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# FRUGIVORY VS. INSECTIVORY IN MARSUPIALS OF THE ATLANTIC FOREST: TRADE-OFFS IN THE USE OF VERTICAL STRATA

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**Abstract:** Space and diet are frequently considered the two most important dimensions of an organism niche, but in tropical forests, these two dimensions are associated, with fruits more accessible in the canopy and upper strata of the forest, and arthropods more abundant in the forest litter. This constitutes a genuine macroecological pattern, potentially common to all tropical forests. We tested the existence of this trade-off between frugivory-insectivory in the vertical strata, and if it results from feeding specializations, using didelphid marsupials as a model group. We compared nine species, representing different lineages, which differ in diet and use of the forest strata, using phylogenetically independent contrasts. We classified species according to their use of the vertical strata into four categories based on the literature (terrestrial-semiaquatic, terrestrial-understory, underestory-subcanopy-canopy, and canopy only). Diet was analyzed by the proportion of nutrients (carbohydrates, fibers, proteins and lipids) in a cafeteria food preference experiment: more frugivorous diets have higher carbohydrate and fiber content, whereas more carnivorous and insectivorous diets have higher protein and lipid content. Along the phylogeny, increases in use of the vertical strata were significantly associated with increases in carbohydrate and fiber contents, and reductions in lipid content. Levels of protein content also reduced with increasing use of the vertical strata, but this association was not significant. The macroecological pattern of increasing frugivory with use of the upper strata is supported by the results for didelphid marsupials, which also indicate specialization is a mechanism involved. The contribution of didelphid marsupials to the ecosystem process of frugivory and seed dispersal is performed by a subset of species, despite being broadly described as omnivorous. Future studies should evaluate this macroecological pattern in more specialized taxonomic groups that vary in the use of the vertical strata, and if specialization is the general mechanism involved.

**Keywords:** Didelphidae; diet; independent contrasts, small mammals; vertical stratification.

## INTRODUCTION

Species differ in the use of the vertical strata of forests, which allows interspecific and intraspecific niche differentiation, reducing risks of competition (Harney & Dueser 1987, Dickman 1989, Cunha & Vieira 2002), predation (Prevedello *et al.* 2008), allowing the use of a greater range of environments (Layne 1970, Saetnan *et al.* 2009), and the coexistence of ecologically and morphologically similar species (Albanese *et al.* 2011). Species also differ in feeding habits, which adds another important dimension to community structure (Batzli & Lesicure 1991, Brown *et al.* 1994). These two dimensions, space and diet, are frequently considered the two most important dimensions of an organism niche (Schoener 1974, Cunha & Vieira 2002).

In tropical forests, structural complexity is an important factor that contributes to a richer arboreal fauna, due to variety of resources that it provides (Levin 1972, Emmons 1980, August 1983). However, resources are not evenly distributed through the forest strata; fruits are obviously more accessible in the canopy and upper strata of the forest. Therefore, species that use the upper strata have more access to fruits (*e.g.* Rader & Krockenberger 2006). This could be common to all forests and organisms consuming fruits, constituting a genuine macroecological pattern. Fruit in the upper strata being consumed by a subset of species supports the existence of compartments of plant-frugivore interactions in the upper strata, which has consequences for ecosystem functionning (Schleuning *et al.* 2011, Stevenson *et al.* 2015). In addition, the mechanism generating this pattern remains an open question: frugivory in the upper strata could be simply opportunistic, or a specialization favored by natural selection.

Didelphid marsupials of South America are a particular appropriate group to test if frugivory by more arboreal species is opportunistic - just a consequence of the higher availability of fruits in the upper strata - or if it indeed use of the upper strata involves specialization and adaptation to frugivory. First, phylogenetic relationships between major lineages are well established (Jansa *et al.* 2013), which allows to determine if increased frugivory along the phylogeny is associated with increased use of the upper strata. Second, vertical stratification and habitat use by didelphid marsupials are also well established (Charles-Dominique *et al.* 1983; Julien Laferrière & Atramentowicz 1990, Malcolm 1995, Passamani 1995, Santori *et al.* 1995, Leite *et al.* 1996, Voltolini 1997, Freitas *et al.* 1997, Fernandez *et al.* 1997, Cunha & Vieira 2002, Grelle 2003, Abreu & Oliveira 2014). Associations between habitat use and diet composition are frequently suggested (Charles-Dominique *et al.* 1981, Leite *et al.* 1996, Cáceres *et al.* 2002, Vieira & Astúa 2003). However, field studies of diet and habitat are commonly conducted separately, and associations between these two characteristics are based on literature information (Albanese *et al.* 2011, Abreu & Oliveira 2014), and on the frequency of captures on ground and understory traps (Cáceres *et al.* 2002). Generally, arboreal species are considered more frugivorous and cursorial species more insectivorous (Leite *et al.* 1994, Cáceres *et al.* 2002, Vieira & Astúa 2003). Last, diet nutritional composition is available for all major lineages, which allows detailed comparison of carbohydrate, lipid and protein content (Pèrissé *et al.* 1988, Fonseca & Kierluff 1989, Malcolm 1991, Santori *et al.* 1997, Astúa *et al.* 2003, Santori *et al.* 2015). Detailed information on diet nutritional composition demonstrates clear differences between lineages in the relative consumption of animal and plant material, and the proportion of macronutrients in their diet. This detailed information was only possible through laboratory studies on food preference – also known as 'cafeteria' experiments – which allows the measurement of the amount food items and nutrient consumption (Pèrissé *et al.* 1988, Santori *et al.* 2015). Selected items in the laboratory are affected only by the intrinsic factors that drives food choice, determined by morphological and physiological attributes (Finotti *et al.* 2015). Whereas diet composition in field studies are influenced by seasonal and spatial variation in food resources, and identification and quantification of food items in stomach or feces contents have many limitations (Ceotto *et al.* 2009, Lessa & Costa 2010). Therefore, results from field studies vary largely and do not enable a clear definition of species diet. For example, *Caluromys philander* is considered the most frugivorous species among didelphids (Fonseca *et al.* 1996, Leite *et al.* 1996), but in some conditions a higher proportion of

insects and animal matter can be found in its diet (Carvalho *et al.* 1999, De Camargo *et al.* 2017).

The aim of this study was to determine if frugivory is evolutionarily associated with the use of the upper strata of the forest, and conversely, if insectivory is associated to the use of the forest floor, using didelphis marsupials as a model group. We identified some general patterns were identified based on the observations made on locomotion and diet studies made independently for many ecosystems, despite the spatial and seasonal variation found for these characteristics (Vieira & Camargo 2012). Until now, the association between use of vertical strata and diet of didelphid marsupials was not directly tested. One great possible restriction for this is that the majority of data on diet composition is provided by field studies using fecal and stomach contents, which are variable in space and time and dependent on resources availability. Therefore, the measure of a mean, general diet for a specie is a hard, maybe impossible task to do, based on this type of data. At this study, we tested the relation between vertical stratification and food habits in a group of nine species of didelphid marsupials collected at many Brazilian localities and submitted to a laboratory preference experiment (Pèrissé *et al.* 1989). We used diet nutritional composition, obtained in these cafeteria preference experiments, and correlated to the species vertical habitat use of the forest, based on literature data. Results of cafeteria experiments are related to the intrinsic factors of diet selection that related to morphological and physiological species characteristics and its relation to the physical and chemical food characteristics. Therefore, it represents the food choice made independent of seasonal and spatial variations (Finotti *et al.* 2015). The habitat vertical use based on literature data enables a specie classification based on the more common vertical strata that individuals of a specie occupy, what can also be considered a result of the adaptive locomotor characteristics that enables a particular specie to occupy more frequently a particular habitat stratum. Thus, these data represent mean species conditions on both factors analyzed.

Such comparative analyzes based on data of species with different relationships pose a problem of statistical dependence: the more closely related a pair of species, the more related are their characteristics (Martins & Hansen 1996). To overcome this problem, we used here a comparative method to contrast vertical strata use and diet along branches of the phylogeny (Felsenstein 1985). This is the first study to test the association between use of the strata of the forest and diet of didelphid marsupials using a comparative method to obtain independent data points.

## MATERIAL AND METHODS

The species used in this study were *Didelphis aurita* (Wied-Neuwied 1826), *Didelphis albiventris* Lund 1840, *Philander frenatus* (Olfers 1818), *Metachirus nudicaudatus* (É. Geoffroy 1803), *Caluromys philander* Linnaeus 1758, *Gracilinanus agilis* (Burmeister 1854), *Marmosa paraguayana* (Tate 1931), *Monodelphis domestica* (Wagner 1842), and *Lutreolina crassicaudata* (Desmarest 1804). Individuals were collected in several Brazilian localities (see Supplementary Material 1 for localities description).

Each species received a score from 1 to 4 based on its use of arboreal strata according to Vieira and Camargo (2012), and confirmed by using other references (Stallings 1989, Fonseca & Kierluff 1989, Malcolm 1991, Vieira 1997, Voltolini 1997, Grelle 2003) (Table 1). We used nutritional data published elsewhere (Astúa *et al.* 2003), where food preference and nutritional content of the diet were calculated for each species through cafeteria experiments of alimentary preference (Pèrissé *et al.* 1989). We used as diet variables the proportion of nonstructural carbohydrates, lipids, proteins and fibers (Table 2) instead of traditional broad and unprecise categories of feeding habits (herbivores, carnivores, omnivores). According to the chemical composition of food items (Franco 1987, Mendez *et al.* 1995), (1) species with higher protein or lipid proportion in the diet consume more animal matter than species with lower protein content, and (2) species with higher proportion of nonstructural carbohydrates (glucids) and fibers in the diet consume a greater amount of plant matter.

Initially we tested the existence of a phylogenetic signal using a Mantel Z-test (Manly 2004) of association between the matrices of use of the vertical strata, diet similarity, and phylogenetic distance. We calculated the matrix of phylogenetic

distance based in the branch lengths of the phylogenetic hypothesis of Jansa *et al.* (2013) (Table 3). The matrix of diet similarity was constructed using as distance between species, the sum of the square root of the product of the four macronutrients (Marroig & Cheverud 2001). The matrix of use of the vertical strata was constructed using the ratio between the ranks of each pair of species, being the denominator always the higher rank (this provides an index between 0 and 1). We tested the hypothesis that the use of the vertical strata determines the consumption of fruits and invertebrates using the method of independent contrasts (Felsenstein 1985), regressing the phylogenetic contrasts of use of the vertical strata against phylogenetic contrasts of carbohydrates, fiber, protein and lipid contents in the diet (Harvey & Pagel 1991).

## RESULTS

The Mantel Test (Z) showed a significant correlation between the phylogenetic distance matrix and diet (n = 10, r = 0.89, $p$ = 0.05), use of the vertical strata (n = 10, r = 0.97, $p$ = 0.02), and between use of the vertical strata and diet (r = 0.85, $p$ = 0.01).

The regression between contrasts of use of the vertical strata and diet contrasts was clearly significant for carbohydrates and fiber (Table 3, Figure 1a, b), and can be considered significant for proteins (Figure 1d). Carbohydrates and fiber content increase with increasing use of the forest terrestrial strata, whereas protein content reduces with the increase of the use of arboreal strata (Table 3, Figure 1).

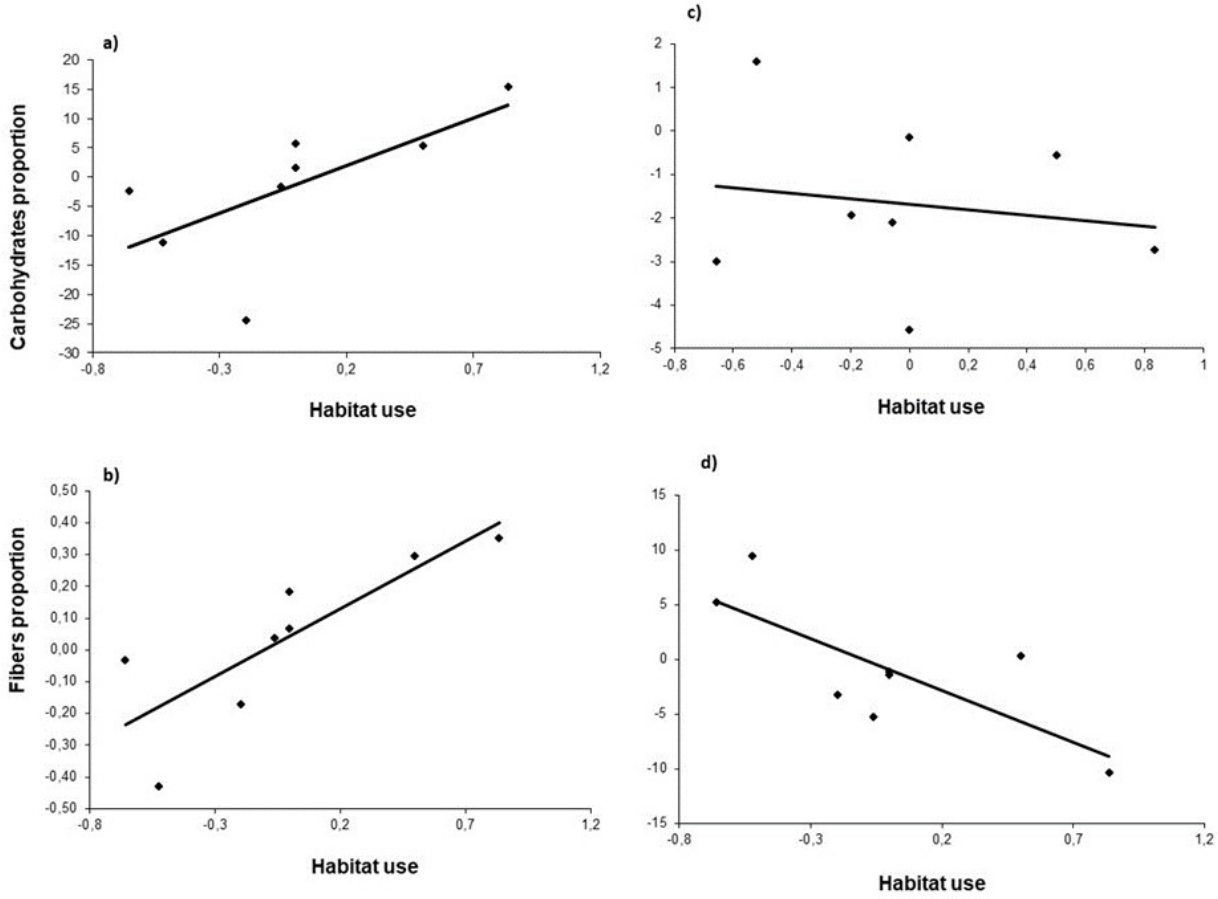


**Figure 1.** Relationship between phylogenetically independent contrasts of use of the vertical strata on contrasts of (a) carbohydrate proportion, (b) fiber proportion, (c) lipid proportion, and (d) protein proportion in the diet.

**Table 1.** Scores ascribed to species according to the degree of vertical strata used according to Vieira & Camargo (2012).

| Species | Habitat use | Scores |
|---|---|---|
| *Didelphis aurita* | Understory, Sub-canopy and canopy | 3 |
| *Didelphis albiventris* | Understory, Sub-canopy and canopy | 3 |
| *Philander frenatus* | Terrestrial/understory | 2 |
| *Metachirus nudicaudatus* | Terrestrial | 1 |
| *Caluromys philander* | Arboreal/canopy | 4 |
| *Gracilinamus agilis* | Understory, Sub-canopy | 3 |
| *Marmosa paraguayana* | Arboreal/canopy | 4 |
| *Monodelphis domestica* | Terrestrial | 1 |
| *Chironectes minimus* | Terrestrial/aquatic | 1 |
| *Lutreolina crassicaudata* | Terrestrial/aquatic | 1 |

**Table 2.** Proportion of macronutrients used for each species in a diet choice experiment (Astúa *et al.* 2003).

| Species | Proteins (%) | Non structural carbohydrates (%) | Lipids (%) | Fiber (%) |
|---|---|---|---|---|
| *Didelphis aurita* | 33.87 | 55.55 | 10.57 | 1.94 |
| *Didelphis albiventris* | 35.49 | 47.40 | 17.11 | 1.68 |
| *Philander frenatus* | 42.70 | 48.00 | 9.29 | 1.76 |
| *Metachirus nudicaudatus* | 37.14 | 54.74 | 8.11 | 1.96 |
| *Caluromys philander* | 7.15 | 91.61 | 1.23 | 2.70 |
| *Gracilinamus agilis* | 26.43 | 67.26 | 6.32 | 2.53 |
| *Marmosa paraguayana* | 20.80 | 73.51 | 5.70 | 2.81 |
| *Monodelphis domestica* | 60.03 | 27.88 | 12.09 | 1.03 |
| *Chironectes minimus* | 50.32 | 44.70 | 4.98 | 2.24 |
| *Lutreolina crassicaudata* | 53.92 | 31.95 | 14.13 | 1.60 |

## DISCUSSION

Frugivory in didelphid marsupials was indeed associated with use of upper strata of the forest, independent of phylogenetic relationships as the association between independent contrasts demonstrated. Consequently, higher fruit consumption by marsupials in the upper strata is done by a subset of species; those more specialized in the use of upper strata. The interaction strength between plants and more frugivore didelphids, which use the upper strata, must be more intense than with didelphids as whole, supporting the existence of compartments of plant-frugivore interactions in the upper strata (Schleuning *et al.* 2011).

The use of higher strata provides resources that are not available on the ground and reduces predation risk by terrestrial predators (Rader & Krockenberger 2006, Prevedello *et al.* 2008, Abreu *et al.* 2010, and Vieira & Camargo 2012). The highest vertical stratum (canopy) have many structural and resource differences compared to the other strata, being a different adaptive zone available to organisms that holds morphological adaptations to explore it (Tobin 1995, Martins & Gribel 2007). In this case, the possibilities to explore new types of habitats or the increase in efficiency in their use are reflected in the diet, and contribute to higher diversity of species and functions they perform in the system.

The use of precise nutritional diet content and a robust classification of use of the forest strata allows the reduction of uncontrolled variation, and can be considered independent from seasonal and spatial variation, representing the mean or

more common condition for the species studied. These metrics and classification are estimates for whole species, based on controlled laboratory experiments made with individuals from different localities for the same species (nutritional diet content), or reviews of available information in the literature (use of the vertical strata) also analyzing the vertical strata use on different ecosystems or laboratory experiments. A higher fiber proportion in the diet is a result of consumption of more plant items, which are more difficult to digest. The use of arboreal strata opens the possibility to explore fruits and seeds directly, before they fall on the ground, but also give access to items such as green fresh buds, nectar and insects that occurs exclusively on the tree canopies (Tobin 1995, Martins & Gribel 2007). Conversely, on the forest floor, probably, arthropods are more abundant available to these animals, mainly because of leaf litter, being an important component of the diet of mainly semi-terrestrial didelphids such as Didelphis aurita and Philander frenatus (Freitas *et al.* 1997). A negative relationship between use of the vertical strata of the forest and the proportion of lipids was also expected. However, as didelphids are mainly omnivorous, the ingestion of plant items with high fat content can compensate for the lower animal matter in the diet of more arboreal species. Some fruits used in the cafeteria preference experiments – where the data came from - like orange, banana, grapes and apple have a relatively high fat content (Astúa *et al.* 2003).

**Table 3.** Coefficient of determination ($r^2$), test t value, and significance level (p) for the regression between each nutrient contrast and the habitat use contrast.

| | Carbohydrates | Proteins | Lipids | Fibers |
|---|---|---|---|---|
| $r^2$ | 0.48 | -0.41 | 0.0002 | 0.70 |
| t | 2.54 | -2.20 | 0.04 | 4.02 |
| *p* | 0.04 | 0.06 | 0.97 | 0.003 |

Use of the vertical strata and diet preferences are well defined for each genus of didelphid marsupials. Species of *Caluromys* are more frugivorous and strictly arboreal species, species of *Didelphis* have a broad diet and amplitude of use of the forest strata, and species of *Monodelphis* are terrestrial and have a more insectivorous diet (Casella & Cáceres 2006, Vieira & Camargo 2012). Species of Didelphis are omnivorous and scansorial whereas species of *Philander* have a larger diversity of items in their diets, therefore being considered more omnivorous but with a higher animal content in its diet (Ceotto *et al.* 2009, Fonseca *et al.* 1991, Santori *et al.* 2015). Use of the vertical strata seem to vary between sites (Pèrissé *et al.* 1988, Freitas *et al.* 1997, Santori *et al.* 2015), but climbing and arboreal walking performance of *Philander* are like other arboreal didelphids (Antunes 2003; Delciellos & Vieira 2006; 2007; 2009a, Delciellos & Vieira, 2009b). In an evolutionary perspective, these differences may be related to the radiation events in history of these lineages. Basal lineages of didelphids inhabited South American moist forests since the Early Oligocene (26,3 Ma) and only diversified into more xeric habitats by the Miocene (Meredith *et al.* 2011, Jansa *et al.* 2013). *Caluromys* lineage was the first to differentiate from other didelphid lineages at this time (Jansa *et al.* 2013). It is reasonable to suppose that the habitat characteristics at this time, in a humid forest with many strata layers can furnish the niche's opportunities to this early radiation. Species of *Caluromys* have the more drastic adaptations to the arboreal life among didelphids, such as locomotor performance (Delciellos & Vieira 2009a), and functional morphology (*e.g.* Youlatos 2008). In addition, *Caluromys philander* was the species with the highest association between digestive tract measurements (caecum and large intestine), and its frugivorous food habits (Santori *et al.* 2004).

The hypothesis that vertical use of the forest strata involves specializations to frugivory is supported by the case of didelphid marsupials, and support the existence of compartments of plant-frugivore interactions in the upper strata of the forest. The contribution of didelphid marsupials to the ecosystem process of frugivory and seed dispersal is therefore performed by a subset of species, despite being broadly described as omnivorous. If even overall such omnivorous animals become more specialized on frugivory by using the upper strata, the same is likely to occur in other more specialized taxonomic groups that vary in the use of the vertical strata, such as bats (*e.g.* Bernard 2001), birds (*e.g.* Pearson 1971), and Lepidoptera (*e.g.* Schulze *et al.* 2001). The

possibility that specialization on frugivory is generally associated with use of the upper forest strata constitutes a genuine macroecological pattern with a clear mechanism involved, which can furnish insights in the direction of character change and functioning of the forest as an ecosystem and deserves attention in future studies.

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**Supplementary Material 1.** Localities where animals were collected.

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