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HABITAT BUT NOT BODY SHAPE AFFECTS PREDATOR ATTACK FREQUENCY ON LIZARD MODELS IN THE BRAZILIAN CERRADO

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ABSTRACT: Predators use characteristics such as pattern and shape in forming search images of prey, thereby influencing the evolution of prey morphology. In lizards, sit-and-wait foraging species are thought to have body shapes that enhance their ability to remain cryptic to predators. Structurally complex habitats provide more opportunities for prey to avoid detection, thus predator foraging efficiency is predicted to be higher in structurally simple habitats. I used clay lizard models to test whether predation varies among lizards with different body shapes and whether predation varies among habitats in the Brazilian Cerrado with different structural characteristics. Predator attack frequency was highest in the most structurally complex habitat, but the probability of being attacked was higher in more open microhabitats. Attack frequencies did not significantly differ among the four lizard model shapes. Lizards and birds were the main attackers of models and attacks were primarily directed toward the models' heads. My results demonstrate that predator-prey interactions are largely influenced by the environmental context and scale, and that body shape alone does not efficiently promote crypsis.

Key words: Antipredator defense; Crypsis; Escape behavior; Foraging mode; Predation; Predator–prey interactions

PREDATION is a major selective force in the evolution of morphological characteristics of organisms (Edmunds, 1974; Endler, 1986). Conspicuous colors or structures can deter predator attacks (aposematism and mimicry), whereas cryptic colors and patterns interfere with the predator's ability to detect prey (Endler, 1986, 1991; Ruxton et al., 2004). Predators form search images of cryptic prey using features such as pattern and shape (Edmunds, 1974; Ruxton et al., 2004), and thus prey species that rely on crypsis should have both patterns and shapes that enhance their ability to remain undetected. The effectiveness of pattern and shape in promoting crypsis is inherently dependent on the substrate. Habitats with high structural complexity offer a high diversity of microhabitat patches that can be mimicked by prey organisms rendering them cryptic, thereby reducing predator foraging efficiency (Denno et al., 2005; Ruxton et al., 2004).

Many lizard species have evolved cryptic colorations and patterns in response to selective pressures exerted by predators (Greene, 1988; Martins, 1996; Pianka and Vitt, 2003). In addition to color and pattern, lizard body shapes may be influenced by predation through a link with foraging mode (Huey and Pianka, 1981). Lizard foraging modes typically are characterized as either sit-and-wait or active, and the mode employed has consequences for other aspects of the species' ecology such as antipredator behavior (Huey and Pianka, 1981). Actively foraging species typically use flight as an antipredator tactic and have body shapes that promote rapid locomotion, whereas sit-and-wait foraging species typically rely upon crypsis and have body shapes that enhance their ability to avoid detection (Huey and Pianka, 1981; Vitt and Congdon, 1978; Vitt and Price, 1982). Morphological characteristics that optimize one of these strategies often occur at the expense of the other strategy (i.e., body shapes that enhance locomotor performance impair crypsis; Vitt and Congdon, 1978). Thus, predation pressure is predicted to influence body shape in lizards, but whether predation varies among different body shapes remains uninvestigated.

Predation studies in nature often are difficult to conduct because of the rarity of observing predation events. Alternatively, clay models have proven effective in previous predation studies involving lizards and snakes (Brodie, 1993; Castilla and Labra, 1998; Diego-Rasilla, 2003; Husak et al., 2006;

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Pfennig et al., 2001). Herein, I used clay lizard models to test the hypotheses that predation on lizards varies across habitats of differing structural complexity and that predation varies among lizards with different body shapes. The first hypothesis predicts that predator attack frequency should be reduced in structurally complex habitats and the second hypothesis predicts that sit-and-wait foraging lizards should be attacked less frequently than active foraging species. I further examined predator attack patterns with respect to different classes of predators (birds versus lizards) and whether predators cued in on specific morphological characteristics of a lizard's body.

Materials and Methods

I conducted this study in the Jalapão region of the state of Tocantins, Brazil, from 1–9 December 2004. The Jalapão region (10°33′ S, 46°45′ W) covers approximately 53,340 km^2 of relatively undisturbed Brazilian Cerrado. The Cerrado Biome is a savanna-like ecosystem and covers approximately 22% (2 million km^2) of Brazil's land surface (Oliveira-Filho and Ratter, 2002). Lizard species diversity is high in the Cerrado (Colli et al., 2002) as is the diversity of birds that prey on lizards (Macedo, 2002; Sick, 1993).

I purchased flexible plastic lizards (Safari Ltd., Miami, Florida, USA) representative of four different lizard body shapes and painted them with gray primer spray paint. I dipped lizard models into melted Plastalina modeling clay (sculptor gray; Van Aken International, Rancho Cucamonga, California), allowed some of the liquefied clay to run off, and then let the clay on the models cool. The clay formed a thin coating that maintained the model's body shape characteristics while remaining soft so that predator attacks could be scored. All models were unpatterned and identical in color (gray) so that body shape could be examined independently of color and pattern (Fig. 1). Size and shape of models were similar to lizard species that occurred in the study area (Fig. 1; confirmed by morphological analysis described below). Because real lizards are often colored, using gray-colored models may have some limitations. For example, predators that cue in on a particular color may not attack as frequently and the lack of color may affect the chromatic contrast with some backgrounds, also influencing attack frequency. However, gray is the best option because attempts to manipulate color are far more likely to create problems than provide solutions (Bennett et al., 1994; Endler, 1990). Color is more subject to variation in the predator visual system and varies considerably with ambient light (Endler, 1990, 1993). For example, a red model would change in contrast relative to its background with time of day and its appearance would vary in the forest compared to open habitats (Endler, 1993). Conversely, a gray model provides relatively even reflectance across the spectrum (Endler, 1990), thus the model should appear more similar to a wider variety of predators and under a wider range of light conditions than would a colored model (Endler, 1993).

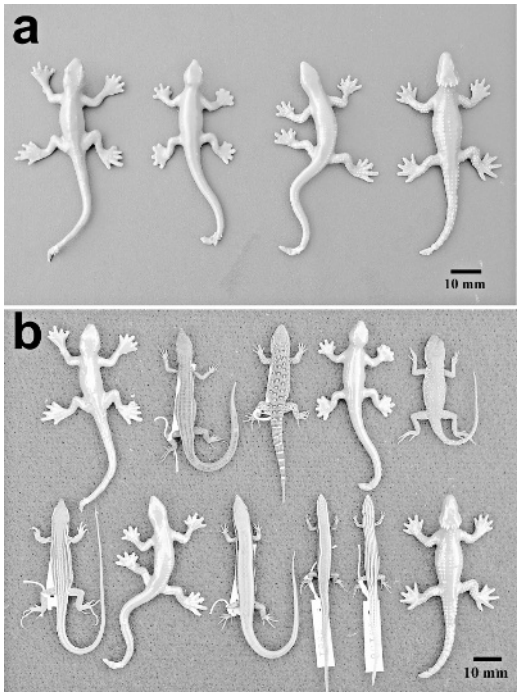


Fig. 1.—Clay-covered lizard models used in the study (a) and lizard models with real lizards from the study area (b). In a (left to right): models A, B, C, and D. In b (top row, left to right): model A, *Cercosaura ocellata*, *Gymnodactylus carvalhoi*, model B, *Tropidurus oreadicus*; (bottom row, left to right): *Cnemidophorus* sp., model C, *Mabuya heathi*, *Micrablepharus maximiliani*, *Vanzosaura rubricauda*, model D.

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I used digital calipers to measure (to the nearest 0.01 mm) the following morphological variables on 20 models of each shape: snout–vent length (SVL), tail length, head width at the widest point, head length from the tip of the snout to the posterior edge of the articulation of the jaw, head height at its highest point, trunk width at its widest point, and trunk height at its highest point. To determine how well the models approximated lizard species in the study area and which species were morphologically similar to each model, I used data, consisting of the same measurements, on lizards from the Jalapão region collected 13 Feb to 10 March 2002, and 21 November 2004 to 05 January 2005 (L. J. Vitt and G. R. Colli, unpublished data). Twenty-six species of lizards have been documented from the Jalapão region (Vitt et al., 2005), and I included 16 species in my analysis, omitting amphisbaenids ($n = 4$) and six species for which too few data existed (*Briba brasiliana*, *Hemidactylus mabouia*, *Cercosaura ocellata*, *Tupinambis duseni*, *Polychrus acutirostris*, and *Hoplocercus spinosus*). The sample size for *Anolis nitens* from Jalapão was small, but data from Parque Estadual de Cantão, Tocantins, approximately 375 km WNW, were available and added to the data set (L. J. Vitt and G. R. Colli, unpublished data). To increase the sample size of lizards with complete morphological data, I estimated tail length for individuals with broken or regenerated tails. For each species, I used the equation generated from a linear regression of $\log_e$-SVL versus $\log_e$-tail length using lizards with complete tails to predict the tail length of individuals with broken or regenerated tails. I did not distinguish between sexes within a species, assuming that intersexual variation within a species is low compared to interspecific variation. In total, I used data on 1297 individuals of 16 lizard species along with data on the lizard models.

I conducted this experiment in three habitats (Fig. 2) with different vegetation characteristics: (1) *cerrado sensu stricto*, (2) *cerrado campo sujo*, and (3) *cerrado sensu stricto queimado*. *Cerrado sensu stricto* (strict sense) is characterized as having a well-developed herbaceous layer and being dominated by shrubs and small trees (3–8 m in height), *cerrado campo sujo* (dirty field) consists of primarily C_4 grasses and scattered shrubs and small trees, and *cerrado sensu stricto queimado* (strict sense burned) is recently burned *cerrado sensu stricto* (Oliveira-Filho and Ratter, 2002; Ottmar et al., 2001). Fire occurs frequently and is an integral component of the Cerrado ecosystem

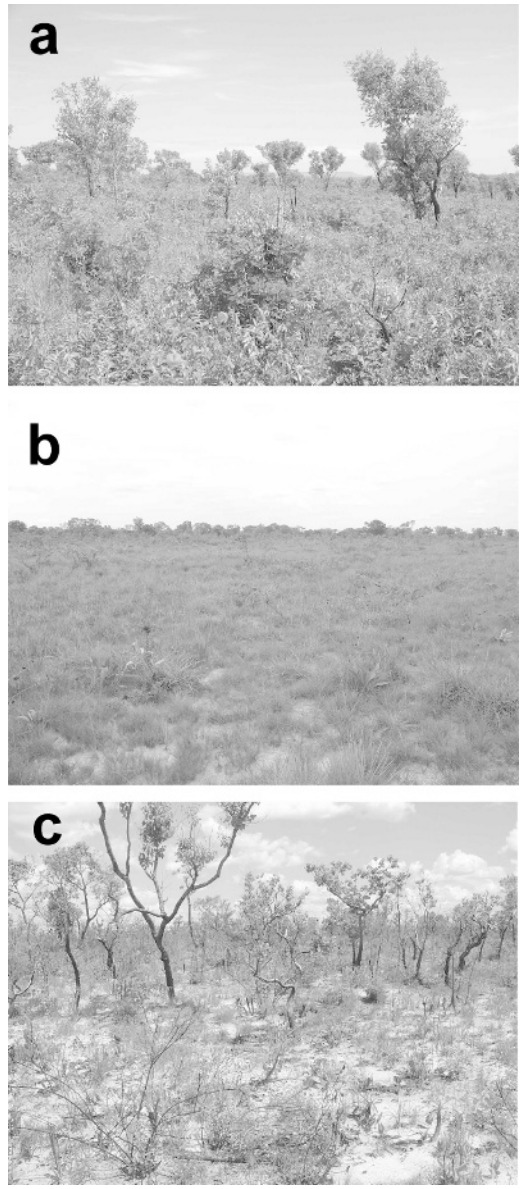


FIG. 2.—Study areas in the three different Cerrado habitats (a) *cerrado sensu stricto*, (b) *campo sujo*, and (c) *cerrado sensu stricto queimado*.

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(Miranda et al., 2002). The *cerrado sensu stricto queimado* site appeared to have burned a few weeks prior to the study and showed little regeneration of herbaceous cover. Distance between habitats ranged from 2.1 to 6.4 km.

Within each habitat, I ran two parallel 475-m transects separated by 100 m. I marked 20 stations along each transect, spaced 25 m apart, for 40 stations per habitat. At each station, I placed one of the four models 4 m from the center in each cardinal direction (N, S, E, and W), randomizing the model that was placed in each direction. Each of the three habitats had 40 models of each of the four body shapes for a total of 480 models. To quantify differences in vegetative structure among habitats, I measured canopy cover and ground cover at the center of each station using a concave spherical densiometer. Canopy cover was measured in the four cardinal directions whereas ground cover was measured once in a random direction.

It was not possible to deploy all models in a single day, so I offset the starting and ending dates in each habitat by deploying models on three consecutive days (one day per habitat). I allowed models to be exposed to predators for six days within each habitat. I deployed and collected models at approximately the same time of day in each of the habitats, so exposure time was equal for all models. Models were placed on bare ground in locations visible from overhead. Locations were similar for all model types and were typical of many of the real lizard species in the study area (e.g., *Ameiva*, *Cnemidophorus*, *Tropidurus*, *Vanzosaura*). Models generally were easy to relocate for collection, but in some instances predators had moved them from their initial location. In these cases, I thoroughly searched a 4-m radius around the spot where the lizard model should have been based on the distance and bearing from the station center. Upon collection, I examined lizard models for evidence of predator attacks. Birds and lizards (e.g., *Ameiva ameiva*) are potential visually oriented predators on the models, but marks made by each are different and distinguishable. Bird marks are V-shaped and lack tooth imprints whereas lizard marks are more U-shaped with distinct tooth imprints (Brodie, 1993; Husak et al., 2006; D. B. Shepard, personal observation). Cases where marks could not be assigned to a particular predator class were classified as unknown. In most of these cases, the model had been attacked with such intensity that no specific marks could be used to identify the predator positively. Marks made by ants (mandibles) and rodents (incisors) also were distinct and not counted as predator attacks because they were not considered predation attempts (Brodie, 1993; Brodie and Janzen, 1995). I also recorded the body region of the model where the attack occurred (head, trunk, tail, or limbs). If an attack included multiple regions (e.g., head and trunk), it was scored for the body region with the highest attack intensity. In some cases, the entire model was attacked with equal voracity and I classified these as a separate category (all).

Statistical Analyses

I used contingency analyses (chi square and log-likelihood ratio tests) to test for differences in attack frequency among habitats, between different predator classes (bird and lizard), and among body regions of the lizard models. Cases where the predator class could not be determined (i.e., category unknown) were omitted from analyses involving predator class, and cases where the entire model was attacked (all) were omitted from analyses involving body region of attack.

Because all morphological measurements were related to body size and highly intercorrelated, I used Principal Components Analysis (PCA, varimax rotation) to reduce them to a smaller number of independent variables. I pooled data from all species/models and regressed each $\log_e$-transformed variable against $\log_e$-SVL, then used the standardized residuals in the PCA. I retained components with eigenvalues greater than 1.0, calculated mean factor scores for each species/model, and plotted them to make qualitative comparisons.

I used ANOVA with post-hoc Tukey HSD tests to compare canopy cover and ground cover among habitats. Canopy cover and ground cover (percentages) were converted to proportions then arcsine transformed before analysis (Sokal and Rohlf, 1995).

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TABLE 1.—Results from Principal Components Analysis (PCA, varimax rotation) on size-adjusted lizard morphological variables including factor loadings, eigenvalues, and the percent variance explained by each factor.

Variable	PC1	PC2
Tail length	0.242	−0.889
Head width	0.546	0.738
Head length	0.910	−0.001
Head height	0.939	0.122
Trunk width	0.343	0.823
Trunk height	0.589	0.459
Eigenvalue	2.53	2.24
% Variance explained	42.17	37.29

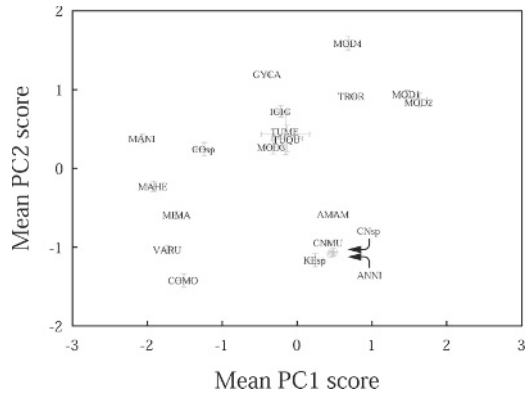


FIG. 3.—Plot of mean (± SE) factor scores for the two Principal Components (PC) based on six size-adjusted morphological variables from 16 lizard species and the four models used in the study. Abbreviations are as follows: *Ameiva ameiva* (AMAM, $n = 197$), *Anolis nitens* (ANNI, $n = 80$), *Cnemidophorus mumbuca* (CNMU, $n = 199$), *Cnemidophorus* sp. (CNsp, $n = 67$), *Colobosaura modesta* (COMO, $n = 19$), *Coleodactylus* sp. (COsp, $n = 18$), *Gymnodactylus carvalhoi* (GYCA, $n = 234$), *Iguana iguana* (IGIG, $n = 25$), *Kentropyx* sp. (KEsp, $n = 19$), *Mabuya heathi* (MAHE, $n = 32$), *Mabuya nigropunctata* (MANI, $n = 44$), *Micrablepharus maximiliani* (MIMA, $n = 72$), *Tropidurus oreadicus* (TROR, $n = 236$), *Tupinambis merianae* (TUME, $n = 2$), *Tupinambis quadrilineatus* (TUQU, $n = 5$), and *Vanzosaura rubricauda* (VARU, $n = 48$), Model A (MOD1, $n = 20$), Model B (MOD2, $n = 20$), Model C (MOD3, $n = 20$), and Model D (MOD4, $n = 20$).

Because vegetative attributes at a model's location may affect its probability of being attacked, it was necessary to test for and remove their influence before examining differences in attack frequency among model shapes. Therefore, I used multiple logistic regression with attacked (yes or no) as the dependent variable, model shape as the independent variable, and canopy cover and ground cover at the model's location as covariates. Results were considered significant at $P \leq 0.05$.

RESULTS

Size-adjusted lizard morphological variables were reduced to two factors that explained 79.5% of the variation (Table 1). The first factor (PC1) accounted for 42.2% of the variance and loaded highest with head length and head height (Table 1). The second factor (PC2) accounted for 37.3% of the variance and loaded strongest with tail length, head width, and trunk width (Table 1). Based on the morphological measurements taken, model shapes A and B were morphologically similar to each other and were most similar to the sit-and-wait forager *Tropidurus oreadicus*. Model shape C was similar to the active foraging teiids *Tupinambis*. Model shape D was most similar to *Tropidurus oreadicus* in PC1 and similar to the sit-and-wait foraging gecko *Gymnodactylus carvalhoi* in PC2 (Fig. 3).

Most lizard models were recovered (468 of 480). Although missing models may represent cases where a predator removed the model, I conservatively chose to score them as not attacked in analyses because of uncertainty. Conclusions were the same regardless of how they were scored. Overall, habitats differed in canopy cover ($F_{2,117} = 3.54$, $P = 0.03$) and ground cover ($F_{2,117} = 83.49$, $P < 0.001$) with *cerrado sensu stricto* having the highest canopy and ground cover, *campo sujo* having the lowest canopy cover, and *cerrado sensu stricto queimado* having the lowest ground cover (Fig. 4). The frequency of predator attacks on models varied among habitats ($\chi^2 = 23.77$, df = 2, $P < 0.001$) and was highest in *cerrado sensu stricto* (Table 2).

Canopy cover ($B = -0.03$, $\chi^2 = 4.72$, df = 1, $P = 0.03$) and ground cover ($B = -0.1$, $\chi^2 = 24.48$, df = 1, $P < 0.001$) at a model location were both negatively related to the model's probability of being attacked. After accounting for their influence, attack frequency did not differ among the four lizard model shapes ($\chi^2 = 1.38$, df = 3, $P = 0.71$).

Based on identifiable marks left on the models, lizards attacked models almost twice

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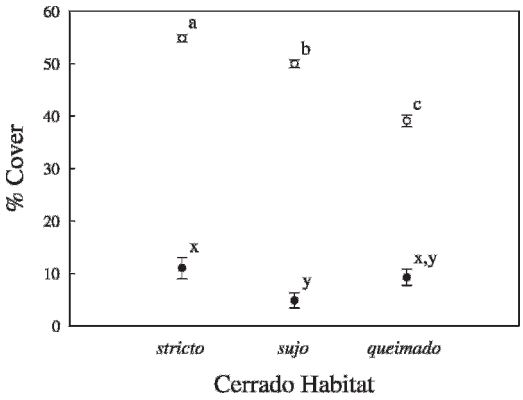


FIG. 4.—Mean canopy cover (closed circle) and ground cover (open circle) with SE bars for the three Cerrado habitats in the study area (*cerrado sensu stricto*, *campo sujo*, and *cerrado sensu stricto queimado*). For both canopy and ground cover, means labeled with different letters are significantly different from each other ($P < 0.05$); $n = 40$ for all groups.

as frequently as birds (Table 3), but the difference was not significant ($\chi^2 = 2.79$, df = 1, $P = 0.09$). Lizards and birds did not differ in their attack frequencies on the four model shapes ($G = 2.56$, df = 3, $P = 0.46$; Table 3). The head was the most frequent location of predator attacks ($\chi^2 = 52.20$, df = 3, $P < 0.001$) regardless of the model shape (Table 4) or the predator class (Table 5).

TABLE 2.—Number of lizard models attacked out of the 40 of each shape that were deployed in each habitat.

	Lizard model shape			
Habitat	A	B	C	D
Cerrado sensu stricto	6	11	6	6
Campo sujo	2	3	4	3
Cerrado sensu stricto queimado	2	0	0	1

TABLE 3.—Number of lizard models attacked, listed by predator class, out of the 120 models of each shape that were deployed.

	Predator		
Lizard model shape	Bird	Lizard	Unknown
A	1	6	3
B	4	5	5
C	3	3	4
D	2	5	3

TABLE 4.—Locations of attacks on lizard models by model shape.

	Lizard model shape			
Attack location on model	A	B	C	D
Head	5	12	6	4
Trunk	2	0	2	1
Tail	1	0	0	2
Limbs	0	0	0	0
All	2	2	2	3

DISCUSSION

Stationary lizard models should be attacked by primarily visually oriented, active foraging predators (Huey and Pianka, 1981). These predators would be able to detect prey more easily in open habitats because they would have a clearer line of sight and because prey lack cover (Denno et al., 2005). Thus, I predicted that predator attack frequency would be negatively related to habitat structural complexity. Of the three habitats, the recently burned *cerrado sensu stricto queimado* was considered the least structurally complex because of the lack of herbaceous cover, and therefore was expected to have the highest attack frequency. Attacks on models, however, were most frequent in *cerrado sensu stricto*, the most structurally complex site.

The higher attack frequency in *cerrado sensu stricto* was likely a reflection of higher predator abundance and diversity compared to other sites. Local species diversity and abundance, including predators, are usually positively correlated with habitat structural complexity (Denno et al., 2005; Ricklefs and Schluter, 1992). Based on my general observations during the study, lizards and birds were more abundant in the *cerrado sensu stricto* site compared to other sites. A higher number and diversity of predators is expected

TABLE 5.—Locations of attacks on lizard models by predator class.

	Predator		
Attack location on model	Bird	Lizard	Unknown
Head	10	9	8
Trunk	0	4	1
Tail	0	2	1
Limbs	0	0	0
All	0	4	5

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to result in a higher number of attacks and an increased diversity of attacks, which would select for increased diversity in antipredator tactics among prey (Schall and Pianka, 1980). The low number of attacks in *cerrado sensu stricto queimado* was likely related to the recent fire. Fires in the Cerrado are most frequent near the end of the dry season and remove vegetative cover (Macedo, 2002; Miranda et al., 2002; see Fig. 2c), resulting in a decreased prey base. Vertebrate diversity and abundance generally decrease immediately following fire and rebound after the vegetation regenerates (Christensen and Kimber, 1975; Macedo, 2002; Miranda et al., 2002).

Predator attack frequency did not vary among the three habitats in the predicted manner, but predators and prey interact at multiple spatial scales (Denno et al., 2005). Ground cover and canopy cover at a model location were negatively related to the model's probability of being attacked. Thus, as predicted, predator attack frequency was negatively related to habitat structural complexity, but only on a microhabitat scale. How habitat and microhabitat differences affect predation risk in lizards is not well known (Smith and Ballinger, 2001). Some studies have used the frequency of broken tails to estimate predation level and make comparisons among different habitats (Schall and Pianka, 1980; Smith and Ballinger, 2001), but few have examined factors at the microhabitat scale. Variation in microhabitat characteristics has been shown to affect lizard escape behavior (Diego-Rasilla, 2003; Martín and López, 1995; Schulte et al., 2004). Because variation in escape behavior often is related to perceived predation risk (Cooper, 2003; Cooper et al., 2003; Lima and Dill, 1990), microhabitat also is predicted to influence predation risk. My results showed that predation risk varies with microhabitat characteristics; specifically, predation risk was higher in more open microhabitats.

Sit-and-wait foragers have body shapes that promote crypsis whereas active foragers have body shapes that facilitate escape (Huey and Pianka, 1981; Vitt and Congdon, 1978). Thus, I predicted that models with body shapes most like sit-and-wait foragers would have lower attack frequencies than models with body shapes more similar to active foragers. However, contrary to this prediction, attack frequencies did not significantly differ among the four model shapes. Although models were similar to lizard species in the study area (Figs. 1 and 3), some models were similar to each other and significant areas of lizard morphospace were devoid of a representative model. For example, no models were similar to the active foraging gymnophthalmids *Colobosaura modesta*, *Micrablepharus maximiliani*, and *Vanzosaura rubricauda* in either PC1 or PC2 (Fig. 3). High PC1 scores were associated with larger (i.e., positive residuals) head lengths and head heights, and high PC2 scores were associated with larger head widths and trunk widths, and smaller tail lengths (Table 1). Morphologically, lizard foraging modes appeared to separate best on PC2. Sit-and-wait foraging lizards (e.g., *Tropidurus* and *Gymnodactylus*) had wider heads and trunks and shorter tails (high PC2 values) whereas active foragers (e.g., *Ameiva*, *Cnemidophorus*, and gymnophthalmids) had longer tails and slimmer heads and trunks (low PC2 values). Of my models, A, B, and D grouped nearest to sit-and-wait foraging lizards, although their morphologies were a bit extreme, and model C grouped closer to active foraging lizards (Fig. 3). Considering the amount of variation among real lizards (Fig. 3), my models did not explore the full range of body shapes. Within the limited range of model body shapes used, my experiment failed to demonstrate a difference in attack frequencies due to shape. Models that better explored lizard morphological variation would provide a more robust test of the hypothesis about foraging mode and body shape.

Bird and lizard attack patterns on models were similar. The teiid *Ameiva ameiva*, a known predator of lizards (Vitt and Colli, 1994), was one of the most common lizards in the study area (L. J. Vitt and G. R. Colli, unpublished data) and was the most frequent attacker of models, based on the size and shape of bite marks. Birds are known predators of lizards in the Neotropics and some species' diets include a large proportion of lizards (Martins, 1996; Poulin et al., 2001; Sick, 1993). Potentially, bird predation may be

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underestimated in this study if birds were responsible for a high number of the missing models (e.g., flying off with them). The site with the highest attack level, *cerrado sensu stricto*, was also the site with the highest attack frequency by birds and the most missing models (9 of 12), indicating this may be the case. No snake attacks were observed in my study. Snakes primarily use chemosensory cues to locate prey; however, vision is also important, particularly for some diurnal active foraging species (Ford and Burghardt, 1993). Husak et al. (2006) found that coachwhips (*Masticophis flagellum*), a diurnal active foraging snake, attacked colored models meant to represent collared lizards (*Crotaphytus collaris*), a species specific to rocky open habitats (Smith, 1946). Vision would be important for diurnal snakes in habitat patches where encounters are frequent, such as when prey are concentrated due to habitat specificity, and when prey are highly visible (e.g., exposed basking and behavioral display sites). Within my study area, the diurnal active foraging snakes that eat lizards include species of the genera *Mastigodryas*, *Philodryas*, and *Chironius* (Vitt et al., 2005); however, exposed rocky habitats are absent. These snakes also use vision during foraging, but because of the characteristics of the habitat, vision would be most important after prey or patches containing prey have been located using chemical cues. Models do not produce lizard chemical cues, thus the probability of a snake encountering a model is likely small.

Most predator attacks were directed at the head of the models (Tables 4 and 5), suggesting that the head may be an important cue for predators. PC2 loaded high with head width (Table 1), high values of which were characteristic of the sit-and-wait foraging lizards *Tropidurus oreadicus* and *Gymnodactylus carvalhoi* (Fig. 3). Smith (1973, 1976) found that avian predators of reptiles have an innate disposition to attack the head; thus, wider heads in lizards may be associated with higher attack rates by visually oriented, active foraging predators. Alternatively, the head may only be important during the subjugation phase of the predatory encounter and predators may cue in on other characteristics during the detection phase (Endler, 1986). Because predator attack frequencies did not differ among models, the head appears to be more of a cue for targeting a predatory strike than for use in detection.

Characteristics such as pattern, body shape, behavior, and microhabitat use are likely co-evolved suites of traits that provide the best antipredator defense by acting together (Brodie, 1992; Cooper, 1994, in press; Schulte et al., 2004; Vitt and Price, 1982). A cryptic pattern may provide some protection independent of body shape, but whether an individual avoids detection will depend on its behavior and microhabitat. Prey morphology is a product of the pressures exerted by the suite of predators in the environment, plus their sensory capabilities, and the ecology of the prey organism (Endler, 1986; Schulte et al., 2004). A portion of morphological attributes such as body shape may also be deeply rooted in the phylogenetic history of lizards (see Harmon et al., 2003), similar to ecological and behavioral traits (Cooper, 1994; Vitt and Pianka, 2005; Vitt et al., 2003). Examining traits as co-evolved suites in a phylogenetic context may help to elucidate the relative roles of phylogenetic history and ecological interactions, and provide important insight into the evolution of prey morphology and behavior.

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