

Detecting Variation in Microhabitat Use in Low-Diversity Lizard Assemblages across Small-Scale Habitat Gradients

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ABSTRACT.—If community structure is influenced by habitat structure at a local level, then it should be possible to tie species occurrence to key habitat variables. We used a pitfall-trap system to determine the relationship of species composition, species diversity (relative abundance), and community structure to habitat structure along a transect through a habitat gradient in the Brazilian Cerrado. A total of 531 individuals of 12 lizard species were sampled. A species accumulation curve based on EstimateS and a curve-fitting protocol predicted 12 species at day 22 and all species by about day 40. We registered 12 species at day 11. Trapping success declined through time, likely because of a combination of removal along the transect and seasonal environmental change (wet to dry). The more open end of our transect experienced higher temperatures in all microhabitats sampled, suggesting thermal structure associated with vegetative structure. A Canonical Correspondence Analysis showed that lizard species composition and relative abundance respond to variation in vegetative and physical structure of the habitat at small scales. Consequently, maintenance of habitat gradients should be considered in programs aimed at maintaining local biodiversity.

Habitat structure is known to influence plant and animal distributions at several scales (Hamer and Hill, 2000; Levin, 2000; Gering et al., 2002; Johnson et al., 2003). It is well known, for example, that mammals (Lindenmayer et al., 1999), birds (Renjifo, 1999; MacFaden and Capen, 2002; Rodewald and Yahner, 2002; Bennett et al., 2004), reptiles (Rocha and Bergallo, 1997; Bini et al., 2000; Fisher et al., 2002; Marchand and Litvaitis, 2004a,b), amphibians (Welsh and Lind, 2002; Guerry and Hunter, 2002; Lowe and Bolger, 2002), and terrestrial invertebrates (Bestelmeyer and Wiens, 2001; Chust et al., 2003; Summerville et al., 2003) respond to variation in habitat structure at different scales in a wide variety of environments throughout the world. We introduce a study designed to examine lizard diversity and community structure at a small spatial scale.

Specifically, we examined one lizard assemblage in the Brazilian Cerrado. The Cerrado has only recently become the focus of conservation efforts even though its biodiversity is more threatened than that of the Amazon or Atlantic rain forest (e.g., Mittermeier et al., 2000; Myers et al., 2000) because of rapid and uncontrolled development for agriculture and large scale hydroelectric projects (Ratter et al., 1997; Oli-

veira and Marquis, 2002; Cavalcanti and Joly, 2002). Biodiversity of the Cerrado remains poorly documented, but 1992 estimates suggested that at least 160,000 species of plants, animals, and fungi were represented (Dias, 1992; see also Ratter et al., 1997). Many previously unknown species have been added to the Cerrado faunal and floral lists, indicating that much of the diversity remains undiscovered (e.g., see chapters in Oliveira and Marquis, 2002; Colli et al., 1998, 2003a,b). Identification and protection of areas with high biodiversity require surveys and inventories of existing flora and fauna. Large regions of the Brazilian Cerrado Biome were transformed from natural habitat to agriculture prior to biotic surveys, with few patches of undisturbed Cerrado remaining today (e.g., Ratter et al., 1997).

Because the Cerrado contains a mosaic of habitats, it offers an ideal opportunity to examine the effect of habitat structure on vertebrate assemblages at relatively small scales. Lizards, which have proven to be excellent models for ecological research (Milstead, 1967; Huey et al., 1983; Vitt and Pianka, 1994), are abundant but often difficult to observe in the Cerrado (Vitt, 1991; Colli et al., 2002). We designed a study to test the hypothesis that lizard assemblages vary on a microgeographic scale and that their distribution on such a scale is predictable based on habitat structure.

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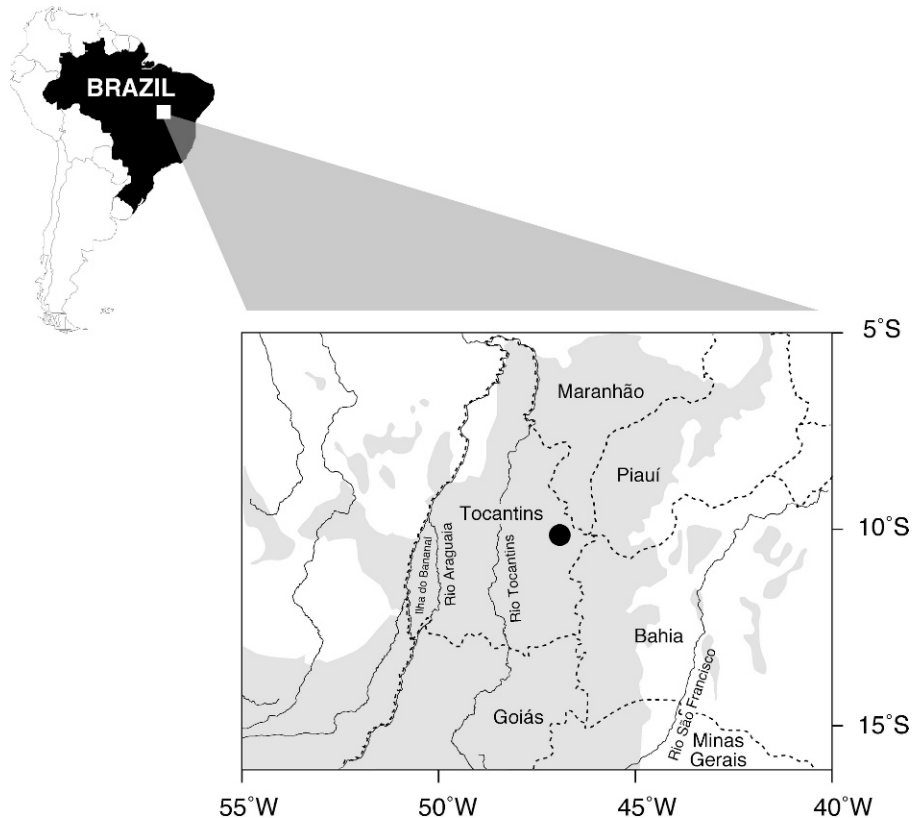


FIG. 1. Map showing location of the study site in eastern Tocantins State, Brazil. Shaded area is Cerrado and the study site is situated near the center of the Jalapão area.

MATERIALS AND METHODS

The Jalapão Site.—We conducted the study from 13 February to 10 March 2002 near “Escola D. Isabel Barreira de Oliveira” ($10^{\circ}15'46''S$, $46^{\circ}33'56''W$), approximately 35 km northwest of the city of Mateiros, Tocantins State, Brazil, in a region known as Jalapão (Fig. 1). Located in the eastern part of the state of Tocantins, with portions in southern Maranhão and Piauí, and western Bahia, the Jalapão region covers approximately 53,340 km² of relatively undisturbed Brazilian Cerrado. Much of it has recently been designated as national and state reserves, including the Área de Proteção Ambiental da Serra de Tabatinga (61,000 ha), Estação Ecológica Serra Geral do Tocantins (716,306 ha), Parque Estadual do Jalapão (158,885.5 ha), and Parque Nacional das Nascentes do Rio Parnaíba (729,813.55 ha). These contiguous reserves form the largest protected tract of Cerrado in Brazil. The habitat is relatively open, with gallery forests associated with streams and large as yet unexplored buttes harboring quite different vegetation than surrounding flatlands.

Field Methods.—We selected a study site that varied from open grassland with sparse stunted trees to grassland with higher density of trees, a partial canopy, and leaf litter. Soils were sandy throughout. We established a linear set of 75 pitfall trap arrays, each of which consisted of a central 20-liter plastic bucket (40 cm in height with 30 cm top diameter) sunk into the ground with the top flush with the surface, three 5-m drift fences at angles of 120° from each other, and a 20-liter bucket also sunk flush with the ground surface at the end of each drift fence. Thus, each array had four bucket traps (total of 300 traps). Thirty-eight of the arrays were evenly spaced along a 1,437-m transect, there was a break of about 100 m along a dirt road, and the remaining 37 pitfall trap arrays were evenly spaced along a 1,257-m transect. Traps were monitored four times per day (early morning, late morning, early afternoon, and late afternoon) to minimize mortality resulting from thermal stress during 23 consecutive days of sampling. Considering each day as a trap day and each bucket as a trap, we completed 6,900 trap days.

We identified each lizard to species and recorded time of day and identity of array.

We removed all lizards captured, humanely killed them following standard approved protocols (Anonymous, 1987), gave each individual a unique numbered tag, took a series of morphological measurements, and preserved them. Thus, our sampling protocol was a total removal one. This protocol allowed us to examine the effect of continual sampling on a local population as well. We used linear regression with day as the independent variable and number of lizards collected as the dependent variable to determine whether trapping success was a function of time.

To examine success rate in terms of species sampling, we assembled a matrix that contained lizard species as rows and day of collection as columns. Entries in the matrix were the number of lizards of each species collected per given day. We then calculated a species accumulation curve using EstimateS Version 7.5.0 (Colwell and Coddington, 1994; Colwell, 2005). Shape of species accumulation curves based strictly on empirical data is determined by the order in which samples are added. EstimateS randomizes sample order to generate smooth species accumulation curves. To generate estimators of diversity, 1,000 randomizations without replacement were performed. Resulting values are numbers of species expected based on empirical data (Colwell et al., 2004). The Abundance-based Coverage Estimator (ACE) was used to estimate completeness of sampling (Chazdon et al., 1998; Chao et al., 2000). Then we used likelihood ratios between three curve fitting models, Clench, logarithmic, and exponential, to determine best fit using methods and software described by Díaz-Francés and Soberón (2005). The model providing the best fit can then be used to estimate the asymptote of the species accumulation curve. Species accumulation curves most accurately predict species richness when the number of rare species is low; species richness is relatively low such that the probability of picking up additional rare species over time is low and, most important, when the species accumulation curve reaches a plateau (Thompson and Withers, 2003; Thompson et al., 2003).

We measured the following vegetative and structural habitat variables in each array: (1) leaf litter mass; (2) percent open ground; (3) percent of surface open to the sky; (4) number of plant stem contacts; (5) number of burrows in ground; (6) number of termite nests within 6 m; (7) distance to the nearest tree; (8) trunk circumference as a measure of tree size; and (9) total number of fallen logs. To do this, we used wooden dowels to construct a 0.5×0.5 -m grid with cross strings placed at 0.1-m intervals to form 25 equal-sized squares. In each area delineated by drift fences within each array, the

square was thrown over the researcher's shoulder, and its landing point was used as our random sample site. We counted squares represented by more than 50% open ground, squares not under canopy (open to sky). All leaf litter under the grid was collected and weighed. At the center of the spot where the square landed, we placed a vertical stake with a 1-m horizontal dowel 20 cm above ground and rotated the stick 360° . We counted the number of plant stem contacts with the horizontal stick. Then we measured distance to nearest tree from the center of the square. This procedure yielded three independent measurements for each variable in each array. We used means for each array for analysis. From 1 m beyond end of wings (6 m from center of array), we counted all burrows, all termite nests, and the total number of fallen logs within the array. All habitat variables were \log_{10} -transformed prior to analyses.

In addition to collecting data on the vegetative and structural characteristics of the habitats, we used TidBit electronic temperature recording devices (made by Onset Computer, Pocasset, MA) to examine thermal characteristics of the arrays at ground level (where lizards live). These devices have been shown to estimate lizard operative temperatures (Vitt and Sartorius, 1999; Shine and Kearney, 2001). However, we used them specifically to test for thermal differences in microhabitats within arrays, making no assumptions about thermal preferences of lizards using the habitats. We sampled four microhabitats that lizards use (1) under grass clump; (2) under small shrub; (3) in leaf litter; and (4) on open ground (exposed to sun). Because we had a limited number of TidBits, we arbitrarily assigned them to nine arrays (yielding nine replicates) at the open habitat end of the linear sampling area and nine in the more closed end of the habitat gradient. We combined data for each set of nine replicates for a simple comparison between more open and more closed Cerrado, recognizing that some transitional detail is lost in the comparison. However, our intent was only to determine whether some thermal structure might exist between relatively open versus relatively closed Cerrado. Each replicate sampled temperature at 5-min intervals over a 48-h period. These data were collected during an eight-day period from 22 February through 29 February. We calculated means and SD for all replicates for each microhabitat to provide a 24-h representation of temperature changes throughout the day with data from all days combined.

We used vegetation and structural habitat variables to characterize the habitat within individual arrays (total of 75) and lizard species identities and relative abundance as a measure of

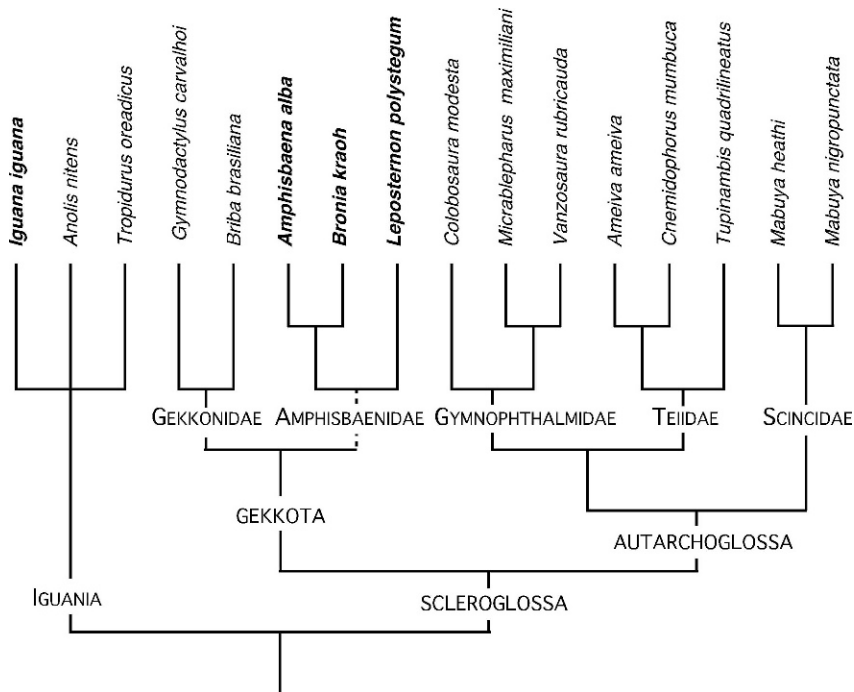


FIG. 2. Phylogenetic relationships among lizard species observed near the Jalapão site. Species in bold text were not observed on the pitfall array sites. Relationships of lizards based on Pellegrino et al. (2001) for gymnophthalmids, Presch (1974, 1983) for teiids, and Frost et al. (2001) for iguanians. The three iguanians shown are in different families. They are, from left to right, Iguanidae, Polychrotidae, and Tropiduridae.

lizard community structure within individual arrays. To examine the relationship between lizard species and microhabitat characteristics, we performed a Canonical Correspondence Analysis (CCA; Ter Braak, 1986), a multivariate ordination procedure that directly associates variation in one matrix (lizard assemblage as the dependent variable) to variation in another matrix (habitat characteristics as the independent variable). The independent variables consisted of a matrix with mean values for each habitat variable as columns and array identity as rows. The dependent variables consisted of a matrix with number of individuals of each lizard species as columns and array identity as rows. Thus, in this analysis, we asked whether an association exists between specific habitat characteristics and abundance of particular lizard species. CCA was performed with CANOCO 4.5 (Ter Braak and Smilauer, 1998), with the following options: focus scaling set on symmetric, biplot scaling type, downweighting of rare species, Monte Carlo test with 1,000 permutations of the reduced model, and unrestricted permutations.

RESULTS

The Jalapão Lizard Fauna.—A total of 531 lizards of 12 species was sampled with pitfall

arrays, including representatives from the three major lizard clades: Iguania, Gekkota, and Autarchoglossa (Fig. 2). Mean body size (SVL) varied from 31.5 ± 0.3 mm in *Vanzosaura rubricauda* to 254 mm in *Tupinambis quadrilineatus* (Fig. 3). Four additional species were collected in the area but primarily not on our plots. They were *Iguana iguana*, an arboreal iguanid lizard distributed primarily along gallery forest, and three species of subterranean amphisbaenians; *Leposternon polystegum*, *Amphisbaena alba*, and *Bronia kraoh*, which are not easily collected in pitfalls. We do not consider these further. Trapping success was greatest during the first 10 days, dropping off considerably by the 23rd day (Fig. 4). The reduction in trapping success was significant ($r_s = -0.8$, $P = 0.0002$). Six species were moderately common, two were very common, and four were uncommon (Fig. 5). Although we had collected all 12 species in the arrays by day 11, the simulated species accumulation curve estimated 11 species at day 11 and continued to rise slightly up until day 23, approaching 12 species (Fig. 6). Among the three models tested, the best-fit model is the Clench model, described as $(az) / [1 + (bz)]$, where a and b are estimated parameters and z is the number of trap days. This model reaches a plateau by about day 20, rising slowly to reach

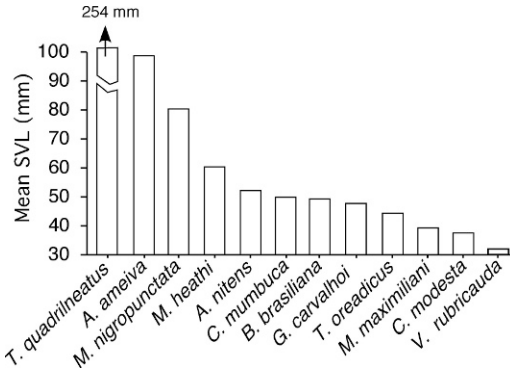


FIG. 3. Body sizes of Jalapão lizards ranked from largest to smallest (mean values). Size for *T. quadrilineatus* is based on data from Colli et al. (1998). Mean values are biased by varying proportions of juveniles collected. Rank order of size based on maximum SVL is, from largest to smallest: *Tupinambis quadrilineatus*, *Ameiva ameiva*, *Mabuya nigropunctatus*, *Tropidurus oreadicus*, *Mabuya heathi*, *Anolis nitens*, *Cnemidophorus mumbuca*, *Gymnodactylus carvalhoi*, *Briba brasiliiana*, *Colobosaura modesta*, *Micrablepharus maximiliani*, and *Vanzosaura rubricauda*.

11 species by a projection to day 60. Thus, the Clench model, even though best fit, slightly underestimated the actual (12) or simulated (12) number of species. The ACE estimated species richness at 12.5, 0.5 species greater than observed or estimated with EstimateS.

Habitat Type Comparison.—Microhabitat temperatures were significantly higher (all *P*-values < 0.0001 based on ANOVA) in arrays at the more open end of the habitat gradient than at the more closed end of the habitat gradient (Fig. 7). Daily fluctuations of microhabitat temperatures indicate that temperatures in microhabitats of more open Cerrado were higher than those in more closed Cerrado during the time

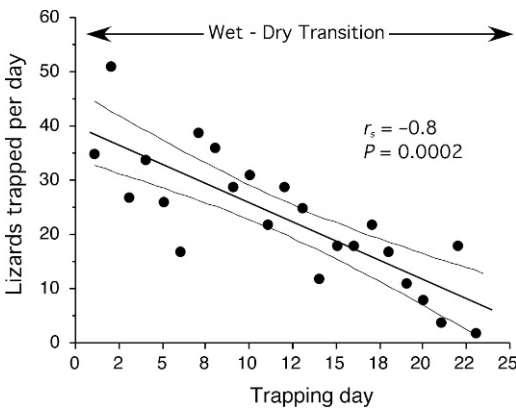


FIG. 4. Relationship between trapping success (number of lizards captured) and time in days.

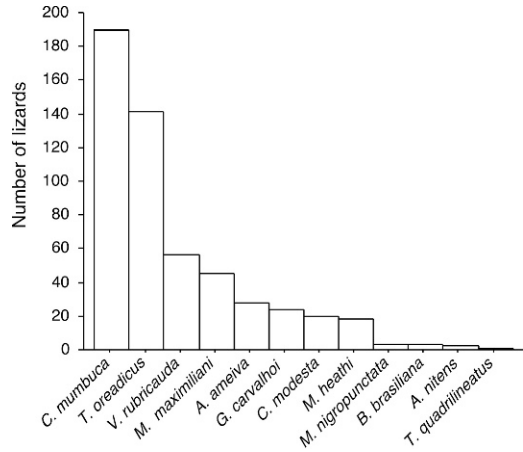


FIG. 5. Number of individuals of each lizard species collected during 23 continuous days of sampling. Species are ranked from highest to lowest abundance.

period in which lizard activity occurs, with the exception of the open-ground microhabitat. Open-ground microhabitats remained lower in temperature in the closed Cerrado portion of the gradient until about 1130 h, at which time the open-ground microhabitats exceeded those in the open Cerrado portion of the gradient.

A summary of vegetation and physical habitat characteristics in lizard-trapping arrays appears in Table 1. Based on 1,000 permutations of a Monte Carlo test and the first canonical axis, a significant association existed between habitat structure within arrays and lizards found there (eigenvalue = 0.335, $F_{8, 64} = 12.73$, $P < 0.001$). In addition, all canonical axes were

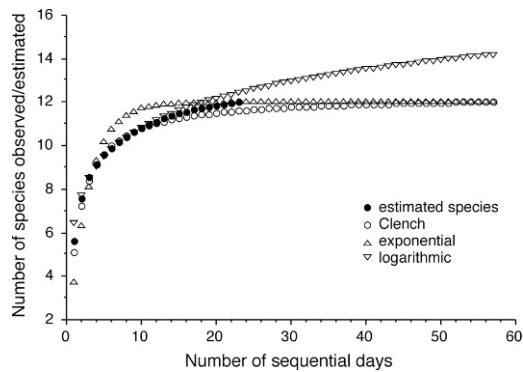


FIG. 6. Species accumulation curve for 75 arrays based on 1,000 randomizations from empirical data using EstimateS. Predictions over longer time periods are shown based on commonly used models. The Clench model is best fit and both Clench and exponential models predict the number of species that we observed.

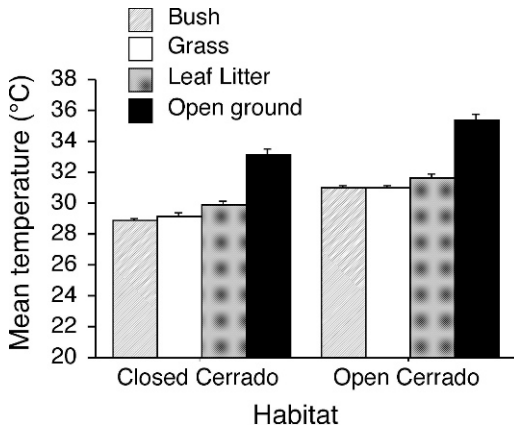


FIG. 7. Mean temperatures \pm SE for four microhabitats sampled within trap arrays in open and closed Cerrado sites based on nine array replicates. SE of means are shown.

significant (trace = 0.543, $F_{8, 64} = 2.611$, $P < 0.001$). *Vanzosaura rubricauda*, *Tropidurus oreadicus*, and *Cnemidophorus mumbuca* were associated with open sky (Fig. 8). *Briha brasiliana* was associated with the nearest tree. *Mabuya heathi* was associated with fallen logs. *Mabuya nigropunctata*, *Colobosaura modesta*, and *Gymnodactylus carvalhoi* were associated with leaf litter.

DISCUSSION

Pitfall trap arrays are highly successful for censusing reptiles and amphibians and crucial for sampling lizards in habitats where they are difficult to observe and collect (Gibbons and Semlitsch, 1981; Jones, 1986). We were able to determine species composition and relative abundance in a relatively short period of time at Jalapão. However, number of lizards collected dropped off significantly ($r_s = 0.0002$) with time indicating that (1) linear trapping and removal reduced density along the linear transect; (2) real changes had occurred in lizard populations during the study; or (3) changes in

population structure resulted in variances in trapping success. The first two explanations are most likely. During the first 14 days of sampling, number of lizards collected per day remained stable, and no significant effect was evident ($P = 0.0569$). However, numbers of lizards trapped dropped off by the 15th day, when a significant effect of time became detectable ($P = 0.0297$). This may result from site fidelity for species that defend territories (e.g., *T. oreadicus*) and active foraging species (e.g., *C. mumbuca*) that patrol home ranges. Relative effects of this remain unstudied. Coincident with the drop-off in trapping success was a transition from the end of the wet season to the beginning of the dry season. A portion of the drop-off in lizard numbers may have resulted from reduced lizard activity associated with a change in resources resulting from season change (wet to dry). We find little support for the third hypothesis. We tested *a posteriori* for potential changes in population structure (distributions of SVL) either related to trapping or short-term population phenomena (e.g., hatching events) that might influence trapping success (i.e., nonrandom sampling with respect to size). We chose the four most commonly collected species for this comparison and divided data into four near equal time periods of six days each. Based on Kruskal-Wallis tests, three species showed no change in population structure; *M. maximiliani* ($H_{3, 47} = 6.76$, $P = 0.080$), *T. oreadicus* ($H_{3, 145} = 2.43$, $P = 0.488$), and *V. rubricauda* ($H_{3, 40} = 0.026$, $P = 0.998$). In *C. mumbuca*, a significant effect of time period on SVL distributions was found ($H_{3, 194} = 11.6$, $P = 0.009$). Only a single juvenile was collected during the first six days. In each consecutive time period, more juveniles were added, indicating that hatching was occurring after the first week resulting in a change in population structure detectable in our sampling. Removing juveniles from the analysis resulted in no population structure effect in adults among time periods ($H_{3, 179} = 1.30$, $P = 0.725$).

TABLE 1. Means for vegetative and structural habitat characteristics of 75 lizard-trapping arrays in the Jalapão region of Brazil.

Habitat characteristic	Mean \pm SE	Minimum–maximum
Leaf litter mass (g)	200.5 \pm 24.4	11.7–965.0
Number of squares open ground	17.4 \pm 0.5	5.0–25.0
Number of squares open to sky	22.2 \pm 0.5	8.3–26.0
Number of plant stem contacts	3.8 \pm 0.3	0–14
Number of burrows	0.1 \pm 0.0	0–1
Number of termite nests	0.9 \pm 0.2	0–10
Distance to nearest tree (m)	1.93 \pm 0.14	0.32–5.85
Trunk circumference (m)	0.22 \pm 0.02	0.05–1.04
Number of fallen logs	1.8 \pm 0.2	0–9

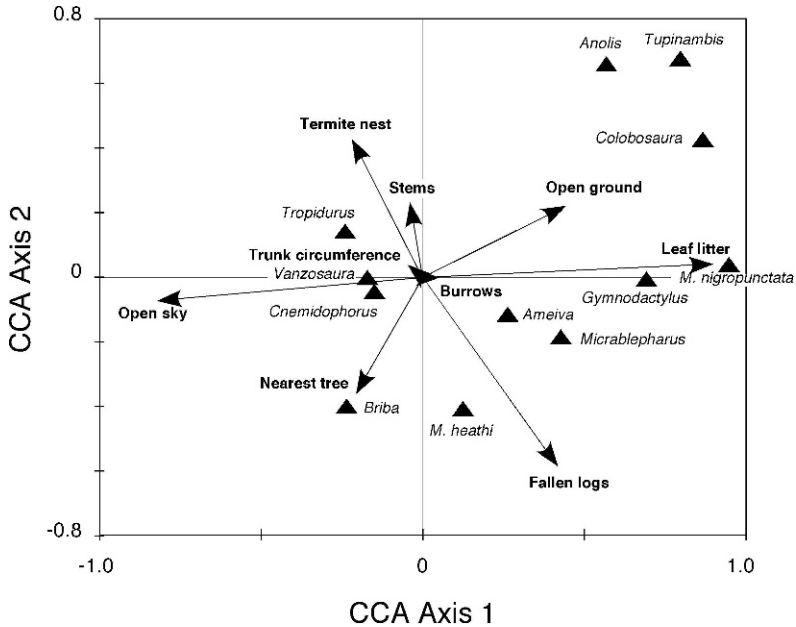


FIG. 8. Plot of Canonical Correspondence Analysis comparing matrices of structural habitat characteristics with lizard sampling data. The plot shows the position of each lizard species among arrays on first two canonical axes. Characteristics that are associated with one other with respect to occurrence of lizard species are more closely distributed than those seldom coassociated with a particular lizard species. The origin at 0.0 represents the lowest common denominator of overall lizard distributions summed across the 75 arrays. Lengths of microhabitat vectors indicate significance strength and points of arrows represent centroids of impact of microhabitat variables on each species' distributions among arrays.

Lizard species are often associated with particular microhabitats, not only in Cerrado, but also in habitats as different as Amazonian rain forest (Vitt and Zani, 1996) and Australian deserts (Pianka, 1973, 1986) on a global level (Vitt et al., 2003). The CCA shows that lizard species are tied to specific vegetative and physical characteristics of Cerrado habitats on a microgeographic level. Absence of leaf litter, open sky, or fallen logs, for example, would result in absence or, at best, rarity of some species. Similar to our results, studies of birds in northern temperate habitats identified microhabitat as the most important contributor to bird distributions at several scales based on a CCA (MacFadden and Capen, 2002).

Our results have broad implications for conservation biology in general and, in particular, for conservation and management of the Jalapão region. First, lizards are important components of natural ecosystems, particularly in arid and tropical lands where their species diversity and abundance is greatest (e.g., Pianka, 1973, 1986; Duellman, 1978, 1987; Lieberman, 1986). Second, they are excellent models for examining patterns of occurrence and relative abundance on microgeographic scales, because they can be easily trapped, identified, and monitored. Finally, as we

have shown, many species depend on specific vegetative or structural aspects of the habitats in which they live. The ability to identify microhabitat characteristics essential to presence of individual species provides necessary information to develop conservation and management plans for ecosystems. In this example, removal of trees, leaf litter, fallen logs, and termite nests from relatively closed Cerrado sites would have immediate and measurable effects on lizard diversity and community structure. Hydroelectric projects will flood or otherwise impact gallery forests, which are well known to provide a link between Amazon and Atlantic rain forests (Costa, 2003; da Silva, 1996). Loss of these habitats is likely to interfere with gene flow for those species using gallery forests for dispersal. As we've shown, animal species are not distributed uniformly across the Cerrado (see also Nogueira et al., 2005). Rather, microgeographic variation in habitat structure affects species composition and relative abundance such that species assemblages will easily be changed by habitat modification. These results should be easily applicable to other vertebrates.

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