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Artículo

FEEDING ECOLOGY OF *Marmosa demerarae* (THOMAS, 1905) AND *Marmosops bishopi* (PINE, 1981) (MAMMALIA, DIDELPHIDAE) IN FOREST FRAGMENTS OF THE SOUTHERN AMAZON

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ABSTRACT. We assessed the relative diet composition and level of trophic niche overlap of two sympatric didelphids, *Marmosa demerarae* and *Marmosops bishopi*, through the evaluation of food items consumed in forest fragments of different sizes in the southern Amazon region. The stomach contents of 107 individuals (42 *M. demerarae* and 65 *M. bishopi*) were analyzed by volume and frequency. The degree of similarity between the diets of the two species was quantified using Pianka's index. The relative importance of the different food items consumed was quantified with the Index of Alimentary Importance. Both species revealed flexibility in their feeding preferences but consumed predominantly coleopterans. Vegetable items were only identified in the diet of *M. demerarae*. Trophic niches of these species overlapped greatly (76%), suggesting strong competition for food items between them in the sampled fragments. *Marmosa demerarae* presented a broader trophic niche, consuming a greater variety of items than *M. bishopi*. Temporal changes in diet composition was attributed to fluctuations in the availability of food resources and to influence from the pasture matrices within these environments.

RESUMO. Ecologia alimentar de *Marmosa demerarae* (Thomas, 1905) e *Marmosops bishopi* (Pine, 1981) (Mammalia, Didelphidae) em fragmentos florestais no sul da Amazônia. Avaliamos a composição relativa da dieta e o nível de sobreposição de nichos de dois marsupiais simpátricos, *Marmosa demerarae* e *Marmosops bishopi*, através da avaliação de itens alimentares consumidos em fragmentos florestais de diferentes tamanhos na região sul da Amazônia. Nós analisamos o conteúdo estomacal de 107 indivíduos, 42 *M. demerarae* e 65 *M. bishopi*, de acordo com os métodos de taxa volumétrica e frequência. O grau de similaridade entre as dietas das duas espécies foi quantificado utilizando o índice de Pianka. A importância relativa dos diferentes itens alimentares consumidos foi estimada pelo Índice de Importância Alimentar. Ambas as espécies revelaram flexibilidade em suas preferências alimentares consumindo predominantemente coleópteros. Os itens vegetais foram identificados apenas em *M. demerarae*. A avaliação de itens alimentares mostrou sobreposição de 76% entre os nichos tróficos das duas espécies, sugerindo a existência de uma forte competição por itens alimentares

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entre eles nos fragmentos amostrados. *Marmosa demerarae* mostrou um nicho trófico mais amplo, consumindo uma maior variedade de itens em relação a *M. bishopi*. A alteração na composição das dietas foi atribuída a flutuações na disponibilidade de recursos alimentares e à influência das matrizes de pastagem nesses ambientes.

Key words: Coleopterans. Diet overlap. Forest fragments. Pasture matrix.

Palavras-chave: Coleópteros. Fragmentos florestais. Matriz de pastagem. Sobreposição de dieta.

INTRODUCTION

The conservation of biodiversity is one of the biggest challenges of this century, due to the elevated levels of anthropogenic disturbance on natural ecosystems, which have resulted in the increased fragmentation and loss of important habitats (Michalski & Peres 2005). A large part of remaining forests in South America, such as Atlantic and Amazon forests, exists only as highly disturbed, isolated and poorly protected fragments (Viana 1995). Despite being severally fragmented, these environments still harbor a diverse community of small non-volant mammals (Santos-Filho et al. 2012). Among these small mammals, the Neotropical endemic family Didelphidae is widely distributed throughout the Americas (Gardner 2007). Currently, about 95 didelphid species have been identified, of which 39 are known to occur in the Brazilian Amazon (Azevedo-Ramos et al. 2006, Gardner 2007, Brandão et al. 2015). Didelphid marsupials have diverse life histories, from predominately arboreal species (e.g. *Caluromys philander*), to semi-aquatic (e. g. *Chironectes minimus*), and terrestrial species (e. g. *Didelphis albiventris*). Some species can be diurnal (e. g. *Monodelphis americana*), whereas others are nocturnal (e. g. *Philander frenatus*). Feeding habits are also variable, with a predominance of omnivory within the family (Passamani 1995, Vieira & Astúa de Moraes 2003, Cáceres 2004, Gardner 2007, Rossi et al. 2012, Camargo et al. 2014).

Variation in feeding habits may occur both within and between species. Specific studies have shown that different didelphid species present different variants of an omnivorous diet, with varying levels of frugivory, carnivory or insectivory (Fonseca et al. 1996, Cáceres 2002, Cáceres 2004, Astúa de Moraes et al. 2003). Interspecific variation in feeding preferences facilitates niche differentiation between a great number of species within communities at local and regional scales (Vieira 2006). At the intraspecific level, the diet composition may vary according to season, resource availability, age, environment, and sex (Albanese et al. 2012, Camargo et al. 2014). Therefore, understanding the feeding ecology of the study species is the first step to understand more complex ecological relationships, such as competition, niche occupation, natural history, and the influence of the environment on the species or population (Jones & Barmuta 1998, Albanese et al. 2012, Camargo et al. 2014).

The use of food resources can influence the distribution of sympatric and syntopic species within a fragmented landscape or fragment. This process is accounted by the niche complementarity hypothesis of Loreau & Hector (2001), which suggests that a high overlap in one dimension of the niche may be compensated by a low overlap in another. The narrowing of specific niche breadths, such as differences in diet and habitat use, reduces competition (Pianka 1981). As mentioned above, didelphid species show differences in habitat use and, to varying degrees, in their temporal activity (Passamani 1995, Cáceres & Machado 2013), which have been shown to be important factors for the coexistence of different didelphid species in fragmented areas (Malcolm 1995).

Partitioning of food resources among these species has been assessed within Atlantic forest (Leite et al. 1996, Pinheiro et al. 2002) and Cerrado (Martins 2004) habitats but is poorly studied within the Amazon forest fragments.

Our hypothesis is that diet varies according to species, sex, time of the year and fragment size. Our goals are to evaluate one niche dimension, namely diet, in two sympatric and syntopic didelphids—*Marmosa demerarae* (Thomas 1905) and *Marmosops bishopi* (Pine 1981)—focusing on evaluating the influence of those factors on diet composition.

MATERIALS AND METHODS

Species

Marmosa demerarae, commonly known as the wooly mouse opossum, is widely distributed in northern South America, including northern and northeastern regions of Brazil, Guyana, Suriname, French Guyana, Venezuela, northern Venezuela, southern Peru and northern of Bolivia (Gardner 2007). This species is a midsize opossum (total length of body and head varying between 378 and 500 mm), with wooly hair which extends to more than 30 mm in the proximal part of the tail (Brandão et al. 2015). This opossum is relatively abundant in secondary forest and disturbed environments.

Marmosops bishopi, commonly known as Bishop's slender opossum, is distributed in northwestern Brazil (Mato Grosso, Rondônia, Acre and Amazonas States), northeastern Bolivia and southern Peru (Patton et al. 2000, Gardner 2007). This opossum is a small sized species, with total length of body and head size varying between 90 and 105 mm, and tail length between 116 and 137 mm (Brandão et al. 2015). This species inhabits mostly primary forests.

Study area

We conducted this study in the southern edge of the Amazon, within the municipality of Alta Floresta (09º 53' S, 56° 28' W), located in northern Mato Grosso (**Fig. 1**). The study area is under the domain Amazon (Souza 2006), which is characterized by a warm and humid tropical climate with well-defined dry and rainy seasons and an average annual temperature between 23 and 25 °C (Vourlitis et al. 2002). The vegetation is characterized by open tropical rain forest, tropical dense forest and transition zones (ecotones) (Loureiro et al. 1982). The study site is situated in a region that has suffered severe deforestation and rapid loss of large swathes of forest, the "Arc of Deforestation" (Fearnside 2005). This destructive process began in the 1970s with the onset of agricultural land conversion and

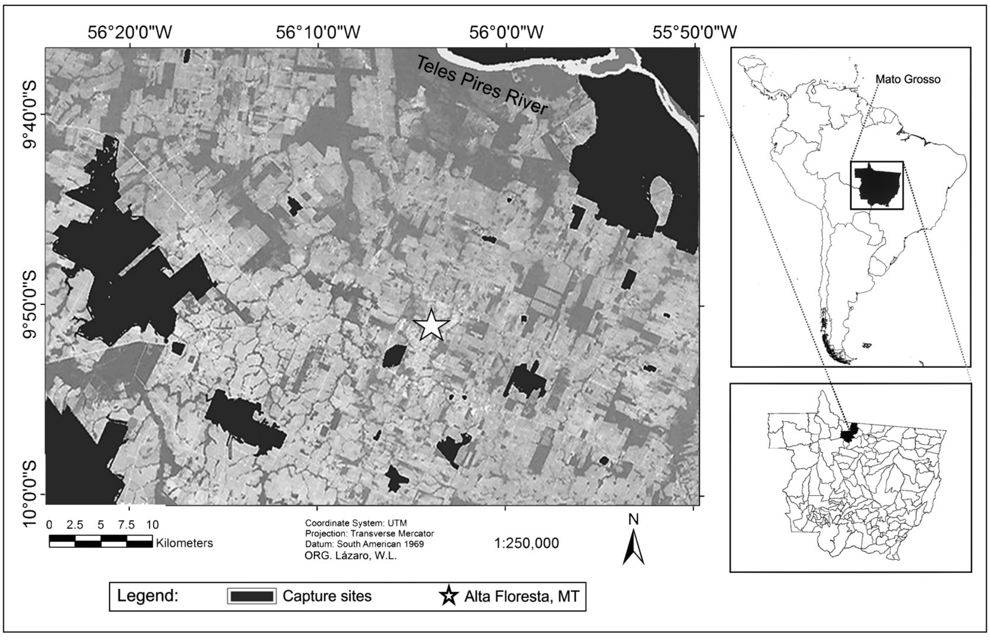

Fig. 1. Location of collection areas of *Marmosa demerarae* and *Marmosops bishopi* in forest fragments.

road-building programs, and is still ongoing (Lees & Peres 2006). This process has resulted in a hyper-fragmented landscape with forest patches of varying sizes, shapes and degrees of connectivity, embedded in a pasture matrix (Michalski & Peres 2005).

Sampling system

Sampling was conducted in 14 forest fragments which vary in size from 2 to 1763 ha, during 10 consecutive nights in each, between May and September 2009. Conventional traps baited with banana and peanut butter (wire-mesh traps with dimensions 145 x 145 x 410 mm, and box live traps, 80 x 90 x 230 mm) and intercepting pitfall traps (60 L buckets) were used to capture specimens. The sampling modules for conventional traps were set with three main parallel tracks, each 80 m long and placed 50 m apart, inside the fragments. Five sampling points (at 20 m intervals) were set in each transect, in which one wire-mesh trap and one box live trap were placed 3 m apart (3 transects x 10 traps). One sampling module was installed within small fragments and three within the mid to large sized fragments. Each module was placed 500 m apart. Intercepting pitfall traps were installed using four 60 L buckets buried in a "Y" formation (three buckets on outer points with one in the centre), connected by a 70 cm-high guide fence made of black plastic tarpaulin. The tarpaulin was buried 5 cm into the ground. One pitfall trap module was installed in the small fragments, which was placed in the center of each area, between the tracks of the conventional traps. The stomachs analyzed in the present study were obtained from 107 specimens collected in the project "Community structure of small mammals in fragments in southern Amazonia"; theses specimens were sacrificed using potassium cloride (KCL) intracardiac injection are vouchers deposited at the Laboratório de Mastozoologia, Universidade do Estado de Mato Grosso (UNEMAT), Cáceres, Mato Grosso, Brazil. List of specimens with the field number of *Marmosa demerarae*: MSF 1422, 1437, 1451, 1455, 1459, 1466, 1467, 1469, 1486, 1514, 1525, 1536, 1538, 1550, 1551, 1567, 1570, 1571, 1580, 1602, 1605, 1607, 1608, 1622, 1630, 1653, 1661, 1679, 1698, 1705, 1714-1716, 1727, 1730, 1731, 1732, 1741, 1742, 1746, 1747, 1749 and *Marmosops bishopi*: MSF 1414,-1417, 1423, 1424, 1441, 1442, 1461, 1464, 1495, 1499, 1508, 1542, 1548, 1573, 1586, 1588, 1599, 1600, 1611, 1614, 1626, 1631, 1634, 1635, 1636, 1642, 1659, 1660, 1662, 1667, 1674, 1678, 1680, 1688, 1691-1693, 1699-1701, 1706, 1708, 1713, 1736, 1788, 1807, 1817, 1824, 1863-1866, 1868, 1899, 1900-1904, 1912, 1916-1918.

The dietary composition was determined by the analysis of stomach contents (Uieda 1994). The stomach of each specimen was removed and stored in formaldehyde (10%) for one day, after which stomachs were washed in freshwater and transferred to 70% alcohol. Stomach contents were then removed and dissolved in 20 ml of distilled water in millimetre-scaled Petri dish and analyzed using a stereoscopic microscope (Fernandes et al. 2006). Food items were identified and classified into eight categories, including one category for baits used in the traps (Leiner & Silva 2007, Pinheiro et al. 2002).

To determine the percentage of stomach volume (Vol %) that each item occupies we measured the displacement of the water volume, related to the total volume found for the stomach. The smaller volumes of some food items were assessed by placing the material on a Petri dish millimeter to 1 mm high, which was then converted into cubic milliliters (Hynes 1950, Hyslop 1980). For larger items, the volumetric method was conducted using a graduated cylinder, checking the displacement of the water volume. We also estimated the stomach repletion degree based on the amount of food within the stomach at the time of capture (not including bait). The frequency of occurrence of food categories (F %) is the percentage of the total volume occupied by each category.

Data analysis

The baits were separated from stomach contents and not included in the analyses. The stomach repletion degree was classified in four categories according to Uieda (1994): stomach partially or totally empty (Gr1, 0-25%), stomach with intermediate or low amounts of food (Gr2, 25-50%), stomach with high amounts of food (Gr3, 50-75%), and stomach full of food (Gr4, 75-100%). The frequency of occurrence and the specific prey abundance (numeric frequency), for each specimen and for each food item identified, were considered as a consumption record, regardless of the total amount of food (Hynes 1950, Hyslop 1980, Uieda 1994). To evaluate the relative importance of the preys (dominant or rare) and the degree of homogeneity of prey selection in the predator population, we used Costello's (1990) diagram method. We combined data of specific prey abundance and volume, aiming to determine the Index of Alimentary Importance (IAI) which was calculated as the ratio of prey-specific abundance (**Pi**) and its frequency of occurrence (**Fi**). The prey-specific abundance was calculated by the following formula: % $\mathbf{Pi = (\Sigma Si / \Sigma Sti) \times 100}$, where **Si** = number of stomachs containing only prey **i**; **Sti** = total number of stomachs in which prey **i** occurs. The frequency of occurrence was obtained by the following formula: % **Fi = (Ni / N) x 100**, where **Ni** = number of predators with prey **i** in the stomach; **N** = total of predators with stomach contents (variable from 0 to 1), which allowed an evaluation of the food regimen of the especies (Kawakami & Vazzoler 1980). To analyze the overlap between trophic niches of the species, we used the food overlap index proposed by Pianka (1973), as implemented in Ecosim version 7.2 software (Gotelli & Entsminger 2011). This index is quite suitable for analysis of trophic niche overlap, including those based on the proportions of the food items found in the stomachs (Krebs 1999). The Pianka overlap index ranges from 0 (no overlap) to 1 (complete overlap).

Variation in volumes of food items between the sexes and months of the year was examined with by Chi-Square tests. The relationship between the abundance of the most consumed prey category and the size of the sampled fragments was examined using general linear models (GLM). All statistical analyzes were performed using the R 9.0 statistical interface (R Development Core Team 2009).

The arthropods and plant material were identified by specialists from Universidade do Estado de Mato Grosso, Cáceres, Brazil.

RESULTS

We analyzed the stomach contents of 42 *M. demerarae* individuals (21 males and 21 females) and 65 *M. bishopi* individuals (48 males and 17 females). Food items were identified and classified into 8 categories, including one category for the bait used in traps (**Table 1**).

With the exception of baits, with frequencies of occurrence of 47.65%, fruits were the most frequently identified food items in the *M. demerarae* diet (43.98%), while the least frequent item was hymenopteran insects (5.27%). Conversely, fruit had the lowest frequency in the stomachs of *M. bishopi* (3.81%) (**Table 1**). Arthropods and coleopterans were the most frequently identified items (**Table 1**). Despite small variations, the Index of Alimentary Importance (IAI) of coleopterans and arthropods were constant throughout the study period.

Costello's diagram showed no dominance of any food item for either species. However, fruits and seeds were the main items in *M. demerarae* whereas the frequency was three times higher in *M. bishopi* (**Table 1**). Pianka's food index of dietary overlap between *M. demerarae* and *M. bishopi* was 0.76.

Stomac repletion in *M. demerarae* varied as follows: 14.28% (n = 6) of had empty stomachs, 16.66% (n = 7) were partially empty, 30.95% (n = 13) partially filled and 38. 09% (n = 16) completely filled. The majority of *M. bishopi* specimens had empty stomachs 30.96% (n = 20),

Table

Percentage of stomach volume (Vol %), frequency of occurrence (F %), and Index of Alimentary Importance (IAI) of two sympatric marsupials, *Marmosa demerarae* and *Marmosops bishopi*, in forest fragments of the southern Amazon, Mato Grosso, Brazil.

Food item	*Marmosa demerarae*			*Marmosops bishopi*		
	Vol (%)	F (%)	IAI	Vol (%)	F (%)	IAI
Fruits	0.703	43.980	0.270	0.175	3.810	0.101
Seeds	0.072	4.108	0.224	0.000	0.000	0.000
Unidentified vegetables	0.369	22.166	0.097	0.010	18.180	0.033
Coleoptera	0.358	19.747	0.078	0.189	58.149	0.418
Hymenoptera	0.102	5.274	0.028	0.005	0.980	0.000
Unidentified insects	0.694	25.322	0.105	0.156	53.130	0.386
Other arthropods[1]	0.363	23.692	0.166	0.200	75.216	0.622
Baits	0.714	47.651	0.312	0.053	49.064	0.435

[1]Insecta: Blattodea, Lepidoptera, Hemiptera, Isoptera; and unidentified Chelicerata

whereas 27.69% (n = 18) had partially empty stomachs, 16.92% (n = 11) had partially filled stomachs, and 24.61% (n = 16) had completely filled stomachs.

The food volume at stomachs of *M. demerarae* and *M. bishopi* showed no temporal variation throughout the sampling months, (p = 0.67, df = 39, and p = 0.76, df = 13, respectively).

In the case of the distribution of percentages of the degrees of repletion (**Fig. 2**), *M. demerarae* showed predominance of Gr4 in May and September, and 100% of Gr3 in June and August, there is no sample from July; while for *M. bishopi* Gr1 stomachs were more common in May, June and August, and Gr2 in July and September.

There is no significant variation for composition and amount of each kind of food items comparing male and females of *M. demerarae* (p = 0.32, df = 39) and *M. bishopi* (p = 0.32, df =13).

There was no significant difference across fragments between the frequency of coleopterans (the most abundant food item) in the diet of either species (**Fig. 3**).

DISCUSSION

The prevalence of some items, such as arthropods, fruits and seeds in the diets of the current study species has been documented for other species of the same genera (Fonseca et al. 1996, Cáceres et al. 2002, Leiner & Silva 2007). The presence of feathers and bone fragments in the stomachs of *M. demerarae* indicates predation on birds and small vertebrates. Larger didelphids, such as *Philander opossum* and *Metachirus nudicaudatus*, have been known to act as mesopredators, often consuming small vertebrates (Emmons & Feer 1997) and preying on bird nests (Barbini & Passamani 2003).

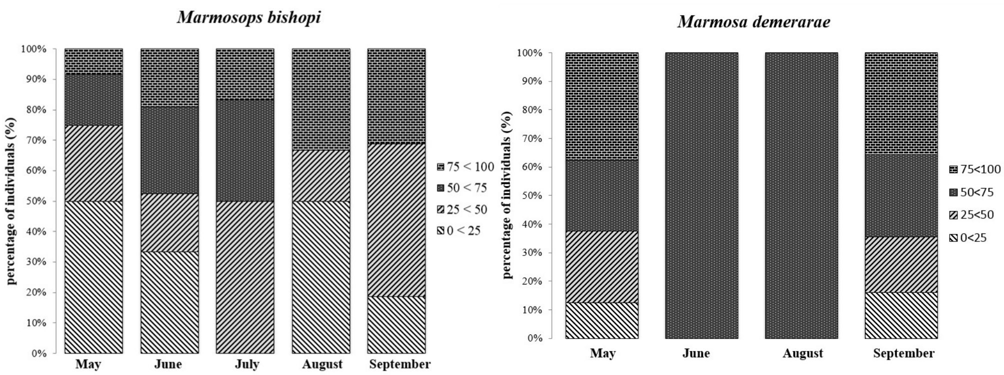

Fig. 2. Diagrammatical columns of the stomachic repletion index of *Marmosa demerarae* and *Marmosops bishopi* in forest fragments during the period from May to September (Rd1 = 0<25, Rd2 = 25<50, Rd3 = 50 <75 and Rd4 = 75<100).

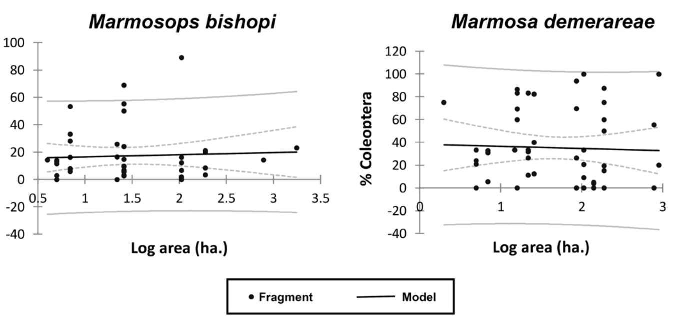

Fig. 3 GLM Model of the effect of the size of forest fragment sampled [Area (ha.)] on the relative volume of beetles found in the stomachs of *Marmosa demerarae* (A) and *Marmosops bishopi* (B) in Amazonian forest fragments in the year 2009.

Within the plant items found, flower remnants were present in the stomach contents of *M. demerarae*, which may indicate the species serves as a pollinator, as confirmed for *Caluromys lanatus* and *C. philander* (Gribel 1988). The high occurrence of fruits in the diet of *M. demerarae* and the percentage of intact seeds found in the lower digestive tract may suggest dispersion via fecal matter. Studies demonstrating the dispersal of seeds by marsupials in Atlantic Forest regions have shown that marsupials can contribute to the recovery of deforested areas and ensure the ecological plasticity of forest fragments (Cerqueira et al. 1993; Cáceres & Monteiro-Filho 2000; Cáceres et al. 2002).

The highest repletion rate for *M. demerarae* was found in September, which coincides with the onset of the rainy season, indicating a greater supply of insects and fruits during that season (Vasconcelos 1990; Brown 2000; Santos-Filho et al. 2008). The feeding behavior of these two species may be indicative of invertebrate abundance, especially beetles, in forest fragments (M. Santos-Filho, personal observation). Beetles are preferred prey of various faunal groups due to their high energy value and the relatively low energy expenditure involved in their capture and digestion (Pianka 2000).

It appears that the coleopteran fauna may be sustaining the population of *M. bishopi* within the study area as the overwhelming majority of food items (about 80%, **Fig. 4**) found in the stomach and intestines of this species consisted of coleopterans. A similar pattern was found by Castilheiro & Santos-Filho (2013) for *Monodelphis glirina* in the same areas. *Marmosa demerarae* is a more generalist species, using other items within the fragments, overlapping in part in the use of beetles with *M. bishopi* in the study area.

Pardini (2004) suggested that *M. demerarae* tend to increase their density in altered environments due to edge effects. These areas generally have a greater abundance of fruits and arthropods, especially beetles (Montenegro et al. 1996; Santos-Filho at al. 2008), which are a major component of the diet of this species (Pinheiro et al. 2002). The abundance of these arthropods makes the foraging activity of this species far more efficient, but does not prevent the active search for preys (Astúa de Moraes et al. 2003). The high abundance of beetles is maintained by the presence of cattle dung throughout the surrounding matrix, which can actively migrate, and become abundant, especially in small fragments (Blume 1985; Cervenka & Moon 1991; Castilheiro & Santos-Filho 2013).

The results of this study on *M. demerarae* in the Amazon rainforest, compared with other Atlantic Forest area, suggests a pattern of insectivorous-frugivorous diet (Carvalho et al. 2005; Casella & Cáceres 2006). Items of vegetal origin were not found in the diet of the *M. bishopi*; however, frugivory cannot be

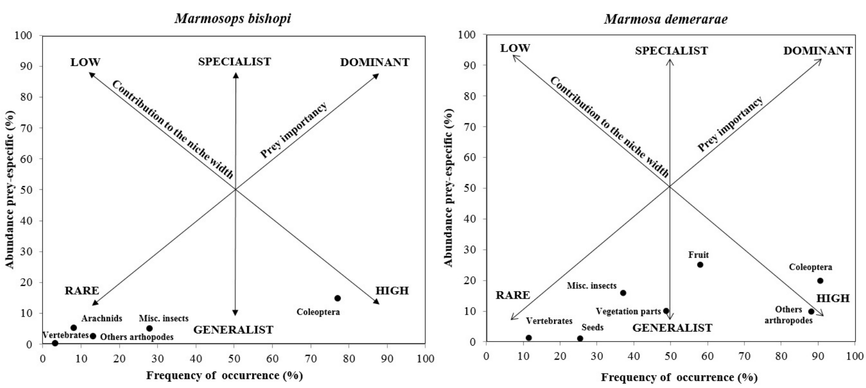

Fig. 4. Abundance of the Preys and the Frequency of Occurrence on the alimentary items between *Marmosa demerarae* and *Marmosops bishopi* in forest fragments on Southern Amazonia.

ruled out because it is common to catch this species using banana and peanut butter as bait in the traps.

The large number of *M. bishopi* captured with empty stomachs may have been influenced by the capture period and the kind of trap, as about 70% of its specimens were captured on pitfall traps, possibly before foraging in the early evening. A thin layer of paste was found in several of the *M. bishopi* empty stomachs. This may have been a residue of digested fruits, which are usually digested and quickly pass through the digestive tract. Studies conducted on other species of the same genus, such as *Marmosops paulensis* and *Marmosops incanus* have found high consumption of carbohydrates and fiber from a frugivourous diet (Astúa de Moraes et al. 2003; Leiner & Silva 2007).

In our study, we did not observe any notable differences in the types of food items ingested by males and females of *M. demerarae* and *M. bishopi*, suggesting a high degree of similarity of food items consumed by both sexes. The uniformity in items of diet between sexes in small marsupials are commonly reported, and may be related to the species behavioral response in relation to the ecosystem in which they live (Pinheiro et al. 2002), even in highly fragmented areas.

The results show the importance of arthropods, mainly coleopterans, in the diet of both species in the Amazonian forest fragments (Malcolm 1997; Lambert et al. 2006). Given that fragmented areas have more arthropods near their edges (Malcolm 1994), it is likely that foraging efficiency on these prey items is highly increased in these types of areas. The high trophic niche overlap value (76%) does not necessarily indicate competitive exclusion of either species, as they may differ in other aspect of their ecological niches. *Marmosa demerarae* was frequently observed in activity in the early evening whilst *M. bishopi* was observed to be more active later in the night (M. Santos-Filho pers. obs.), suggesting temporal differentiation. It is possible that *M. bishopi* is more specialized for insectivory, a common response to high trophic niche overlap (Hutchinson 1957; Astúa de Moraes et al. 2003; Crouzeilles 2010).

Compared to other studies involving the diet of different marsupial species (Cáceres 2004; Cáceres 2006), we observed a relatively low diversity of food items in the diets of *M. bishopi* and *Micoureus demerarae*. These results are probably due to the effect of the pasture matrix in the areas surrounding fragments, which tends to reduce the variety of available food items. At these same areas, beetles are significantly more abundant in smaller fragments (see Castilheiro & Santos-Filho 2013). However, we found no difference in the number of food items between species. Fluctuations in the abundance of beetles throughout the year can increase the degree of niche overlap between these two marsupial species in times of scarcity.

The advancement of deforestation and conversion of forest into pasture in the Amazon have modified the natural habitats. The high occurrence of beetles in the diet of both species and the possible divergence via the insectivorous specialization of *M. bishopi* (Fonseca et al. 1996; Cáceres 2004; Casella & Cáceres 2006; Leiner & Silva 2007) show the importance of understanding the new reality posed by habitat fragmentation in the structure of forest communities.

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