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# Diet composition and tropic niche overlap of *Ameivula ocellifera* Spix 1825 (Squamata: Teiidae) and *Tropidurus cocorobensis* Rodrigues 1987 (Squamata: Tropiduridae), sympatric species with different foraging modes, in Caatinga

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Lizard diets can be influenced by several factors, such as age, physiological aspects, food availability, behaviour and foraging mode. The latter can be an important predictor of the type of prey consumed. This study analysed *Ameivula ocellifera* and *Tropidurus cocorobensis* diets, both of which are psammophiles and coexist in an area of Caatinga in north-eastern Brazil, but use different foraging modes. Lizard stomachs were examined, and prey categories were quantified by frequency of occurrence, number, volume and relative importance index. We used PERMANOVA and SIMPER analyses to understand the dissimilarities among diets. Additionally, we estimated the degree of trophic niche overlap between species using the Pianka index. The most frequently consumed food item by *A. ocellifera* was Isoptera and Formicidae (Hymenoptera) for *T. cocorobensis*. The trophic niche overlap between the species was approximately 0.24 and, although there were many consumed prey categories in common, the proportion at which these prey categories were consumed was quite divergent. For example, the consumption of plant material, which was present in the diet of both species, was much more important for *T. cocorobensis* compared to the active forager *A. ocellifera*. Our results indicate that despite sharing the same space and consuming the same prey types, these species have significant differences in their diets. Furthermore, these divergences can be explained by several factors in the environment and even by the evolutionary history of each species, which are included in different families and are not evolutionarily close to each other.

*Keywords*: diet, niche overlap, foraging mode, plant consumption, competition

## INTRODUCTION

The diet composition of lizard species is an important source of information on trophic interactions between these reptiles, other animals, plants, and the environment in general (Duffield & Bull, 1998). Additionally, dietary composition is influenced by the ecological characteristics of species, such as foraging mode, which can affect energy expenditure, morphology, life history traits, and prey selection (Huey & Pianka, 1981; Verwaijen & Van Damme, 2007). Huey & Pianka (1981) observed that small to medium-sized foraging lizards ingest abundant prey that have high rates of movement, e.g. ants, since lizards that exhibit this type of foraging strategy encounter this type of prey more frequently. In contrast, small to medium-sized active foraging lizards ingest proportionally more sedentary, conglomerate prey, such as insect larvae and termites, as well as large and often inaccessible prey for sit-and-wait lizards (e.g. scorpions).

Environmental factors may also influence the dietary patterns of lizards (Griffiths & Christian, 1996; Whitfield & Donnelly, 2006; Perez-Cembranos et al., 2016), especially in regions with defined climate seasonality. This is the case of the Brazilian Caatinga, an ecoregion with high annual average temperatures (25–30 °C), particularly during the long dry season, and a rainfall regime which is restricted to three months of the year (annual average 773 mm) (De Andrade et al., 2018). This type of seasonality affects the trophic ecology of lizards, specifically, by reducing the diversity of ingested prey categories during the dry season, thereby generating physiological challenges which must be overcome (Vasconcellos et al., 2010; Sannolo & Carretero, 2019). Consequently, the trophic niches of lizard species in this environment are dynamic, both in relation to intraspecific niche breadth and niche overlap between species (Ribeiro & Freire, 2011; Ferreira et al., 2017).

The sharing of dietary resources among sympatric species is an important element when considering trophic niche (Huey & Pianka, 1977; Sutherland, 2011; Sousa et al., 2017), particularly when competition is involved. Hypothetically, niche overlap between two or more sympatric species should be limited in

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coexisting taxa (Pianka, 1974). For example, in desert regions, congeneric fossorial lizards tend to eat different sized prey when in sympatry, compared to when in allopatry, thus they appear to segregate trophic niches and consequently reduce competition (Pianka, 1973). According to this niche theory, sympatric species must differ in at least one of the niche dimensions (spatial, temporal or trophic) for their coexistence to be viable (Pianka, 1974).

In this study we explore the diet composition and trophic overlap between two heliophilous lizard species, *Ameivula ocellifera* Spix 1825, and *Tropidurus cocorobensis* Rodrigues 1987, that are often sympatric in the Brazilian Caatinga (Rodrigues, 1996; Menezes et al., 2011; Pedrosa et al., 2014), considering their distinct foraging strategies. *Ameivula ocellifera* is a small to medium-sized (males up to ~ 100 mm SVL and females up to ~ 80 mm SVL), active foraging teiid lizard (Menezes et al., 2006; Zanchi-Silva et al., 2014; Sales & Freire, 2015), whose diet is based on small arthropods, and commonly predates upon termites and larvae (Sales & Freire, 2015; Ferreira et al., 2017). *Tropidurus cocorobensis* is a small-sized iguanian lizard (males up to ~ 73 mm SVL and females up to ~ 62 mm SVL), which uses a sit-and-wait foraging strategy, and is restricted to sandy environments (Rodrigues, 1987; 2003). There is currently no published data on its diet.

## METHODS

### Study Area

This study was carried out in the Catimbau National Park (hereafter PARNA Catimbau), a conservation unit inserted in the Caatinga ecoregion, between the geographical coordinates 08°24'' S and 08°36' S and 37°09' W and 37°14' W, in the state of Pernambuco, Brazil. The PARNA Catimbau comprises approximately 62,000 ha, with an altitude varying between 700 m and 1000 m a.s.l (PROJETO RADAMBRASIL, 1983), and located in a transition zone between the Brazilian mesoregions known as Agreste and Sertão. The climate in the region is considered hot semi-arid (BSh), according to the Köppen classification, with an average precipitation of 600 mm and an average annual temperature of 26 °C (Gomes et al., 2006). The PARNA Catimbau area is covered by outcrops of sand conglomerates and sandy soil (PROJETO RADAMBRASIL, 1983) and the vegetation is typical of the Caatinga, i.e. predominantly xeromorphic, where families such as Cactaceae, Euphorbiaceae, Mimosaceae and Fabaceae are the most common (Gomes et al., 2006). In general, the landscapes of the PARNA Catimbau are similar to other areas in the Caatinga. During the dry season (usually from March to May) the climate is warm and dry and it is possible to observe dry plants without their leaves, however during the rainy season (usually from September to January) the plants bloom fully, their leaves sprout and some flooded areas can be formed due to rainwater accumulation.

### Data Collection

The *A. ocellifera* and *T. cocorobensis* specimens were collected during two expeditions to the PARNA Catimbau in November 2020 and January 2021, during the dry season (Fig. 1). Lizards were collected using pitfall traps (Cechin & Martins, 2000; Foster, 2012) and by lasso ("noosing" in Fitzgerald, 2012). There is no evidence of significant differences between the methods used for stomach content analyses of captured lizards (Costa et al., 2008). Soon after collection the subjects were euthanised using an overdose of liquid lidocaine, based on experimental procedures which were approved by the Committee of Ethics on Animal Use (CEUA-UFPE process 0004/2020). All collections were authorised by the Brazilian government environmental entities (permit SISBIO #73617). All collected specimens were deposited in the Herpetological Collection of the Federal University of Pernambuco (CHUFPE).

In the laboratory the stomach and intestines of each specimen were removed and the contents analysed under a stereomicroscope. The ingested prey categories were identified to the Order level and, specifically for Hymenoptera (Formicidae), at the Family level. Prey category measurements (maximum length and width) were taken using a digital caliper (precision of 0.1 mm).

### Data Analysis

For each prey item category, we calculated the frequency of occurrence, and the number and volume (in $mm^3$) of prey per stomach. The volume was estimated using the ellipsoid formula, using the length (l) and width (w) of each prey item, according to Dunham (1983):

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right)$$

Additionally, we calculated the relative importance index (R.I) (Howard et al., 1999) for each type of prey that was ingested. Wheren X represented the average number of times that item X was repeated within the stomachs; fX: the number of stomachs in which item X was found and vX: the average volume of food item X in $mm^3$. N, F and V correspond, respectively, to the general sum of the number, frequency and volume of all grouped prey categories:

$$Ix = \frac{\left[\left(\frac{nX}{N}\right) + \left(\frac{vX}{V}\right) + \left(\frac{fX}{F}\right)\right]}{3}$$

We also calculated the food niche overlap (Ojk) between species according to Pianka's (1974) index, considering the volumetric proportion of each prey category in the lizards' diets. In the formula, "pij" corresponds to the proportion of prey categories in the diet of *A. ocellifera* and "pik", to the proportion of prey categories in the diet of *T. cocorobensis*:

$$Ojk = \frac{\sum pij * pik}{\sqrt{\sum pij^2 * pik^2}}$$

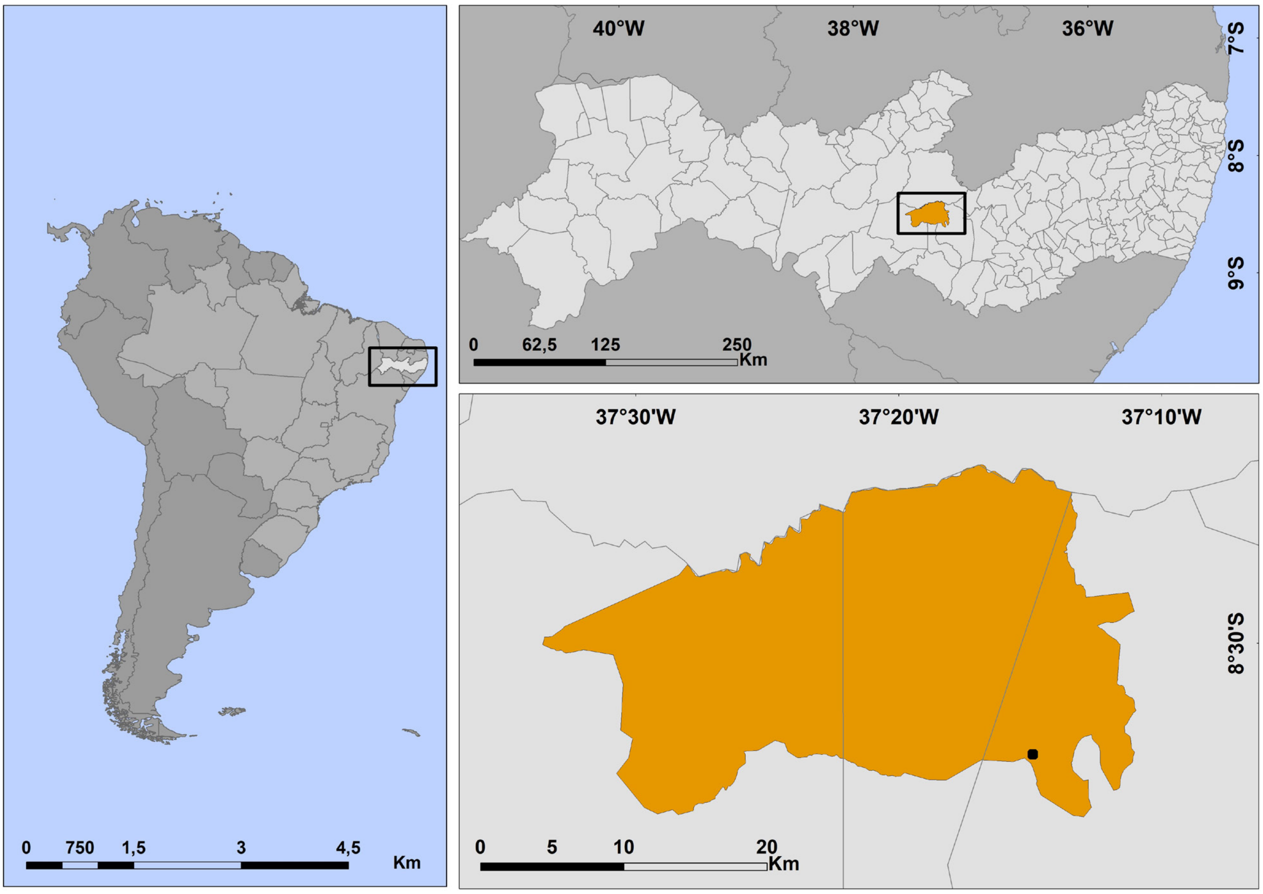


**Figure 1**. Map with the location of Catimbau National Park. The black dot represents the collection area.

To compare the diet compositions of the two different species, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA), based on a similarity matrix of the number of individuals of each item per stomach, using the Bray-Curtis index (Anderson, 2014), using the 'vegan' package (Oksanen et al., 2019) in R 3.5.1 (R Core Team, 2022). In order to identify the cumulative contributions of the most influential prey types to the dissimilarity between the diets of each species, we used the Analysis of Similarity Percentages (SIMPER) also using the 'vegan' package (Oksanen et al., 2019) in R 3.5.1 (R Core Team, 2022).

## RESULTS

In total, 31 *A. ocellifera* specimens (14 during the first and 17 during the second expedition) and 53 *T. cocorobensis* specimens (30 during the first and 23 during the second expedition) were collected, all of which were adults. The average size (SVL) was 66.43 mm for *A. ocellifera* and 71.32 mm for *T. cocorobensis*. All the lizards, of both species, had food in their stomachs. Interspecific comparisons demonstrated that the diets of *A. cellifera* and *T. cocorobensis* differed significantly, when taking into account the number (N) of cover type of prey, as indicated by the results of the PERMANOVA analysis (Factor Species~ Number (N): $p<0.001$). And, according to the SIMPER analysis, the prey types responsible for the main differences between the species' diets are Hymenoptera Formicidae (0.720) and Isoptera (0.408).

The *A. ocellifera* and *T. cocorobensis* specimens sampled in the PARNA Catimbau most frequently ingested insects (Table 1). No digestive tracts were found empty. In general, the number of prey categories ingested by the two species was very similar, where 17 different categories were ingested by *A. ocellifera* and 18 by *T. cocorobensis*. The most frequently identified prey in the diet of *A. ocellifera* was Isoptera (present in 24.66 % of stomachs) (Table 1), and Formicidae (Hymenoptera) (28.75 %) in the diet of *T. cocorobensis* (Table 1). Considering the volumetric proportion of food, the main item for *A. ocellifera* was Blattodea (6049.95 $mm^3$) and for *T. cocorobensis* the main item was plant material (in total, 37033.5 $mm^3$) (Table 1). Among the types of plant materials found, flowers occupy a greater volume in the diet composition of *T. cocorobensis* (23154.22 $mm^3$) and in the stomach contents of *A. ocellifera*, leaves occupy a greater volume (2014.58 $mm^3$).

Regarding the Relative Importance index, Isoptera was the most important item for *A. ocellifera*, where R.I=0.47 (Table 1, Fig. 2). The other prey categories ingested by the species were quite distant from this value, where the second and third most important prey categories presented values of 0.14 (Blattodea) and 0.07 (Hymenoptera) (Table 1, Fig. 2). In the *T. cocorobensis* diet, plant material had the highest R.I (in total, 0.38),

**Table 1**. Diet composition of *Ameivula ocellifera* and *Tropidurus cocorobensis* in Catimbau National Park, Pernambuco, Brazil. F represents the frequency of items in the diet, N represents the number, V the volume in mm³ and R.I the value of the relative importance.

| | *Ameivula ocellifera* (N=31) | | | | *Tropidurus cocorobensis* (N=53) | | | |
|---|---|---|---|---|---|---|---|---|
| Prey Types | F (%) | N (%) | V (mm³) | R.I | F (%) | N (%) | V (mm³) | R.I |
| **Hexapoda** | | | | | | | | |
| Blattodea | 2 (2.74) | 4 (0.37) | 6049.95 | 0.14 | 1 (0.65) | 1 (0.06) | 121.88 | 0.00 |
| Coleoptera | 3 (4.11) | 5 (0.47) | 294.73 | 0.02 | 4 (2.61) | 9 (0.54) | 523.34 | 0.01 |
| Coleoptera (Larvae) | 5 (6.85) | 5 (0.47) | 247.55 | 0.03 | 2 (1.31) | 13 (0.79) | 86.61 | 0.01 |
| Diptera | - | - | - | - | 3 (1.96) | 3 (0.18) | 41.03 | 0.01 |
| Hemiptera | - | - | - | - | 2 (1.31) | 3 (0.18) | 34.61 | 0.01 |
| Homoptera | 1 (1.37) | 1 (0.09) | 11.24 | 0.01 | 3 (1.96) | 4 (0.24) | 21.78 | 0.01 |
| Hymenoptera | | | | | | | | |
| Formicidae | 11 (15.06) | 33 (3.08) | 301.75 | 0.07 | 44 (28.75) | 826 (49.97) | 2658.63 | 0.28 |
| Formicidae (Larvae) | - | - | - | - | 3 (1.96) | 3 (0.18) | 3.18 | 0.01 |
| Non Formicidae | 10 (13.69) | 14 (1.14) | 928.63 | 0.07 | 28 (18.30) | 44 (2.66) | 1905.32 | 0.08 |
| Isoptera | 18 (24.66) | 957 (89.36) | 4125.17 | 0.47 | 15 (9.80) | 483 (29.22) | 3870.43 | 0.16 |
| Mantodea | - | - | - | - | 2 (1.31) | 2 (0.12) | 324.86 | 0.01 |
| Odonata | 1 (1.37) | 1 (0.09) | 194.98 | 0.01 | - | - | - | - |
| Orthoptera | 3 (4.11) | 5 (0.47) | 1534.46 | 0.05 | 3 (1.96) | 3 (0.18) | 530.91 | 0.01 |
| Phasmatodea | 1 (1.37) | 1 (0.09) | 6.70 | 0.01 | 1 (0.65) | 2 (0.12) | 15.16 | 0.00 |
| Unidentified Insect | 3 (4.11) | 3 (0.28) | 775.38 | 0.03 | - | - | - | - |
| **Arachnida** | | | | | | | | |
| Araneae | 4 (5.48) | 4 (0.37) | 533.41 | 0.03 | 3 (1.96) | 3 (0.18) | 2064.75 | 0.02 |
| Pseudoscorpiones | 2 (2.74) | 2 (0.19) | 2.16 | 0.01 | 1 (0.65) | 1 (0.06) | 1.32 | 0.00 |
| Scorpiones | 1 (1.37) | 1 (0.09) | 75.30 | 0.01 | - | - | - | - |
| **Chilopoda** | | | | | | | | |
| Scolopendromorpha | 1 (1.37) | 1 (0.09) | 183.99 | 0.01 | - | - | - | - |
| **Mollusca** | | | | | | | | |
| Gastropoda | 4 (5.48) | 4 (0.37) | 53.75 | 0.02 | 1 (0.65) | 1 (0.06) | 8.68 | 0.00 |
| **Vertebrate** | | | | | | | | |
| Squamata | - | - | - | - | 1 (0.65) | 1 (0.06) | 363.92 | 0.00 |
| **Matter Plant** | | | | | | | | |
| Flowers | 2 (2.74) | 4 (0.37) | 659.39 | 0.05 | 20 (13.07) | 144 (8.71) | 23154.22 | 0.23 |
| Leaves | 1 (1.37) | 26 (2.43) | 2014.58 | 0.02 | 16 (10.46) | 121 (6.47) | 13879.28 | 0.15 |
| **Total** | | **1071** | **17993.12** | | | **1653** | **49609.90** | |

followed by Formicidae (Hymenoptera) and Isoptera (0.28 and 0.16) respectively (Table 1, Fig. 2). The trophic niche overlap between both species was 0.2465 (24.65 %). In addition, here we observed the second record of saurophagy for the species *T. cocorobensis* (first: Oliveira & Nunes, 2020), in the present study the prey was a juvenile individual of *A. ocellifera*.

## DISCUSSION

*Ameivula ocellifera* and *Tropidurus cocorobensis* ingest a wide variety of different insects, and a few other animal groups such as arachnids and gastropods, however, plant material appears to be the main item in the diet of *T. cocorobensis* (Table 1). Although these lizards are sympatric in the study area and their diets are composed of many of the same prey categories, the proportions of these prey categories are notably different, thus their diets are significantly distinct (Table 1). Isoptera was the most frequently ingested item by *A. ocellifera* specimens (24.66 %), followed distantly by Formicidae (15 %), whereas Formicidae (28.75 %) and plant material (23.53 %) were the most frequently consumed items in the *T. cocorobensis* diet, with similar frequency values. Such

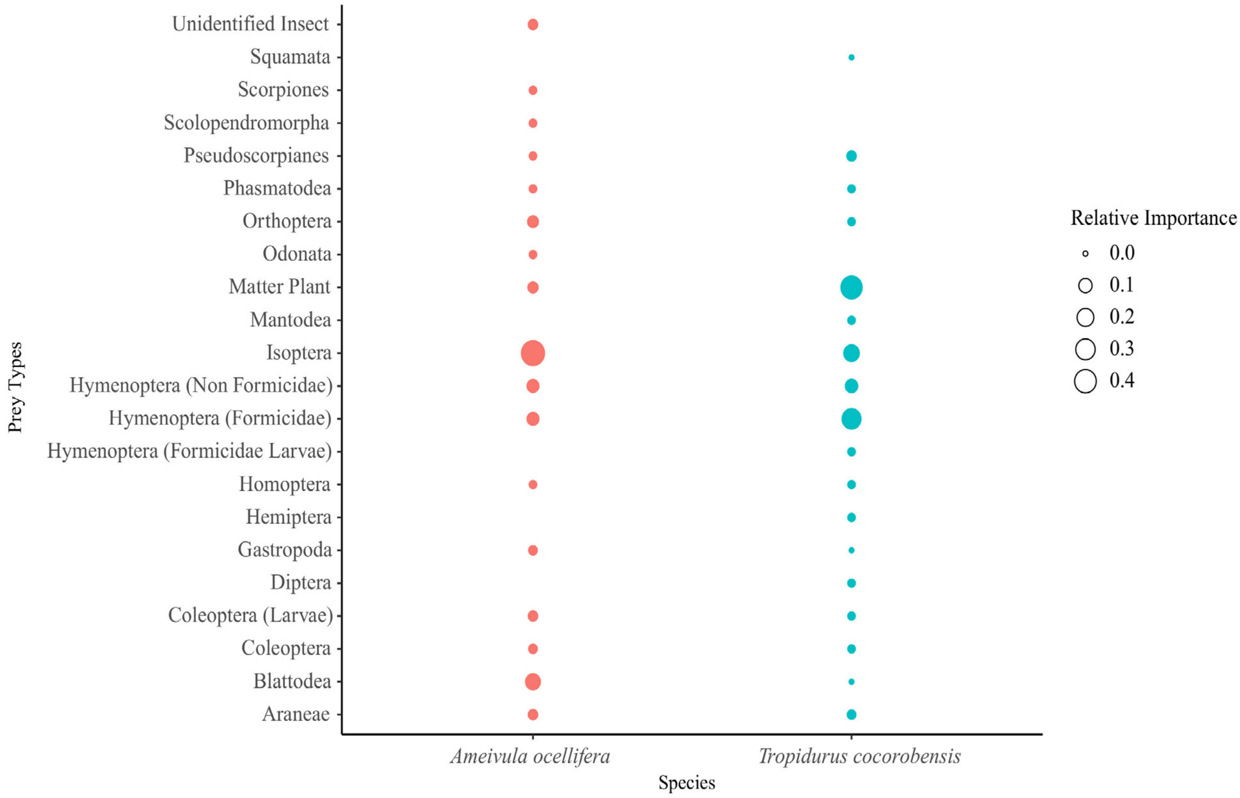


**Figure 2**. Graph representing the relative importance (R.I) of each item ingested by the species *Ameivula ocellifera* (first column) and *Tropidurus cocorobensis* (second column) collected at Catimbau National Park. The larger the symbol, the greater relative importance of prey.

differences in the most frequently consumed prey items of these lizards are in accordance with the observations of Huey & Pianka (1981).

If niche segregation is achieved, then competition should decrease, thus favoring the coexistence of different species (Pianka, 1973; 1974). In this study, *A. ocellifera* and *T. cocorobensis* seemed to share similar spatial (Pedrosa et al., 2014) and temporal niches, since both species are diurnal and heliophilous lizards (Rodrigues, 1987; Menezes et al., 2011). Differences regarding niche segregation are theoretically possible, but we lack information on important variables such as the time of day for peak of activity and the time of day at which foraging starts, among others, which are only known for *A. ocellifera* in other areas of north-eastern Brazil (Menezes et al., 2011; Albuquerque et al., 2018).

Considering that both species share many ecological similarities, including the same microhabitat (both psamophiles) and temporal niches, niche differentiation may be mainly trophic, as our results suggest for the populations in the PARNA Catimbau. Furthermore, foraging strategy appears to be an important factor when considering diet. The sit-and-wait forager, *T. cocorobensis*, consumes a higher frequency of active prey (i.e. ants), whereas the more active forager, *A. ocellifera*, ingests fewer active prey items (i.e. termites), and these prey items represent exactly the greatest dissimilarity between the diets of these lizards. These results corroborate the previously cited proposals by Huey & Pianka (1981).

However, historical influences should also be considered as an important factor influencing the differences in the proportions of consumed prey categories by both species (i.e. by number, frequency, and volume), which are nested in very distant clades within Squamata (Teiioidea and Iguania; Pyron et al., 2013; Simões & Pyron, 2021). The consumption of plant material is vastly documented, for Iguania and Tropiduridae in particular (e.g. Fialho et al., 2000; Van Sluys et al., 2004; Kolodiuk et al., 2010; Garda et al., 2012; Siqueira et al., 2013; Verrastro & Ely, 2015; García-Rosales et al., 2020; Tan et al., 2020), where Tropiduridae is included as one of the families whose diet comprises the highest percentage of omnivorous species and the highest average percentage of plant material in their diet (Cooper & Vitt, 2002).

This high intake of plant material seems to be a result of historical heritage. Although the primitive condition of Iguania seems to be carnivory, and the primitive condition of Tropiduridae is uncertain, plant consumption is widespread throughout the crown groups of the family and appears to be the condition at the root of the *torquatus* group, in which *T. cocorobensis* is nested (Frost et al., 2001; Cooper & Vitt, 2002). On the other hand, carnivory appears to be the primitive condition for all Scincoidea species, for the family Teiidae, and for the genus *Ameivula* (Cooper & Vitt, 2002). Furthermore, there are records of plant material consumption by some teiid lizards in Brazil, but at much lower levels compared to tropidurids (Menezes et al., 2006; 2011; Sales et al., 2011; Sales & Freire, 2015). However, plant consumption in the family Teiidae is greatly reduced when compared with the observed in Tropiduridae (Cooper & Vitt, 2002).

In the present study, all data were collected during the dry season, but it is important to consider the different responses of each species to environmental variations when comparing the use of food resources, especially in environments with marked seasonality, such as the Caatinga. In this environment the ingestion rates of some species of *Tropidurus*, such as *T. hispidus* and *T. semitaeniatus*, may vary depending on the different seasons, consuming mainly ants and termites in both seasons, and becoming opportunistic predators of arthropod larvae during the rainy season, this prey being poorly available in the warmer season (Ribeiro & Freire, 2011). In some species of the Teiidae family, seasonal changes in trophic ecology are not present, for example *Glaucomastix littoralis* in coastal sandbank environments, which experience reduced seasonality and constantly high air humidity and rainfall (Teixeira-Filho et al., 2003). On the other hand, in a population of *A. ocellifera* in the Caatinga, seasonal changes in diet have been recorded for the three most important prey categories during each season (insect larvae, termites and orthopterans during the rainy season, contrasting with spiders, hemipterans and insect larvae during the dry season) (Sales & Freire, 2015), which seems to reinforce the influence of seasonality on diet.

Despite inhabiting the same microhabitat, there is a low trophic niche overlap between *A. ocellifera* and *T. cocorobensis* and their diets differ significantly. The predation of termites by *A. ocellifera* in the Caatinga and Cerrado ecoregions is well documented (Menezes et al., 2011; Sales & Freire, 2015), but populations of this species in Amazonian savannahs mainly consume orthopterans (Mesquita & Colli, 2003). Specimens of *T. cocorobensis* consume several of the same prey categories as their congeners and ants are the most frequently ingested prey category, similar to *T. hispidus* and *T. semitaeniatus* (Ribeiro & Freire, 2011), which are also sympatric with *T. cocorobensis* and *A. ocellifera* in the Catimbau National Park (Pedrosa et al., 2014).

Our results show that although the study species share microhabitats and the same food resources, the trophic niche overlap between these species is low and their diets differ significantly. This may be related to competition strategies, historical constraints, and/or responses to environmental variations. We suggest that future studies consider the possible temporal niche overlap of these species, in order to provide more information on the activity period of *T. cocorobensis*. Our study contributes to the knowledge of resource sharing among sympatric species of lizards from different families in the Caatinga.

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