

Escape by the Balearic Lizard (*Podarcis lilfordi*) is affected by elevation of an approaching predator, but not by some other potential predation risk factors

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Submitted on: 2011, 6th April; revised on: 2nd September; accepted on: 5th September.

Abstract. Many predation risk factors to affect escape behavior by lizards, but effects of some potential risk factors are unknown or are variable among species. We studied effects of several risk factors on escape responses by the Balearic lizard (*Podarcis lilfordi*, Lacertidae) on escape responses. Escape was elicited by an approaching experimenter who recorded flight initiation distance (predator-prey distance when escape begins) and distance fled. When an experimenter approached from above (upslope), flight initiation distance and distance fled were longer than when the experimenter approached from below. This novel effect suggests that lizards exposed to aerial predation might have been naturally selected to respond rapidly to predators approaching from above or that effects of path inclination of escape ability may differ between predators and prey in a manner requiring a larger margin of safety during approaches from above than below. Although sex differences in aspects of escape occur in some lizards, including lacertids, no sex difference was observed in *P. lilfordi*. Because vigilance and some other aspects of antipredatory behavior exhibit cortical lateralization, we tested effects of approach from the left and right sides of lizards. As predicted by optimal escape theory, side of approach did not affect flight initiation distance. Because many lizards have color vision and respond to pigmentation of conspecifics in social settings, researchers have often worn only drably colored clothing when simulating predators. This precaution may be unnecessary because flight initiation distance did not differ among investigator shirt colors (red, orange, olive).

Keywords. Escape behavior, flight initiation distance, distance fled, laterality, predation risk, Squamata.

INTRODUCTION

Optimal escape theory successfully predicts effects of many risk factors on escape decisions (Stankowich and Blumstein, 2005; Cooper and Frederick, 2007, 2010; Cooper

2010a). Although optimal escape theory was developed to predict flight initiation distance, the distance separating prey from an approaching predator when the prey begins to flee, its principles regarding predation risk, cost of escaping, and prey fitness are often applicable to other escape variables, including distance fled and probability of entering refuge (Martín and López, 2003; López et al., 2005). Numerous predation risk factors are known to affect escape decisions (Lima and Dill, 1990; Stankowich and Blumstein, 2005; Cooper, 2010a). Flight initiation distance increases with risk for diverse risk factors, and mounting evidence indicates that distance fled and probability of entering refuge also increase with predation risk in many circumstances (Stankowich and Blumstein, 2005; Cooper, 2010a).

Despite extensive study in the past 15 years, effects of some potential risk factors on escape decisions remain unstudied. One such factor is the elevation of an approaching terrestrial predator with respect to the prey. Many prey are subject to both aerial and terrestrial attack. Because aerial predators often approach more rapidly than terrestrial predators and may be more maneuverable during chases, risk may often be high when prey are approached from above. Even for terrestrial predators, greater maximal approach speed may be possible while moving downhill. Predators approaching on the ground from below a prey's position may have slower top running speed or acceleration than when on level ground (Irschick and Jayne, 1999; Vanhooydonck and Van Damme 2001; Warner and Shine, 2000). In these circumstances, it may be predicted that flight initiation distance is longer when prey are approached from above than from below. For prey that do not enter refuges, distance fled is also predicted to be longer for approaches from above than below. Predictions regarding refuge entry are less clear, but if risk is great enough to elicit hiding in refuge by a high proportion of individuals, a greater proportion of individuals are predicted to enter refuge when approached from above than from below.

Sex differences in escape behavior may occur for several reasons, including differences in body size, detectability, and escape ability. Over a wide range of taxa, about one third of prey species exhibit sex difference in flight initiation distance (Stankowich and Blumstein, 2005). Among 30 lizard species, flight initiation distance is longer in males than females in at least one population in five species, longer in females than males in only one species; it does not differ between sexes in the remaining 24 (80%) species (Johnson, 1970; Shallenberger, 1970; Snell et al., 1988; Burger and Gochfeld, 1990; Braña, 1993; Bulova, 1994; Stone et al., 1994; Smith, 1996; Whiting, 2002; Cooper, 2003a, 2006, 2009, in press; Lailvaux et al., 2003; Capizzi et al., 2007; Cooper and Wilson, 2007a; Vanhooydonck et al., 2007; Brecko et al., 2008; Cooper and Avalos, 2010). A sex difference in distance fled has been detected in only one of 21 lizard species studied (Snell et al., 1988; Stone et al., 1994; Smith, 1996; Whiting, 2002; Cooper, 2003a, 2006, 2009a, in press; Lailvaux et al., 2003; Cooper and Wilson, 2007a; Vanhooydonck et al., 2007; Brecko et al., 2008; Cooper and Avalos, 2010); males fleeing a greater distance in that species (Cooper, 2006). A sex difference in probability of entering refuge occurs in 2 of 5 lizard species, conspicuous males being more likely than less conspicuous females to enter refuge in both cases (Lailvaux et al., 2003; Cooper, in press).

Another possible risk factor is the side from which a predator approaches a prey. Because sidedness affects many activities, prey having different escape latencies when approached from right or left (Lippolis et al., 2002) or prey that exhibit left-right pref-

erences for maintaining vigilance (Martín et al., 2010) might also exhibit differences in flight initiation distance between approaches by predators from the left and right. If such differences occur, flight initiation distance is predicted to be longer for approaches from the side for which escape latency is shorter. If differential vigilance between sides is important, flight initiation distance might be longer during approaches from the side where the prey is more vigilant. On the other hand, because natural selection should favor prey able to escape from attacks from any angle, the side of approach may not affect flight initiation distance if the prey has detected the predator at a distance greater than the optimal flight initiation distance (Cooper and Frederick, 2007). Many lizards have excellent color vision, and many species have bright, socially significant coloration (Cooper, 1992). Therefore, it has been common practice for researchers who simulate predators approaching lizards to wear drab coloration to avoid possible effects of color on escape behavior (e.g., Martín and López, 1999; Cooper 2003b). However, it has never been established whether the color of clothing worn by researchers affects escape parameters.

Here we examine possible influences on escape decisions by Balearic lizards (*Podarcis lilfordi*) of two predation risk factors not previously studied in any prey species, the elevation of an approaching predator with respect to the prey and the coloration of clothing used by investigators. In addition, we investigated the poorly known effect of the side from which the predator approaches and the possibility that the sexes differ in flight initiation distance and distance fled.

METHODS

Animals and study sites

Podarcis lilfordi is a small, omnivorous lacertid lizard that occurs at high population densities on many islets off the coasts of the large islands Mallorca and Menorca (Pérez-Mellado and Corti, 1993; Pérez-Mellado et al., 2008), Balearic Islands, Spain. We conducted field experiments on effects of experimenter elevation during approach, lizard sex, and shirt color on escape on Dragonera Island adjacent to Mallorca and of side from which approach occurred on Aire adjacent to Menorca. All data were collected in late June 2010 in sunny conditions when lizards were active. Males are slightly larger than females on Aire (67.8 mm vs. 59.3 mm snout-vent length) and some other, but not all, islets (Pérez-Mellado et al., 2000). Only large adults were included in observations.

On Dragonera data were collected during 09:00-14:25 h at air temperatures of 27-29 °C in the study of elevation, 28-29 °C in the study of side of approach, and 23-25 °C in the study of shirt color. Lizards were observed on and adjacent to unpaved pedestrian paths. Lizards there escaped off the paths and could seek refuge beneath vegetation or in rock crevices, including those in stone fences in several locations. Human beings are continually present on Dragonera, a natural park where boats daily bring tourists to the islet who walk along the paths occupied by lizards. Many known and potential predators are present. These include raptors, especially kestrels (*Falco tinnunculus*) and booted eagles (*Aquila pennata*), seagulls that capture lizards occasionally (yellow-legged gull, *Larus michahellis*; Audouin's gull, *L. audouinii*; Cramp and Simmons, 1983)), and ship rats (*Rattus rattus*), which are potential predators.

On Aire data were collected during 11:15-18:00 h at temperatures 22-26 °C. Lizards were observed on open ground amidst patches of sparse vegetation. Available refuges were low bushes, rock crevices, and holes at the bottom of some stone fences, as well as burrows from introduced rab-

bits (*Oryctolagus cuniculus*). Aire has lacked permanent residents since the 1960s, but biologists, lighthouse maintenance personnel, and boaters often visit it during spring and summer. Potentially predatory birds on Aire include kestrels (*Falco tinnunculus*), booted eagles (*Aquila pennata*), seagulls of both species noted for Dragonera, and shrikes. Kestrels eat lizards in southern Europe (Cramp and Simmons, 1980). Kestrels are major predators on *P. lilfordi* populations on some Menorcan islets, especially on islets where they breed. They often visit Aire, but have not bred there for several years. The seagull *Larus michahellis* is abundant on Aire, but this species is not known to eat *P. lilfordi* in Cabrera (Araújo et al., 1977) or *P. atrata* in the Columbretes Islands (Gómez, 1991; Catalá et al., 1990). Shrikes (*Lanius* spp.) are major predators of lizards and occur on Menorca and some of its islets, particularly during spring migration. However, they were only occasionally observed on Aire. Mammalian and ophidian predators are absent from Aire (Pérez-Mellado, 1989).

Simulation of approach by a predator

An investigator walked directly toward a lizard to elicit escape behavior. People are not natural predators of *P. lilfordi*. However, biologists and amateur collectors have removed many of these lizards from natural populations. Even if such human predation has been unimportant, prey subject to attack by diverse predators are likely to be naturally selected to flee when approached directly by any potential predators. Consequently, use of researchers as simulated predators is effective for study of escape responses in diverse prey (Stankowich and Blumstein, 2005), including lizards (e.g., Cooper, 1997a, 2000a; Martín and López, 1999b; Martín et al., 2003a,b; Cooper and Wilson, 2007a,b). Studies of escape by lizards using human simulated predators have consistently validated predictions of optimal escape theory about flight initiation distance for numerous predation risk factors and for factors that affect cost of fleeing (e.g., Heatwole, 1968; Burger and Gochfeld, 1990; Martín and López 1996; Cooper 1997a-c, 1999, 2000; Cooper et al. 2003a; Cooper et al. 2006; Cooper and Whiting, 2007).

Simulation of a predator by a researcher has some important advantages. This method is efficient because humans can traverse rough terrain much better than inanimate predator models can. It also precludes actual predation that might occur if natural predators were used and facilitates control of differences among experimental conditions.

Several potential problems with this method have proven to be unimportant. One possible drawback is that apparent escape responses to people might be motivated by avoidance of trampling rather than avoidance of a predator. Another is that some prey, such as chameleons, exhibit different responses to different types of predators (Stuart-Fox et al., 2006). In *Sceloporus virgatus*, a lizard similar to *P. lilfordi* in being primarily terrestrial, no qualitative differences in escape occurred in response to approaching people and models of snakes and birds (Cooper, 2008). Predator-specific responses are unknown in *P. lilfordi*, which escapes by fleeing and often enters refuges (Cooper et al., 2009a, b, 2010).

To avoid experimenter bias, another potential drawback, we approached lizards in a standardized fashion: the same gait was used in all approaches and approach speeds were practiced to ensure consistency across trials. Approach speeds were 0.8 ± 0.0 (SE) m/s in the experiment on the effect of side from which the lizard was approached and 1.4 ± 0.1 (SE) m/s in the other experiments. Sample sizes for the speeds were 10 each. For each experiment the treatment order was selected prior to data collection to eliminate any unconscious choice of treatments to favor predicted outcomes. All approaches were made by WEC.

Experimental design and analysis

All experiments were conducted independently of each other. In the study of the effects of elevation of the approaching predator with respect to the prey, lizards were approached by an inves-

tigator walking along a path either from below (downslope) or above (upslope). Data were collected where slopes were moderate (ca. 15-30 °, corresponding to a difference of 30-60° between approaches from above and below). The experimenter walked upslope during several successive trials, and then downslope for the next series of trials in a different location. The overall number of trials was the same for each elevation ($n = 26$), and no sequential biases were possible due to differences in time of day, temperature, or other variables. In this and the other studies, the experimenter moved very slowly to a position 6-8 m from a lizard located on the ground, stopped for a few seconds, approached directly, and then stopped approaching as soon as the lizard began to flee. Data recorded were sex of lizard, flight initiation distance and distance fled to the nearest 0.1 m, and whether or not the lizard entered refuge. Analysis of variance for a single factor experiment was used to test for sex differences in flight initiation distance and distance fled. An analysis of covariance with flight initiation distance as covariate was used to further examine the effect of elevation of approacher on distance fled. In the absence of a sex difference, similar analyses were used to assess the significance of the difference between approaches from above and below in the two distance variables. A Fisher exact probability test was used to examine the difference in proportion of individuals that entered refuge during approaches from above and below.

To study the effects of side from which a lizard was approached, an investigator approached a the lizard's left or right side from angles in an 60 ° arc centered perpendicular to the lizard's longitudinal axis. Eight-eight lizards were tested in counterbalanced sequence ($n = 44$ each). To study effects of shirt color the investigator wore a red, orange or olive t-shirt during approaches. Fifteen lizards were tested using orange and olive shirt color and 20 were tested using red shirt color. Five trials were conducted in sequence for a given shirt color before the investigator changed shirts to another color. In the studies of effects of approach side and shirt color, only flight initiation distance was measured. ANOVA for single-factor experiments was used in each experiment to for differences in treatments.

Prior to analyses of variance, the assumptions of normality and homogeneity of variance were evaluated using Kolmogorov-Smirnov and Levene's tests, respectively. Effect sizes are reported as η^2 , for which values < 0.30 are considered small (Cohen, 1992). Assumptions were met in all cases. Significance tests were two-tailed with $\alpha = 0.05$.

RESULTS

Predator elevation and lizard sex

Flight initiation distance was significantly greater ($F_{1,50} = 10.19$, $P = 0.0024$) when the predator approached from above than from below lizards on an inclined path (Fig. 1). In an analysis of variance, distance fled was significantly longer ($F_{1,50} = 6.51$, $P = 0.0145$) for lizards approached from above (1.0 ± 0.1 m) than from below (0.7 ± 0.1 m). Distance fled increased as flight initiation distance increased for all lizards ($r = 0.28$; $F_{1,50} = 4.39$, $P = 0.041$). This relationship was significant for approaches from above ($r = 0.42$; $F_{1,24} = 5.04$, $P = 0.034$), but not from below ($r = 0.05$; $F_{1,24} = 0.06$, $P = 0.81$). Slopes of distance fled on flight initiation distance differed substantially, but not significantly ($F_{1,48} = 2.48$, $P = 0.12$). In an ANCOVA using flight initiation distance as covariate, the distance fled remained significantly greater during approaches from above than from below ($F_{1,49} = 3.40$, $P = 0.036$). The effect sizes were small: $\eta^2 = 0.20$ for flight initiation distance and $\eta^2 = 0.12$ (ANOVA) or 0.06 (ANCOVA) for distance fled.

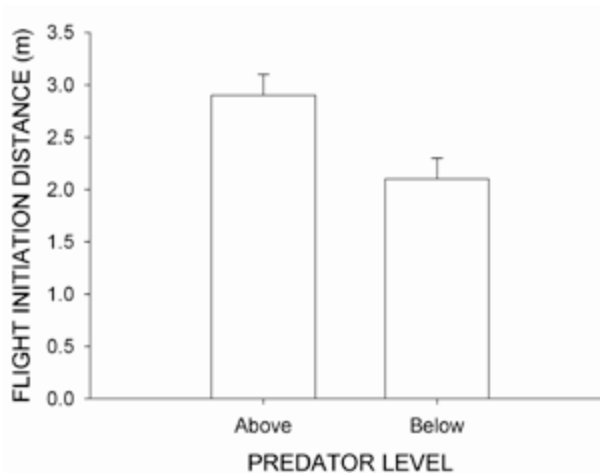


Fig. 1. Flight initiation distances of *Podarcis lilfordi* approached from above and below. Error bars represent 1.0 SE.

Table 1. Flight initiation distance (m) and distance fled (m) by *Podarcis lilfordi* when approached by an investigator wearing a shirt having one of the listed colors.

Shirt color	Flight initiation distance		Distance fled		Entered refuge		n
	Mean	SE	Mean	SE	Yes	No	
Olive	3.1	0.2	0.6	0.1	3	12	15
Orange	3.0	0.3	0.7	0.1	5	10	15
Red	2.8	0.2	0.8	0.1	5	15	20

Few lizards entered refuges: 3 of 26 when approached from above and 4 of 26 when approached from below. The approaching predator's elevation did not affect the probability of entering refuge (Fisher $P = 0.71$).

Flight initiation distance did not differ significantly between sexes (2.4 ± 0.7 m for males, $n = 29$; 2.6 ± 0.8 m for females, $n = 23$; $F_{1,50} = 0.57$, $P = 0.45$). Neither did distance fled for the same individuals (0.9 ± 0.4 m for males, 0.8 ± 0.5 m for females; $F_{1,50} = 0.06$, $P = 0.81$).

Approach side and shirt color

Flight initiation distance did not differ significantly ($F_{1,86} = 0.05$, $P = 0.82$) between approaches from the lizard's left (2.3 ± 0.1 m) and right (2.3 ± 0.2 m) sides ($n = 44$ each). The investigator's shirt color (Table 1) did not significantly affect flight initiation distance ($F_{2,47} = 0.21$, $P = 0.81$), distance fled ($F_{2,47} = 1.53$, $P = 0.23$), or probability of entering refuge (Fisher $P = 1.00$ for olive versus red, 0.68 for olive versus orange, and 0.71 for red versus orange).

DISCUSSION

Lizards permitted closer approach before fleeing and fled for shorter distances when the experimental predator approached along a path from below than from above. These effects, although novel, were small. In several species of lizards approached on level ground when perched on trees, flight initiation distance increases as perch height decreases (Cooper, 1997a, 2006, 2009c). In effect, individuals higher on tree trunks are closer to refuge, i.e., to being out of reach above the predator. For lizards on the ground, flight initiation distance increases as distance to refuge increases because a longer time is required to flee into a more distant refuge (Bulova, 1994; Cooper, 1997a, 2000). In the studies of lizards on trees, flight initiation distance is longer when the predator is higher with respect to the lizard, but for a different reason in *P. lilfordi*. In the present study, approach from above positioned the experimenter higher with respect to the lizard than approach from below, but the distance to the nearest refuge would have been the same regardless of the elevation of approach.

One hypothesis to explain the longer flight initiation distance and distance fled by lizards approached from above than below is that natural selection has favored long flight initiation distance and distance fled in response to aerial predators that approach more rapidly than terrestrial predators. This hypothesis assumes that lizards interpret standing human beings as aerial predators, which they might be more likely to do when approached from above than from below. Because the predator approached at the same speed in all trials, the hypothesis also requires that natural selection has favored longer flight initiation distance at a given approach speed when the approach is from above than below.

A second hypothesis is that flight initiation distance and distance fled are longer during approaches from above than below because terrestrial predators can run and/or accelerate fasterly when moving downslope than upslope (Irschick and Jayne, 1999; Jayne and Irschick, 2000). On steep slopes, flight initiation distance by the phrynosomatid lizard *Sceloporus virgatus* did not differ from that in other terrestrial microhabitats, but distance fled was longer on the slopes (Cooper and Wilson, 2007b). The effect of slope on distance fled is opposite that of predator elevation in *P. lilfordi*. By fleeing upslope, *S. virgatus* could escape without incurring costs of entering refuge because the predator's ability to pursue was diminished on the slope. No information is available about approach from above on escape by *S. virgatus*, but the different effects on distance fled in the two lizard species appear to reflect different aspects of escape strategies. Future studies of effects of predator elevation during terrestrial approach on escape decisions should be conducted to verify the new findings, determine how widespread the effects are among lizards, and to ascertain the importance of the steepness of the approach slope.

The infrequency of refuge use in this experiment despite the presence of abundant refuges might be a consequence of habituation to human presence. In areas where other lizard species frequently encounter human beings, flight initiation distance is shorter (Burger and Gochfeld, 1990; Labra and Leonard, 1999; Eifler, 2001; Cooper, 2006, 2009c, 2010b; Cooper and Whiting, 2007b; Cooper and Avalos, 2010). In Columbian black-tailed deer, distance fled increases as flight initiation decreases, and both variables are shortened by habituation (Stankowich and Coss, 2007). In species that use refuges, shorter distance fled by habituated individuals presumably is accompanied by a lower probability of entering refuge when the effect of initial distance from refuge is taken into account.

Among diverse lizard taxa, sex differences in flight initiation distance occur in only a small proportion of species (Cooper, in press). In Lacertidae, flight initiation distance is longer in males than females in two of five species studied, *Iberolacerta horvathi* and *Zootoca vivipara* (Braña, 1993; Capizzi et al., 2007; Brecko et al., 2008). However, no difference in flight initiation distance between sexes has been detected in *Podarcis* (*P. lilfordi*: this study; *P. melisellensis*: Brecko et al., 2008; *P. muralis*: Braña, 1993). Although the proportion of lacertid species having sex differences in flight initiation distance is more than twice that in all other lizards combined, the sample size for lacertids is too small to assess this difference with adequate statistical power. Distance fled rarely differs between sexes in lizards, having been detected only in one species (*Anolis gundlachi*: Cooper, 2006) of 22 species tested, including *P. lilfordi* and others reviewed by Cooper (in press).

The side from which a predator approached a lizard did not affect flight initiation distance. Brain function of many vertebrates is lateralized, the right eye and left hemisphere feeding being dominant in foraging and the left eye and right hemisphere in antipredatory contexts (Martín et al., 2010). In the common wall lizard (*Podarcis muralis*), the left eye is preferentially used to monitor predators once a lizard has entered refuge (Martín et al., 2010). In horses, distance moved was greater when a person on the horse's left than right side opened an umbrella (Austin and Rogers, 2007), suggesting a relationship between side bias and escape behavior. The absence of any laterality in flight initiation distance suggests that neural lateralization may not affect flight initiation distance in lizards.

The decision to begin fleeing is based on degree of predation risk, cost of fleeing, and the prey's initial fitness (Cooper and Frederick, 2007, 2010). Only risk is likely to be affected by the side from which a predator approaches. Laterality of flight initiation distance may be expected to occur only if escape ability differs between approaches from the left and right, which might occur due to interhemispheric differences in control of fleeing or to morphological asymmetry. Lateralization is believed to be advantageous in allowing more rapid responses (Mandel et al., 2008). However, in the scenario of optimal escape theory, a prey monitors the approach of a predator prior to fleeing. Given time for monitoring and risk assessment, lateralization seems unlikely to affect flight initiation distance. Nevertheless, lateralization might affect rapidity of response when a predator is closer than the optimal flight initiation distance. This can occur if the prey does not detect the predator until immediate flight is required (Blumstein, 2003; Stankowich and Coss, 2006; Cooper and Frederick, 2007). In such circumstances, more rapid detection of a predator on one side could favor shorter latency to escape and, therefore, slightly longer flight initiation distance.

The color of an investigator's shirt did not affect flight initiation distance by *P. lilfordi*. Although experimenters have been cautious about possible effects of clothing color on lizard escape behavior (Martín and López, 1999; Cooper, 2003b), wearing drab clothing of similar coloration throughout an experiment does not appear to be necessary in studies of flight initiation distance. It remains possible that colors known to affect lizard social behavior (Cooper and Crews, 1987; Cooper, 1992; Martín and Forsman, 1999; Weiss, 2006) might affect flight initiation distance, this seems very unlikely. Given the huge differences in body size and shape between lizards and human beings, lizards are unlikely to misidentify researchers as conspecifics no matter what the colors of clothing worn by the researchers.

ACKNOWLEDGEMENTS

The research was funded by the research project: CGL200912926C0202 from the Spanish Ministry of Science and Innovation. We thank Martí Mayol for permits allowing our research and providing accommodations in the Natural park of Dragonera. We are grateful to Mario Garrido and Ana PérezCembranos for logistical help in Aire Island. We are also thankful for the scientific capture permits issued by the Conselleria de Medi Ambient of Balearic Government.

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