

Ontogenetic change in plant consumption by *Tropidurus psammonastes*, Rodrigues, Kasahara & Yonenaga-Yassuda, 1988 (Tropiduridae), a lizard endemic to the dunes of the São Francisco River, Bahia, Brazil<sup>1</sup>

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**Abstract:** We analyze the diet of *Tropidurus psammonastes* Rodrigues, Kasahara & Yonenaga-Yassuda, 1988 (Tropiduridae) a species endemic to the dunes of the São Francisco River in the Brazilian Caatinga, and compare diets among lizards of the species of different body sizes at different times of the year. Fieldwork was carried out in Ibiraba, Bahia. During field campaigns conducted from 1996 to 1997, lizards were captured in pitfall traps. We inferred diets through analysis of stomach contents based on mass, frequency of specific food items and recurrence of food categories. We attempted to determine whether morphometric variables of the lizards correlated with masses of the heaviest items ingested and with total dietary volume of the main food categories ingested. *T. psammonastes* consumed mainly flowers and ants, as seems to be plesiomorphic for Tropidurinae, and flowers were an important part of the lizard diet during the dry season. In addition, smaller lizards consumed mainly ants, whereas larger lizards consumed primarily plant material.

**Key words:** lizards, *Tropidurus*, ecology, diet.

**Resumo:** Variação ontogenética no consumo de vegetais por *Tropidurus psammonastes* Rodrigues, Kasahara & Yonenaga-Yassuda, 1988 (Tropiduridae), um lagarto endêmico das dunas do Rio São Francisco, Bahia, Brasil. A dieta de *Tropidurus psammonastes*, uma espécie endêmica das dunas do Rio São Francisco na Caatinga brasileira, foi avaliada e comparada com as dietas de outros lagartos da espécie com diferentes tamanhos de corpo em diferentes épocas do ano. O trabalho de campo foi realizado em Ibiraba, Bahia. Durante as campanhas de campo conduzidas de 1996 a 1997, os lagartos foram capturados por armadilhas do tipo *pitfall*. A dieta foi inferida a partir do conteúdo estomacal baseada na massa, frequência de itens alimentares específicos e recorrência de categorias alimentares. Avaliou-se se as variáveis morfométricas dos lagartos exibiam correlações com a massa dos itens ingeridos mais pesados e com o volume total da dieta das principais categorias alimentares ingeridas. *T. psammonastes* consumiu principalmente flores e formigas, o que parece ser plesiomórfico para Tropidurinae, sendo que flores constituíram uma importante parte da dieta dos lagartos durante a estação seca. Adicionalmente, lagartos pequenos consumiram principalmente formigas, enquanto que os lagartos maiores consumiram primariamente material vegetal.

**Palavras-chave:** lagartos, *Tropidurus*, ecologia, dieta.

## INTRODUCTION

Although it is unusual to find lizards that are strictly herbivorous, among lizard families, incorporation of plant material into the diet is prevalent and widespread. In a review of the literature, COOPER & VITT (2002) determined that plant consumption occurs in 247 species, slightly more than half of the species (from 23 families) for which volumetric data are available. The authors also found that plants constitute more than 10% of dietary volume in approximately 12% of those species.

Lizard body size is one of the most well known correlates of herbivory in lizards. HURTUBIA & DI CASTRI (1973) found a positive correlation between body size and dietary plant volume in *Liolaemus* species from Chile and made comparisons to other similar data in literature. POUGH (1973), based on original and secondary data concerning lizard species from 10 families, showed that an herbivorous diet is common only in lizards weighing 100g or more. The author suggested that, since smaller lizards are more agile and have higher mass-specific metabolic rates than do larger lizards, they are more prone to feed on mobile, energetic arthropods, such as insects. Larger lizards, on the other hand, would be unable to meet caloric demands on a diet strictly based on insects and must rely on vegetation as source of food, the collection of which demands less energy expenditure. In the previously cited review by COOPER & VITT (2002), the authors also found a significant (albeit weak) correlation between lizard species length and percentage of plant material included in the diet. The evolutionary analysis presented in their study supports the hypothesis that increased body size is a consequence of greater plant consumption.

In larger lizards, some level of ontogenetic shift in the diet (age-related increase in the consumption of less energetic items) is predicted in the energetic model presented in the POUGH (1973) study cited above. In fact, such a shift has been documented for various species, including some whose adult mass is less than 100g (ROCHA, 1998; COOPER & VITT, 2002). However, additional data on ontogenetic shifts in proportional dietary contribution of plants are needed in order to allow a better comprehension on the

frequency of these shifts and the reasons for interspecific differences (COOPER & VITT, 2002).

Tropiduridae is a neotropical family of small to medium-sized lizards endemic to savanna-like and coastal habitats in South America (RODRIGUES, 1987). Recent studies have shown that species within this family consume arthropods and plants (VAN SLUYS, 1993; VITT, 1993, 1995; ROCHA & BERGALLO, 1994). New species of endemic *Tropidurus*, some recently included in the genus *Eurolophosaurus* (FROST *et al.* 2001), have been found in a desert-like habitat in the Brazilian Caatinga, namely the sand dunes of the middle São Francisco River, Bahia (RODRIGUES, 1986; RODRIGUES *et al.*, 1988). Body mass of adult animals of these species reaches usually less than 40g. In this study, we analyzed the diets of lizards of different body sizes within a population of one of those species, *Tropidurus psammonastes*, Rodrigues, Kasahara & Yonenaga-Yassuda, 1988 (RODRIGUES *et al.*, 1988) at various times during 1996 and 1997.

## MATERIALS AND METHODS

**Study area:** The study site was among the dunes on the west bank of the São Francisco River, in the village of Ibiraba (10°48'S, 42°50'W), in the state of Bahia, Brazil (Fig. 1). The dunes present a very pronounced topography, with summits reaching up to 40m above river level. According to ROCHA *et al.* (2004), plant cover ranges from sparse to progressively denser, providing shady areas where there are clusters of trees, while still leaving some open areas where sandy soil is fully exposed to sunlight. Mean annual air temperature in the area is the highest in the state, reaching 26.2°C (BAHIA-SEPLANTEC, 1978) and mean annual rainfall is 692mm. The dry season is from April to September, and most of the rain falls between January and March (NIMER, 1979).

**Field data collection:** We captured lizards during the months of February and March (the height of the wet season) in 1996 and 1997, September (the height of the dry season) in 1996 and December (the beginning of the wet season) in 1996. This was done using 40-liter dry pitfall traps with drift fences. During successive field campaigns, traps were installed every

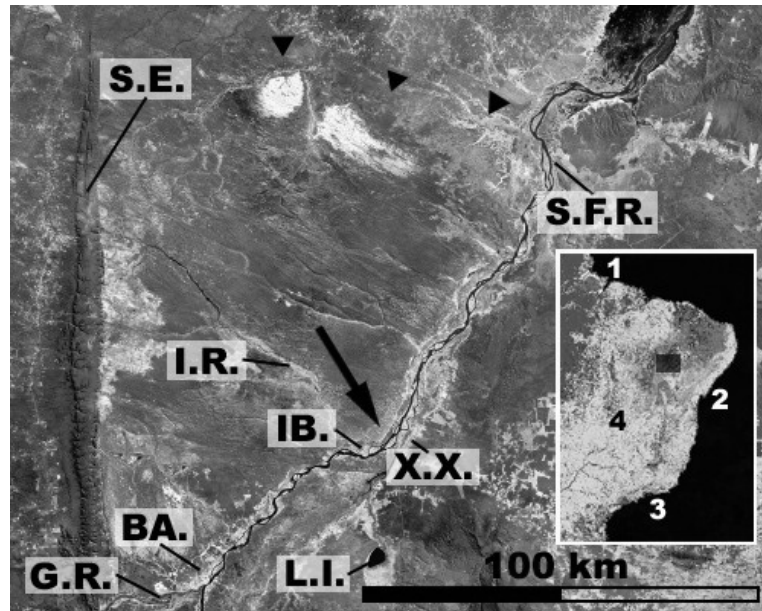


Figure 1. Map showing the geographic location of the study area. The inset shows the easternmost part of Brazil and four important cities as reference points: 1.) Belém, state of Pará; 2.) Salvador, state of Bahia; 3.) Rio de Janeiro, state of Rio de Janeiro; 4.) Brasília, Distrito Federal (Federal District). 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 (BA.) 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.

7m in a grid ( $n \cong 120$  per grid) and grids were at least 250m apart. We visited traps at dawn and dusk for 10 days during each campaign, collecting *T. psammonastes* (IBAMA license # 3451/93-13-AC) and removing arthropods from the traps in order to prevent the lizards from consuming them. Still, our methodology relies on the premise that lizard diets were not changed by consumption in the traps. Lizards were anesthetized using chloroform and then euthanized with an overdose of the same anesthetic. Subsequently, they were fixed in formalin 10% and conserved in alcohol 70%. For laboratory analysis, we sub-sampled lizards captured in campaigns in which more than 50 animals had been collected. All specimens were deposited as voucher in the collection of the Museu de Zoologia da Universidade Federal da Bahia.

**Laboratory data collection:** After dissection, we extracted the stomach contents and analyzed them

under a binocular microscope in order to record the frequency (F) of items per food category, the masses of each food category per stomach and the recurrence, defined as the number of stomachs containing the item. Food categories were based on taxonomy (usually defined by order for arthropods). We computed F as the minimal number of detectable individuals based on the fragments found. After removing excess water with blotting paper, we measured the masses of each food category per stomach (to the nearest 0.01g). Any given food category whose mass was less than 0.01g in one stomach was recorded arbitrarily as 0.002g. We excluded the categories "sand", "unidentified material" and "nematodes" from the diet analysis. In order to perform correlation analysis, we recorded the mass of the heaviest item (MHI) in each stomach, as well as snout-vent length (SVL) measured using digital calipers (0.01mm).

**Diet analysis and morphometric correlations:** The collected lizards fell naturally into two non-overlapping size classes based on SVL. We graphically compared diet (based on total mass ingested per food category) between these classes in each campaign. Then we looked for positive association between SVL and three diet variables (MHI and the total mass of the two most important food categories) based on one-tailed correlation tests, using either Spearman or Pearson's index, depending on the normality of data distribution (ZAR, 1999). Scatterplots of these associations within each size class were produced and their significances were also evaluated. The significance level adopted for computing critical values was 0.05.

## RESULTS

We captured a total of 163 *T. psammonastes*. However, since only four were captured in the campaign conducted at the height of the dry season (Sept/1996), data from this campaign were excluded from the subsequent analyses. We randomly sub-sampled 96 of the remaining 159 lizards. Each of these 96 fell naturally into one of two rather distinct size classes. The first consisted of smaller individuals (SVL from 25.62mm to 47.30mm), commonly found at the height of the wet season (52 out of the 56 captured during Feb-Mar/1996 and 19 out of the 24 captured during Feb-Mar/1997 fell into this category). The second consisted of larger individuals (SVL from 57.05mm to 94.26mm), the only type captured at the beginning of the wet season (16 animals in Dec/1996). The body mass recorded for the heaviest lizard was 38.4g. The smaller lizards typically weighed approximately 4g, and the larger lizards approximately 15g.

Empty stomachs were found in only 1 larger lizard and 11 smaller lizards. The near 9g of stomach contents analyzed included 1973 items classified into 18 food categories (Tab. 1).

Based on the total sample (all three campaigns), 84% of the mass consumed by *T. psammonastes* fell into one of five food categories: 30.4% was plant material (mainly flowers); 23.2% was Formicidae; 12.5% was insect pupae, larvae and eggs (mainly larvae); 9% was Coleoptera; and 8.8% was Arachnida. Items

in the plant material and insect larvae categories were, on average, one order of magnitude heavier than those in the categories Formicidae and Coleoptera, and the weight of Arachnida items was intermediary. Comparison of diets among campaigns showed a pronounced dietary mass of plant material and Formicidae in all three campaigns, together constituting 38.7% up to 53.1% of the total mass ingested. Although ants were always consumed by at least twice as many lizards as those consuming plants, the total mass of plant material was always greater than that of ants. Ingestion of both items was greatest at the beginning of the wet season. At the height of the wet season, especially in 1997, total mass of insect larvae ingested increased, although it was consumed by only about 6% of individuals. Also during the rainy seasons, we found significant mass of a fourth food category, consisting of Arachnida (in 1996) and Orthoptera (in 1997). Comparison of diet (based on mass) between the two body-size classes revealed that smaller lizards feed mainly on Formicidae and that usually there was not a conspicuous amount of plant material in their diet, whereas larger lizards fed mainly on plants. Consumption of Formicidae by larger lizards increased at the beginning of the wet season and consumption of larvae by smaller and larger lizards increased during Feb-Mar/1997 (Fig 2).

Most MHI values were below 0.02g for smaller lizards and above 0.05g for larger lizards. When we analyzed all lizards together, positive correlation was demonstrated between MHI and SVL ( $r_{\text{spearman}} = 0.723$ ,  $n = 84$ ,  $p < 0.001$ ). Positive (albeit weak) correlation was found between MHI and SVL for smaller lizards: ( $r_{\text{spearman}} = 0.440$ ,  $n = 61$ ,  $p < 0.001$ ). However, no such correlation was found in the case of larger lizards (SVL:  $r_{\text{pearson}} = 0.113$ ,  $n = 23$ ,  $p = 0.304$ ). The scatterplots are presented in Figure 3. Dietary volume of plant material and of Formicidae both correlated positively with SVL ( $r_{\text{spearman}} = 0.371$ ,  $n = 81$ ,  $p < 0.001$  and  $r_{\text{spearman}} = 0.787$ ,  $n = 81$ ,  $p < 0.001$ , respectively). Separate analysis of data from smaller and larger lizards revealed positive correlations with Formicidae (small:  $r_{\text{spearman}} = 0.683$ ,  $n = 59$ ,  $p < 0.001$ ; large:  $r_{\text{pearson}} = 0.386$ ,  $n = 22$ ,  $p = 0.038$ ), but not for plant material (small:  $r_{\text{spearman}} = 0.070$ ,  $n = 59$ ,  $p = 0.299$ ; large:  $r_{\text{pearson}} = 0.298$ ,  $n = 22$ ,  $p = 0.089$ ) (Fig. 3).

Table 1. Results from the analysis of stomach contents of *T. psammonastes* from Ibiraba, Bahia, Brazil sampled in three field campaigns. Values in the body of the table represent percentage of frequency (F), percentage of mass (M) and percentage of recurrence (R). Food categories are ranked by total M.

Food Categories	Field Campaigns									Total		
	Feb-Mar/1996			Dec/1996			Feb-Mar/1997			(n = 96)		
	(n = 56)			(n = 16)			(n = 24)					
	F (%)	M (%)	R (%)	F (%)	M (%)	R (%)	F (%)	M (%)	R (%)	F (%)	M (%)	R (%)
Plant material	5.1	31.4	11.9	4.3	34.7	11.1	3.0	22.8	12.7	4.5	30.4	12.0
Formicidae	70.0	21.7	31.8	74.6	29.5	25.9	71.8	15.8	25.3	71.2	23.2	28.9
Larvae and eggs	1.4	15.6	6.6	4.0	3.0	5.5	2.2	22.3	6.3	2.0	12.5	6.3
Coleoptera	13.3	6.1	19.2	10.4	11.2	20.4	12.5	9.7	20.2	12.6	9.0	19.7
Arachnida	4.6	16.2	10.6	1.8	6.8	9.3	5.0	1.9	17.7	4.2	8.8	12.3
Orthoptera	0.6	3.2	4.0	1.2	2.6	5.5	0.4	12.3	2.5	0.7	5.4	3.9
Diplopoda	-	-	-	0.6	7.5	3.7	0.2	0.4	1.3	0.2	3.0	1.0
Lepidoptera	-	-	-	0.9	2.1	5.5	0.4	7.2	2.5	0.3	2.7	1.8
Blattodea	1.0	3.2	2.7	0.3	2.3	1.9	0.2	2.5	1.3	0.7	2.7	2.1
Other Hymenoptera	0.1	0.1	0.7	-	-	-	0.2	3.8	1.3	0.1	1.0	0.7
Diptera	1.1	0.6	5.3	0.6	0.1	3.7	2.6	0.7	5.0	1.4	0.4	4.9
Thysanura	0.3	0.5	2.0	0.3	0.1	1.9	0.2	0.4	1.3	0.3	0.3	1.8
Chilopoda	0.1	0.6	0.7	-	-	-	-	-	-	0.1	0.2	0.4
Isoptera	1.7	0.3	2.0	-	-	-	0.9	0.1	1.3	1.2	0.1	1.4
Hemiptera	0.5	0.1	1.3	0.6	0.1	3.7	0.4	0.1	1.3	0.5	0.1	1.8
Homoptera	0.2	0.2	0.7	-	-	-	-	-	-	0.1	0.1	0.4
Gastropoda	0.1	0.2	0.7	-	-	-	-	-	-	0.1	0.1	0.4
Embioptera	-	-	-	0.3	0.1	1.9	-	-	-	0.1	-	0.4
Total (%)	100	100	100	100	100	100	100	100	100	100	100	100
Total analyzed	1182 items	3.142 grams	56 lizards	327 items	3.488 grams	15 lizards	464 items	2.374 grams	24 lizards	1973 items	9.004 grams	96 lizards

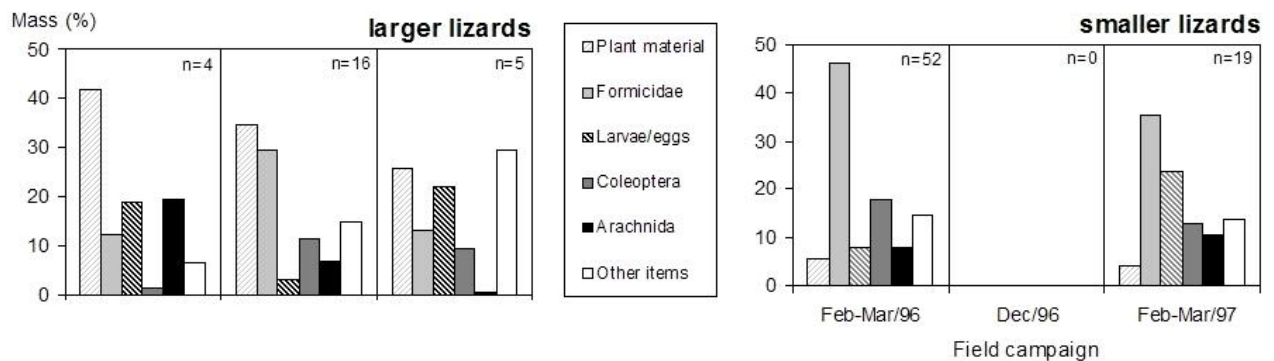


Figure 2. Comparison of diets (based on percentage of mass) among larger and smaller (*T. psammonastes*) lizards from Ibiraba, Bahia, Brazil based on data from three field campaigns. Food categories are ordered by total dietary volume.

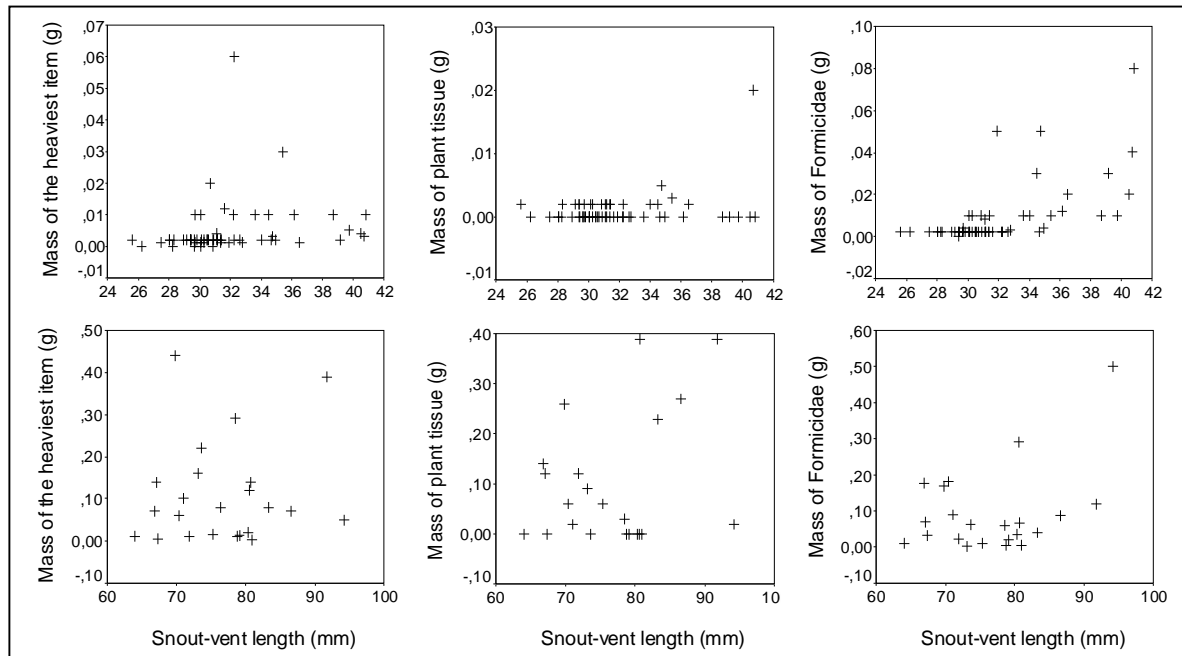


Figure 3. Scatterplots showing correlation between snout-vent length of smaller (top) and larger (bottom) *Tropidurus psammonastes* lizards from Ibiraba, Bahia, Brazil, as well as mass of the heaviest item in the stomach (left), mass of plant material in the stomach (center), and mass of Formicidae in the stomach (right).

## DISCUSSION

**Diet composition:** Our data revealed that, in addition to plant material and ants, *T. psammonastes* also consumed insect larvae and eggs, beetles, and spiders. Plants and eggs, that represent immobile items, are not supposed to be abundant in the pitfall traps. Moreover, pitfall traps collected very few arthropods during the phase of activity of *T. psammonastes* individuals (i.e., between dawn and dusk). ROCHA (1998) has shown that ants, beetles, and spiders are much less active during the day than during the night, as estimated by pitfall trapping in the dunes. Therefore, we believe that our premise that estimation on diet of the lizards was not influenced by consume inside the traps holds. Finally, the presence of food items inside the traps would influence equally small and large lizards. Therefore, our conclusions on diet ontogeny are likely to represent a natural phenomenon.

VITT & CALDWELL (1996) suggested that diet composition among many species of *Tropidurus* is

similar and that, among the potential prey present in the environment, these animals preferentially select ants, insect larvae, and bugs. Ants were also found to be an important part of the diets of other Brazilian tropidurids: *Liolaemus lutzae* from restinga areas in the State of Rio de Janeiro (ROCHA, 1989); *Eurolophosaurus divaricatus* (previously *Tropidurus divaricatus*: Frost *et al.*, 2001), syntopic with *T. psammonastes* (ROCHA & RODRIGUES, 2005); *T. torquatus* from restinga areas in the State of Espírito Santo (BERGALLO & ROCHA, 1994); *T. itambere* from the city of Campinas in the State of São Paulo (VAN SLUYS, 1993, 1995); *T. oreadicus* from the Chapada dos Guimarães region in the State of Mato Grosso do Sul (COLLI *et al.*, 1992); and *T. hispidus* in savanna-like habitats in the state of Roraima (VITT & CALDWELL, 1993; VITT & CARVALHO, 1995). However, tropidurids found in open formations in Brazil are also known to feed on plant material. These include *T. torquatus* and *Liolaemus lutzae* in the restinga (ROCHA & BERGALLO, 1994; ROCHA, 1989; ROCHA, 2000; FIALHO *et al.*, 2000), *T. itambere* in fields around Campinas (VAN

SLUYS, 1993), *T. hispidus* and *T. semitaeniatus* in the Caatinga (schrubland) (VITT, 1995) and *Tropidurus* found in savanna-like vegetation within Amazonia (VITT, 1993). Comparing these data to the phylogeny proposed by FROST *et al.* (2001), which is based on molecular and morphological characteristics, it seems clear that the ability to feed on both ants and plants is a plesiomorphic habit of Tropidurinae, since it occurs in stem branches (e.g., *Eurolophosaurus*), intermediate branches (e.g., *T. semitaeniatus*, *T. itambere*, *T. psammonastes*) and crown branches (e.g., *T. oreadicus*, *T. hispidus*). It is possible that this is even more common within the family, given the known diet of some populations of *Liolaemus* as cited above.

Selecting plant materials with high water content, such as fruits, may allow lizards to get enough water to survive in habitats where temperatures are quite high and access to free water is limited (ROCHA, 1991, 1996; FIALHO *et al.*, 2000). Flowers, which can also be a source of water, represent the main food item for several Coleoptera and Thysanoptera in the deserts, as well as being important sources of food for certain rodents and larger mammals (COSTA, 1995). Plant blooming in the Caatinga seems to be closely associated with rainfall. However, several plant species in the dunes (ROCHA *et al.*, 2004) and in other areas bloom during the dry season, possibly due to the continuous activity of pollinators (CASTRO, 1994). The availability of flowers during the drought and the beginning of the wet season, prior to the period of insect reproduction, may represent a significant source of water and energy for the tropidurids in the dunes. In fact, larger lizards increased consumption of both flowers and ants (low-quality food) at the beginning of the wet season (Dec/1996), although insect larvae (high-quality food) consumption increased at the height of wet season.

**Ontogenetic shift in diet:** Smaller lizards were found in great numbers only at the height of the wet season, suggesting a seasonal pattern of reproduction correlated with rainfall. The very low rate of successful capture at the height of the dry season, together with the fact that only larger lizards were captured at the beginning of the wet season, suggests that *T. psammonastes* become less active under stressful environmental conditions.

The results of our correlation tests based on the total sample show that there is a direct correlation between lizard body size and dietary volume of ants and flowers. However, in the sub-samples of smaller and larger lizards, only the mass of ants ingested was found to increase with body size. This means that slight increases in body size result in higher consumption of ants, but only significant increases in body size result in a higher consumption of plants. This reflects the considerable ontogenetic drift shift in the diet of *T. psammonastes*: the diet of larger lizards was found to consist mainly of plant material and that of smaller lizards to consist mainly of ants. However, flowers were present in the habitat when these animals were captured, as evidenced by the diets of larger lizards captured during the same campaign. This pattern is clear for both campaigns conducted at the height of the wet season. Since the mass of the heaviest item is correlated with body size in the case of smaller lizards but not in the case of larger lizards, it seems that the proportions of the animal impose limits on the ingestion of available food items only in early life. This fact could reveal a morphological constraint related to the diet shift detected. A second complementary explanation based on nutrition is also plausible. A protein rich diet is important for lizards that are still growing, and animals of some species grow at a faster pace when their diets are animal-based rather than plant-based (POUGH, 1973; ROCHA, 1998 and references cited therein). Therefore, plant-based diets could have a negative effect on early lizard development, since young lizards may have a preference for small animals such as ants and bugs. Finally, the low proportion of plant material in the diet of smaller lizards corresponds with the model presented by POUGH (1973), in which the author predicts that smaller lizards may have physiological restrictions in digesting plant material. At least one additional species of *Tropidurus* (*T. torquatus*) has been shown to increase consumption of plants (fruit) during ontogeny (FIALHO *et al.*, 2000).

Our results present two significant findings concerning *T. psammonastes*. First, this species, endemic to the desert-like sand dunes of the São Francisco River, represents another example of a small

omnivorous lizard whose diet includes considerable amounts of soft plant material and ants, a pattern, which seems to be plesiomorphic for its genus. Secondly, its diet changes during ontogeny, evidenced by plant consumption increasing concomitantly with body size, regardless of the availability of items (mainly ants) preferred by smaller individuals.

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