

INTER AND INTRASPECIFIC DIFFERENCES IN FOOD RESOURCES SELECTION AND USE IN CAPTIVE *PHILANDER FRENATUS* AND *DIDELPHIS AURITA* (DIDELPHIMORPHIA; DIDELPHIDAE)

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ABSTRACT

The opossums *Philander frenatus* and *Didelphis aurita* are sympatric throughout most of their distribution ranges and share several ecological traits, including natural diet. However, experimental studies on feeding habits of didelphid marsupials in captivity have revealed important differences between the nutritional contents of their diets, based on experimental food choice. Our aim was to assess inter and intraspecific differences in the diets of the two species. We hypothesized that comparisons of inter and intraspecific food habits variations in captivity can provide insights to understand the effects of differential use of food resources on niche differentiation and diversification. Thus, we used a cafeteria test with 26 different kinds of foods. Food selection and use by the two species were analyzed and calculated niche breadth (Czekanowski's Proportional Similarity - PS index) and overlap (Pianka's index). Both *P. frenatus* and *D. aurita* had similar diets between sexes and age classes. However, *D. aurita* specimens used or tried a broader range of resources than those of *P. frenatus* for all compared categories. In *P. frenatus* males had a more generalist diet than females. Adults of this species were more generalist than younger specimens, and juveniles and subadults had similar indexes. In *D. aurita* the preferred diet was also very similar across sexes and age classes. In this species, males have a narrower diet than females. In juveniles niche breadth and diet amplitude were superior to those of subadults, while adults had the highest indexes of all three age classes. There was a high dietary overlap in all intraspecific, and interspecific comparisons performed. Our results show that selection and use of food resources in field and in laboratory coincided and are complementary, but intraspecific analysis revealed different strategies of food use in each species, which in nature may influence in niche partitioning and affect trophic structure in mammal communities.

Keywords: diet overlap; feeding ecology; food habits; food preference; opossums.

INTRODUCTION

The development of ecological models and theories depends on the basic information about animal life. Thus, knowledge of what small mammals eat in the wild, for example, can provide important insights on how their communities are structured. Food habits of didelphid marsupials have been considered generalist, with some exceptions, varying from “insectivores/omnivores” to “frugivores/omnivores” (Santori *et al.* 2012). But, the use of such general trophic categories is sometimes inadequate, mainly for poorly studied species, because they hide important information on the ecology of the species and the trophic structure of their communities (Astúa de Moraes *et al.* 2003, Lessa and Geise 2010).

To assess food use of small mammals, laboratory studies on diet selection and composition may be used to assess aspects that complement those addressed in field studies. Four factors can influence the selection of food resources: availability, palatability, accessibility and the energetic gain from food (Owen 1982). Studying experimentally comparative diet selection, independently from resource availability, and without any accessibility restrictions reflects more clearly the intrinsic factors that lead to distinct food preferences by each species, because it removes the effects of variation that are related to accessibility to and availability of food resources (Astúa de Moraes *et al.* 2003). Such studies also allow a quantitative nutritional assessment of the diet and its relation to the consumed

items and to morphological features of the trophic apparatus, which are more difficult to study with field data (Astúa de Moraes *et al.* 2003, Finotti *et al.* 2012, Santori *et al.* 2012). Intrinsic factors are those related to the ability of an organism to identify, find, obtain and process food resources. These factors are conditioned by pre- and post-ingestion stimuli associated with features of the trophic apparatus, such as tooth morphology, morphology and physiology of the digestive tract (Penry 1993, Santori *et al.* 1995b, Astúa de Moraes 1998, Cáceres 2005), and with the ability of identifying, acquiring and handling these resources (Shuttleworth *et al.* 1993).

Reflex responses to chemical or visual stimuli, such as color, scent and shape, or any other feature of the food items that can be identified prior to ingestion are considered pre-ingestion stimuli (Zuwang *et al.* 1987, Augner *et al.* 1998). Experiments with laboratory rats suggest that food preferences in mammals are shaped by learning, through flavors present in the mother’s milk, or through smells and food fragments found on her fur (Galef and Girauldeaut 2001), as well as through direct observation of foraging adults. These factors are responsible for the recognition of feeding groups by juveniles (Galef 1993, Galef and Wright 1995, Suarez and Kravetz 1998). Pre-ingestion stimuli are related to responses to a positive or negative feedback following the ingestion of food, when different food items features are associated with the “experience” or “reward” obtained from that food item (Belovsky and Schmitz 1994,

Lawler *et al.* 1998, Magnus *et al.* 1998). Such stimuli are closely related to the morphology, physiology and plasticity of the digestive tract, which can determine both nutrient absorption efficiency and nutrient and energy uptake rates (Penry 1993, Santori 1995a, Koteja 1996, Corp *et al.* 1997, Owl and Batzli 1998). Thus, food preference results from several physiological, behavioral and ecological mechanisms that act upon each individual. Such mechanisms act on the optimal energy ingestion and on the selection of a nutritionally balanced diet (Louw 1993). In our study, we tested the hypothesis of intra and interspecific differences in food use and preference of *D. aurita* and *P. frenatus*, which may be reflecting variation in reception and processing of pre- and post-ingestion stimuli associated with morphological differences in the trophic apparatus of each species and intraspecific groups.

Individuals from a single species can have variation in their diets that derive, probably, from the diet quality (Langer 2003, Del Valle *et al.* 2006), from the different physiological states and trophic apparatus maturity stages in which they are at each moment (Langer 2003), or even from individual preferences when food items are selected (Pires *et al.* 2013). Different concentrations of several enzymes needed for detoxification and digestion and differential plasticity in the digestive tract between individuals may result in variation in the amounts and types of food items used. It is at this individual variation level that natural selection mechanism can act, as long as such variation is inheritable (Arsenos *et al.* 2000).

The opossums *Philander frenatus* (Olfers, 1818) and *Didelphis aurita* (Wied-Neuwied, 1826) are sympatric throughout most of their distribution ranges (Cerdeira and Tribe 2008, Patton and Silva 2008), and share several ecological traits, such as food resources, activity patterns and habitat (Cerdeira *et al.* 1993, Leite *et al.* 1994, Cáceres 2004, Ceotto *et al.* 2009, Santori *et al.* 2012).

Experimental studies on feeding habits of didelphid marsupials in captivity have revealed important differences in nutritional contents between the diets of *Philander frenatus* and *Didelphis aurita* (Astúa de Moraes *et al.* 2003, Santori *et al.* 2012). However, field studies based on the analysis of fecal contents indicate that they use similar items in their diets (Périssé *et al.* 1988, Cáceres 2004, Ceotto *et al.* 2009, Casella 2011). Such studies have the advantage of allowing analyses of the use of available food sources and resource partitioning, including in time (Charles-Dominique *et al.* 1981, Leite *et al.*, 1994, Passamani 1995). However, techniques routinely used for the analysis of fecal and stomach contents have limitations when it comes to adequate identification and quantifying ingested items (Dickman and Huang 1988, Robinson and Stebbings 1993, Lessa and Geise 2014). Traditional methods used for establishing the natural diet of a species do not always succeed in properly identifying all of the items that are actually consumed by wild small mammals (Caron *et al.* 1985, Dickman and Huang 1988). These results are tied and dependent upon the taxonomic

level to which consumed prey can or are identified, thus influencing the final estimates of parameters such as niche breadth and overlap (Greene and Jaksic 1983). But the limitations of estimates resulting from field methods can be complemented or refined by studying feeding preferences and feeding habits in captivity, as the resource availability can be controlled, and consumed items can be identified and quantified in detail (Caron *et al.* 1985, Jenkins and Bollinger 1989, Périssé *et al.* 1989).

Intraspecific and interindividual variation in the diet of didelphid marsupials have been increasingly studied in the field (Cantor *et al.* 2013, Martins *et al.* 2008, Araújo *et al.* 2010, Pires *et al.* 2013, Camargo *et al.* 2014), but studying comparisons of intraspecific food habits variations in captivity can provide insights to understand the effects of differential use of food resources on niche differentiation and diversification between Didelphidae species (Périssé *et al.* 1988, Santori *et al.* 1997). In this study, we experimentally analyze food selection and use by *P. frenatus* and *D. aurita*, through food preference experiments, in order to assess inter and intraspecific differences in the diets of the two species, and to assess experimentally the relation between use and resource selection.

MATERIAL AND METHODS

Specimens

We used 45 specimens of *Philander frenatus* (27 males and 18 females), which consisted of 6 juveniles (3 males and 3 females), 12 sub-adults (7 males

and 5 females) and 27 adults (17 males and 10 females). We used 34 specimens of *Didelphis aurita* (17 males and 17 females), which consisted of 17 juveniles (7 males and 10 females), 4 sub-adults (2 males and 2 females) and 13 adults (8 males and 5 females). Age classes followed Tyndale-Biscoe and Mackenzie (1976) and were based on the eruption sequence of molars and on the presence or absence of the third deciduous pre-molar. Specimens classified as juveniles still had the third deciduous premolar and an incomplete molar dentition, specimens classified as sub-adults had the third deciduous premolar and all four molars, but the fourth molar was not functional, and specimens classified as adults had the permanent third premolar and all four molars functional with some level of wear. Only specimens freshly arrived from the field were used in the experiments, and pregnant and lactating females were not submitted to the experiments. Specimens were housed individually in polypropylene boxes (410 x 340 x 170mm) with wired metal lids, at an average room temperature of 24°C and at the natural photoperiod of Rio de Janeiro (Hingst *et al.* 1998). Between experiments specimens were fed with species and age-specific balanced diet based on the method established by Périssé *et al.* (1989). This diet included a diversity of fruits according to season availability, quail eggs (*Coturnix japonica*), mice (*Mus musculus*), beef or chicken, *Tenebrio molitor* larvae (Coleoptera), cod liver oil and commercial dog food. As both species are nocturnal,

food was offered at late afternoon, and water was freely available in drinking bottles attached to the boxes. Lining of the boxes consisted of vermiculite and shredded newspapers (Hingst *et al.* 1998). This study was performed before ethics committees were established in the authors institution by Brazilian government (Brasil 2008). However, our procedures were in accordance with international guidelines and agree with international rules of animal use and ethics (Gannon *et al.* 2007).

Food preference experiments

We compared food selection between the two species using the method developed by Périssé *et al.* (1989), with modifications on offered items and offer breadth (Finotti *et al.* 2012). The food choice test consisted in offering each specimen 26 different food crop items, for a period of 18–24 hours. All items were weighed before and after the experiment, and the difference was used to estimate item consumption. Food items included animal matter, leaves, fruits, roots, tubers and seeds never tried by the animals. A preference index (PI) was determined for each item touched or tasted by the tested specimen (Périssé *et al.* 1989). A food item is considered preferred by the species if 50% or more of the specimens tested attain a $PI \geq 1.0$ (Périssé *et al.* 1989). When a food item is not touched, it is considered not preferred ($PI = 0$), and when $PI < 1.0$ or $PI \geq 1.0$ for less than 50% of the specimens tested, the item is considered marginally preferred, meaning it can be considered a sub-optimal resource that could be used in case a better or preferred item

is missing. Thus, the species' preferred diet consists of all items with $PI \geq 1.0$ for 50% or more of the specimens tested. All food items were offered freely, and in the event of a specific resource being totally consumed, the experiment was excluded from the analyses. This ensures that only preferred resources were used, and that the tested specimen did not choose sub-optimal items due to the depletion of a preferred item. Experiment food items were always offered towards the end of the afternoon, thus minimizing possible differences due to differences in activity peaks.

Data analyses

We compared the experimental diets within and between species through the graphs of food preference for each food item and the percentage of specimens for which such indexes were attained. This is a qualitative approach that provides a preliminary approximation to the space of selected resources within the universe of available items. We also calculated niche breadth (Feisinger *et al.* 1981) and niche overlap (Pianka 1973). Niche breadth was measured with Czekanowski's Proportional Similarity (PS) Index (Feisinger *et al.* 1981). This can be considered a special case of similarity, presented by the intersection between the frequency distribution of available and used resources (Feisinger *et al.* 1981). A value of $PS = 1.0$ indicates a generalist habit, meaning that the specimen selected resources in a direct proportion of its availability. The closer the index is to 0, the more specialized the feeding habits are (Fisher and Dickman 1993). Pianka's overlap index

(Oik) was used to quantify the intra and interspecific overlap of experimentally determined diets (Pianka 1973).

RESULTS

Diet preference and breadth

Both *P. frenatus* and *D. aurita* had similar diets between sexes and among age classes (Figures 1 and 2). Both species preferred items of animal origin (egg, arthropods and meat), as well as fruits. However, *D. aurita* specimens used or tried a broader range of resources than those of *P. frenatus* for all compared categories.

In *P. frenatus* males had a broader niche, indicating a more generalist diet than that of females (Figures 1 A and B), selecting a broader variety of items from the universe of available resources. Adults were more generalist than younger specimens, and juveniles and subadults had similar indexes (Figure 1 C, D, and E).

In *D. aurita* the preferred diet was also very similar across sexes and age classes, and preferred food items are basically the same between all categories (Figure 2 A to E). Similarity indexes indicated that males have a narrower diet than females (Figure 2 A and B). The preferred diet of juveniles did not include egg, but its niche breadth and diet amplitude were still superior to those of subadults, while adults had the highest indexes of all three age classes (Figure 2 C to E).

Dietary overlap

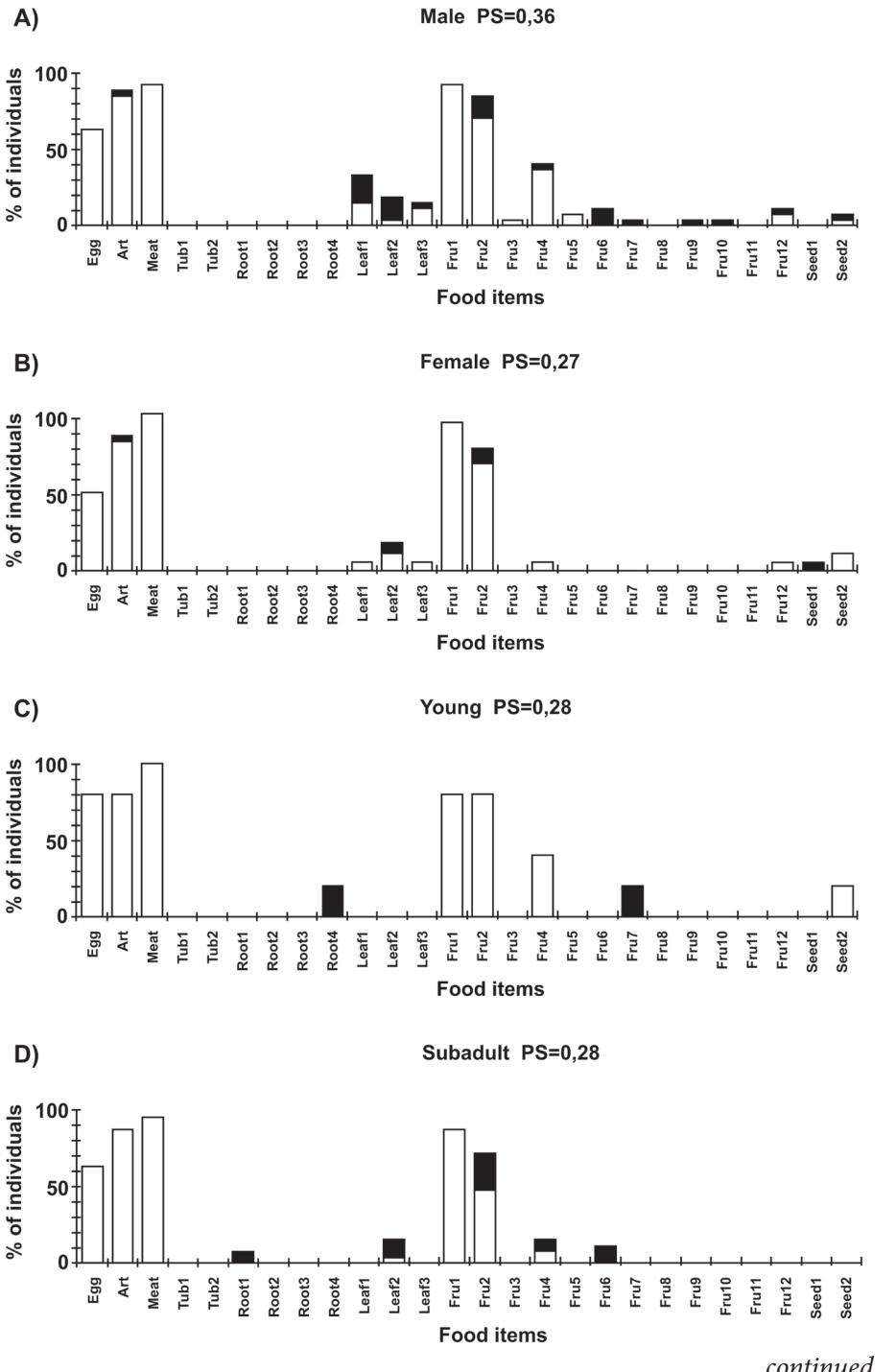
There was a high dietary overlap in all intraspecific comparisons performed

in both species (Table 1). In *D. aurita* overlaps were slightly lower than those found in *Philander frenatus* but can still be considered high. Dietary overlap between the two species was also high.

DISCUSSION

Our results showed that selection and use of food resources in field and in laboratory by *P. frenatus* and *D. aurita* are coincident and complementary, but intraspecific analysis revealed different strategies of food use in each species, which in nature may influence in niche partitioning and trophic structure in small mammal communities. *Didelphis aurita* had a more generalist diet than *P. frenatus* in all intraspecific categories analyzed. The preferred (optimal) diet was the same in all intraspecific groups tested in both species, except for juveniles *D. aurita*. Food items touched, but not preferred, played an important role in intra and interspecific diet variation. Intraspecific analysis showed differences in the two species. Males and females of both species presented high diet overlap index, but in both the sex more feeding generalist differ between them. In the same way, diet variation also occurred among age classes, with difference as for that more feeding generalist between the two species.

It has been demonstrated that food preference measured in captivity is consistent with natural diets (Rodgers and Lewis 1986). Results from diets we obtained experimentally for *P. frenatus* e *D. aurita* agreed with those obtained by Périssé et al. (1988), who found a food preference in both species for



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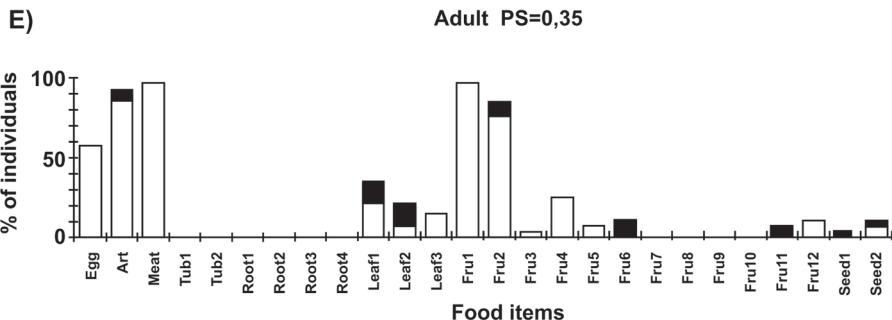
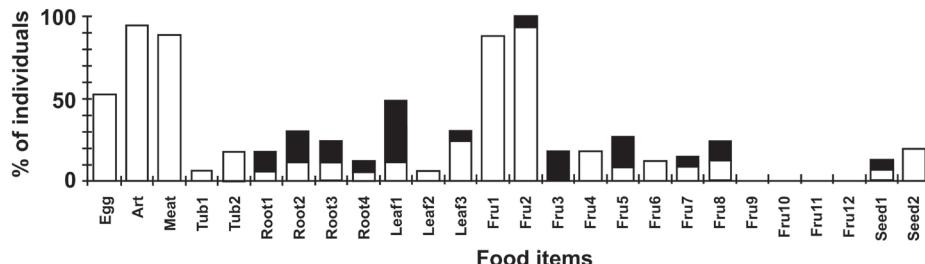
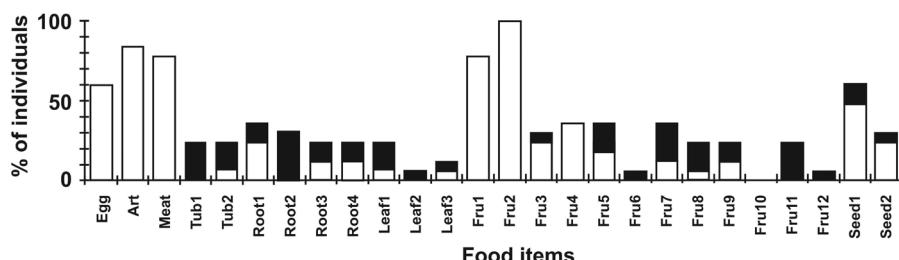
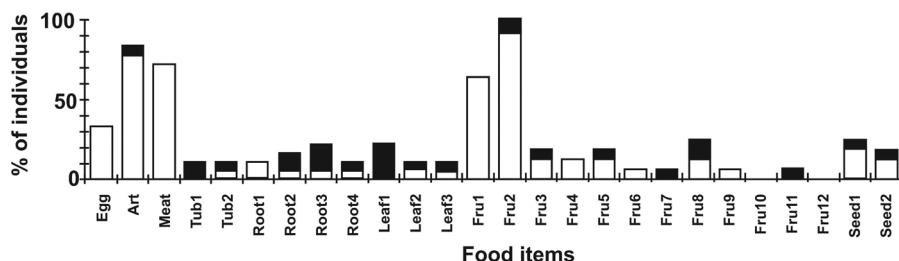
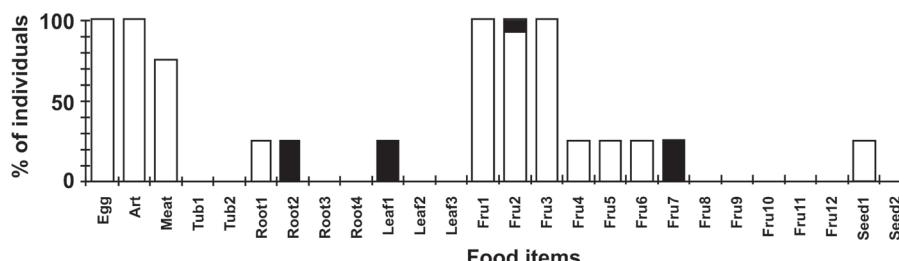


Figure 1. Food resource use in the food preference experiment, by sex and age class, in *Philander frenatus*. White bars indicate the percentage of specimens that reached a Preference Index $P \geq 1.0$ for any particular food item, and black bars the percentage of specimens that reached a Preference Index $0 < P < 1.0$. Codes and definitions of food: Egg - quail egg; Art - shrimp; Meat – beef; Tub1 – yam; Tub2 – cassava; Root1 – carrot; Root2 – turnip; Root3 – beet; Root4 - sweet potato; Leaf1 – lettuce; Leaf2 – cabbage; Leaf3 – spinach; Fru1 – banana; Fru2 – orange; Fru3 – pumpkin; Fru4 – tomato; Fru5 – cucumber; Fru6 – red pepper; Fru7 – chayote; Fru8 – zucchini; Fru9 - scarlet eggplant; Fru10 - string beans; Fru11 – okra; Fru12 – pea; Seed1 – peanut; Seed2 – corn. PS – Proportional Similarity index.

meat, shrimps, eggs, and some fruits, and with the natural diet of the two species (Freitas *et al.* 1997, Santori *et al.* 1997, Cáceres 2004, Ceotto *et al.* 2009, Casella, 2011). Therefore, selection and use of food resources in captivity and in field coincide and are complementary.

Didelphis aurita had a more generalist diet than *P. frenatus* in all intraspecific categories analyzed. With the same experimental method, Périsse *et al.* (1988) found a similarity index (Kulczinski's index) of 0.83. Cerqueira *et al.* (1994) then used multivariate statistical methods to analyze food preference indexes obtained in these experiments. They found 6.5% of *P. frenatus* specimens classified as

D. aurita, based on their feeding preferences, while the latter species had 100% of its specimens correctly classified, showing a small part of the tested individuals of *P. frenatus* preferring the same food items as the other. This means that food items preferred by *P. frenatus* are included in diet of *D. aurita*. Astúa de Moraes *et al.* (2003) found significant differences in nutrient consumption between these two species, based on laboratory food preference experiments, showing that the preferential diet of *D. aurita* suggest also a more generalist habit than *P. frenatus*, which was found to be more carnivorous than *D. aurita*. In this study, we could not detect, with the array

A)**Male PS=0,47****B)****Female PS=0,57****C)****Young PS=0,45****D)****Subadult PS=0,35***continued...*

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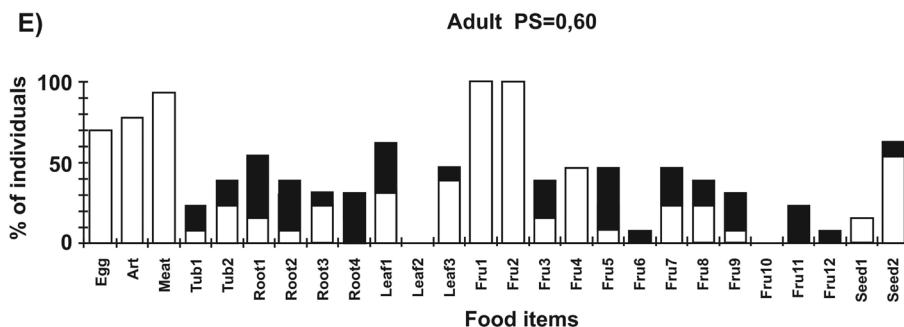


Figure 2. Food resources use in the food preference experiment, by sex and age class, in *Didelphis aurita*. White bars indicate the percentage of specimens that reached a Preference Index $P \geq 1$ for any particular food item, and black bars the percentage of specimens that reached a Preference Index $0 < P < 1$. Codes and definitions of food: Egg - quail egg; Art - shrimp; Meat - beef; Tub1 - yam; Tub2 - cassava; Root1 - carrot; Root2 - turnip; Root3 - beet; Root4 - sweet potato; Leaf1 - lettuce; Leaf2 - cabbage; Leaf3 - spinach; Fru1 - banana; Fru2 - orange; Fru3 - pumpkin; Fru4 - tomato; Fru5 - cucumber; Fru6 - red pepper; Fru7 - chayote; Fru8 - zucchini; Fru9 - scarlet eggplant; Fru10 - string beans; Fru11 - okra; Fru12 - pea; Seed1 - peanut; Seed2 - corn. PS - Proportional Similarity index.

Table 1. Pianka's Indexes of dietary overlap between compared groups.

Comparisons	Overlap Index (Oik)	
	<i>Philander frenatus</i>	<i>Didelphis aurita</i>
Juveniles vs Adults	0.95	0.89
Juveniles vs Subadults	0.97	0.87
Adults vs Subadults	0.97	0.83
Males vs Females	0.97	0.92
<i>Philander frenatus</i> vs <i>Didelphis aurita</i>	0.85	

of offered food items, higher levels of carnivory in *P. frenatus*, possibly because the majority of the offered items are of vegetal origin and only three out of 26 items were of animal origin.

The preferred (optimal) diet was the same in all intraspecific groups tested

in both species, except for juveniles *D. aurita*. Thus, the observed difference in niche breadth was due to food items considered sub-optimal, i.e. those that did not reach a $PI \geq 0$ for 50% or more of the tested specimens, or those that had a $0 < PI < 1.0$.

Périssé *et al.* (1988) found similarity indexes between the diets of *P. frenatus* and *D. aurita* very close to the ones we found in this study, even using different indexes. In intraspecific comparisons, Santori *et al.* (1997) found a similarity of 0.87 between juveniles and adults in *P. frenatus*, using Kulczinski's index. Périssé *et al.* (1988), with the same index, found a similarity of 0.84 between males and non-lactating females in *P. frenatus*, and of 0.76 between males and lactating females. Overlap indexes for all comparisons in this study were high for *D. aurita*. Périssé *et al.* (1988) calculated a Kulczinski's similarity index of 0.76 between males and females in *D. aurita*. The overlap index between diets of males and females in *D. aurita* was high, just as in *P. frenatus*. However, and in contrast with *P. frenatus*, females of *D. aurita* were more generalist than males, which could be reflecting different nutritional needs.

Juveniles of *D. aurita* used a more generalist diet than sub-adults, the opposite of what was seen in *P. frenatus*. As resources were provided freely, and all specimens had the same opportunities to select any available resource, these results indicate that in *P. frenatus* juveniles and sub-adults use food resources in a similar yet different way than adults. In *D. aurita*, the small sample of sub-adult specimens prevented drawing several conclusions.

Diet overlap between juveniles, sub-adults and adults in both species showed a similar use of part of the food resources, as observed by Santori *et al.* (1997) in *P. frenatus*. However, the

diet breadth indexes that we calculated showed that juveniles and sub-adults use more restricted food resources than adults. Resource use and food preferences graphs show that the food items preferred by juveniles and sub-adults are included among those of adults. Thus, the set of food resources used by younger age classes appear as a subset of the universe of resources explored by adults.

Males of *P. frenatus* had a more diverse use of food items, but had the same preferred as females, as well as a high overlap with them. In *D. aurita*, although the preferred diet was also the same for males and females, these latter used a wider array of food resources, and also showed high overlap with males. This shows that the overlap index is strongly affected by those resources that were consumed by the highest proportions of specimens.

The classification of specimens in three age classes showed differences in the diets of juveniles and adults in both species. All offered items had approximately the same volume, and the only items that could have any sort of obstacle that could hamper its consumption would be the egg and the shrimp, because of the shell and exoskeleton, respectively. In natural conditions, obstacles are greater, as food items are almost always alive, and may be in hard to reach places, meaning that the differences between age classes could be even larger. Analysis of the wild diet of *P. frenatus* showed that juveniles prey less frequently on vertebrates (Santori *et al.* 1997). Such results are not reflected

in the food choice experiments results found here, as the available food items did not present as many obstacles to capture and manipulation as items in its wild diet. Ontogenetic differences in Didelphidae were reported by Cordero and Nicolas (1987) in *D. marsupialis*. They found that juveniles prey mostly on invertebrates, while adults prey additionally on small vertebrates. However, *D. aurita* pups can suckle until 150 days of age, but pups from 91 to 100 days old (with a dentition of) already behave as insect and mice pups predators, and may even attack the mother and siblings, with cannibalism events being not uncommon in captivity (Motta 1988). Thus, the incomplete dentition is not an obstacle to prey animals by young *D. aurita*. A similar trait is shared by *Didelphis albiventris* and *Monodelphis domestica* (Streillein 1982), and for *Monodelphis dimidiata* (Voss 1975).

In spite of the differences in niche breadth between sub-adults and adults in both species, the high overlap in the choice of the experimental diet suggests that the incomplete dentition in sub-adults does not affect the food choice in captivity. However, these data do not allow a proper assessment of the influence of the number of teeth and their wear on the capture, processing and use of the different prey that may be part of the diet of these species. It is possible that with changes in tooth wear, mainly molar wear, there could be a shift in the species of predated arthropods that may have different levels of hardness in their exoskeletons (Strait 1993a, 1993b, 1993c).

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