immobile to reduce the likelihood of being detected and attacked. At temperatures low enough to preclude escape by running, some lizards abandon fleeing altogether, switching to defense by biting (Hertz, Huey and Nevo, 1982). At temperatures too low to permit escape at maximal speed, but high enough to allow some chance of successful escape by running, some lizards may delay fleeing until the predator is closer than the optimal FID at preferred body temperature. Because an approaching predator may not have detected the prey, movement by a slowed prey may increase the joint probability of being detected and captured by fleeing too soon.

In this view, slower running speed shifts the balance between escape ability and detectability, resulting in a shorter FID than that of lizards at preferred body temperature. Escape is still attempted by a prey slowed by low body temperature when the predator reaches an FID at which the probability that the predator has already detected the prey in combination with probability of escape by fleeing at the slower speed out-

weighs the cost of being detected due to escape movements. At still lower body temperatures, FID is zero, either because escape attempts at all distances are useless or physical incapacitation precludes escape.

The findings for *P. lilfordi* verify predictions of escape theory for several risk factors, in particular approach speed and directness, predator persistence, and conspicuousness of the prey. Findings for weather conditions appear to be consistent with escape theory based on effects of weather on thermoregulation and a shift in escape strategy as running speed declines due to decrease in maximum escape speed. Further study is needed to isolate effects of temperature and wind speed and to test the hypothesis that strategy changes as escape capacity declines.

The risk factors that we studied strongly affect escape behavior by taxonomically and ecologically diverse lizards. This applies also to the limited sample of tests of lacertids. No obvious qualitative differences appear among representatives of several iguanian and scleroglossan families. Similar effects occur in insectivores, omnivores, and herbivores, as well as in ambush foragers and active foragers. Thus, predictions of escape theory about effects of risk factors appear to apply very broadly to lizards that rely on running to escape.

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