# Universal Optimization of Flight Initiation Distance and Habitat-Driven Variation in Escape Tactics in a Namibian Lizard Assemblage

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## Abstract

Some aspects of escape predicted by theoretical models are intended to apply universally. For example, flight initiation distance (distance between an approaching predator and prey when escape begins) is predicted from predation risk and the costs of escaping. Escape tactics and refuge selection are not currently predicted by theoretical models, but are expected to vary with structural features of the habitat. One way of studying such variation is to compare aspects of antipredatory behavior among sympatric species that differ in habitat or microhabitat use. In an assemblage of lizards in northwestern Namibia, we conducted experiments to test predictions of escape theory for three risk factors in representatives of three families and observed escape tactics in additional species. As predicted by escape theory, flight initiation distance increased with directness of a predator's approach and predator speed in Agama planiceps, Mabuya acutilabris, and Rhotropus boultoni, and with distance from refuge in M. acutilabris. As predicted by theory, the probability of entering refuge increased with risk in R. boultoni. All available data indicate that flight initiation distance and refuge entry by lizards conform to theoretical predictions. Escape tactics varied greatly as a function of habitat type: (1) arboreal species fled up and around trees and sometimes entered tree holes; (2) saxicolous species used rock crevices as refuges, but differed in tactics prior to entering refuges; and (3) terrestrial species fled into bushes or other vegetation, often to the far sides of them. Some M. acutilabris entered small animal burrows or buried themselves in sand beneath bushes. Escape tactics varied even among congeners in Mabuya, highlighting the important effect of habitat structure on them. Although habitat partitioning has traditionally been viewed as favoring species coexistence, an interesting by-product appears to be structuring of escape tactics in lizard communities.

## Introduction

Some aspects of antipredatory behavior are predictable from general considerations of costs and benefits that presumably apply to all prey that match the scenario of escape theory. When a prey detects an approaching predator, escape theory predicts that the prey will not flee immediately if the predator is sufficiently distant. The prey should monitor the predator's approach and flee when the fitness cost of not fleeing due to predation risk equals the cost of escaping (Ydenberg & Dill 1986) or at the distance where the prey's expected lifetime fitness after the encounter is maximized (Cooper & Frederick 2007). Similar considerations determine how long a prey should remain inside a refuge before emerging (Martín & López 1999a; Cooper & Frederick in press).

Escape theory makes many testable predictions about effects of predation risk and opportunity costs of escape (e.g. lost foraging time and social opportunities) on flight initiation distance, the distance between predator and prey when the prey begins to flee. Predictions that flight initiation distance increases as risk increases and decreases as escape costs increase have been verified in diverse lizards for many risk (Rand 1964; Heatwole 1968; Burger & Gochfeld 1990; Martín & López 1995, 1996; Cooper 1997a,b,c, 1998a, 2000a) and cost factors (e.g. Cooper 1999, 2000b; Cooper et al. 2003; Cooper & Pérez-Mellado 2004).

Among the best-studied risk factors are predator approach speed and directness of approach. Prey are predicted to have longer flight initiation distances for faster than slower approach speed because a faster predator would overtake the prey sooner and at a shorter distance if the prey did not reach refuge first. Increase in flight initiation distance as predator approach speed increases has been verified in several taxa (e.g. Ydenberg & Dill 1986; Lima & Dill 1990), including several lizards (e.g. Martín & López 1995; Cooper 1997a, 2003a,b).

Flight initiation distance is predicted to be longer during direct than indirect approaches by predators. A predator approaching directly either has detected the prey or is very likely to do so by continuing on its path whereas a predator moving on a tangential trajectory becomes increasingly unlikely to detect the prey as the minimum distance separating prey and predator along the predator's project path increases. This prediction has been supported in birds (Burger & Gochfeld 1981) and several lizards (e.g. Burger & Gochfeld 1981; Bulova 1994; Cooper 1997a, 2003a,b; Cooper et al. 2003). An exception is a crab having inadequate depth perception to assess risk during direct approaches (Hemmi 2005).

A third factor strongly affecting flight initiation distance is distance between a prey and the nearest refuge. Escape theory (Ydenberg & Dill 1986; Cooper & Frederick 2007) predicts that flight initiation distance increases with distance from refuge as time required to reach refuge increases, giving the predator longer to overtake the prey. Accordingly, prey in several taxa have longer flight initiation distance when further from refuge (e.g. Grant & Noakes 1987; Dill & Houtman 1989; McLean & Godin 1989; Dill 1990), and this relationship occurs in lizards (e.g. Bulova 1994; Cooper 1997b, 2003a,b; Cooper et al. 2003; Martín & López 2003).

Models predicting emergence time have not been used to predict when prey should enter refuges, but can do so. Because refuge use is costly, time between entry into a refuge and emergence is predicted from the combined gain from avoiding predation and thermal and opportunity costs of staying in the refuge (Martín & López 1999a,b; Cooper & Frederick in press). When risk is low enough relative to cost, predicted emergence time is zero. For prev not in refuge, this is equivalent to predicting that they will not enter. Thus, it may be predicted that for fixed costs of refuge use, prey should be more likely to enter refuges when risk is high and cost is low than when risk is low and cost of entering is high. Data for several taxa, including lizards, support these prediction (Sih 1997; Amo et al. 2003; Whiting et al. 2003; Hamilton 2004; Stapley & Keogh 2004; Hemmi 2005; López et al. 2005).

Among many aspects of escape and refuge use not predicted by current theoretical models are escape tactics and types of refuges selected. Considerable information about these topics is scattered in the literature, but has not been synthesized. For lizards, some information exists about relationships among morphological variables, substrate types, and escape tactics (Losos et al. 1993, 2002; Losos & Irschick 1996; Schulte et al. 2004). Consistent differences in escape tactics and refuges selected were detected among 11 species of lacertid lizards from diverse locations (Vanhooydonck & Van Damme 2003) and in four species of phrynosomatid lizards, two each in two different locations (Smith & Lemos-Espinal 2005).

We present data on escape and refuge use by sympatric lizards representing several families. To further assess the generality of escape and emergence theories with respect to predation risk factors, we conducted field experiments using three species belonging to different families. For all three we studied effects of directness of approach on probability of fleeing and flight initiation distance and of approach speed on flight initiation distance; for one of them we studied the effect of distance from refuge on flight initiation distance. For these species and several additional lizards, we recorded escape tactics used and refuge types to examine variation among species and habitats.

# Materials and Methods

# Animals and Habitat

In October 1994 we conducted studies of escape behavior at Farm Bergevellei (19°37'S, 14°40'E) 20 km west of Kamaniab in northeastern Namibia. We conducted observations of escape and experiments on effects of predation risk factors on flight initiation distance in Agama planiceps (Agamdiae), Mabuya acutilabris (Scindidae, subfamily Lygosominae), and Rhotropus boultoni (Gekkonidae). At Farm Bergvellei, A. planiceps and R. boultoni occur on rock outcrops. Agama planiceps typically perches on tops of rocks, whereas R. boultoni usually rests on sides of rocks. Mabuya acutilabris is terrestrial, occurring on loose to hard-packed sand where available refuges vary from grass and bushes to holes at the bases of bushes. We also observed escape tactics and types of refuges used by six other species of Mabuva.

# Methods of Observation and Experimentation

Observations were made on warm, sunny days when lizards were fully active. We ensured that each individual was tested no more than once per experiment or set of observations (except in repeated measures experiments) by moving to a new location after observing an individual and not returning to the same site during that experiment of set of observations.

We simulated approaching predators to induce escape by lizards. Because people are not major predators on the lizards, any specific defenses evolved against major predators such as snakes and birds (Stuart-Fox et al. 2006) might be overlooked. On the other hand, researchers can traverse rough terrain much better than model predators, allowing them to approach lizards in a natural manner in sites inaccessible to models. Numerous studies using human-simulated predators have shown that flight initiation distance of lizards is affected by variation in both predation risk factors (e.g. Burger & Gochfeld 1990; Bulova 1994; Martín & López 1996; Cooper 1997a,c, 2003a,b; Cooper et al. 2003) and costs of escaping (Cooper 1999, 2000b; Cooper & Pérez-Mellado 2004; Cooper et al. 2006) as predicted by escape theory (Ydenberg & Dill 1986; Cooper & Frederick 2007).

To characterize escape tactics and destinations, an observer sighted a lizard, turned to face it, walked toward it until it fled, and recorded its methods of escape and refuges used. Unless otherwise state, the investigator stopped moving as soon as a lizard began to flee. In other cases, the investigator continued to approach (pursue) the lizard to force it to select a refuge. In the experiments, an investigator walked toward a lizard on a predetermined path at a practiced speed, then recorded whether the lizard fled, flight initiation distance, escape methods, and destinations.

In A. planiceps we studied effects of directness of approach on probability of fleeing and flight initiation distance and the effect of approach speed on flight initiation distance. We observed escape tactics when the experimenter stopped approaching as soon as a lizard fled and when the experimenter pursued it. To study the effect of directness of approach, we approached lizards at a slow, practiced speed (ca. 65 m/min) directly or on linear paths along which the investigator would pass by the lizard at a minimum distance of 5 or 10 m. Each of 17 lizards (five males, 12 females) was tested using all three approach paths. Sequence of paths was counterbalanced (the final replication including only five of six possible sequences) to preclude bias due to order of testing. If a lizard did not flee, flight initiation distance was recorded as the minimum bypass distance. We studied effects of approach speed by directly approaching at either a slow (ca. 45 m/min, n = 7lizards) or a fast approach speed (ca. 120 m/min, n = 9 lizards). In *M. acutilabris* we studied effects of directness and speed of approach using the same methods with the following exceptions. Bypass distances were 0, 2, and 4 m (n = 18). We used a repeated measures design with counterbalancing to study the effect of approach speed (n = 6). We examined the effect of vegetative cover on flight initiation distance during slow, direct approach for lizards on open sand (n = 9) and in vegetation providing some cover (n = 6).

In *R. boultoni* we studied effects of directness of approach (n = 12) and we used a counterbalanced repeated measures design to study the effect of approach speed (n = 6). We studied the effect of degree of risk on use of crevices as refuges by comparing frequencies of refuge use at different approach speeds and directness of approach.

# **Statistical Analyses**

Effects of directness of approach on probability of fleeing were tested for significance using sign tests. Because three separate tests were conducted, significance was assessed using a sequential Bonferroni procedure (Wright 1992). Unadjusted p values are reported, but significance is indicated following adjustment. Friedman two-way analysis of variance was used to test significance of differences in flight initiation distance among approach types because many individuals did not flee when approached indirectly, producing non-normal distributions. Effects of sex in A. planiceps on probability of fleeing during 5 m bypass trials and on flight initiation distance during direct approaches were examined using a Fisher exact probability test and analysis of variance, respectively. The effect of cover on flight initiation distance in M. acutilabris was tested for significance by analysis of variance. The effect of risk on use of crevices as refuges by R. boultoni was assessed by comparing frequencies of refuge use in trials with lower and higher risk using pooled data from experiments on directness of approach and approach speed by sign test.

To detect the predicted effect of directness of approach on flight initiation distance, it is necessary for flight initiation distance to be greater during direct than indirect approaches. This requires testing at an appropriate bypass distance. In all experiments the longer bypass distance was greater than flight initiation distance during direct approaches, which was in turn somewhat greater than the shorter bypass distance in two of three species. If a lizard did not flee when bypassed, but had a flight initiation distance less than the minimum bypass distance when approached directly, there is no way to know whether the minimum bypass distance that would have induced it to flee would have been greater than its flight initiation distance during direct approach. We therefore conducted sign tests using numbers of individuals that (1) had flight initiation distances for direct approaches that were greater than or equal to the shorter of the two bypass distances, but did not flee when bypassed; (2) fled during both approaches and had greater flight initiation distance during direct approaches; and (3) numbers of individuals that fled in both trials and had greater flight initiation distance when bypassed. Individuals that fled in both trials and had equal flight initiation distances were excluded.

Differences in flight initiation distance between approach speeds were assessed for significance using a t-test for *A. planiceps* and repeated measures analyses of variance for the other species. Levene's tests (*A. planiceps*) or Hartley's  $F_{max}$  tests (*M. acutilabtris* and *R. boultoni*) were used to ascertain that variances were homogeneous. Data are presented as  $\bar{x} \pm 1.0$ SE. All statistical tests are two-tailed unless noted otherwise. Alpha was 0.05 when no adjustment was required, or a lower adjusted value for some comparisons using the sequential Bonferroni procedure.

## Results

#### Agama planiceps

The directness of approach strongly affected probability of fleeing (Fig. 1a). All individuals approached directly fled, whereas progressively fewer fled approached on paths bypassing them by 5 and 10 m, respectively. The probability of fleeing was significantly greater during direct approaches than five m



**Fig. 1:** Proportions of individuals that fled varied with directness of approach. Error bars are 1.0 standard error of a proportion. (a) Agama planiceps (n = 17), (b) Mabuya acutilabris (n = 18), (c) Rhotropus boultoni (n = 12)

bypasses (sign test, p = 0.0024) and 10 m bypasses (sign test, p = 0.00006). The probability of fleeing did not differ significantly between the two bypass distances (sign test, p > 0.10). When trials with flight initiation distances less than 5 m are excluded, the probability of fleeing remains higher for direct approaches than 5 m bypasses (sign test, p =0.0039). No males and four of 12 females fled during 5 m bypass trials (Fisher exact test, p > 0.10).

Flight initiation distance differed significantly among conditions (Friedman test, H = 18.72, df = 2, p < 0.00011, n = 17). However, flight initiation distance was significantly greater for 10 m bypasses than the other conditions (p < 0.01 each), which is not informative about the effect of directness of approach on flight initiation distance, and did not differ significantly between direct approaches and 5 m bypasses (p > 0.10). Despite flight initiation distances less than 5 m by seven lizards during direct approaches, mean flight initiation distance was slightly greater during direct approaches than 5 m bypasses (Table 1). Three of the four lizards that fled during 5 m bypasses had flight initiation distance = 5.0 m. Flight initiation distance for direct approach did not differ between sexes (F = 0.61; df = 1, 15; p > 0.10) and variances were homogeneous (Levene's F = 0.90; df = 1,15; p > 0.10).

Directness of approach nevertheless affected flight initiation distance. Six individuals had flight initiation distances greater than or equal to 5 m during direct approaches, but did not flee during 5 m bypasses. Another three individuals that fled during both direct approaches and 5 m bypasses had greater flight initiation distances during direct approaches. For one lizard the flight initiation distance was 5 m during both direct approaches and 5 m bypasses.

**Table 1:** Mean flight initiation distances ( $\pm$ 1.0 SE) for lizards approached directly or indirectly are presented in three columns corresponding to direct approach, intermediate bypass distance, and greatest bypass distance. Because bypass distances varied among species, they are shown in parentheses following the flight initiation data. For individuals that did not flee, flight initiation distances were taken to be the minimum bypass distance

Bypass distance			
Direct	Intermediate	Greatest	n
$6.2\pm0.9$ (0 m)	$5.5\pm0.3$ (5 m)	$10.5\pm0.5$ (10 m)	17
$2.5\pm0.3$ (0 m)	$2.0\pm0.1$ (2 m)	$4.0\pm0.0$ (4 m)	18
$2.6\pm0.3$ (0 m)	$3.0\pm0.0$ (3 m)	$6.0\pm0.0$ (6 m)	12
	Bypass distance           Direct $6.2 \pm 0.9 (0 \text{ m})$ $2.5 \pm 0.3 (0 \text{ m})$ $2.6 \pm 0.3 (0 \text{ m})$	Bypass distanceDirectIntermediate $6.2 \pm 0.9 (0 \text{ m})$ $5.5 \pm 0.3 (5 \text{ m})$ $2.5 \pm 0.3 (0 \text{ m})$ $2.0 \pm 0.1 (2 \text{ m})$ $2.6 \pm 0.3 (0 \text{ m})$ $3.0 \pm 0.0 (3 \text{ m})$	Bypass distanceDirectIntermediateGreatest $6.2 \pm 0.9 (0 \text{ m})$ $5.5 \pm 0.3 (5 \text{ m})$ $10.5 \pm 0.5 (10 \text{ m})$ $2.5 \pm 0.3 (0 \text{ m})$ $2.0 \pm 0.1 (2 \text{ m})$ $4.0 \pm 0.0 (4 \text{ m})$ $2.6 \pm 0.3 (0 \text{ m})$ $3.0 \pm 0.0 (3 \text{ m})$ $6.0 \pm 0.0 (6 \text{ m})$

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Only one individual fled during both types of approach, but had greater flight initiation distance during the 5 m bypass. The remaining individuals are irrelevant to the analysis because they fled only during direct approaches, but at flight initiation distances shorter than 5 m. Excluding the single tie, nine of 10 individuals that fled at distances of at least 5 m had greater flight initiation distances during direct approaches than 5 m bypasses. Thus, significantly more individuals fled at distances greater than 5 m during the direct than indirect approaches (sign test, p = 0.022).

Approach speed significantly affected flight initiation distance (t = 6.48, df = 13, p = 0.0016), which was greater during faster ( $8.0 \pm 0.4$  m, range 6.2–10.0, n = 9) than slower approaches ( $3.8 \pm 0.5$  m, range 3.0–6.0, n = 9). Variances were homogeneous (Levene's test, F = 0.84; df = 1,13; p > 0.10).

When the investigator stopped approaching as soon as a lizard started to flee, escape diversity was relatively great: Lizards fled higher (n = 2) on a rock, to the far side (n = 3) of the rock, to the next rock (n = 2) away from the investigator, or into a crevice (n = 6) under a rock. However, when pursued, all of 12 (nine females, three males) individuals ran away first, went to the far side of the rock, and then entered a crevice, indicating escape calibrated to threat level. Some individuals fled from rock to rock up a slope before eventually entering crevices. We also noted at other times that A. planiceps climbs trees, especially in midday heat, and flees down the trees to rocks. When approached in trees, this species also attempts to stay on the far side of the tree.

#### Mabuya acutilabris

The directness of approach strongly affected probability of fleeing (Fig. 1b). All individuals fled when approached directly, whereas only half fled when bypassed by 2 m and a single individual fled when bypassed by 4 m. The probability of fleeing was significantly greater during direct approaches than 2 m bypasses (sign test, p = 0.0039) and 4 m bypasses (sign test, p = 0.0022). With trials in which flight initiation distance was less than 2 m excluded, the probability of fleeing remained significantly higher for direct approaches than 2 m bypasses (sign test, p = 0.022). With trials in which flight initiation distance was less than 2 m excluded, the probability of fleeing remained significantly higher for direct approaches than 2 m bypasses (sign test, p = 0.0039).

Flight initiation distance differed significantly among conditions (Friedman test, H = 27.91, df = 2,

 $p < 1 \times 10^{-5}$ , n = 18). Flight initiation distance was significantly greater for 4 m bypasses than the other conditions (p < 0.01 each), which is not informative about the effect of directness of approach on flight initiation distance because many individuals did not flee, and did not differ significantly between direct approaches and 2 m bypasses (p > 0.10). Despite flight initiation distances less than 2 m by five lizards during direct approaches, mean flight initiation distance was slightly greater during direct approaches than 2 m bypasses (Table 1). Eight of the nine lizards that fled during 2 m bypasses had flight initiation distance = 2 m.

Four individuals had flight initiation distances of at least 3 m during direct approaches, but did not flee during 2 m bypasses. Another individual that fled during both direct approaches and 5 m bypasses had greater flight initiation distance during direct approaches. Two individuals fled at less than 3 m during direct approaches, but at 3 m during 2 m bypasses. The remaining individuals fled only during direct approaches and had flight initiation distances shorter than 3 m. They are irrelevant for comparison of flight initiation distance between the two treatments. Overall, five of seven individuals that fled at distances of at least 3 m had greater flight initiation distances during direct approaches than 2 m bypasses. Flight initiation distances did not differ significantly between the direct approaches and 2 m bypasses (sign test, p > 0.10) when analysis was appropriately restricted.

Approach speed significantly affected flight initiation distance (F = 38.17; df = 1,5; p = 0.0016), which was greater during faster (4.6  $\pm$  0.5 m, range 2.5–5.5 m) than slower approaches (2.2  $\pm$  0.4 m, range 1.2–4.0 m, n = 6 each). Variances were homogeneous (F<sub>max</sub> = 1.48; df = 2,5; p > 0.10).

Proximity to refuge strongly affected escape behavior. In an area with hard-packed soil with leafless bushes having low-lying branches providing both cover and obstruction from pursuit, 15 of 16 lizards approached slowly and directly in the open fled away from the approaching investigator under plants into dense cover, often stopping on the far side of a plant where they were obscured from view (Table 2). Another individual fled further under a plant, but not into denser cover. In a nearby population on loose sand with isolated bushes, all of 15 lizards fled into bushes. When pursued, these lizards frequently buried themselves in the sand (n = 12)or entered animal burrows at the base of bushes (n = 3; Table 2). When the lizards were dug out of the burrows and chased, they dove into the sand head first and buried themselves. Flight initiation distance was over twice as great for lizards in the open as for those under partial cover of vegetation (F = 29.56; df = 1,13; p < 0.00012). Lizards resting vegetation permitted closer approach under  $(2.2 \pm 0.4 \text{ m}, \text{ range } 1.2\text{--}4.0 \text{ m}, \text{ n} = 6)$  at slow approach speed than did those on open sand  $(4.9 \pm 0.3 \text{ m}, \text{ range } 3.7-6.0 \text{ m}, \text{ n} = 9).$ 

## Other Mabuya

Each species of *Mabuya* exhibited characteristic escape behaviors and/or refuge types as a function of the habitat it occupied (Table 2). *Mabuya spilogaster* all fled up and around trees or into tree holes, and *M. binotata* readily entered tree holes. *Mabuya laevis, M. striata,* M. sulcata, and *M. variegata* all fled into crevices in or under rocks.

#### Rhotropus boultoni

The directness of approach strongly affected probability of fleeing (Fig. 1c). All lizards fled when approached directly, whereas only one-fourth fled when bypassed by 3 m and none fled when bypassed by 6 m. The probability of fleeing was significantly greater during direct approaches than 2 m

Species	Substrate	Escape tactics	Refuge	n
Agama planiceps	Rock	Higher on rock, to far side, to more distant rock	Crevice	17
Mabuya acutilabris	Ground	Flee to bushes	Bushes, animal burrows, bury in sand	31
M. binotata	Tree	Enter hole	Tree hole	2
M. laevis	Rock	Down far side	Under rock	1
M. spilogaster	Tree, ground	Up and around tree	Height or tree hole	14
M. striata	Rock	Away, toward crevice	Crevice	4
M. sulcata	Rock	Away, toward crevice	Crevice	14
M. variegata	Rock, ground	Away to rock or toward crevice	Crevice	15
Rhotropus boultoni	Rock	Usually down, to far side, or into deeper shade	Crevice	19

 Table 2: Typical substrates where sighted, escape tactics, and types of refuges

bypasses (sign test, p = 0.0039) and 6 m bypasses (sign test, p = 0.00049). Frequency of escape did not differ significantly between 3 and 6 m bypasses (sign test, p > 0.10). When flight initiation distances less than 3.0 m are excluded, the only difference that approaches significance is that between direct approaches and 3 m bypasses (sign test, p = 0.031, one-tailed).

Flight initiation distance differed significantly among conditions (Friedman test, H = 18.77, df = 2. p < 0.00008, n = 12). Flight initiation distance was significantly greater for 6 m bypasses than the other conditions (p < 0.01 each), which is not informative about the effect of directness of approach on flight initiation distance because many individuals did not flee, and did not differ significantly between direct approaches and 3 m bypasses (p > 0.10). Due to flight initiation distances less than 3 m by seven of 12 individuals during direct approaches, mean flight initiation distance was slightly less than 3 m during direct approaches (Table 1). The three individuals that fled during approaches using 3 m bypass distance all fled at 3.0 m as the investigator reached the closest point and one additional individual retreated slightly after the investigator had passed the nearest point.

Directness of approach nevertheless affected flight initiation distance. Six individuals had flight initiation distances greater than or equal to 2 m during direct approaches, but did not flee during 2 m bypasses. Another six individuals that fled during both direct approaches and 5 m bypasses had greater flight initiation distances during direct approaches. Two lizards began to flee at less than 2.0 m during direct approaches, but 2.0 m during 2 m bypasses. For one lizard the flight initiation distance was 2.5 m during both direct approaches and 2 m bypasses. The remaining individuals are irrelevant to the analysis because they fled only during direct approaches, but at flight initiation distances shorter than 2.0 m. Excluding the single tie, 12 of 14 individuals that began to flee at distances of at least 2.0 m had greater flight initiation distances during direct approaches than 2 m bypasses. Thus, flight initiation distances were significantly more likely to be greater during direct than indirect approaches (sign test, p = 0.012).

Variances of raw data for flight initiation distance differed significantly between the slow and fast approach conditions ( $F_{max(2,6)} = 12.14$ , p < 0.01), but were homogeneous for square-root transformed data ( $F_{max(2,6)} = 3.73$ , p > 0.10). Approach speed significantly affected flight initiation distance ( $F_{1.5} =$ 

29.20, p = 0.0017), which was greater during faster (4.2  $\pm$  0.7 m, range 2.2–8.0 m) than slower approaches (1.4  $\pm$  0.2 m, range 0.8–2.2 m, n = 7 each).

In both experiments the lizards consistently entered rock crevices when escaping (Table 2). In the experiment on effect of directness of approach, 10 of 12 lizards entered crevices when approached directly; two of four that fled in trials with 3 m bypasses also entered refuges.

In the experiment on effect of approach speed, all seven lizards escaped into crevices when approached rapidly, but only three entered crevices when approached slowly. This difference is not significant, but is highly suggestive given the small sample size (sign test, p = 0.0625, one-tailed). Pooling data for the two experiments, 17 of 19 lizards entered refuges in the riskier condition and five of 11 lizards that fled entered refuges in the less risky condition. Lizards were significantly more likely to use crevices as refuges when risk was greater (sign test, p < 0.016, one-tailed). Individuals that did not enter refuges remained visible on rock surfaces or hid in shadows or on the far sides of rocks (Table 2).

# Discussion

Risk factors affected escape behavior as predicted in *A. planiceps, M. acutilabris,* and *R. boultoni.* For all three, probability of fleeing was greater for direct than indirect approaches. It also was greater for the shorter than longer of two bypass distances in *M. acutilabris.* The difference in probability of escape between the two bypass distances was in the predicted direction for the other species, but was not significant, presumably because few individuals fled.

These findings are consistent with previous findings for other groups of lizards (Iguanidae - Dipsosaurus dorsalis; Cooper 2003a; Phrynosomatidae -Holbrookia propingua; Cooper 2003b; Scindicdae: Scincinae - Plestidon (formerlyEumeces) laticeps, Cooper 1997a; Teiidae - Cnemidophorus murinus; Cooper et al. 2003). Our data extend the relationship between probability of fleeing and directness of approach to Agamidae, Gekkonidae and the scincid subfamily Lygosominae. Mounting evidence suggests that lizards that rely on escape rather than extreme crypsis (e.g. Chamaeleo chameleo; Cuadrado et al. 2001) assess that risk of being detected and attacked is greater during direct than indirect approaches and therefore are less likely to flee as bypass distance increases.

Published data show that flight initiation distance increases with directness of approach in the iguanids

*C. similis* (Burger & Gochfeld 1990) and *D. dorsalis* (Cooper 2003a), the phrynosomatids *C. draconoides* (Bulova 1994), *C. texanus* (Bulova 1994), and *H. propinqua* (Cooper 2003b), the scincine *P. laticeps* (Cooper 1997a), and the teiid *C. murinus* (Cooper et al. 2003). Similarly, time spent in refuge before emerging is greater after direct than indirect approach in the lacertid *Lacerta monticola* (Martín & López 1999a).

In the above studies flight initiation distance was significantly greater during direct approaches than indirect approaches for at least one bypass distance. This obviously will not be the case for sufficiently large bypass distances, i.e. all bypass distances greater than the flight initiation distance for a direct approach at the given speed. To show that directness of approach affects mean flight initiation distance, it is necessary to use relatively short bypass distances. The bypass distances used in the present study were too large for mean flight initiation distance to be greater than the shortest bypass distance even if no lizards fled when bypassed. Although mean flight initiation distance for direct approaches was not significantly greater than that for the shorter bypass distance, it was numerically greater for A. planiceps and M. acutilabris. Our findings are less clearcut than for other studies because some lizards did not flee when bypassed, but fled at distances shorter than the minimum bypass distance when approached indirectly.

Excluding these cases, however, flight initiation distances were greater during direct than indirect approaches at the shorter bypass distance in all three species. Our data thus extend the relationship between directness of approach and flight initiation distance to representatives of Agamidae, Gekkonidae and the subfamily Lygosominae. They provide further confirmation of the predictions of escape theory (Ydenberg & Dill 1986; Cooper & Frederick 2007) for directness of approach as a predation risk factor, and suggest that for a broad diversity of diurnal, surfaceactive lizards, short bypasses distances exist for which flight initiation distance is shorter than during direct approaches.

Predator approach speed is a strong indicator of risk because rapid, direct approach implies a high probability that the predator has detected the prey and is attacking. Flight initiation distance increased markedly with approach speed in all three species. This relationship has been found in all species studied, representing diverse lizard taxa: Iguanidae – *Dipsosaurus dorsalis* (Cooper 2003a); Lacertidae – *Psammodromus algirus* (Martín & López 1999c); Phrynosomatidae – *Holbrookia propinqua* (Cooper 2003b); Scincidae: Scincinae – *P. laticeps*; Cooper 1997a; Teiidae – *C. murinus*; Cooper et al. 2003), now extended to Agamidae, Gekkonidae, and Lygosominae, and may be nearly universal. This provides strong confirmation of the prediction of escape theory (Ydenberg & Dill 1986; Cooper & Frederick 2007) that flight initiation distance increases with approach speed.

Distance from refuge is an important risk factor because prey farther from refuge are more likely to be captured before reaching refuge, and perhaps because they are more likely to be attacked. A study using plasticine lizard models showed that the probability of being attacked increased with distance from vegetative cover (Castilla & Labra 1998). Because M. acutilabris usually flee to plants and often to their far sides, individuals in plant cover are in or very close to refuges. That flight initiation distance was over twice as long for lizards in the open as for those in vegetation indicates that lizards in refuges had shorter flight initiation distances than did those in the open away from refuges. An alternative hypothesis to explain the finding of this experiment is that lizards under plants were less conspicuous, reducing risk of detection. However, because the bushes lacked leaves and had only thin branches, the lizards remained readily detectable. Thus, the degree of protection afforded by plants presumably accounts for the shorter flight initiation distance by lizards under plants.

Qualitatively, this finding reinforces those showing that flight initiation distance increases with distance from refuge in other lizards (Phrynosomatidae – *C. draconoides*, Bulova 1994; *C. texanus*, Bulova 1994; *H. propinqua*, Cooper 2000a; Lacertidae – *Acanthodactylus erythrurus*, Martín & López 2003; *P. algirus*, Martín & López 1995, 1996; Scincidae – *P. laticeps*, Cooper 1997b) and extends them to Scincinae. These experimental findings strongly support the prediction of escape theory (Ydenberg & Dill 1986; Cooper & Frederick 2007) for a third factor affecting cost of not fleeing, i.e. distance from refuge.

The only apparent exception is that flight initiation distance of *Scincella lateralis* was not affected by the availability of cover in a laboratory experiment in which lizards were approached by a model predator mounted on a board (Smith 1997). However, it is questionable whether the lizards in that experiment recognized the matchbox covers as potential refuges during the 5-min habituation period prior to trials because they were restrained in glass cylinders that did not allow them to move through the experimental chamber.

Entry into refuges is expected to increase with predation risk, which accounts for the finding that a higher proportion of R. boultoni entered refuges when risk was greater using pooled data from the experiments on directness of approach and predator approach speed. A similar finding is that H. propingua are less likely to enter refuges when approached slowly than rapidly (Cooper 2003a). When approached twice in succession, A. erythrurus enter vegetation that is larger and provides more obstructive cover during the second approach (Martín & López 2003) and P. laticeps enter refuges more frequently because a predator's persistence indicates higher risk (Cooper 1997c). Lizards from populations of Podarcis muralis exposed to intense predation were also more likely to enter refuge when approached than lizards from populations exposed to less intense predation (Diego-Rasilla 2003). All available evidence suggests that the probability of entering refuge increases with predation risk as predicted by opportunity costs while in refuge, and by thermal costs (Martín & López 1999a,b).

Although flight initiation distance and refuge use match theoretical predictions in virtually all species studied, other aspects of escape and refuge use differed among species in the lizard assemblage at Farm Bergvellei. Agama planiceps fled higher up on large boulders and away from the approaching predator, sometimes moving out of sight on the far sides or moving to a rock further away, and escaped into rock crevices when pursued. Mabuya laevis, M. striata, M. sulcata, and M. variegata escaped into rock crevices, but none of these species ran up rocks or to upper, elevated surfaces of nearby rocks during escape. Rhotropus boultoni escaped into rock crevices, but differed from the above species in starting on nearly vertical sides of rocks and stopping on rock sides, usually in obscuring shadows, when they did not enter refuges.

Hiding in rock crevices or under rocks is typical for saxicolous lizards and some other species living in areas where rocks are available (e.g. Hertz et al. 1982; Cooper et al. 1999, 2000; Whiting 2002; Stapley & Keogh 2004; Amo et al. 2006; Eifler & Fogarty 2006). Nevertheless, as shown for the lizard assemblage at Farm Bergvellei, species using crevices as refuges differ in greatly in escape behaviors in ways presumably depending on their substrates, distances from refuges, crypsis, and types of major predators.

Mabuya spilogaster and M. binotata were associated with trees and used them as refuges. The two

*M. binotata* that we observed were sighted by openings of tree holes and appeared to be very wary, fleeing into the tree holes at substantial flight initiation distance. The escape behavior of *M. spilogaster* was typical of that in many arboreal and semiarboreal lizards that flee up and around tree trunks, attempting to stay out of view by 'squirreling' (e.g. Williams 1983; Cooper 1998b, 2006). They used both height in the tree and tree holes as refuges, also typical for arboreal lizards (e.g. Williams 1983; Cooper 1997a, 1998b).

Some aspects of escape behavior, such as flight initiation distance (Ydenberg & Dill 1986; Cooper & Frederick 2007) and emergence time (Martín & López 1999a: Cooper & Frederick in press), appear to be determined by costs and benefits associated with escaping or using refuges. The costs, benefits, and predictions appear to apply universally. Other aspects of escape, including tactics such as squirreling and fleeing to sites that allow the lizard to view the predator while having a boulder obstruct its approach path (A. planiceps), and types refuges used are strongly influenced by interspecific differences in microhabitat use. It is unfortunate that we lack data for the abundant lacertid species at Farm Bergvellei (a field notebook was lost). However, our personal observations suggest that the terrestrial lacertids in the vicinity (Castanzo 1991; Bauer 1993; Castanzo & Bauer 1993) escape by running across the ground, sometimes stopping where plainly visible, but often hiding on the ground under bushes, often on the sides of bushes away from the predator.

Limited data from other studies indicate variation in escape tactics among habitats in groups of fairly closely related lizard species. Escape tactics in Anolis vary among ecomorphs in the Greater Antilles (Williams 1972, 1983; Schneider et al. 2000; Cooper 2006) and with both morphology and habitat structure (Losos & Irschick 1996). In Liolaemus lizards the distance fled during escape runs is affected by openness of the microhabitats occupied (Schulte et al. 2004). In four species of Mexican phrynosomatid lizards, species on trees employed squirreling and escaped on trees, whereas those found on primarily rocks sometimes ran to the far side of the rocks and often used crevices in or beneath rocks as refuges (Smith & Lemos-Espinal 2005). Our personal observations of lizards at various sites in southern Africa, North America, Central America, and Europe suggest that such relationships are widespread and strongly affect the structure of escape strategies and refuge use in lizard communities. Microhabitat partitioning appears to play a key role in structuring the nature

and distribution of escape tactics and refuges used in lizard assemblages.

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