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Research Article

Habitat type and seasonality influence the isotopic trophic niche of small mammals in a neotropical savanna

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Abstract

Knowing the trophic ecology of the species that occur in a given location is crucial for understanding the factors that allow their co-existence. Using stable isotope ratios (δ^{13}C and δ^{15}N) and metrics of the isotopic niche, we evaluated the trophic level of 22 small mammal species from the Brazilian Cerrado (neotropical savanna) through the assimilation of three groups of food items (C_3 plants, C_4 grasses, and invertebrates). In addition, we investigated trophic assimilation during dry and rainy seasons in the three main Cerrado vegetation formations (grassland, savanna, and gallery forest). We assessed the effects of differences in availability and diversity of food resources and of variation in habitat complexity (i.e., increase in forest cover) on trophic behavior. Overall, we confirmed that omnivory is the predominant feeding category of small terrestrial mammals from the Brazilian savanna, but certain trophic specializations were detected, such as the high frugivory (C_3 source) of arboreal forest species (*R. macrurus* and *O. cleberi*) and insectivory of terrestrial swamp rats (*Oxymycterus* spp.). The amplitude of the trophic niche of some species increased as a positive response to food availability, both in forest and savanna areas in comparison to grassland areas, and in the rainy season compared to dry season. Inside forests, insectivorous rodents showed a broader isotopic niche during the rainy season (when resource availability is higher) than in the dry season but an opposite pattern arose for frugivorous species. Our results indicated that the influence of habitat complexity and food resources on the isotopic trophic niche is species-dependent and not unidirectional, thus being difficult to make general predictions of species response. Moreover, the patterns of isotopic assimilation indicated that habitat-generalist species are also isotopic generalists.

Introduction

Knowing how species of the same community use available resources is crucial for understanding the factors that allow their co-existence (Chase, 2005; Macarthur and Levins, 1967). The resource use by these species may change as a function of several factors, such as intra- and inter-specific competition, resource availability, and habitat complexity. The understanding of how sympatric species partition resources and the relative importance of these factors has historically being one of the pivotal issues for ecologists (Begon et al., 2005; Pianka, 1986; Schoener, 1974; Brown and Wilson, 1956). Particularly for the role of competition and use of food resources, the relevance of trophic interactions in determining the composition of communities has recently been pointed out as one of the 100 fundamental questions in pure ecology (Sutherland et al., 2013).

A more recent approach for evaluation of trophic interactions in animals is the analysis of stable isotope ratios in their tissues, mainly carbon (δ^{13}C), which refers to the basal source of food resource and nitrogen (δ^{15}N), which refers to the trophic level of the sampled individual. This approach is generally known as the evaluation of isotopic niche (Galetti et al., 2016; Newsome et al., 2012; Flaherty and Ben-David, 2010; Martínez et al., 2009; Newsome et al., 2007). The isotopic niche of a consumer is comprised in the "Hutchinsonian niche", an n-dimensional hypervolume that defines all biotic and abiotic requirements needed for a species to exist (Hutchinson, 1957). Stable isotope analysis provides evidence of how assimilation of food resources occurs (Quillfeldt et al., 2005; Morrison and Hobson, 2004; Dahl et al., 2003) and how distinct habitats are exploited (Rubenstein and Hobson, 2004; Hobson, 1999). These factors are the main dimensions of the organism's isotopic niche (Quillfeldt et al., 2008; Bearhop et al., 1999), whose measurement is a powerful method for evaluating trophic niche width (Bearhop et al., 2004).

Stable isotope analysis has been shown to be a reliable complementary approach for classic dietary studies, based on fecal and stomach content analysis (Codron et al., 2015; Ambrose and DeNiro, 1986). The evaluation of stable isotope assimilation indicates trophic level and the contribution of the food sources. The dietary information obtained from stable isotope analysis may reflect food consumed over a longer period than information obtained from analysis of stomach contents. Furthermore, stable isotope analysis may provide information hardly accessible for a broad spectrum of species through traditional methods, such as geographical origins of the food items eaten (Salvarina et al., 2013) and foraging behavior of the animal (Crawford et al., 2008). For non-volant small mammals, it may reveal potential displacement between vegetation formations of individuals in search for food. The carbon isotope signature allows, for example, to determine whether the food sources assimilated by the organism were predominantly derived from grassland, where plants that use the C_4 carbon fixation pathway occur, or forest, dominated by plants that use the C_3 carbon fixation pathway (Leichliter et al., 2016; Ambrose and DeNiro, 1986).

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In the Brazilian Cerrado (neotropical savanna), non-volant small mammals are locally abundant, highly diverse (>100 species, Paglia et al., 2012) and widely distributed in the three main vegetation formations that occur in this phytogeographic domain (i.e., grassland, typical savanna, and gallery forest). Although most of these animals are specialists to a specific type of vegetation (Mendonça et al., 2018; Alho et al., 1986; Mares et al., 1986), there are also habitat generalists such as the sigmodontine rodents *Necromys lasiurus* and *Oligoryzomys nigripes* (Marinho-Filho et al., 1994; Alho et al., 1986). The great diversity of species, habitat selection and feeding strategies, combined with the variability of isotopic ratios associated with the distinct vegetation types (Coletta et al., 2009), make this an extremely noteworthy group in which to assess isotopic niches. Moreover, the Cerrado is characterized by strong seasonality, with well-defined rainy and dry seasons (Oliveira-Filho and Ratter, 2002), which causes strong effects on the temporal availability of food sources for small mammals (Pinheiro et al., 2002; Fonseca et al., 2001). Thus, the assessment if their isotopic trophic niches may provide insights on habitat use, niche partitioning and coexistence mechanisms among small mammals, and also on potential effects of seasonal environmental changes on these ecological aspects.

Here we investigated the isotopic assimilation and trophic position of 22 species of small mammals from the Cerrado (five marsupials and 17 rodents), for 14 of these species there is no current information on trophic niche. We estimated the contribution of each food group (i.e., C_3 plants, C_4 grasses, and invertebrates) for each species, aiming at comparing our results with the available studies on the dietary habits of those species (e.g., Camargo et al., 2014, 2011; Pacheco and Peralta, 2011; Pinotti et al., 2011; Bocchiglieri et al., 2010; Lessa and Costa, 2009; Ellis et al., 1998; Talamoni et al., 2008; Casella et al., 2006; Martins et al., 2006; Vieira, 2003; Cáceres, 2002; Campos et al., 2001; Castellarini et al., 1998; Meserve et al., 1988). We anticipated that investigating the isotopic niche of small mammals in the Cerrado would help in shedding light on feeding habits and ecological relationships that have remained unclear with commonly used methods.

We evaluated the seasonal variation (i.e., rainy versus dry seasons) of isotopic assimilation through the description of the food groups assimilated (i.e., C_3 plants [fruits], C_4 grasses, invertebrate consumers of C_4 plants, and invertebrate consumers of C_3 plants) in different vegetation formations (grassland, savanna, and gallery forest). Moreover, for small mammals sampled in more than one vegetation formation or season, we assessed intraspecific variations of the isotopic niche related to these factors. We expected that more food resources would be available in the most complex habitat (i.e., forests) and in the rainy season in comparison with the dry one. In that case, we predicted that such availability leads these ubiquitous species to narrow their isotopic niches in the rainy season in comparison with the dry season and in forested habitats in comparison with non-forested ones (also influenced by increased interspecific competition).

Materials and methods

Study area

The Cerrado, which occupies approximately 2.0 million km^2 of the Brazilian territory (Ratter et al., 1997), contains several vegetation formations including open areas (e.g., open grasslands [locally known as *campo limpo*] and grassland with scattered shrubs [*campo sujo*], savanna formations with increased woody plant cover (e.g., cerrado *sensu stricto* and rocky savanna), and forest formations (e.g., gallery forests) (Oliveira-Filho and Ratter, 2002). Local climate, classified as Aw according to the Köppen, 1948 climate classification system, is characterized by a dry season from May to September with marked water deficits in most soils, and a rainy season from October to April.

We carried out the study in the Chapada dos Veadeiros National Park, hereafter called PNCV (from the original name in Portuguese). This Federal conservation unit is located in the municipality of Alto Paraíso, federal state of Goiás (14°5′5.32″ S, 47°42′18.67″ W). The park has an area of 240611 ha and altitude ranging from 1100 to 1300 m a.s.l.

Field methods

We conducted field samplings in the area once in each season (i.e., rainy and dry) between 2012 and 2013. We established 13 linear transects of 270 m, placed 300–1000 m apart. These transects were established in four forest formations (all gallery forests), five savanna formations (four cerrado *sensu stricto* [typical savanna-like formation] and one rocky cerrado), and four grassland formations (two wet grasslands and two dry grasslands [*campo limpo*]). The gallery forests are narrow forest strips that surround water coursers. In the study area they suffered some level of disturbance, with average width ranging from 15 to 168 m and open canopies in several places, probably due to recurrent fires in this conservation unit (Fiedler et al., 2006).

Small-mammal captures

In each transect, we installed 8 60 l plastic buckets (pitfall traps), five Tomahawk live traps, 25 small Sherman® live traps (9×9.5×23 cm), and five large Sherman traps (11×12.5×37 cm). The Tomahawk and Sherman traps were placed on the ground at every 10 m, forming a linear capture transect with Tomahawk traps at every sixth trap location. The pitfall traps were placed 5 m from each other and were interconnected with 50 cm tall plastic drift fences. They were installed at the edges of each transect, forming two 25 m transects arranged perpendicularly to the main live-trap transect. Sampling in each plot (including the main transect and the two perpendicular pitfall transects) consisted of 8 subsequent nights of capture, resulting in 1376 trap-nights per plot and 17888 trap-nights in total.

We used a standardized mixture of mashed banana, cod liver oil, corn meal, peanut butter, and vanilla essence as bait in all traps. We recorded the species, gender, reproductive status, body measurements, and weight of all captured individuals. We used a clean scissor for cutting and collecting hair samples from the dorsal region of each individual and stored samples in sealed plastic vials. After these procedures they were released in the same trap location. Voucher specimens were collected and maintained in the mammal collection of the Department of Zoology of the University of Brasília (UnB, Brasília city, Brazil).

Sampling of food items

We estimated the abundance of zoochorous fruits during each sampling period by counting the number of fruits available on trees and fallen on the ground at 15 plots of 8×8 m (64 m^2 per plot, totaling 960 m^2 sampled in each transect) placed along the transect (distance between plots=14 m). Subsequently, we pooled all the fruits available in the plots in each transect for calculating the average fruit density per transect for each vegetation formation (forests, savanna, and grassland formations) and season (dry and rainy seasons).

We calculated the "true" diversity of fruits (Shannon index with Hill number=1, Jost, 2006) for each transect and estimated the average diversity per transect for vegetation formation and season. For each species of plant that produced fruits during the sampling period, we collected vegetative and reproductive parts for confirming the identification of species. Moreover, we collected fruit samples (average of five fruits for each species) from all species and determined their dry mass after 48 h in a drying oven at 60 °C.

For invertebrate sampling, we installed 30 pitfalls in each transect every sampling season. These pitfalls consisted of 500 ml plastic cups buried so that the soil was flush with the cup edge. To ensure invertebrate capture and storage, the cups held 400 ml of solution consisting of water (95%), 10% formaldehyde (5%), and a few drops of detergent. We placed two of these traps in each transect of the mammal pitfall traps (see previous section), the remaining 28 forming a linear transect parallel to the main live-trap transect. These pitfall traps remained in the field for three consecutive nights. The material was then screened in the lab, the invertebrates identified at the order level and total dry biomass was obtained after 72 h in a drying oven at 60 °C. We estimated invertebrate availability through the mean total dry biomass per transect for each vegetation formation and season. As for fruits, we also calculated the "true" diversity of invertebrate orders (Shannon in-

dex, Jost, 2006) for each transect and calculated the average diversity per transect for vegetation formation and season.

Samples for isotopic analysis

For the small mammals, whenever possible, we collected samples of all species in each season and vegetation formation, obtaining hair samples from a total of 124 individuals. Residues were removed from the hair samples by rinsing with distilled water, immersing them in a 2:1 mixture of chloroform and methanol for 30 min, and rinsing again with distilled water. The hair samples were then oven dried overnight at 65 °C, shredded, and weighed (minimum sample weight=1.5 mg) in tin capsules on an analytical scale (0.001 g precision). We performed isotopic analyses of 22 species of small rodents and marsupials, with number of sampled individuals per species ranging from 1 to 17 (median=5.5 samples; Table S1).

For the isotopic analyses, we selected fruit species (C_3) that are more frequently described in dietary studies of small mammals (e.g., Camargo et al., 2011; Pinotti et al., 2011; Bocchiglieri et al., 2010; Lessa and Costa, 2009; Ellis et al., 1998; Talamoni et al., 2008; Casella et al., 2006; Campos et al., 2001; Castellarini et al., 1998; Meserve et al., 1988 and were abundant in the sampled vegetation formations (i.e., *Melastomataceae*, *Rubiaceae*, *Sapindaceae*, *Smilacaceae*, *Vochysiaceae*, *Apocynaceae*, and *Erythroxylaceae*). We conducted isotopic analysis of 22 samples from C_3 species. Seven species were sampled in the open grasslands, including 6 that produced zoochorous fruits in the rainy season: *Byrsonima verbascifolia*, *Chomelia* sp., *Miconia albicans*, *Myrcia tomentosa*, *Psidium myrsinites*, and *Rourea* sp., and seeds of one anemochorous species that was highly abundant in the study area during the dry season (*Qualea* sp.). In the savanna areas, we sampled 5 C_3 species (dry season: one unidentified *Leguminosae* species, *Syagrus deflexa*, and *Matayba* sp.; rainy season: *Smilax* sp. and *Hancornia speciosa*). In the forest areas we evaluated samples of the following 10 C_3 plant species: rainy season — *Buchenavia* sp., *Erythroxylum engleri*, *Leandra* cf. *deflexa*, *Smilax fluminensis*, *Mauritia flexuosa*, *Miconia stenostachya*, and *Protium heptaphyllum*; dry season — *Psychotria* cf. *mapourioides*, *Tibouchina stenocarpa*, and *Chionanthus* sp. We also analyzed samples of seeds from one locally abundant C_4 species, *Schizachyrium sanguineum* (*Poaceae*).

We selected for isotopic analysis invertebrate morphotypes belonging to the most frequently reported orders in small-mammal dietary studies (Camargo et al., 2014; Santori et al., 2012; Camargo et al., 2011; Pinotti et al., 2011; Lessa and Costa, 2009; Martins and Bonato, 2004; Cáceres, 2002) and the most abundant ones in each vegetation type and season. We used δ^{13}C measurements to classify invertebrates into two groups according to the origin of the resource used by these prey species, namely C_3 invertebrates (woody plants) or C_4 invertebrates (grasses). High values of carbon indicated that the food source originated from grassy areas, whereas low values of carbon indicated that the food source originated from forested areas. We assigned the invertebrates to each group using mean value of carbon isotope distribution range (δ^{13}C) by defining the average value as the cut-off value between groups.

We analyzed samples corresponding to a total of 92 invertebrate morphotypes obtained with the pitfalls, categorized according to season and vegetation formation (grassland: rainy season, n=17 morphotypes; dry season, n=10; savanna: rainy season, n=10, dry season, n=21; forest: rainy season, n=12, dry season, n=22). These morphotype samples (one sample for each morphotype) were dried for 96 h in a drying oven at 60 °C and then crushed and weighed (minimum sample weight=1.5 mg) in tin capsules over an analytical scale.

The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios of each hair, invertebrates and vegetation sample were determined at the Stable Isotope Facility of the University of California, Davis, USA. The isotopic compositions were analyzed using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer. Internal, certified laboratory standards are routinely interspersed with target samples during analysis runs. Long-term standard deviations of internal standards used at the Stable Isotope Facility are of 0.2‰ for carbon and 0.3‰ for nitrogen (further analytical details at http://stableisotopefacility.ucdavis.edu/l3candl5n.html). The results were reported using delta notation (δ) in parts per thousand (‰), relative to standard international references (VPDB-Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen).

Time required for the assimilation of ingested food (i.e., time from ingestion until isotopes are incorporated into the tissue and subsequent excretion) is species- and tissue-specific (Hobson and Clark, 1992). Accordingly, we corrected the data obtained from hair samples by the specific isotopic renewal rate (or turnover) based on a half-life of 47.5 days value found for carbon in hairs of non-volant small mammals (Tieszen et al., 1983). Because isotope fractionation varies according to consumer characteristics such as diet composition and feeding rate (Post, 2002; Vander Zanden and Rasmussen, 2001), we adjusted the isotope values of rodents and marsupials using the average fractionation of 2.2‰ (±1.5 SD) for δ^{13}C (Sponheimer et al., 2003; Tieszen et al., 1983) and 3.0‰ (±1.5 SD) for δ^{15}N (DeNiro and Epstein, 1981).

Statistical analyses

Bayesian models are appropriate for evaluating isotopic signatures and discrimination of consumed resources (Moreno et al., 2010; Newsome et al., 2007; Ogle et al., 2012). To estimate the trophic level of small mammal species, we used the Markov Chain Monte Carlo (MCMC) method with 500000 permutations (Parnel et al., 2010). Based on δ^{13}C and δ^{15}N values, this analysis produces a relative contribution probability curve for each food resource and for each hair sample. Measured isotope ratios were adjusted using the above-mentioned fractionation values for δ^{13}C and δ^{15}N, and food resources were classified into three groups (C_3 plants, C_4 plants, and invertebrates) for evaluating the trophic level of the species. In this way, we estimated the average contribution of each food resource for each sampled mammal species (i.e., diet evaluation through isotopic signature). Analyses were performed within the R environment, version 2.15.3 (R Development Core Team, 2013) using the SIAR package (Parnel and Jackson, 2011).

We also calculated the trophic level for the species in each season and vegetation formation using the MCMC method with 500000 permutations. For this analysis, we categorized food sources into four groups (C_3 plants, C_4 grasses, forest invertebrates, and grassland-invertebrates), because the subdivision of mammalian samples into season and vegetation formation limited the analysis to a maximum of four food sources (Boecklen et al., 2011). We classified the invertebrates according to their assimilation of the distinct plant sources (i.e., C_3 plants and C_4 grasses). This classification was used for inferring strategies of space use by the studied small mammals, as there is an inverse relation between availability of C_4 grasses and structural complexity of Cerrado phytophysiognomies (Lehmann et al., 2011).

We calculated isotopic niche metrics for each species, according to season and vegetation formation. We used these metrics to evaluate possible adaptation of the species' diet related to differences in structural complexity and seasons. These differences, in their turn, may promote changes in the availability and diversity of food items. Based on the distribution of samples in each analyzed scenario, we calculated four isotopic niche metrics (Jackson et al., 2011; Layman et al., 2007) that reflect trophic diversity, considering the δ^{13}C-δ^{15}N biplot, as follows: (i) δ^{15}N range, which correlates to the diversity of trophic levels used by the species; (ii) δ^{13}C range, which correlates to the isotopic range of basal resources that the species assimilated; (iii) SEAc, which is a standard ellipse area corrected for sample size, equivalent to a bivariate standard deviation that can be interpreted as a measure of the core isotopic niche of a population (Jackson et al., 2011); (iv) the average of the Euclidean distance of each individual in relation to the centroid of the polygon defined by all individuals in the δ^{13}C-δ^{15}N space (CD), a measure that reflects the average trophic diversity of each individual within the population.

We also evaluated two metrics that reflect aggregation (i.e., trophic redundancy) or dispersion of individuals in the 2-dimensional space (δ^{13}C-δ^{15}N biplot) of the isotopic niche (Jackson et al., 2011; Layman et al., 2007). The first metric, mean nearest neighbor distance

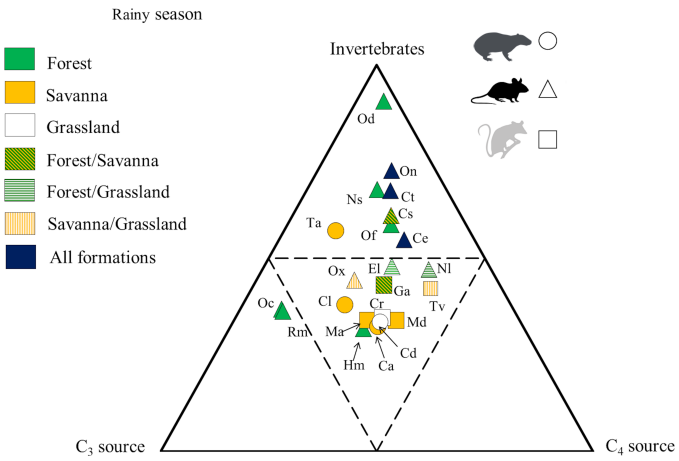

Figure 1 – Ternary plot indicating the trophic status of the small terrestrial mammal species captured at the National Park Chapada dos Veadeiros (central Brazil) in a neotropical savanna (Cerrado). The proximity of the symbols to the apex of the triangle is proportional to the averaged potential contribution of each isotope source (invertebrates, C_3 plants, and C_4 plants). Letter codes refer to studied species (Didelphid marsupials: Ga=*Gracilinanus agilis*, Cr=*Cryptonanus agricolai*, Tv=*Thylamys velutinus*, Ma=*Monodelphis americana*, Md=*Monodelphis domestica*; Sigmodontinae rodents: Ce=*Calomys expulsus*, Ct=*Calomys tener*, Od=*Oxymycterus delator*, Ox=*Oxymycterus* sp., Nl=*Necromys lasiurus*, Ns=*Nectomys squamipes*, Of=*Oligoryzomys fornesi*, On=*Oligoryzomys nigripes*, Hm=*Hylaeamys megacephalus*, El=*Euryoryzomys lamia*, Cs=*Cerradomys scotti*, Rm=*Rhipidomys macrurus*, Oc=*Oecomys cleberi*; Caviomorph rodents: Ca=*Cavia aperea*, Cd=*Carterodon sulcidens*, Cl=*Clyomys laticeps*, Ta=*Thrichomys apereoides*). Taxonomic groups are represented by the following symbols: square=marsupials, triangle=sigmodontinae rodents, circle=caviomorph rodents. Symbol patterns indicate where each species was captured considering the three habitat types sampled (grasslands, typical savanna and forests). The position of four species for which the three sources contributed to the diet in similar proportions (Ca, Hm, Csu, and Cap; in the center of the ternary graph) were slighted moved for clarity (see Tab. S2 for exact values).

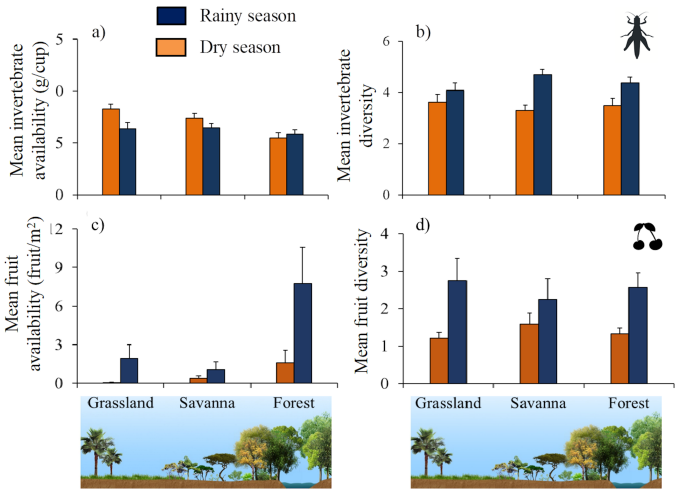

Figure 2 – Availability and diversity of invertebrates and fruits (mean and standard error) according to season and vegetal formation (forest [four sites sampled], savanna [five sites sampled], and grassland [four sites sampled]). Left column shows food availability and right column shows food diversity (expressed by exp^H, where H=Shannon index) for invertebrates (a, b) and fruits (c, d). Illustrations on the bottom represent the vegetation formations (modified from Ribeiro and Walter, 1998).

(MNND), is the mean Euclidean distance between individuals of a species. Thus, the smaller the MNND, the more similar is the trophic ecology among individuals of that species (i.e., greater trophic redundancy within the species). We also considered a measure of uniformity between individuals of a species in the δ^{13}C-δ^{15}N space, that is the standard deviation of the mean nearest neighbor distance (SDMNND), which is less influenced by sample size.

Results

Trophic level of small mammals of the Cerrado

We analyzed samples from 124 individuals, comprising 22 small mammal species (five marsupials and 17 rodents). There was a mean sample size of 5.6 individuals sampled per species (range 1–17; Tab. S1). The relative contribution of the three food groups assessed (C_3 source, C_4 source, and invertebrates) indicated a predominance of omnivory in the studied assemblages, but with some degree of dietary specialization for several species (Fig. 1; Tab. S2). Two forest rodents had diets primarily based on C_3 plants (*Oecomys cleberi* and *Rhipidomys macrurus*) and 8 small mammals were predominantly invertebrate eaters. Among the 12 species with more balanced contribution of the three food-source types (i.e., within the inner triangle of the isotopic ternary graph [Fig. 1]), three assimilated mainly invertebrates but also with a relevant contribution of C_4 grasses (*Thylamys velutinus*, *Monodelphis domestica* and *Necromys lasiurus*), and three were mainly insectivorous (*Gracilinanus agilis*, *Oxymycterus* sp., and *Euryoryzomys lamia*). The dietary pattern was less pronounced for the remaining 6 species assessed (Fig. 1; Tab. S2).

Availability and diversity of food resources

We recorded 19 invertebrate orders: 16 in forested, 16 in savanna, and 18 in grassland formations. The availability of invertebrates on the ground were slightly higher in the dry season than in the rainy season in the open environments (savanna and grassland formations) but not in the forested ones (Fig. 2A). However, diversity of invertebrate orders was greater in the rainy season than in the dry season for all formations, but this pattern was less pronounced in grasslands (Fig. 2B). In relation to plant resources, we identified 95 species of zoochorous fruiting plants during the field sessions: 48 species fruiting in forested, 41 in savanna, and 31 in grassland formations. Availability and diversity of fruit were greater in the rainy season in all sampled environments (Fig. 2C,D).

Isotopic patterns for the distinct habitat types and seasons

The results indicated that three species consumed different proportions of each food group in different habitat types (i.e., showed spatial feeding flexibility), namely *Calomys expulsus*, *E. lamia* and *Cerradomys scotti*. Two forest-exclusive species, the rodents *Oligoryzomys fornesi* and *Nectomys squamipes*, showed between-season feeding plasticity. Moreover, five species that occurred in more than one vegetal formation (*G. agilis*, *Calomys tener*, *N. lasiurus*, *Oligoryzomys nigripes* and *C. scotti*) varied in the proportions of each food group across vegetal formations and seasons (Fig. 3).

Marsupials tended to be insectivores in all sampled environments (mean δ^{15}N±SD=6.5‰±1.3, range=4.4 to 8.6‰), but some species showed differences in terms of feeding source assimilated by consumed invertebrates (forest or grassland invertebrates; Fig. 3). *Thylamys velutinus* and *Cryptonanus agricolai*, sampled exclusively in non-forest areas (i.e., savanna and grassland), apparently assimilated grassland invertebrates (Fig. 3A and 3C). *Monodelphis domestica*, in turn, assimilated forest invertebrates in both seasons in the savanna, but in the rainy season this species apparently also assimilated grassland invertebrates (Fig. 3C and 3D). The diet of other marsupial, *G. agilis*, was based on forest invertebrates both in grassland areas (rainy season) and savannas (dry season). In forest formations, however, this marsupial apparently changed its diet from forest invertebrates in the rainy season to grassland invertebrates in the dry season (Fig. 3D, E and F).

Most Sigmodontinae rodents showed relevant assimilation of invertebrates, as indicated by high values of δ^{15}N in their hair samples (mean δ^{15}N±SD=5.4‰±2.2, range=1.7 to 10.6‰) but also of C_3 and C_4 plants (Fig. 3). However, *Oxymycterus* species (*O. delator* and *Oxymycterus* sp.) showed isotope values consistent with a more insectivorous diet (mean δ^{15}N±SD=9.2‰±0.8, range=7.2 to 10.6‰), with assimilation of grassland invertebrates across the seasons and habitats assessed (Fig. 3). *Calomys tener* and *O. fornesi*, in turn, maintained the assimilation of both forest and grassland invertebrates regardless of habitat or season. On the other hand, some species varied the assimilation of direct and indirect C_3 and C_4 sources according to season

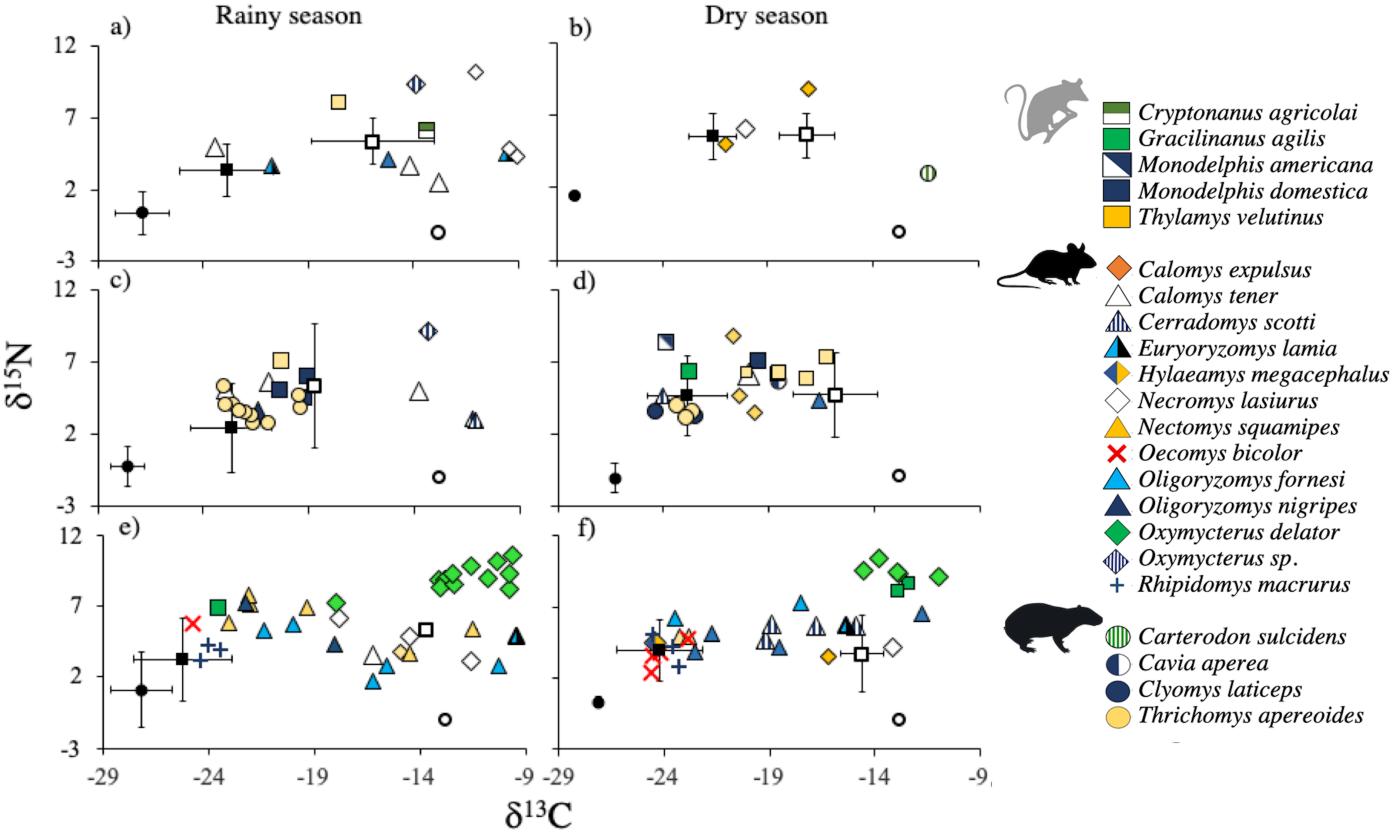

Figure 3 – Assimilation of stable isotopes $\delta^{13}C$ and $\delta^{15}N$ in small mammals captured in three vegetation formations of a neotropical savanna (Cerrado) (marsupials=squares, caviomorph rodents=circles, sigmodontinae rodents=all other symbols). Results for the food sources are reported as mean and standard deviation (error bars) when more than one sample was available (small black circle=C_3 plants; small black square=C_3 plant-feeding invertebrates, small white square with thick line=C_4 plant-feeding invertebrates, and small white circle with thick line=C_4 plants). Habitats studied were grassland (a, b), savanna (c, d) and gallery forest (e, f), all of them sampled during rainy (left column) and dry (right column) seasons.

(e.g., *N. squamipes*, *N. lasiurus*, and *C. scotti*), vegetation type (e.g., *C. expulsus*), or even by both factors (e.g., *O. nigripes*) (Fig. 3).

The patterns of isotopic assimilation for the caviomorph rodents were less clear mainly because of the limited sample size for most species (1–2 individuals of *Cavia aperea*, *Carterodon sulcidens*, and *Clyomys laticeps*; Tab. S1). Notwithstanding, *Thrichomys apereoides* (14 individuals sampled) assimilated forest invertebrates in savanna environments (Fig. 3C and D) and *C. sulcidens* assimilated C_4 vegetable matter in grassland environments during the dry season (Fig. 3B).

Within-species variation

For five species, isotopic niche metrics could be compared across seasons in the same vegetation formation, or across different vegetation formations in the same season (Tab. 1). In relation to between-habitat differences, during the rainy season the rodent *C. tener* showed higher trophic diversity and plasticity ($\delta^{15}N$ range, $\delta^{13}C$ range, and SEAc), and lower between-individual trophic redundancy in grassland formations compared to savanna habitats (i.e., higher MNND and SDMNND; Tab. 1). For another rodent, *N. lasiurus*, we also detected a higher trophic plasticity ($\delta^{15}N$ range) in less complex formations (grassland) in comparison to forested habitats. This rodent, however, showed a higher overall trophic diversity (SEAc) in forests than in grasslands, which was a consequence of increased $\delta^{13}C$ range for forest individuals (Tab. 1).

In relation to seasonal differences, the rodents *T. apereoides*, in the savanna, and *O. delator*, in the forest formations, showed similar patterns. Both species narrowed their isotopic niche (lower $\delta^{15}N$ range, $\delta^{13}C$ range, and SEAc; and higher redundancy between sources – lower MNND) during the dry season in comparison to the rainy season. On the other hand, *R. macrurus*, a forest specialist, showed an opposite pattern, with an increase in trophic diversity (CD) and reduction in trophic redundancy (higher MNND and SDMNND) in the dry season compared to the rainy season (Tab. 1).

Discussion

This study is the first published report describing the diets of non-volant small mammals in the Brazilian Cerrado based on isotopic assimilation. Overall, we confirmed that omnivory is the predominant feeding category of small terrestrial mammals in this neotropical savanna, but also detected certain trophic specializations, such as the high frugivory (C_3 source) of arboreal forest specialists (*R. macrurus* and *O. cleberi*) and insectivory in terrestrial swamp rats (*Oxymycterus* spp.). The amplitude of the trophic niche of some species increased in response to greater food availability, both in forest and savanna areas in comparison to grassland areas, and in the rainy season compared to dry season. Inside forests, insectivorous rodents showed broader isotopic niches during the rainy season (when resource availability was higher) than in the dry season, but frugivorous species showed an opposite pattern. Moreover, the patterns of isotopic assimilation indicated that habitat-generalist species also are isotopic generalists as well.

Among the studied mammal species, some of them showed to be primary frugivorous, like the forest-specialists *O. cleberi* and *R. macrurus*. Other small mammals, like the swampy rats (*Oxymycterus* spp.) and the water-rat (*N. squamipes*) occupied high trophic levels consistent with insectivory. Nevertheless, some species varied not only the trophic level but also the resource source according to the vegetal formation or the season. Habitat complexity influenced differently the isotopic niche of grassland species (*C. tener*) and habitat generalists (*N. lasiurus*). Moreover, trophic level also played a relevant role on seasonal changes in isotopic niche width. From wet to dry season, the insectivorous *T. apereoides* and *O. delator* narrowed markedly their isotopic niche whereas the frugivorous *R. macrurus* enlarged its niche.

Contribution of food groups to the diets of Cerrado small mammals

The general omnivory for the small-mammal assemblage that our results indicated based on isotopic assimilation is consistent with previous

Table I – Isotopic niche metrics (Jackson et al., 2011; Layman et al., 2007) for small mammal species in the central Brazilian savanna (Cerrado) with three or more samples. Values are presented for vegetation formations (grassland, savanna, and forest) and seasons (dry and rainy). δ^{15}N range indicates the trophic diversity, δ^{13}C correlates with number of assimilated basal resources, Standard Ellipse Area (SEAc) indicates the overall trophic diversity of the species isotopic niche, mean distance to centroid (CD) averages degree of trophic diversity between individuals, mean nearest neighbor distance (MNND) is inversely related to within-species trophic redundancy, and standard deviation of the mean nearest neighbor distance (SDMNND) measures the uniformity of δ^{13}C-δ^{15}N space among conspecific individuals.

	δ^{13}C range	δ^{15}N range	SEAc	CD	MNND	SDMNND	N
Rainy season							
Calomys tener							
Grassland	10.71	2.45	17.7	3.96	2.82	4.49	3
Savanna	9.17	0.61	8.41	4.09	1.04	1.2	3
Necromys lasiurus							
Grassland	1.94	5.83	1.56	2.23	1.54	2.67	3
Forest	6.22	2.94	3.91	2.57	1.73	1.2	3
Savanna formation							
Thrichomys apereoides							
Rainy	3.61	2.62	3.31	1.68	0.72	0.56	11
Dry	0.72	0.87	0.79	0.42	0.34	0.41	3
Forest formation							
Oxymycterus delator							
Rainy	8.34	3.35	5.18	2.88	2.22	2.81	12
Dry	3.58	1.29	2.27	1.43	0.76	0.71	4
Rhipidomys macrurus							
Rainy	0.94	1.14	1.43	0.63	0.34	0.39	3
Dry	1.26	2.25	1.96	1.01	0.66	0.76	3

studies that analyzed fecal and stomach contents of this group (e.g., Camargo et al., 2014, 2011; Pacheco and Peralta, 2011; Pinotti et al., 2011; Bocchiglieri et al., 2010; Lessa and Costa, 2009; Ellis et al., 1998; Talamoni et al., 2008; Casella et al., 2006; Vieira, 2003; Cáceres, 2002; Campos et al., 2001; Castellarini et al., 1998; Meserve et al., 1988). The detected patterns of stable isotope assimilation also indicated the contribution of different food categories to the diets of the small mammals, allowing us to categorize the studied species into three distinct dietary groups.

Our results clearly indicated a group of mainly fleshy-fruit eaters, which included the arboreal forest dwellers *O. cleberi* and *R. macrurus*. Both species are commonly regarded as frugivorous and seed predators (Paglia et al., 2012), but at least for the former we found no published studies on dietary patterns to support such statement. *Rhipidomys macrurus*, in turn, showed an intermediary position along the δ^{15}N axis, possibly indicating some consumption of invertebrates. A mixed diet of plant matter and, to a lesser extent, on invertebrates, has also been reported for other congeneric species (Pacheco and Peralta, 2011; Pinotti et al., 2011; Montenegro-Diaz et al., 1991).

The most species-rich dietary group consisted of genuinely omnivorous species (12 species in the inner triangle of Fig. 1). Most of them assimilated mainly invertebrates, but also included a high proportion of plants in their diet. Among those, two marsupials (*Thylamys velutinus* and *Monodelphis domestica*) and one rodent (*Necromys lasiurus*) also showed a relevant contribution of C_4 food sources. Direct consumption of C_4 plants by both marsupials would not be expected, since these marsupials are reported as carnivore-insectivores (Vieira, 2003; Vieira and Palma, 1996). Thus, the observed assimilation of C_4 sources was probably derived from invertebrates that feed on C_4 grasses in grasslands and savanna habitats (i.e., grassland invertebrates), where these mammals were captured. For *N. lasiurus*, however, the observed proportion of invertebrates and C_4 plants (grasses) in the diet was already expected (Vieira, 2003; Ellis et al., 1998; Talamoni et al., 2008).

A third dietary group consisted of predominantly insectivorous species (the upper inner triangle in Fig. 1). This group included the semiaquatic rodent *N. squamipes*, *Oxymycterus* spp., and the echimyid rodent *T. apereoides*. This observed pattern for the latter is consistent with results based on fecal analysis (Lessa and Costa, 2009), raising doubts on the consistency of the frugivore-herbivore classification suggested by Paglia et al. (2012). Some of the predominantly insectivorous species (or congeneric ones) of this group have been described in the literature as omnivores-frugivores with greater consumption of vegetal matter, such as *Calomys* spp. (Ramos, 2007; Campos et al., 2001; Castellarini et al., 1998; Ellis et al., 1998), *Euryoryzomys* sp. (Pinotti et al., 2011), *Cerradomys* sp. (Vieira, 2003), *O. nigripes*, and *O. fornesi* (Pinotti et al., 2011; Talamoni et al., 2008; Vieira et al., 2006; Vieira, 2003; Ellis et al., 1998; Meserve et al., 1988). Therefore, our results highlight the insufficiency of the current knowledge on the diet of neotropical mammals and the dietary plasticity of these species, which clearly indicate the need of improved and complimentary approaches such as stable isotope analysis for adequate diet evaluation of these animals.

We detected that some species occupy an indeterminate trophic position (e.g., *Cryptonanus agricolai*,*Monodelphis americana*, *Cavia aperea*), with apparent similar contributions of all sampled food groups. However, small sample sizes limited our inferences of some species. This is a recurring issue in analysis of mammals' isotopic niches (Ambrose and DeNiro, 1986; Codron et al., 2015; **?**; Galetti et al., 2016; Symes et al., 2013), and because of this limitation some of these results should be considered merely indicative of the isotopic signature. However, for several species investigated in this study, information about feeding habits in the Cerrado is extremely scarce or even nonexistent (e.g., *M. americana*, *H. megacephalus*, *O. cleberi*, *R. macrurus*, *E. lamia*, *Clyomys laticeps*, and *C. sulcidens*). For the rare echimyid *C. sulcidens*, its position in the isotopic graph (Fig. 3B) clearly indicates that this rodent is a strict herbivore that feeds on C_4 grasses, as suggested in the first description of a non-fossil specimen (Reinhardt, 1852).

Isotopic niche space of non-volant small mammals

Our overall results (Fig. 1) suggest that sigmodontine rodents as a group present a broader isotopic niche space than marsupials, considering the three habitat types sampled. This pattern was also indicated by Galetti et al., 2016 for Atlantic forest sites. Even considering that we sampled fewer species of marsupials (n=5) than sigmodontine rodents (n=13), the spread of rodents along the ternary graph (Fig. 1), with rodents distributed in distinct trophic levels and with a wide range of carbon sources supports the assumption of a broader isotopic niche for this group in comparison to marsupials.

The trophic structure of the studied assemblages encompassed up to 2.96 trophic levels, considering an average trophic enrichment of ≈3.0‰ per trophic level (Vanderklift and Ponsard, 2003), similar to those reported for other tropical small-mammal assemblages (Galetti et al., 2016; Hyodo et al., 2010). The marsupials encompassed about 1.40 trophic levels, with a lower total isotopic niche area than the rodents. These latter encompassed about 2.96 trophic levels, indicating a high trophic diversity. The highest values of the δ^{15}N isotopic axis corresponded to the rodents *Oxymycterus* sp., *Oxymycterus delator*, *Calomys expulsus*, and the marsupials *T. velutinus*, *Monodelphis americana*, *M. domestica* and *Gracilinanus agilis*. Among these, only for *C. expulsus* the values indicated an unexpected degree of insectivory, as this species has been reported as frugivorous-granivorous (Paglia et al., 2012).

The rodents *C. tener*, *N. lasiurus* and *O. nigripes* presented a wide spread along the δ^{13}C axis, reaching enriched δ^{13}C values (between -12.74‰ and -9.04‰; Fig. 3). This isotopic axis is related to the variety of basal resources in the species diets and a similar pattern was also pointed out for the two later species in the Atlantic forest (Galetti et al., 2016). Species in the genera *Calomys*, *Necromys*, and *Oligoryzomys* are reported as generalist feeders (Vieira, 2003; Ellis et al., 1998) and the trophic niche width of these species is probably related to their adaptive wide habitat selection.

Species of the genus *Calomys* are considered opportunists in terms of habitat use (Vieira, 1999; Mills et al., 1991), being able to switch from an omnivorous diet to an invertebrate-based diet after disturbance in savanna habitats (Vieira and Briani, 2013). For *N. lasiurus*, in

turn, feeding plasticity may contribute to the overall high local abundance and large geographic range reported for this rodent, which is common in the Cerrado biome (Mendonça et al., 2018; Marinho-Filho et al., 1994). Ecological characteristics of this species, which has a broad ecological niche driven by flexible diet and habitat use, are often considered to be important for successful colonization, establishment and spread of invasive species (Pettitt-Wade et al., 2015; Marvier et al., 2004). Indeed, *N. lasiurus* has invaded disturbed areas within the Atlantic Forest biome (Estavillo et al. , 2013; Bonvicino et al., 2002) and a "flexible" use of the environment may allow this species to persist even in anthropogenic-transformed areas, as suggested for African rodents (Symes et al., 2013). Another species with broad values along the δ^{13}C isotopic axis, *O. nigripes*, also has a broad geographical range from south to central Brazil, occurring in several habitat types (Dalmagro and Vieira, 2005).

Our results indicated a relatively higher insectivory of terrestrial species captured inside forests (e.g., *N. squamipes*, *C. scotti*, and *O. delator*) in comparison with arboreal forest dwellers. This pattern corroborates previous findings (Galetti et al., 2016; Vieira, 2003; Malcolm, 1995; but see Symes et al., 2013) and likely results from a higher invertebrate availability (and lower fruit availability) on the ground in comparison with the upper layers of the forest and also by the increasing difficulty in finding, pursuing, capturing, and subjugating prey in the canopy in comparison with the ground (Emmons, 1995). Moreover, differences in the isotopic space between groups of species that occupy distinct forest strata suggest the relevance of the vertical dimension for trophic niche partitioning in small-mammal assemblages (as suggested by Galetti et al., 2016).

Stable isotope analysis has been widely used in trophic ecology studies (Boecklen et al., 2011) but it must be pointed out that "isotopic niche width" is not the same that "trophic niche width" (*sensu* Bearhop et al., 2004. The isotopic approach, has clear limitations, including the difficulty for identifying specific food items within the same trophic position, particularly in complex environments (Ben-David and Flaherty, 2012; Phillips and Gregg, 2003). This method, however, is considered a helpful tool for the evaluation of resource partitioning in small mammals (Symes et al., 2013). In the present study, stable isotope analysis indicated clear trophic niche segregation between similar species, as the higher trophic level of *Oxymycterus delator* in comparison to the congeneric *Oxymycterus* sp. On the other hand, we observed high similarity in isotopic niche between other congeneric species pair *Monodelphis* spp. and between pair of species with similar habitat requirements (*O. cleberi* and *R. macrurus*, both arboreal forest dwellers). Such patterns suggest that, for the studied small mammal assemblages, in some cases other mechanisms than dietary niche segregation may be relevant for allowing species coexistence (e.g., differences in activity time, Kronfeld-Schor and Dayan , 2003). In addition to that, methodological limitations might be hindering the detection of differences in feeding habitats (e.g., consumption of distinct resource items with similar isotopic signature).

Despite these methodological constraints and some contrasting patterns, our study clearly indicated a wider range of the isotopic niche space (along both the δ^{13}C and δ^{15}N axes) and higher niche packing in the most complex habitats (i.e., gallery forests) in comparison to the non-forested habitats. This high packing in isotopic trophic niche possibly contributes to the highest richness generally observed in gallery forests (Camargo et al., 2018b; Mendonça et al., 2018). Moreover, this reinforces the need for conservation of these forests, which show low resilience to disturbances such as wildfires, which are common in neotropical savannas (Miranda et al., 2002). The structural simplification caused by fire (Camargo et al., 2018a) reduces the opportunities for trophic niche segregation among small mammals, potentially decreasing local richness associated to forests. Nonetheless, this hypothesis still holds to be adequately investigated in Cerrado environments, possibly affecting mainly diet-specialist species, such as *R. macrurus* and *O. bicolor*.

Within-species variations in isotopic assimilation

The observed within-species variation in the isotopic niche metrics according to season and vegetation formation is probably a response to the variation in availability and diversity of food items in each habitat, as already reported for other groups of animals (e.g., snakes, Willson et al., 2010; fish, penguins, and sea-wolves, Cherel, 2008; Cherel et al., 2007).

The assimilation of invertebrates from both grassland (C_4) and savanna/forested (C_3) areas by the agile mouse opossum *G. agilis* suggests an ability of this marsupial for exploiting a range of habitats. Indeed, this species occurs in dense savanna formations, woodland forests, and gallery forests and may alter its trophic niche seasonally, consuming more food items in the rainy season than in the dry season in Cerrado dry woodland forests (locally known as "cerradões"; Camargo et al., 2014, 2011.

In forests, the rodent *O. delator* predominantly consumed grassland invertebrates, which indicates that this species forages in forest gaps close to swampy areas, which are the preferred habitat type of this habitat-specialist genus (Bonvicino et al., 2002; Vieira and Marinho-Filho, 1998; Hershkovitz, 1994; Hinojosa et al., 1987). This species expanded its food-source spectrum (higher range of δ^{15}N, δ^{13}C, and SEAc) during the rainy season in response to increased food-resource diversity, which apparently was not accompanied by a marked increase in invertebrate availability (Fig. 2). Thus, this rodent enlarged its isotopic niche width as a response to a higher food diversity even when the overall food availability did not increase markedly. The abundance of this wet-grassland specialist inside forests also indicates the degraded condition of these formations in the study area.

The standard isotopic ellipse area (SEAc) of *T. apereoides* also increased in the rainy season in savanna formations compared to the dry season. This echimyid rodent assimilated both C_3 plants and invertebrates, indicating a high trophic diversity. In the rainy season, the savanna formations also showed greater invertebrate diversity (but lower availability; see Fig. 2) and higher diversity and availability of fruits in comparison to the dry season. The C_3 plant sources used by this species are mainly seeds and fruits, as suggested by a previous study based on fecal analysis, which also indicated higher consumption of plant matter in the rainy season compared to the dry season (Lessa and Costa, 2009).

We observed an opposite pattern for the arboreal rodent *R. macrurus* in comparison with *O. delator* and *T. apereoides*. The former showed lower trophic diversity in the rainy season in comparison with the dry season. Differently from the latter two rodents, *R. macrurus* is highly arboreal (Cáceres et al., 2010; Camargo et al., 2018b) and primarily assimilated C_3 plants. Thus, the high diversity of fruits in the rainy season likely allowed higher food selectivity, resulting in lower SEAc value than in the dry season. This pattern indicates that a greater variety of food resources not necessarily leads to increased diversity of assimilated food items.

In a South African savanna, a general pattern of reduction in between-individual differences in δ^{13}C and δ^{15}N values during the rainy season in comparison to the dry season was reported at least for the locally dominant rodents (Codron et al., 2015). Our results did not follow a similar trend, since variation in isotopic niche between seasons or across habitats failed to show a clear common pattern across the sampled species. Both habitat-generalist rodents (*C. tener* and *N. lasiurus*), however, reduced their invertebrate consumption (narrow δ^{15}N range) in more complex habitat types, even though invertebrate availability or diversity in these more complex formations was not reduced. This narrowing in δ^{15}N range may be related with increased competition for invertebrates and potentially more niche packing in the formations with higher complexity (Willis et al., 2005; August, 1983). For *N. lasiurus* individuals, the highest SEAc — value in the most complex habitat (forest), which was influenced mainly by an increase in the δ^{13}C range, suggests that this species frequently assimilated both C_3 and C_4 plants, directly or through invertebrates, in this habitat type. Thus, our results suggest that the influence of the availability and diversity of food

items on the isotopic trophic niche is mediated by idiosyncratic species characteristics.

In summary, we confirmed that omnivory is the predominant feeding category of small terrestrial mammals from the Brazilian savanna, but also detected certain trophic specializations, such as the high frugivory (C_3 source) of arboreal forest species (*R. macrurus* and *O. cleberi*) and insectivory of terrestrial swamp rats (*Oxymycterus* spp.). Inside forests, insectivorous rodents showed a broader isotopic niche during the rainy season (when resource availability is higher) than in the dry season but an opposite pattern arose for frugivorous species. Taken together, our results suggest that the influence of habitat complexity and food resources on the isotopic trophic niche is species-dependent and not unidirectional, thus being difficult to make general predictions of species response. Moreover, the patterns of isotopic assimilation indicated that habitat-generalist species also have a broad isotopic niche.

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Supplemental information

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

Table S1 Number of individuals sampled for isotopic analysis, by habitat.

Table S2 Proportional contribution of each food-source group.