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Influence of Life History Traits on Trophic Niche Segregation between Two Similar Sympatric *Tupinambis* Lizards

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Abstract. Segregation of habitat resources is an important mechanism that allows the coexistence of species. The diet is an important and dynamic component that can generate interactions among co-existing species. Differences in food resource use between related sympatric species have been associated frequently with divergence in multiple phenotypic traits; hence, it is interesting to explore how phenotypic differences allow sympatric species to minimize niche overlap. We aimed to evaluate trophic niche segregation between *Tupinambis merianae* and *T. rufescens* in relation to life history traits in a sympatric zone. We compared the volume of the stomach food items between species considering sexual dimorphism, body size classes, sexual maturity and reproductive activity. The obtained Morisita's index indicated trophic niche overlap between *T. merianae* and *T. rufescens*; however, considering particular food items, we observed differences in diet composition. Moreover, our results indicate that body size, sexual maturity and reproductive activity are relevant factors influencing the diet of these species. Life history traits of these two species of *Tupinambis* are important because they shape diet composition, contributing to interspecific segregation of the trophic niche and, therefore, allowing species coexistence.

Keywords. Activity pattern; Body size; Feeding ecology; Phenotypic traits; Sexual dimorphism; Squamata; Sympatry; Trophic niche overlap.

Resumen. La segregación de los recursos del hábitat es un importante mecanismo que permite la coexistencia de especies. La dieta es un componente importante y dinámico, que puede generar interacciones entre especies co-existentes. Las diferencias en la dieta entre especies relacionadas en simpatría han sido frecuentemente asociadas a la divergencia en múltiples caracteres fenotípicos, por lo tanto es interesante explorar cómo las diferencias fenotípicas permiten que las especies simpátricas minimicen la superposición del nicho. Nuestro objetivo fue evaluar la segregación del nicho trófico entre *Tupinambis merianae* y *T. rufescens* en una zona de simpatría y entender de qué manera los caracteres de historia de vida podrían influenciar la ecología trófica de estos lagartos. Analizamos el contenido estomacal comparando el volumen de presas consumidas entre especies, considerando además el dimorfismo sexual, las clases de tamaño corporal, la madurez sexual y la actividad reproductiva. El índice de Morisita obtenido indica superposición del nicho trófico entre *T. merianae* y *T. rufescens,* pero considerando algunas presas en particular, observamos que las especies muestran diferencias en la composición de la dieta. Por otro lado, nuestros resultados indican que el tamaño corporal, la madurez sexual y la actividad reproductiva son factores relevantes que influyen en la dieta de las especies. Los caracteres de historia de vida de estas dos especies de *Tupinambis* son importantes porque determinan la composición de la dieta, contribuyendo a la segregación interespecifica del nicho trófico y en consecuencia a la coexistencia de las especies.

INTRODUCTION

Under the resource-utilization niche concept, two species cannot occupy the same *n*-dimensional ecological niche without exerting strong competition on each other (Shoener, 2009; Chillo *et al.,* 2010). Therefore, resource partitioning often occurs between sympatric populations of species with similar ecological niches. Segregation of habitat resources is an important mechanism that allows the coexistence of species (Chillo *et al.,* 2010; Salvidio, 2012). Interspecific interactions play an important role in shaping the structure of communities. The diet is an important and dynamic component that can generate interactions among co-existing species (Duffield and Bull, 1998; Raine *et al.,* 2007; Huang, 2010; Ribeiro and Freire, 2011). Foraging habits of species with similar phenotypic traits can lead to ecological and behavioral interactions in food resource use (Werneck *et al.,* 2009). Moreover, these competitive interactions are strong between phylogenetically closely related sympatric species (Loveridge and Macdonald, 2003; Di Bitetti *et al.,* 2009, Chillo *et al.,* 2010).

In lizards, coexistence of species is often possible due to morphological and behavioral differences that allow niche segregation (Vitt and Zani, 1998, Huey *et al.,* 2001; Teixeira, 2001; Colli *et al.,* 2003, Gainsbury and Colli, 2003; Freitas, 2012). Species can differ in diet composition as a result of competition-reducing mechanisms (Ribeiro and Freire, 2011), such as morphological differences, which can lead to consumption of different types of prey items (Mesquita *et al.,* 2006). Differences in food resource use between related sympatric species have been

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associated frequently with divergence in multiple phenotypic traits (Mori and Vincent, 2008; Lelièvre *et al.,* 2012); hence, it is interesting to explore how intra- and interspecific phenotypic differences allow sympatric species to minimize niche overlap. It is known that intrinsic life history factors have a strong influence on feeding ecology (Pianka, 1986; Sales *et al.,* 2012); factors such as body size, sex, and ontogenetic changes are important in differentiating diet composition (Vitt, 2000; Sales *et al.,* 2012). Individual specialization in trophic resources influenced by individual differences in bioecological factors, such as morphology or activity, has important ecological and evolutionary consequences in relaxing intraspecific competition (Svanbäck *et al.,* 2008). Intrinsic life history factors can also cause a decrease in interspecific niche overlap; therefore, assessing the role of life history traits in the feeding ecology of species might help elucidate how trophic interactions relax to favor the coexistence of similar sympatric species.

Significant associations between body size and prey dimensions have been reported in lizards (Van Sluys *et al.,* 2004). The smallest individuals appear to be more limited in the type of prey they can acquire (Freitas *et al.,* 2012). Moreover, similar-sized species ingest similar-sized prey, probably overlapping their trophic niches (Faria and Araújo, 2004). However, body size might also be a key factor allowing diet segregation in individuals of certain size classes. For instance, if juveniles of two species are of similar size but adults differ, we would expect that trophic niches overlap in juveniles but diverge in adults. Furthermore, morphological differences have a strong influence on foraging strategy. In lizards, body size has a fundamental effect on habitat use, with implications for the amount of food acquired (Irschick and Jayne, 2000; Freitas *et al.,* 2012).

Trophic niche overlap between species can also depend on the diet of each sex. Diet can vary in one sex but not in the other sex. Sex can influence prey type and size due to differences in morphology and/or behavior between males and females (Vitt, 2000; Sales *et al.,* 2011). In species with sexually dimorphic body size, the occurrence of dietary differences between sexes is expected because the larger sex has the potential to consume larger or more diverse prey (Sales *et al.,* 2012). Therefore, sexual dimorphism in body size, which is often related to different ecological functions such as feeding (Canovas *et al.,* 2006), might reveal sex-dependent differences in the trophic niche of a species.

Reproductive behavior is another key factor that can influence feeding ecology. Numerous studies have reported ontogenetic changes in the diet of lizards, with immature individuals using less energy and consuming less food than mature individuals (Sironi *et al.,* 2000). Before maturation, energy is allocated to maintenance and growth, whereas after maturation it is also allocated to reproduction (Wapstra *et al.,* 2001). Moreover, during the activity period, mature individuals of hibernating species often develop feeding and reproductive activities at different moments (Yanosky, 1993); therefore, interspecific niche differences may be associated with temporal reproductive behaviors of the activity pattern (Cooper and William, 2011). Furthermore, during the mating period not all individuals reach the reproductive condition; therefore, the particular condition of each individual might influence its feeding behavior.

Tupinambis merianae (Duméril and Bibron, 1839) and *T. rufescens* (Günther, 1871) provide a good model system to examine the role of life history factors in trophic niche divergence because they share several bioecological traits. They have similar body size, being the largest lizards in their distribution area, and share external morphological traits and general foraging habits (Williams *et al.,* 1993; Castro and Galetti, 2004). Phylogenetic studies in the genus have demonstrated that *T. merianae* and *T. rufescens* are sister species (Fitzgerald *et al.,* 1999; Cabaña *et al.,* 2014). In Argentina, they occur in parallel allopatric zones from approximately 10–40°S (*T. rufescens* occurring further west than *T. merianae*) (Cei, 1993; Lanfri *et al.,* 2013); however, they also co-habit in a large contact zone (Cei, 1993; Fitzgerald, 1994; Cardozo *et al.,* 2012; Lanfri *et al.,* 2013). Cardozo *et al.* (2012) explored habitat requirements at a landscape level for *T. merianae* and *T. rufescens* in allopatric and sympatric zones. These species differ in habitat requirements in allopatric areas, but in the contact zones the species use the same landscape-habitat resources. Moreover, *T. merianae* and *T. rufescens* select landscapes patterns with a greater proportion of forest and shrubs than the mean landscape availability in contact zones (Cardozo *et al.,* 2012).

We aimed to evaluate trophic niche segregation between the two *Tupinambis* species in a contact zone of their distributions and understand how life history traits (body size, sexual body size dimorphism, sexual maturity and reproductive activity) might influence the feeding ecology of these lizards and lead to trophic niche differentiation between species.

MATERIALS AND METHODS

Study site

We conducted fieldwork in the southernmost distribution area of both species, in central Argentina (31°25′59″S, 63°41′04″W to 31°40′55″S, 63°22′30″W). Lizards were captured in diverse localities with different levels of syntopy in the contact zone between the phytogeographic regions of Chaco forest and the Espinal (Cabrera, 1994). The vegetation of the study area is characterized by *Celtis tala, Aspidosperma quebracho-blanco,* *Schinus fasciculata, Larrea divaricata, Condalia microphylla, Aloysia gratísima, Ziziphus mistol, Geoffroea decorticans, Acacia* spp. and *Prosopis* spp. (Zak, *et al.,* 2004). Exotic forest species such as *Melia azedarach* and *Morus* sp. are also present.

Capture of specimens

Tupinambis merianae and *T. rufescens* are included in Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES); in Argentina, commercial harvest is allowed (Porini, 2006; Res. 11/2011, Secretaría de Ambiente y Desarrollo Sustentable de la Nación). *Tupinambis* individuals were caught weekly from wild populations by local authorized hunters in central Argentina between October–March. We accompanied authorized local people to standardize the sampling according to scientific capture. Specimens were killed for the legal skin trade, in accordance with AVMA Guidelines on Euthanasia (AVMA, 2007). A total of 503 lizards were captured (429 *T. merianae:* 227 were males and 202 females; 74 *T. rufescens:* 54 were males and 20 females) during the activity period described for these species (October–March) from 2008–2012.

Determination of bioecological factors

We determined body size by measuring snout–vent length (SVL) with calipers (to the nearest 0.1 cm). We differentiated mature from immature individuals by considering the SVL of the smallest reproductive female and male (Madsen *et al.,* 2006; Cardozo and Chiaraviglio, 2011; Naretto *et al.,* 2014). Thus, size at sexual maturity was 32.0 cm SVL for females of both species and 29.5 and 30.5 cm SVL for males of *T. merianae* and *T. rufescens,* respectively. We assigned mature individuals to size classes: C1 (size at sexual maturity–38 cm), C2 (38.1–43.5 cm) and C3 (43.6–49 cm). We considered the reproductive period to be October–December and the non-reproductive period to be January–March (Naretto *et al.,* 2014). Males were categorized as reproductive when they presented turgid testes or semen in deferent ducts, whereas females were categorized as reproductive when they presented vitelogenic follicles (> 6 mm diameter), oviductal eggs or corporea lutea.

Sample processing

In the field, we removed digestive tracts completely and stored them individually. We transported samples and stored them in the laboratory under cold conditions (Colli *et al.,* 1998). In the laboratory, we followed standard procedures for stomach content analysis (Korschgen, 1987). We measured the total volume of the content of each digestive tract (Mercolli and Yanosky, 1994) and recorded the number of empty stomachs to calculate the feeding rate. We washed the contents and passed them through sieves of different mesh sizes to separate and identify food items with a Nikon SMZ1500 optical magnifier. We measured the volume of each food item using the water displacement technique with graduated cylinders of 10, 50, 100, 250 mL (Magnusson *et al.,* 2003). We recorded food displacing < 0.1 mL as "trace" (Bonino *et al.,* 2009). We identified vertebrate prey at the class taxonomic level and invertebrate prey at the order taxonomic level (Rocha and Siqueira, 2008). We identified seeds and fruits to the taxonomic level of genus or species, if possible, using reference collections, and consulting specialists and taxonomic literature (Sérsic and Cocucci, 2006), and assigned the seeds and fruits found in stomachs either to a native or exotic group.

Data analyses

We considered two indicators to quantify the importance of each prey type (Varela *et al.,* 2008):

1. Relative frequency: Frequency of item *a* / ∑ frequencies of total items × 100
2. Relative volume: Volume of item *a* / volume of total items × 100

We calculated the relative importance of each food item in the diet of *Tupinambis merianae* and *T. rufescens* using the Index of Relative Importance (IRI), which integrates frequency of occurrence and volume:

$$IRI = 100\ (F_o \cdot V_i) / \sum (F_o \cdot V_i)$$

where F_o indicates the relative frequency and V_i the relative volume; values range from near 0 (low importance) to near 100 (high importance) (Bonino *et al.,* 2009; Hart *et al.,* 2003). We also applied the Hierarchical Index (HI), which takes the highest IRI value to calculate the percentage of all the other IRI values. According to the HI value, a food item can be fundamental (100–75%), secondary (75–50%), accessory (50–25%) or accidental (below 25%) (Sanabria, 2005). We calculated the HI for the entire population and for each sex. We measured similarity or niche overlap between species and between males and females of each species using the Simplified Morisita Index (CH):

$$CH = 2 \cdot \sum Pij \cdot Pik / \sum Pij^2 + \sum Pik^2$$

where j and k are categories to be compared, and Pij . Pik is the proportion represented by item i in such categories;

Table 1. The diet of *Tupinambis merianae* and *T. rufescens* (n = 503). Nu = number of stomachs containing prey category, RF = relative frequency; RV = relative volume; HI = Hierarchical Index of the Index of Relative Importance. Scientific names of fruits and seeds are followed by local common names in parentheses.

	Tupinambis merianae				***Tupinambis rufescens***			
	Nu	RF	RV	HI	Nu	RF	RV	HI
Native fruits and seeds	**9**	**2.48**	**5.13**	**0.6**	**19**	**19.2**	**50.2**	**100**
Celtis tala (Tala)	3	1.12	0.25		0	0	0	
Prosopis alba (Algarrobo)	0	0	0		1	1.16	0.09	
Geoffroea decorticans (Chañar)	5	1.87	10		5	5.81	40.1	
Ziziphus mistol (Mistol)	0	0	0		13	15.1	31.3	
Exotic fruits and seeds	**28**	**7.71**	**2.46**	**0.9**	***8***	**7.07**	**4.16**	**3**
Melia azedarach (Paraíso)	29	10.9	4.43		5	5.81	2.44	
Morus sp. (Mora)	1	0.37	0.51		2	2.33	3.33	
Lantana camara (Lantana)	0	0	0		1	1.16	0.14	
Arthropoda	**194**	**53.4**	**42.4**	**100**	**46**	**46.5**	**16**	**77**
Malacostraca								
Isopoda	1	0.37	0.22		2	2.33	0.29	
Arachnida								
Aranae	4	1.5	0.36		4	4.65	1.1	
Insecta								
Orthoptera	38	14.2	12.1		5	5.81	1.08	
Coleoptera	185	69.3	72.1		41	51.2	18.2	
Hymenoptera	1	0.37	0.22		1	1.16	0.43	
Miriapoda								
Chilopoda	0	0	0		3	3.49	1.56	
Mollusca	**36**	**9.92**	**2.53**	**1.1**	**8**	**8.08**	**16.2**	**14**
Gastropoda								
Pulmonata	36	9.92	2.53	1.1	8	8.08	16.2	
Squamata	**19**	**5.23**	**7.66**	**1.8**	**8**	**8.08**	**3.42**	**2.9**
Aves	**26**	**7.16**	**17.3**	**5.5**	**2**	**2.02**	**2.23**	**0.5**
Mammalia	**51**	**14.1**	**22.5**	**14**	**9**	**9.09**	**7.78**	**7.3**

values near 0 indicate low similarity and values near 1 indicate high similarity (Krebs, 1999).

We determined the trophic niche breadth using Levin's Index (Nb) (Villavicencio *et al.,* 2005):

$$Nb = (\sum Pij^2)^{-1}$$

where Pij is the percentage of the item i in the sample j. Then, we calculated the standardized Levin's Index:

$$Bsta = (B_{obs}–B_{min}) / (B_{max}–B_{min})$$

where B_{obs} is the calculated Nb; $B_{min} = 1$ considering that at least one item prey should be consumed, and B_{max} is the amount of prey items found. Bsta values close to 0 indicate that the species is a specialist and values close to 1 indicate that the species is a generalist. We used the Wilcoxon or Kruskal Wallis test to compare the volume of the consumed food items between sexes, species, maturity condition, reproductive condition or among body size classes, considering the level of confidence at 0.95 (P = 0.05). Body mass was used as covariable. We used a Principal Component Analysis (PCA) and MANOVA to detect differences in diet among species and sexes. An a posteriori test (Hotelling) was also performed. We performed all statistical analyses using InfoStat (Di Rienzo *et al.,* 2015).

RESULTS

Levin's Index was 0.23 for *Tupinambis merianae* and 0.11 for *T. rufescens*. Feeding rates were 0.76 for females and 0.75 for males of *T. merianae* and 0.95 for females and 0.89 for males of *T. rufescens*. Morisita's Index (CH = 0.92) indicates considerable trophic niche overlap between *T. merianae* and *T. rufescens*. The comparison between sexes at the intraspecific level showed a Morisita's Index value of CH = 0.97 for *T. merianae* and CH = 0.95 for *T. rufescens*. Considering particular food items, we observed that diet composition differed (Table 1). HI values indicate that the diet of *T. merianae* included mainly Arthropoda and Mammalia, whereas that of *T. rufescens* comprised mainly native fruits and seeds, and Arthropoda. We found sexual size dimorphism in both species (*T. merianae:* W = 37708, $P < 0.0001$; *T. rufescens:* W = 373,

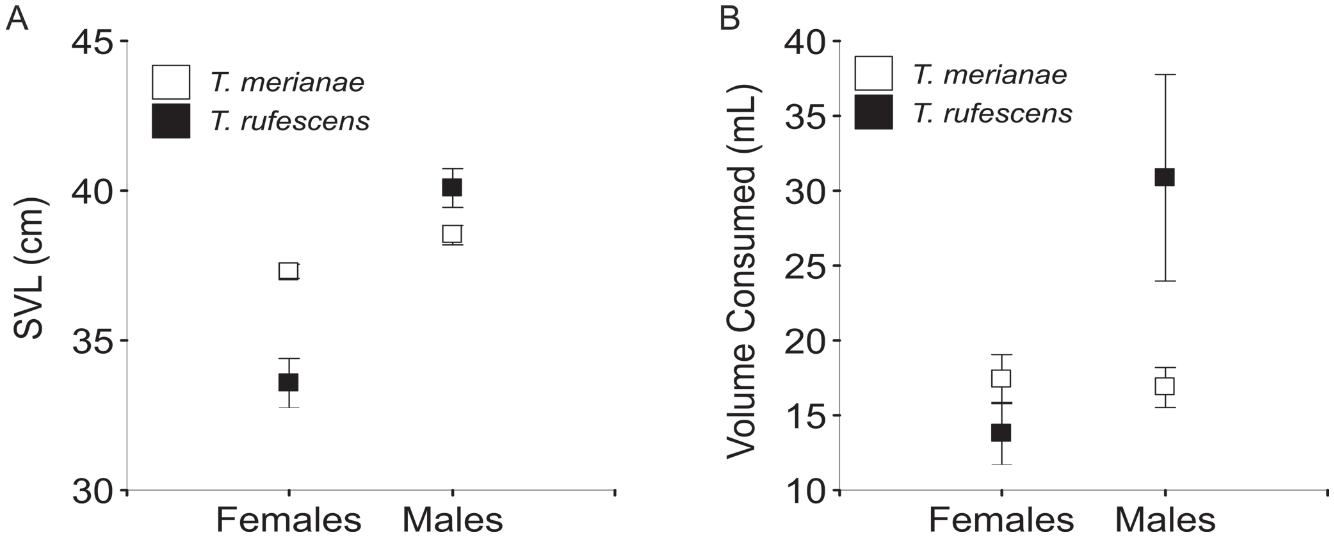

Figure 1. Sexual dimorphism measured as mean ± SE of **(A)** snout–vent length (SVL) and **(B)** volume of food consumed in females and males of *Tupinambis merianae* and *T. rufescens.*

Table 2. Diet composition (Hierarchical Index of the Index of Relative Importance) of *Tupinambis merianae* and *T. rufescens* males and females.

HI	Native fruits and seeds	Exotic fruits and seeds	Arthropoda	Mollusca	Squamata	Aves	Mammalia
T. merianae ♂	1.67	1.19	**100**	0.65	3.73	6.3	19.86
T. rufescens ♂	**100**	3.24	58.22	17.83	4.46	0.72	5.43
T. merianae ♀	0.01	0.51	**100**	1.31	0.64	4.99	8.57
T. rufescens ♀	19.71	0.45	**100**	0.74	0	0	8.21

$P < 0.0001$), as well as differences in body size between species for each sex (males: W = 8757.5, $P = 0.0284$; females: W = 1082, $P < 0.0001$) (Fig. 1A). Males and females of *T. merianae* and *T. rufescens* consumed a similar volume of food (ANCOVA: *T. merianae:* sex effect, $F_{1,421} = 0.94$, $P < 0.3325$; covariate effect $P < 0.0079$ and *T. rufescens:* sex effect, $F_{1,65} = 0.13$, $P < 0.7167$; covariate effect $P < 0.0079$) (Fig. 1B). Furthermore, we observed differences between species in the volume consumed in males (W = 8987.50, $P = 0.0101$) but not in females (W = 2350, $P = 0.6597$). Regarding diet composition, females of both *T. merianae* and *T. rufescens* consumed mainly Arthropoda, but they differed in the consumption of other food items. In males, diet composition differed markedly between species (Table 2). The PCA showed the widest and most diverse trophic niche in males of *T. rufescens,* whereas the niche of males and females of *T. merianae* and females of *T. rufescens* were similar (MANOVA, dependent variables: PC1 and PC2, independent variables: sex-species, F = 5.14, $P < 0.0001$) (Fig. 2).

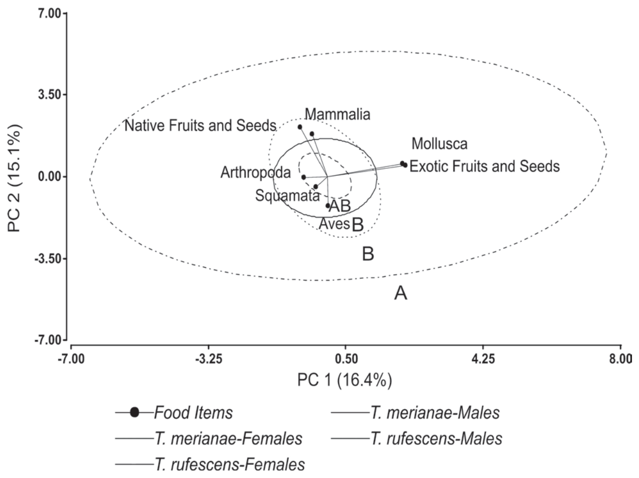

Figure 2. Principal Component Analysis characterizing trophic niche overlap in *Tupinambis merianae* and *T. rufescens*. An a posteriori test (Hotelling) was also performed: Different letters indicate significant differences.

The volume of food consumed by mature and immature individuals was similar (ANCOVA: *Tupinambis merianae:* maturity effect, $F_{1,421} = 1.73$, $P < 0.1895$; covariate effect $P < 0.006$ and *T. rufescens:* maturity effect, $F_{1,65} = 0.02$, $P < 0.8920$; covariate effect $P < 0.0078$). Moreover, mature individuals of *T. rufescens* consumed a higher volume of food than mature individuals of *T. merianae* (W = 18712.50, $P = 0.0048$), with no difference in immature ones between species (W = 114.5, 266, $P = 0.6017$) (Fig. 3). In mature individuals, the volume of some items differed between species (exotic fruits and seeds W = 134, $P = 0.05$; Arthropoda W = 3709, $P = 0.007$), but in immature individuals there were no differences between species (Table 3). Moreover, within mature individuals,

Table 3. Mean volume ± SD of each prey type consumed by immature and mature *Tupinambis merianae* and *T. rufescens* (* = $P < 0.05$).

	Immature		**Mature**	
	T. merianae	***T. rufescens***	***T. merianae***	***T. rufescens***
Native fruits and seeds	0	2.5 ± 0.71	17.66 ± 23.70	28.17 ± 62.17
Exotic fruits and seeds	3.2 ± 2.55	0.8 ± 0.00	2.28 ± 2.53	6.68 ± 7.25*
Arthropoda	1.81 ± 1.63	1.4 ± 1.12	6.13 ± 9.38	3.55 ± 5.08*
Mollusca	6 ± 0.00	0	1.71 ± 3.83	19.96 ± 30.57
Squamata	0	0	11.11 ± 12.96	4.2 ± 4.80
Aves	5 ± 0.00	0	18.85 ± 23.28	10.95 ± 14.21
Mammalia	5.5 ± 0.71	0	12 ± 18.68	8.5 ± 10.71

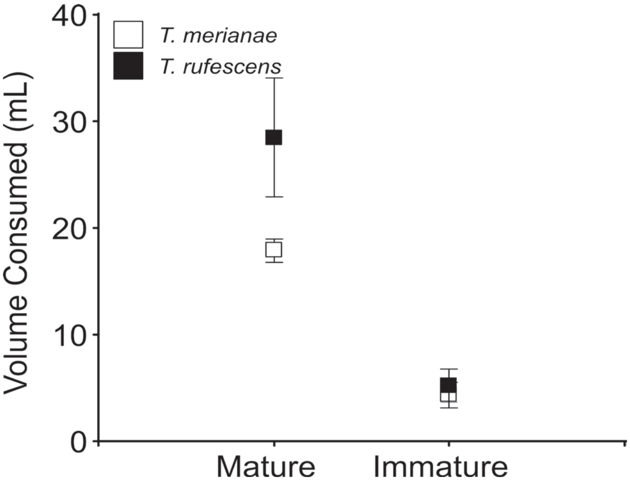

Figure 3. Mean volume ± SE of food consumed by immature and mature individuals of *Tupinambis merianae* and *T. rufescens*.

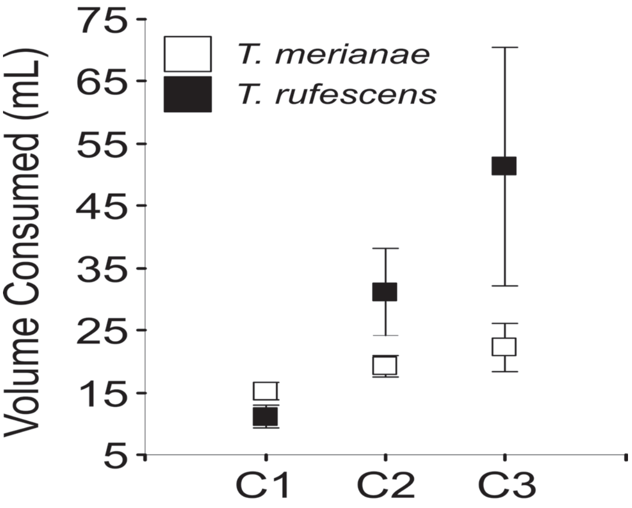

Figure 4. Mean volume ± SE of food consumed according to body size classes (C1–C3) of mature individuals of *Tupinambis merianae* and *T. rufescens*. See text for definition of size classes.

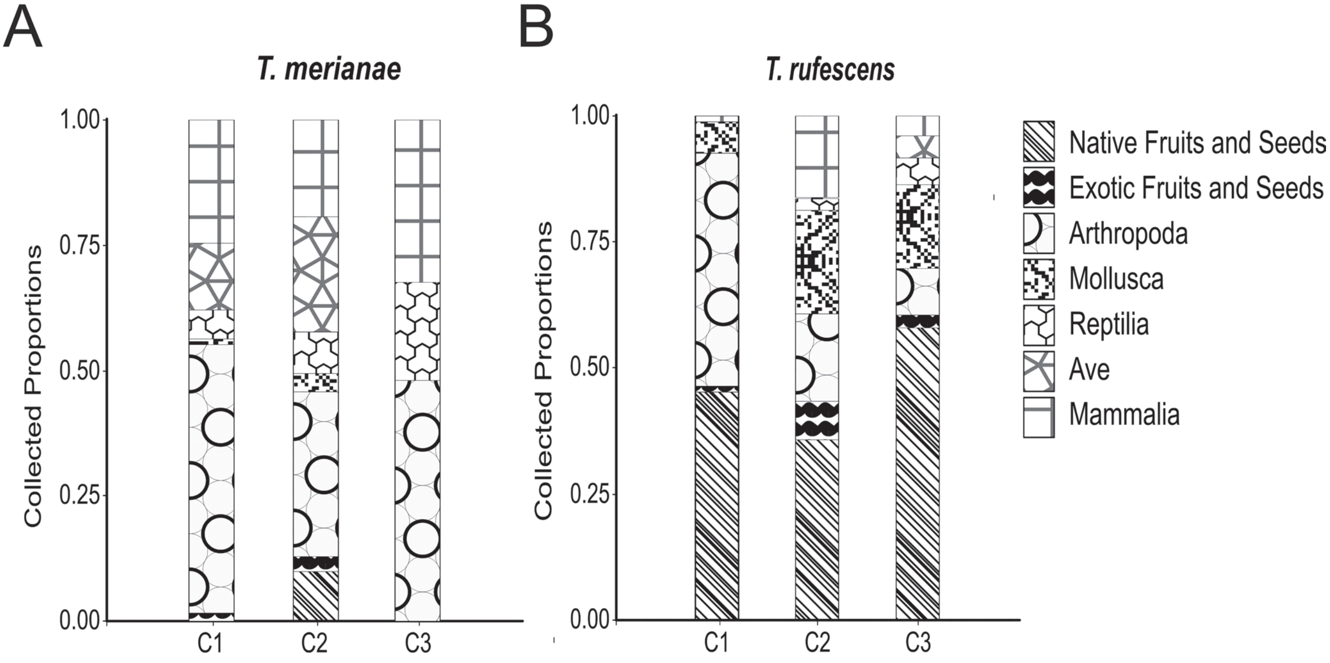

Figure 5. Variation in the volume of food consumed of each preys according to body size classes of **(A)** *Tupinambis merianae* and **(B)** *T. rufescens*.

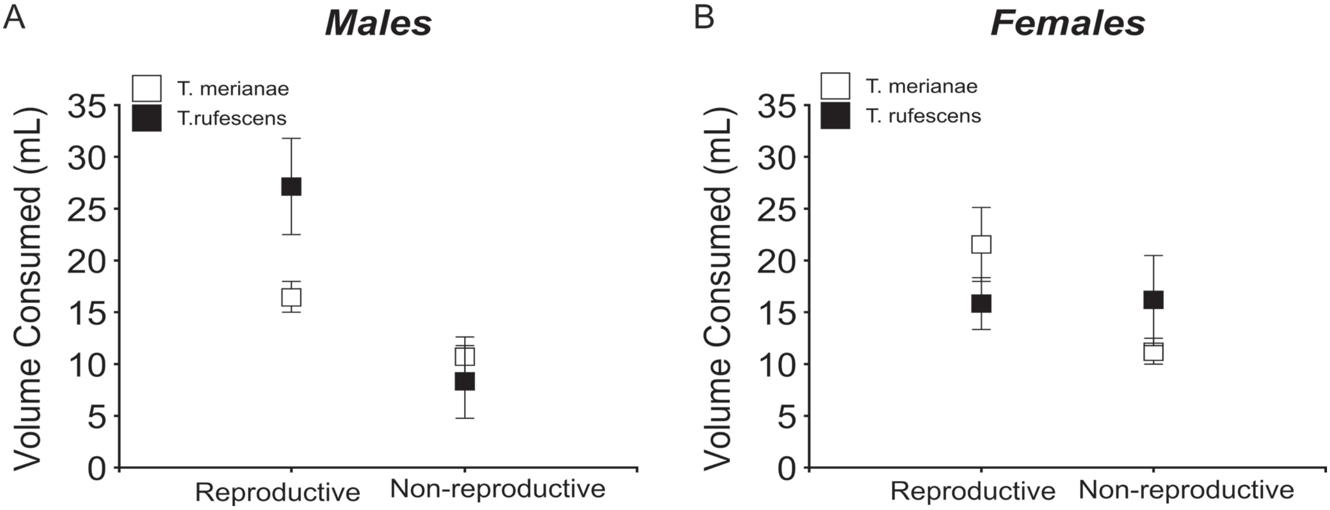

Figure 6. Temporal variation in the mean volume ± SE of food consumed by *Tupinambis merianae* and *T. rufescens* males **(A)** and females **(B)** (October–December: reproductive period, January–March: non-reproductive period).

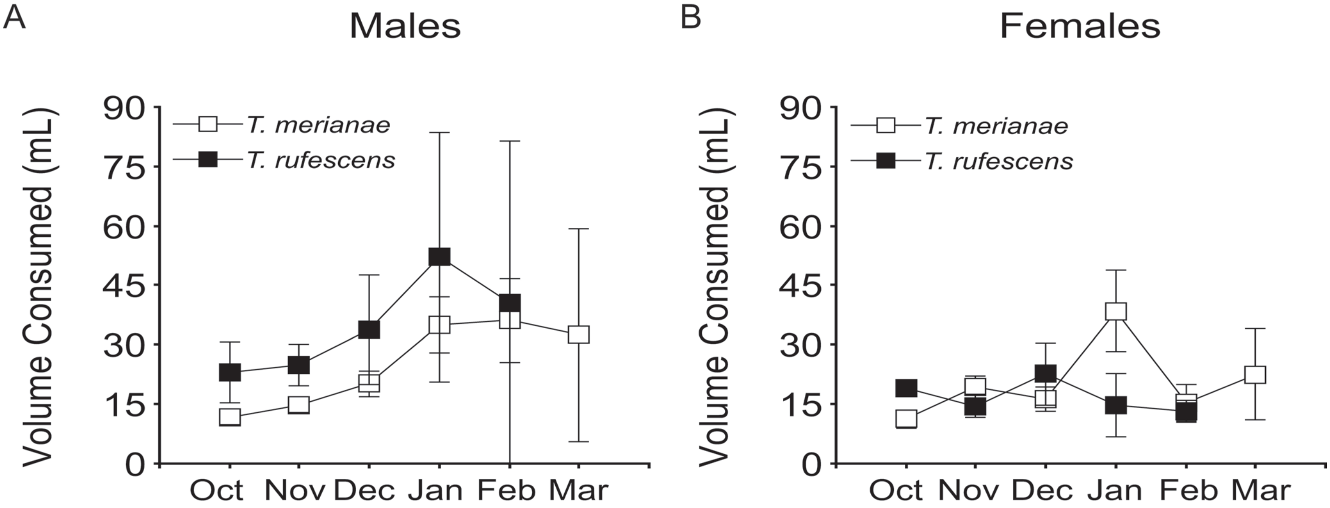

Figure 7. Mean volume ± SE of food consumed taking into account the reproductive condition of *Tupinambis merianae* and *T. rufescens* **(A)** males and **(B)** females.

the volume consumed differed between species in C2 (H = 5.65, $P = 0.0172$) and C3 (H = 5.24, $P = 0.0219$) but not in C1 (H = 0.03, $P = 0.8699$) (Fig. 4). C1 individuals consumed a great proportion of Arthopoda in both species, C2 individuals presented high diversity of food items in both species, and C3 individuals of *T. merianae* based their diet on fewer food items than C3 individuals of *T. rufescens* (Fig. 5).

Mature males and females of *Tupinambis merianae* consumed a lower volume in the reproductive period than in the non-reproductive period (Male H = 17.15, $P = 0.0039$; Female H = 16.97, $P = 0.0042$). Mature males and females of *T. rufescens* consumed a similar volume in both reproductive and non-reproductive periods (Males: H = 1.18, $P = 0.8809$; Females: H = 1.61, $P = 0.8051$) (Fig. 6A–B). Furthermore, reproductive males consumed a significantly greater food volume than non-reproductive males in both species (*T. merianae:* W = 7312.50, $P < 0.0001$, *T. rufescens:* W = 57.50, $P < 0.0001$) (Fig. 7A). Reproductive males of *T. rufescens* consumed a significantly higher food volume than their *T. merianae* counterparts (W = 4042, $P = 0.0052$). In *T. merianae* reproductive females consumed a significantly greater food volume than non-reproductive females, but in *T. rufescens* non-reproductive females consumed a greater food volume than reproductive females (*T. merianae:* W = 11837.50, $P < 0.0001$, *T. rufescens:* W = 101.50, $P < 0.0001$) (Fig. 7B).

DISCUSSION

Our findings show that *Tupinambis merianae* and *T. rufescens* feed on diverse plant and animal prey items. Accordingly, Williams *et al.* (1993) reported omnivory in

T. rufescens from northwestern Argentina. However, the Levin's Index values indicate that, although both species are omnivorous, they exhibit a tendency to be specialists, with some items being dominant, such as Arthropoda in the diet of *T. merianae* and native fruits and seeds in the diet of *T. rufescens.*

The values of Morisita's index indicate broad trophic niche overlap between species. However, although both species share several prey items, the relative importance of each item varied between them. These differences may be important for niche segregation, mainly because the prey items considered fundamental were different between species, suggesting a differential use of certain resources (Lelièvre *et al.,* 2012). Accordingly, Cardozo *et al.* (2012) observed that although morphological similarity should induce niche similarity. Despite of both species selected the same landscape *T. rufescens* are associated with greater forest cover than *T. merianae,* which could be related to their diet preference for native fruits and seeds. Moreover, Cardozo *et al.* (2012) found that *T. merianae* is associated with anthropogenic areas with cultural vegetation and remnant shrublands where few vertebrate species remain (Chebez, 2008), which could explain the low diversity of food items and the dominance of arthropods and some rodents in the diet composition.

The feeding rate was higher for *Tupinambis rufescens* than for *T. merianae.* Body size has important effects on individual feeding rates because larger predators consume more prey than smaller individuals (González-Suárez *et al.,* 2011). Males of *T. rufescens* have a large body size, which might contribute to the high feeding rate in this species. However, females, which are small-sized, also presented a high feeding rate. These differences in feeding rate between species might be caused by a need to consume a greater amount of food items or to differences in digestion rate related to different type of prey items consumed.

Tupinambis merianae and *T. rufescens* showed sexual size dimorphism biased to males; therefore, we would have expected differences in trophic niche between sexes. However, Morisita's Index showed trophic niche overlap between sexes of both species. Similarly, other studies focused on sexually dimorphic lizards did not find sexual differences in the types of selected prey (e.g., Zaluar and Rocha, 2000; Kolodiuk *et al.,* 2010; Sales *et al.,* 2011, 2012). Therefore, morphological differences could be also shaped by other selective pressures such as sexual selection forces (Naretto *et al.,* 2014). However, differences in the diet between males and females would be greater in *T. rufescens* than in *T. merianae,* which could be associated with the different degree of sexual dimorphism between species. Likewise, the volume of consumed items was similar between sexes in *T. merianae.* The great volume of native fruits and seeds consumed by *T. rufescens* males might be related to the high energetic requirements imposed by their large body size and reproductive behaviors (Naretto *et al.,* 2014). Native fruits are considered an important food resource for wild animals because they provide important nutrients, such as sugars and, therefore, a quick energy source (Silva *et al.,* 2000; Nogués *et al.,* 2013).

We observed that *Tupinambis rufescens* males are larger and consumed a greater volume than males of *T. merianae.* We also observed that females of *T. merianae* are of greater body size than *T. rufescens* females, which is expected to contribute to diet segregation between females of different species. Indeed, *T. merianae* females complemented their diet with larger prey, such as Mammalia, whereas *T. rufescens* females consumed smaller items, such as native fruits and seeds. Differences in body size between sympatric lizards explained by sexual differences would be associated with differences in the size of the ingested prey. Body size can clearly limit the size of the prey consumed by lizards at both inter- and intraspecific levels (Carretero *et al.,* 2006; Freitas, 2012); hence, lizard size, which is related to bioecological constraints such as gape limitation or small territory, may prevent small lizards from choosing large prey species (Suarez *et al.,* 2000).

Immature individuals consumed a similar amount of food in both species; at maturity, however, individuals of *Tupinambis rufescens* consumed a greater volume than individuals of *T. merianae.* These observations indicate that sexual maturity is an important factor differentiating diet between species. The high food requirement after maturity could lead to specific diet diversification in adults; in fact, we observed interspecific divergence in the consumption of some food items by mature individuals. In addition, diet composition was more varied in mature than in immature individuals. Immature individuals often show a narrower spectrum of prey sizes than adults (Pianka, 1986; Carretero, 2006), which could be related to the amount of energy allocated to reproduction (Wapstra *et al.,* 2001). Moreover, juvenile lizards are limited by their smaller body, head and mouth than adults, resulting in a narrower range in the size of potential prey available (Vitt, 2000); they are also limited by bite force (Erickson *et al.,* 2003; Herrel and O'Reilly, 2006) and prey handling performance (Mehta, 2003, Sales *et al.,* 2012).

Within mature individuals, the volume of food consumed increased in animals of large body size, suggesting an intensification of competition on food resource in bigger-sized classes. Accordingly, our results indicate that in group C1, in which food volume consumed is low and consequently competition would also be low, both species base their diets on arthropods. By contrast, in group C2, competition might lead to diet diversification and differentiation between species. In group C3, the niche becomes broader, with dominance of native fruits and seeds for *Tupinambis rufescens,* whereas for *T. merianae* diversification of prey items is limited and Arthropoda is dominant (probably due to the limitation in prey availability in anthropogenic environments). Body size probably affects not only diet volume but also diet composition (Magnusson and da Silva, 1993); consequently, as we observed in *T. rufescens,* despite incorporating larger prey into their diet, the largest size classes continue to consume small prey consistently, leaving minimum prey size constant and increasing niche breadth (Sales, 2011). In *T. merianae* consumption of large prey such as Mammalia is not only feasible but also advantageous in terms of energy gain, although some large lizards may also consume small and abundant prey available in the habitat, such as Arthopoda, due to the low energy costs associated with their capture and ingestion (e.g., Siqueira *et al.,* 2013). Therefore, the observed differences in the diet associated with body size reveal that interspecific niche segregation in the largest size class.

Regarding the relationship between reproduction and feeding, during the reproductive period individuals of both species in general consumed a lower volume than in the non-reproductive period. This difference may be caused by the greater time devoted to reproductive activities (territory defense and mate search, courtship and copulation, egg incubation) at the expense of feeding. Furthermore, during the reproductive period the individuals that reached the reproductive condition consumed a greater amount of food than non-reproductive individuals. In reproductive males, gonad and sexual character development might involve high costs (Olsson *et al.,* 1997; Kvarnemo and Simmons, 2013; Naretto *et al.,* 2014; Blengini *et al.,* 2014), probably increasing food consumption. Similarly, reproductive females likely consume a great amount of food to sustain their enormous energy allocation to reproduction (Starostová, 2013). Food resource availability has been invoked as one of the most important drivers of reproductive investment, affecting clutch and offspring size trade-offs (Jordan and Snell, 2002; Olsson *et al.,* 2002). However, in *Tupinambis rufescens* reproductive females consume less food than non-reproductive females. In some reptile species, pregnant females have been found to reduce food intake or even stop feeding, a phenomenon known as anorexia (Shine, 1988). Anorexia may be due to several causes: abdominal space limitation to accommodate both embryos and prey items; a loss of appetite intrinsically associated with gestation, due to changes in hormonal balance (Bonnet *et al.,* 2001); low foraging success due to behavioral changes in gravid individuals (i.e., thermal needs or predator avoidance) (Lourdais *et al.,* 2002).

Our results provide evidence for the important of native forest as a food source for *Tupinambis*. *Tupinambis rufescens* was strongly dependent on fruits of native vegetation, whereas *T. merianae,* despite being more generalist in the use of trophic resources, relied on local biodiversity for feeding. The loss of native habitat and the associated reduction in food quality will make it more difficult for animals to meet their nutritional and energy needs (Hoyos *et al.,* 2010; Nelson *et al.,* 2000). Further, native vegetation has been highly modified in several ecosystems by anthropogenic activities, and this change in habitat structure may increase the risk for lizards (Whittingham and Evans, 2004).

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