

# Between-individual variation drives the seasonal dynamics in the trophic niche of a Neotropical marsupial

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**Abstract** The dynamics of population niches result from the variation in resource use within individuals and also from the variation between individuals. The prevalence of one mechanism or the other leads to competing hypotheses about the major mechanisms underlying the empirical observations of the contraction/expansion dynamics of the trophic niche in natural populations. In this study, we investigated how within- and between-individual variation in resource use shapes the food niche dynamics of the woolly mouse opossum, *Marmosa paraguayana* (Didelphimorphia: Didelphidae), in a remnant of the highly seasonal Cerrado in south-eastern Brazil. To do so, we analysed the faecal samples of live-trapped individuals to determine their diets within the wet and dry seasons. In addition to a seasonal shift in the composition of the diet, the population trophic niche was significantly wider during the dry season than the wet season. This expansion resulted from larger between-individual variation in the dry season that was not related to sex preferences, whereas the individual niche widths did not significantly increase from the wet to the dry seasons. Our findings add to the growing list of animal populations that show individual-level variation in resource use. Furthermore, these results represent a pattern of individual-level response to seasonal changes that is different from patterns reported for other organisms. We suggest that a pathway to build more realistic foraging models and produce more accurate predictions on population and community dynamics is to consider between-individual variation and short-term niche dynamics.

**Key words:** Cerrado, Didelphidae, diet breadth, inter-individual variation, niche width.

## INTRODUCTION

Optimal Foraging Theory (OFT) predicts that the trophic niche width of a population will expand (or contract) when resource availability is low (or high) (Schoener 1971; Pyke *et al.* 1977; Stephens & Krebs 1987). In fact, such OFT predictions have received extensive empirical support (e.g. Schoener 1971; Pianka 1986; Pulliam 1986; Tome 1994; Ben-David *et al.* 1997; Vieira 2003). Both the theory and empirical observations carry the implicit assumption that individuals within populations respond similarly to variation in the availability of food resources (Tinker *et al.* 2008).

By assuming no individual variation in resource use, most studies have not addressed the question of how

such variation may affect population niche dynamics (e.g. Pulliam 1986; Tome 1994; Ben-David *et al.* 1997). Indeed, the dynamics of the population niche result from the variation in resource use within individuals (i.e. the expansion/contraction of individual niche width) and also from variation between individuals (i.e. a reduction/increase in niche overlap among individuals; Tinker *et al.* 2008; Bolnick *et al.* 2010). Although both types of variation are not mutually exclusive, the prevalence of one mechanism or the other leads to competing hypotheses about the major drivers of empirical observations of contraction/expansion dynamics of the niche in natural populations (Bolnick *et al.* 2007; Tinker *et al.* 2008).

The few studies (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007) that have investigated the within- and between-individual variation as drivers of population niche dynamics have shown that the balance between these two components fluctuates in

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response to changes in population density, which affect the availability of resources. Resource availability can vary in response to the consumer regulatory effect (Svanbäck & Bolnick 2007), but also fluctuates in response to environmental factors, such as climatic factors operating on intra-annual timescales (Grant & Grant 2002). Thus, a relevant question is whether niche dynamics imposed by natural short-term changes in the environment are predominantly shaped by within-individual or between-individual variation in natural populations. If on the one hand niche dynamics driven by occasional changes in consumer density can be episodic (e.g. Svanbäck & Persson 2004), niche dynamics resulting from intra-annual climatic fluctuations should, in theory, be more regular and thus could be related to adaptive responses (e.g. Willson *et al.* 2010). In this sense understanding the mechanisms underlying niche dynamics may provide insights into the suite of strategies that individuals employ to deal with the environmental fluctuations and enhance our ability to predict the response of populations facing a changing environment.

In this study, we investigated how within- and between-individual variation in resource use shape the food niche dynamics of the woolly mouse opossum, *Marmosa paraguayana* (Didelphimorphia: Didelphidae; until recently *Micoureus paraguayanus*; see Voss & Jansa 2009). *Marmosa paraguayana* is a medium-sized (58–132 g), solitary, arboreal and nocturnal Neotropical didelphid marsupial that occurs in eastern Paraguay, north-eastern Argentina, and south-eastern and southern Brazil (Gardner & Creighton 2008). Although this large distribution includes disparate habitats, such as the Atlantic rainforest and Cerrado (Brazilian savanna), we focus on a population inhabiting a remnant of the highly seasonal savanna-like Cerrado in south-eastern Brazil. The marked seasonality in the Cerrado affects the availability of the food resources that are potentially used by the marsupials, such as fruits (Batalha & Martins 2004) and arthropods (Pinheiro *et al.* 2002a). Thus, the marsupials inhabiting this environment are well suited to the study of the contraction/expansion dynamics of the population niche on intra-annual timescales and the role of individual-level processes in such dynamics.

We first describe the seasonality in *M. paraguayana* diet composition and niche dynamics and then investigate whether such dynamics are caused mainly by variation in resource use within individuals or the variation between individuals. If population niche dynamics is mainly shaped by within-individual variation, we should expect that population niche and individual niches vary accordingly, that is, both would expand or contract. Conversely, if changes in the population niche are not mirrored by changes in the individual niches, between-individual variation should be the main mechanism determining the population niche

dynamics. Because males and females differ in their energetic needs especially during the reproductive season (Martins *et al.* 2006), we also investigate whether males and females have different niche dynamics.

## METHODS

### Study area

Our study was carried out at the Reserva Biológica de Mogi Guaçu (RBMG) (22°15′/22°18′S, 47°08′/47°13′W), located in the city of Mogi Guaçu in south-eastern Brazil. The vegetation at the RBMG consists of Cerrado, which is a tropical savanna formation comprising different vegetation physiognomies (Oliveira-Filho & Ratter 2002). At the RBMG, there is a remnant of the physiognomy that is locally known as ‘Cerrado *sensu stricto*’, which is woodland with scattered trees that are 5–8 m tall and closed scrub (Oliveira-Filho & Ratter 2002). Even though the temperatures do not change markedly throughout the year (monthly mean temperature range = 18–23°C), the rainfall is strongly seasonal, with most of the precipitation occurring from October to March (average rainfall for the period = 175 mm), whereas the dry months are mainly between April to September (average rainfall for the period = 50 mm, pluviometric data from: [http://www.cpa.unicamp.br/outras-informacoes/clima\\_muni\\_348.html](http://www.cpa.unicamp.br/outras-informacoes/clima_muni_348.html), accessed 29 October 2012).

### Trapping

The diet of *M. paraguayana* was determined by analysis of the faeces sampled from individuals captured between September 2005 and August 2006 (Fernandes *et al.* 2010). From September to November 2005, the sampling was performed every 15 days over two consecutive nights. Thereafter, the sampling was performed over 10 consecutive days each month except during February and April 2006, when sampling was not possible because of logistical issues. The individuals were captured in an 11 × 11 trapping grid, with 121 trapping stations located 15 m from each other. A Sherman live-trap (dimensions 7.5 × 9.0 × 23.5 cm) was set in a tree at each trapping station, approximately 1.75 m above the ground and baited with banana and peanut butter. The individuals were marked with a numbered ear-tag, and their sex was recorded.

### Dietary analysis

The faecal samples on the trap floor and those defecated by the adult individuals during manipulation were collected, preserved in 70% ethanol and transported to the laboratory. In the laboratory, the faecal pellets were carefully broken apart in Petri dishes and analysed with a binocular stereomicroscope with magnification range of 6× to 66×. All samples were examined exhaustively for any fragments of animal or vegetal matter. Although the bait used in live trapping was

often found within samples, it did not affect the identification of food items as they were mostly seeds or arthropod fragments, which are easily identifiable. The food resources detected in the faecal samples were identified to the level of order and, in some cases, to family and genus using taxonomic keys (Borror *et al.* 1989) and/or by direct comparison with a reference collection of arthropods and fruits systematically collected in the study area while performing a pilot study (F. R. Fernandes, unpubl. data, 2005).

Faecal analysis has limitations, such as the differential digestion of dietary items and the individual variation in the digestion of different prey items (Hume 2006; Pires *et al.* 2011). Nonetheless, faecal analysis is considered reliable for organisms that consume mainly arthropods (Dickman & Huang 1988) and has the advantage that individuals need not be killed. Moreover, several studies using faecal samples to determine the diet of Neotropical marsupials (e.g. Martins *et al.* 2006, 2008; Leiner & Silva 2007) have successfully recovered soft-bodied invertebrate fragments and fruits usually found in the analyses of stomach contents (Martins & Bonato 2004), suggesting that the inference of dietary diversity is not strongly affected by the differential digestibility of food items in these species. Also, because our main questions rely on comparisons among individuals, presumably subjected to the same biases in diet description, any potential biases are less problematic here than if our objective were to provide a detailed description of the species diet. Finally, dietary studies based on faeces also allow one to obtain longitudinal samples such that the repeated observations of the diet of an individual over time are possible. In this sense, faecal analysis was the most adequate method for the objectives of the present study.

To describe the diet composition of the *M. paraguayana* population we calculated the per cent occurrence, that is, the proportion of faecal samples containing a particular food resource (Korschgen 1987). For the remaining analysis, where we computed niche width and niche overlap measures, we used the estimated minimum number of items of each resource category consumed by an individual. This measure was obtained by counting the number of parts of a prey's body for arthropods and of seeds for fruits found in faecal samples. To obtain conservative estimates of the number of items ingested by an individual, we used different approaches for arthropods and fruits. For the arthropods, we estimated the number of a given prey category using the minimum number of items detected in a given sample (e.g. two ants were only recorded if more than six ant legs or two ant antennae were found). Because we did not have accurate estimates of the numbers of seeds that each fruit contains, we used the natural logarithm of the numbers of seeds found in each sample in the following analyses. The indices to quantify individual variation (see below) are more strongly affected by those resources that are found in larger proportion in the diets of individuals. By using a transformation we avoided overestimating the number of ingested fruits and consequently differences among individuals, allowing a more conservative estimate of the degree of individual variation.

We first tested whether the population diet composition changed with the seasons. To do that we compared the number of occurrences of each food category between the dry and wet seasons using the *G*-test of independence (Zar 1999). We used all of the categories whose expected

frequency on the contingency table built for the *G*-test was less than 5 for both seasons. To estimate the population trophic niche width, we used the Shannon index of diversity and compared the estimates between the seasons using Hutchenson's *t*-test (Krebs 1989).

To assess whether the niche width of individuals varied between the seasons, we calculated the Shannon index within each season for those individuals that were captured in both seasons, as a measure of individual niche widths, and tested whether the individual niche width differed among the seasons. To allow for direct comparisons, we used an approach that controls for differences in the number of faecal samples collected per individual in each season. We used a rarefaction algorithm that takes random subsamples of the items in the diet of an individual in a given season generating several subsamples (10 000 simulations) of smaller size. The index is then computed for each subsample and the averages can be compared. This equates the number of items detected in both seasons, thus, allowing comparisons for similar sampling sizes (Heck *et al.* 1975). The Shannon index calculations and rarefactions were performed using the Ecosim 7.0 program (Gotelli & Entsminger 2005). The differences in the individual niche widths between the seasons were then tested with the Wilcoxon signed rank test for paired samples. If the niche widths of the individuals and the population varied accordingly (i.e. both the individual and population niches contracted or expanded), the changes in the population niche width would correspond to the changes in the individual's niche widths; otherwise, we might expect that the dynamics of population niche occurred because of variation in the between-individual component.

To assess how the degree of between-individual niche variation varied across the seasons, we used the individual-level diet variation index, *E* (Araújo *et al.* 2008). The *E* index is an estimate of the between-individual variation, which is obtained by averaging the pairwise dietary dissimilarity among individuals. *E* ranges from 0, when the individual diets are identical and there is no diet variation, towards 1, as the variation in the diet increases (see Araújo *et al.* 2008 for further detail). To test the null hypothesis that there was no diet variation between individuals, we used a null model approach to test the significance of the index in each season. We used a bootstrap procedure in which each individual was reassigned the same number of food items that was detected in its faecal samples, drawn randomly from the population diet distribution via multinomial sampling (Araújo *et al.* 2008). The null hypothesis could be rejected if the observed  $E > 95\%$  of the null values. Because the number of individuals and resources varies between seasons the values of *E* need to be corrected to be comparable. To allow comparison between the *E* values computed for each season we calculated the relative value of *E*,  $E^* = (E - E_{\text{null}})/E_{\text{null}}$ , where  $E_{\text{null}}$  is the average value of *E* computed for the null model. Because the null model uses the actual data to generate the theoretical expectation it accounts for possible effects of limited sampling in the variation index. To double check if our estimate of *E* was affected by our limited sample size we used a rarefaction approach. We generated rarefied samples of 95%, 85%, 75%, . . . , 25% of the total number of individuals by randomly removing individuals and calculating *E* for each rarefied sample (1000 per fraction). If *E* was strongly affected by the number of sampled individuals we should expect that

rarefied samples would show  $E$  values largely different from the value calculated for the total sample. We performed analyses using our own code written in R (R Development Core Team 2010).

To verify whether the degree of between-individual diet variation was related to the sex of individuals, we used the pairwise diet overlap measure,

$$w_{ij} = 1 - 0.5 \sum_{k=1}^K |p_{ik} - p_{jk}|,$$

where  $p_{ik}$  is the frequency of category,  $k$ , in the diet of an individual,  $i$ , and  $p_{jk}$  is the frequency of category,  $k$ , in the diet of an individual,  $j$ . Thus, we separated the pairwise overlap measures into two groups: overlap among individuals of the same sex and among individuals of different sexes. We tested the null hypothesis that the diet overlap did not differ among these groups using randomization tests (1000 simulations) in which the diets were randomly assigned to males and females, and the dietary overlap was then calculated. For each simulation, we calculated the difference in the average dietary overlap between the two groups. If the observed difference was significantly higher than the difference values obtained in the randomizations, the between-individual variation in the population could be, at least in part, attributed to gender differences in dietary preferences.

## RESULTS

We analysed 165 faecal samples (67 from males and 98 from females) from 20 individuals (13 males and 7 females). The average number of faeces per individual was smaller in the wet season (mean  $\pm$  SD =  $4.50 \pm 5.30$ ) than in the dry season ( $9.30 \pm 10.50$ ). We found arthropods from 11 orders and seeds representing five plant genera (Table 1). Ants, beetles, hemipterans and *Miconia* fruits were the most frequent resources detected in the samples (Table 1). Termites and non-Formicidae hymenopterans were found with intermediate frequencies, whereas other resources, such as spiders and *Passiflora* fruits, were detected with low frequencies (Table 1). The composition of the population diet differed significantly between the seasons ( $G = 30.43$ , d.f. = 3,  $P < 0.001$ ); notably, the frequency of beetles and fruits detected in the samples decreased substantially from the wet to the dry seasons (Table 1). In contrast, the frequency of termites detected in the samples increased considerably during the dry season (Table 1).

**Table 1.** Percentage of occurrence (%) and frequency ( $n$ ) of each resource category detected in the faecal samples of *Marmosa paraguayana* throughout the year, and in the warm-wet and the cool-dry season separately

Food resource	Year total		Wet season ( $n = 16$ individuals)		Dry season ( $n = 9$ individuals)	
	%	$n$	%	$n$	%	$n$
<b>Insecta</b>						
Hymenoptera						
Formicidae	88	146	100	72	81	75
Apoidea	6	10	4	3	8	7
Not identified	10	16	10	7	10	9
Coleoptera	43	71	74	53	19	19
Isoptera	12	20	4	3	18	17
Blattodea	3	5	4	3	2	2
Hemiptera						
Heteroptera	29	48	25	18	32	30
Auchenorrhyncha	2	3	4	3	0	0
Lepidoptera	1	2	0	0	2	2
Diptera	6	11	10	7	4	4
Orthoptera	4	6	4	3	3	3
Arachnida	6	7	7	5	2	2
Myriapoda	4	6	7	5	2	2
<b>Fruits</b>						
Melastomataceae						
<i>Miconia</i>	36	59	69	50	10	9
Passifloraceae						
<i>Passiflora</i>	5	8	0	0	9	8
Malvaceae						
<i>Pavonia</i>	27	44	47	34	11	10
Moraceae						
<i>Ficus</i>	2	3	1	1	2	2
Rubiaceae						
<i>Tocoyena</i>	1	1	1	1	0	0

The population food niche was significantly wider in the dry season ( $H' = 1.80$ ) than in the wet season ( $H' = 1.61$ ,  $t = 2.67$ , d.f. = 27.90,  $P = 0.01$ ). However, the niche width of individuals that were captured in both seasons did not significantly increase in the dry season (average difference between seasons = 0.06; Wilcoxon paired-test:  $V = 11$ ,  $P > 0.99$ ), suggesting that the increase in the population niche width in the dry season was not achieved via the expansion of the individual niches. Instead, it was the reduction in the niche overlap among the individuals that caused the population niche expansion. Even though the absolute value of  $E$  was similar for both seasons, we found a higher between-individual diet variation than expected by chance in the dry season ( $E = 0.44$ ,  $E_{\text{null}} = 0.28$ ,  $E^* = 0.58$ ,  $P < 0.001$ ), whereas the diets did not differ significantly among the individuals in the wet season ( $E = 0.43$ ,  $E_{\text{null}} = 0.45$ ,  $E^* = -0.04$ ,  $P = 0.66$ ; Fig. 1). The rarefaction analysis indicated the significant value of  $E$  for the dry season was not a product of limited sample size (see Appendix S1 in Supporting Information). The pairwise dietary overlap in the dry season was not smaller between the males and females than within males or within females ( $P = 0.99$ ), suggesting that the variation found was not related to sex.

## DISCUSSION

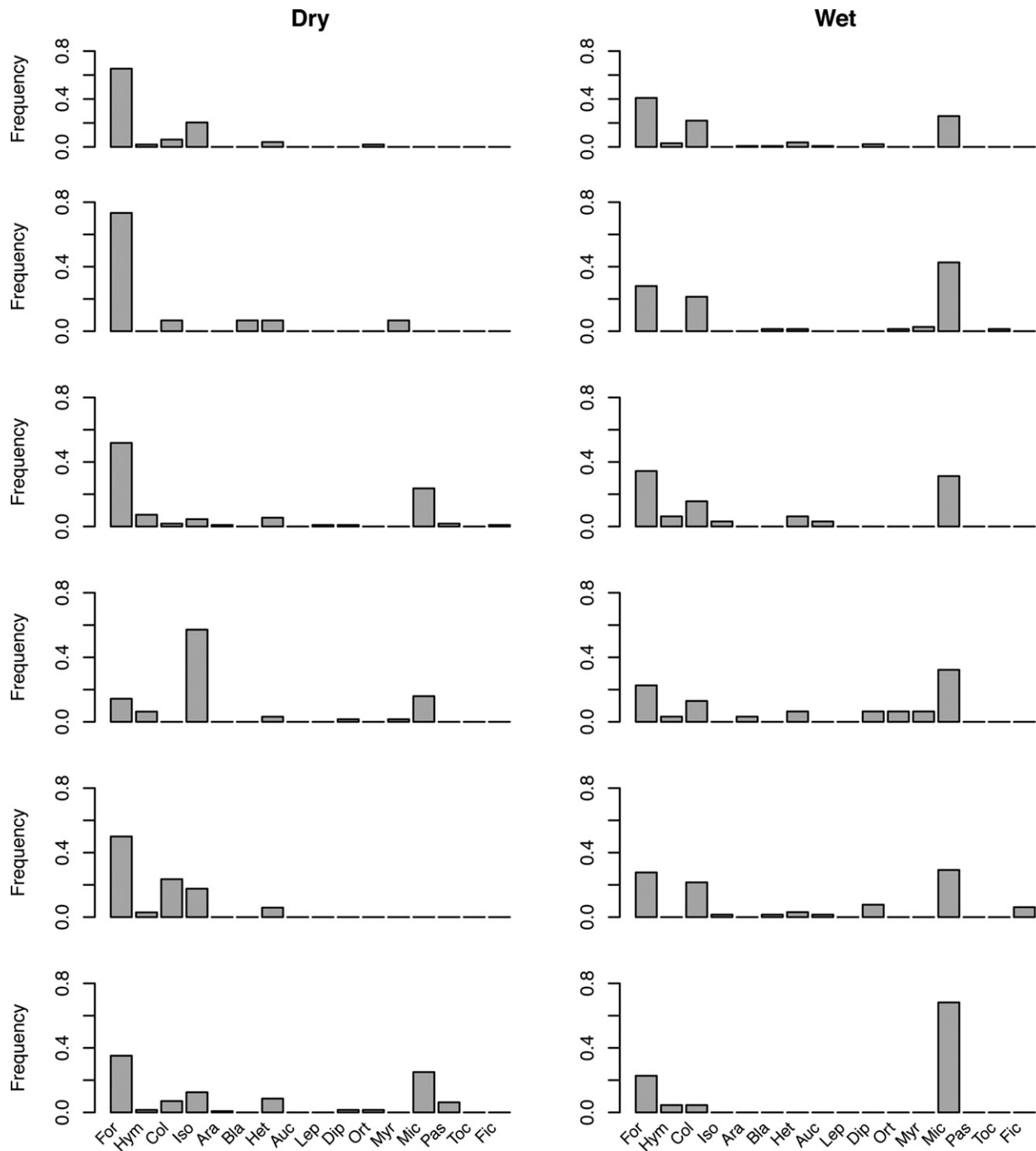
Similar to the previous studies on the diet of *M. paraguayana* that were conducted in the Atlantic rainforest (Leite *et al.* 1996; Carvalho *et al.* 1999; Cáceres *et al.* 2002; Pinheiro *et al.* 2002b; Casella & Cáceres 2006), our results showed that the studied population of *M. paraguayana* in a remnant of the highly seasonal Cerrado consumed a wide variety of arthropods and fruits. However, in contrast to previous studies, our results showed that, at the population level, both the diet composition and trophic niche width of *M. paraguayana* varied with the seasons in the study area. Seasonal shifts in the diet composition and niche space are a common feature of species living in highly seasonal environments, where resource availability fluctuates at intra-annual timescales (e.g. Aragona & Setz 2001; Martins *et al.* 2006; Leiner & Silva 2007). The didelphid *Marmosops paulensis* for instance, relies mainly on fruits of Piperaceae species in the wet season, but increases the consumption of fruits from other species and arthropods expanding its diet in the dry season when fruits from Piperaceae are less available (Leiner & Silva 2007). The diet composition of *M. paraguayana* also seemed to reflect the seasonal availability of the resources in the Cerrado. Although ants were frequently consumed in both seasons, ants have a large proportion of indigestible matter and also lower caloric content in comparison with other resources such as larger arthropods and fruits. Therefore, even though ants stand

out because of the frequency of consumption, other resources consumed less frequently are an important part in the diet of *M. paraguayana*. For example, beetles and fruits were often frequent in the faecal samples obtained in the wet season, when there were peak abundances of these resources in the Cerrado (Mantovani 1984; Pinheiro *et al.* 2002a), but were rarely detected in samples collected in the dry season. Conversely, termites usually peak during the dry season in the Cerrado (Pinheiro *et al.* 2002a), and in fact, we detected this food resource more frequently in the samples collected during that season.

Consistent with the OFT predictions (Schoener 1971), we found that the food niche width of *M. paraguayana* increased in the Cerrado dry season. At first, this expansion could be interpreted as a simple average response to reduced resource availability (Stephens & Krebs 1987): as highly used resources, such as beetles and fruits, become scarce, individuals increase the proportion of other food resources, such as hemipterans and termites, in their diet. However, in spite of the population niche expansion, the individual niches did not expand in the dry season; instead, the larger niche width observed in the dry season was accompanied by a larger between-individual variation (i.e. a reduced niche overlap).

In contrast to the present work, a recent study addressing the intrapopulation diet variation of frogs in the Cerrado (Araújo *et al.* 2007) found larger inter-individual diet variation in the wet season, when resource availability is supposed to be the highest. This increase in the between-individual variation was attributed to a higher selectivity of individuals when the resources were abundant. This response, however, is expected only if individuals have distinct preference ranks for resources (Svanbäck & Bolnick 2005). Conversely, if individuals share the same top-ranked resources but have different rankings for alternative resources or if all of the individuals have identical rank preferences but differ in the willingness to include alternative resources in their diets, the between-individual variation is expected to increase when the resources become scarce (Svanbäck & Bolnick 2005; Araújo *et al.* 2010). Individual's rank preferences arise from the interplay between the factors that depend on resource properties (e.g. prey evasiveness, caloric content and defences) and those that affect the consumer skills (e.g. experience, morphology and physiology). In this sense, the complex interactions between resource traits, environmental heterogeneity, social interactions and consumer traits are responsible for an individual's actual resource usage (Bolnick *et al.* 2003).

Between-individual variation could also occur because of resource patchiness if the individuals forage in different places (Durell 2000). We lack the data on resource distribution dynamics, covering different spatial scales, needed to perform a formal test to



**Fig. 1.** Relative frequency of each resource category in the diet of the six individuals of *Marmosa paraguayana* that were captured in both seasons. Note diets are much more similar within the wet season than within the dry season. For, Formicidae; Hym, non-Formicidae Hymenoptera; Col, Coleoptera; Iso, Isoptera; Ara, Arachnida; Bla, Blattodea; Het, Heteroptera; Auc, Auchenorrhyncha; Lep, Lepidoptera; Dip, Diptera; Ort, Orthoptera; Myr, Myriapoda; Mic, *Miconia*; Pas, *Passiflora*; Toc, *Tocoyena*; Fic, *Ficus*.

evaluate the role of resource patchiness in the niche dynamics we report here. However *M. paraguayana* forages actively and has high mobility, moving on average about 500 m per night and up to 1100 m per night (Morales & Chiarello 2005) so that foraging areas usually overlap. Therefore it is unlikely that resource

patchiness alone is the process underlying niche seasonal dynamics. Because didelphid marsupials are solitary and lack a social organization, which could explain the differing diets among the individuals, it is also unlikely that social status has an important role in the patterns of niche dynamics.

Although we discuss our results mainly as a response to seasonal changes in fruit and insect availability, a well-known pattern in Brazilian Cerrado (Batalha & Mantovani 2000; Pinheiro *et al.* 2002a), other factors possibly subjected to intra-annual climatic variation such as changes in activity levels due to temperature and precipitation variation could also affect niche dynamics. Sorting out the contribution of different factors that might trigger niche dynamics is beyond the scope of this study. However any difference among individuals in the way they respond to such environmental changes would still represent inter-individual variation in foraging behaviour.

Our results do not allow us to go beyond proposing candidate mechanisms that generate between-individual variation in the studied population, but they contribute to our understanding of niche dynamics by bringing in a pattern of individual-level response to seasonal changes that differs from patterns previously described. The frogs studied by Araújo *et al.* (2007) showed larger between-individual variation in the Cerrado wet season. Similarly, Martins *et al.* (2008) reported a decrease in between-individual diet variation for the didelphid *Gracilinanus microtarsus* from the wet to the dry season in Cerrado, but only among males. The pattern we report here for *M. paraguayana* is a third, distinct pattern of seasonal niche dynamics in which population niche width expands in the dry season in response to an increase in between-individual variation that was not related to sex.

Significant between-individual diet variation, such as that reported here, has been shown for many different species, suggesting that the individual-level variation in resource use is widespread (Bolnick *et al.* 2003, 2011; Araújo *et al.* 2007, 2009; Martins *et al.* 2008; Tinker *et al.* 2008). Our results not only add a further member to this growing list, but also empirically demonstrate a mechanism of individual-level response by which seasonal changes might affect population niche dynamics that is distinct from those reported for other organisms. The pervasiveness of the individual-level variation in resource use, and the diversity of mechanisms by which population niche dynamics can be affected by individual-level responses, suggest that studies on population and community dynamics and OFT models will be more realistic and their predictions will be more accurate when considering the between-individual variation in the trophic niche (Bolnick *et al.* 2003, 2011; Svanbäck & Bolnick 2005; Araújo *et al.* 2008).

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## SUPPORTING INFORMATION

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

**Appendix S1.** Rarefaction analysis of the inter-individual diet variation index.