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INFLUENCE OF RISK ON HIDING TIME BY BALEARIC LIZARDS (*PODARCIS LILFORDI*): PREDATOR APPROACH SPEED, DIRECTNESS, PERSISTENCE, AND PROXIMITY

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ABSTRACT: Cost–benefit models predict that hiding time in refuge increases with predation risk. Studies of diverse prey confirm this prediction for various single risk factors, but much less is known regarding joint effects of variation in multiple factors. For single risk factors, we predicted that Balearic lizards (*Podarcis lilfordi*) hide longer after faster and more direct approaches by predators and when predators attack persistently or remain close to the refuge. We predicted that effects of approach speed on hiding time would interact with those of directness of approach and predator proximity to the refuge. We simulated attacking predators by approaching lizards ourselves. Predictions for all single risk factors were confirmed: hiding time was greater after faster and more direct approaches, second than first attacks, and when an investigator stood closer to the refuge. These findings agree with those for other prey that are ecologically and phylogenetically diverse, suggesting that optimality theory is broadly applicable to refuge use. The predictions of interaction of approach speed were confirmed for both directness of approach and predator proximity, but the interaction between approach speed and predator proximity was opposite that predicted. Knowledge of the shapes of curves relating joint risks to hiding time are needed to use optimality theory to predict joint effects of multiple risk factors, but these shapes are unknown. Comparative studies are needed to detect quantitative effects of ecological and phylogenetic differences on hiding time.

Key words: Antipredatory behavior; Emergence time; Hiding time; Predation risk; Refuge use; Squamata

TIME spent hiding in refuge after escaping an attack by a predator (hiding time) can have strong impacts on the probability of being attacked again upon emergence (Hugie, 2003) and time that can be used for other activities that may increase fitness. Hiding time has been studied more thoroughly in lizards than in any other prey taxon (e.g., Amo et al., 2006; Cooper, 1998; Cooper and Wilson, 2008; Martín and López, 1999a, 2004; review for other taxa: Cooper, 2009), but much remains to be learned about factors that affect hiding time, interactions among them, their possible relationships to ecological factors, and their universality.

Refuge-use theory that predicts hiding time based on cost–benefit logic is fairly new, having first been adapted from escape theory (Martín and López, 1999a) by substituting hiding time for flight initiation distance as the dependent variable. The duration of hiding in this model is predicted to be the time when cost of emerging equals cost of hiding (Martín and López, 1999a), both costs being measured

in expected fitness units. Cost of emerging is a consequence of exposure to possible attack, whereas cost of hiding is expected loss of fitness due to inability to engage in fitness-enhancing activity outside the refuge, to physiological costs such as progressive lowering of body temperature as time spent in refuge increases, and to risks in refuge.

Because prey can select hiding times corresponding to higher expected fitness than in the previous model, Cooper and Frederick (2007) developed an optimality model that predicts hiding time to be the time that maximizes expected fitness after the predator–prey encounter. Although quantitative predictions about hiding time differ between the models, in a large majority of circumstances their predictions at the ordinal level are identical. Both models predict that hiding time is greater when cost of emerging (predation risk) is greater and is shorter when cost of remaining in refuge is greater. Until functions relating hiding time to precise levels of fitness associated with predation risk factors and cost of hiding factors are available, ordinal predictions are the best that can be made.

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Such predictions apply very generally to a range of risk and cost of hiding factors, and are likely to differ between the two models of hiding time primarily when fitness gains due to early emergence can be retained even if the prey is killed (Cooper and Frederick, 2007).

Numerous tests of economic models of hiding time in lizards have verified predictions. These include predictions for risk factors associated with predator behavior (approach speed: Cooper, 1998, 2009; Cooper et al., 2003; Martín and López, 2004; directness of approach: Cooper, 2009; Cooper et al., 2003; Martín and López, 1999a; proximity of predator to the refuge: Cooper, 2009; Martín and López, 2004, 2005; persistence of a predator in attacking: Amo et al., 2006; Cooper, 1998, 2009; Martín and López, 1999b, 2001; Polo et al., 2005). Predictions also have been confirmed for opportunity costs of hiding (food and nutritional state: Amo et al., 2007; Cooper, 2009; Cooper et al., 2006; Martín et al., 2003a; presence of conspecific males or females outside the refuge: Díaz-Uriarte, 1999; Martín et al., 2003b) and other costs of occupying refuges (thermal costs: Amo et al., 2004; Cooper and Wilson, 2008; Martín and López, 1999a, 2001, 2005; Martín et al., 2003b; different predator in refuge: Amo et al., 2006).

All tests cited in the preceding paragraph apply to only five species. Two are iguanian ambush foragers, the phrynosomatid *Sceloporus virgatus* (Cooper et al., 2001) and the tropidurid *Tropidurus hispidus* (Vitt et al., 1996). The others are actively foraging sceloproglossans, the skink *Plestiodon* (formerly *Eumeces*) *laticeps* (Cooper et al., 2001) and two lacertids, *Iberolacerta cyreni* (Martín and Salvador, 1997) and *Podarcis muralis* (Verwajen and Van Damme, 2008).

Here we extend tests of the optimal hiding time model to the lacertid *Podarcis lilfordi*, the Balearic lizard. This lizard differs from previously tested species in being an omnivore having high dietary plant content (Pérez-Mellado and Corti, 1993). Although it sometimes climbs plants to access flowers and sometimes scales walls (W. Cooper, D. Hawlena, and V. Pérez-Mellado, personal observations), *P. lilfordi* is primarily terrestrial. It occurs on vertical surfaces much

less frequently than *P. muralis* and is much less closely associated with rocks than *I. cyreni*.

We report experiments on effects on hiding of four risk factors: predator approach speed, directness of approach, predator persistence as indicated by repeated attacks, and proximity of the predator to the refuge while the prey hides. Each of these factors is known to affect hiding time in three or four lizard species. Our goals are (1) to add comparative data to permit eventual assessment of the universality of the effects or their variation with ecological factors, (2) to address the previously unstudied issue of the nature of graded effects of approach speed on hiding time, and (3) to examine little-studied interactions between risk factors. In the study of effect of approach speed we used three speeds to obtain a first assessment of whether hiding time increases linearly as approach speed increases.

Refuge-use theory predicts hiding time based on degree of predation risk and other factors that affect fitness, notably the prey's residual reproductive value and benefits that may be obtained by emerging (Cooper and Frederick, 2007). Most tests of theory have examined effects of variation in single factors that affect predation risk, but prey typically must assess risk based on levels of several factors that operate simultaneously. We conducted an experiment to ascertain whether effects of directness of approach vary with approach speed or are independent of it. We predicted that these factors would interact. Greater risk implied by rapid than slow approach is likely to cause prey to be cautious about emerging regardless of directness, especially for indirect approaches on paths that lead the predator close to the prey, but bypass it. After slow approach, a greater difference in risk of emerging is likely to be assessed after direct than indirect approach. We also examined a possible interaction between approach speed and predator proximity to refuge on hiding time. We predicted that the effect of approach speed would be masked when the predator remains near the refuge because risk remains high as long as the predator is at hand, rather than decaying over time as does the effect of approach speed. When the predator is farther from the

refuge, we predicted that hiding time would be greater after rapid than slow approaches.

MATERIALS AND METHODS

Lizards, Study Site, and Predators

All observations were of adult *P. lilfordi* and all were conducted on Rei, an islet near the harbor city of Mao on Menorca, Balearic Islands, Spain, during 1–6 May 2005. All data were collected on sunny days. Temperatures were in the low 20s °C, but lizards attained much higher body temperatures by basking and were fully active. No appreciable wind occurred except during two experiments having repeated-measures designs in which wind conditions were similar during both trials for each individual. Refuges used by *P. lilfordi* on Rei include spaces beneath stones and boards, and holes around the concrete foundations of abandoned buildings. No permanent human occupants were on Rei in 2005, but people were present for restoration of some buildings and as visitors, possibly habituating lizards somewhat to human contact.

To study effects of predation risk factors on hiding time, we simulated predators by approaching lizards until they entered refuges. Human beings are not natural predators of *P. lilfordi*, although people have collected these lizards for the pet trade and museum specimens. The major predators of lizards that occur on Rei are kestrels (*Falco tinnunculus*); other avian predators such as shrikes (*Lanius* spp.) may visit the islet (Cramp and Simmons, 1982). Rats, which may eat lizards, occur on Rei, and dogs formerly occupied it.

Simulation of Predatory Approach

To study hiding time in refuge, we simulated predatory attacks by approaching lizards, which induced them to flee into refuges. Human beings are not natural predators of *P. lilfordi*, but biologists and amateurs have collected many of them from Menorcan islets. Simulation of predators has been very effective in studies of escape behavior (reviewed by Stankowich and Blumstein, 2005; fish: Grant and Noakes, 1987; frogs: Cooper et al., 2009a,b; lizards: e.g., Cooper, 1997a–c, 1999, 2000a,b; Cooper and Wilson, 2007a,b; Martín

and López, 1995; Martín et al., 2003a; birds: Blumstein, 2003; Cárdenas et al., 2005; mammals: Blumstein and Pelletier, 2005; Stankowich and Coss, 2006; insects: Cooper, 2006; and other taxa Hemmi, 2005, and refuge use, e.g., Amo et al., 2007; Blumstein and Pelletier, 2005; Cooper, 1998, 2000a; Hemmi, 2005; Kramer and Bonenfant, 1997; Martín and López, 1999a,b).

Experimenter bias is possible because the experimenters knew the hypotheses being tested and the experimental designs. To minimize the potential for bias, we standardized approaches by practicing speeds to ensure consistency among trials and attempted to approach using the same gait in all trials. We alternated order of conditions in experiments using repeated-measures designs, thereby precluding biased selection of treatments to match lizards or refuges. During the experiment on effect of approach speed, speeds were interspersed throughout the experiment, preventing any artifacts due to differences in environmental conditions.

Data Collection

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 flight initiation distance (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 (W. Cooper, unpublished data). Findings for the lizard *Sceloporus virgatus* suggest that 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.

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.

Experimental Designs

To study the effect of predator approach speed on hiding time, we used an independent groups design in which each lizard was tested only once at one of three approach speeds. Sample sizes were 16 for slow, 18 for intermediate, and 19 for fast approach speeds. An investigator began a trial by walking directly toward a lizard, not stopping when it began to flee, but continuing to approach until it entered a refuge. When the lizard entered the refuge, the investigator began timing the duration of hiding, moved to a position 6–8 m from the opening of the refuge, and stood immobile. Hiding time was the number of seconds from immergence to complete emergence of the body from the refuge. If a lizard did not emerge within 600 s, the trial was terminated and hiding was recorded as 600 s. We reduced pseudoreplication by having each investigator work in largely separate sites and moving to new spots between trials. It might have occurred at most very infrequently when we worked in overlapping areas.

The other three experiments had repeated-measures designs. In each we alternated which of the two conditions was used in the first trial of a lizard to preclude possible bias due to order of testing, including any effects of predator persistence on hiding time. With exceptions noted below, procedures for each trial were as in the preceding experiment. The experimenter remained immobile after recording hiding time for a lizard's first trial, and approached again until the lizards entered the refuge. Second approaches were begun while lizards were immobile near the refuges within several seconds of emerging, long enough to record the first hiding time.

We examined the effect of directness of approach by approaching lizards directly or indirectly along a linear path that would pass by them at a distance of 1.0 m if they did not flee. Hiding times were measured for each lizard using both direct and indirect approaches. Fourteen lizards were tested using the fast speed and 23 using the intermediate approach speed. Trials were terminated after 300 s, in which case 300 s was assigned as the hiding time.

The possible effect of predator persistence was examined by repeatedly attacking the same lizard ($n = 41$). To simulate a persistent predator attacking again as soon the prey emerged from refuge, the investigator approached a lizard directly at the intermediate speed until it entered a refuge, recorded hiding time as above, approached again immediately in the same manner, and recorded the second hiding time. Trials were terminated after a maximum of 300 s. Strong breezes occurred during this experiment.

The relationship between proximity of the predator to the refuge while the prey is hiding and hiding time was assessed using a repeated-measures design in which hiding time was measured twice for each lizard, once while an investigator stood close to the refuge (1 m) and once far from the refuge (6–8 m). We approached using the intermediate speed and fast speeds. Trials were terminated after 600 s, in which case 600 s was assigned as the hiding time. Strong breezes occurred at times during this experiment.

Statistical Analyses

Analysis of variance (ANOVA) appropriate for independent groups or repeated measures

was the primary means of evaluating significance of differences among treatments and conditions. We used single-factor ANOVA to assess the main effect of approach speed and predator persistence and factorial ANOVA to assess main effects and interaction terms in the studies of effects of approach speed and directness and of approach speed and predator proximity. We tested the assumptions of normality using Kolmogorov–Smirnov tests and of homogeneity of variance using Levene’s tests for independent groups and either Box’s tests for equality of covariances or Hartley’s tests for repeated-measures designs. If assumptions were violated, data were logarithmically transformed, the assumptions validated, and analysis was conducted using the transformed data if assumptions were then met. The assumption of normality could not be met using logarithmically transformed data for predator proximity. Therefore, separate analyses were conducted using (1) two-way ANOVA to estimate the strength of interaction between proximity and approach speed, and (2) nonparametric tests of ranked data to assess the effects of main factors (Sokal and Rohlf, 1995). Differences among pairs of treatment means in the study that employed three approach speeds were tested for significance using Levene’s tests.

For the study of approach speed, a linear regression of mean hiding time on approach speed was conducted. In the study of effects of directness of approach, a Fisher’s exact probability test was used to examine the interaction between approach speed and directness of approach based on frequencies of relative magnitudes of hiding time. A sign (binomial) test examined the effect of directness at the slower speed on frequencies of relative magnitudes of hiding time. In the study of predator persistence, a binomial test was used to assess the difference in frequency of longer hiding time between first and second approaches. In the study of predator proximity, a Wilcoxon signed-ranks matched-pairs test was conducted to corroborate the findings of ANOVA for the main effect of proximity. We examined the effect of predator proximity on the likelihood of hiding until the trial ended using Fisher’s exact tests.

All tests of significance were two-tailed except where stated otherwise and justified by a directional prediction, with $\alpha = 0.05$. Effect sizes were estimated as η^2 for ANOVA, g for binomial tests, and $r_{\text{equivalent}}$ for Fisher’s exact probability tests and a Wilcoxon signed-ranks matched p -pairs test (Cohen, 1992; Rosenthal and Rubin, 2003).

RESULTS

Approach Speed

Raw hiding times were nonnormally distributed ($d = 0.16$, $P = 0.003$) because 9 of 53 individuals did not emerge within 5 min and, therefore, had assigned hiding time = 300 s. Using logarithmically transformed hiding times, the distribution did not deviate significantly from normality ($d = 0.11$, $P = 0.10$), and variances were homogeneous among approach speeds (Levene’s $F_{2,50} = 0.82$; $P = 0.45$). Using transformed data, hiding time differed significantly among approach speeds ($F_{2,50} = 28.44$; $P < 1 \times 10^{-6}$; $\eta^2 = 0.53$).

Hiding times were over 4.5 times longer at the fastest approach speed than the slowest (Fig. 1) and were of intermediate duration at the intermediate approach speed. The regression of mean hiding time on approach speed is significant despite the small sample ($n = 3$; $F_{1,1} = 607.80$; $P = 0.026$), the equation $HT = 2.35AS - 74.81$ s accounting for $R^2 = 0.998$ of the variance, where HT is hiding time and AS is approach speed. Hiding time was significantly greater at the fastest approach speed than for the slowest speed (Tukey’s HSD test, $P = 0.036$) and the intermediate speed ($P < 0.001$), and for the intermediate than for the slowest approach speed ($P = 0.023$).

Directness of Approach

Raw hiding times had nonnormal distributions for direct ($d = 0.21$, $P = 0.01$) and indirect ($d = 0.29$, $P < 0.01$) approaches. Both distributions were normal for logarithmically transformed data (direct: $d = 0.09$, $P > 0.20$; indirect: $d = 0.11$, $P = 0.20$), and covariances were homogeneous (Box’s test, $F_{3,26589} = 1.19$; $P > 0.31$). Hiding time was significantly shorter for indirect than direct approach ($F_{1,35} = 7.46$, $P = 0.0098$; $\eta^2 = 0.07$; Fig. 2), but this cannot be interpreted

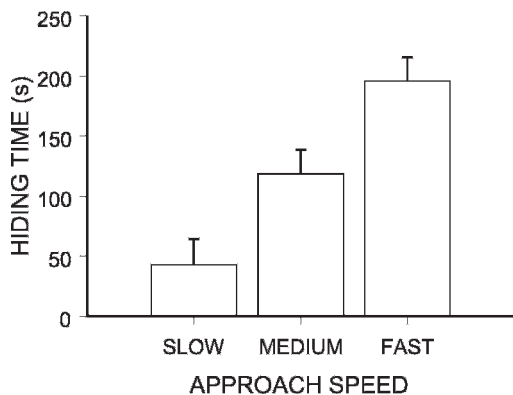


FIG. 1.—Time spent hiding in refuge before emerging increases linearly with predator approach speed.

simply because the interaction between directness and approach speed was significant ($F_{1,35} = 3.88$, $P = 0.029$, one-tailed; $\eta^2 = 0.04$). The effect of approach speed was not significant ($F_{1,35} = 0.56$, $P = 0.46$; $\eta^2 = 0.02$). Mean hiding times were greater after fast than slow approaches for both direct and indirect approaches, but the difference in hiding time between direct and indirect approaches was much greater for slow than fast approaches, as predicted (Fig. 2). Analysis of the simple effects showed that hiding times did not differ significantly between direct and indirect approaches at the faster approach speed ($F_{1,22} = 0.30$; $P = 0.59$; $\eta^2 = 0.01$), but varied strongly with directness of approach following slow approaches ($F_{1,13} = 16.49$; $P = 0.0013$; $\eta^2 = 0.56$).

The interaction term was significant only using a one-tailed test, but nonparametric analyses suggest a stronger interactive effect. At the slower approach speed, hiding time was longer for 13 of 14 (0.93) individuals during direct than indirect approach. At the faster approach speed, 11 of 22 (0.50) individuals hid longer when approached directly than indirectly. Thus, a significantly greater proportion of lizards hid after fast than slow approaches (Fisher's exact test, $P = 0.013$; $r_{\text{equivalent}} = 0.37$). A significantly greater proportion of lizards approached at the slower speed had longer hiding times when approached directly than indirectly (binomial $P = 0.002$; $g = 0.498$), but at the faster approach speed the proportions that hid longer were equal for direct and indirect

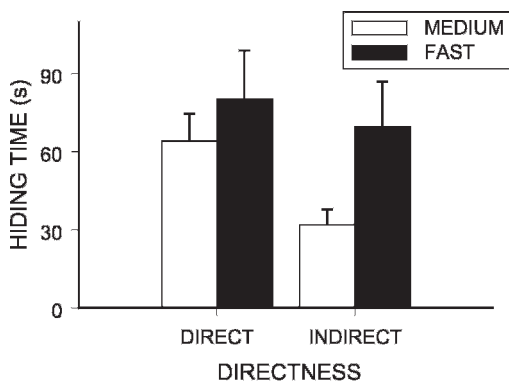


FIG. 2.—Hiding time is greater following direct than indirect approaches that bypass the prey without contact at medium approach speed, but not at the fast approach speed.

approaches. The findings of these nonparametric tests indicate that the marginal interaction term in the ANOVA reflects a real effect difference in between approach speeds in effects of directness of approach on hiding time.

Predator Persistence

Variances of hiding times were significantly heterogeneous ($F_{\max 2,40} = 2.45$; $P < 0.05$), but were homogeneous for logarithmically transformed data ($F_{\max 2,40} = 1.45$; $P > 0.10$). Distributions of first and second hiding times did not depart significantly from normality for the transformed data (first: $d = 0.10$, $P > 0.10$; second: $d = 0.08$, $P > 0.10$). Using transformed data, hiding times were significantly longer following second than first approaches ($F_{1,40} = 13.93$; $P = 0.00059$; $\eta^2 = 0.26$). Raw hiding time data were 53.1 ± 8.9 s (range 1–251 s) after first approaches and 93.8 ± 13.9 s (range 5–300 s, including five lizards that hid the full 300 s) after second approaches.

Although the mean hiding time was greater following second approaches, the difference was far from uniform. Among 41 adults, almost all of which were males ($n = 2$ females were identified), 30 hid longer after second approaches, 10 hid longer after first approaches, and there was one tie for an individual that emerged after only 6 s in both trials. A significantly higher proportion (0.75) of lizards hid longer after second than first approaches

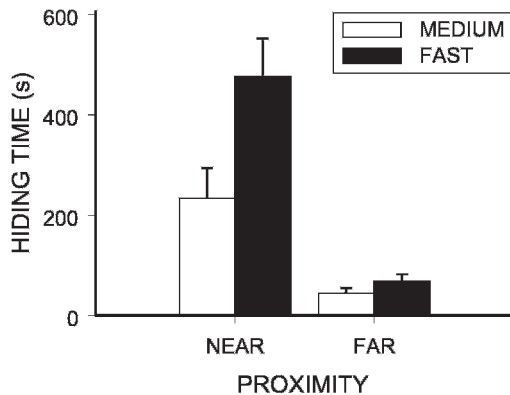


FIG. 3.—Hiding time is longer when the predator stays near the refuge than farther from it, and the difference between distances is greater after approaches at the fast than the medium speed.

than hid longer after first approaches (0.25, binomial $P = 0.0026$; $g = 0.497$).

Predator Proximity

Because many lizards did not emerge when the predator was close to the refuge, especially after rapid approach, distributions of hiding time were intractably nonnormal. Analysis of variance in violation of the assumption of normality showed a significant interaction between approach speed and predator proximity ($F_{1,21} = 5.37$; $P = 0.000002$; $\eta^2 = 0.41$; Fig. 3). The main effects, which cannot be interpreted simply, were $F_{1,21} = 6.95$ ($P = 0.015$; $\eta^2 = 0.08$) for approach speed and $F_{1,21} = 40.32$ ($P = 0.000003$; $\eta^2 = 0.01$) for predator proximity.

Proximity had a stronger influence than approach speed on hiding time (Fig. 3). A Wilcoxon signed-ranks matched-pairs test of data pooled for both approach speeds also shows that hiding time was significantly greater when the predator stood close to the refuge than when farther from the refuge ($T = 3$, $n = 23$; $P = 0.000040$; $r_{\text{equivalent}} = 0.74$). Another indication of the importance of approach speed and dependence of its effect on predator proximity is that lizards delayed emergence beyond the end of the 10-min trial significantly more frequently when the predator was close to the refuge (Fisher's exact $P = 0.0131$; $r_{\text{equivalent}} = 0.44$) after fast (7 of 9 did not emerge) than slow approaches (3 of 14 did not emerge). All lizards emerged long

before the ends of trials when the observer stood farther from the refuge. Using data pooled for both approach speeds, the probability of emerging was significantly lower when the predator stood closer to the refuge (0.57) than farther from refuge (1.00, sign test $P = 0.002$; $g = 0.498$).

DISCUSSION

Effects of the Four Risk Factors and Hiding Time

All predictions based on cost-benefit models of hiding time were confirmed. The relationship between approach speed and hiding time had a large effect size and was linear at the three speeds used. Hiding time increased rapidly with approach speed, as indicated by a slope of 2.4 for hiding time on approach speed. Because negative hiding time is meaningless, the negative intercept of 75 s suggests that linearity cannot extend to zero approach speed.

Approach speed interacted with directness of approach as predicted (i.e., with a greater difference in hiding time between direct and indirect approach at the slower than the faster approach speed). Although significant, this effect was not strong using parametric analyses. However, nonparametric tests revealed the same relationship with lower P -values and larger effect sizes. Directness of approach strongly affected hiding time after slow approaches, but not after rapid approaches. It appears that the greater risk implied by a rapidly approaching predator overrides the effect of directness of approach. Rapid approach might similarly affect responses to certain other risk factors, especially those having small effect sizes. Our findings differ from those of Cooper et al. (2003) for *I. cyreni*, in which speed and directness affected hiding time independently. The greater habituation of *I. cyreni* to human presence and cooler refuges at high elevation might have both minimized interactive effects by shortening hiding times.

Balearic lizards appeared to assess second attacks as riskier than first attacks. This conclusion is supported by the longer mean hiding time after second than first approach (1.8 times longer) and the higher proportions

of individuals that hid longer after second than first approaches. Estimates of effect sizes were intermediate for the parametric test, but very large for the nonparametric test. Nevertheless, one-fourth of individuals hid longer after first than second approaches, indicating a less reliable effect of predator persistence than approach speed. One reason for the inconsistency could be the relatively low risk implied at intermediate approach speed. Other possible explanations for lack of uniformity among individuals are variation in uncontrolled aspects of refuges, such as security and temperature (Martín and López, 1999a,b), and of body temperatures of lizards following second approaches (Polo et al., 2005). If body temperature falls while a lizard hides after a first attack, it may emerge sooner after a second attack if decrease in body temperature offsets increased risk upon emergence.

Predator proximity while lizards hid strongly affected hiding time. Lizards remained in refuges 6.4 times longer when the predator stood close to the refuge than farther from it. This strong effect indicates that while lizards hide, they monitor the environment outside to assess risk of emerging. Sometimes they could be seen dimly while looking out from within refuges. Such monitoring of predator position is consistent with observations of other lizards that move to locations where they remain hidden, but can see outside, or emerge only partially (Martín and López, 1999a,b) and with willingness to assume some risk to monitor predator activity while outside refuge (Cooper, 2008b). When the predator is detected nearby, emergence is delayed.

Analysis of variance revealed a significant interaction between predator proximity and approach speed, but this finding must be interpreted cautiously because the assumption of normality was violated. However, interaction is clear in Fig. 3 and nonparametric analyses substantiated influences of approach speed and proximity in an apparently interactive manner. The prediction that approach speed would have a stronger effect on hiding time when the predator was farther from refuge was contradicted. Hiding time was greater after fast than slow approaches when the predator was closer to the refuge, but was

similar at the two speeds when the predator was farther from refuge. When the predator stood close to the refuge, the proportion of lizards that did not emerge before trials ended was greater after fast than slow approaches, but no such difference occurred when the predator stood farther away.

In *I. cyreni* predator proximity and approach speed independently affected hiding time when each lizard was tested using the same speed in both trials (Martín and López, 2004). A marginally nonsignificant interaction between risk level and proximity was found in *P. muralis*, but risk level was based on combinations of two factors (slow, indirect approach for low risk and fast, direct approach for high risk [Martín and López, 2005]). Reasons for interspecific differences in independence versus interaction between predator proximity and other risks are uncertain, but may be related to differences in thermal conditions in refuges and habituation to people that result in much faster emergence in *I. cyreni*. Because speed and directness themselves interact, but speed interacted with proximity in the opposite direction in *P. lilfordi*, the opposing effects might have obscured or contributed to interaction in *P. muralis*.

Hiding Time: Theory, Ecology, and Phylogeny

Current theory (Cooper and Frederick, 2007) accurately predicts relative magnitude of hiding times by lizards responding to variation in numerous risk factors as noted above. Present results for each of the four risk factors considered singly confirm previous findings and extend them to *P. lilfordi*. For each of the four risk factors that we studied, the relationship between risk and hiding time was qualitatively identical in *P. lilfordi* and previously studied species (cited above, this paper). The uniformity of findings for these factors suggests that predictions of escape theory apply widely to lizards regardless of important ecological differences in factors such as foraging mode, diet, and microhabitat use. Foraging mode influences many aspects of lizard ecology and behavior (e.g., Cooper, 1995, 1997d; Huey and Pianka, 1981; Vitt and Congdon, 1978), including defense (Vitt, 1983; Vitt and Price, 1982). However, hiding

time increases with risk for several risk factors in the ambush forager *S. virgatus* and four active foragers (reviewed by Cooper, 2009, this paper). Similar findings about effects of various risk factors on hiding time have been reported for a phrynosomatid, a skink, and three lacertids (Cooper, 2009, this paper). Limited findings for other prey taxa suggest that theory (Cooper and Frederick, 2007; Martín and López, 1999a) successfully predicts hiding times in diverse vertebrates and invertebrates that escape into refuges (Cooper, 2009).

Optimality theory (Cooper and Frederick, 2007) successfully predicts hiding time due to variation in single risk factors, but the theoretical basis for predicting interactive effects between risk factors is unclear. To make predictions with assurance, one must know the shapes of the risk curves. For single factors, a curve relating risk of emerging to time spent in refuge is greater for the higher risk at all times until emergence. However, if levels of more than one risk factor are allowed to vary, shapes of the joint risk curves are unknown. Thus, predictions are based on suppositions about effects of variation of one risk factor on risk assessment by prey for another factor. The suppositions appear to have been correct about interaction between approach speed and directness: high risk at fast approach speed may overwhelm the difference in directness, but the effect of directness is larger after slower approach, presumably because the low risk due to speed allows greater expression of the effect of directness of approach.

The prediction of interaction between predator proximity and approach speed, although based on logic similar to that for interaction between approach speed and directness, was incorrect given that the interaction was in the direction opposite that predicted. The stronger effect of approach speed when the predator is closer to refuge suggests that lizards assess the combination of rapid approach and remaining near the refuge as indicating a determined predator posing higher risk than implied by a high risk level for single factors or both additively. Another interpretation is that low risk of emerging when a predator is far from the refuge may

lessen the importance of the initial approach speed. Our disparate findings for the two interactions show that pairs of factors may interact in different ways that may be difficult to predict a priori.

Interactions between risk factors and between risk and cost factors appear to be common in lizards, but some factors may have independent effects or interactions only apparent when risk levels vary sequentially. When two risk levels (slow, indirect versus fast direct approach) were varied in a sequence of two or three attacks, the interaction between persistence and sequence of risk levels was significant in both *I. cyreni* and *P. muralis*, with greater increase in emergence time in second trials when the second approach was fast (Martín and López, 2004, 2005). In the only lizard studies that varied risk and cost of remaining in refuge, repeated approach and temperature inside refuge influenced hiding time independently in *I. cyreni* (Polo et al., 2005), as did approach speed and female presence outside refuge for males (Martín et al., 2003b).

Few studies report interactions involving hiding time in nonlizard taxa. In the turtle *Mauremys leprosa*, risk level was varied by a combination of duration of handling and tapping on the shell, by presence or absence of the experimenter during hiding, and by microhabitats (Martín et al., 2005). Experimenter presence had no effect because turtles could not monitor it while the head was withdrawn into the shell (Martín et al., 2005). Risk level and microhabitat interacted because hiding time increased with risk on land, but not in water where emergence could facilitate escape (Martín et al., 2005). Degree of risk indicated by chemical cues to a predator appeared to interact with frequency of exposure to affect hiding time by the crayfish *Orconectes virilis* (Pecor and Hazlett, 2003). Duration of handling by an experimenter and amount of food did not interact in the hermit crab *Pagurus acadianus*, but amount of food did not affect hiding time (Scarratt and Godin, 1992).

No variation in effects of risk factors on hiding time attributable to ecological or phylogenetic differences has been reported. Comparative studies using phylogenetic meth-

ods offer great potential for examining quantitative differences among species. Such studies are beginning to make important contributions to our knowledge of effects of ecological and taxonomic differences on flight initiation distance in birds (e.g., Blumstein, 2006; Møller, 2008a,b), and are likely to prove fruitful for understanding determinants of hiding time in other prey.

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