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Aerial Predator Recognition by Free-ranging *Sceloporus occidentalis*

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To successfully avoid an attacking predator, prey must identify danger and respond appropriately—sometimes by escaping to a hiding place. Correct recognition of a predator is paramount to survival and to avoid an inappropriate escape response. False alarms prevent an animal from otherwise foraging, defending territory, thermoregulating, or conserving energy (Ydenberg and Dill, 1986). While it is to an animal's advantage to identify every feature of its environment, it is more probable that a combination of cues signals to an animal what is dangerous and what is not. Unfortunately, we know little about the stimulus control of antipredator behavior in reptiles, and most of what we do know is from controlled laboratory studies (Gallup, 1973; Scudder and Chiszar, 1977;

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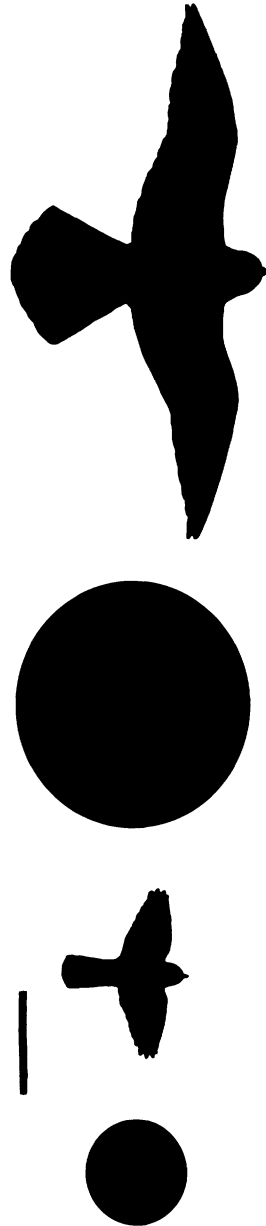


FIG. 1. The models used in the experiment. Surface areas as follows: Kestrel model (610 cm²), Big Circle model (610 cm²), Sparrow model (137 cm²), and Small Circle model (137 cm²). All models were constructed from brown masonite, 1 cm thickness. Scale bar = 10 cm.

Burghardt and Greene, 1988; Greene, 1988; Fleishman, 1992; Macias Garcia and Drummond, 1995).

I investigated the cues used by the western fence lizard, *Sceloporus occidentalis* (Phrynosomatidae), to identify predators and developed a method for assessing responses of wild lizards to predator models. Models that varied in shape, size, and speed were pre-

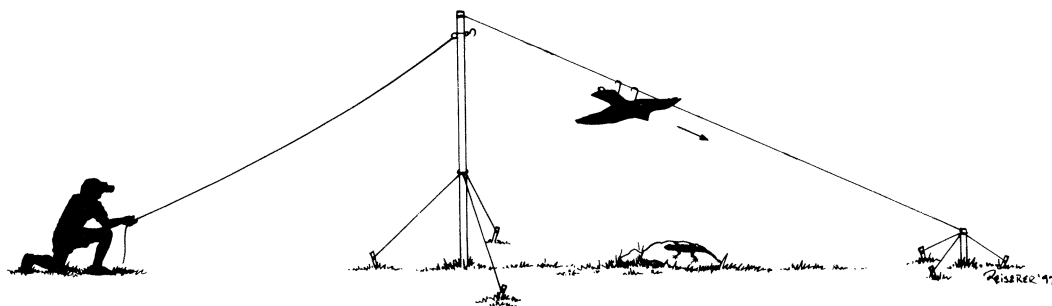


FIG. 2. The experimental setup. Drawing not to scale.

sented overhead to free-ranging *S. occidentalis* in a controlled motion pattern simulating a gliding bird. *Sceloporus occidentalis* relies on vision to recognize danger and responds to an approaching predator by locomotor escape into a refuge (Greene, 1988). Earlier work on this species included a report of the lizard encountering and ignoring a Brown Towhee (*Pipilo tuscus*), even though similarly sized aerial predators such as the American Kestrel (*Falco sparverius*) commonly prey upon *S. occidentalis* (Fitch, 1940; Balgooyen, 1976).

This experiment was conducted at Briones Regional Park, Contra Costa County, California (37°56'N, 152°09'W, 350 m elevation) from 16 April to 3 June 1995. The habitat was rangeland, punctuated with oak trees and rock outcrops. I tested the lizards only on sunny days and between 1230 and 1700 h at air temperatures above 15 C. After finding a lizard basking on a rock, I carefully erected the experimental apparatus around it. The setup took approximately one hour and the lizard always resumed basking behavior before the experiment began. Fourteen individual *S. occidentalis* were involved in the study. They were not captured or subjected to any stress other than that due to the models flown overhead and my presence in the area. I visually categorized the lizards into small, medium and large classes (*S. occidentalis* has a SVL from 5–10 cm).

Experiment I consisted of four trials with each individual lizard. Four masonite models (Kestrel, Big Circle, Sparrow, and Small Circle, Fig. 1) were released to glide along a lubricated 6 m 50 lb. test monofilament line between two aluminum poles (3 m and 0.5 m tall) at a 15 degree incline from the horizontal (Fig. 2). The models glided from the tall pole to the short pole due to gravity. Lead weights were attached to the top of the smaller models so that they matched the speed of the larger ones; all models travelled from 1.2–1.4 m sec⁻¹, approximating the velocity and motion pattern of a slowly diving hawk.

Eight individuals were tested with all four of the models. The remaining six individuals were tested with two or three of the models because changing weather stopped the experiment. The order of presentation of the models was randomized. I was at least 10 m from the lizard and watched its reactions with 7 × 42 binoculars. Before each trial, I took a 60 sec control observational period to determine whether the experimental setup affected the behavior of the lizard. The models began their trajectory toward the lizard

after I pulled a string connected to a releasing mechanism (Fig. 2). After the model passed over the lizard, its behavior was noted and if it fled to its refuge, the time was measured from the moment of escape until the lizard returned to view. This measurement is hereafter referred to as "hiding time" and was used to determine whether the lizards had different responses to the various models. After the lizard returned to view, I waited until it resumed basking behavior before starting a new trial. I used Kruskal-Wallis non-parametric tests to assess differences in the statistical distribution of variables (Zar, 1996).

Experiment II tested the importance of motion for predator recognition and began after completion of Experiment I for five individuals. I tethered the Kestrel model to a 15 m string. Staying 10 m away, I released the model down the monofilament line by hand so that it moved less than 1 cm sec⁻¹. This trial was identical to the Kestrel trial in Experiment I above except for the speed of the model. Experiment II was performed in the absence of wind to keep the model from swaying from side to side. I compared the results of Experiment II to the Kestrel model data in Experiment I using a one-tailed Sign test (Zar, 1996).

During the control observational period, lizards always remained immobile, basking on top of their rock. When a model was released, a lizard either showed no reaction, flinched but did not leave its perch, or fled from atop its perch into its hiding place beneath it. A hiding lizard waited from seconds to several minutes before climbing back to its perch. Only the small models caused no reaction or flinches (Table 1). Large models (Kestrel: $\bar{x} \pm SE = 139.31 \pm 34.73$ sec; Big Circle: 110.54 ± 27.68 sec) caused longer hiding times than small models (Small Circle: 69.69 ± 32.73 sec; Sparrow: 37.57 ± 11.33 sec) ($\chi^2 = 12.1795$, $df = 1$, $P < 0.0005$) (Table 1). However, there was no significant difference in hiding time between Kestrel and Big Circle, nor between Sparrow and Small Circle ($\chi^2 = 0.0693$, $df = 1$, $P > 0.7$) (Table 1). Hiding times, when analyzed with Kruskal-Wallis tests, did not vary significantly with time of day, day of year, size of lizard, order of model presentation, and effect of the subsequent model. For Experiment II, zero of five of the lizards reacted to the slow Kestrel model, even when it was directly overhead, less than 1.5 m from the lizard, while in Experiment I, 13 of 13 lizards fled their perch from the Kestrel model ($P < 0.05$) (Table 1).

The shape of a Kestrel, probably the most important aerial predator of *S. occidentalis* in California, was per-

TABLE 1. Responses of lizards to different models.

Model	Number of lizards tested	Number that hid/flinched/did not react	Avg. hiding time, $\bar{x} \pm SE$ (sec)	Statistical result
Kestrel	13	13/0/0	139.31 \pm 34.73	Bird-shaped models' hide times are not different than circle-shaped (Kruskal-Wallis, $P > 0.7$). Large models cause longer hide times than small (Kruskal-Wallis, $P < 0.0005$). Slow Kestrel caused different reaction than Kestrel trial above (Sign Test, $P < 0.05$).
Big Circle	13	13/0/0	110.54 \pm 27.68	
Sparrow	11	6/3/2	37.57 \pm 11.33	
Small Circle	13	9/3/1	69.69 \pm 32.73	
Slow Kestrel	5	0/0/5	0	

ceived by the lizard as just as dangerous as a circle of identical area. But when the Kestrel model was moved over the lizard at a very slow speed, it caused no reaction. This suggests that it is not the shape of an object that frightens the lizard but rather a combination of size and motion cues that signal danger, consistent with the notion that these lizards have a limited ability to identify shapes at different orientations (Fleishman, 1992). A flying hawk has many different apparent shapes, depending on the way it holds its wings, to its angle of approach, and other factors. However, its size and motion pattern stay relatively constant, and recognizing these may be more efficient and feasible for the lizard's sensory system.

While classic ethological studies have shown that mammals and birds are quite adept at recognizing their predators by shape (Tinbergen, 1948; Moore and Mueller, 1982; Klump and Curio, 1983; Walters, 1990), squamate reptiles may be largely insensitive to shape and instead depend on size, speed, motion pattern, and presence of eyes. Rattlesnakes (*Crotalus viridis* and *Sistrurus catenatus*) responded defensively to a moving canid and a moving human face while a static canid and a static human face did not elicit a response (Scudder and Chiszar, 1977). Aquatic garter snakes (*Thamnophis melanogaster*) selected prey models with respect to size and movement, but not with respect to shape (Macias Garcia and Drummond, 1995). *Anolis auratus* identified prey, recognized conspecifics and potential mates primarily by their specific motion patterns, and will not attack immobile prey (Fleishman, 1992). Black iguanas (*Ctenosaura similis*) fled sooner from humans with a larger eye mask than smaller eye mask, and from humans with eyes compared with humans with eyes covered with hair (Burger et al., 1991; Burger and Gochfeld, 1993). Neonate hognose snakes (*Heterodon platirhinos*) took longer to recover from tonic immobility when in the presence of a direct gaze than from an averted gaze (Burghardt and Greene, 1988). The lizard *Anolis carolinensis* remained in tonic immobility longer when in the presence of a stuffed Cooper's Hawk (*Accipiter cooperi*) with eyes than without eyes (Gallup, 1973). These studies, along with my data, indicate that squamates use cues about an object's size, motion, and whether it has eyes directed toward the subject much more than cues about its shape. My study emphasizes that this problem can be addressed in an experimental field context, and future studies on other squamates will clearly be of interest.

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Niche Differences among Three Sympatric Species of *Ameiva* (Reptilia: Teiidae) on Hispaniola

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Four species of *Ameiva* (*chrysoleama*, *leberi*, *taeniura*, and *lineolata*) occur sympatrically in the xeric woodlands west of Oviedo on the Barahona Peninsula, Dominican Republic. Three of the four species are moderate (*taeniura*) to large (*chrysoleama*, *leberi*) in size. This community is unique in the West Indies because it is the only area where three species of similar size co-occur. Whereas *Ameiva* appear to differ ecologically from other sympatric species of lizards, a substantial degree of niche overlap seems to exist among these three species. All are ground-dwelling, active foragers, which superficially appear syntopic. Many community studies have demonstrated significant partitioning of resources among sympatric lizard species (Hillman, 1969; Pianka, 1969; Huey et al., 1974; Laerm, 1974; Pianka and Pianka, 1976). However, few studies have addressed niche differences among *Ameiva* (Hirth, 1963; Hillman, 1969), or teiids in general (Milstead, 1965; Medica, 1967; Scudday and Dixon, 1973).

The purpose of our study was to characterize some aspects of the ecological niches of the *Ameiva* in this community by quantifying the niche dimensions of diet and habitat. *Ameiva chrysoleama* is widespread in Hispaniola and contains 16 subspecies (Schell et al., 1993a). This large-sized species has been characterized as xerophilic, inhabiting *Acacia* scrub and woods, xeric woodlands (especially areas with sparse ground cover), and scrublands (Schwartz and Henderson, 1991). The Barahona Peninsula population, *Ameiva chrysoleama ficta*, is disjunct from conspecifics, and reaches a maximum snout–vent length (SVL) of 121 mm (females to 113 mm SVL) (Schell et al., 1993a). *Ameiva leberi* is a monotypic species (males to 129 mm SVL, females to 119 mm) (Schell et al., 1993a). Its range is restricted to xeric habitat in the lower Bar-

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