Research Article

Age and habitat quality matters: isotopic variation of two sympatric species of rodents in Neotropical Forest

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Abstract

Dietary studies allow us to understand important ecological patterns such as intra- and interpopulation variation and interspecific differences regarding the use of food sources. Stable isotopes have been successfully employed to detect dietary differences between species and feeding shifts within a species, as a response to age, habitat use, and resource availability. Here we investigated the stable isotope compositions of carbon and nitrogen of young and adult specimens of *Euryoryzomys russatus* and *Sooretamys angouya* and their stomach contents, in a complex mosaic of vegetation in the Brazilian Atlantic Forest. Isotopes indicated a pronounced inter- and intraspecific plasticity in resource use for *E. russatus* and *S. angouya*. Plant sources were the prevalent feeding itens for *E. russatus*, with low to intermediate consumption of arthropods. For *S. angouya*, plants were dominant in the stomach content, but arthropod arose as an important source. *E. russatus* showed more variation in isotopic signature between grids than *S. angouya*, suggesting that the former was more affected by habitat changes. These results allow us to better understand the ontogeny, diet and the behavioral responses to environmental variations of both species. Finally, our study contributes to reduce the lack of knowledge about sympatric species ecology and aggregates information for their conservation.

Introduction

How closely related species co-occur and interact in a community has long fascinated ecologists. Resource distribution and resource use are two of the many ecological factors that influence the niche of a given species (Elton, 1927; Hutchinson, 1957). Sympatric species with similar life-history traits, such as different species of rodents in the same habitat, should be able to coexist because they share resources through time and/or space (Gause, 1934). Niche partitioning can be the result of numerous factors including past and present competition, arrival order, relative abundances, resistance to disturbance and their combination (Olmos, 1991; Barton, 2014), generally leading to avoidance of competition allowing coexistence (Turnbull et al., 2013; Galetti et al., 2016). One of the resources that might be shared among coexisting species is food, and the comparison of the diets between sympatric species can help to detect the occurrence of dietary niche partitioning as a mechanism to avoiding the competition (Kotler and Brown, 1988; Biro et al., 2005).

The Atlantic Forest of Brazil, a global hotspot for biodiversity (Myers et al., 2000), hosts several sympatric species of rodents, as it harbors a high diversity of non-volant small mammals including 22 species of marsupials (Didelphidae) and 97 species of small rodents (da Silva et al., 2004; Visconti et al., 2011; Paglia et al., 2012). However, little is known about how species co-habit in the same assemblages and how they use food resources, especially rodents. For this group, there is a particular difficulty in evaluating their diet based on stomach or fecal samples contents due to the intense chewing process food resources go through when digested, which transforms animal and plant items in very small fragments (Hansson, 1970). The difficulties of conducting dietary studies have long been discussed (Norman, 1970; Duffy and Jackson, 1986; Pinotti et al., 2011) and available studies support the use of other techniques in order to generate more precise and comprehensive knowledge on dietary habits of rodent species.

The analysis of natural occurrence of stable isotopes, especially the isotopic ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$), has been used to differentiate and better understand the diet habits and trophic dynamics of different species (Fry, 1988; Forsberg et al., 1993; Dalerum and Angerbjorn, 2005). Stable isotopes techniques can detect dietary differences between different species and also intraspecific diet shifts related to habitat use and resource availability (Blüthgen et al., 2003; Sare et al., 2005; Nakagawa et al., 2007; Voigt et al., 2008; Galetti et al., 2016). The variation of diet within (age, sex and sampling sites) and between species may be present at some developmental stages throughout an individual's lifetime (Lambin, 1994), therefore contributing towards an individual fitness, the structure and density of the population where it belongs, and the ecological interactions in which the species is involved (Ricklefs, 1990; Hughes et al., 1997).

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Euryoryzomys russatus (Wagner, 1848) and *Sooretamys angouya* (Fischer, 1814) are two sympatric, phylogenetic related species, that also exhibit similar life-history traits (Carvalho et al., 1999; Bergallo and Magnusson, 2002; Casella et al., 2003; Vieira et al., 2006; Pinotti et al., 2011; Galetti et al., 2016), being therefore a suitable model system to investigate food resource partitioning. Both species are members of the tribe Oryzomyini (Sigmodontinae, Cricetidae), and co-occur from the Serra do Espinhaço in Minas Gerais and Espírito Santo states to the Rio Grande do Sul state in north-south direction, and from the Atlantic coast of Southern Brazil to the eastern Paraguay and northern Argentina in east-west direction (Percequillo, 2015a,b), being syntopic in several sites throughout this region.

These two rodents have been shown to respond differently to changes in successional stages of forest habitat and habitat fragmentation in the Atlantic forest of Brazil (Pardini, 2004; Pardini et al., 2005; Pardini and Umetsu, 2006; Umetsu et al., 2008; Pardini et al., 2010). For example, Umetsu and Pardini (2007) showed that abundance of the russet rice rat *E. russatus* (a forest specialist species endemic to the Atlantic biome and considered an endangered species in São Paulo State (SMA, 2014), is correlated to landscape structure. In particular, abundance of *E. russatus* showed a strong positive response to the amount of forest and forest patch size (Umetsu et al., 2008; Pardini et al., 2010). Regarding *S. angouya*, it is not clear whether the quality of the fragment (e.g. size and percentage of forest cover) may or may not influence its abundance, but the connectivity among patches might have a positive effect on this species (Pardini et al., 2005; Pardini and Umetsu, 2006).

In this study, we aimed to verify if there were significant differences in the diet and isotopic assimilation between *E. russatus* and *S. angouya*. Considering that both species are syntopic, exhibiting ecologic and phylogenetic affinities, we aim to compare their diets to detect the occurrence of dietary partitioning as a mechanism to avoiding the competition. At first, we assessed the intraspecific differences related to age, sex and sampling sites for both species, prior to test interspecific differences, in order to evaluate possible mean ontogenetic dietary shifts. We subsequently compared these results to a pool of food sources such as plant and arthropods sampled at the same sites, testing the differences among species and their habitats. Also, we assessed stomach contents of adult individuals and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition of hair from juvenile and adults from a locality of the Atlantic Forest Plateau in southeastern Brazil. We expect that the patterns observed in this study may enlighten our knowledge of an endangered and of an elusive species, *E. russatus* and *S. angouya*, respectively.

Materials and methods

Study site

The Reserva Florestal do Morro Grande (RFMG), located at 23°29'-23°48' S, 47°1'- 46°55' W, is a forest reserve in Cotia municipality, São Paulo State (Fig. 1); it has an area of 10870 ha of continuous forest, assembling a complex mosaic of vegetation with secondary forests in different regeneration stages and areas which probably passed through clear cutting (Metzger et al., 2006). The RFMG represents one of the more extensive forested patches in the Atlantic Plateau of São Paulo State (Veloso et al., 1991), and it is recognized by its high conservation value (Metzger et al., 2006). The vegetation is classified as lower montane Atlantic Rain Forest (Veloso et al., 1991; Oliveira-Filho and Fontes, 2000; Catharino et al., 2006), with summer temperature ranging from 19.7 °C to 20.6 °C and winter temperature from 13.3 °C to 17.7 °C. Precipitation occurs throughout the year, with rain peaks from November to March and July to September.

Data collection

We sampled three grids, each at one different RFMG location. Each grid covered an area of two hectares (100×200 m), using 11 trap lines separated by 20 meters; each trap line consisted of 11 trap stations apart 10 m, and each station have a single Sherman live-trap (H.B. Sherman Traps, Inc., Tallahassee, Florida) on the ground, with large

(37.5×10.0×12.0 cm) and small (23.0×7.5×8.5 cm) traps placed alternately along the trap line; additionally, we employed five pitfall trap lines consisting of 11 units of 60 L buckets (53.0 cm in depth and 40.0 cm in diameter) connected by a 50-cm high plastic fence, placed along five of the trap lines. All grids (M1, M2 and M3) were placed in secondary forest in intermediary stage of regeneration in order to represent similar successional stages, but there were some differences on the structure of each forest, as M3 area was characterized by a dense understory and higher and more closed canopy than the other two (Fig. 1). All Sherman traps were baited with a mixture of sardines, peanut butter, banana, and cornmeal. Pitfall traps were not baited. All small mammals and food sources were sampled at these three grids inside the RFMG.

Small mammals

We conducted monthly surveys at each site simultaneously for five days from April 2009 to January 2010, and two campaigns in July 7th to 23th, 2010 and January 14th to 28th, 2011. We marked all individuals with numbered ear tags (Small Animal Tags OLT; A. Hartenstein GmbH, Würzburg-Versbach, Germany), recording their sex, body size, proportion of head and hind foot to body size, and other morphological characteristics (Bonvicino et al., 2008). We considered here only juvenile and adult individuals following the criteria of the change of hair and reproductive stage (Percequillo, 2003) to avoid the transitional diet of sub-adults, as long as we are not interested in the turnover of the dietary shift. All collected hair samples were placed in labeled Eppendorf tubes and stored in −16 °C freezer before laboratory processing. All capture, handling, and tagging techniques followed the guidelines of the American Society of Mammalogists (Sikes, 2016).

Plant sources

We sampled plant sources from July 7th to 23th, 2010 and January 14th to 28th, 2011. We took samples of fruits and seeds in all trap lines used for small mammals trapping. All trap lines were surveyed throughout their extension once in each campaign to search and collect fruits and seeds available in the trees or in the soil. We pooled together the samples from both field campaigns. We collected 435 fruits and seeds and identified them to the maximum taxonomic level. The samples were stored at −16 °C in a freezer before the laboratory processes.

Arthropod sources

We sampled arthropods from July 7th to 23th, 2010 and January 14th to 28th, 2011. We collected arthropods with small pitfall traps (400-ml plastic cups) filled with 92% alcoholic Ethanol solution installed in the Sherman-only trapping lines. Each line had six pitfall traps installed
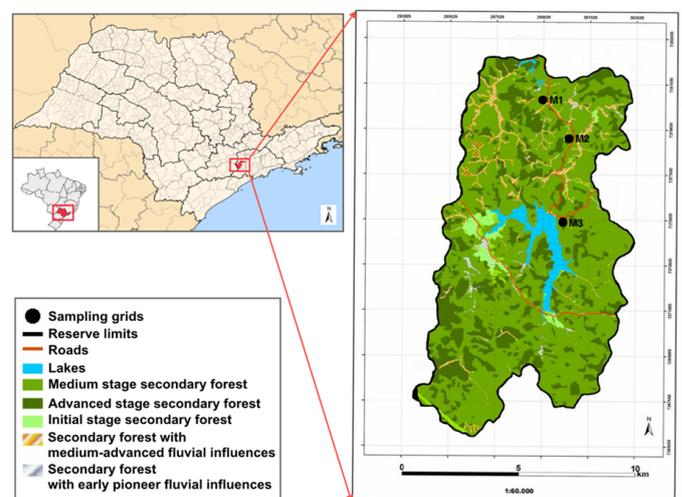

Figure 1 – Map of the São Paulo state, Brazil, highlighting the Morro Grande Reserve, where the three locations Ml, M2 and M3 are plotted (source: LEPaC, adapted).

distant 20 meters to each other. Each grid has six Sherman traps lines adding to 36 pitfall traps for arthropods per day per grid. The pitfall traps remained open during 16 days on July and 14 days during January, with daily maintenance. Also, we pooled together the samples from both field campaigns. We obtained a total of 216 pitfall trap samples. We counted the arthropod individuals and identified them to the maximum taxonomic level (order or family) possible. We estimated the frequency of occurrence of each arthropod order in the wild by calculating the ratio between the number of individuals of the group and the total number of arthropod individuals. The voucher material of arthropods is housed at the Laboratório de Zoologia de Vertebrados, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo.

Stomach content

We obtained adult individuals for stomach content analyses during two capture sessions, July 7th to 23th, 2010 and January 14th to 28th, 2011, trapped as described above. The collected specimens were deposited in the Museu de Zoologia of the Universidade de São Paulo, under the license SISBIO-15733-1. For analyses, we pooled together the individuals from both field campaigns. We analyzed stomachs that showed a considerable amount of food, counting three stomachs of *E. russatus* from grid M1 (field numbers: 6529, 6627, 6863); four stomachs of *E. russatus* from M3 (6509, 6510, 6513, and 6792) and only one specimen of *S. angouya* (6852) from grid M3; no stomachs were available from grid M2. We employed on the stomach content analyses individuals sampled with pitfall traps, as their stomachs contents do not possess bait employed in the traps; we also included in the analyses, specimens caught with conventional traps that presented no traces of bait at the stomach. Astra blue dye (1%) was used to color the cellulose and Safranin dye (0.25%) was employed for lignin, in order to differentiate particles of plant sources from the animal ones (Hansson, 1970). Further, the stomach contents were screened in Petri dish and examined under a stereomicroscope.

Arthropod fragments found in stomach contents were separated and identified to the order or family taxonomic levels. We estimated the frequency of occurrence of each group of arthropods by calculating the ratio between the number of stomachs where it occurred and the number of stomachs analyzed. The identification of the stomach contents was based on the available literature (Gallo et al., 1988; Almeida et al., 1998) and also provided by specialists from the Departamento de Entomologia e Acarologia of Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo (ESALQ-USP) and Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil.

In order to assess how much each food category (arthropods, plants and not identified) contributed to the amount of stomach contents, we dry weighted the contents and calculated the ratio between the categories of food items by the total amount of contents for each stomach. We then calculated the average and standard deviation of these proportions by species (Swynnerton and Worthington, 1940; Hynes, 1950). As there is one stomach available of *S. angouya*, we ought to be conservative and cautious regarding most aspects of its contents; we are aware that our statements are easily falsified. However, this is the first instance on the description of the stomach content of this species, and represents a valuable opportunity to discuss under the light of the isotopic evidence.

Stable isotope treatment

Plant and arthropod sources

All the fruits and seeds were analyzed separately, as species or morphogroup, to compare the isotopic composition of each plant item to the isotopic composition of the consumers (Ben-David and Flaherty, 2012). The arthropods were analyzed similarly, but they were grouped by order rather than by species or morpho-group.

Small mammals

We used hair samples as our source of isotopic composition from the small mammals because they represent a long-term average of an individual diet (Tieszen et al., 1983). Regarding the variation in tissue turnover rates among organs (Peterson and Fry, 1987; Lajtha and Michener, 1994), hairs are a good source to estimate the general diet from specimens captured in the wild and provide precise information about their ages and consumed items. Besides, hair samples have been widely used in isotopic analyses (Panarello and Fernández, 2002; Cryan et al., 2004), and they are easily collected without requiring the euthanasia of the animal (Sare et al., 2005; Nardoto et al., 2006; Navarro, 2009).

Hair samples were collected from the hindquarter dorsal pelage with tweezers for every captured individual of *E. russatus* and *S. angouya*. In total, we obtained 100 hair samples for *E. russatus* (Table S1), and 32 for *S. angouya* (Table S2), though later we excluded samples from subadult in our analyses. We avoided the use of subadult samples because mammals change hair throughout their development, thus isotopic values from subadult hairs might represent a past diet but not the current one (Miller et al., 2008).

Isotopic analytical procedures

The food source samples were ordered by genera or species level for plants, and by order or family level for arthropods. All samples (plants, arthropods and small mammal hairs) were dried in a laboratory oven at a temperature of 65 °C for up to three days until they had achieved constant weight, and then fragmented into smaller pieces. The samples were put separately in tin capsules and analyzed in a Carlo Erba CHN-1110 elemental analyzer coupled to a Thermo Finnigan Delta Plus mass spectrometer. The adjustment standards used were fossil Belemnite calcareous rock of Pee Dee formation (PDB) for carbon and atmospheric air for nitrogen. The sample mass used and the standard deviation in each capsule was 1.26 ± 0.42 and the standard deviation for replicate samples used in this analysis was 0.14‰ for $\delta^{13}C$ and 0.08‰ for $\delta^{15}N$. The isotopes analysis was conducted on Laboratório de Ecologia Isotópica – CENA-USP. We calculated and used the isotope Carbon/Nitrogen ratio using the formula:

$$ratio = (cb/n)*(-1)$$

in which: $cb=\delta^{13}C$ (Carbon value extract from hair samples); $n=\delta^{15}N$ (Nitrogen value extract from hair samples) and reference -1 (Ishiwatari and Uzaki, 1987).

Intraspecific variation analyses

The stable isotope technique can be very sensitive to environmental variability related to the forest structure and plant diversity (Tieszen, 1991). Thus, when was possible, we used samples from the same grid to perform the statistical analyses for each species separately, in order to reduce the interference of habitat variability in the intraspecific analyses.

We performed a non-parametric Mann-Whitney test to compare mean isotopic ratio values between adult males and females for both species, to exclude the possibility of the influence of sex of the individuals on comparisons between ages and/or species. We used the samples from grid M3 for *E. russatus*, but we pooled together, just for this analysis, the samples from three grids for *S. angouya*, because the sample size of this species precluded such detailed statistical approach to verify dimorphism. There were no statistical differences between males and females of both species for $\delta^{13}C$ and $\delta^{15}N$ values (all $p>0.05$; Table S3). Therefore, we pooled both sexes on all subsequent univariate analyses.

We used the samples of *E. russatus* from the area M2 and the sample of *S. angouya* from area M3 to verify separately the variation related to age. We constructed scatterplots with 95% confidence interval bars (Zar, 1996; Simpson et al., 2003) using the $\delta^{13}C$ and $\delta^{15}N$ values for age classes and food sources by area. We considered that when confidence intervals do not overlap, there is a statistically significant difference between the means at the 5% level (Cox and Hinkley, 1974; Zar, 1996; Cumming et al., 2007; Krzywinski and Altman, 2013).

Interspecific variation analyses

For interspecific comparisons, we used the data only from M1 and M3 grids, because we did not obtain stomachs with food items in the grid

M2. We used the isotopic data from *E. russatus*, *S. angouya* and the food sources from M1 and M3 separately, to avoid possible habitat influence in the statistical analyses. Also, we constructed scatterplots plotted with individual values as well as the 95% confidence interval bars (Zar, 1996; Simpson et al., 2003) for each isotopic value for species and food sources (plants: species or morpho-group; arthropod: order or family) from each area (Ben-David and Flaherty, 2012).

We further created 9 Linear Mixed Effects Models using maximum likelihood estimation (in the `lme4` package; Bates et al., 2015) in program R to test the effects of grid, plant and arthropod sources and their interactions in the models (Table S4) for the isotopic values of Carbon/Nitrogen ratio of *E. russatus* and *S. angouya*. We fitted models to a Gaussian distribution for isotope values. Having fitted these models, we then compared them by their AIC value (where the best model had the lowest AIC value). For the best model we assessed the relative importance of variables using model averaging by the `MuMIn` package (Barton, 2014) in R.

Results

Small mammals

Our total trapping effort was 9,680 trap-nights for each grid, including 5,280 live trap-nights and 4,400 pitfall trap-nights. We captured 100 individuals of *E. russatus* (Table S1) and 32 *S. angouya* in M1, M2 and M3 (Table S2). For *E. russatus* we captured 84 adults, 9 sub-adults and 7 juveniles and for *S. angouya* we capture 10 adults, 12 sub-adults, 10 juveniles. We captured most of individuals of *S. angouya* in M3 (N=25), and most of *E. russatus* in M2 (N=40).

Food sources

The fruits and seeds collected belonged to eight plant species in grid M1 (*Solanum* sp., *Ocotea* sp., *Pauterea* sp., *Dicella holosericea*, *Merostachys riedeliana*, Rubiaceae sp.2, *Syagrus rommanzoffiana*, *Miconia cinnamomifolia*), 10 species in M2 (*Campomanesia* sp., *Eugenia* sp., *Mollinedia* sp., *Myreia* sp., *Tovomitopsis paniculata*, *Psychotria suterella*, *Mendoncia velloziana*, *Scheflera* sp., *Alibertia edulis*, *Cupania oblongifolia*) and 11 species on grid M3 (*Podocarpus sellowii*, *Eugenia* sp., *Cedrela ordorata*, *Lytocarium hoehnei*, *Geonoma* sp., *Psychotria* sp., *Euterpe edulis*, Rubiaceae sp.1, Rubiaceae sp.2, *Syagrus rommanzoffiana*, *Miconia cinnamomifolia*).

Regarding the arthropod sampling, we collected and identified 13 arthropod groups present in all grids: Acari, Araneae, Archaeognatha,

Blattodea, Coleoptera, Crustacea (woodlouse), Dermaptera, Diptera, Hymenoptera Fomicidae, Hemiptera, Hymenoptera (excluding Formicidae), Opiliones and Orthoptera.

Intraspecific variation

We found that age differences were significant between juveniles and adults for *E. russatus* only for $\delta^{15}N$, as their confidence intervals did not overlap (Fig. 2). Juveniles presented significantly enriched values of $\delta^{15}N$ in comparison to adult *E. russatus* and food sources. Both age classes for *E. russatus* had significantly higher carbon isotope mean values than the food sources. However, *S. angouya* did not show significant variation due to age for isotopic values (Fig. 3), and both ages showed lower $\delta^{15}N$ values than arthropod items and higher than plant ones. The species also presented higher $\delta^{13}C$ mean value than plant sources.

### Interspecific variation

Stomach contents

The bulk of dry weighed of food items on the stomach contents of *E. russatus* present in both grids was plant material followed by unidentified material and arthropods (Tab. 1). We found that all stomachs from *E. russatus* in both M1 and M3 areas contained ants (Formicidae) and most of them also beetles (Coleoptera, Fig. S1 and S2). Although these were the most frequently consumed arthropod groups, they presented lower frequency of occurrence in the grids than Diptera, which was the most common arthropod group sampled in both areas. Concerning other arthropod groups, *E. russatus* from M1 presented Diptera, Aranae and Myriapoda. The individuals from M3 consumed other groups, as Blatoidea, Hymenoptera (excluding ants), Orthoptera, Psocoptera and Acari. Groups as Archaeognatha, Crustacea, Dermaptera, Hemiptera, and Opiliones, although were found in the grids, they were not identified in the stomach contents of *E. russatus*. Nevertheless, Myriapoda and Psocoptera, which were detected as food items, were not found in the pitfall traps. Concerning *S. angouya*, the contents of the only stomach analyzed, 93.38% of the dry biomass was plant material, 6.62% unidentified materials and only one small arthropod fragment belonging to Araneae (Fig. S2), with negligible mass.

Stable isotopic signatures

E. russatus and *S. angouya* presented different enrichment patterns of $\delta^{15}N$ and $\delta^{13}C$ compared to each other (Tab. 2). Both species presented significantly enriched values of $\delta^{15}N$ and $\delta^{13}C$ in comparison to
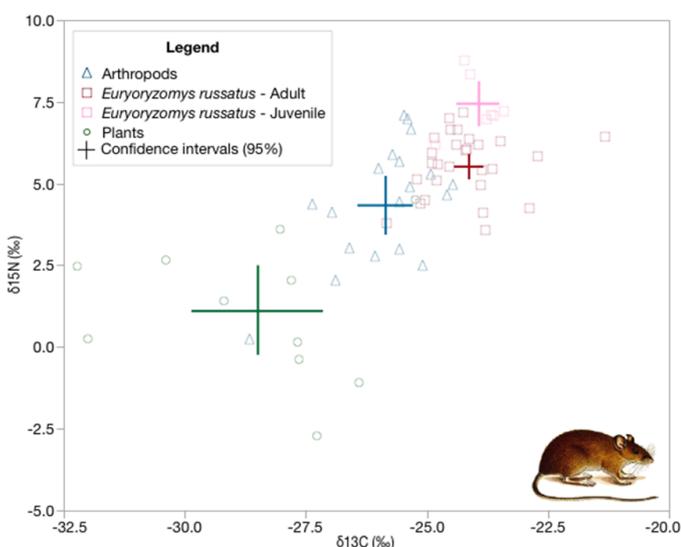
Figure 2 – Scatterplot showing the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition of hair from juvenile (pink square) and adult (red square) individuals of *Euroryzomys russatus* from M2 sampling area, and its arthropod (blue triangles) and plant (green circles) food sources. The bars represent 95% confidence intervals and they cross at the mean value of each isotope composition of each category of correspondent color.
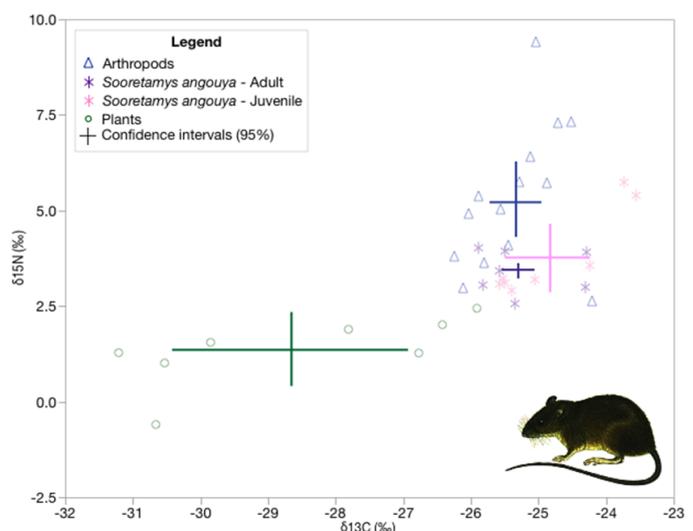
Figure 3 – Scatterplot showing the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition of hair from juvenile (pink crosses) and adult (purple crosses) individuals of *Sooretamys angouya* from M3 sampling area, and its arthropods (blue triangles) and plants (green circles) food source. The bars represent 95% confidence intervals and they cross at the mean value of each isotope composition of each category of correspondent color.

Table 1 – The mean percentage (Mean), standard deviation (SD), minimum(Min) and maximum (Max) values of dry weighed of plant material, arthropod, and unidentified material of the stomach contents of *Euryoryzomys russatus* in grid M1 and M3.

Species	Resources	Grids	Mean	SD	Min	Max
Euryoryzomys russatus	Plant material	M1	72.1%	4.4%	65.8%	75.7%
		M3	84.7%	1.4%	82.8%	86.2%
	Artropods	M1	1.2%	0.9%	0.1%	2.4%
		M3	1.0%	0.6%	0.1%	1.7%
	Unidentified material	M1	26.6%	5.3%	21.7%	34.0%
		M3	14.2%	1.2%	12.8%	16.1%

Table 2 – Stable isotopes Nitrogen ($\delta^{15}N$) and Carbon ($\delta^{13}C$) mean values (Mean) with standard deviation (SD), minimum (Min), maximum (Max) and significance difference (Sig; *=$p<0.05$) between *Euryoryzomys russatus* and *Sooretamys angouya* on grids M1 and M3.

Species	Grids	Stable isotopes	Mean	SD	Min	Max	Sig
Euryoryzomys russatus	M1	$\delta^{15}N$	6.52	0.94	4.54	8.87	*
		$\delta^{13}C$	-23.97	1.11	-25.44	-20.46	*
	M3	$\delta^{15}N$	3.99	1.20	2.69	8.48	
		$\delta^{13}C$	-25.18	0.85	-26.14	-21.89	
Sooretamys angouya	M1	$\delta^{15}N$	4.43	0.67	3.95	4.90	*
		$\delta^{13}C$	-23.73	0.62	-24.20	-23.26	*
	M3	$\delta^{15}N$	3.41	0.56	2.57	4.01	
		$\delta^{13}C$	-25.24	0.67	-25.88	-24.28	
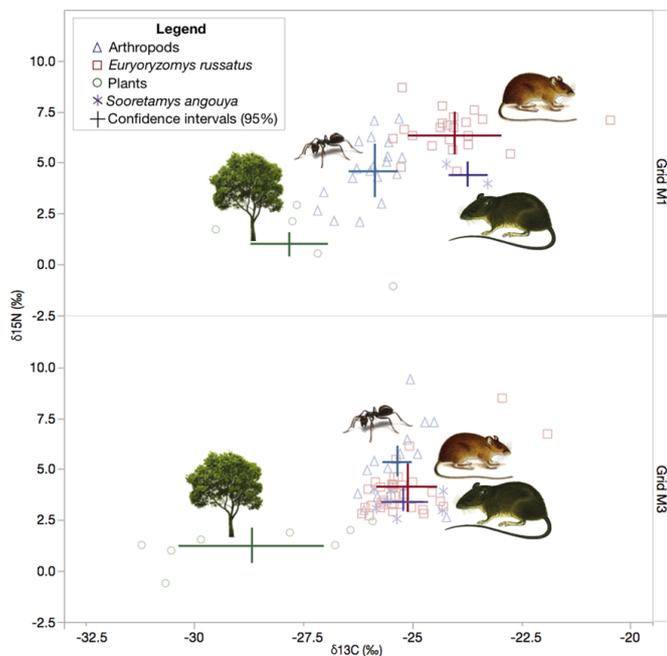
Figure 4 – Scatterplot showing the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition of hairs from adult individuals of *Sooretamys angouya* (purple crosses) and *Euryoryzomys russatus* (red squares) from two trapping grids (M1 and M3) and arthropod (blue triangles) and plant (green circles) food sources for each grid. The bars represent 95% confidence intervals and they cross at the mean value of each isotope composition of each category of correspondent color.

Factors influencing isotopic values

The variable Grid explained best the variation in C:N ratio for *E. russatus* (AICc=317.46; AICcWt=0.40; F=45.6; $p<0.0001$; Table S7). The relative importance of variables in the averaged models for this species was higher for Grid with 1.00, followed by plant sources with 0.31 and arthropod sources with 0.24 (Table S8). In the other hand, arthropod explained best the variation in C:N ratio for *S. angouya* (AICc=42.03; AICcWt=0.53; F=51.4; $p<0.001$; Table S9). The relative importance of variables in the averaged models for this species was higher for arthropod sources with 0.76, followed by Grid with 0.16 and plant sources with 0.15 (Table S10).

Discussion

Intraspecific variation: age

Our results showed that the shift in diet from juvenile to adult stage is more noticeable in *E. russatus* than in *S. angouya*. These results suggest that *E. russatus* juveniles presented a clear enrichment in ^{15}N, and a possible explanation is that juveniles exhibit a diet richer in protein, as a developmental requirement. This hypothesis is supported by other study (Clark, 1980b), who suggested that juveniles of *Rattus rattus* from Galapagos Islands tend to present more animal food in their stomach contents than older individuals. The author suggested that growing rats could prefer more protein-enriched foods. The smaller stomach capacity may also lead to the higher demand for animal protein, since it is easier to digest animal items in comparison to plant items, making the former more energetically efficient (Needham, 1964; Clark, 1980a). Although older individuals could present more efficiency in capturing animal prey (Polsky, 1977), younger rats could explore more animal food items due to their limited masticatory capacity at this age (Lakars and Herring, 1980). Juveniles do not present a completely developed buco-masseteric apparatus, which could limit their access to harder food items like some seeds and nuts, and resulting in their preference for softer items such as larvae of arthropods, soft seeds and nuts (Lakars and Herring, 1980). Thus, the high levels of $\delta^{15}N$ and $\delta^{13}C$ of young *E. russatus* could be resultant of: i) milk consumption (Babicky et al., 1975; Goode et al., 1981); ii) an increment of animal items on post-weaning diet (Babicky et al., 1975); iii) or, more likely, a combination of both. Camargo et al. (2014) showed that *Gracilinanus agilis*, a small Neotropical marsupial, exhibit a shift on food items related to size, establishing that adults (larger) specimens are more insectivorous in comparison to young (smaller) individuals, an opposite shit dietary pattern compared to our results, in

plant food sources, and *E. russatus* presented significantly enriched value for $\delta^{15}N$ in both M1 and M3 grids in comparison to *S. angouya* (Fig. 4). *E. russatus* and *S. angouya* did not present significant difference between them concerning $\delta^{13}C$ in M1 and M3. *S. angouya* from grid M3 presented significantly lower $\delta^{15}N$ values when compared to the arthropod food items. Although both species presented higher isotopic values in M1 in comparison to M3, the adults of *E. russatus* and *S. angouya* differed significantly on $\delta^{15}N$ and $\delta^{13}C$ in M1, but not in M3.

which young specimens apparently uses more animal items than adult specimens (Camargo et al., 2014). Nonetheless, authors highlight that physiology of juveniles can differ than that of adults affecting Nitrogen enrichment (Minagawa and Wada, 1984; Jenkins et al., 2001; Miller et al., 2008). Nevertheless, some studies show that differences in Nitrogen values between juveniles and adults might not be simply be the result of dietary differences, but can be related to different pathways for milk production and processing in capital versus income breeders (Miller et al., 2011) and the internal metabolic process (Minagawa and Wada, 1984; Smith et al., 2010). Nitrogen isotopic enrichment is well documented in the red-backed vole *Clethrionomys gapperi* (Sare et al., 2005), and in other mammalian groups, such as ungulates, carnivores, rodents and lagomorphs (Jenkins and Breck, 1998; Jenkins et al., 2001; Polischuk et al., 2001; Dalerum et al., 2007).

The maintenance in $\delta^{15}N$ and $\delta^{13}C$ values through age classes observed in *S. angouya* suggests that juveniles and adults may be exploring similar food sources in the RFMG area. For *S. angouya*, similarity of isotopic values between adult and juveniles remain yet to be investigated, and it is unclear why they did not show the same pattern that *E. russatus* (see below intespecific comparison, that may account to this intraspecific difference). Nevertheless, our results of ontogenetic variation for *E. russatus* agree to what should be expected for rodents (Mendl, 1988; Jenkins et al., 2001; Bergallo and Magnusson, 2002; Champagne et al., 2003; Miller et al., 2011; Stewart and McAdam, 2014).

Interspecific variation: area and species variation

Regarding food sources, our results were similar to those presented by Pinotti et al. (2011), who registered plant material and high diversity of arthropods (such as a frequency of 26% of Opiliones, 17% of Formicidae, 17% of Orthoptera, 12% of Coleoptera and 0.27% of other arthropods) in the stomach contents of *E. russatus*. Pinotti et al. (2011) also showed that other terrestrial rodents from RFMG, *Delomys sublineatus* and *Thaptomys nigrita*, consumed both plant and arthropod sources in high quantities, as demonstrated for other terrestrial sigmodontine rodents (Bergallo and Magnusson, 1999, 2002; Vieira et al., 2003, 2006).

To the best of our knowledge, no published studies have described in detail the diet of *S. angouya* (Olmos, 1991; Fonseca et al., 1996). Here, we report the presence of a fragment of Araneae and a predominance of plant material in the stomach contents of *S. angouya*. When compared to the stomach contents of *E. russatus*, the only stomach studied presented higher dry weight of plant material and a very poor diversity of arthropods. These results could be misleading, but considering that the best model for isotopic ratio signature for this species is the variable "arthropod sources" (indicating the enrichment of $\delta^{15}N$), that we interpret as a consequence of a possible arthropod consumption.

The diversity of arthropod groups found in the stomach contents of *E. russatus* may be influenced by the availability of each item in its habitat (Ellis et al., 1976; Pinotti et al., 2011). As *E. russatus* is exclusively terrestrial and *S. angouya* is predominantly arboreal (Olmos, 1991; Pardini et al., 2005; Graipel et al., 2006; Cademartori et al., 2008; Melo et al., 2011), some insect groups and other animal food sources could be more accessible for the terrestrial *E. russatus* compared to the arboreal *S. angouya*. Pinotti et al. (2011) found few food items of animal origin for other arboreal rodent (*Rhipidomys mastacalis*) in comparison to the terrestrial species mentioned above, a pattern already discussed by (Emmons, 1995), who suggested that arboreal species would rely more on canopy products, as "fruits, leaves, and nectar". A possible explanation for this general trend could be related to arboreal habitats, where food items could be less diverse (Brown and Lugo, 1990; Clark, 1996; Guariguata and Ostertag, 2001; Miller et al., 2011).

Regarding isotopic signatures, we also found clear discrimination between *E. russatus* and *S. angouya* for $\delta^{15}N$ values, especially on area M1. However, the $\delta^{13}C$ mean values were statistically similar to each other, with slightly higher values for *S. angouya* in both grids. These differences are in concordance with the diets described above. Although it was possible to detect differences in diet and isotopic composition between both species in both areas, this interspecific variation

seems to be affected by other environmental factors (Andreo et al., 2009; Bergallo, 1994). However, the $\delta^{13}C$ mean close values between species does not mean that these species do not differ on type of sources used, but possibly they might feed on different items with similar isotopic signatures (Phillips and Gregg, 2003).

The best model showed that amongst all variables considered, "grid" was the main variable responsible for the variation on the ratio of isotopic values for *E. russatus*. In addition, arthropod and plant sources were important predictors for *E. russatus* models. These results suggest that even with the small variations in the sources between grids *E. russatus* may respond to them (Bergallo and Magnusson, 1999). On the other hand, arthropod sources were the best factor explaining the variation on the ratio of isotopic values for *S. angouya*, independently of grid. The isotopic values of *S. angouya* were not different between grids and the other factors had no strong relative importance on mean values amongst the set of models fitted.

These results on the stable isotopic signatures for *E. russatus* and *S. angouya* and their relationship with the food sources and area, may exhibit some relation to the predictions of the responses of species to environmental disturbances based on their habitat requirements (Wiegand et al., 2005; Swihar et al., 2006; Pandit et al., 2009; Filippi-Codaccioni et al., 2010; Püttker et al., 2013). *E. russatus* is a species that is affected by landscape habitat fragmentation and percentage of forest cover (Pardini et al., 2010), indicating that habitat changes associated to this fragmentation affect its abundance (Püttker et al., 2013). Our results show that *E. russatus* exhibit tolerance to some level of habitat change, as this species apparently shifted its diet and, consequently, its isotopic signature in response to minor habitat differences: even though the areas (M1 and M3) were considered to represent similar successional stages (Püttker et al., 2013), there are some differences between the areas, as demonstrated by the isotopic signatures of our plant and arthropod sources. We expect that this species will not exhibit a flexible feeding strategy that will allow it to cope with more profound changes on the habitat (as evidence available shows that this species is one of the most affected in small mammal assemblages by fragmentation process), but future analysis will be needed to test this hypothesis or alternative hypothesis, as a high plasticity of *E. russatus* to adapt to deeper habitat changes. On the other hand, *S. angouya* is a species more tolerant to habit fragmentation (Pardini et al., 2010; Püttker et al., 2013) and is apparently more conservative on its diet, exhibiting lesser isotopic signature variation regardless of the isotopic differences observed on the habitat.

Hence, we argue that there are differences in dietary strategies among the sympatric species *E. russatus* and *S. angouya*. These differences could be related to their diet segregation, and also to their terrestrial versus arboreal behavior, as it is expected that syntopic species generally exhibit different dietary strategies (Fonseca et al., 1996; Vieira and Monteiro Filho, 2003). Nonetheless, these isotopic responses suggest differences in niche specialization between both species and that this variation needs to be taken into account to predict responses to disturbance events based on their niche requirements.

Conclusion

Isotopic evaluation indicates a pronounced inter- and intraspecific plasticity in resource use between *E. russatus* and *S. angouya*. Plant source consumption may be most developed in these two rodents with small to intermediate consumption of arthropod by *E. russatus*. Due the understory or canopy foraging by *S. angouya*, plants it appears to be dominant in the stomach content, even we have only one sample. In understory or canopy arthropod sources may be less abundant that on the forest ground, but nevertheless arose as an important source for *S. angouya*. *E. russatus* a ground dwelling species showed more isotopic variation between grids, seeming to be the more affected by habitat changes than *S. angouya*. Future studies designed to answer questions of ontogenetic dietary shifts on these species using stable isotope and physiology technique should enlighten the patterns observed in this study for *E. russatus* and *S. angouya*, and if these patterns we found are applicable to other populations. ✍

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Individuals of *Euryoryzomys russatus*.

Table S2 Individuals of *Sooretamys angouya*.

Table S3 Mann-Whitney test.

Table S4 Concurrent candidate models for *E. russatus* and *S. angouya* isotopes values.

Figure S5 Frequency of occurrence of arthropod groups - grid M1.

Figure S6 Frequency of occurrence of arthropod groups - grid M3.

Table S7 Linear mixed effect models - *E. russatus*.

Table S8 Relative variable importance on predict models - *E. russatus*.

Table S9 Linear mixed effect models - *S. angouya*.

Table S10 Relative variable importance on predict models - *S. angouya*.