

Feeding ecology of *Tropidurus torquatus* (Wied) (Squamata, Tropiduridae) in two areas with different degrees of conservation in Marambaia Island, Rio de Janeiro, Southeastern Brazil

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ABSTRACT. We compared the effects of habitat disturbance on the feeding ecology of two local populations of *Tropidurus torquatus* (Wied, 1820) in restinga habitats on Ilha da Marambaia, Southeastern Brazil. Both populations presented a relatively diverse diet and differ in the number ($D_{Max} = 0.22$, $DF = 2$, $p = 0.00$) and volume of prey consumed ($D_{Max} = 0.82$, $DF = 2$, $p = 0.00$). Ants were the most frequent and numerous preys in both areas, and plant matter and coleopterans were the most important alimentary items in volume. The population from the disturbed area presented a larger niche breadth for number of prey items consumed ($Bi_{num} = 3.06$) and volume ($Bi_{vol} = 2.98$), when compared to the other population ($Bj_{num} = 2.44$, $Bj_{vol} = 1.52$). Niche overlap was higher for number of items consumed between the populations ($Oij_{num} = 0.82$) but lower for volume ($Oij_{vol} = 0.05$). Our data suggest dietary differences between the two lizard populations, and these differences may be associated with environmental modifications. Our main hypothesis to explain the dietary differences is based in the Optimal Foraging Theory. However, the alimentary behavior, and consequently the diet of these lizards, seems to be constrained phylogenetically, with a pattern that may have evolved in the ancestor of all iguanids.

KEY WORDS. Diet; lizards; Optimal Foraging Theory.

RESUMO. **Ecologia Alimentar de *Tropidurus torquatus* (Wied) (Sauria, Tropiduridae) em Duas Áreas com Diferentes Níveis de Conservação na Ilha da Marambaia, Rio de Janeiro, Sudeste do Brasil.** Comparamos os efeitos da degradação ambiental sobre a ecologia alimentar de duas populações de *Tropidurus torquatus* (Wied, 1820) em áreas de restinga da Ilha da Marambaia, sudeste do Brasil. Ambas as populações apresentaram dieta relativamente diversa e diferiram em número ($D_{Max} = 0,22$; $DF = 2$; $p = 0,00$) e volume de presas consumidas ($D_{Max} = 0,82$; $DF = 2$; $p = 0,00$). Formigas foram os itens mais freqüentes e numerosos em ambas as áreas, e material vegetal e coleópteros os mais importantes em volume. A população da área perturbada apresentou maior largura de nicho alimentar para número de presas consumidas ($Bi_{num} = 3,06$) e volume ($Bi_{vol} = 2,98$), quando comparada à outra população ($Bj_{num} = 2,44$; $Bj_{vol} = 1,52$). A sobreposição de nicho foi mais marcante para o número de itens consumidos entre as populações ($Oij_{num} = 0,82$) e menos marcante para volume ($Oij_{vol} = 0,05$). Nossos dados sugerem diferenças nas dietas entre as duas populações de lagartos, e estas diferenças parecem estar associadas à degradação ambiental. Nossa principal hipótese para explicar as diferenças nas dietas embasa-se na Teoria do Forrageamento Ótimo. Entretanto, o comportamento alimentar, e conseqüentemente a dieta dos lagartos, mostraram-se limitadas filogeneticamente, com um padrão que pode ter evoluído no ancestral de todos os iguanídeos.

PALAVRAS-CHAVE. Dieta; lagartos; Teoria do Forrageamento Ótimo.

The diet of any species is related to aspects of the local ecology of its populations as well as the evolutionary history of the taxon. Lizards present alimentary patterns well defined and constrained by their phylogeny (VITT *et al.* 2003, VITT & PIANKA 2005). Two widely recognized main feeding strategies define these patterns: "widely" versus "sit-and-wait foragers"

(HUEY & PIANKA 1981). Examples of the first strategy are lizards of the genus *Ameiva* Meyer, 1795 and *Cnemidophorus* Wagler, 1830, which seek food by actively probing the leaf litter with their tongue (ARAUJO 1991, ZALUAR & ROCHA 2000, ROCHA *et al.* 2000). The Tropidurid genus *Tropidurus* Wied-Neuwied, 1825 is a good example of the sit-and-wait strategy. This speciose

genus of open formations dwellers found in tropical and subtropical South America, including the Galapagos Islands (RODRIGUES 1987, LOPES *et al.* 1992, FROST *et al.* 2001), presents several adaptations related to this strategy, such as cryptical coloration, robust body, territorial behavior, and diet based on mobile prey (RAND & RAND 1966, RODRIGUES 1987, BERGALO & ROCHA 1994). In Brazil, *Tropidurus* is present in the Amazon, Cerrado, Caatinga and Atlantic Forest, including the coastal Restingas (RODRIGUES 1987, ROCHA 2000).

Tropidurus torquatus (Wied, 1820) is the most widely distributed lizard in the genus, occurring from Southeastern Brazil to the north of Argentina (RODRIGUES 1987). Its diet is based on highly vagile arthropods, primarily ants, and vegetal matter, especially fruits (ARAÚJO 1991, ROCHA & BERGALO 1994, FIALHO *et al.* 2000). Several aspects of its diet, foraging mode, and behavioral ecology were studied (RAND & RAND 1966, BERGALO & ROCHA 1994, TEIXEIRA & GIOVANELLI 1999, ROCHA *et al.* 2000). However, the effects of environmental modifications to its feeding ecology have not been considered yet.

Changes in the environmental conditions can affect prey offer, patterns of diet, and costs of foraging. According to the Optimal Foraging Theory (MACARTHUR & PIANKA 1966), lizards from species-rich feeding areas would present narrower food niche breadth, while lizards from areas with less dense and less nutritive prey would present larger alimentary niche breadth in order to compensate for the low quality of the prey (MACARTHUR & PIANKA 1966, SCHOENER 1971). Consequently, lizards living in a stressed environment would reduce their spatial niche to use only the best patches (MACARTHUR & PIANKA 1966). Therein, we tested this assumption by comparing the effects of habitat disturbance on the feeding ecology of two local populations of *Tropidurus torquatus* that occur in restinga habitats on Ilha da Marambaia, Rio de Janeiro, Southeastern Brazil, one preserved, and the other disturbed.

MATERIAL AND METHODS

This work was developed on Ilha da Marambaia, located in Rio de Janeiro, Southeastern Brazil (23°04'S, 43°53'W). Marambaia presents a marked spatial heterogeneity, including rain forests on the hills (Atlantic Forest), restinga (long sand bars connecting the hills to the continent, covered with open vegetation), and mangrove (MENEZES & ARAUJO 2005). Two sites in the restinga habitat with different degrees of conservation were chosen for sampling the lizards (Fig. 1). The first, called Bravo-meia (23°04'16.36"S, 43°56'43.43"W) presents a well-preserved mosaic of shrubs. The other, called Heliporto (23°03'40.50"S, 43°59'24.47"W) is a small and isolated restinga area, bordered by secondary forest outgrow, both deforested and burned periodically; trash is also dumped in the area by residents.

Fieldwork was undertaken from February 2003 to September 2004. The diets were compared analyzing stomach contents. We collected 37 specimens from Heliporto and 32 from Bravo-meia, totalizing 69 lizards. The animals were euthanized

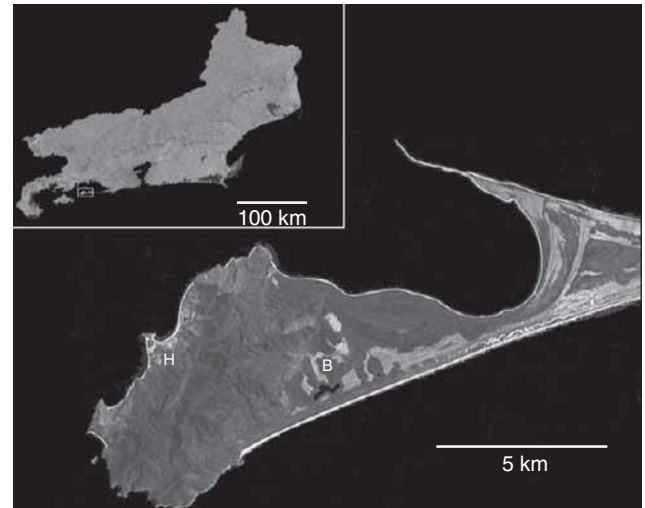


Figure 1. Map of the State of Rio de Janeiro, with the location of Marambaia (square). Enlarged, Marambaia Island with part of the restinga and indication of study areas: (H) Heliporto, (B) Bravo-meia.

with an overdose of lidocain 0,5% and fixed in formalin 10% while in the field. The collected lizards were posterior sexed and measured (snout-vent-length) in laboratory. The animals were then dissected for the investigation of the stomach contents, using a stereomicroscope. All alimentary items were counted and measured with a caliper (length and breadth, ± 0.05 mm). The volume of the alimentary items were estimated through the ellipsoid formula (COLLI *et al.* 1992).

$$Volume = \frac{(\pi \cdot length \cdot width^2)}{6}$$

We calculated the alimentary niche breadth for number of items and volume consumed, for the two areas, following PIANKA (1973). Where P is the proportional utilization of the prey item i and n is the number of prey categories used.

$$B = \frac{1}{\sum_{i=1}^n P_i^2}$$

To evaluate the similarity between the diets of the two lizard populations, we used the niche overlap index (PIANKA 1973), symbols the same as above, but j and k represent each lizard population.

$$\phi_j = \frac{\sum_{i=1}^n P_{ji} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ji}^2 \sum_{i=1}^n P_{ik}^2}}$$

We tested differences in size between the two lizard's

populations using the T Test. Diet differences were tested using Kolmogorov-Smirnov. The Z Test was performed to evaluate differences in the consumption (number and volume) of each prey category separately. To evaluate differences in the mean number, size and volume of prey items consumed in the two areas, we used the Mann-Whitney Test. The relationship between the snout-vent-length (SVL) and number and volume of prey items consumed was evaluated using linear regression analysis. The statistical methodology followed ZAR (1999).

RESULTS

According to T Test, the two lizard populations do not differ in size ($T = 0.33$, $DF = 67$, $p = 0.74$). Both populations presented a relatively diverse diet, with 19 prey categories consumed by the population from Bravo-meia and 18 prey categories consumed by the population from Heliporto. However, just 15 prey categories are common to both populations (Tab. I). Despite the similarity in the number of prey categories consumed, the populations differed in number (Kolmogorov-Smirnov, $D_{Max} = 0.22$, $DF = 2$, $p = 0.00$) and volume of preys consumed (Kolmogorov-Smirnov, $D_{Max} = 0.82$, $DF = 2$, $p = 0.00$). Ants were

the most frequent and numerous prey items in both areas. Volumetrically, vegetal matter was the most important alimentary category for the population from Bravo-meia, while for Heliporto it was Coleoptera (Tab. I). The Z Test indicated differences in the proportion of volume consumed for the majority of prey items and to half of them, in numerical proportion (Tab. II). Similarity in the numerical consumption of the prey items was observed just for those less-consumed categories.

The population from Heliporto presented a larger niche breadth for number of prey items consumed ($Bi_{num} = 3.06$) and volume ($Bi_{vol} = 2.98$) while the population from Bravo-meia presented lower values ($Bj_{num} = 2.441$, $Bj_{vol} = 1.52$). The niche overlap was superior for number of items consumed between the populations ($Oij_{num} = 0.82$) and lower for volume ($Oij_{vol} = 0.05$).

The results of the Mann-Whitney Test indicated that the mean number ($U = 525.50$, $\chi^2 = 0.64$, $DF = 1$, $p = 0.42$), mean size ($U = 444.00$, $\chi^2 = 3.17$, $DF = 1$, $p = 0.07$) and mean volume ($U = 610.00$, $\chi^2 = 0.05$, $DF = 1$, $p = 0.83$) of prey items consumed by the lizards from the two areas were not statistically different.

The linear regression analysis indicated no relationship between body size and number (Heliporto: $r^2 = 0.01$, $F = 0.22$, p

Table I. Number of items, volume (mm³) and frequency of each prey consumed by the two populations of *Tropidurus torquatus* studied on Ilha da Marambaia, Rio de Janeiro.

Prey	Bravo-meia (n = 32)			Heliporto (n = 37)		
	Items (%)	Volume (%)	Frequency	Items (%)	Volume (%)	Frequency
Acarina	1 (0.002)	4.81 (<0.001)	0.03	–	–	–
Aranae	8 (0.015)	1621.91 (0.044)	0.19	5 (0.005)	113.48 (0.005)	0.11
Blattaria	8 (0.015)	635.07 (0.017)	0.16	6 (0.006)	344.48 (0.014)	0.11
Chilopoda	2 (0.003)	93.54 (0.002)	0.03	2 (0.002)	44.71 (0.002)	0.05
Coleoptera	18 (0.034)	326.81 (0.009)	0.34	61 (0.064)	13382.06 (0.550)	0.59
Diplopoda	–	–	–	1 (0.001)	83.73 (0.003)	0.03
Diptera	11 (0.020)	93.26 (0.002)	0.03	3 (0.003)	112.90 (0.005)	0.08
Egg	–	–	–	1 (0.001)	32.66 (0.001)	0.03
Formicidae	332 (0.622)	1107.91 (0.030)	0.84	389 (0.409)	2895.87 (0.119)	0.89
Gastropoda	1 (0.002)	3.39 (<0.001)	0.03	2 (0.002)	6.40 (<0.001)	0.05
Hemiptera	2 (0.004)	8.70 (<0.001)	0.06	16 (0.017)	1180.99 (0.048)	0.27
Homoptera	2 (0.004)	52.86 (0.001)	0.06	5 (0.005)	1156.85 (0.047)	0.11
Hymenoptera	24 (0.045)	1187.35 (0.032)	0.28	44 (0.046)	1065.37 (0.044)	0.46
Isopoda	–	–	–	8 (0.008)	212.93 (0.009)	0.13
Isoptera	59 (0.110)	87.75 (0.002)	0.12	371 (0.390)	867.78 (0.036)	0.30
Larva	9 (0.017)	844.11 (0.023)	0.18	30 (0.031)	2494.52 (0.102)	0.40
Mantodea	1 (0.002)	29.44 (<0.001)	0.03	–	–	–
Neuroptera	1 (0.002)	49.06 (0.001)	0.03	–	–	–
Odonata	1 (0.002)	4.24 (<0.001)	0.03	–	–	–
Orthoptera	11 (0.021)	901.96 (0.024)	0.31	2 (0.002)	35.02 (0.001)	0.05
Scorpiones	1 (0.002)	13.84 (<0.001)	0.03	1 (0.001)	0.46 (<0.001)	0.03
Vegetal matter	42 (0.079)	29603.81 (0.807)	0.59	5 (0.005)	312.36 (0.001)	0.13
Total	534	36669.83		952	24342.62	

= 0.64 – Bravo-meia: $r^2 = 0.02$, $F = 0.52$, $p = 0.48$) or volume (Heliporto: $r^2 = 0.09$, $F = 0.78$, $p = 0.38$ – Bravo-meia: $r^2 = 0.09$, $F = 3.05$, $p = 0.09$) of prey items consumed.

Table II. Results of the Z Test for differences in the proportion of consumption (number and volume) of each prey category used by the two populations of *Tropidurus torquatus* studied on Ilha da Marambaia, Rio de Janeiro. Significant p values are in bold face.

Taxon	Number of items		Volume	
	Z	P	Z	P
Acarina	1.336	0.091	1.630	0.052
Aranae	1.932	0.027	28.798	0.000
Blattaria	1.662	0.048	3.066	0.001
Chilopoda	0.587	0.279	1.862	0.031
Coleoptera	-2.504	0.006	0.000	0.000
Diplopoda	-0.749	0.227	-11.189	0.000
Diptera	3.341	0.000	-4.316	0.000
Egg	-0.749	0.227	-6.945	0.000
Formicidae	7.887	0.000	-43.356	0.000
Gastropoda	-0.094	0.462	-1.640	0.050
Hemiptera	-2.208	0.014	-42.243	0.000
Homoptera	-0.407	0.342	-40.001	0.000
Hymenoptera	-0.113	0.455	-7.301	0.000
Isopoda	-2.124	0.017	-17.902	0.000
Isoptera	-11.389	0.000	-32.412	0.000
Larva	-1.696	0.045	-42.251	0.000
Mantodea	1.336	0.091	3.489	0.000
Neuroptera	1.336	0.091	5.155	0.000
Odonata	1.336	0.091	1.630	0.052
Orthoptera	3.674	0.000	22.766	0.000
Scorpiones	0.415	0.339	2.938	0.002
Vegetal matter	5.472	0.000	192.230	0.000

DISCUSSION

Our data suggest dietary differences between the two lizard populations. Given that lizards from the two populations do not differ in size, these differences may be associated with environmental differences between the two areas and not to morphometrical differences between the populations. Our main hypothesis to explain the dietary differences is based in the Optimal Foraging Theory (MACARTHUR & PIANKA 1966, SCHOENER 1971). According to this theory, as prey offer (and quality) deteriorates in a given area, the alimentary niche breadth is enlarged (MACARTHUR & PIANKA 1966).

The values for alimentary niche breadth found for the two lizard populations support these assumptions. Lizards from the disturbed area (Heliporto) presented larger alimentary niche

breadth, indicating a more generalist diet. However, the total number of prey categories consumed was similar for the two populations, with 15 (out of 22) items in common, indicating that, in general, diets were not radically different. The high consumption of ants by the two populations, for example, reinforce a well-known pattern of item consumption among tropidurids, that are sit-and-wait lizards (HUEY & PIANKA 1981) and present diet dominated by some common mobile items like ants (VITT *et al.* 2003, VITT & PIANKA 2005).

Several works report large usage of ants by sit-and-wait lizards, especially among *Tropidurus*. The consumption of ants is extremely common in species of different habitats and localities. Good examples of the frequency of this behavior are *T. oreadicus* Rodrigues, 1987 (ARAUJO 1987, FARIA & ARAUJO 2004), *T. itambere* Rodrigues, 1987 (VAN-SLUYS 1993, FARIA & ARAUJO 2004), and *T. spinulosus* (Cope, 1862) (COLLI *et al.* 1992) from Brazilian Cerrado; *T. hispidus* (Spix, 1825) (VITT *et al.* 1996) in isolated rock outcrops in Amazonia; or *T. melanopleurus* Boulenger, 1902, an Andean species (PEREZ-MELLADO & DE-LA-RIVA 1993). The tropidurid genus *Liolaemus* Wiegmann, 1834 is another example of a similar dietary pattern. *L. lutzae* Mertens, 1938, a sand dune lizard of coastal formations from Rio de Janeiro, Brazil, in addition to high consumption of vegetal matter, uses insect larva, coleopterans, and ants in large amounts (ROCHA 1989).

The amount of vegetal matter consumed was notably altered, being lower in Heliporto when compared to Bravo-meia. These results suggest that modifications in the local flora caused by burn, deforestation, and soil overturn may affect the diet of the lizards by altering the availability of items. *Tropidurus torquatus* is known for its consumption of vegetal matter (TEIXEIRA & GIOVANELLI 1999, FIALHO *et al.* 2000). In Maricá, another area of restinga in Rio de Janeiro, FIALHO *et al.* (2000) documented high utilization of fruits by this species. Fruits of *Erythroxylon ovalifolium* Peyritsch, 1879 (Erythroxylaceae) represented about 50% of the diet of adult males sampled during the summer, the peak of this plant's fruit-bearing season.

FIALHO *et al.* (2000) also showed that vegetal matter consumption was positively correlated to the body size of the lizards, pointing to an increase of herbivory during lizard growth. Considering the significant use of plants reported for *Tropidurus torquatus*, and confirmed in this work for the lizards from the more intact restinga area, we can suppose that changes in the composition of plants may have been caused by environmental disturbances – changing or depressing the offer of eatable fruits, leaves and flowers – and that it may have affected the lizard's diet, perhaps altering ontogenetic feeding preferences. The importance of vegetal matter in the diet of the *Tropidurus* is reinforced by analyzing the niche overlap value for volume. The low value obtained indicates that vegetal matter is volumetrically one of the most important items, differing sensitively in the diet of the two *Tropidurus* populations studied.

Our results also indicate that besides the depression of herbivory, changes in the frequency of consumption of some

other items were recorded in the disturbed area. It is possible that these events are associated. Therefore, in order to compensate for the reduction of vegetal matter in the diet, the lizards apparently substitute other items in higher frequency, for example coleopterans, as registered for the population from Heliporto. Despite some differences regarding prey items in the diet of the two populations, the common prey do not differ in size or volume, indicating that the disturbed area, in general, sustains a similar supply of arthropods that possibly differ in frequency, as observed in the stomach contents of the lizards.

Another hypothesis that can account for the differences in the frequency of consumption of different groups of arthropods among the two areas relates to the possibility of incoming and/or increasing of some arthropod populations that would not be present, or in high density, in the area under normal, undisturbed, conditions. Unfortunately, during the fieldwork, samples of the available arthropods were not taken. Therefore, we cannot properly evaluate this hypothesis.

In addition to the aforementioned, in Heliporto, the lizards are commonly observed visiting the forested area near the restinga, using trunks and branches as perches for thermoregulation, and possibly as foraging sites. The use of this boundary may be reflected in the diet of the lizards from Heliporto.

No relationship between lizards body size and prey number and volume were observed in both areas studied, contrary to what was expected according the Optimal Foraging Theory (MACARTHUR & PIANKA 1966, SCHOENER 1971). This theory predicts that an optimal prey size would be consumed with reduced time of prey handling by the predator. However, it is possible that this expected effect on generalist lizards like *Tropidurus torquatus* is less strong than in more specialized ones; however, this will require further investigation.

In summary, analysis of the stomach contents in addition to consideration of lizards as good samplers of the food offer, the data indicate that environmental modifications may affect the feeding habits of *Tropidurus torquatus*, especially in plant consumption, as predicted by the Optimal Foraging Theory. The availability of prey items needs to be measured in future studies. Overall, however, the dietary pattern of this lizard species seems to be conservative, following a diet phylogenetically determined perhaps in the common ancestor of all iguanids (VITT *et al.* 2003, VITT & PIANKA 2005), since this behavior has been observed even in altered conditions.

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