

Frugivory by the black-eared opossum *Didelphis aurita* in the Atlantic Forest of southern Brazil: Roles of sex, season and sympatric species

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Abstract

Our objective in this study was to examine the frugivory performed by the black-eared opossum, *Didelphis aurita* Wied-Neuwied, 1826, in an area of the coastal Atlantic Forest of southern Brazil, including differences between sexes, seasonal variation, and relationships to other sympatric marsupials. We collected 63 fecal samples from a trap grid over a six-month period and analyzed seed presence, seed number and richness, and diversity of fruit species in feces. Diversity of fruit items was estimated by the Shannon index. Results showed a high variability in fruit consumption along the seasons, but no sexual difference in consumption. Sympatric marsupial species, including *D. aurita*, showed substantial differences in frugivory which may be related to body size, space use and differences in the foraging behavior of such species.

Key words: coexistence, food partitioning, fruit consumption, Neotropical marsupial

Resumo

Frugivoria pelo gambá-de-orelha-preta *Didelphis aurita* em Floresta Atlântica do sul do Brasil: o papel do sexo, estação do ano e espécies simpátricas. Nosso objetivo neste estudo foi examinar a frugivoria desempenhada pelo gambá-de-orelha-preta *Didelphis aurita* Wied-Neuwied, 1826 em uma área de floresta atlântica da costa do Brasil, incluindo diferenças entre sexos, variação sazonal e relações com espécies simpátricas. Nós coletamos 63 amostras fecais em uma grade num período de seis meses. Foram analisadas a presença e o número de sementes e a riqueza e a diversidade de frutos nas fezes. A diversidade de frutos nas fezes foi estimada

pelo índice de Shannon. Os resultados mostraram alta variabilidade no consumo de espécies de frutos ao longo dos meses, mas não havendo diferenças entre os sexos. As espécies de marsupiais simpátricas, incluindo *D. aurita*, mostraram diferenças substanciais quanto à frugivoria as quais devem estar relacionadas a diferenças de tamanho do corpo, uso do espaço e comportamento de forrageio dessas espécies.

Unitermos: coexistência, frugivoria, marsupiais neotropicais, partição de recursos

Introduction

Several vertebrate species have been identified as frugivores, being specialists or generalists. One of the main implications of this is the role of frugivory in the seed dispersal. The degree of specialization towards frugivory is variable among species. Many attributes of fruit are responsible for animal specialty and hence the capacity to attract a consumer, such as fruit size, form, color, smell, and position in the stem, besides fruit quality. More generic attributes are also important, such as crop size, time and intensity of fruit production, plant habit, and dispersal syndrome (Howe and Smallwood, 1982; Van der Pijl, 1982; Fleming et al., 1993; Fleming and Sosa, 1994; Da Silva and Tabarelli, 2000).

On the other hand, frugivores have specific characteristics as well, such as vision or olfaction acuity, reduced or modified teeth, large caeca and hard guts, and/or arboreal habitats (Vieira and Astúa de Moraes, 2003; Cáceres, 2005). Toucans, guans, several primates, and some carnivores, such as kinkajous, are good examples of specialized fruit eaters among vertebrates (Galetti and Pedroni, 1994; Peres, 1994; Galetti et al., 1997; Julien-Laferrrière, 1999; Da Silva and Tabarelli, 2000).

Generalist frugivores are not necessarily fruit dependent, but typically utilize a variety of food items of both animal and plant sources. This category of consumers is often recognizable as opportunist in nature, feeding on fruits or other items in proportion of their availability. Among vertebrate guilds, omnivores usually carry out this role, consuming all food types, and it is known that these consumers are not specialists in any food category. Peccaries, foxes, opossums, and even some primates are examples of such omnivores (Chivers and Hladik, 1980; Atramentowicz, 1988; Bodmer, 1991; Motta-Júnior et al., 1994; Santori et al., 1995; Motta-Júnior, 2000; Cáceres and Monteiro-Filho, 2001).

In addition, the role of coexistence of related animals in nature has been investigated, and results have shown reasonable niche segregation in the feeding habits of sympatric species, particularly for small and medium-sized omnivorous or frugivorous mammals (Charles-Dominique et al., 1981; Müller and Reis, 1992; Julien-Laferrrière, 1999; Motta-Júnior, 2000).

The southern black-eared opossum *Didelphis aurita* Wied-Neuwied, 1826 is a common marsupial species of eastern Brazil for which a lot of ecological data exists, particularly on food habits, but little for the populations of southern Brazil. Given its abundance in nature, only few studies on diet have substantially assessed the degree of frugivory by this species (Leite et al., 1996; Cáceres and Monteiro-Filho, 2001; Carvalho et al., 2005), and thus there is a general absence of such studies in the Atlantic Forest emphasizing the frugivory and hence the role in seed dispersal performed by this opossum.

In addition, particular associations of related and sympatric species are poorly known for Neotropical marsupials when considering food partitioning. With regard to the entire extent of the Atlantic Forest, there are data available on this subject for no more than four sites regarding all marsupial species living in that biome. These few studies have analyzed two or three marsupial species simultaneously (Leite et al., 1996; Cáceres et al., 2002; Cáceres, 2004; Carvalho et al., 2005; Casella and Cáceres, 2006).

In order to examine the frugivory performed by the Neotropical food-generalist marsupial *Didelphis aurita* in an Atlantic coastal rainforest area of southern Brazil, a six-month field study was carried out in the area. Fruit composition, and its differences regarding seasons, sexes, and sympatric marsupial species were assessed. Fruits in the diet of sympatric marsupials occurring in the study area (see Cáceres et al., 2002) were compared

to those occurring in the *D. aurita* diet, in order to assess niche segregation among related species.

Study area

The study was carried out in a coastal region of southern Brazil, covered by 65-year-old second-growth rainforest (Floresta Ombrófila Densa Submontana *sensu* Klein 1990), on Santa Catarina Island (Parque Municipal da Lagoa do Peri), at 27°43'S and 48°32'W. The area is located in the Lagoa do Peri Reserve, which is 20.3km² in size, including 5.2km² of lagoon surface (CECCA, 1997). Except for the eastern side, forested hills rise to 500m above sea level surrounding the lagoon. The study area was located on the lower slopes, from five to 60m in elevation. Average annual temperature, humidity, and rainfall in the region are 20.5°C, 84 % and 1384mm, respectively. Rainfall is not well marked, but generally the hottest period is wet. The hottest period is from November to April (mean = 22.8°C, range 20.8 to 24.3°C), and the colder period is from May to October (mean = 17.8°C, range 16.4 to 19.2°C) (GAPLAN, 1986). During the study, rainfall was high during the colder months (May to July), March being the driest month. Mean temperature was low in April and May (around 16°C) and high in March (18°C) and July to August (around 20 to 23°C).

Material and Methods

Didelphis aurita was trapped with a grid of 127 traps set in the study area, including 73 traps set on the ground and 54 at 2m height in the understory. Twenty traps installed on the ground were of medium size (45x21x17cm) and the others were small (26x19x9cm), as were all the traps in the understory. The trap grid had a 11x7 configuration between columns and lines, with stations being 15m apart. Traps were baited with banana mixed with peanut butter, and they were monitored daily for four consecutive days each month (March to August, 1999). A compilation of trapping data is shown in Graipel et al. (2003).

When an animal was trapped, it usually defecated on the trap floor. Its feces were thus collected, but only after marking (with ear hole combination) and releasing

the animal. We considered one fecal sample as all feces produced by one animal in a night. Feces were then washed in the laboratory through a 1mm mesh sieve (avoiding loss of small seeds) and dried for examination.

Seed presence and number in feces of the opossum were investigated by searching and counting seeds in feces under a stereoscope, discriminating individual feces by sex and age of the opossum, and month of collection. Feces obtained by successive captures (i.e., on consecutive days) of the same individual were discarded from the analyses. Records of the palm *Syagrus romanzoffiana* were recorded in feces in a different way because only its fibers were seen (and not seeds). Thus, the percentage of the partial volume of such fibers regarding all other items in a given fecal sample was estimated.

To compare diets between sexes, only adults or subadults were considered, based on tooth eruption (Tyndale-Biscoe and Mackenzie, 1976). The seasonality of frugivory was tested using the means of the observed fruit consumption (seen by seed number and fiber percentage in feces) along time (cumulative number of months), through Spearman correlation analyses. Assuming the non-normality of the data, Mann-Whitney *U* test was used for testing sexual differences in overall consumption by considering the total seed number per fecal sample. Based on each fruit species consumed and its respective seed number, feeding differences between sexes were tested for significances by the Wilcoxon test. All except the *U* test included only the main, identifiable seed species in feces. The statistical program used was BioEstat 3.0 (Ayres et al., 2003).

In order to compare the degree of frugivory among sympatric marsupial species at the study site, seeds in feces of *D. aurita* were analyzed and compared to seeds found in feces of the marsupials *Lutreolina crassicaudata* (Desmarest, 1804) and *Micoureus paraguayanus* (Tate, 1931). *Didelphis aurita* was trapped at Lagoa do Peri Reserve following the same trapping methods and period used for the *L. crassicaudata* and *M. paraguayanus* study (Cáceres et al., 2002). The specific name of *M. paraguayanus* follows Voss and Jansa (2003). In order to assess differences of the frugivory performed by these

sympatric species in the study area, we used the Morisita index of overlap (Krebs, 1989). Fruit diversity in the diet of marsupials was estimated by the Shannon index, and tested for differences using the *t* test (Zar, 1984). The Program PAST (Hammer et al., 2001) was used.

Results

Fruit consumption

Based on 63 fecal samples collected mostly from March to August and from 19 individuals of *D. aurita* (17 adults, 1 subadult and 1 young, and 7 female and 12 male), the opossum fed on at least 8 fruit species on Santa Catarina Island, averaging 527 ± 1328 seeds per fecal sample. Cecropiaceae (*Cecropia* spp. and *Maclura tinctoria*) and palm fruits were the main species consumed, but Piperaceae (*Piper* and *Ottonia* species) and Moraceae (*Ficus* spp.) were frequently consumed as well. Fruit species were from canopy (*Ficus* and *Cecropia*) as well as from understory (Piperaceae) plants (Table 1).

The main fruit species consumed regarding total quantities of seeds and means of seeds per scat were, in decreasing order, *Cecropia glazioui*, *Ficus* spp., *Piper*

sp., *C. hololeuca*, *M. tinctoria*, *Ottonia martiana*, and *Ficus luschnatiana*; other non-identified species were not important in terms of seed numbers. Regarding frequency of occurrence in feces, *C. glazioui* was the most consumed fruit species (81%), followed by *Syagrus romanzoffiana* was the second one (77%). Fruits of *Piper* sp. (34%), *Ficus* spp. (27%), and *C. hololeuca* (17%) were not so common but were reasonably frequent in the opossum diet. Fruit species of *M. tinctoria*, *O. martiana* and *F. luschnatiana* were the least consumed items (< 7%) (Table 1).

Effects of season and sex

The consumption of *S. romanzoffiana* increased positively and significantly with time (March to August) ($r_s = 0.92$, $P < 0.0001$), while *Piper* sp. and *C. glazioui* decreased significantly with time ($r_s = -0.67$, $P = 0.015$, and $r_s = -0.76$, $P = 0.004$, respectively). Hence, the two last species, and also *C. hololeuca*, were negatively correlated with *S. romanzoffiana* ($r_s = -0.62$, $P = 0.03$; $r_s = -0.71$, $P = 0.01$; $r_s = -0.71$, $P = 0.01$, respectively). Then *C. glazioui* and *Piper* sp. were positively correlated between themselves ($r_s = 0.77$, $P = 0.003$), with higher numbers of seeds in feces during March and April, decreasing toward June and July, and again beginning

TABLE 1: Frequency of occurrence (%) and number of seeds found in feces of the black-eared opossum *Didelphis aurita* in the Lagoa do Peri Reserve, Santa Catarina Island, southern Brazil. N is the number of times each item appeared in feces. Mean is regarding the number of seeds per sample, which is given in percent for *S. romanzoffiana*. SD = standard deviation. Total = total number of seeds found in all samples. The total number of feces analyzed was 63.

Fruit species	%	N	Mean \pm SD	Total
ARECACEAE				
<i>Syagrus romanzoffiana</i> (Cham.) Glassm.	77	49	34 \pm 27	-
CECROPIACEAE				
<i>Cecropia glazioui</i> Snethlage	81	52	414 \pm 1261	26,144
<i>Cecropia hololeuca</i> Miq.	17	11	6 \pm 21	383
<i>Maclura tinctoria</i> D. Don.	6	4	0.3 \pm 1.6	21
MORACEAE				
<i>Ficus</i> spp.	27	17	92 \pm 387	5,796
<i>Ficus luschnatiana</i> (Miq.) Miq.	2	1	-	1
PIPERACEAE				
<i>Piper</i> sp.	34	22	13 \pm 53	842
<i>Ottonia martiana</i> Miq.	3	2	0.1 \pm 0.6	6
Non-identified	22	14	-	-

to increase slightly in August. There was no correlation between *Ficus* spp. and time ($P > 0.05$) (Figure 1).

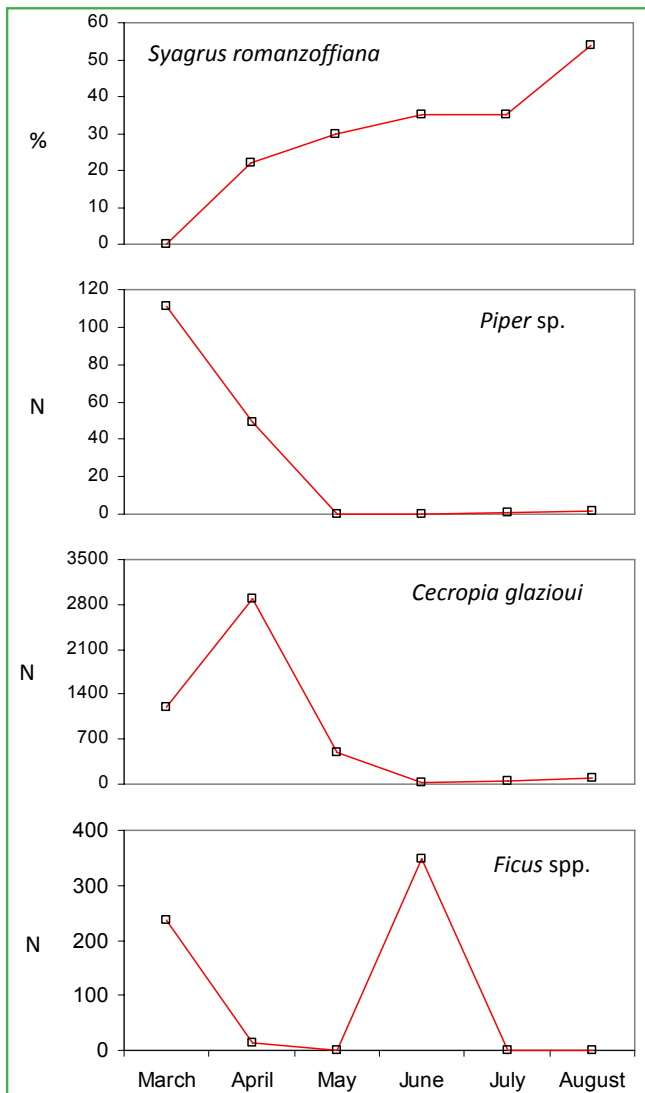


FIGURE 1: Monthly consumption of five fruit types by the opossum *Didelphis aurita* in a coastal Atlantic Forest in southern Brazil. N is the mean number of seeds in feces, and % is the mean percentage of fibers found regarding the entire fecal sample. Numbers of feces per month were 5, 5, 7, 13, 19, and 13, respectively.

Analyses of fruit consumption between sexes did not reveal significant differences ($P > 0.17$, $n = 6$ fruit species, Wilcoxon paired test). Moreover, on seed number per scat, females had a mean number of seeds per fecal sample (526.4; $n = 31$) similar to that of males (576.6; $n = 29$) ($U = 431$; $P = 0.78$).

Resource partitioning among sympatric marsupials

Didelphis aurita had the highest fruit diversity in the samples analyzed regarding the other two sympatric species, being only comparable to that of *M. paraguayanus*. However, that difference was significant ($P = 0.05$; $t = -1.97$). *Lutreolina crassicaudata* had the lowest value for fruit diversity, which differed significantly from that of *D. aurita* ($P = 0.001$; $t = 3.63$) (Table 2).

The similarity of the frugivory among sympatric species was in general high. It was relatively lower between *D. aurita* and *M. paraguayanus* (0.65), and relatively higher between *D. aurita* and *L. crassicaudata* (0.75). However, similarity assumed the highest value between *L. crassicaudata* and *M. paraguayanus* (0.88).

Discussion

The frugivory by the opossum

The black-eared opossum *D. aurita* proved to be a consumer of many fruit species in the Atlantic forest of southern Brazil. This is emphasized by the high intensity of fruits consumed, which was estimated both by frequencies of occurrence and numbers of seeds

TABLE 2: Comparative approach of general characteristics of three sympatric species of Neotropical marsupials regarding their frugivory in lowland Atlantic Forest of Santa Catarina Island, southern Brazil. N is the number of feces analyzed. Mean is the mean number of seeds per fecal sample. R is the richness of fruit species in feces. H' is the Shannon index of diversity for fruits. Data for marsupials other than *D. aurita* are from Cáceres et al. (2002).

Species	Mass (g)	Habit	N	Mean	R	H'
<i>Didelphis aurita</i>	1000	Scansorial	63	580	8	1.61
<i>Lutreolina crassicaudata</i>	600	Cursorial (around water courses)	13	765	4	1.07
<i>Micoureus paraguayanus</i>	100	Arboreal	30	25	5	1.41

found in feces. This happened mainly during the warmer months, but it also occurred during the colder and dryer months (June to August) when *S. romanzoffiana* was intensively consumed. Certain fruit species are very important for frugivorous animals during the season of scarcity (Smithe, 1970; Foster, 1982; Howe and Smallwood, 1982; Julien-Lafférière, 1999), a role which was performed by *S. romanzoffiana* here for *D. aurita*. Fruits of this palm species are important elsewhere for several mammal species (e.g. Motta-Júnior et al., 1994; Quadros and Cáceres, 2001).

The pattern of fruit consumption by *D. aurita* did not differ between sexes as observed elsewhere (Carvalho et al., 2005), but evidence of such differences has already been for *D. aurita* in Araucaria mixed forest, perhaps related to onset of the reproductive season and behavioral differences related to mates and parental care (Cáceres, 2003).

Didelphis aurita has been considered as mostly omnivorous (Santori et al., 1995; Astúa de Moraes et al., 2003), but sometimes it is characterized as being mostly frugivore as well (Stallings, 1989; Cáceres and Monteiro-Filho, 2001; Carvalho et al., 2005). In fact, this species is very opportunistic, consuming food resources according to their availability in the environment (Cáceres et al., 1999; Cáceres, 2003).

For example, *S. romanzoffiana* was consumed in an increasing rate over the time, reaching a high consumption rate in August, a period of cold and dryness, reflecting the known fruiting pattern of this plant species (Lorenzi, 2002). Fruits such as those of *S. romanzoffiana* should be important for frugivores since they would help animals to cross the winter months in good health conditions, particularly for marsupials, which begin to reproduce during this time (Cáceres, 2000). On the other hand, fruit species of *Cecropia* and *Piper* were consumed mainly during the warmer and rainy months (March to April), decreasing toward the winter. This pattern of fructification is in part in accordance with the fruiting patterns of these species (V.A.O. Dittrich, personal communication for *Piper*) in which main fructification occurs during the warmer wet season (Lorenzi, 2002). Many fruiting plants have flesh fruits available during this time, with a decreasing rate towards the winter

(Smithe, 1970; Foster, 1992). However, discrepancies sometimes happen regarding this pattern as was reported for *C. glazioui* which apparently has a year-round fructification elsewhere (Ferraz et al., 1999).

Massive fruiting is expected during warmer months in seasonal habitats (Smithe, 1970; Foster, 1992), which is correlated to the peak of reproduction for marsupials, with a predominance of rather frugivorous young individuals during this time (Cáceres, 2000 and 2002). In a different pattern, *Ficus* is known to offer ripe fruits year-roundly and asynchronously (Charles-Dominique et al., 1981; Foster, 1982; Lorenzi, 2002), this pattern also being in concordance with our data, with high and low peaks during the time, reflecting the asynchronous fructification of the genus (França, 2003). Fruits are important to opossums on account of their nutritional values, such as sugars (Atramentowicz, 1988). The intensity of fruit consumption evidenced here and their nutritional values are thought to help opossums to growth, as is the case of free-ranging young during warmer months (Cáceres, 2000), and also to help fat accumulation in adults (Cáceres and Monteiro-Filho, 1999) during the autumn. Related to this, the positive role of this opossum species in seed dispersal has already been reported (Cáceres et al., 1999; Grelle and Garcia, 1999; Cáceres and Monteiro-Filho, 2001), particularly for small-seeded species.

The opportunism of *D. aurita* can be noted by the observed change in fruit consumption according to elevation and site characteristics. For example, it regularly feeds on *Cecropia* fruits in lowland areas and coastal regions (Carvalho et al., 1999, 2005), like the study area, but feeds on other equivalent fruit species in mountainous areas, such as solanaceous and passifloraceous fruits (Cáceres and Monteiro-Filho, 2001). *Cecropia* species occur mostly in lowland tropical forests with a predominately warmer climate (Lorenzi, 2002; S. M. Silva, personal communication), which are not available to *D. aurita* populations of mountainous cold regions.

Although *D. aurita* is able to feed on large-seeded fruits (Atramentowicz, 1988), only small-seeded species cross its digestive tract, a fact that is evidenced here by the presence of fibers of *S. romanzoffiana* in feces only,

on account of the fact that this is a large-seeded species (> 15mm in seed length).

Resource partitioning among marsupial species

Since all fruits ingested by the opossum here have hundreds and thousands of small seeds (usually less than 5mm), interspecific comparisons could be made in terms of quantities ingested, which would be useful to infer the volumes of fruits consumed.

By comparing *D. aurita* with the sympatric species *L. crassicaudata* and *M. paraguayanus*, the amount of fruits consumed is clearly related to body size (Fleming et al., 1993). The larger the body size, the more fruits (or eventually seeds) will be found in the diet of such animal. This can be exemplified by *C. glazioui* consumption since it was frequently consumed by the three species: the largest species *D. aurita* was found with a mean of 414 seeds, the intermediate size *L. crassicaudata* with a mean of 206 seeds, and the smaller species *M. paraguayanus* with 28 seeds on average (see Cáceres et al., 2002).

However, this body-size related pattern is not so clear for *Piper* or *Ficus*, the other main species consumed by the three marsupial species (see Cáceres et al., 2002), which could be related to food preferences or even microhabitat segregation (Leite et al., 1996; Carvalho et al., 2005). For instance, *L. crassicaudata* based its consumption strongly on *Ficus* and *Piper* fruits (Cáceres et al., 2002), this being one of the reasons for the low fruit diversity in its diet.

In fact, *D. aurita* is a scansorial forest dweller, *L. crassicaudata* is a cursorial, mostly marshland or stream sided dweller, and *M. paraguayanus* is mostly arboreal in lifestyle (Marshall, 1978; Grand, 1983; Leite et al., 1996; Cunha and Vieira, 2002; Graipel, 2003; Graipel et al., 2003; Vieira, 2006). These differences in habitat use could be in part responsible for the observed differences in fruit consumption rather than accounting only for body size. In addition, we inferred that habitat use is responsible more for differences in the quality of fruits consumed, whereas body size is linked to the quantity of fruits consumed. Support for this is the type of frugivory shown by the small body-sized *M. paraguayanus* in

which low quantities of fruits are seen in its feces but an array of fruit species is recorded, showing that the species forages in a variety of habitats for fruits (Cáceres et al., 2002).

By comparing diet similarities based on fruits, *D. aurita* revealed a diet more similar to that of the cursorial *L. crassicaudata* than to that of the arboreal *M. paraguayanus*. Since *D. aurita* and *L. crassicaudata* have more terrestrial habits, this similarity in frugivory matches with this more similar use of habitat, since terrestrial animals will explore resources more similarly when compared with fully arboreal species (Vieira, 2006). But in a general view, the two smaller body-sized opossums (*L. crassicaudata* and *M. paraguayanus*) were the most similar species in fruit consumption, a fact that places this type of species interaction as complex, given the number of factors that can be acting on such species segregation in the environment.

Didelphis aurita appears to exploit more fruit species that are highly available in the environment (e.g. *C. glazioui* and *S. romanzoffiana*) and *M. paraguayanus* exploits fruits more uniformly (Cáceres et al., 2002; Carvalho et al., 2005), the former species being more opportunistic and generalist comparatively (Cáceres and Monteiro-Filho, 2001; Graipel et al., 2001). Nevertheless, *D. aurita* and *M. paraguayanus* revealed higher fruit diversity in their diets when compared to *L. crassicaudata*, which reveals the trend towards frugivory for the former two species (Stallings, 1989). Indeed, the partial (*D. aurita*) and full (*M. paraguayanus*) relationships of both former species with the arboreal lifestyle corroborate these patterns of fruit richness and diversity in their diets, according to Vieira and Astúa de Moraes (2003).

The interactions of factors determining frugivorous habits in Neotropical marsupials, such as habitat utilization, body size, and feeding specialization (Leite et al., 1996; Cunha and Vieira, 2002; Cáceres, 2003, 2004; Santori et al., 2004; Vieira, 2006), are responsible for the patterns of segregation in frugivory seen in the Atlantic Forest of southern Brazil. The marsupial *D. aurita*, as a generalist and scansorial species, can interact with either cursorial or arboreal sympatric species through food partition.

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References

- Astúa de Moraes D.; Santori, R. T.; Finotti, R.; Cerqueira, R. 2003. Nutritional and fibre contents of laboratory established diets of neotropical opossums. In: Jones, M.; Dickman, C. & Archers, M. (Eds). **Predators with pouches: The biology of carnivorous marsupials**. CSIRO, Collingwood, Canada, p.229-237.
- Atramentowicz, M. 1988. La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. **Revue d'Ecologie Terre et Vie**, **43**: 47-57.
- Ayres M.; Ayres, M. Jr.; Ayres, D. M.; Dos Santos, A. S. 2003. **BioEstat 3.0: Aplicações estatísticas nas áreas das ciências biológicas e médicas**. Sociedade Civil Mamirauá, Manaus, Brasil, 291pp.
- Bodmer, R. E. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. **Biotropica**, **23**: 255-261.
- Cáceres, N. C. 2000. Population ecology and reproduction of the white-eared opossum, *Didelphis albiventris* (Mammalia, Marsupialia), in an urban environment of southern Brazil. **Ciência & Cultura**, **52**: 171-174.
- Cáceres, N. C. 2002. Food habits and seed dispersal by the white-eared opossum *Didelphis albiventris* in southern Brazil. **Studies on Neotropical Fauna & Environment**, **37**: 97-104.
- Cáceres, N. C. 2003. Use of the space by the opossum *Didelphis aurita* Wied-Neuwied (Mammalia, Marsupialia) in a mixed forest fragment of southern Brazil. **Revista Brasileira de Zoologia**, **20**: 315-322.
- Cáceres, N. C. 2004. Diet of three didelphid marsupials (Mammalia, Didelphimorphia) in southern Brazil. **Mammalian Biology**, **69**: 430-433.
- Cáceres, N. C. 2005. Comparative lengths of digestive tracts of seven didelphid marsupials (Mammalia) in relation to diet. **Revista Brasileira de Zoologia**, **22**: 182-185.
- Cáceres, N. C.; Dittrich, V. A. O.; Monteiro-Filho, E. L. A. 1999. Fruit consumption, distance of seed dispersal and germination of solanaceous plants ingested by the common opossum (*Didelphis aurita*) in southern Brazil. **Revue d'Ecologie Terre et Vie**, **54**: 225-234.
- Cáceres, N. C.; Ghizoni-Jr, I. R.; Graipel, M. E. 2002. Diet of two marsupials, *Lutreolina crassicaudata* and *Micoureus demerarae* in a coastal Atlantic Forest island of Brazil. **Mammalia**, **66**: 331-340.
- Cáceres, N. C.; Monteiro-Filho, E. L. A. 1999. Tamanho corporal em populações naturais de *Didelphis* (Mammalia, Marsupialia) do Sul do Brasil. **Revista Brasileira de Biologia**, **59**: 461-469.
- Cáceres, N. C.; Monteiro-Filho, E. L. A. 2001. Food habits, home range and activity of *Didelphis aurita* (Mammalia, Marsupialia) in a forest fragment of southern Brazil. **Studies on Neotropical Fauna & Environment**, **36**: 85-92.
- Carvalho, F. M. V.; Fernandez, F. A. S.; Nessimian, J. L. 2005. Food habits of sympatric opossums coexisting in small forest fragments in Brazil. **Mammalian Biology**, **70**: 366-375.
- Carvalho, F. M. V.; Pinheiro, P. S.; Fernandez, F. A. Z.; Nessimian, J. L. 1999. Diet of small mammals in Atlantic Forest fragments in southeastern Brazil. **Revista Brasileira de Zoociências**, **1**: 91-101.
- Casella, J.; Cáceres, N. C. 2006. Diet of four small mammal species from Atlantic forest patches in south Brazil. **Neotropical Biology and Conservation**, **1**: 5-11.
- CECCA – Centro de Estudos e Cultura e Cidadania. 1997. **Unidades de Conservação e Áreas Protegidas da Ilha de Santa Catarina: Caracterização e legislação**. Insular, Florianópolis, Brasil, 160pp.
- Charles-Dominique, P.; Atramentowicz, M.; Charles-Dominique, M.; Gerard, H.; Hladik, A.; Hladik C. M.; Prévost, M. F. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: interrelations plantes-animaux. **Revue d'Ecologie Terre et Vie**, **35**: 341-435.
- Chivers, D. J.; Hladik, C. M. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. **Journal of Morphology**, **166**: 337-386.
- Cunha, A. A.; Vieira, M. V. 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. **Journal of Zoology London**, **258**: 419-426.
- Da Silva, J. M. C.; Tabarelli, M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. **Nature**, **404**: 72-74.
- Ferraz, D. K.; Artes, R.; Mantovani, W.; Magalhães, L. M. 1999. Fenologia de árvores em fragmento de mata em São Paulo, SP. **Revista Brasileira de Biologia**, **59**: 305-317.
- Fleming, T. H.; Sosa, V. J. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. **Journal of Mammalogy**, **75**: 845-851.
- Fleming, T. H.; Venable, D. L.; Herrera, L. G. 1993. Opportunism vs. specialization: The evolution of dispersal strategies in fleshy-fruited plants. In: Fleming, T. H. & Estrada, A. (Eds). **Frugivory and seed dispersal: Ecological and evolutionary aspects**. Kluwer, Belgium, p.107-120.
- Foster, R. B. 1982. The seasonal rhythms in fruitfall on Barro Colorado Island. In: Leigh-Jr., E. G. (Ed.). **The ecology of a tropical forest**. Smithsonian Institution, Washington, USA, p.151-172.
- França L. F. 2003. **Frugivoria e abundância de tucano (*Ramphastus toco*) durante a estação seca no Pantanal Sul**. MSc. Dissertation, Universidade Federal do Mato Grosso do Sul, Brasil, 49pp.
- Galetti, M.; Martuscelli, P.; Olmos, F.; Aleixo, A. 1997. Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic Forest of Brazil. **Biological Conservation**, **82**: 31-39.

- Galetti, M.; Pedroni, F. 1994. Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in south-east Brazil. **Journal of Tropical Ecology**, **10**: 27-39.
- GAPLAN. 1986. **Atlas de Santa Catarina**. Gabinete de Planejamento e Coordenação Geral, Rio de Janeiro, Brasil, 173pp.
- Graipel, M. E. 2003. **Contribuição ao estudo da mastofauna do estado de Santa Catarina, sul do Brasil**. PhD. Thesis, Pontifícia Universidade Católica do Rio Grande do Sul, Brasil, 226pp.
- Graipel, M. E.; Cherem, J. J.; Miller, P. R. M.; Glock, L. 2003. Trapping small mammals in the forest understory: a comparison of three methods. **Mammalia**, **67**: 551-558.
- Graipel, M. E.; Cherem, J. J.; Ximenez, A. 2001. Mamíferos terrestres não voadores da Ilha de Santa Catarina, sul do Brasil. **Biotemas**, **14**: 109-140.
- Grand, T. I. 1983. Body weight: its relationship to tissue composition, segmental distribution of mass, and motor function. III. The Didelphidae of French Guyana. **Australian Journal of Zoology**, **31**: 299-312.
- Grelle, C. E. V.; Garcia, Q. S. 1999. Potential dispersal of *Cecropia hololeuca* by the common opossum (*Didelphis aurita*) in Atlantic forest, southeastern Brazil. **Revue d'Ecologie Terre et Vie**, **54**: 327-332.
- Howe, H. F.; Smallwood, J. 1982. Ecology of seed dispersal. **Annual Review of Ecology and Systematic**, **13**: 201-228.
- Hammer, Ø.; Harper, D. A. T.; Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. **Palaeontologia Electronica** **4**: 1-9.
- Julien-Laferrrière, D. 1999. Foraging strategies and food partitioning in the neotropical frugivorous mammals *Caluromys philander* and *Potos flavus*. **Journal of Zoology London**, **247**: 71-80.
- Krebs, C. J. 1989. **Ecological methodology**. Harper and Row, New York, USA, 654pp.
- Lorenzi, H. 2002. **Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil**. Instituto Plantarum de Estudos da Flora, Nova Odessa, Brasil, 368pp.
- Leite, Y. L. R.; Stallings, J. R.; Costa, L. P. 1996. Diet and vertical space use of three sympatric opossums in a Brazilian Atlantic forest reserve. **Journal of Tropical Ecology**, **12**: 435-440.
- Marshall, L. G. 1978. *Lutreolina crassicaudata*. **Mammalian Species**, **91**: 1-4.
- Motta-Júnior, J. C. 2000. Variação temporal e seleção de presas na dieta do lobo-guará, *Chrysocyon brachyurus* (Mammalia: Canidae), na Estação Ecológica de Jataí, Luiz Antônio, SP. In: Santos, J. E. & Pires, J. S. R. (Eds). **Estação Ecológica de Jataí**. RIMA, São Carlos, Brasil, p.331-347.
- Motta-Júnior, J. C.; Lombardi, J. A.; Talamoni, S. A. 1994. Notes on the crab-eating fox (*Dusicyon thous*): seed dispersal and food habits in southeastern Brazil. **Mammalia**, **58**: 156-159.
- Müller, M. F.; Reis, N. R. 1992. Partição de recursos alimentares entre quatro espécies de morcegos frugívoros (Chiroptera: Phyllostomidae). **Revista Brasileira de Zoologia**, **9**: 345-355.
- Peres, C. A. 1994. Primate responses to phenological changes in an Amazonian terra firme Forest. **Biotropica**, **26**: 98-1994.
- Quadros, J.; Cáceres, N. C. 2001. Ecologia e conservação de mamíferos na Reserva Volta Velha, Estado de Santa Catarina, Brasil. **Acta Biológica Leopoldensia**, **23**: 213-224.
- Santori, R. T.; Astúa de Moraes, D.; Cerqueira, R. 1995. Diet composition of *Metachirus nudicaudatus* and *Didelphis aurita* (Marsupialia, Didelphoidea) in Southeastern Brazil. **Mammalia**, **59**: 511-516.
- Santori, R. T.; Astúa de Moraes, D.; Cerqueira, R. 2004. Comparative gross morphology of the digestive tract in ten Didelphidae marsupial species. **Mammalia**, **68**: 27-36.
- Smithe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. **American Naturalist**, **104**: 25-35.
- Stallings, J. R. 1989. Small mammal inventories in an eastern Brazilian park. Bulletin of Florida Museum of Natural History, **Biological Science**, **34**: 153-200.
- Tyndale-Biscoe, C. H.; Mackenzie, R. B. 1976. Reproduction in *Didelphis marsupialis* and *D. albiventris* in Colombia. **Journal of Mammalogy**, **57**: 249-265.
- Van der Pijl, L. 1982. **Principles of dispersal in higher plants**. Springer-Verlag, Berlin, Germany, 215pp.
- Vieira, E. M.; Astúa de Moraes, D. 2003. Carnivory and insectivory in neotropical marsupials. In: Jones, M.; Dickman, C. & Archers, M. (Eds). **Predators with pouches: The biology of carnivorous marsupials**. CSIRO, Collingwood, Canada, p.271-284.
- Vieira, M. V. 2006. Locomoção, morfologia e uso do habitat em marsupiais neotropicais: uma abordagem ecomorfológica. In: Cáceres, N. C. & Monteiro-Filho, E. L. A. (Eds). **Os Marsupiais do Brasil: Biologia, ecologia e evolução**. Editora da UFMS, Campo Grande, Brasil, p.145-158.
- Voss, R. S.; Jansa, S. A. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. **Bulletin of American Museum of Natural History**, **276**: 1-82.
- Zar, J. H. 1984. **Biostatistical analysis**. 2nd ed. Prentice-Hall, Englewood Cliffs, UK, 718pp.