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ELECTIVITIES AND RESOURCE USE BY AN ASSEMBLAGE OF LIZARDS ENDEMIC TO THE DUNES OF THE SÃO FRANCISCO RIVER, NORTHEASTERN BRAZIL

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ABSTRACT

*This study describes the pattern of resource use by one assemblage of lizards inhabiting a desert-like dune field in the Brazilian Caatinga. We evaluated food and microhabitat availability and phases of lizard activity, as well as use of, and electivities for, food and microhabitats. Six of the seven most abundant species are endemic to the dunes, and their diets under-represented arthropods possessing chemical defenses. The two fossorial gymnophthalmids were similar in presenting no electivities for microhabitat but differed in diet, electivities for food and phase of activity. The five species of epigeous lizards include one group presenting positive electivities for protected and shaded microhabitats (*Procellosaurinus erythrocerus*, *Briba brasiliiana*, and *Tropidurus psammonastes*) and another presenting negative electivities for such microhabitats (*Eurolophosaurus divaricatus* and *Cnemidophorus spec. nov.*). The tropidurid *T. psammonastes* presented the earliest activity in the morning, the strongest positive electivities for protected and shaded areas and negative electivity for exposed areas, and was the only species to present high positive electivity for ants. The only other tropidurid in the area, *E. divaricatus*, also ate ants but presented positive electivity for flowers. The medium-sized teiid *Cnemidophorus spec. nov.* showed the highest negative electivity for shaded areas, high positive electivity for open areas, and high negative electivity for protected areas. This pattern leads to use of microhabitat that is similar to that of *E. divaricatus*, which has a very different diet, and different from that of *T. psammonastes*, whose diet is comparable in the consumption of insect larvae and large-sized items. We discuss the evolution of the detected patterns of resource electivities.*

KEYWORDS: Caatinga; Diet; Dunes; Electivity; Microhabitat; Phase of activity; Lizards.

INTRODUCTION

The research developed so far on lizard assemblages has been based on a very limited sample of the current diversity (Vitt & Pianka, 1994; Vitt & Zani, 1996). Many of the best contributions to the field come

from studies on the *Anolis* (Polychrotidae) fauna from Antilles (Roughgarden, 1995) and from taxonomically more diversified faunas from deserts (Pianka, 1986). These studies have focused on the influence of biogeographical and ecological factors on the diversity and pattern of resource use. Recently, herpetologists started

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to include phylogenetic methods in their analyses in order to evaluate hypotheses of phylogenetic inertia on the patterns of resource use by lizard assemblages from desert (Losos, 1994) and other (Vitt, 1995; Vitt & Zani, 1996; Vitt *et al.*, 2003) habitats.

Many of these analyses are based on the pattern of resource use without evaluating resource availability in the habitat. When based only on rates of use by species, these measurements reflect the interaction between the species, and the resource and are better interpreted as phenotypic features. In order to demonstrate that the pattern of differential use of resources results from evolutionary divergence among competitors, *i.e.* it has genetic bases (Connell, 1980), it is necessary to evaluate the electivity of the species for the resource under analysis, that is, its preference by the resource or its ability in using it (Lawlor, 1980; Schoener, 1974a, b). The evaluation of electivities depends on quantification of resource availability in the environment, which is usually difficult to achieve (Pertraitis, 1979).

Analyses of electivities in studies focusing lizards have been restricted almost exclusively to diet, and the difficulty in evaluating the availability of the food items in the habitat has been cautiously avoided by using the total of food consumed by the assemblage as a representative sample of the food effectively available to it (Pianka, 1986). Studies evaluating habitat or microhabitat availability have been much less common (e.g. Rocha, 1991), although, in many circumstances, such evaluation could be easily made in the field. It is sometimes assumed that habitat availability is represented by the total use of the community (Moermond, 1979). However, in many cases, there is an implicit assumption, hardly justifiable, that different habitats are equally available in the environment (e.g. Pianka, 1975; Vitt, 1995).

The present study is the first of a series intended to evaluate the relative importance of local and historical factors (*i.e.* ecological interactions and phylogeny) on patterns of resource use by assemblages of lizards present in the desert-like dune fields in the semiarid Brazilian Caatinga. These dunes were referred to by Captain Richard Burton (1869) as "The little Sahara along the São Francisco River", and represent a paleodesert inside the semiarid Brazilian Caatinga morphoclimatic domain (Barreto, 1996; de Oliveira *et al.*, 1999). We have chosen these assemblages for a number of reasons. First, the dunes are inhabited by a diverse and abundant lizard community (Rodrigues, 1996), allowing meaningful analyses. Second, as the superficial area of the dunes (ca. 7000 km²) represents

only 1% of the area of the Brazilian Caatinga and many of the squamate species (and some of the genera) are endemic (Rodrigues, 1996), ecological interactions among these small populations of different species are likely to generate evolutionary effects (Endler, 1977) that could be detected by ecological analyses. Third, the dunes are located along both banks of the São Francisco River, and vicariant communities include closely related species, allowing phylogenetic comparisons. Forth, good phylogenies are available for many of the most abundant species in the area (Benozzati & Rodrigues, 2003; Frost *et al.*, 2001; Pellegrino *et al.*, 2001), making phylogenetic comparisons of ecological data credible.

In this first study, we describe the pattern of resource use and the electivities for food and microhabitat variables by the most abundant lizards captured in one location within the dunes. We then discuss the likelihood that the pattern is derived mainly from the history of the taxa or from ecological interactions.

MATERIALS AND METHODS

Study Area

The dunes are located along a strip of land, presenting both arid and semiarid climates, extending southwest from Raso da Catarina, along the middle São Francisco River valley, where mean annual temperatures are the highest in the state of Bahia, exceeding 26.2°C (Bahia-Seplantec, 1978). Records from Barra (ca. 50 km SW of Ibiraba), indicate mean annual rainfall of 692 mm (ranging from 400 to 800 mm). Typically, the dry season is from April to September and the wet season is from October to March (Nimer, 1979) (Fig. 1). Fieldwork was carried out in the sand dunes at Ibiraba

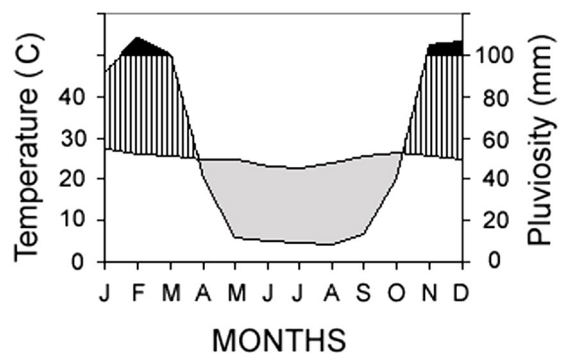


FIGURE 1. Climate diagram for the municipality of Barra, State of Bahia (from Nimer, 1979), generated by the meteorological station closest to the study area (Ibiraba).

in the municipality of Barra in the state of Bahia, Brazil (10°48'S, 42°50'W) (Fig. 2). The study area is approximately 500 m from the nearest village and comprises mainly lowlands in the floodplain of the São Francisco River, near the Icatu River. The dunes have apparently been undisturbed by recent human activity, except for some extraction of firewood. Indeed, the local human demographic density (3.58 inhabitants km⁻²) is one of the lowest in the State (www.sei.ba.gov.br, Mar/2004).

The studied area represents one of the five geomorphologic dominions of the sandy seas in the middle São Francisco River, as described by Barreto (1996), who also provided a full description of the geology

and geomorphology of the area. In this dominion of dunes with sharp morphology, dune summits stand about 40 m above the river level, and up to 20 m above the dune valleys. Vegetation physiognomy on the dunes differs from that on the neighboring alluvial plain, the former presenting trees and bushes that are shorter and more scattered and lack of conspicuous herbaceous covering even in the wet season. Therefore, most of sandy soil remains exposed, except for patches of terrestrial bromeliad *Bromelia antiacantha* Bertol., small cacti *Tacinga inamoena* (K. Schum.) N.P Taylor & Stuppy, and ground litter. A full description of the local flora and physiognomy has been presented (Rocha *et al.*, 2004). The soil is composed mainly of very thin eolic

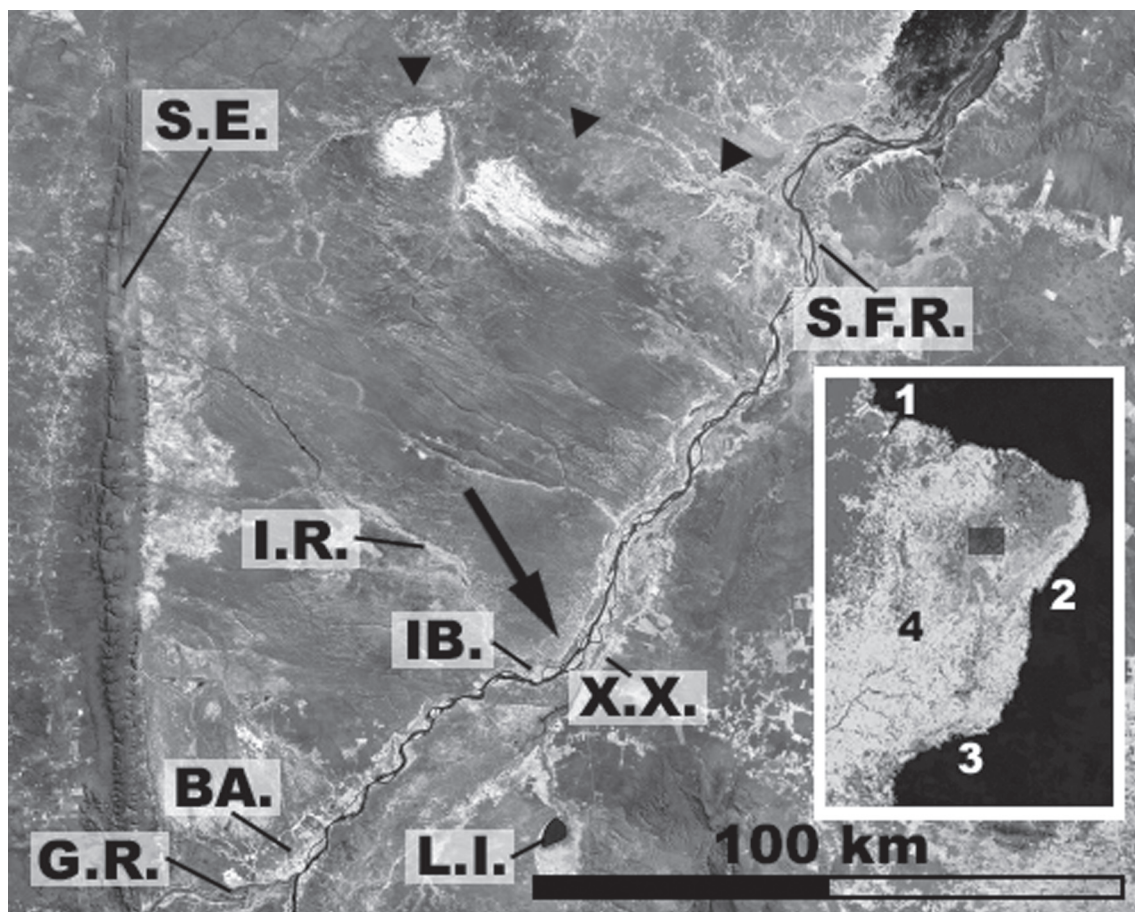


FIGURE 2. Map showing the geographic location of the study area. The inset shows the easternmost part of Brazil and four important cities as reference points: 1.) Belém, State of Pará; 2.) Salvador, State of Bahia; 3.) Rio de Janeiro, State of Rio de Janeiro; 4.) Brasília, Distrito Federal (Federal District). The darker, diagonal area surrounded by lighter areas represents the shrublands and dry forests of the Caatingas, bordered on the west and east by forest and degraded forest and on the south by the Cerrado grasslands. The area delimited by the smallest darker rectangle is magnified to show the dune fields on the west bank of the São Francisco River (S.F.R.) The dune field is bordered on the west by the Serra do Estreito (S.E.). Its northern limit is represented by the small triangles. The Icatu River (I.R., the only perennial river crossing the dunes), the Grande River (G.R.), and the Lagoa de Itaparica (L.I.), as well as the urban centers of the municipalities of Barra (BAR.) and Xique-Xique (X.X.) are shown for geographic reference. The fieldwork was performed in the dunes with sharp morphology (lighter strip along the SFR; black arrow) near the village of Ibiraba (IB.). The coordinates of the central point in this image are 10°30'S-42°45'W.

sand and less than 15% clay (Bahia-Septantec, 1978; Barreto, 1996), resulting in a lack of any standing water (even temporary) in the dunes, and there are no rock outcroppings in the area. Additional descriptions of the dunes can be found in the study conducted by Rodrigues (1996).

Data Collection

Data collection in the field: We carried out fieldwork during four campaigns: two at the peak of the wet season (Feb-Mar/1996 and Feb-Mar/1997), one at the peak of the dry season (Sep/1996), and one at the beginning of the wet season (Dec/1996). We have complied with all applicable institutional Animal Care guidelines and obtained all required state and federal permits (IBAMA license 3451/93-13-AC). In each campaign, we used pitfall-traps and sampled animals continually over a period of at least 10 days. Each trap consisted of a 15 or 20 liter dry bucket (height: 30 or 40 cm respectively) and three radial 1.5 x 0.4-m drift fences. We distributed the traps in grids (approximately 120 traps spaced 7 meters apart) and plotted each one at least 250 m from the grids used in the previous campaign.

We checked traps twice a day, at dawn (mean \pm standard deviation: from 0624 h \pm 0031 h to 0853 h \pm 0059 h) and dusk (from 1625 h \pm 0111 h to 1800 h \pm 0027 h), when we collected all the captured vertebrates and removed from buckets all arthropods captured in order to avoid consumption by the lizards. For four days during the first campaign (peak of the

wet season) and for 10 days during the second (peak of the dry season), we preserved (in 70% alcohol) all arthropods larger than 1 mm in order to estimate prey availability for lizards. We recorded the microgeographic position (MGP) of each trap in the dunes (Huey & Pianka, 1974) as a categorical variable whose levels are summit, slope, valley, and plateau (Fig. 3, left). We also produced drawings of the habitat circumscribed by a circle 3 m in diameter around each trap, representing the following six quantitative variables: area covered by ground litter (LIT), shrubs (SHR), subshrubs (SUB), terrestrial bromeliad *Bromelia antiacantha* (BRO) and the small cactus *Tacinga inamoena* (TAC) – and summation of areas of horizontal projection of individual trees (TRE) (Fig. 3, right). We considered that these seven microhabitat variables to be very good descriptors of the variability in the local micro-conditions that are important to the local smaller fauna (rodents, lizards, and arthropods) (e.g., Rocha, 1991; Rocha *et al.*, 2004; Rodrigues *et al.*, 1988; Xavier & Rocha, 2001).

Data collection in the laboratory: After euthanizing the lizards with chloroform, we recorded their mass (BM, g) using portable Pesola[®] suited for the mass of the individual. We then fixed each lizard in 10% formalin for three days and stored it in 70% alcohol. In the laboratory, we also recorded snout-vent length (SV, mm), jaw length (JL, mm) and head width at the skull-jaw joint (HW, mm). When the number of individuals collected per campaign for a given species (N_{ind}) was more than 30, we randomly choose a sub-sample (N_{anal} ; usually 30 individuals) for diet analysis. Based on data regarding consumption by these analyzed individuals (C_{anal}),

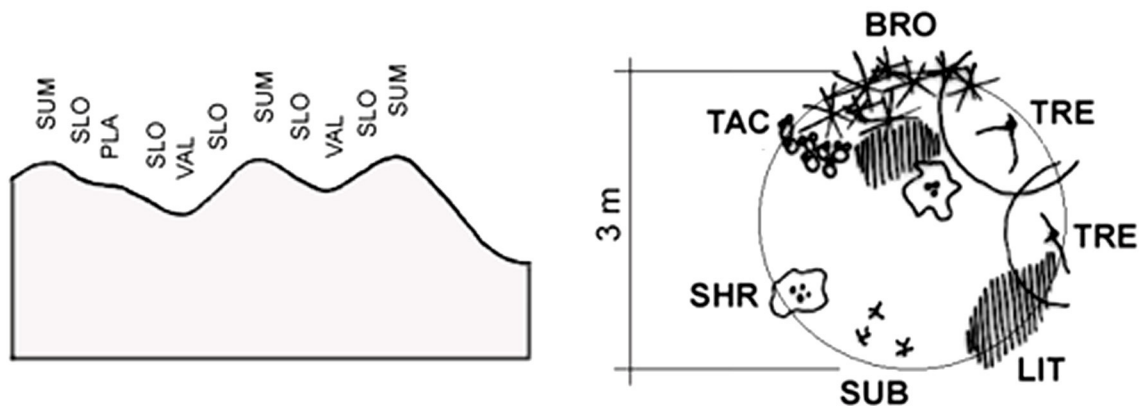


FIGURE 3. Left: schematic profile of the dunes showing microgeographic positions: summit, slope, plateau, and valley. Right: an example of a drawing used to quantify six quantitative microhabitat variables: area covered by ground litter, shrubs, subshrubs, the terrestrial bromeliad *Bromelia antiacantha*, the small cactus *Tacinga inamoena*, and area of horizontal projection of trees.

we estimated total consumption (C_{tot}) by all individuals collected using the equation:

$$(C_{tot} = C_{anal} * N_{ind} * N_{anal}^{-1})$$

We dissected the animals and removed their stomach contents in order to evaluate their diets. Food categories were initially recorded by morphospecies and then grouped by broader classes (usually orders for arthropods). We recorded, for each food category per stomach, frequency (F) and, after removing excess water with blotting paper, wet mass (M) to within 0.01 g. When a given food category in one stomach weighed less than 0.01 g, we designated the value as 0.002 g. In the prey categories, we measured mass instead of volume because of the strong correlation between the two (Magnusson & Silva, 1993) and because of considerable criticism regarding bias in the way that volume has traditionally been estimated (Magnusson *et al.*, 2003). We recorded the number of stomachs containing each prey category as recurrence (R). We analyzed the arthropods collected in the pitfall traps, recording the frequency of morphospecies and grouping the data based on higher taxonomic levels (usually order). Finally, we digitized the drawings of the habitat surrounding each trap in order to calculate the value of each of the six ground-cover variables (in cm²) per sampling plot. Vertebrates and arthropods collected were deposited in the Museum of Zoology from Universidade Federal da Bahia.

Data Analysis

Climatological data: In order to evaluate whether rainfall during the study was representative of the mean conditions of the region, we obtained complete historical rainfall data for four locations in the Barra vicinity from the National Institute of Meteorology. The series were evaluated visually based on graphs. In order to build the graphs, we included only months in which there were adequate records for all days.

Phase of activity: We determined the preferential phase of activity (nocturnal or diurnal) for each lizard species based on the number of captures per phase using the chi-square goodness-of-fit test, assuming (in the case of no preference) the effective sampling effort (number of traps) per phase as the theoretical proportion. We used the Bonferroni method in order to adjust levels of significance to 0.05.

Microhabitat: In order to detect orthogonal sets of microhabitat variables that are strongly correlated, we reduced the matrix of microhabitat values per plots by applying principal-components analysis PCA (correlation matrix), extracting factors with eigenvalues greater than 1,000 and applying VARIMAX rotation, an orthogonal method that simplifies the interpretation of the factors (Kleibaun *et al.*, 1988:620). We transformed the categorical variable MGP into two binary (*dummy*) variables designated “summit” (SUM), and “valley” (VAL). To preclude the collinearity effect, the third and fourth levels of the categorical variable were not transformed into a binary variable (Kachigan, 1986:268-9; Kleibaun *et al.*, 1988:260-1). After preliminary analysis of the data, we replaced the variables TRE and SHR with the variable “summation of areas of horizontal projection of individual trees and shrubs” (T&S = TRE + SHR). The proportion of objects (*i.e.* plots: $n = 484$) to number of variables (seven) in our analysis is in accordance with the general rules for factor analysis (Kachigan, 1986:383). We determined the electivities (*sensu* Lawlor, 1980) of each lizard species for the levels of the categorical variable MGP based on the number of captures per level using the chi-square goodness-of-fit test. We assumed as the theoretical proportion in the case of no electivity, the one effectively available in the habitat (as sampled by the distribution of traps along the grids).

Significant differences based on Bonferroni-adjusted alpha values (significance levels) were considered “detected electivities”. Significant differences based on standard analysis (without Bonferroni adjustment) were considered “marginally significant electivities”. In the case of quantitative microhabitat variables (TRE, SHR, T&S, SUB, BRO, TAC), we used the Kruskal-Wallis Test (followed by the Dunn’s multiple comparisons versus control test) to compare the distribution of the values of the variable in the habitat (as sampled by the distribution of traps along the grids; control) with the distribution of the values in all capture events by species. Each capture contributed to the last distribution with the value of the habitat variable represented in the plot around the trap. Significant differences were considered “detected electivities”. Significant differences found through Mann-Whitney tests comparing distribution of each species with distribution in the habitat were considered “marginally significant electivities”. Sets of similar lizard species were identified through visual inspection of scatter plots representing BM x SV (lizard size and form) and HW x JL (feeding apparatus size and

form) and by applying Dunn's multiple comparison test to each variable.

Diet: In our analysis, we assumed that the most important food categories in the diet of a given species were those presenting the highest contributions to the total mass ingested (highest M%) and ingested by majority of the individuals sampled (highest R%). We considered a given food category important for a lizard species if it represented at least 30% of the total mass ingested by the species and was ingested by at least 30% of the individuals. However, high importance of one category does not necessarily indicate high electivity for the category by a given lizard species. In order to detect electivities, we compared item consumption with item availability. When the numerical difference between the percentage of consumption and percentage of availability of a given food category was greater than 20, we considered that the lizard species had a high positive electivity for that food category. When that difference was less than -20, we considered that the species had high negative electivity for the food category. Although 20 certainly is an arbitrary limit, we believe that using differences larger than that will generate conservative results and higher confidence in the detection of electivities. We believe this method to be superior to the estimation method proposed by Lawlor (1980) because it does not overestimate electivity values for rare items. Estimation of food availability usually varies widely depending on the methodology applied (Winemiller & Pianka, 1990).

In order to determine the distribution of availabilities for the assemblage of lizards, we compared and used the results of two different methods: (a) estimation based on total consumption (C_{tot}) by the assemblage (e.g., Pianka, 1986) based on frequency data; and (b) estimation based on the total frequencies of items collected (in our case, using pitfall traps) directly from the habitat (H_{tot}). For our study, availability of mobile terrestrial items (as most arthropod groups are) was estimated by using the latter method (b), and availability of immobile items (some arthropods, eggs and larvae, gastropods or plant matter) was estimated by former (a), since it is known that successful capture with pitfall traps is influenced not only by species density but also by level of activity (Adis, 1979; Greenberg *et al.*, 1994; Van der Aart & Smeenk-Enserink, 1975).

In order to detect homogeneous groups of lizard species based on the morphometric attributes of their diets, we applied Dunn's multiple comparison test (Zar, 1996:227) to the masses of the heaviest food items

found in the stomach (MH). In order to compare species based on total diet composition, we calculated the symmetrical coefficient of niche overlap (ϕ) (Pianka, 1973) for each pair of species based on the proportions of resource use (by mass) using the formula:

$$\phi_{jk} = \frac{\sum_{i=1}^n p_{ij} \cdot p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \cdot \sum_{i=1}^n p_{ik}^2}}$$

where I represents the resource category, p represents the proportion of the resource used in the category I , n represents the total number of categories, and j and k represent the lizard species. Finally, we evaluated the incidence of positive correlations between JL and HW and among morphometric attributes of lizard diets using the (one-tailed) Spearman correlation coefficient and visually inspecting scatterplots.

We used the software SigmaStat for Windows (Version 2.0 – Jandel Corporation, 1992-1995) and SPSS for Windows (Version 6.0 – SPSS Inc., 1989-1993) for the statistical analyses. We adopted a significance level of 0.05 to obtain critical values (a) and, when indicated, Bonferroni adjustment for repeated tests.

List of codes used in figures: The codes used in figures to refer to variables measured are listed below in alphabetical order. Inside parenthesis we indicate the unity of measurement and kind of variable: BM: body mass of lizards (g; ratio scale); BRI: *Briha brasiliiana* (level of the categorical variable *species*); BRO: area covered by *Bromelia antiacantha* (cm²; ratio scale); CAL: *Calyptommatius leiolepis* (level of the categorical variable *species*); CNE: *Cnemidophorus* spec. nov. (level of the categorical variable *species*); EUR: *Eurolophosaurus divaricatus* (level of the categorical variable *species*); HW: head width (mm; ratio scale); JL: jaw length (mm; ratio scale); LIT: area covered by ground litter (cm²; ratio scale); MH: wet mass of the heaviest food item in the stomach (g; ratio scale); NOT: *Notobachia ablephara* (level of the categorical variable *species*); PLA: plateau (level of the categorical variable MGP); (dummy variable); PRO: *Procellosaurinus erythrocerchus* (level of the categorical variable *species*); SHR: area covered by shrubs (cm²; ratio scale); SLOP: slope (level of the categorical variable MGP); SUB: area covered by subshrubs (cm²; ratio scale); SUM: summit (level of the categorical variable MGP); (dummy variable); SV: snout-vent length (mm; ratio scale); T&S: area

of horizontal projection of trees plus shrubs; TAC: area covered by *Tacinga inamoena* (cm²; ratio scale); TRE: area of horizontal projection of trees (cm²; ratio scale); TRO: *Tropidurus psammonastes* (level of the categorical variable species); VAL: valley (level of the categorical variable MGP); (dummy variable).

RESULTS

Climatological Data

Climatological data from Barra for the study period is presented in Fig. 4 (top) with rainfall his-

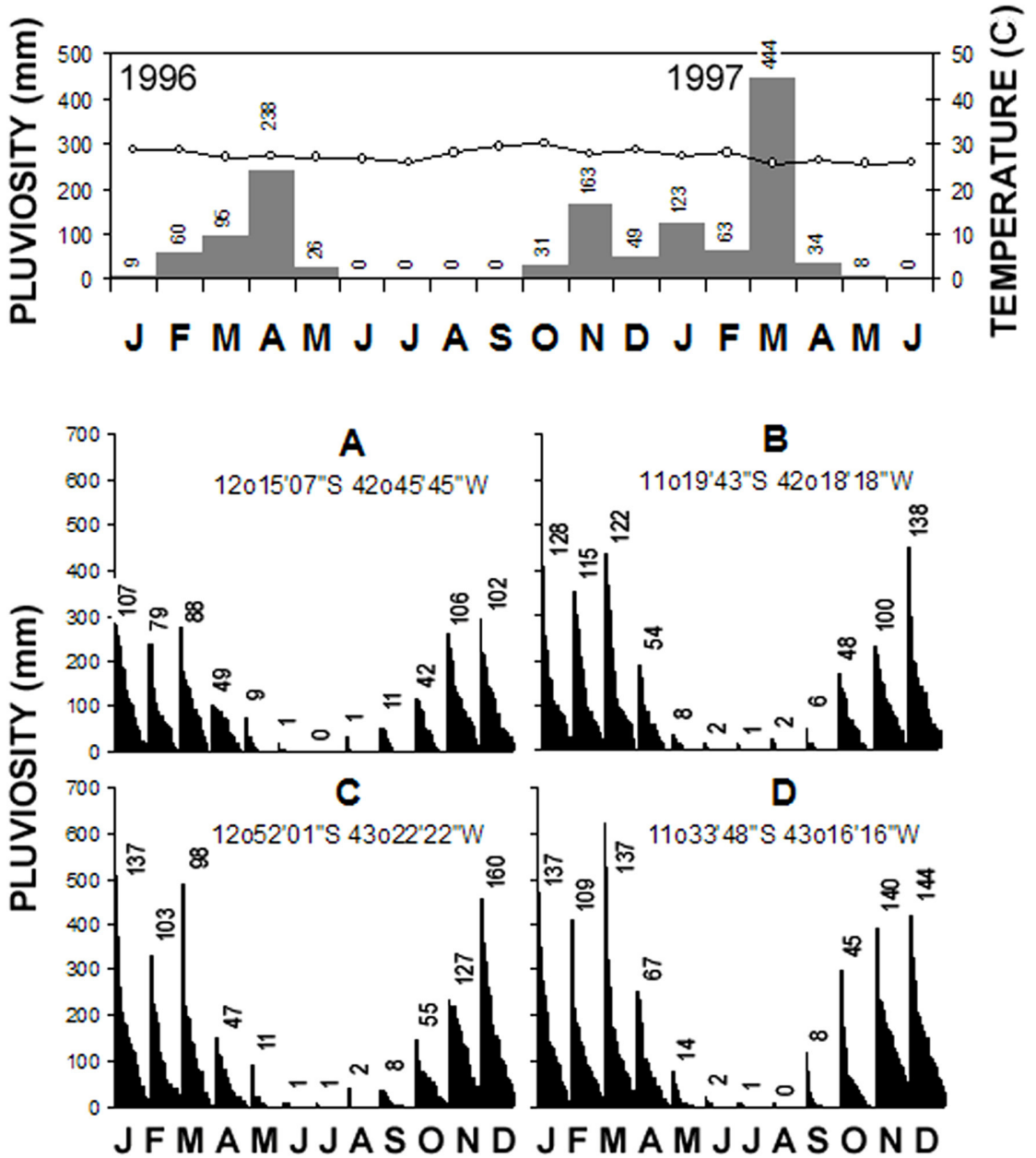


FIGURE 4. Climatological data from the town of Barra, State of Bahia, Brazil, during the study period compared to complete historical series of rainfall data from four locations in the vicinity. Top: monthly rainfall and mean temperatures from January 2000 to March 2001 as recorded at the Barra meteorological station. Values over bars are the monthly rainfall values. Bottom: monthly rainfall (records ranked in inverse order by month) recorded by the National Institute of Meteorology (INMET) at: (A) Station Ponte BR-242, Bahia (1972-1999); (B) Station Fazenda Cabaceiras, Ibipeba, Bahia (1972-1999); (C) Station Gameleira da Lapa, Sítio do Mato, Bahia (1962-1999); (D) Station Morpara, Bahia (1945-1999). Values over bars are mean monthly rainfall values.

torical data for four locations in the Barra vicinity (bottom). Visual inspection of the graphs in Figs. 1 and 4 reveals that, during the study period, rainfall peaked later than usual for both years. In 1996, January was anomalously dry and April was anomalously rainy; cumulative rainfall during the first three months (165 mm) was approximately half the mean of the historical data for the vicinity (274-383 mm). In 1997, on the other hand, March was quite rainy and the accumulated rainfall during the first three months was approximately twice (630 mm) the historical mean.

Lizards Captured

Using the pitfall traps, we captured 846 lizards (11 species), 770 anurans (8 species) and 17 snakes (4 species) (Table 1). Total squamate and anuran intensity of activity, as estimated by captures in pitfall traps, was much lower at the peak of the dry season and at the beginning of the wet season. In both campaigns conducted at the peak of the wet season, lizards were outnumbered by anurans and their total mass was also lower. Analyses of anuran (Santos *et al.*, 2003) and snake species are or will be presented elsewhere.

TABLE 1. Sampling effort and vertebrate captures during the four campaigns in Ibiraba in the State of Bahia, Brazil. Total mass of lizards and anurans captured are also presented.

	Field campaign				Total
	Feb-Mar/96	Sep/96	Dec/96	Feb-Mar/97	
Number of traps in the sampling grid	128	120	119	117	—
Sampling effort (number of traps x days)	1478	1440	1232.5	1462.5	5613
Anurans: captures; total mass (g)	304 ; 638.6	0 ; 0.0	26 ; 98.7	440 ; 1701.5	770 ; 2438.8
Bufonidae					
<i>Bufo granulosus</i>	143	0	9	42	194
<i>Bufo paracnemis</i>	7	0	0	0	7
Microhylidae					
<i>Dermatonotus mulleri</i>	0	0	0	26	26
Leptodactylidae					
<i>Leptodactylus fuscus</i>	0	0	1	0	1
<i>Leptodactylus ocellatus</i>	3	0	0	3	6
<i>Leptodactylus podicipinus</i>	0	0	0	7	7
<i>Physalemus albifrons</i>	130	0	3	115	248
<i>Pleurodema diplostris</i>	21	0	13	247	281
Lizards: captures; total mass (g)	232; 424.0	154 ; 164.0	240 ; 934.7	238 ; 931.0	864 ; 2454.7
Gekkonidae					
<i>Briha brasiliiana</i>	2	4	6	5	17
<i>Lygodactylus klugei</i>	0	0	1	0	1
<i>Phyllorhynchus pollicaris</i>	0	1	0	0	1
Teiidae					
<i>Cnemidophorus</i> spec. nov.	16	1	29	43	89
Gymnophthalmidae					
<i>Calyptommatius leiolepis</i>	109	125	143	119	496
<i>Notobachia ablephara</i>	3	2	7	1	13
<i>Procellosaurinus erythrocerus</i>	6	9	16	3	34
Tropiduridae					
<i>Eurolophosaurus divaricatus</i>	13	9	19	13	54
<i>Tropidurus psammonastes</i>	81	3	16	54	154
Scincidae					
<i>Mabuya beatbi</i>	2	0	0	0	2
Amphisbaenidae					
<i>Amphisbaena hastata</i>	0	0	3	0	3
Snakes: captures	0	3	8	6	17
Colubridae					
<i>Apostolepis gaboi</i>	0	2	4	1	7
<i>Philodryas nattereri</i>	0	1	1	0	2
<i>Phimophis scriptoribatus</i>	0	0	2	5	7
<i>Waglerophis merremii</i>	0	0	1	0	1
Total captures:	536	157	274	687	1651

Among lizards, *Lygodactylus klugei* and *Phyllorhynchus pollicaris* (Gekkonidae), as well as *Mabuya heathi* (Scincidae) and *Amphisbaena hastata* (Amphisbaenidae), were captured in low numbers (together representing less than 1% of all lizards captured) and were therefore excluded from any subsequent analyses. *Briba brasiliiana* (Gekkonidae), *Eurolophosaurus divaricatus* and *Tropidurus psammonastes* (Tropiduridae), *Calyptommatius leiolepis*, *Nothobachia ablephara* and *Procellosaurinus erythrocerus* (Gymnophthalmidae), and *Cnemidophorus* spec. nov. (Teiidae), were the most abundant species and are the object of the following analyses. All but *Briba brasiliiana* are endemic to the main dune field on the west bank of the São Francisco River. During the September 1996 campaign, capture rates for *Cnemidophorus* spec. nov. and *T. psammonastes* were quite low. The same was true for *P. erythrocerus* in the Feb-Mar/1997 campaign, *B. brasiliiana* in the first three campaigns and *N. ablephara* in all campaigns.

The scatterplot of body mass versus snout-vent length (Fig. 5a) shows that both *C. leiolepis* and *N. ablephara* differed from the remaining species due to their slender bodies. The gymnophthalmids were significantly lighter than the other species in the dunes (body mass below 2.0 g). *P. erythrocerus* (BM below 0.7 g) included also the shortest individuals (snout-vent length typically less than 30 mm). The four species with heaviest specimens (average body mass above 1.0 g) showed a similar body mass to snout-vent length relationship. Of the four, *B. brasiliiana* was the lightest (body mass below 3.0 g),

and *Cnemidophorus* spec. nov. had a significantly longer body length than did the other species. The scatterplot of head width versus jaw length (Fig. 5b) shows two clear patterns. First, there is a clear distinction between the size of the jaw apparatuses in gymnophthalmids (significantly shorter jaws and narrower heads) and that seen in the larger bodied species (longer jaws and broader heads). Second, the fossorial species and the teiid have narrower heads and longer jaws, whereas specimens of *P. erythrocerus*, the tropidurids and *B. brasiliiana* have comparatively broader, shorter heads.

Distributions of body mass values per campaign (Figs. 6 and 7) suggest that recruitment of *C. leiolepis*, *P. erythrocerus*, and *B. brasiliiana* occurs at the peak of the dry season and at the beginning of the wet season, and that recruitment of tropidurids, *Cnemidophorus* spec. nov. and (possibly) *N. ablephara* occurs at the peak of the wet season. Rodrigues (1991a) and Moraes (1993) found the same pattern for *Calyptommatius* species.

Phase of Activity

The results of chi-square goodness-of-fit tests (Table 2) showed that, of the seven most abundant species, only *C. leiolepis* and *B. brasiliiana* were primarily nocturnal. The other species were diurnal. In trap checks performed at dawn, the diurnal *T. psammonastes* was the only species frequently found (37%).

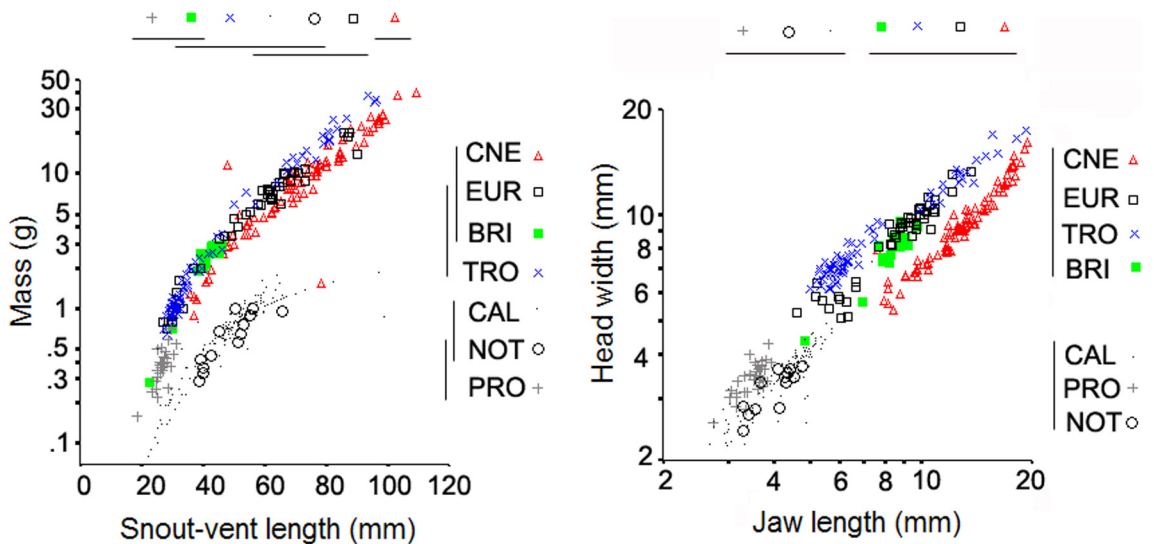


FIGURE 5. Scatterplots of body mass versus snout-vent length (A) and head width versus jaw length (B) based on data from seven lizard species endemic to the dunes of Ibiraba, State of Bahia, Brazil.

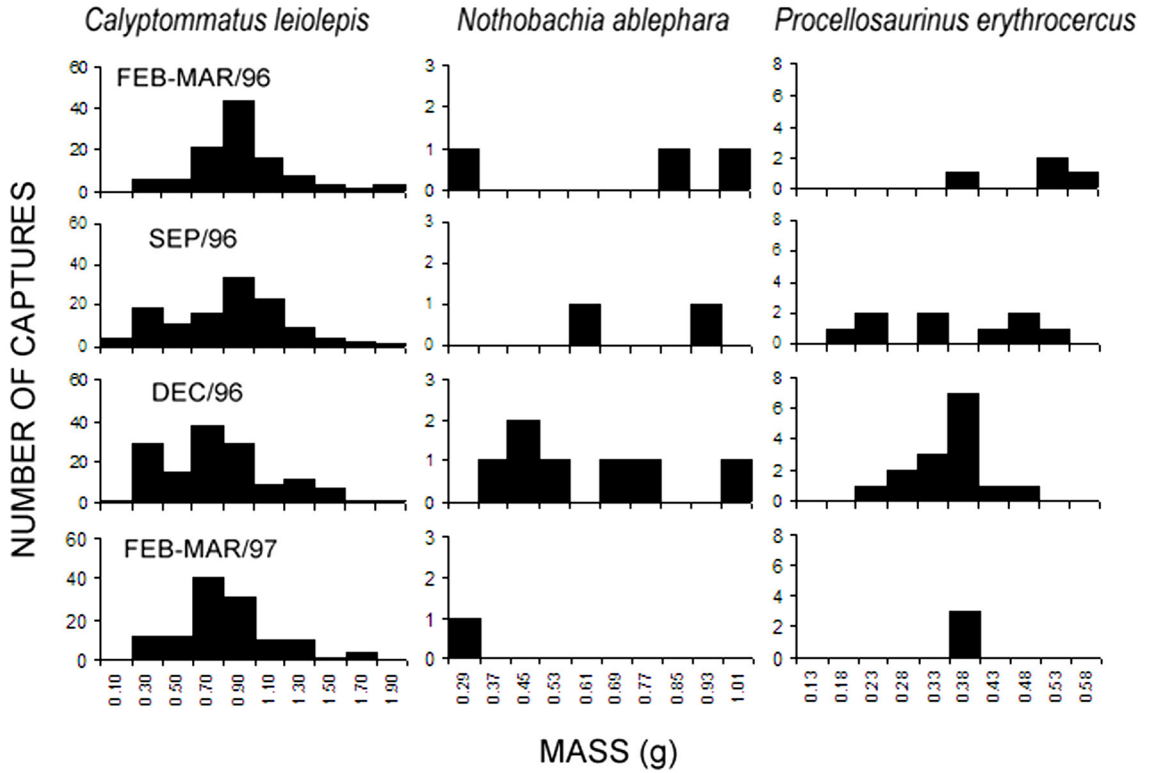


FIGURE 6. Distributions of sizes in gymnophthalmid (based on mass) in four field campaigns conducted in the dunes of Ibiraba, State of Bahia, Brazil.

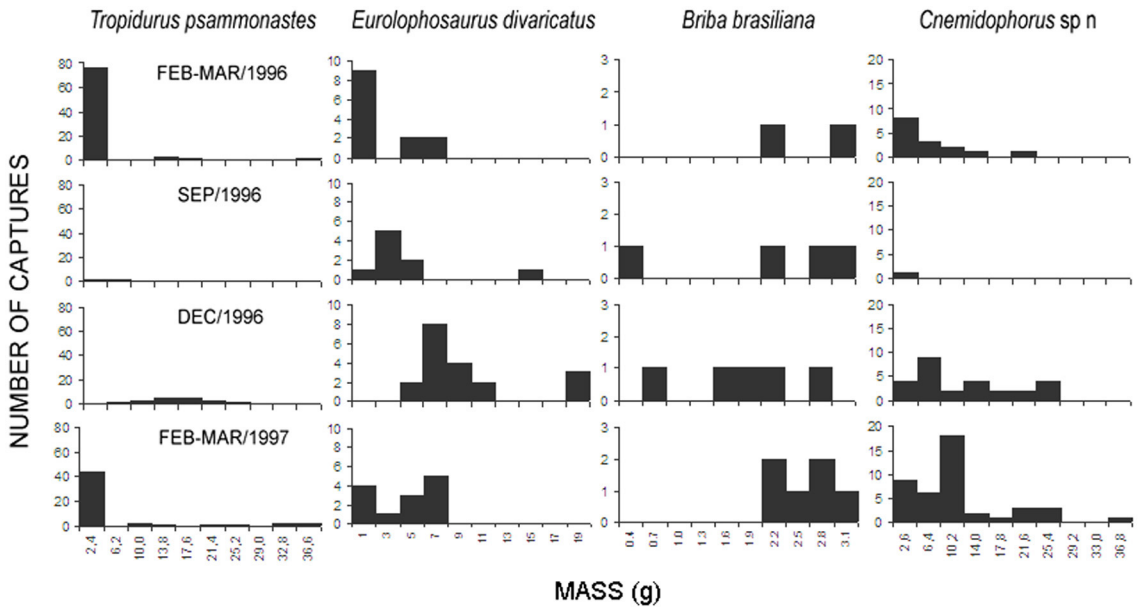


FIGURE 7. Distributions of sizes of *Tropidurus psammonastes*, *Eurolophosaurus divaricatus*, *Briba brasiliana* and *Cnemidophorus* spec. nov. based on mass in four field campaigns conducted in the dunes of Ibiraba, State of Bahia, Brazil.

TABLE 2. Results of the analysis of preferential phase of activity for the seven most abundant lizard species in Ibiraba in the State of Bahia, Brazil. Significance level adjusted for seven tests by the Bonferroni method = 0.007. The symbol (*) indicates significant results.

Species	Captures			Goodness-of-fit test (theoretical proportion: 1:1) (traps x phases: 11,226)	
	Night (%)	Day (%)	Total number	χ^2	Probability
<i>Briba brasiliiana</i>	94	6	16	10,539	< .005 *
<i>Calyptommatius leiolepis</i>	96	4	496	430,461	<< .001 *
<i>Cnemidophorus ocellifer</i>	13	87	87	47,195	<< .001 *
<i>Notobachia ablephara</i>	0	100	8	6,137	< .0025 *
<i>Procellosaurinus erythrocerus</i>	9	91	34	21,489	<< .001 *
<i>Eurolophosaurus divaricatus</i>	13	87	55	29,162	<< .001 *
<i>Tropidurus psammonastes</i>	37	63	160	10,579	< .005 *

Microhabitat

The PCA analysis of the microhabitat variables based on total data obtained in all campaigns extracted two components that explain approximately 50% of the original variance. The first component (first environmental gradient) shows the positive correlation between valley areas, amount of coverage by *Bromelia antiacantha* and by *Tacinga inamoena*. The second component (second environmental gradient) shows a negative correlation between coverage of trees plus shrubs, coverage with litter, summit areas, and subshrub coverage. Figure 8 shows the availability of each microhabitat variable and its use by each lizard species, as well as indicating significant and marginally significant electivities. We were unable to detect any microhabitat electivity for the fossorial gymnophthalmids *C. leiolepis* and *N. ablephara*. On the other hand, the gymnophthalmid *P. erythrocerus*, which dwells above ground, showed significant positive electivities for litter and *Bromelia antiacantha*. The gekkonid *B. brasiliiana* showed a marginally significant positive electivity for *Bromelia antiacantha*. The tropidurid *E. divaricatus* showed marginally significant negative electivity for valley areas, litter and *Bromelia antiacantha*. However, the tropidurid *T. psammonastes* showed significant positive electivities for valley areas, projection of trees and trees plus shrubs, marginally significant positive electivities for litter and shrubs, and marginally significant negative electivity for subshrubs. Finally, the teiid *Cnemidophorus* spec. nov. showed significant negative electivity for valley areas and litter, significant positive electivity for summit areas, marginally significant negative electivity for trees, trees plus shrubs, and *Bromelia antiacantha*, and marginally significant positive electivity for shrubs. Figure 9 synthesizes the results of PCA and electivity analyses and shows that fossorial gymnophthalmids use the environmental gradients

indiscriminately. The other species can be divided into two groups that use the environmental gradients in complementary ways. *P. erythrocerus*, *B. brasiliiana*, and *T. psammonastes* prefer (or are better able to use) microhabitats presenting high values of one or both environmental gradients and *E. divaricatus* and *Cnemidophorus* spec. nov. prefer (or are better able to use) microhabitats presenting low values of both gradients.

Diet

We analyzed the stomach contents of 384 lizards and recorded 3102 food items (a total of 30.7 g of material) distributed across 97 primary categories, which were grouped into 29 broader classes. In order to estimate food availability, the total consumption (C_{tot}) by the lizard assemblage (857 captured lizards) was calculated, resulting in 6924 food items. In the pitfall traps, we also captured 9,115 invertebrates distributed across 27 classes. Figure 10 shows the frequencies of food items based on both methodologies. The general patterns determined by both methodologies are quite similar. However, the availability of low-mobility items such as termites, homopterans, arthropod eggs, insect larvae, snails, flowers and other plant tissues was better sampled by lizard diets than by pitfall trapping. On the other hand, the estimated values of some food categories, such as Diplopoda, Hymenoptera (except Formicidae), Scorpiones, Chilopoda, Phasmida, and Mantodea, were one order of magnitude higher in pitfall trap results than in stomach content analysis. This indicates that, among the lizards captured, overall consumption of such items was low.

The percentages of frequency, wet mass, and recurrence per species and the related important food categories are presented in Table 3. The comparison between food availability and food consumption per

species and the determination of high electivities are presented in Fig. 11. Tropicidurids were the only species showing no negative electivity for ants. In fact, *T. psammonastes* presented positive electivity for ants, which were also its only important food category. The

other tropidurid, *E. divaricatus*, presented high positive electivity for flowers, which were also its only important food item. The teiid *Cnemidophorus* spec. nov. and the nocturnal gymnophthalmid *C. leiolepis* presented high electivity for insect larvae, which were also their

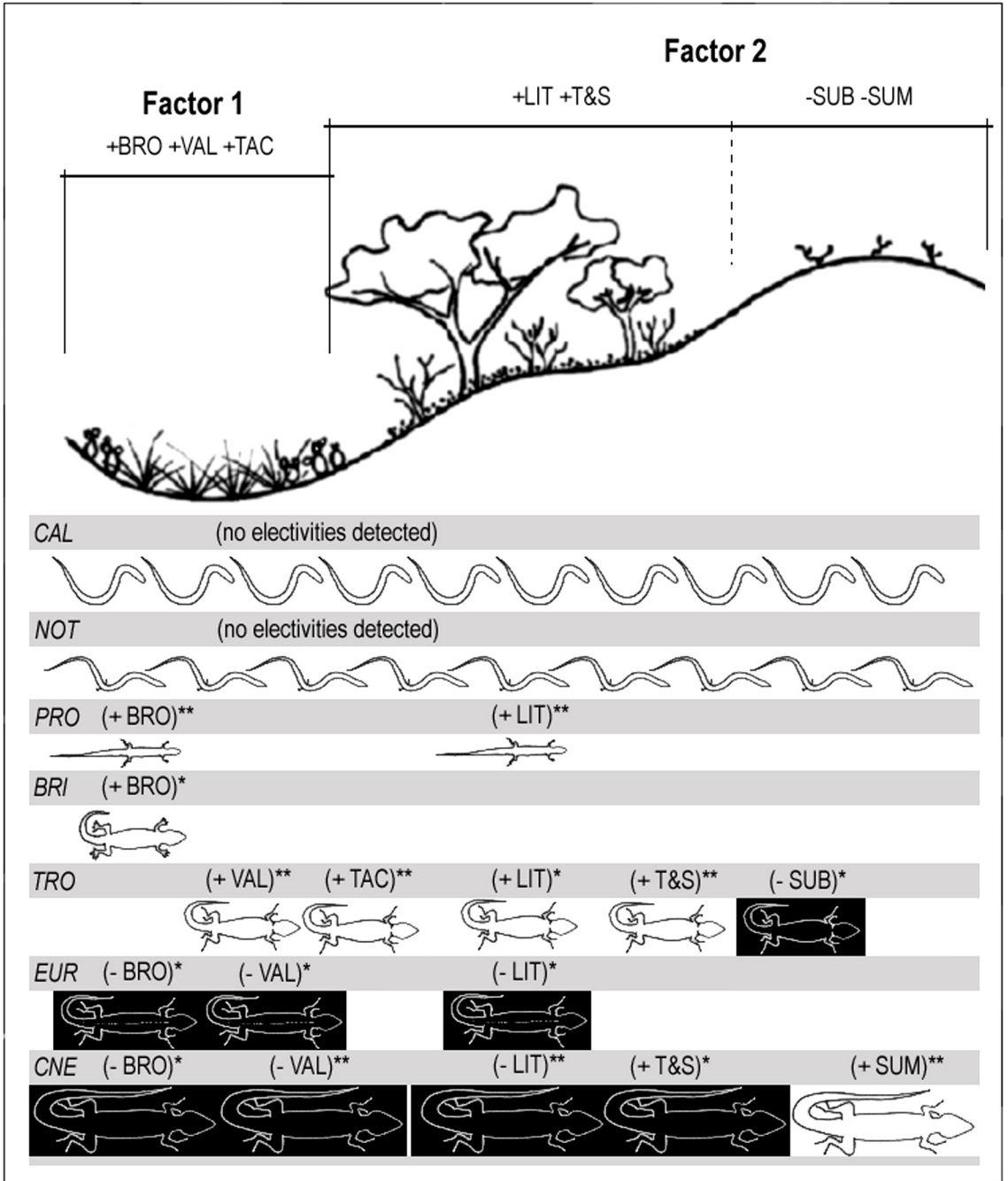


FIGURE 9. Synthesis of the ordination analysis of microhabitat variables and microhabitat electivity among the seven most abundant lizard species endemic to the Ibiraba dunes, State of Bahia, Brazil. Profile of the dunes (top) represents the variables highly correlated in factor 1 and 2. Identical symbols represent positive correlation. Lizard drawings (below) represent significant (**) and marginally significant (*) positive electivity (white), and negative electivity (black) of each species for microhabitat variables.

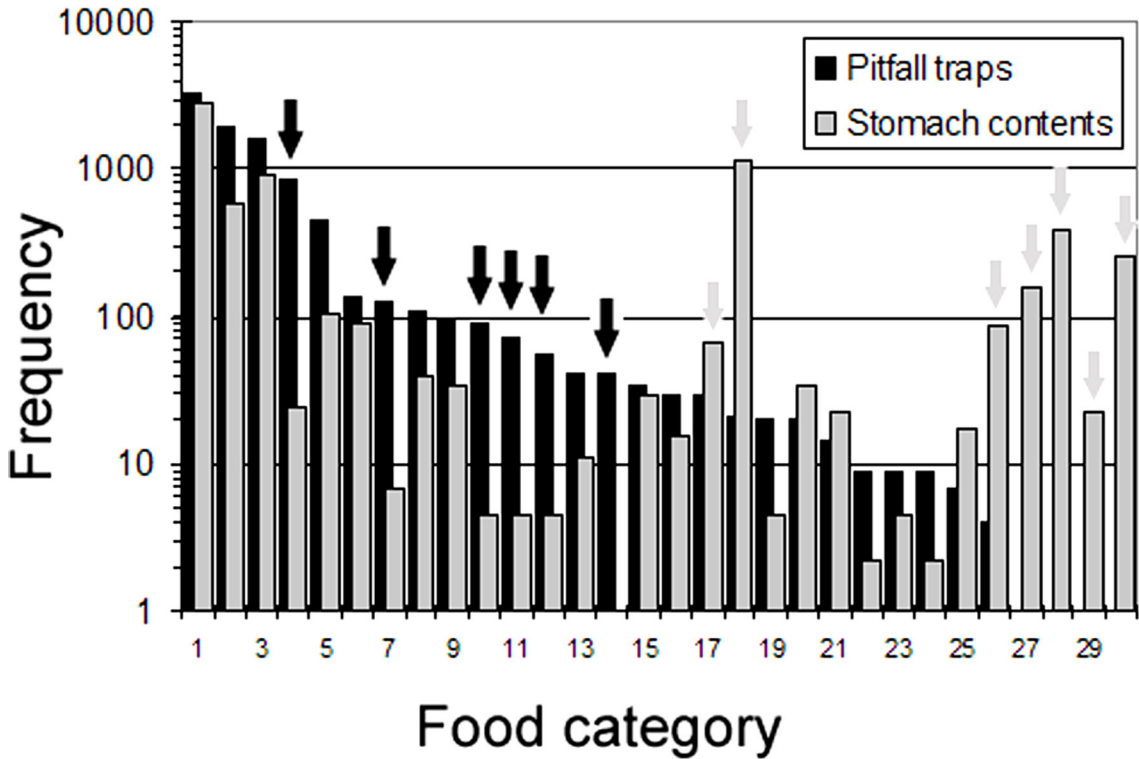


FIGURE 10. Frequency of food items available in the dunes of Ibiraba, State of Bahia, Brazil, estimated by captures in pitfall traps (black bars) and by total consumption by the lizard assemblage (gray bars). Black arrows indicate food categories of low consumption by the assemblage and gray arrows show food categories better estimated by lizard consumption. Food categories: 1 = Formicidae; 2 = Araneae; 3 = Coleoptera; 4 = Diplopoda; 5 = Thysanura; 6 = Ensifera; 7 = Hymenoptera (except Formicidae); 8 = Solifugae; 9 = Acari; 10 = Scorpiones; 11 = Chilopoda; 12 = Phasmida; 13 = Blattaria; 14 = Mantodea; 15 = Diptera; 16 = Hemiptera; 17 = Homoptera; 18 = Insect larvae and pupae; 20 = Pseudoscorpiones; 21 = Lepidoptera; 22 = Caelifera; 23 = Collembola; 24 = Neuroptera; 25 = Embioptera; 26 = Isoptera; 27 = Arthropod eggs; 28 = Flowers; 29 = Gastropoda; 30 = Plant matter (except flowers).

only important food item. In contrast, the gekkonid *B. brasiliiana* presented high electivity for arthropod eggs, but its important food items were insect larvae and crickets. Although very small larvae (mass < 0.01 g) constituted from 67 to 95% of the larvae consumed by these three species, 95% of the mass of larvae ingested by the teiid lizard consisted of larvae heavier than 0.01 g. However, 95% of the mass of larvae ingested by the gymnophthalmid and 33% of that ingested by the gekkonid consisted of larvae smaller than 0.01 g (Fig. 12). *P. erythrocerus*, which dwells above ground, did not present high positive electivity for any food item and consumed mainly spiders and crickets. Finally, the gymnophthalmid *N. ablephara* presented high positive electivities for spiders (its important food item), insect larvae and pseudoscorpions.

Dunn's test of the mass of the heaviest item per stomach detected three homogeneous species groups: *Cnemidophorus* spec. nov. + *E. divaricatus*, which ingested

the heaviest items; *T. psammonastes* + *B. basiliiana* + *P. erythrocerus* + *C. leiolepis* + *N. ablephara*, which ingested the lightest items; and *E. divaricatus* + *T. psammonastes*, intermediate to the first two groups (Figs. 13 and 14). Based on total diet, the comparisons among *C. leiolepis*, *N. ablephara*, *B. brasiliiana*, and *Cnemidophorus* spec. nov. presented the highest values of the symmetric coefficient of the niche overlap ($\phi \geq 0.7$). The lowest values ($\phi \leq 0.3$) were found between *E. divaricatus* and all other species except *T. psammonastes* ($\phi = 0.6$), and between *P. erythrocerus* and all other species except *N. ablephara* ($\phi = 0.4$) and *B. brasiliiana* ($\phi = 0.6$). Intermediate values ($0.4 \leq \phi \leq 0.6$) were found between *T. psammonastes* and all other species except *P. erythrocerus* (Fig. 13). We found significant correlations between JL and logarithm of MH ($\log MH$) and between HW and logarithm of MH ($r^2 = 0.666$, $P < 0.001$ and $r^2 = 0.679$, $P < 0.001$, respectively; Fig. 14).

TABLE 3. Results of the analysis of stomach contents of the seven most abundant lizard species from Ibiraba in the state of Bahia, Brazil. Darker cells represent important items based on criteria defined in text. F% = percentage of frequency (absolute total represents individuals); M% = percentage of mass (absolute total represents grams); R% = percentage of recurrence frequency (absolute total represents stomachs analyzed).

Food Category	Species																						
	<i>B. brasiliiana</i>		<i>T. psammunastes</i>		<i>E. dinariatus</i>		<i>Cnemidoph. spec. nov.</i>		<i>C. teioides</i>		<i>N. abelphara</i>		<i>P. erythrocerus</i>										
	F%	R%	F%	M%	R%	F%	M%	R%	F%	M%	R%	F%	M%	R%									
Collembola	-	-	-	-	-	-	0.2	0.1	2.4	-	-	-	-	-	-								
Thysanura	9.5	10.2	12.5	1.0	1.0	6.8	0.5	0.2	8.7	1.7	0.3	16.9	-	-	20.0	17.8	20.6						
Embioptera	-	-	-	0.1	0.1	2.7	0.9	0.2	15.2	-	-	-	-	-	-	-	-						
Phasmida	-	-	-	-	-	-	0.3	0.1	4.3	-	-	-	-	-	-	-	-						
Ensifera	9.5	16.9	12.5	0.5	1.9	8.1	0.4	0.3	6.5	2.2	4.1	28.9	-	-	16.0	18.9	26.5						
Caelifera	-	-	-	-	-	-	-	-	-	0.1	0.6	1.2	-	-	-	-	-						
Blattaria	-	-	-	0.1	1.1	1.4	0.1	0.1	2.2	0.2	0.6	3.6	-	-	-	1.3	1.1	2.9					
Isoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
Hemiptera	-	-	-	0.2	0.1	4.1	0.3	0.0	4.3	0.1	0.2	2.4	-	-	-	1.3	1.1	2.9					
Homoptera	-	-	-	0.3	0.2	5.4	0.5	0.1	6.5	1.6	0.3	20.5	2.1	1.2	4.1	5.3	4.4	11.8					
Neuroptera	-	-	-	-	-	-	-	-	-	0.1	0.0	1.2	-	-	-	-	-						
Coleoptera	4.8	1.7	6.3	10.3	10.3	62.2	12.6	6.6	71.7	22.4	25.6	88.0	5.4	3.7	10.6	-	-						
Diptera	-	-	-	0.6	0.5	8.1	0.4	0.5	6.5	0.2	0.0	2.4	-	-	-	1.3	1.1	2.9					
Lepidoptera	4.8	8.5	6.3	0.2	1.0	4.1	0.3	0.5	4.3	0.2	0.0	4.8	0.4	0.3	0.8	-	2.7	2.2	5.9				
Hymenoptera (other)	-	-	-	-	-	-	0.4	0.4	6.5	-	-	-	-	-	-	-	-						
Formicidae	-	-	-	76.9	30.9	82.4	39.8	5.2	73.9	3.9	3.2	27.7	1.7	0.9	3.3	-	-						
Insect larvae	14.3	44.1	18.8	3.9	23.0	25.7	4.6	11.1	34.8	34.8	38.4	96.4	64.7	78.2	60.2	40.0	42.9	25.0					
Arthropod eggs	47.6	8.5	6.3	0.2	0.0	1.4	-	-	-	5.7	0.4	22.9	4.1	1.8	4.9	-	-	4.0	1.1	2.9			
Diplopoda	-	-	-	0.3	5.4	5.4	-	-	-	0.7	0.7	10.8	-	-	-	-	-	1.3	1.1	2.9			
Chilopoda	-	-	-	-	-	-	-	-	-	0.1	0.4	1.2	0.4	3.1	0.8	-	-	-	-				
Araneae	4.8	8.5	6.3	2.5	4.9	32.4	2.2	2.0	26.1	22.5	20.9	96.4	4.1	5.5	8.1	40.0	50.0	37.5	26.7	21.1	47.1		
Acari	4.8	1.7	6.3	0.9	0.0	1.4	-	-	-	0.4	0.0	6.0	-	-	-	-	-	-	-	-	-		
Scorpiones	-	-	-	0.3	0.1	4.1	0.5	0.1	8.7	0.5	0.0	3.6	-	-	-	-	-	-	-	-	-		
Pseudoscorpiones	-	-	-	-	-	-	-	-	-	0.2	1.0	2.4	-	-	-	-	-	-	-	-	-		
Opiliones	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Solifugae	-	-	-	0.1	0.0	1.4	0.7	0.2	8.7	0.9	0.7	8.4	-	-	-	20.0	7.1	25.0	1.3	1.1	2.9		
Gastropoda	-	-	-	0.1	0.0	1.4	-	-	-	0.5	0.1	8.4	-	-	-	-	-	-	-	6.7	18.9	14.7	
Flowers	-	-	-	1.1	18.1	8.1	21.7	57.4	65.2	-	-	-	-	-	-	-	-	-	-	-	-	-	
Plant tissue (other)	-	-	-	0.5	1.4	4.1	13.8	15.0	32.6	0.4	2.2	3.6	1.2	0.3	0.8	-	-	-	-	1.3	1.1	2.9	
Total (%)	100	100	-	100	100	-	100	100	-	100	100	-	100	100	-	100	100	-	100	100	-	100	100
Total (absolute)	21	0.12	16	1212	7.47	74	739	8.32	46	804	13.93	83	241	0.65	123	10	0.03	5	75	0.18	28	75	0.18

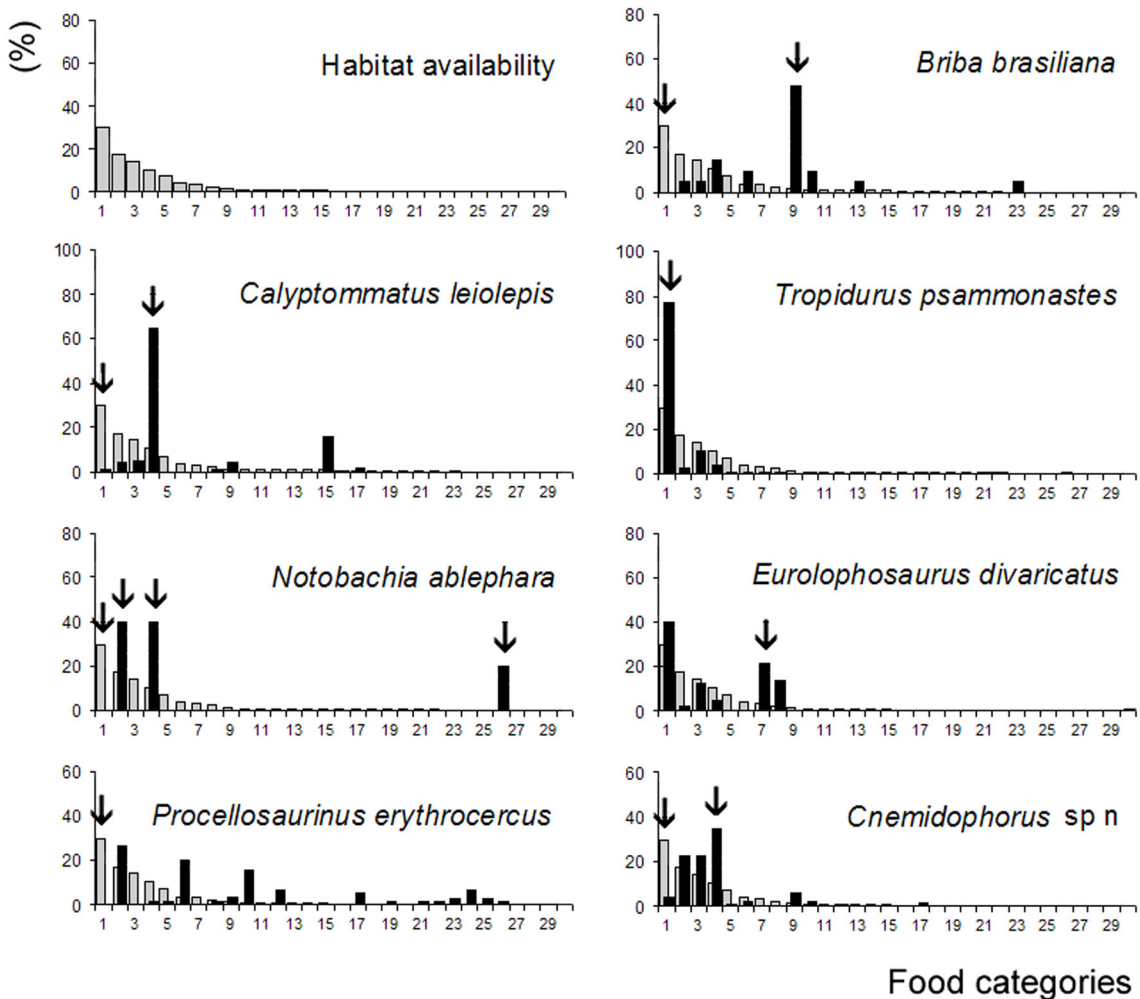


FIGURE 11. Frequency-based comparison among relative food item availability (gray bars) in the Ibiraba dunes, State of Bahia, Brazil, and relative food consumption by the seven most abundant dune-dwelling lizard species (black bars). Black arrows show food categories for which lizards showed electivity (positive or negative) following criteria defined in the text. Food categories: 1 = Formicidae; 2 = Araneae; 3 = Coleoptera; 4 = Insect larvae; 5 = Diplopoda; 6 = Thysanura; 7 = Flowers; 8 = Plant tissues (except flowers); 9 = Arthropod eggs; 10 = Ensifera; 11 = Hymenoptera (except Formicidae); 12 = Solifugae; 13 = Acari; 14 = Scorpiones; 15 = Isoptera; 16 = Chilopoda; 17 = Homoptera; 18 = Phasmida; 19 = Blattaria; 20 = Mantodea; 21 = Diptera; 22 = Hemiptera; 23 = Lepidoptera; 24 = Gastropoda; 25 = Opiliones; 26 = Pseudoscorpiones; 27 = Caelifera; 28 = Collembola; 29 = Neuroptera; 30 = Embioptera.

Synthesis

In synthesis, we found three patterns of microhabitat use by lizards: positive electivity for shaded and protected areas (the medium-sized *T. psammonastes* and *B. brasiliana*, and the small *P. erythrocerus*), positive electivity for exposed areas (the medium-sized *Cnemidophorus* spec. nov.) or negative electivity for shaded and protected areas (the medium-sized *E. divaricatus*), and no microhabitat electivity (the small fossorial gymnophthalmids). As can be seen in Fig. 15, there were differences among the diets of the four

species extensively using exposed areas. *E. divaricatus* was the only species that fed mainly on flowers, and the items ingested by it and by *Cnemidophorus* spec. nov. (a medium-sized species) were heavier than those ingested by smaller species. In addition, the small fossorial gymnophthalmids differed in diet and phase of activity. Such differences were also seen among the five species extensively using protected areas. *T. psammonastes* was the only species that fed mainly on ants. *C. leiolepis* and *B. brasiliana* were nocturnal and ate mainly larvae, which were less prominent in the diet of *C. leiolepis*. *N. ablephara* and *P. erythrocerus* fed mainly

on spiders, and *B. brasiliiana* and *P. erythrocerchus* also ate a considerable number of crickets.

DISCUSSION

Our study aimed to describe the pattern of resource use by the seven most abundant lizard species inhabiting the dune fields of the west bank of the São Francisco River: *Tropidurus psammonastes* and

Eurolophosaurus divaricatus (Tropiduridae), *Briba brasiliiana* (Gekkonidae), *Cnemidophorus* spec. nov. (Teiidae), and *Procellosaurinus erythrocerchus*, *Notobachia ablephara*, and *Calyptommatus leiolepis* (Gymnophthalmid). We found major differences in microhabitat. For species using similarly microhabitat resources, we found major differences in diet attributes (kind or size of food items) and, in some cases, phase of activity. As it is believed

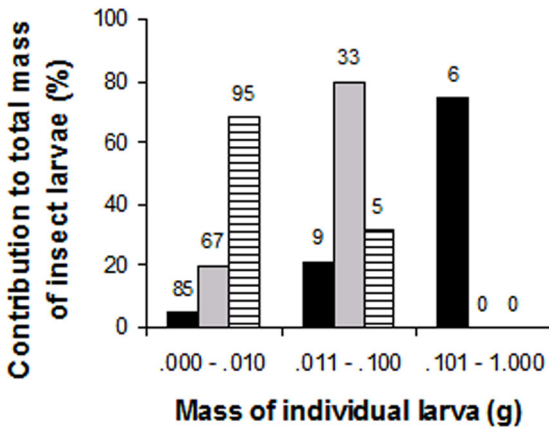


FIGURE 12. Relative contributions of very small, small, and medium-sized larvae to the total mass of larvae ingested by *Cnemidophorus* spec. nov. (CNE- black bars), *Briba brasiliiana* (BRI- gray bars) and *Calyptommatus leiolepis* (CAL- striped bars), the three lizard species endemic to the Ibiraba dunes, State of Bahia, Brazil for which larvae are the most important item in their diets.

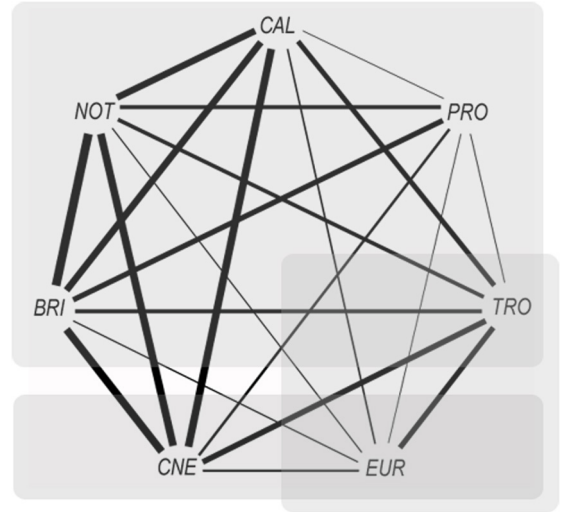


FIGURE 13. Comparison of food use among the seven most abundant lizard species in the Ibiraba dunes, State of Bahia, Brazil. The width of lines connecting each pair of species is proportional to the value of the symmetrical coefficient of the niche overlap (f). Gray areas circumscribe homogenous groups of species based on the mass of the heaviest item ingested.

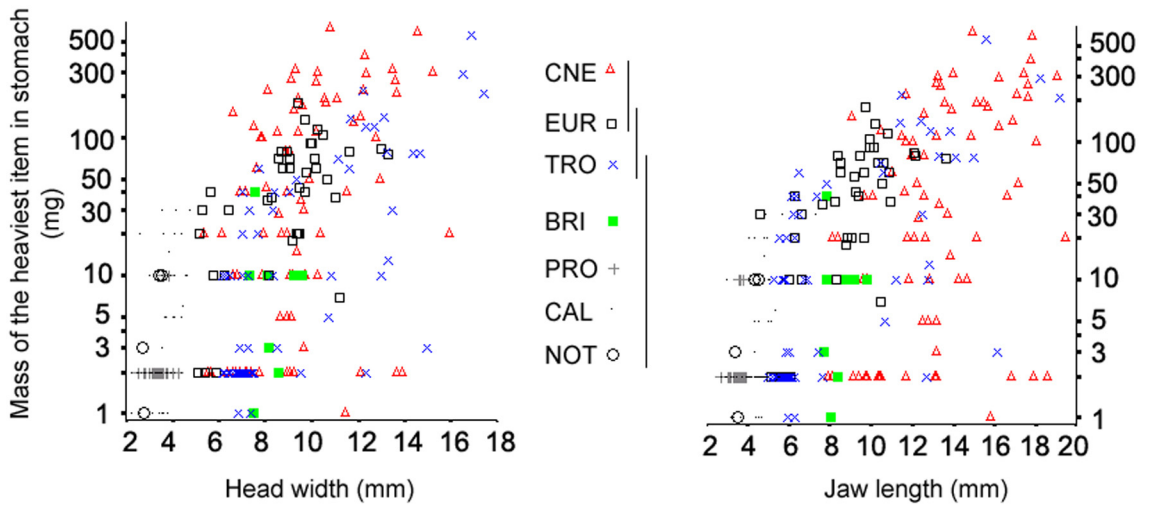


FIGURE 14. Scatterplot of the mass of the heaviest item (MH) in the stomach (in logarithm scale) versus head width (HW) (left) and jaw length (JL) (right) for the seven most abundant lizard species in the Ibiraba dunes, State of Bahia, Brazil. Vertical bars in the legend represent homogeneous groups of mass based on Dunn's multiple comparison test.

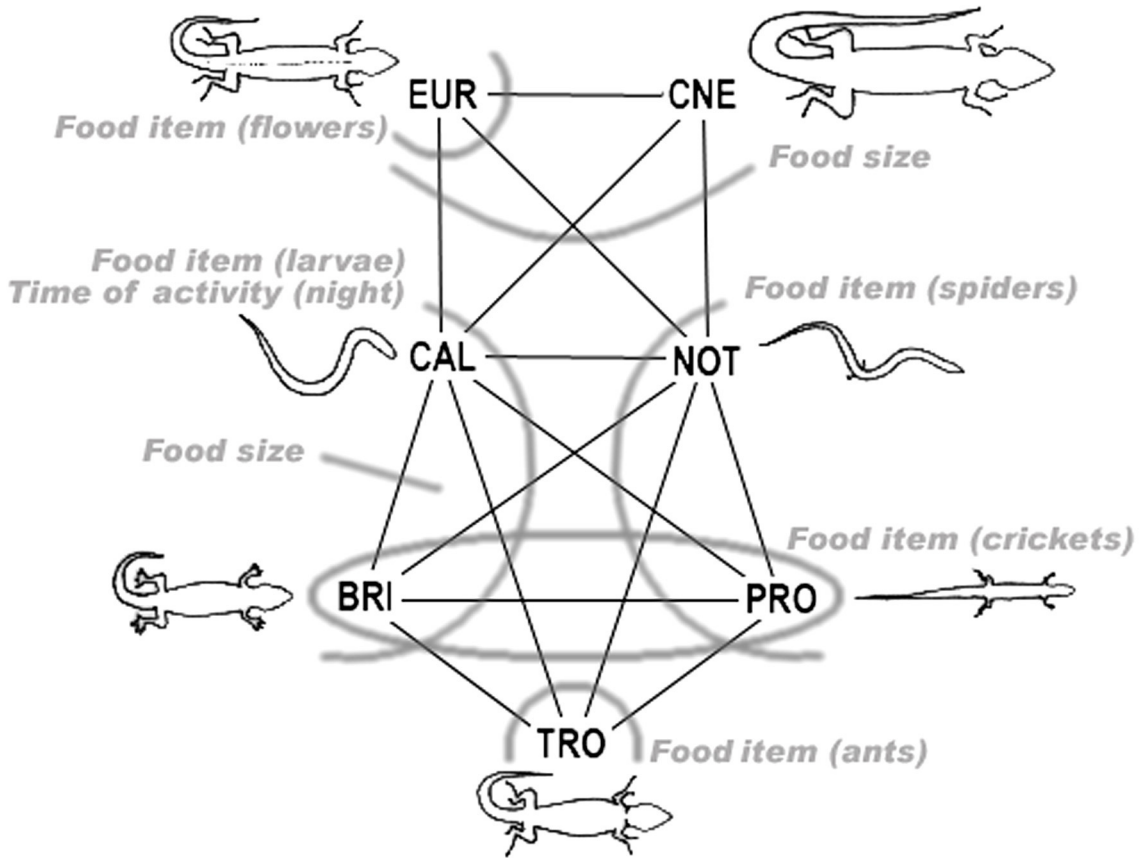


FIGURE 15. Synthesis of the differences in diet (food items and sizes) and phase of activity among the five lizard species extensively using protected microhabitat areas (lower pentagram) and among the four lizard species extensively using exposed microhabitat areas (or avoiding protected areas) (upper square). Black straight lines crossed by gray curved lines show differences in food consumption and phase of activity (indicated in gray letters) between pairs of species.

that coevolution between competing species leads to divergence in their pattern of resource use (Lawlor & Maynard-Smith, 1976), one of the processes underlying the patterns detected could be that of resource partitioning. On the other hand, differences in resource use among species within one assemblage could also be the result of plesiomorphic traits inherited from ancestor lineages. These traits could be expressed if: the assemblage has been composed recently; competition pressure has been weak or diffuse due, for example, to the assemblage being composed of species with wide geographic distribution (since the genetic flow among populations under different selective regimens may limit local genetic differentiation – Endler, 1977); or anagenesis is limited by structural or phylogenetic constraints (Gould, 2002). Therefore, geomorphological, biogeographical, anatomical, and phylogenetic data can bring insights to ecological analysis (e.g., lizards from Brazilian restinga – Araujo, 1991; snakes

from Brazilian Caatinga – Cadle & Greene, 1993; *Anolis* from Bimini Island – Williams, 1983).

With the exception of *B. brasiliensis*, all of the most abundant lizard species studied by us are psamphilic and endemic to the dunes on the west bank of the São Francisco River. In addition, the gymnophthalmids and *E. divaricatus* are included in clades whose evolution is closely related to the geomorphologic history of the dunes (Rodrigues, 1986, 1995, 1996). This pattern is quite different from that seen in the fauna of the Caatinga at large, which is widespread and lacks endemic reptile species (Rodrigues, 2003; Vanzolini, 1974, 1976; Vanzolini *et al.*, 1980). Only a few Caatinga-endemic species are typically found in areas of sandy soil, and our study area represents an exception to this rule (Rodrigues, 2003). Barreto (1996) employed thermoluminescence dating of sedimentary beds, carbon 14 dating and palynological data to study the geological history of the dunes (see also de Oliveira *et al.*, 1999).

He showed that the region in which the dunes are located has had an arid or semiarid climate associated with abundant sand supply, since at least 28,000 years before present (ybp). The author also demonstrated that floristic elements of the Caatinga have been present since at least 11,000 ybp, and that the contemporary pattern of climate and vegetation was established after 4,240 ybp, probably as a result of El Niño-like phenomena. These data suggest that the lizard species studied herein may have coexisted for several thousands of generations in a restricted arid to semiarid area with marked seasonal variation in climate, which is conducive to the evolution of resource partitioning.

Fossorial Lizards

The monophyletic clade containing the fossorial genera *Calyptommatus* and *Notobachia* is the crown group of the gymnophthalmid lineage containing also four legged, diurnal, aboveground dwellers *Procellosaurinus*, *Vanzosaura*, and *Psilophthalmus* (Pellegrino *et al.*, 2001). Among the species studied in the dunes, *N. ablephara* and *C. leiolepis* were the only species presenting no electivities for any of the microhabitat variables analyzed and, within this assemblage, were also the only fossorial lizards. Although *N. ablephara* was captured in small numbers, which could make the detection of electivities difficult, *C. leiolepis* was the most abundant species in the area. Therefore, if fossorial habit precludes electivities for aboveground microhabitat variables, the negative result for *N. ablephara* may be as accurate as that for *C. leiolepis*. Despite presenting similar patterns of microhabitat use and high diet overlap, the two species presented some differences in their diets. Although they had similar-sized feeding apparatuses and they fed on items of similar sizes, *C. leiolepis* fed mainly on larvae, whereas *N. ablephara* fed mainly on spiders. Moreover, they presented different food electivities (spiders, larvae, and pseudoscorpions by *N. ablephara* and larvae by *C. leiolepis*) and phases of activity (*N. ablephara* has retained the plesiomorphic diurnal activity and *C. leiolepis* has shifted to nocturnal habits, as one can infer by distribution of the states of this character in the phylogeny). The lack of an overlap in daily activity may be related to intensity of competition between predators in two fundamental ways: through reduction of direct encounters (minimizing competition created by interference) and through exposition of predators to different prey categories (minimizing competition created by resource exploitation).

Although we have no data on interspecies behavioral interactions, we can assume (since nocturnal activity is an autapomorphy of the genus *Calyptommatus*) that this lack of overlap would be derived from minimizing encounters with *Notobachia* only if the density of *Notobachia* were at least the same as that of *Calyptommatus*, since the rarest species of one competing pair should be more frequently involved in interspecific contacts and the most abundant one should be involved more frequently in intraspecific contacts (Pimentel, 1968). However, in the assemblage we studied, this was not the case. Our data also suggest that, for two different reasons, exposition of a predator to a variety of prey categories is not important. First, the main prey categories (larvae and spiders) ingested by the two species are the same. In fact, the majority of spiders consumed belong to a new species (genus *Leprolochus*) endemic to the dunes, which is the most abundant arachnid in the area (PLBR personal observation). This finding is in agreement with that of Huey & Pianka (1983), who concluded that temporal segregation is only occasionally followed by a reduction in diet overlap. Second, the phase of prey activity is apparently irrelevant to their detection and capture by these predators, given the high consumption of low-mobility items such as larvae and the supposed importance of chemical clues rather than visual clues in the foraging strategy of the lineage (Cooper, 1994). Therefore, regardless of the selective pressures that led to the shift in phase of activity of the genus *Calyptommatus*, there is no unequivocal evidence that this shift was responsible for the differences between *Calyptommatus* and *Notobachia* diets.

There are, however, indications that important changes in diet followed the adoption of the fossorial habit in this lineage gymnophthalmids. Figure 16 synthesizes available diet information for 12 populations of six species of this lineage based on analyses of 682 stomachs by Moraes (1993) and on data from the present study, using the phylogeny proposed by Benozzati & Rodrigues (2003) and Pellegrino *et al.*, (2001). We used values of recurrence frequency, which are comparable among studies. We considered a food category important to a population if it was ingested by at least 30% of the individuals. When no category was consumed by 30% of the individuals, the first two categories in the rank were designated as important. It seems clear that high consumption of spiders is plesiomorphic for the fossorial species and is retained by *N. ablephara*, and that consumption of larvae is an apomorphy of the fossorial clade and is strongly expressed in the nocturnal genus *Calyptommatus*.

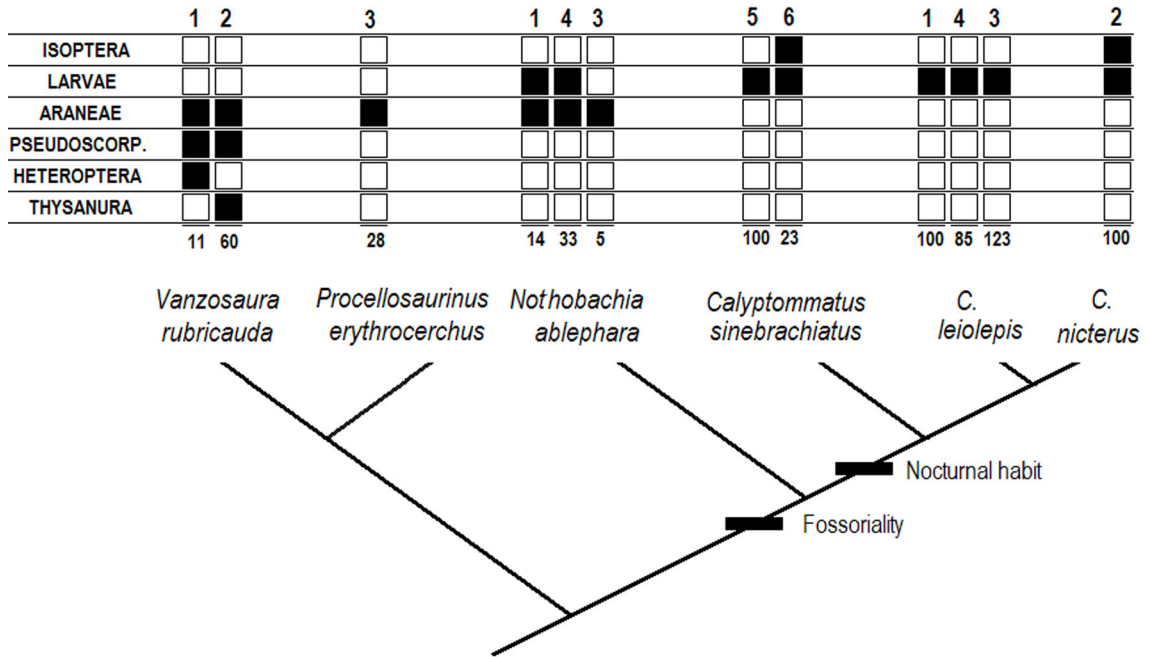


FIGURE 16. Synthesis of available information (Moraes, 1993; present study) on the diet of gymnophthalmids present in the sandy areas along the middle course of São Francisco River, mapped into the phylogeny presented by Pellegrino *et al.*, (2001). Numbers 1 to 6 across the top represent the locations studied (1 = Queimadas; 2 = Vacaria; 3 = Ibiraba; 4 = Alagoado; 5 = Santo Inácio; 6 = Lagoa de Itaparica; see map in Fig. 2). Black squares represent important items in the diet of each population studied, based on recurrence frequency. Numbers below squares represent the number of stomachs analyzed.

Epigeous lizards

Microhabitat variables in the dunes fall mainly into two orthogonal environmental gradients as revealed by PCA analysis. Both may be seen as gradients of protected areas for the small to medium-sized fauna. The first represents a gradient of spiny plant clusters (*Bromelia antiacantha* and *Tacinga inamoena*) associated with valleys. High values of this gradient represent greater protection against medium-sized predators. The second represents a gradient of shaded areas with litter. High values of this gradient represent greater protection against direct sun due to the presence of shelter, including many woody perches. Rocha *et al.*, (2004) observed a similar environmental structure in other land parcels in the Ibiraba dunes. Epigeous lizards use these gradients differently: one group (*P. erythrocerchus*, *B. brasiliiana*, *T. psammonastes*) presents positive electivity for protected areas, and the other group (*E. divaricatus* and *Cnemidophorus* spec. nov.) presents negative electivity for such areas.

The electivity of *P. erythrocerchus* for LIT areas may be comparable to the more frequent capture in this kind of microhabitat of specimens of other species of epigeous gymnophthalmids (*Vanzosaura rubricauda*,

Psilophthalmus paeminus, and *Procellosaurinus tetradactylus*) in sandy areas near the middle course of the São Francisco river (Moraes, 1993; Rodrigues, 1991b, c; Vanzolini *et al.*, 1980). Data presented in these studies were used to evaluate electivities, since availability was not quantified. However, if the findings of these studies do reflect electivities, then the electivity detected in our study must represent a plesiomorphic feature of the clade, as one can infer from mapping the states of this character in the phylogeny, and not an evolutionary response to ecological interactions within the assemblage. We did not detect electivities of *P. erythrocerchus* for any food category, since the most important item in its diet (spiders) was consumed in a ratio only slightly higher than the ratio available in the habitat. Nevertheless, spiders are one of the most common food items for other gymnophthalmids, as discussed above (Fig. 16). There is therefore no reason to assume that consumption of spiders by the dune species is a reflex of competitive interaction with other lizards in the assemblage.

The nocturnal gekkonid *B. brasiliiana* presented weak positive electivity for BRO areas and high positive electivity for arthropod eggs. However, as with the nocturnal *C. leiolepis* and the diurnal *Cnemidophorus* spec.

nov., larvae composed the bulk of the *B. brasiliana* diet, although most of the larvae it ingested were intermediate in size to those ingested by the other two species. The genus *Briba* is monotypic and virtually nothing is known about its biology. The phylogeny of the family is also not known. *B. brasiliana* is said to be nocturnal and arboreal (Vanzolini *et al.*, 1980) as are most members of the family, although the high frequency of captures in our pitfall traps indicates that it does travel on the ground and therefore might interact with terrestrial species of the assemblage. On the other hand, *B. brasiliana* is the only locally abundant lizard species that is not endemic to the dunes. *B. brasiliana* has a wide geographic distribution throughout the Brazilian Caatinga and Cerrado (Vanzolini *et al.*, 1980). Due to ecological interaction with other lizard species (arguments above), *B. brasiliana* is less prone to local specialization. Therefore, microhabitat electivity may mainly reflect selection of patches protected from predators. Similarly, consumption of larvae may mainly reflect larvae availability in the habitat and, in comparison to the other two species, differences in larvae size may mainly reflect the different size of the *B. brasiliana* feeding apparatus, which is intermediate between that of *C. leiolepis* and that of *Cnemidophorus* spec. nov.

The tropidurid *T. psammonastes* was the species presenting the highest positive electivity for protected areas. It was also the only species in the assemblage presenting high positive electivity for ants, which constituted the bulk of their diet. Lima & Rocha (unpublished data) verified that there is an ontogenetic shift in the diet of this species in the dunes of Ibiraba: small animals eat mainly ants and big animals eat mainly flowers and ants. They also suggested, based on the phylogeny of *Tropidurus* (Frost *et al.*, 2001) and on diet data present in the literature, that the ability to consume both plants and ants is plesiomorphic for the Tropidurinae. Vitt *et al.*, (2003) proposed that the historical determinant of myrmecophagy actually dates from at least the origin of Iguania and argued that it derives from their inability to utilize chemical clues to discriminate prey either possessing chemical defense systems or having high energy content. However, our habitat availability and lizard consumption data indicates that all species of Iguania, Gekkota, and Autarchoglossa in the assemblage avoided consumption of arthropod taxa, such as Hymenoptera (except Formicidae), Scorpiones, Chilopoda and Diplopoda, that possess chemical defenses (Cloudslay-Thompson, 1991, 1996; Crawford, 1981) or others, such as Phasmida and Mantodea, that are very cryptic. As a

result, estimates of availability of these items in the habitat based on pitfall trap captures were one order of magnitude higher than those based on assemblage consumption. Additionally, *T. psammonastes* not only ate ants but they ate them in considerably higher proportions than the proportion of their availability in the dunes, suggesting that the lizards choose them. Therefore, myrmecophagy could be better interpreted as a physiological specialization of Iguania to deal with formic acid present in one abundant food resource rather than a lack of sensorial specialization to detect and avoid formic acid in food items.

The other dune-dwelling Tropidurid, *E. divaricatus*, presented high electivity for flowers, their only important food item, and weak negative electivity for protected areas. However, unlike the non-Iguania species of the assemblage, it did not present negative electivity for ants. In fact, it consumed ants in proportions higher than their availability. As discussed above, it is likely that plant-consuming habits, as well as myrmecophagy, are plesiomorphic features of Tropidurinae. However, based on available data, phylogeny alone cannot explain the greatest importance of each food category for the dune-dwelling Tropidurinae species. Morphological differences between lizard species usually led to different foraging places, and microhabitat segregation is common in syntopic sit-and-wait lizards, as most Iguania (Moermond, 1979; Vitt & Carvalho, 1995; Williams, 1983). *T. psammonastes* adults are almost twice as heavy as *E. divaricatus* adults. However, the coincidence in reproductive season for both species and the apparent explosive pattern of reproduction in the first species, as well as the similarity of their diets during this ontogenetic phase, could potentially generate competitive interactions based on food gathering. Therefore, the differential use of microhabitat could be the result of ecological interaction – either evolutionary resource partitioning or contemporary microhabitat displacement of one species by the other based on competition.

The teiid *Cnemidophorus* spec. nov. was the species presenting the highest negative electivity for protected areas, a pattern that seems to be widespread in various Brazilian species of the genus. Mesquita & Colli (2003) compared several Brazilian species of *Cnemidophorus* and reviewed the ecological literature regarding the genus. Their study underscored the view that these lizards have a strong preference for open microhabitats and present high body temperatures. However, the species endemic to the dunes also presented negative electivity for valleys and for areas cov-

ered by *Bromelia antiacantha*. This finding cannot be fully explained by the general pattern for the genus, since, in the dunes, these microhabitat variables were correlated with a factor orthogonal to the one representing a gradient of shaded areas. Mesquita & Colli (2003) also found, within the genus, great interspecific and intraspecific differences in diet (that can include, as the most important item, termites, insect larvae, orthopterans, ants or beetles). The authors suggested that this could be the result of either differences in preference or differences in availability. The most important food item in the diets of the species endemic to the dunes was insect larvae, for which these lizards presented high positive electivity. Since the syntopic lizard *T. psammonastes* adults also ate a great deal of larvae and there is considerable overlap in the size of the heaviest items ingested by both *Cnemidophorus* spec. nov. and *T. psammonastes*, there is a potential for competitive interaction between them. We cannot discard the hypothesis that the differential use of microhabitat by both species results from ecological interaction, in the form of either evolutionary resource partitioning or contemporary microhabitat displacement through interference. Additionally, *Cnemidophorus* spec. nov. and *E. divaricatus* presented similar use of microhabitat variables and ingested similar-sized food items, but both species had less diet overlap with each other than they had with *T. psammonastes*, which used microhabitat variables differently. This pattern does not rule out the hypothesis that ecological interactions play (or have played) a role in the settlement of the contemporary patterns of resource use by these species.

CONCLUSIONS

1. Except for *Briba brasiliana*, the most abundant species of lizards inhabiting the dunes from Ibiraba are endemic from the dunes.
2. Individuals of the fossorial species *Calyptommatus leiolepis* and *Notobachia ablephara* use similarly the micro-habitat, but they differ in diet phase of activity, mainly due to apomorphic habits of the genus *Calyptommatus* (diet based on larvae and nocturnal activity). Differences can not be attributed to competition between these species.
3. Individuals of *Procellosaurinus erythrocerus* presents positive electivities for areas covered by litter, presents no electivities for food and is diurnal. None of these features seem to represent adaptations to the environmental conditions present in the dunes.
4. Individuals of *Briba brasiliana* presents positive electivities for areas covered by the terrestrial bromeliad *Bromelia antiacantha* and for arthropod eggs. It eats mainly medium-sized insect larvae and is nocturnal. Although it is said to be arboreal, it does travel on the ground. None of these features seem to represent adaptations to the dunes.
5. Individuals of *Tropidurus psammonastes* are diurnal, present strong positive electivities for protected areas and for ants and eats many insect larvae. Their ability to develop myrmecophagy can be interpreted as the retention of a plesiomorphic physiological specialization of Iguania.
6. Individuals of *Eurolophosaurus divaricatus* are diurnal, present negative electivities for protected areas and positive electivities for flowers, and eat many ants. Differences in resource electivities of *T. divaricatus* and *Eurolophosaurus divaricatus* can result from ecological interaction (evolutionary resource partitioning or contemporary competition) between both species.
7. Individuals of *Cnemidophorus* spec. nov. are diurnal and present high negative electivity for protected areas and larvae. Diet overlap between *Cnemidophorus* spec. nov. and *E. divaricatus* is smaller than overlap of each species with *T. psammonastes*, but their use of micro-habitat is more similar. This pattern can not be fully explained by retention of plesiomorphic characters by *Cnemidophorus* spec. nov. and it can result from ecologic interaction with syntopic medium sized lizards from the dunes.

RESUMO

Este estudo descreve o padrão de uso de recursos por uma assembléia de lagartos de um campo de dunas da Caatinga. Avaliamos a disponibilidade de recursos e as fases de atividade dos lagartos, bem como seu uso e suas eletividades por alimento e micro-habitats. Seis das sete espécies mais abundantes são endêmicas das dunas, e suas dietas sub-representaram artrópodes com defesas químicas. Os dois gimnoftalmídeos fossórios mostraram-se semelhantes por não apresentar eletividades por micro-habitats, mas diferiram quanto à dieta, às eletividades por alimentos e à fase de atividade. As cinco espécies de lagartos epígeos incluem um grupo com eletividade positiva por micro-habitats protegidos e sombreados (Procellosaurinus erythrocerus, Briba brasiliana e Tropidurus psammonastes) e outro com eletividades negativas pelos mesmos (Eurolophosaurus divaricatus e Cnemidophorus spec. nov.). O tropidurídeo T. psammonastes apresentou atividade mais precocemente pela manhã, as eletividades positivas mais

fortes por áreas protegidas e sombreadas e eletividades negativas por áreas expostas, sendo a única espécie com eletividade positiva alta por formigas. O outro tropidurídeo da área, *E. divaricatus*, também alimentou-se de formigas mas apresentou eletividade positiva por flores. O teídeo de médio porte *Cnemidophorus spec. nov.* apresentou as maiores eletividades negativas por áreas sombreadas e a maior eletividade positiva por áreas abertas, bem como uma alta eletividade negativa por áreas protegidas. Assim, seu padrão de uso de micro-habitat é similar ao de *E. divaricatus*, que possui uma dieta muito distinta, e diferente do padrão de *T. psammonastes*, cuja dieta é semelhante (larvas de insetos e itens de maior tamanho). Discutimos a evolução dos padrões detectados de eletividades por recursos.

PALAVRAS-CHAVE: Caatinga; Dieta; Dunas; Eletividade; Microhabitat; Fase de atividade; Lagartos.

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