

## Food partitioning between the sympatric lizards *Tropidurus torquatus* and *Ameiva ameiva* in the Atlantic rainforest, northeastern Brazil

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**Abstract.** Ecological characteristics of *Tropidurus torquatus* and *Ameiva ameiva* were assessed in an area of the Brazilian Atlantic rainforest, in order to determine the role of diet in the sympatric coexistence of these lizards. A total of 120 *T. torquatus* were collected (77 males and 43 females). Sexual dimorphism in size and weight was detected in this species. Ants were the predominant prey in the diet of this lizard. Twenty-two females had eggs with developed shells, varying in number between two and five. Regarding *A. ameiva*, a total of 49 specimens were collected (30 males and 19 females). Sexual dimorphism was not evident in our studied population. Cockroaches were the predominant prey of *A. ameiva*. Eleven females had eggs with developed shells, varying in number between two and four. Competition for food is apparently minimized by difference in foraging strategy and body size between these sympatric lizards. These traits might be related to the consumption of different types and sizes of prey, allowing them to coexist in the studied forest fragment.

Key words. Squamata, Teiidae, Tropiduridae, diet, fecundity, competition, prey division.

### Introduction

Coexistence of lizard species has been mainly attributed to morphological and behavioural differences (VITT 1995, VITT & ZANI 1998, HUEY et al. 2001, TEIXEIRA 2001, COLLI et al. 2003, GAINSBURY & COLLI 2003). Diet is an important partitioned resource and a proxy for measuring ecological similarity between species (PIANKA 1973, TOFT 1985). In Neotropical lizards, diet composition is considered to be the main factor structuring communities (VITT & ZANI 1996, 1998). Body size is an important element in interspecific and intraspecific competition (PIANKA 1973, VITT 2000). Within a lizard population, differences in body sizes of juveniles and adults may influence the ways in which the lizards utilise space, diet, prey size, and home ranges (VITT 2000, SALES et al. 2011). Foraging strategy is also thought to play an important role in adjusting co-existence in a community (SUTHERLAND 2011).

In Brazil, *Tropidurus torquatus* (WIED, 1820) and *Ameiva ameiva* (LINNAEUS, 1758) co-exist in many different habitats, such as the sandy coastal plain (= restinga), savanna, caatinga, Atlantic Forest, and even in urban areas (RODRIGUES 1988, SARTORIUS et al. 1999). Because these lizards are naturally sympatric, they may be expected to exhibit resource partitioning to reduce interspecific interactions and facilitate coexistence. This makes them excellent

model organisms to test hypotheses on the resource partitioning between co-existing generalist species (*sensu* HUEY & PIANKA 1981).

We compared the diets of the sympatric lizards *T. torquatus* and *A. ameiva* in a fragment of the Atlantic rainforest at Arraial D'Ajuda, southern Bahia State, northeastern Brazil. Our objectives were to examine (1) how prey types and prey sizes are partitioned between these two species, (2) whether there is morphological dimorphism for each species, (3) the sex ratio for each species, and (4) fecundity of each species. We chose these species because of their wide sympatry in Brazil and their relative abundance at our study location.

### Material and methods

Fieldwork was carried out in a fragment of the Atlantic Forest (16°26' S, 39°11' W) in the municipality of Arraial D'Ajuda, situated in southern Bahia State. The sampled area was estimated at 3 km<sup>2</sup> in size. The samples were taken along random transects using an air gun during 15 days (from 8:00 to 12:00 h, or from 14:00 to 18:00 h) in November 2000 and January, February, April, June, and July 2001, respectively.

Lizards were preserved in 10% formalin. After a week, they were washed under running water, and transferred

to 70% alcohol. In the lab, preserved specimens had their snout-vent length (SVL mm) measured, weighed (0.1 g), dissected for identification of sex, stomach content analysis, and counting of shelled eggs. Ingested food items were assessed regarding frequency, number, and wet weight (measured with a digital scale; 0.0001 g precision). Intact prey items were measured with callipers (0.1 mm precision).

We calculated the dietary similarities between the two lizard species using values of number and prey weight as per the equation of SCHOENER (1970):

$$C_{ih} = 1 - \frac{1}{2} \sum |P_{ij} - P_{hi}|$$

where C represents the value of the overlap, and  $P_{ij}$  and  $P_{hi}$  are the frequencies of resource use of species j and h, respectively, in category i. Schoener's diet similarities index varies from zero (no overlap) to one (complete overlap).

All other tests were applied to data from each species individually. A Chi-Square test ( $\chi^2$ ) was used to assess possible differences in sex ratios. Linear regression was used to assess the proportional relationship between prey size and predator size. We used one-way analysis of variance (ANOVA), with sex as the independent variable and SVL and mass as the dependent variables, to test for differences in body size between sexes of adults and juveniles. *A. ameiva* were considered adult when larger than 100.0 mm (VITT & COLLI 1994), and *T. torquatus* at > 65.0 mm (FIALHO et al. 2000). We applied an analysis of co-variance (ANCOVA), with sex as the independent variable, mass as the dependent variable, and SVL as the covariate, to test for differences in the slope of the SVL/weight relationship between sexes. We also tested for differences in mean prey size between these two species of lizards using ANOVA.

Before applying any of the parametric tests mentioned above, the data were tested for normality (Kolmogorov-Smirnov), and the variances for homocedasticity (Bartlett's test; ZAR 1984). When variances were heterocedastic, data were  $\log_{10}$  transformed to fit the assumptions of ANOVA. Voucher specimens of both lizards were deposited in the zoological section of Museu de Biologia Prof. Mello Leitão (MBML) in Santa Teresa-ES.

## Results

### *Tropidurus torquatus*

A total of 120 individuals of *T. torquatus* were collected: 77 were males and 43 females. The Chi-Square test revealed significant differences in the sex ratio ( $\chi^2 = 9.6$ ;  $p < 0.01$ ). Males varied in SVL from 24.8 to 105.0 mm (mean =  $65.6 \pm 19.4$  mm), whereas female SVL varied from 42.6 to 90.4 mm (mean =  $63.0 \pm 11.4$  mm). We observed a case of sexual dimorphism in adult SVL between the sexes (> 59.5 mm SVL;  $F_{1,76} = 7.6$ ;  $p < 0.01$ ). Males were considerably larger than females. Males varied in weight from 0.6 to 60.9 g (mean =  $16.6 \pm 13.4$  g), and females from 4.0 to 31.5 g (mean =  $12.8 \pm 6.8$  g). Additionally, we observed sexual dimorphism in weight between sexes ( $F_{1,76} = 6.7$ ;  $p = 0.01$ ), with males being heavier than females. The ANCOVA-test revealed significant differences in the slope of the SVL/weight between sexes ( $F_{1,117} = 6.2$ ;  $p < 0.01$ ).

All the individuals collected had full or partially filled stomachs. Prey varied in size from 2.8 to 29.5 mm (mean =  $11.0 \pm 6.6$  mm;  $n = 118$ ). Although widely dispersed, the relationship between prey size and SVL was positive and significant ( $r^2 = 0.47$ ;  $p < 0.05$ ; Figure 1). Seventeen prey categories were identified (Table 1). Ants were the domi-

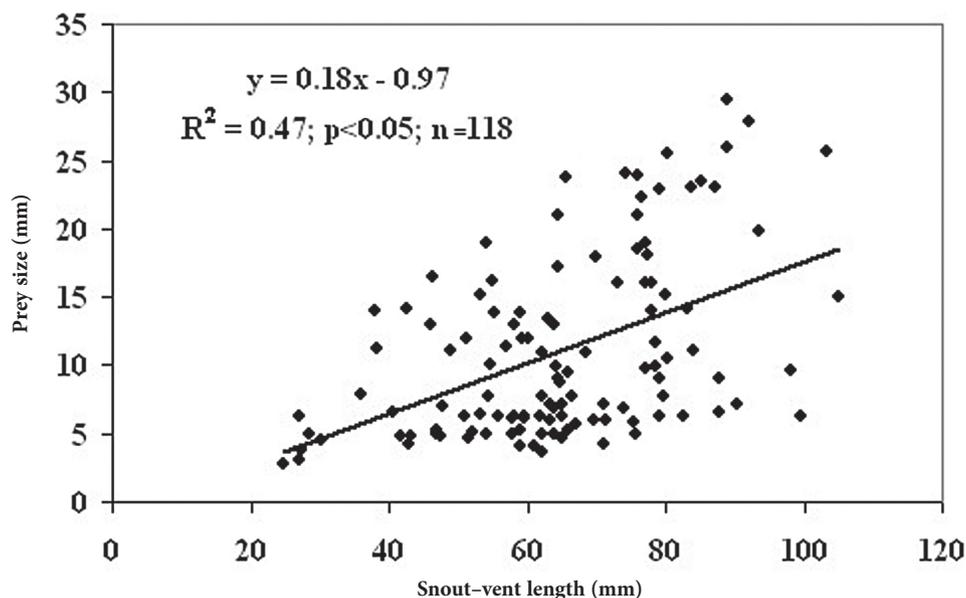


Figure 1. Relationship between prey size and snout-vent length of *Tropidurus torquatus* from a fragment of the Atlantic Forest at Arraial D'Ajuda, Bahia, northeastern Brazil.

Diet of sympatric lizards

Table 1. Prey found in the stomach contents of *Tropidurus torquatus* (n = 120) from Arraial D'Ajuda, Bahia, northeastern Brazil. F= frequency; N= number of prey items; W= prey wet weight (mg).

Prey	F	%F	N	%N	W	%W
INSECTA						
Hymenoptera (Apiidae)	4	3.3	5	0.8	524	1.5
Hymenoptera (Formicidae)	85	70.8	466	77.3	14624	40.6
Blattodea	21	17.5	25	4.1	4635.5	12.9
Coleoptera (adults)	17	15.0	18	3.0	2238.5	6.2
Coleoptera (larvae)	5	4.2	6	1.0	92.5	0.3
Collembola	1	0.8	1	0.2	0.5	0.0
Dermaptera	1	0.8	1	0.2	5.3	0.0
Diptera	2	1.7	9	1.5	214.4	0.6
Hemiptera	4	3.3	6	1.0	54.5	0.2
Lepidoptera (larvae)	18	15.0	20	3.3	4943	13.7
Orthoptera	15	12.5	17	2.8	5552.4	15.4
ARACHNIDA						
Araneae	11	9.2	12	2.0	2147.1	6.0
Pseudoscorpionida	1	0.8	2	0.3	19.5	0.1
CRUSTACEA						
Isopoda	2	1.7	2	0.3	4.4	0.0
MYRIAPODA						
Diplopoda	2	1.7	2	0.3	140.8	0.4
Chilopoda	3	2.5	3	0.5	246.8	0.7
OTHER						
Seeds	3	2.5	8	1.3	597	1.7
Total	-	-	603	100.0	36050.2	100.0

nant prey item ingested in frequency (70.8%), in number (77.3%), and in wet weight (40.6%). Other important prey items were cockroaches and Lepidopteran larvae. Plant

seeds were secondary items. Specimens smaller than 40.0 mm SVL fed almost exclusively on ants, whereas larger individuals fed on a greater diversity of prey (Figure 2).

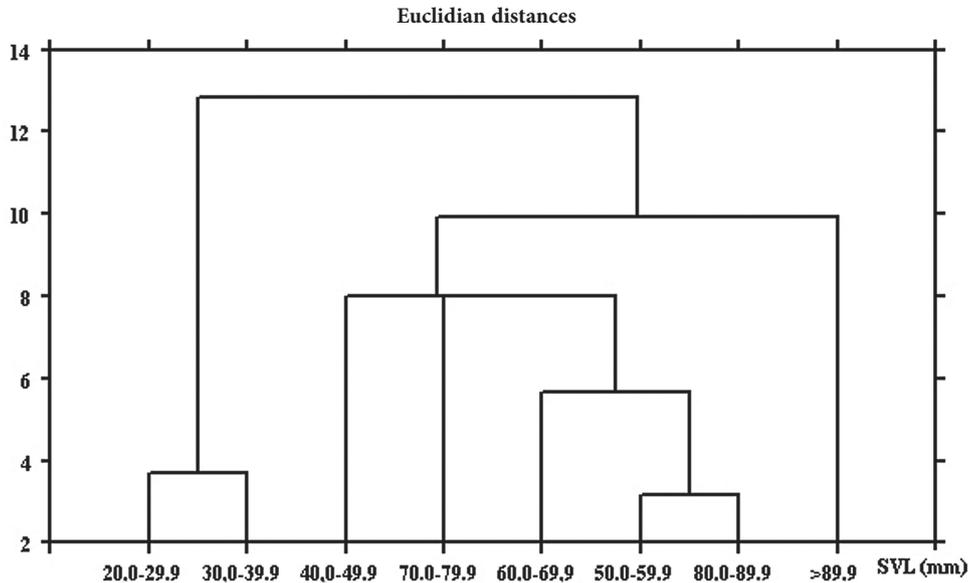


Figure 2. Cluster analysis based on Euclidean distances, facilitating the hypothesis that trophic ontogeny occurs in *Tropidurus torquatus* from a fragment of the Atlantic Forest at Arraial D'Ajuda, Bahia, northeastern Brazil.

We collected developed oocytes from 22 of 43 collected females (51.2%). Clutch size varied from 2 to 5 eggs (mean =  $2.9 \pm 0.8$ ). Gravid females of *T. torquatus* occurred in every sampled month.

#### *Ameiva ameiva*

A total of 49 *A. ameiva* were collected (30 males and 19 females). The sex ratio was not different from 1:1 ( $\chi^2 = 2.5$ ;  $p > 0.11$ ). Males varied in SVL from 39.1 to 135.0 mm (mean =  $89.7 \pm 24.4$  mm), and females from 57.8 to 117.0 mm (mean =  $91.0 \pm 16.9$  mm). There were no significant differences in SVL between sexes ( $F_{1,40} = 2.1$ ;  $p = 0.15$ ) for specimens larger than 59.9 mm SVL. Males ranged in weight from 1.6 to 80.6 g (mean =  $32.7 \pm 24.1$  g), whereas females varied from 6.8 to 45.3 g (mean =  $27.3 \pm 12.4$  g). There was a significant difference in weight between sexes ( $F_{1,40} = 4.2$ ;  $p = 0.04$ ), with males being heavier. There was no significant difference in the slope of the SVL/weight relationship between males and females ( $F_{1,46} = 13.2$ ;  $p < 0.01$ ).

All individuals collected contained at least one prey item in their stomach. Prey varied in size from 8.0 to 30.5 mm (mean =  $17.8 \pm 6.1$  mm;  $n = 30$ ), and its size increased relative to lizard SVL ( $r^2 = 0.71$ ;  $p < 0.01$ ; Figure 3). Thirteen prey categories were identified in the stomachs of *A. ameiva* (Table 2). Cockroaches were the dominant prey item in frequency (71.4%), number of prey ingested (44.0%), and prey wet weight (52.8%). The only other important prey item in the diet of this lizard was Coleopteran larvae. Plant seeds were also a secondary item in the stomach contents of this lizard. Trophic ontogeny was also detected in *A. ameiva* (Figure 4). Individuals smaller than 50.0 mm in SVL fed

mainly upon cockroaches, whereas larger individuals fed upon higher prey diversity.

Of the 19 females collected, 11 (57.9%) contained completely developed oocytes. Clutch size varied from 2 to 4 (mean =  $2.8 \pm 0.7$ ). Gravid females of *A. ameiva* also occurred in all sampled months.

#### Interspecific comparisons

Both species were active during the sampled months. *Ameiva ameiva* was significantly larger in SVL ( $F_{1,118} = 72.6$ ;  $p < 0.01$ ) and mass ( $F_{1,118} = 29.7$ ;  $p < 0.01$ ) than *T. torquatus*. Diet overlap was not large, based on either the number of ingested prey ( $C_{ih} = 0.65$ ) or prey wet weight ( $C_{ih} = 0.58$ ). Both lizard species shared 42.8% of the total identified prey categories. There were significant differences in mean prey size between both lizards ( $F_{1,146} = 26.3$ ;  $p < 0.01$ ). *Ameiva ameiva* predated upon larger prey items than *T. torquatus*. Although *T. torquatus* consumed on average more prey items (mean = 5.0) than *A. ameiva* (mean = 3.6), the former had lighter stomach content on average (300.4 mg) than the latter (516.5 mg).

#### Discussion

In Arraial D'Ajuda, the larger number of *T. torquatus* collected might be related to the more apparent behaviour of this species. Furthermore, the sedentary foraging behaviour of *T. torquatus* might increase individual detectability, because they are easier to catch than *A. ameiva*, which are active foragers, moving constantly in search of prey (VITT

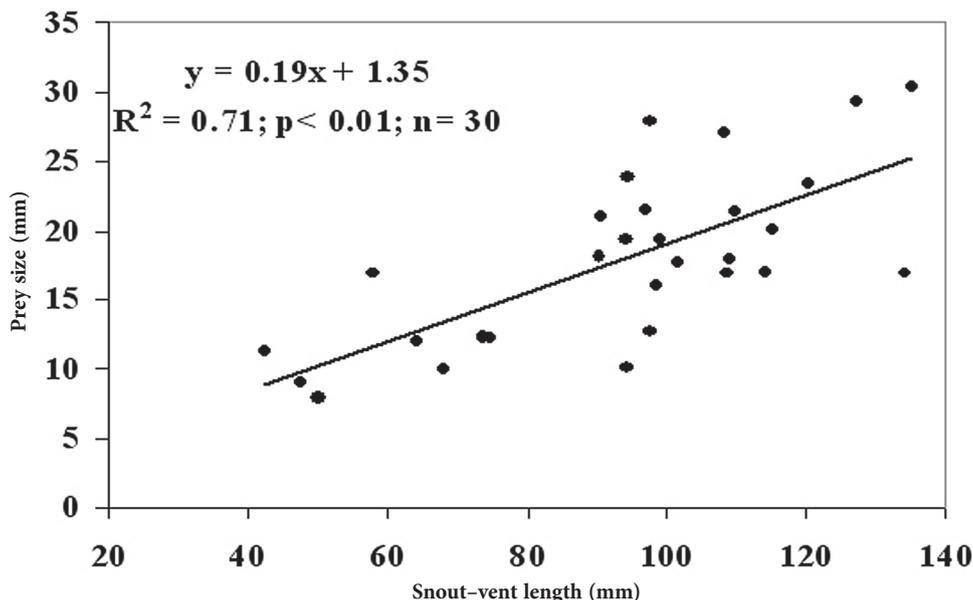


Figure 3. Relationship between prey size and snout-vent length of *Ameiva ameiva* from a fragment of the Atlantic Forest at Arraial D'Ajuda, Bahia, northeastern Brazil.

Diet of sympatric lizards

Table 2. Prey found in the stomach contents of *Ameiva ameiva* (n = 49) from Arraial D'Ajuda, Bahia, northeastern Brazil. F = frequency; N = number of prey; W = prey wet weight (mg).

Prey	F	%F	N	%N	W	%W
INSECTA						
Blattodea	35	71.4	77	44.0	13374.8	52.8
Coleoptera (adults)	5	10.2	5	2.9	698.4	2.8
Coleoptera (larvae)	9	18.4	41	23.4	2972.21	11.7
Hemiptera	1	2.0	1	0.6	107.5	0.4
Lepidoptera (larvae)	4	8.2	11	6.3	1364.6	5.4
Orthoptera	10	20.4	13	7.4	5143.9	20.3
ARACHNIDA						
Araneae	4	8.2	12	6.9	1069.9	4.2
Opilionida	1	2.0	1	0.6	125.4	0.5
MYRIAPODA						
Chilopoda	1	2.0	1	0.6	81.3	0.3
MOLLUSCA						
Gastropoda	1	2.0	1	0.6	17.4	0.1
REPTILIA						
Colubridae	1	2.0	1	0.6	212.5	0.8
OTHER						
Eggs	1	2.0	1	0.6	36.2	0.1
Seeds	3	6.1	10	5.7	106.3	0.4
Total	76		175	100.0	25310.41	100.0

& COLLI 1994). This difference in foraging behaviour could also explain similar findings in the studies conducted by ARAÚJO (1991) and TEIXEIRA (2001) who likewise caught greater numbers of *T. torquatus* than *A. ameiva*.

We collected more males than females of both *T. torquatus* and *A. ameiva*. Other studies of *A. ameiva* also found this to be true (e.g., SILVA et al. 2003, ROCHA 2008). Despite using the same sampling technique as in our study,

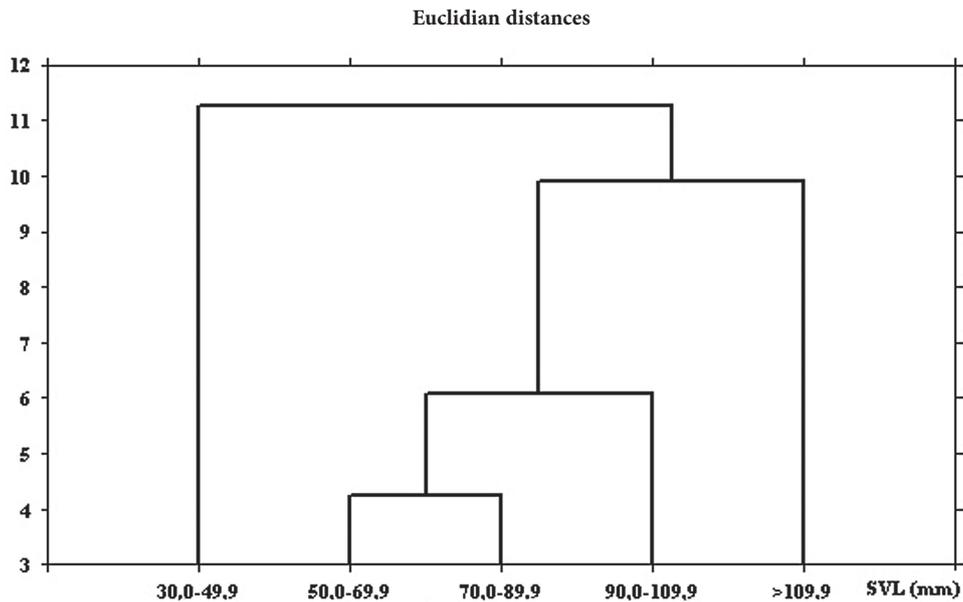


Figure 4. Cluster analysis facilitating the hypotheses that trophic ontogeny occurs in *Ameiva ameiva* in a fragment of the Atlantic Forest at Arraial D'Ajuda, Bahia, northeastern Brazil.

TEIXEIRA & GIOVANELLI (1999) found more female than male *T. torquatus*, which is consistent with studies of other *Tropidurus* species (ROCHA & SIQUEIRA 2008, KOLODIUK et al. 2010, RIBEIRO & FREIRE 2011). Therefore, sex ratio may be variable across populations. The presence or absence of a level sex ratio represents an important factor in the population structure, and can influence the extent of possible conflicts relating to securing mating partners.

The sexual dimorphism observed in our study in *T. torquatus*, also supported by other studies (RODRIGUES 1987, FIALHO et al. 2000), might be related to intersexual selection in this species. Males of this lizard exhibit territorial behaviour (PINTO et al. 2005), precluding smaller males from maintaining high-quality territories (KOHLSDORF et al. 2006). Sexual dimorphism has also been observed in several populations of *A. ameiva* (ANDERSON & VITT 1990, COLLI 1991, SILVA et al. 2003, ROCHA 2008), although not in our study. Although the males of *A. ameiva* in our population were heavier and the largest individuals were male, sexual dimorphism proved not significant when we combined both measured parameters (i.e., SVL and weight). This finding was unpredicted for *A. ameiva*; thus, further studies in our population should be conducted to examine this unexpected result.

It is known that larger lizards that predate upon more agile prey tend to show a higher proportion of empty stomach than smaller species characterized by a more sedentary foraging strategy (HUEY et al. 2001). However, this difference was not observed in our data, due to all individuals of both lizard species having at least one prey item in the stomach. This high level of predation success might be an important trait responsible for the maintenance of these species in a variety of habitats, including anthropogenic ones.

Although we found a larger spectrum of prey types in *T. torquatus* stomachs compared to those of *A. ameiva*, ants (Formicidae) were by far the most common prey item by number in *T. torquatus*, suggesting some degree of specialization. Other studies reported a high consumption of ants for other *Tropidurus* species as well (VITT et al. 1996, RIBEIRO & FREIRE 2011). This prey type is characteristic of sit-and-wait predators, although variation in foraging intensity and changes in feeding strategy according to food availability may also exist (HUEY & PIANKA 1981, ARAÚJO 1991, TEIXEIRA & GIOVANELLI 1999). According to TEIXEIRA & GIOVANELLI (1999), the species saves energy by investing in the procurement of small but abundant prey, such as ants.

The diet composition of the *A. ameiva* population described in the present study is similar to those from other regions (e.g., ARAÚJO 1991, VITT & COLLI 1994, SILVA et al. 2003). These studies detected a large spectrum of prey from sedentary (larvae) to active (Blattodea), demonstrating the ecological plasticity of this lizard. ROCHA & VRCIBRADIC (1998) reported the presence of vertebrates in *A. ameiva* stomachs, which is corroborated by our finding of an ingested colubrid snake. However, no *A. ameiva* examined had preyed upon *T. torquatus*, as had previously been

observed by ROCHA & VRCIBRADIC (1998). Our data is consistent with other studies in showing *A. ameiva* as a dietary generalist, with our population being predominantly insectivorous.

We observed trophic ontogeny in *T. torquatus*, consistent with some other studies (BÚRQUEZ et al. 1986, FIALHO et al. 2000). In our population, specimens smaller than 40.0 mm SVL fed mainly on ants, while larger individuals had a higher diversity of prey in their stomachs. Trophic ontogeny was also observed in *A. ameiva*. Individuals smaller than 50.0 mm SVL fed mainly on cockroaches, and larger individuals on a greater variety of prey types. The smallest individuals of both lizards appear to be more limited as to which prey types they are able to acquire, likely due to constraints such as smaller territory and gape limitation.

The ingestion of plant parts, even in low proportion, by *T. torquatus* and *A. ameiva* might be an indication of omnivory in our population. Variable amounts of plant material have been found in many studies of the genera *Ameiva* and *Tropidurus* (e.g., VITT & DE CARVALHO 1995, FIALHO et al. 2000, FARIA & ARAÚJO 2004, ROCHA & SIQUEIRA 2008, KOLODIUK et al. 2010, SIQUEIRA et al. 2010). However, seeds are not a commonly found plant part in stomachs of *T. torquatus* (SIQUEIRA et al. 2010). Furthermore, no seeds were found in stomachs of lizards from the two nearest studied populations (SIQUEIRA et al. 2010). Differences in the proportion of plant material ingested among populations are probably associated with food availability (SIQUEIRA et al. 2010).

Studies show that *A. ameiva* and *T. torquatus* are active throughout the year in all of the ecosystem types studied (TEIXEIRA-FILHO et al. 1996, SARTORIUS et al. 1999, ZALUAR & ROCHA 2000). Apparently both species at our study site are also not seasonal, because individuals were seen actively searching for food and defending territories throughout the sampled months. This niche dimension is considered the least important in the structuring of lizard communities (TOFT 1985).

Females of both lizards carried developing eggs in every sampled month, suggesting a protracted reproductive period. Studies that have focused more broadly on these species have reported protracted reproductive periods and low fecundity, also detected in congeners (VAN-SLUYS 1993b, TEIXEIRA & GIOVANELLI 1999, WIEDERHECKER et al. 2002, SILVA et al. 2003, KIEFER et al. 2008, ROCHA 2008). KIEFER et al. (2008) suggest that low numbers of eggs are a result of energy investment in large egg size rather than large clutch size.

The mean body size ratio between the two species of lizards is 1:1.3, which is the value suggested as necessary for a coexistence of species based on dietary niche differentiation (HUTCHINSON 1959). *Ameiva ameiva* is significantly larger than *T. torquatus* in Arraial D'Ajuda. In reptiles, size has a fundamental effect on locomotion, with implications for food acquisition (IRSCHICK & JAYNE 2000). Diet partitioning between species often results in morphological differences, even on a small scale, which have a strong influence on foraging strategy (TOFT 1985).

Here we examined the segregation of food type and food size between *A. ameiva* and *T. torquatus*. Seasonality is not an important element of niche segregation between these two species. We suggest future studies evaluate the other three traditional categories of resource dimensions: macrohabitat, microhabitat, and diel spacing (see SCHOENER 1974). Competition between *A. ameiva* and *T. torquatus* is apparently minimized by two traits in our populations. The difference in foraging strategy adopted by each species reflects the consumption of different prey types. Furthermore, differences in body size between these sympatric lizards reflect the differences in the size of their ingested prey. The differences in these behavioural and morphological traits might be a function of the niche partitioning between *A. ameiva* and *T. torquatus*, allowing them to coexist in this forest fragment.

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