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Sex and Season Affect Individual-Level Diet Variation in the Neotropical Marsupial *Gracilinanus microtarsus* (Didelphidae)

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ABSTRACT

Individual-level diet variation was investigated in *Gracilinanus microtarsus*, an insectivorous marsupial whose diet is affected by sex and season in the highly seasonal Brazilian Cerrado. To measure individual-level diet variation, the diets of individual males and females were compared to that of their population in the warm-wet and cool-dry seasons using the proportional similarity index (PS_i). This index varies from 1 (complete overlap between the individual i's and population's diets) toward 0 (decreasing overlap). Mean PS_i values were computed as a measure of the degree of interindividual diet variation (the larger the mean PS_i value, the smaller the variation among individuals' diets). Interindividual diet variation among females was similar between seasons, whereas among males it decreased from the warm-wet to the cool-dry season. Diet variation among males is probably reduced in the cool-dry season because of constraints on food consumption generated by interactions between endogenous (physiological needs associated with high rates of body mass growth) and exogenous (food limitation) factors.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Brazil; Cerrado; food-niche; gracile mouse opossum; intrapopulation variation; savanna.

ECOLOGICAL NICHE THEORY, AS ORIGINALLY FORMULATED (Hutchinson 1957), IS BASED ON the assumption that individuals within populations use similar resources and therefore can be considered as ecologically equivalent (Bolnick *et al*. 2003). Under this framework, the niche is a property of the population as a whole and can be adequately characterized in terms of average resource use. This simplification has been challenged by empirical studies showing that intrapopulation variation in resource use is commonplace and can occur by subdividing the population's niche in a number of different organizational scales, such as sex, age, or morphotype (*e.g.*, Polis 1984, Walls *et al*. 1993, Shine *et al*. 2002). However, patterns of resource use at any given organizational scale often emerge from the collective behavior of large ensembles of individuals showing characteristic variability (Levin 1992). Hence, for populations whose variation in resource use has been shown to be accounted for sex, age, or morphotype, a fundamental question to be asked is: is there individual-level variation in resource use within any of these organizational scales?

This study investigates individual-level diet variation in the Brazilian gracile mouse opossum, *Gracilinanus microtarsus*—a small (20–45 g), sexually dimorphic in size, solitary, arboreal, nocturnal, seasonally breeding (September to December), and insectivorous Neotropical didelphid marsupial commonly found in the Atlantic rain forest and forested physiognomies interspersed in savannas in the Cerrado biome (Emmons & Feer 1997; Martins & Bonato 2004; Martins *et al*. 2006a, b). Recently, using a Poisson regression model, sex and season were shown to significantly affect the number of food items consumed by *G. microtarsus* in the Cerrado (Martins *et al*. 2006a). This analysis also showed that food consumption by males and females is disproportionately affected by season, implying a strong interaction between sex and season. Since sex and season contribute significantly to intrapopulation variation in food consumption in *G. microtarsus*, the aim of this study was to investigate the occurrence of individual-level diet variation within sexes and whether sex and season affect such variation. Specifically, the following questions were addressed: (1) Is there individual-level diet variation within sexes in *G. microtarsus*? (2) What is the degree of individual-level diet variation within each sex? (3) Do males and females differ in the degree of individual-level diet variation? (4) Does the degree of individual-level diet variation within sexes change with season?

This study was done at Clube Náutico Araraquara (21°43′ S, 48°01′ W), located in Américo Brasiliense, *ca* 300 km northwest

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of São Paulo in southeastern Brazil. Vegetation at Clube Náutico Araraquara consists of two forested remnants (*ca* 73 ha and 307 ha) of Cerrado characterized by dense semi-deciduous forest with canopy cover varying from 50 to 90 percent, trees 8–15 m tall and little herbaceous vegetation. The climate of the region has two well-defined seasons: a warm-wet season from October to March and a cool-dry season from April to September (Tolentino 1967).

Traps were set for two consecutive nights every 15 d from January to December 2001, for a total of 23 sampling occasions and 46 days of field work. Animals were captured in the smaller forest remnant (*ca* 73 ha) using a 7 × 7 trapping grid with 49 trapping stations located 10 m apart. A single Sherman live trap (7.5 × 9.0 × 23.5 cm) was set on trees at each trapping station *ca* 1.75 m aboveground and baited with banana, peanut butter, and cod-liver oil. Captured individuals were marked with a numbered leg-band and sex and age were recorded. Age was recorded based on the sequence of tooth eruption and individuals were recorded as adults when all teeth had erupted (Costa *et al.* 2003). A total of 146 feces (100 from males and 46 from females) were sampled from 38 adult individual *G. microtarsus* (25 males and 13 females). Of these, 51 were sampled in the warm-wet season and 95 in the cool-dry season. Description of the procedures of collection, preservation, and identification of food resources detected in feces of *G. microtarsus*, as well as detailed information on diet composition, can be found in Martins *et al.* (2006a).

To measure individual-level diet variation, the diets of individual males and females were compared to that of their populations in the warm-wet and cool-dry seasons using the proportional similarity (PS) index (Feinsinger *et al.* 1981, Bolnick *et al.* 2002). This measure is computed as

$$\mathrm{PS}_i = 1 - 0.5 \sum_j | p_{ij} - q_j |,$$

where p_{ij} is the proportion of the jth food resource in individual's i diet and q_j is the proportion of the jth food resource in the population's total diet (Bolnick *et al.* 2002). PS_i assumes values ranging from q_j, for individuals that specialize in a single food resource j, to 1, for individuals that consume food resources in direct proportion to the population as a whole (Bolnick *et al.* 2002).

Averages of PS_i values were computed for males and females in each season as a measure that summarizes the degree of interindividual diet variation by sex and season. The larger the average PS_i value, the more similar individuals are to the population and to each other and, therefore, the smaller the variation among individual diets (Bolnick *et al.* 2002). Two-factor analysis of covariance was used to test the significance of the effects of sex and season, as well as their interaction, on the mean PS_i values, while controlling for the effects of the number of feces accrued for individual animals on the PS_i estimates. Pairwise comparisons between mean PS_i values by sex and season were done using the Tukey's test. The PS_i values were arcsine transformed prior to the analysis (Zar 1999). Because some individuals were sampled in both warm-wet and cool-dry seasons, one of the PS_i estimate repetitions for each individual was removed from the data set in such a way as to maintain the number of replicates per season as balanced as possible.

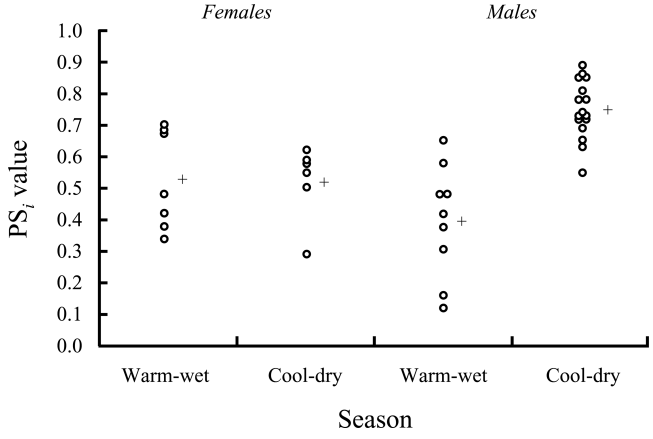

FIGURE 1. Individual proportional similarity estimates (PS_i) in *Gracilinanus microtarsus* by sex and season. PS_i measures the overlap between the individual i's diet and the population's diet and varies from 1 (complete overlap between the individual i's and population's diets) toward 0 (decreasing overlap). The plus sign indicates mean PS_i values, which were computed as a measure of the degree of interindividual diet variation (the larger the mean PS_i value, the smaller the variation among individuals' diets).

There was evidence of individual-level diet variation in *G. microtarsus*, with PS_i values ranging from 0.10 to 0.86 (Fig. 1). The distribution of PS_i estimates for females was similar between the warm-wet and cool-dry seasons, with the individual diets resembling between 30 and 70 percent of the female population's diet in both seasons (Fig. 1). The distribution of PS_i estimates for males in the warm-wet season was similar to that of females, although the mean PS_i value was slightly lower (Fig. 1). In the cool-dry season, however, most of the individuals' diets resembled between 50 and 90 percent of the male population's diet (Fig. 1).

The mean PS_i value was similar across seasons for females, whereas for males the mean PS_i value increased from the warm-wet to the cool-dry season (Fig. 1). There was a significant effect of the interaction between sex and season ($F_{1,33} = 19.13$, $P = 0.001$) on the mean PS_i values. The mean PS_i value of males in the cool-dry season was significantly larger than that of males in the warm-wet season (Tukey's test: $q = 5.45$, df = 33, $P < 0.001$) and that of females in both warm-wet ($q = 1.35$, df = 33, $P = 0.006$) and cool-dry seasons ($q = 1.34$, df = 33, $P = 0.008$). The other pairwise comparisons between mean PS_i values were not significant ($P > 0.10$ in all cases).

Our results showed evidence of individual-level diet variation in *G. microtarsus* and that males and females differ in the timescale over which the degree of interindividual diet variation (measured as the average PS_i values; Bolnick *et al.* 2002, 2003) persists. The mean PS_i value for females was similar between the warm-wet and cool-dry seasons in the Cerrado. In contrast, the mean PS_i value for males was significantly larger in the cool-dry season than in the warm-wet season. This implies more similar diets among individual males during the cool-dry season than in the warm-wet season and that the degree of individual-level diet variation is not constant

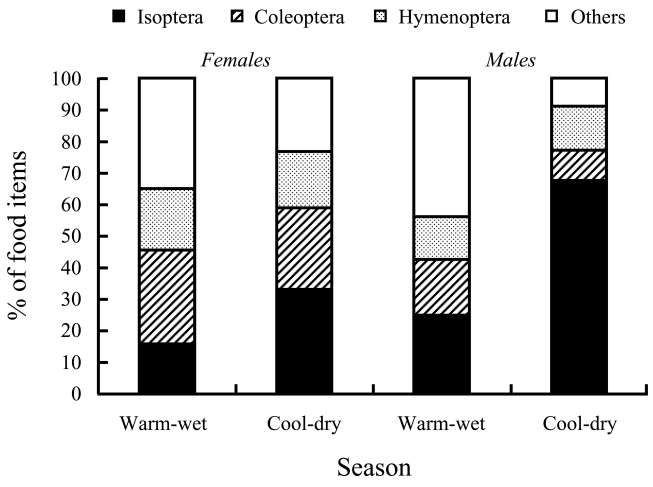

FIGURE 2. Percentage of the number food items of the prey categories detected in feces of male and female *Gracilinanus microtarsus* in the warm-wet and cool-dry seasons in the Cerrado. Note the greater contribution of termites (Isoptera) to the diet of males in the cool-dry season. The category 'Others' includes Araneae, Blattodea, Diptera, Hemiptera, Lepidoptera, Orthoptera, and fruits (*Miconia*, *Passiflora,* and *Solanum*).

across seasons. It is therefore evident that the degree of individual-level diet variation in *G. microtarsus* was affected by an interaction between sex and season.

The greater similarity among individual males' diets in the cool-dry season results from all males consuming large numbers of termites during this time (Martins *et al*. 2006a). Such insects compose the bulk of the diet of males (Fig. 2), when food abundance is low (Pinheiro *et al*. 2002; V. Bonato, pers. obs.). Consuming large numbers of termites when food is limited may be a reward maximizing foraging strategy for individual males because termites are a high-value clumped food resource that are easy to find and capture (Redford & Dorea 1984, Abensperg-Traun & Steven 1997). Thus, adopting such a strategy during the cool-dry season may allow males to maximize net energy income and help to explain their high rates of body mass growth during the last 3 mo of this season (E. G. Martins, pers. obs.).

Growing to a large body size may be important for males to compete for mates during the short mating period that occurs at end of the cool-dry season (Martins *et al*. 2006b). Shortly after the mating period, males suffer high mortality rates that may be caused by detrimental effects of stress generated by aggressive interactions between males competing for matings with many females (Boonstra 2005, Martins *et al*. 2006c). This suggests that increasing to a large body size may be important for males to reproduce successfully. Furthermore, the increase in body mass observed in males may also be associated with the storage of fat reserves, allowing them to supply their energetic requirements associated with searching for mates and in mating (Gittleman & Thompson 1988, Martins *et al*. 2006a).

In conclusion, our results demonstrated the occurrence of individual-level diet variation in both male and female *G. microtarsus* and that the degree of interindividual diet variation was affected by an interaction between sex and season. Males experience the environment during the cool-dry season in such a way that results in reduced diet variation among individuals. Such reduction in interindividual diet variation is likely to be determined by constraints on food consumption generated by strong interactions between endogenous (physiological needs associated with high rates of body mass growth) and exogenous (food limitation) factors.

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