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Effects of risk on flight initiation distance and escape tactics in two southern African lizard species*

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Abstract Escape theory predicts that flight initiation distance increases with fitness costs of not fleeing and decreases with cost of escaping. Habitat structure may affect aspects of escape such as routes and destinations. We studied escape tactics and effects of risk factors on flight initiation distance in Kalahari tree skinks *Trachylepis sparsa* and black girdled lizards *Cordylus niger* by simulating approaching predators. Probability of fleeing and flight initiation distance were greater when lizards were approached directly versus on paths bypassing them. The difference in flight initiation distance was significant in *T. sparsa* and marginal in *C. niger*. *Trachylepis sparsa* on trees used as refuges permitted closer approach than those on the ground. Those on ground had longer flight initiation distances when approached rapidly than slowly. Flight initiation distance in *C. niger* was shorter where they were habituated to human presence than where people were present infrequently. When on ground，*T. sparsa* escaped to trees and less frequently to logs or fallen weaver nests. When on trees，they usually escaped by running to the far side and up，and sometimes entered tree holes or weaver nests. *C. niger* escaped by entering rock crevices. All findings verify predictions of escape theory about flight initiation distance. Differences in escape tactics suggest that each species took advantage of routes and refuges available in its habitat. Habitat structure may affect flight initiation distance when habitats differ in risk，and seems to strongly affect escape tactics [*Acta Zoologica Sinica* 53 (3): 446-453，2007].

Key words Squamata，Antipredatory behavior，Escape，Flight initiation distance，Refuge use，Predation risk

风险对两种南非蜥蜴逃跑启始距离和逃避策略的影响*

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摘 要 逃避理论预测，不逃跑若增大适合度代价则导致逃跑启始距离加长，逃跑若增大代价则导致逃跑启始距离缩短。逃跑路径和去向等受生境结构影响。作者通过模拟捕食者逼近研究喀拉哈里树石龙子（*Trachylepis sparsa*）和黑环蜥（*Cordylus niger*）逃避策略和风险因子对逃跑启始距离的影响。与迂回逼近相比较，直接逼近不仅提高蜥蜴逃跑几率还能缩短其逃跑启始距离。喀拉哈里树石龙子在两种逼近方式下的逃跑启始距离有显著差异，这种差异对黑环蜥而言是边缘性的。喀拉哈里树石龙子以树为避所，树上个体可逼近的距离短于地面个体；快速逼近地面个体的逃跑启始距离比慢速逼近更长。习惯于有人环境的黑环蜥逃跑启始距离比人迹罕至环境中的个体更短。地面喀拉哈里树石龙子多遁至树上而很少逃入倒木或倒伏编巢中。树上喀拉哈里树石龙子通常奔逃至远侧和高处，有时遁入树洞或编巢中；黑环蜥则逃入石缝中。所有发现都证实逃避理论中有关逃跑启始距离的预测。逃跑策略的种间差异表明每一种蜥蜴都利用其生境中逃跑路径和避所的有利条件。在风险不同的生境中，生境结构可影响逃跑启始距离，似乎对逃跑策略亦有重要影响 [动物学报 53（3）：446-453，2007]。

关键词 有鳞类 反捕行为 逃避 逃跑启始距离 避所利用 捕食风险

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Although little is known about antipredatory behaviors in African lizards, certain aspects of escape behavior are predictable using escape theory and others appear to be related to habitat use and availability of associated refuges. Escape theory applies to situations in which a potential prey detects an approaching predator while it is far enough away that escape can be delayed. The prey then monitors the approaching predator and is believed to make an escape in one of two ways. According to a graphical model, the prey begins to flee when the predator reaches the point where the expected fitness costs of escaping equal those of not escaping (Ydenberg and Dill, 1986). Although this model has been highly successful, it does not allow prey to make escape decisions that maximize fitness. Optimal escape theory (Cooper and Fredrick, 2007) makes many of the same qualitative predictions for factors affecting predation risk and cost of escaping, but allows the prey to optimize escape decisions. Both models make predictions about flight initiation distance, the distance between the prey and the predator when escape begins.

Studies of lizards representing several families and higher taxa have verified predictions that flight initiation distance increases as predation risk (cost of remaining) increases and decreases as cost of escaping increases. Cost of remaining factors studied include distance from refuge (Martín and López, 1996; Cooper, 1997a), temperature (Rand, 1964), tail autotomy (Cooper, 2007), direction of predator turning (Cooper, 1998), habituation to predators (Burger and Gochfeld, 1990; Labra and Leonard, 1999; Cooper, 2006), and others such as predator approach speed (references below) and directness of approach (references below) show consistent increase in flight initiation distance as degree of risk increases. Escape costs are primarily lost opportunities. In the presence of food or conspecifics, flight initiation distance by lizards is greater than in their absence (e. g., Cooper, 1999, 2000a; Cooper et al., 2003; Cooper and Pérez-Mellado, 2004; Cooper et al., 2006).

The greatest amount of information is available for predator approach speed and directness of approach as risk factors. Because a more rapidly approaching predator will reach the lizard sooner and may overtake a lizard before it reaches refuge if it delays escape too long, flight initiation distance is predicted to be greater for more rapid than slower approach speed. All lizards tested to date exhibit longer flight initiation distances when approached more rapidly (Iguania: Iguanidae-*Dipsosaurus dorsalis*, Cooper, 2003a; Phrynosomatidae-*Holbrokia propinqua*, Cooper, 2003b; Scleroglossa: Lacertidae-*Psammodromus algirus*, Martín and López, 1995; Scincidae: Scincinae-*Plestiodon* (formerly *Eumeces*) *laticeps*, Cooper, 1997b, Smith, 1997; Teiidae-*Cnemidophorus murinus*, Cooper et al., 2003).

A directly approaching predator may have already detected the lizard and, if not, is likely to detect it if it continues approaching on the same path. On the other hand, suppose that a predator that continues on its current trajectory will pass by the lizard, drawing nearest at some distance greater than zero. Such an indirectly approaching predator is less likely to have detected the prey or to detect it before the prey passes out of its field of view than is a directly approaching predator. Thus, risk decreases as minimum bypass distance increases, leading to the predictions that 1) probability of fleeing decreases as minimum bypass distance increases, and 2) flight initiation distance is greater for direct approach than for indirect approaches at some relatively small bypass distance.

Data for several lizards confirm these predictions (all references in the preceding paragraph except for the lacertid plus the following: Iguanidae-*Ctenosaura similis*, Burger and Gochfeld, 1990; Phrynosomatidae-*Callisaurus draconoides* and *Cophosaurus texanus*, Bulova, 1994). A related finding is that the lacertid *Lacerta monticola* delays emergence from refuge longer when approached directly than indirectly (Martín and López, 1999). Most of the studies cited in this paragraph also examined the probability of fleeing, and consistently found that probability of fleeing decreases as minimum bypass distance increases.

Escape strategies of lizards such as entering refuges, burying themselves in sand, climbing trees, etc., have not been studied systematically. Informal observations about escape strategies are scattered through the literature on lizard natural history, but have not been synthesized and might reveal interesting patterns. Furthermore, species having specialized escape strategies may evolve specialized morphology to enhance escape (e. g., Losos and Sinervo, 1989; Losos et al., 2002) Irschick et al., 2005) or may adopt strategies suitable to morphological features selected for other reasons (Pianka and Parker, 1975).

It may be predicted that escape tactics, destinations, and refuges used should be influenced by the availability of habitat features such as safe refuges and objects that may be used to block a predator's view or access. For example, in an assemblage of *Trachylepis* (formerly *Mabuya*; Bauer, 2003) spp. in northeastern Namibia, species associated with rock outcrops fled into crevices in or under rocks, whereas semiarboreal species fled to trees, up and around them while staying out of view, and into tree holes (Cooper and Whiting, in press).

We conducted field experiments to test the predictions that flight initiation distance and probability of fleeing increase as directness of approach increases in the lygosomine skink *Trachylepis sparsa* and the cordylid *Cordylus niger*, which were selected because each was the single most abundant species at its study site. In the skink we also tested the prediction that flight initiation distance increases with predator approach speed and distance from refuge, and in the cordylid tested the prediction that flight initiation distance is greater in populations habituated to human presence than in populations less frequently exposed to people. We also observed escape strategies of both species. We predicted that the flight initiation distance would conform to predictions of escape theory (Ydenberg and Dill, 1986; Cooper and Frederick, 2007), and that escape strategies would differ based on differences in the types of refuges available in to the lizards. Specifically, we predicted that the semiarboreal *T. sparsa* would flee to and up trees and use large social weaver nests as refuges and the saxicolous *C. niger* would flee into crevices in or beneath rocks.

1 Materials and methods

1.1 Species and study sites

In October 1994 we conducted field studies of lizard escape behavior in Namibia and South Africa. *Trachylepis sparsa* (Scincidae: Broadley, 2000) were observed at an arid location at Farm Arabi in the Kalahari Desert near Aroab in southeastern Namibia (26°25′S, 18°45′E). The habitat was loose sand with sparse vegetation including grass clumps and isolated trees. The lizards occur primarily on and adjacent to larger camel thorn acacia *Acacia erioloba* trees (Cooper and Whiting, 2000). *Cordylus niger* (Cordylidae) were studied at Cape Point in the Western Cape Province of South Africa (34°21′S, 18°30′E), where the lizards perch on low rocks that are often separated by open ground that they traverse in changing perches.

1.2 Methods of observation and experimentation

All data were collected on warm, sunny days when lizards were fully active. Some individuals may have been tested in more than one experiment. To study escape reactions, we simulated approaching predators by walking toward lizards. This technique has been validated by numerous findings that flight initiation distances conform to predictions of escape theory (Ydenberg and Dill, 1986; Cooper and Frederick, 2007) for both predation risk factors (e.g., Burger and Gochfeld, 1990; Bulova, 1994; Martín and López, 1996; Cooper, 1997a, b; 2003a, b; Cooper et al., 2003) and factors that affect cost of escaping (Cooper, 1999, 2000a; Cooper and Pérez-Mellado, 2004; Cooper et al., 2006). Using people as experimental predators precludes detection of any predator-specific defenses that may have evolved and major predators of lizards, which in southern Africa include snakes and birds (Stuart-Fox et al., 2006).

We observed the escape tactics and refuges used by lizards when approached. Upon sighting a lizard, an investigator turned toward it, and walked toward it at a practiced speed. When the lizard began to flee, the investigator stopped moving and recorded flight initiation distance and noted aspects of refuge use. To ensure that each lizard was observed only once in a particular experiment, we moved to a new location after each observation and did not return to the same site during the experiment.

We conducted experiments on effects of directness of approach on flight initiation distance in both lizard species. In the study of *T. s. sparsa*, we approached the lizards at a slow, practiced speed (ca. 65 m/min) either directly ($n = 29$) or on straight paths that bypassed them at a minimum distance of three m ($n = 13$) or six m ($n = 15$). For lizards that did not flee, flight initiation distance was recorded as the minimum bypass distance, which was a conservative overestimate of flight initiation distance for lizards that did not flee. The same methods were used for *C. niger*, but with sample sizes of 21 for direct approaches, 23 for 5 m bypasses, and 23 for 10 m bypasses.

In *T. sparsa* we additionally studied effects of predator approach speed on flight initiation distance and effects of a lizard's initial location on its final location and escape tactics. We studied the effect of predator approach speed by directly approaching at either a slow (ca 45 m/min, $n = 8$ lizards) or a fast approach speed (ca. 120 m/min, $n = 8$ lizards). In the study of effects of initial location, we observed individuals initially sighted on the ground ($n = 20$) or tree trunks below 2.0 m ($n = 61$). After recording its initial location, an investigator approached the lizard directly at an intermediate speed (ca. 80 m/min) until it fled. For lizards initially on the ground, final locations were recorded as visible on a tree or hidden in one of three types of refuge (under log, in a crevice in a log, or in a fallen weaver nest). For lizards on trees, we recorded frequencies of lizards that used escape tactics in the categories around and up, around and down, tree hole, weaver nest, and away along branch. We recorded one tactic per individual. Lizards remained outside refuges except in the categories tree hole and weaver nest.

The effect of habituation to human beings on flight initiation distance in *C. niger* was studied using direct approaches at the slower approach speed in two areas. The high density area was along the edges of a path leading from a parking lot to the view from the cliffs at Cape Point, a major tourist attraction. At this site people walk past the lizards all day long every day. The low density area was well away from parking sites and hiking paths. We observed only one group of people walking near the site, and they did not approach closer than 100 m. Sample sizes were six at the high-density site and 21 at the low density site.

1.3 Statistical analyses

Effects of directness of approach on probability of fleeing were tested for significance using Fisher exact probability tests. A sequential Bonferroni procedure

(Wright, 1992) was used to assess significance because three tests were needed for comparisons of the three pairs of directness treatments. Significance is reported after Bonferroni adjustment, but the unadjusted P values are presented. A median test was used to compare flight initiation distance for direct approach versus the 3m bypass distance for *T. sparsa*. After testing for homogeneity of variance using Levene's test and transforming the data to ensure homogeneity, the effect of being on the ground versus a tree trunk on flight initiation distance was tested using analysis of variance.

Kruskal-Wallis analysis of variance (Zar, 1996) was used to test significance of differences among approach types in *C. niger* because many individuals did not flee when approached indirectly, producing nonnormal distributions of flight initiation distance. Median tests protected by Bonferroni adjustment were used to compare flight intitiation distance between pairs of directness treatments. The effect of speed of approach on flight initiation distance was examined by a t test in association with Levene's test and transformation of data.

Statistical tests were two-tailed. Alpha was 0.05 when no adjustment was required or lower for some comparisons using the sequential Bonferroni procedure. Data are given as $\bar{X} \pm 1.0SE$.

2 Results

2.1 *Trachylepis sparsa*

Probability of fleeing was strongly affected by directness of approach (Fig. 1a). All 29 individuals fled when approached directly, whereas only seven of 13 and none of 15 fled when approached on paths bypassing them by 3 m and 6 m, respectively. The probability of fleeing was significantly greater during direct approaches than 3 m bypasses (Fisher exact test, $P < 0.0001$) and six m bypasses (Fisher exact test, $P < 0.0001$) and during 3 m than 6 m bypasses (Fisher exact test, $P = 0.00028$). With four individuals that had flight initiation distance less than 3.0 m excluded, the probability of fleeing remained significantly higher for direct approaches than three m bypasses (sign test, $P < 0.00013$).

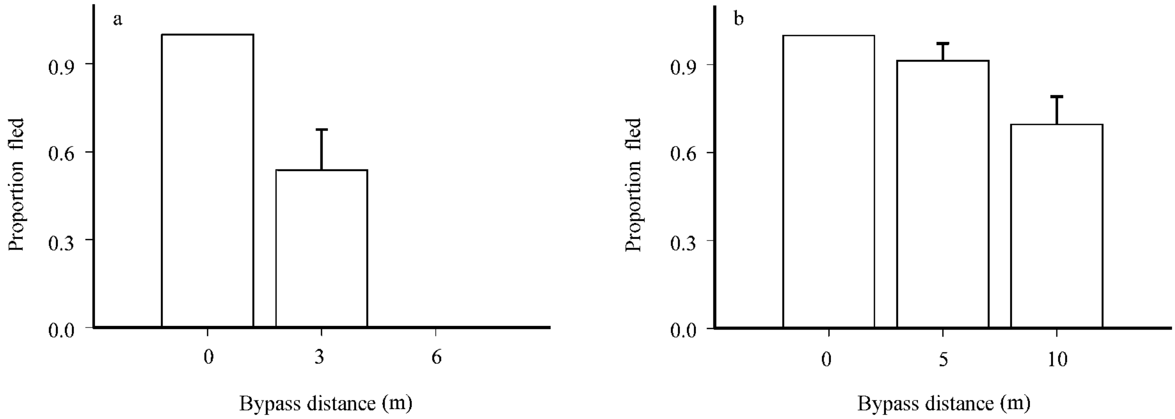

Fig. 1 Proportions of individuals that fled when approached directly and along paths bypassing them by different minimum distances for a) *Trachylepis sparsa* and b) *Cordylus niger*

Error bars are 1.0 *SE*.

Flight initiation distance was significantly longer for lizards approached directly than for those bypassed by three m (Median test, $\chi_1^2 = 18.83$, $P < 0.0001$; Table 1). The large range of flight initiation distances during direct approach was a consequence of differences in initial location of the lizards. Individuals approached directly permitted much closer approach before fleeing when on tree trunks below 2.0 m (3.0 ± 0.4, range 1.1 – 6.0, $n = 15$) than did those on the ground (6.4 ± 0.7, range 3.5 – 11.1, $n = 14$). Variances were significantly heterogenous for the raw data (Levene's $F_{1,27} = 5.67$, $P < 0.025$), but were homogenous following square root transformation (Levene's $F_{1,27} = 0.82$, $P > 0.10$). Using transformed data, the flight initiation distance was significantly greater for lizards initially on the ground than for those on tree trunks ($F_{1,27} = 12.59$, $P = < 0.0001$).

Table 1 Flight initiation distances (FID) in meters for lizards approached directly or on paths by passing them at the minimum distances shown

Species	Bypass distance (m)	FID	*SE*	Range
Trachylepis sparsa				
	0	4.6	0.5	1.1 – 11.1
	3	3.0	0.0	3.0 – 3.0
	6	6.0	0.0	6.0 – 6.0
Cordylus niger				
	0	9.3	1.1	2.0 – 19.0
	5	7.3	0.6	5.0 – 14.0
	10	11.0	0.3	10.0 – 14.0

Flight initiation distance was much greater during faster (6.0 ± 0.7 m, range 4.0 – 9.0) than slower approaches (2.3 ± 0.3 m, range 1.3 – 3.2 m, $n = 8$

each）. Variances were significantly heterogeneous for raw data（Levene's $F_{1,14} = 4.80$，$P < 0.025$），but homogeneous for square-root transformed data（Levene's $F_{1,14} = 1.25$，$P > 0.10$）. Using transformed data，flight initiation data differed significantly between approach speeds（$t_{14} = 5.92$，$P < 0.0001$）.

When on the ground，*T. sparsa* most frequently escaped to nearby trees，but fled to logs and communal weaver *Philetairus socius* nests on the ground to a lesser extent（Table 2）. When on trees，they never descended to the ground，using various escape strategies within trees，including fleeing to the far side of the tree trunk and upward，less frequently fleeing to the far side of the trunk and downward or away along branches not oriented vertically（often on the far side），entering tree holes，and entering nests of social weavers.

Table 2 Destinations and tactics of escaping adult *Trachylepis sparsa*

Initial location	Destinations				
Ground	Tree	Under log	Log crevice		Fallen weaver nest
	12	4	2		2
Tree	Around and up	Around and down	Tree hole	Weaver nest	Away along branch
	29	7	14	4	7

Data are number of individuals that used each destination and tactic.

2.2 *Cordylus niger*

Cordylus niger were very wary，most individuals fleeing at all bypass distances（all during direct approaches，21 of 23 for 5 m bypasses，and 16 of 23 for 10 m bypasses，Fig. 1b）. Nevertheless，the proportion of individuals that fled was significantly greater for lizards approached on a path bypassing them by 10 m than for those approached directly（Fisher exact test，$P = 0.0094$）. Proportions of individuals that fled did not differ significantly between the groups approached directly and using a 5 m bypass or between the 5 m and 10 bypass groups.

Mean flight initiation distance was greatest in the ten m bypass group，least in the five m bypass group，and intermediate in the directly approached group（Table 1）. This unusual pattern is in part a consequence of including all data，even those for individuals that did not flee. Flight initiation distance did not differ significantly among treatments（Kruskal-Wallis test，$\chi^2_2 = 4.92$，$P = 0.086$）although the differences approached significance for the comparisons between direct approaches and five m bypasses（Median test，$\chi^2_1 = 3.19$，$P = 0.074$）and 5 m and ten m bypasses（$\chi^2_1 = 5.06$，$P < 0.028$）. Four of 21 lizards in the directly approached group had flight initiation distances less than 5 m，distances which were impossible in the other groups and may account for the greater variability in the directly approached group.

Lizards from the area with many tourists had much shorter flight initiation distances when approached slowly and directly（1.4 ± 0.4 m，range $0.3 - 3.0$ m，$n = 6$）than those where tourists go infrequently（11.0 ± 0.3，range $10.0 - 14.0$，$n = 21$）. Raw data exhibited significant heterogeneity of variance（Levene's test，$F_{1.25} = 8.82$，$P < 0.0011$），but variances of square root transformed data were homogeneous（Levene's test，$F_{1,25} = 2.63$，$P > 0.10$）. Using transformed data，flight initiation distance was significantly greater in the area having infrequent human presence（$F_{1,25} = 21.24$，$P < 0.0001$）.

Cordylus niger were found consistently on rocks that were too small to permit climbing out of reach. If on solid rocks or on the ground，they escaped by running beneath the rocks on which they were perched or beneath nearby rocks. Lizards on rocks with crevices above ground level sometimes entered these crevices.

3 Discussion

3.1 Directness of approach

Directness of approach strongly affected escape responses by both species，the probability of fleeing increasing as the approach became more direct. For *T. sparsa* the proportion of individuals that fled decreased progressively as the minimum bypass distance increased，but in *C. niger* the only difference detected was a greater probability of fleeing during direct approaches than approaches using either of two minimum bypass distances. The findings verify the qualitative prediction based on risk for both species，and reveal a difference between the species.

Cordylus niger was warier than *T. sparsa*，as indicated by the much higher proportion of individuals that fled during 10 m bypasses in the former than during six m bypasses in the latter species. This is probably a consequence of the open habitat of *C. niger*，which exposes them to rapid attacks by raptors. Both species are eaten by birds and snakes（Stuart-Fox et al.，2006），but *T. sparsa* is typically on tree trunks limit angles of aerial attacks and escape requires merely moving around the trunk. Even individuals on the ground are close to trees or refuges such as fallen weaver nests. Greater vulnerability to aerial attack may account for the greater wariness of *C. niger*，but this species is also eaten by small carnivorous mammals（Branch，1998）.

Other factors may contribute to wariness and the probability of running to escape and/or seeking refuge. *Cordylus niger* belongs to a family that possesses armature, which varies in degree among species and is most highly developed in *Cordylus* (Losos et al., 2002). Cordylids that are more heavily armored run shorter distances and are more likely to enter crevices, in part because sprint speed is inversely related to degree of armature (Losos et al., 2002).

Relationships between proportions of individuals that flee and directness of approach are highly dependent on the minimum bypass distances used. If time is available for investigators to become familiar with escape responses of a species prior to beginning formal data collection, it is a simple matter to discover bypass distances large enough that few if any individuals flee and intermediate distances that elicit escape by some individuals, but not others. That is one reason why reported minimum bypass distances often differ among species (Burger and Gochfeld, 1990; Cooper, 1997b, 2003a, b; Martín and López, 1999; Cooper et al., 2003; this study).

Effects of using different bypass distances are conceptually simple. If all minimum bypass distances selected were too short, all individuals would flee and no effect of directness of approach would be detected. If all minimum bypass distances (other than zero for direct approach) used were too long, no individuals would flee during indirect approaches. In this case probability of fleeing would be greater for direct than indirect approaches, but no difference would be detected among indirect approaches at different bypass distances. In another case, minimum bypass distance would be large enough that some individuals would flee and others would not, depending on individual differences in boldness (López et al., 2005), but differences in bypass distances would be too small to have affect probability of fleeing enough to be detectable without a very large sample. This presumably accounts for the lack of a significant difference in probability of fleeing between five m and 10 m bypass distances in *C. niger*. Only when bypass distances chosen by experimenters are such that prey assess substantial differences in risk among them will a graded pattern of probability of escape attempts be observed, as for *T. sparsa*.

Flight initiation distance in *T. sparsa* was greater for direct approaches than five m bypasses, indicating that lizards assessed greater risk during direct approaches and adjusted flight initiation distance in accordance with the prediction of escape theory. This relationship was not observed in *C. niger*, which had similar flight initiation distances for direct approaches and 5 m bypasses. This is the first reported failure to verify the prediction that flight initiation distance is greater during direct than indirect approaches. The difference was marginal, suggesting that the effect may be detectable with larger sample size and/or slightly shorter bypass distance.

3.2 Distance from refuge, approach speed and habituation

Trachylepis sparsa low enough in trees to be vulnerable to attack had shorter flight initiation distances than individuals on the ground. Because these lizards use trees as refuges and climb out of reach to escape, this finding corroborates evidence that flight initiation distance increases as distance from refuge increases in other lizards (Bulova, 1994; Cooper, 1997b, 2000b; Eifler, 2001). We observed, but did not record, cases of individuals higher in trees not fleeing when we approached the base of the trunk. These lizards were effectively in refuges.

Flight initiation distance by *T. sparsa* was nearly three times greater during faster than slower approaches. This effect has been found in all lizard species studied (references above), and may be universal for species exposed on the surface, but not adapted for extreme crypsis. Approach speed might not affect flight initiation distance in chameleons in bushes, *Phrynosoma* flattened against the ground, or other species that rely primarily on crypsis to avoid detection.

Cordylus niger had flight initiation distances nearly eight times longer in an area of infrequent human activity than in a nearby area with high human density. The sample size was small for habituated lizards, but results were very consistent. Several other lizards that we approached in the high density area, but for which no data were recorded, were very reluctant to flee. These findings are consistent with other reports that flight initiation distance is shorter where prey are habituated to human presence (Burger and Gochfeld, 1990; Labra and Leonard, 1999; Eifler, 2001; Cooper et al., 2003; Cooper, 2006). Risk is assessed as greater if a potential predator is unfamiliar or rarely encountered than if it is familiar and has not attacked. Thus, the finding verifies the prediction that flight initiation distance increases as risk increases. The risk allocation hypothesis that flight initiation distance is shorter because costs of repeated escape and refuge use would be prohibitively high is not credible because people do not attack.

3.3 Escape tactics

Trachylepis sparsa on ground escaped to refuges including trees, logs and fallen weaver nests. Lizards on trees typically fled by moving to the far side and upward, but sometimes moved down the far side or away along branches. If sufficiently threatened they entered holes in tree trunks or weaver nests. These lizards prefer trees offering large amounts of ground cover such as fallen limbs, bark, and weaver nests (Cooper and Whiting, 2000). Such large trees provide multiple refuges. Although larger trees tended to contain more or larger, more complex weaver nests (Cooper and Whiting, 2000), lizards entered them infrequently. Entering weaver nests may be risky due to presence of predatory snakes (Branch, 1998) and possibly nest defense by weavers. *Cordylus niger* escaped from either the ground or rocks to crevices in or beneath rocks. These crevices were the only obvious refuges in the habitat. Refuges may be essential for escape from birds and rapid snakes such as Cape cobras *Naja nivea*.

As in an assemblage of Nambian lizards (Cooper and Whiting, in press), cordylids with differing degrees of body armature (Losos et al., 2002), and anoles varying in microhabitats and morphology (Losos and Irschick, 1996; Cooper, 2006), escape tactics varied predictably between species based on habitat features affecting escape routes and refuges. Interspecific variation in tactics also depends on morphologies (Losos and Irschick, 1996; Losos et al., 2002) presumably evolved to facilitate escape by species exposed to different habitats and predator suites.

Escape tactics are fine-tuned to habitats, morphology, and types of predators. This contrasts with universal or nearly universal optimization of flight initiation distance and time spent in refuge in relation to predation risk and cost of escaping (Ydenberg and Dill, 1986; Martín and López, 1999; Cooper and Frederick, 2007, in press). Flight initiation distance and hiding time are affected by risks and costs associated with habitats, morphology, and predators, but current escape theory does not predict alternative tactics, degree of reliance on refuges, or types of refuges. Thus, in an assemblage of lizard species, escape tactics may vary among species, but ability to escape using those tactics is taken into account by each species in making decisions about flight initiation distance and emergence time.

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References

Bauer AM, 2003. On the identity of *Lacerta punctata* Linnaeus 1758, the type species of the genus *Euprepis* Wagler 1830, and the generic assignment of Afro-Malagasy skinks. Afr. J. Herpetol. 52: 1 - 7.

Branch B, 1998. Field Guide to Snakes and Other Reptiles of Southern Africa. Sanibel Island, Florida: Ralph Curtis Books.

Broadley DG, 2000. A review of the genus *Mabuya* in southeastern Africa (Sauria: Scincidae). Afr. J. Herpetol. 49: 87 - 110.

Bulova SJ, 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. Copeia 1994: 980 - 992.

Burger J, Gochfeld M, 1990. Risk discrimination of direct versus tangential approach by basking black iguana *Ctenosaura similis*: variation as a function of human exposure. J. Comp. Psychol. 104: 388 - 394.

Cooper WE Jr, 1997a. Escape by a refuging prey, the broad-headed skink *Eumeces laticeps*. Can. J. Zool. 75: 943 - 947.

Cooper WE Jr, 1997b. Threat factors affecting antipredatory behavior in the broad-headed skink *Eumeces laticeps*: repeated approach, change in predator path, and predator's field of view. Copeia 1997: 613 - 619.

Cooper WE Jr, 1998. Direction of predator turning, a neglected cue to predation risk. Behaviour 135: 55 - 64.

Cooper WE Jr, 1999. Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard *Eumeces laticeps*. Behav. Ecol. Sociobiol. 47: 54 - 59.

Cooper WE Jr, 2000a. Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink *Eumeces laticeps*. Behaviour 137: 1 175 - 1 189.

Cooper WE Jr, 2000b. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard *Holbrookia propinqua*. Behaviour 137: 1 299 - 1 315.

Cooper WE Jr, 2003a. Risk factors affecting escape behaviour in the desert iguana *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. Can. J. Zool. 81: 979 - 984.

Cooper WE Jr, 2003b. Effect of risk on aspects of escape behavior by a lizard *Holbrookia propinqua* in relation to optimal escape theory. Ethology 109: 617 - 626.

Cooper WE Jr, 2006. Risk factors affecting escape behaviour in Puerto Rican *Anolis* lizards. Can. J. Zool. 84: 495 - 504.

Cooper WE Jr, 2007. Compensatory changes in escape and refuge use following autotomy in the lizard *Sceloporus virgatus*. Can. J. Zool. 85: 99 - 107.

Cooper WE Jr, Frederick WG, 2007. Optimal flight initiation distance. J. Theor. Biol. 244: 59 - 67.

Cooper WE Jr, Frederick WG, 2007. Optimal time to emerge from refuge. Biol. J. Linn. Soc. In press.

Cooper WE Jr, Pérez-Mellado V, 2004. Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard *Podarcis lilfordi*. Herpetologica 60: 321 - 324.

Cooper WE Jr, Whiting MJ, 2000. Islands in a sea of sand: use of *Acacia* trees by tree skinks in the Kalahari Desert. J. Arid Environ. 44: 373 - 381.

Cooper WE Jr, Whiting MJ, In press. Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. Ethology.

Cooper WE Jr, Pérez-Mellado V, TA Baird, TA Baird, JP Caldwell, LJ Vitt, 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards *Cnemidophorus murinus*. Behav. Ecol. 14: 288 - 293.

Cooper WE Jr, Pérez-Mellado V, Hawlena D, 2006. Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards *Podarcis lilfordi*. Behav. Ecol. 17: 554 - 559.

Eifler D, 2001. *Egernia cunninghami* (Cunningham's skink). Escape behavior. Herp. Rev. 32: 40.

Irschick DJ, Carlisle E, Elstrott J, Ramos M, Buckley C, Vanhooydonck B, Meyers J, Herrel A, 2005. A comparison of habitat use, morphology, clinging performance and escape behaviour among two divergent green anole lizard *Anolis carolinensis* populations. Biol. J. Linn. Soc. 85: 223 - 234.

Labra A, Leonard R, 1999. Intraspecific variation in antipredator response of three species of lizards *Liolaemus*: possible effects of human presence. J. Herpetol. 33: 441 - 448.

López P, Hawlena D, Polo V, Amo L, Martín J, 2005. Sources of shy-bold variations in antipredator behaviour of male Iberian rock lizards. Anim. Behav. 69: 1 - 9.

Losos JB, Irschick DJ, 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: Laboratory predictions and field tests. Anim. Behav. 51: 593 - 602.

Losos JB, Sinervo B, 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. J. Exp. Biol. 145: 23 - 30.

Losos JB, Mouton PLFN, Bickel R, Cornelius I, Ruddock L, 2002. The effect of body armature on escape behaviour in cordylid lizards. Anim. Behav. 64: 313 - 321.

Martín J, López P, 1996. The escape response of juvenile *Psammodromus lizards*. J. Comp. Psychol. 110: 187 - 192.

Martín J, López P, 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav. Ecol. 10: 487 - 492.

Pianka E, Parker WS, 1975. Ecology of horned lizards: A review with special reference to *Phrynosoma platyrhinos*. Copeia 1975: 141 - 162.

Rand AS, 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45: 863 – 864.

Smith DG, 1997. Ecological factors influencing the antipredator behaviors of the ground skink *Scincella lateralis*. Behav. Ecol. 8: 622 – 629.

Stuart-Fox D, Whiting MJ, Mousalli A, 2006. Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. Biol. J. Linn. Soc. 88: 437 – 446.

Wright SP, 1992. Adjusted p-values for simultaneous inference. Biometrics 48: 1 005 – 1 013.

Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. Adv. Stud. Behav. 16: 229 – 249.

Zar JH, 1996. Biostatistical analysis. Upper Saddle River, New Jersey: Prentice Hall.