

Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil

André A. Cunha and Marcus V. Vieira*

Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Rio de Janeiro RJ, 21941-590, Brazil

(Accepted 11 February 2002)

Abstract

Didelphids use vertical strata in different ways, suggesting the existence of a wider variety of niches than simply arboreal or terrestrial. This variety could be related to the differential ability to deal with support diameters and inclines, and might be important for the coexistence of species in local assemblages. From data obtained with the spool-and-line technique, the use of the vertical space and above-ground supports is described in four species of an assemblage of didelphid marsupials in south-east Brazil. The stratification in this and other assemblages in the Atlantic forest and in the Amazon is also compared. Animals were trapped in Serra dos Órgãos, state of Rio de Janeiro, and equipped with a spool-and-line device before release. The paths were tracked by measuring variables related to support diameter, incline, distance and height moved above ground. The diameter of supports used was positively related to body size, and the incline to the dominant direction of movement (horizontal *vs* vertical). The more cursorial species, *Metachirus nudicaudatus*, only once moved above ground in > 3200 m of paths followed. *Didelphis aurita* moved mostly on the ground, but was the only species that occasionally reached the canopy. *Philander frenata* also moved mostly on the ground, occasionally used the understorey, but never reached the canopy. The more arboreal species, *Marmosops incanus*, moved mostly in the understorey, but never in the canopy. This pattern of stratification is similar to that observed in other sites in the Atlantic forest and in the Amazon.

Key words: climbing ability, spool-and-line, community structure, vertical stratification, small mammals, didelphids, marsupials

INTRODUCTION

Neotropical forests are unique in their heterogeneity in vertical strata and in diversity of microhabitats (Richards, 1996). Richness of small mammal species is dependent on the complexity of this environment (*sensu* August, 1983), especially in the vertical strata (August, 1983; Malcolm, 1995). Species of didelphid marsupials differ in their specialization for feeding on meat, arthropods, or fruits, but all are omnivorous to some degree, with a potentially large overlap in their diets (Table 1). Therefore, segregation along the vertical strata of neotropical forests could favour coexistence and resource partitioning between species of didelphids.

The differential use of the forest strata by small mammals in the neotropics was first quantified by Charles-Dominique *et al.* (1981), using a combination of nocturnal observations and traps in the canopy. Two

major assemblages were identified, one of the canopy (*Micoureus demerarae* [= *Marmosa cinerea*] and *Caluromys philander*), and another of the understorey-forest floor (*Marmosa murina*, *Philander opossum* and *Didelphis marsupialis*). Within these assemblages there was a continuum of body size with little overlap between species (Charles-Dominique *et al.*, 1981). Subsequent studies confirmed the vertical stratification of small mammals in the Amazon (Terborgh, Fitzpatrick & Emmons, 1984; Janson & Emmons, 1991; Julien-Laferrière, 1991; Malcolm, 1991; Voss & Emmons, 1996), and in the Atlantic forest of Brazil (Fonseca & Kierulff, 1989; Stallings, 1989; Passamani, 1995; Leite, Costa & Stallings, 1996; Palma, 1996; Voltolini, 1997; E. M. Vieira, 1998, 1999; Grelle, in press). In these studies, species of *Caluromys* were the more arboreal species, mostly captured in the canopy. Species of *Didelphis* and *Micoureus demerarae*, were captured at all heights, but *Didelphis* more frequently on the forest floor and *M. demerarae* more frequently above ground. There was often one species captured more frequently

*All correspondence to: Marcus V. Vieira.
E-mail: mvvieira@biologia.ufrj.br

Table 1. Food habits of some didelphid marsupials

Species	Food habit	Reference ^a
<i>Caluromys philander</i>	Omnivorous – frugivorous	1, 2
<i>Micoureus demerarae</i>	Omnivorous – insectivorous	1, 2
<i>Marmosops incanus</i>	Omnivorous – insectivorous	2, 3, 4
<i>Didelphis aurita</i>	Omnivorous	1, 2, 5, 6
<i>Philander frenata</i>	Omnivorous – carnivorous	2, 7
<i>Metachirus nudicaudatus</i>	Omnivorous – insectivorous	2, 5, 6

^a 1, Leite *et al.* (1996); 2, Astúa de Moraes *et al.* (in press); 3, Fonseca & Kierulff (1989); 4, Stallings (1989); 5, Santori *et al.* (1995a); 6, Freitas *et al.* (1997); 7, Santori *et al.* (1995b).

in the understorey, usually of the genus *Marmosa* or *Marmosops*. Species of *Philander* were more terrestrial than *Didelphis*, but captured occasionally in the understorey. The more terrestrial species was *Metachirus nudicaudatus*.

There may be more subtle differences in the vertical use of the forest by these species that could contribute to resource partitioning, such as the use of different support diameters and inclines (Charles-Dominique *et al.*, 1981). Indeed, size and shape differences between didelphids suggest that segregation along the vertical strata is more complex than simply arboreal vs terrestrial habits. Size differences alone could limit the climbing ability of different species (M. V. Vieira, 1997). Besides, differences in shape between didelphids do exist, and suggest different degrees of adaptation for climbing (M. V. Vieira, 1997; Lemelin, 1999). Accordingly, the relative long claws and broad foot of *Didelphis aurita* compared to *Philander frenata* could be a specialization for climbing in *D. aurita* (M. V. Vieira, 1997), and the length of the digits relative to palm and sole breadth also suggest varying degrees of climbing specialization in didelphids (Lemelin, 1999).

Studies based only on traps at two or three heights are not able to detect subtle differences in the vertical use of the forest. Traps do not reveal how animals climb to or move through upper strata of the forest. Besides, baits attract animals away from their natural path, introducing an unknown amount of error. Detailed studies of the vertical use of space by didelphids require alternative methods, such as direct observation combined with radio-tracking (Charles-Dominique *et al.*, 1981; Atramentowicz, 1982; Charles-Dominique, 1983) and spool-and-line (Miles, Souza & Póvoa, 1981; Boonstra & Craine, 1986), providing a detailed picture of the path of the animal on the ground and in the vertical strata of the forest.

Our first objective was to detail the vertical use of the forest by four didelphids of a local assemblage in the Atlantic forest ('Mata Atlântica') of Brazil, using a spool-and-line technique: *Didelphis aurita* (Wied-Neuwied, 1826), *Philander frenata* (Olfers, 1818), *Metachirus nudicaudatus* (Desmarest, 1817), and *Marmosops incanus* (Lund, 1840). Second, we compared the stratification of didelphids in this assemblage with other assemblages in the literature. Our hypothesis of stratifi-

cation is that *D. aurita* uses the canopy more frequently than the others, that *M. incanus* uses the understorey more frequently, that *P. frenata* is more terrestrial than *D. aurita*, and that *M. nudicaudatus* is strictly terrestrial. We further hypothesize that these species use different support diameters and inclines, and differ in the distance moved above ground and in their use of fallen logs and trunks.

MATERIAL AND METHODS

Study area

The area is in the coastal forest of the Serra do Mar, a subdivision of the Atlantic forest biome (Dinerstein *et al.*, 1995), located in the mountain range of Serra dos Órgãos, in the Parque Nacional da Serra dos Órgãos (PARNA/SO), in the municipality of Guapimirim, state of Rio de Janeiro, Brazil, locally known as Garrafão (22°28'28", 42°59'86"W). The forest of the region is part of one of the largest continuous stretches of Atlantic forest remaining (SOS Mata Atlântica/INPE/ISA, 1998). Canopy reaches 20–25 m, with diameter of trees varying from 40 to 60 cm, sometimes reaching 1 m. A sub-canopy and understorey are present, but generally it is not possible to distinguish them clearly. Lianas, palm trees, epiphytes, ferns, and bromeliads are frequent. Common tree species belong to the genera *Sloanea*, *Ficus*, *Cedrela*, *Cariniana*, *Vochysia*, *Cecropia*, among others. Common species of the sub-canopy and understorey include tree ferns of the genera *Alsophila*, *Cyathea*, and *Hemitelia*, and the palm tree *Euterpe edulis* (Rizzini, 1979). Currently, the area is surrounded by holiday houses that could have some influence on the structure and composition of the forest (Freitas, 1998).

Trapping and handling of animals

Animals were captured in bi-monthly trapping sessions of 5 consecutive nights each, from January 1998 to June 2000, as part of a mark-recapture study of small mammal populations of the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro. The 4 species studied were the more abundant didelphid marsupials during the period of study. Of the 72 individuals of these species tracked, there were 19 males and 16 females of *Didelphis aurita* ($x = 928$ g, $SD = 462$), 8 males and 5 females of *Philander frenata* ($x = 292$ g, $SD = 155$), 9 males and 10 females of *Metachirus nudicaudatus* ($x = 391$ g, $SD = 123$), and 3 males and 2 females of *Marmosops incanus* ($x = 95$ g, $SD = 50$). Three other species occur in the area, but were not included in the study because of their scant captures: *Micoureus demerarae*, *Caluromys philander* and *Gracilinanus agilis*. These species are captured mostly in the canopy, but traps were set in the canopy only after June 2000.

Three grids of 0.64 ha were established in the area at altitudes of 748 m, 652 m and 522 m. Each grid had 25

Table 2. Variables measured along the path of the animals to characterise the use of the vertical strata of the forest

Number of climbing up movements / total thread recovered (m)	NCLIMB
Total above-ground movement approximately horizontal (m) / total thread recovered (m)	MOVEABOVE
Total movement on fallen logs (m) / total thread recovered (m)	MOVELOG
Diameter of supports used for climbing up	DIAMUP
Diameter of supports used for climbing down	DIAMDOWN
Diameter of supports used for above-ground movements approximately horizontal	DIAMABOVE
Diameter of fallen logs and trunks used	DIAMLOG
Incline in degrees of supports used for climbing up	INCLUP
Incline in degrees of supports used for climbing down	INCLDOWN
Maximum height reached in a climbing up movement	MAXHT

trapping stations 20 m apart, 2 traps/station, 1 Tomahawk (41 × 14 × 14 cm) and 1 Sherman (30.5 × 9.8 × 8 cm), both on the ground. After identification, marking with ear-tags if necessary, and measuring, some animals were equipped with a spool-and-line device based on Boonstra & Craine (1986). Anaesthetics were not necessary because the animals were handled quickly and without harm. Quilting cocoons no. 5 or no. 10 of nylon thread were used (Culver Textiles Corp., New York) weighing *c.* 1.7 g (175 m of thread) and 4.5 g (480 m of thread), respectively. The size of the cocoon used depended on the size of animal: the small cocoon was used for all *Marmosops incanus* and young of the other species, whereas the large cocoon was used for adult *Philander frenata*, *Metachirus nudicaudatus* and *Didelphis aurita*. Cocoons of 5 colours were used to facilitate the identification of threads of different individuals in the field. Colours were also used to find the other end of the thread when it broke. The cocoon was covered with heat-shrinking plastic, and wrapped with masking tape to form the spool. The spool was attached to the fur between the shoulders with Superbond, an ester-cyanocrylate based glue. Any marks of cocoon or glue had disappeared in animals recaptured 1 or 2 trapping sessions later. Most animals were tracked the next day after release, although some were tracked on the same day of release to locate their nest with certainty. In these cases, tracking began at least 1 h after release of the animal to avoid disturbance, and continued the next day starting from the nest.

Data analyses

The use of vertical strata by each species was compared first by the frequency of individuals with at least 1 climbing up movement, 1 above-ground movement approximately horizontal, and 1 movement on fallen logs. Complementarily, the use of vertical strata by each individual was characterized by measuring 10 variables along its paths (Table 2). Diameter and incline of support were measured for each support used in a climbing up or down movement. An individual could use > 1 support when climbing up or down, and could climb up and down more than once along its path. Total displacement on and above ground was calculated by multiplying the weight (g) of thread collected by the ratio of total cocoon thread (m) to cocoon weight (g).

The frequency of individuals with at least 1 climbing up movement, 1 above-ground movement, and 1 movement on fallen logs was compared with a *G*-test (Sokal & Rohlf, 1995). The significance of differences among variables of Table 2 was tested with the Kruskal–Wallis test for 3 variables (*H*-statistic) or the Mann–Whitney test for 2 variables (*U*-statistic). These non-parametric tests are appropriate for these variables, whose measurement confirms that 1 value is higher than another, but not accurately by how much. Significance of *a posteriori* pair-wise comparisons was tested with Dunn's test for pair-wise comparisons (*T*-statistic; Dunn 1964, in Neave & Worthington, 1988).

RESULTS

In *M. nudicaudatus*, only one out of 19 individuals (5%) had an above-ground movement (1 m high) after 3200 m of thread recovered. The opposite occurred in *M. incanus*, where all individuals had above-ground movements (Table 3). Hence, *M. nudicaudatus* was excluded in comparisons between species involving above-ground movements. The other three species are hereafter denominated scansorial. Most individuals of *D. aurita* and *P. frenata* had above-ground movements, but not all (Table 3). The use of logs was proportional to the use of vertical strata, *M. incanus* using logs more frequently, and *M. nudicaudatus* using them less frequently (Table 3). However, the frequency of these above-ground movements did not differ significantly between species in *G*-tests (Table 3).

Species differed significantly from each other in all variables except for MOVELOG and DIAMLOG (all $H > 7.209$, $P < 0.030$). The difference in DIAMLOG was only marginally significant ($H = 5.783$, $P = 0.055$), and was not significant in MOVELOG ($H = 0.674$, $P = 0.714$).

Along the path of animals, *M. incanus* moved more frequently above ground than the other species, either climbing up more frequently (NCLIMB) or moving longer distances above ground (MOVEABOVE) (Table 4). *Didelphis aurita* and *P. frenata* moved above the ground with a similar frequency (Table 4). Values of *M. incanus* compared to the other species were significantly higher for NCLIMB, for MOVEABOVE compared to *D. aurita*, and marginally significant for MOVEABOVE compared to *P. frenata* (Table 5).

Table 3. Proportion of individuals with at least one above-ground movement per species of didelphid marsupial. Number of individuals is in parenthesis. *G* statistic and associated probability of the *G*-test

Category of above-ground movements	<i>Didelphis aurita</i> (35)	<i>Marmosops incanus</i> (5)	<i>Metachirus nudicaudatus</i> (19)	<i>Philander frenata</i> (13)	<i>G</i>	<i>P</i>
Climbing up	0.60	1.0	0.05	0.54	3.27	0.19
Horizontal	0.49	1.0	0.00	0.46	4.81	0.09
On fallen logs	0.34	0.60	0.16	0.31	1.34	0.51

Table 4. Median of variables measured along the path of each animal per species of didelphid marsupial. Values are relative to 100 m of the path of an animal. Minimum and maximum values are in parentheses. See Table 2 for a description of the variables

	<i>Didelphis aurita</i> <i>n</i> = 24	<i>Marmosops incanus</i> <i>n</i> = 5	<i>Metachirus nudicaudatus</i> <i>n</i> = 5	<i>Philander frenata</i> <i>n</i> = 8
NCLIMB (frequency)	1.25 (0.00–7.92)	4.87 (2.47–30.13)	0.00 (0.00–1.82)	1.16 (0.00–2.51)
MOVEABOVE (%)	2.06 (0.00–47.51)	14.66 (4.93–49.69)	0.00 (0.00–0.00)	3.24 (0.00–14.84)
MOVELOG (%)	0.06 (0.00–39.43)	2.62 (0.00–15.76)	1.50 (0.00–6.35)	0.66 (0.00–13.67)

Table 5. Comparisons between species in the variables measured along the path of animals. Values are Dunn statistic [*T*], and associated probability. Bold, significant values. See Table 2 for a description of the variables

Variable	<i>D. aurita</i> vs <i>P. frenata</i>	<i>D. aurita</i> vs <i>M. incanus</i>	<i>P. frenata</i> vs <i>M. incanus</i>
NCLIMB	0.15 <i>P</i> > 0.30	2.66 <i>P</i> < 0.05	2.40 <i>P</i> < 0.05
MOVE-ABOVE	0.04 <i>P</i> > 0.30	2.60 <i>P</i> < 0.05	2.27 0.05 < <i>P</i> < 0.10
DIAMUP	0.87 <i>P</i> > 0.30	2.28 0.05 < <i>P</i> < 0.10	2.60 <i>P</i> < 0.05
DIAM-DOWN	1.10 <i>P</i> > 0.30	2.89 <i>P</i> < 0.05	1.21 <i>P</i> > 0.30
DIAM-ABOVE	0.50 <i>P</i> > 0.30	3.33 <i>P</i> < 0.05	2.18 0.05 < <i>P</i> < 0.10
INCLUP	2.13 0.05 > <i>P</i> < 0.10	4.25 <i>P</i> < 0.05	0.94 <i>P</i> > 0.30
INCLDOWN	1.09 <i>P</i> > 0.30	3.04 <i>P</i> < 0.05	1.28 <i>P</i> > 0.30
MAXHT	2.41 <i>P</i> < 0.05	7.24 <i>P</i> < 0.05	1.64 0.25 < <i>P</i> < 0.30

Philander frenata and *D. aurita* did not differ significantly in NCLIMB or MOVEABOVE (Table 5).

Within each scansorial species, there was no difference between the diameter of supports used for climbing up (DIAMUP), climbing down (DIAMDOWN), and for horizontal movements above ground (DIAMABOVE) (*D. aurita*: *H* = 0.213, *P* = 0.899; *M. incanus*: *H* = 0.134, *P* = 0.935; *P. frenata*: *H* = 2.499, *P* = 0.294). The incline of supports used for climbing up (INCLUP) and for climbing down (INCLDOWN) did not differ either (*D. aurita*: *U* = 1310.5, *P* = 0.485; *M. incanus*: *U* = 1096.5, *P* = 0.936; *P. frenata*: *U* = 199.5, *P* = 0.966).

Species differed significantly in the diameter of support used, although all used the thinnest supports more frequently for climbing up, down, and for hori-

zontal movements above ground (Fig. 1a–c). *Didelphis aurita* used large supports (> 12 cm) more frequently, whereas *M. incanus* used thin supports (< 3 cm) more frequently (Fig. 1a–c). The diameter of supports used more frequently by *P. frenata* were intermediate between those of the other two species. Accordingly, *D. aurita* and *M. incanus* differed significantly in DIAMABOVE and DIAMDOWN, and marginally significant in DIAMUP (Table 5). *Philander frenata* and *M. incanus* differed significantly in DIAMUP, and marginally significant in DIAMABOVE (Table 5). *Didelphis aurita* climbed trunks as large as 1 m diameter, whereas the largest trunks climbed by *P. frenata* were 0.20 m diameter. Nevertheless, these two species did not differ significantly in the diameter of any support used (all $|T| < 1.097$, *P* > 0.300 in Table 5).

In the incline used (Fig. 2 a, b), nearly vertical supports (incline > 75°) were more frequently used by *D. aurita*, followed by *P. frenata* and *M. incanus*. Lower inclines were more frequently used by *M. incanus*. Accordingly, *D. aurita* differed significantly from *M. incanus* in INCLUP, INCLDOWN, and marginally significantly from *P. frenata* in INCLUP (Table 5). *Philander frenata* and *M. incanus* did not differ from each other (Table 5).

Maximum heights (MAXHT) also differed significantly between species (Fig. 2 c). Heights reached by *D. aurita* were significantly higher than heights reached by *P. frenata* and *M. incanus* (Table 5). *Marmosops incanus* did not differ significantly from *P. frenata* in this variable (Table 5). The maximum value of MAXHT for each species was 20 m for *D. aurita*, 10 m for *M. incanus*, and 8 m for *P. frenata*.

DISCUSSION

The exclusively terrestrial way of life of *Metachirus*

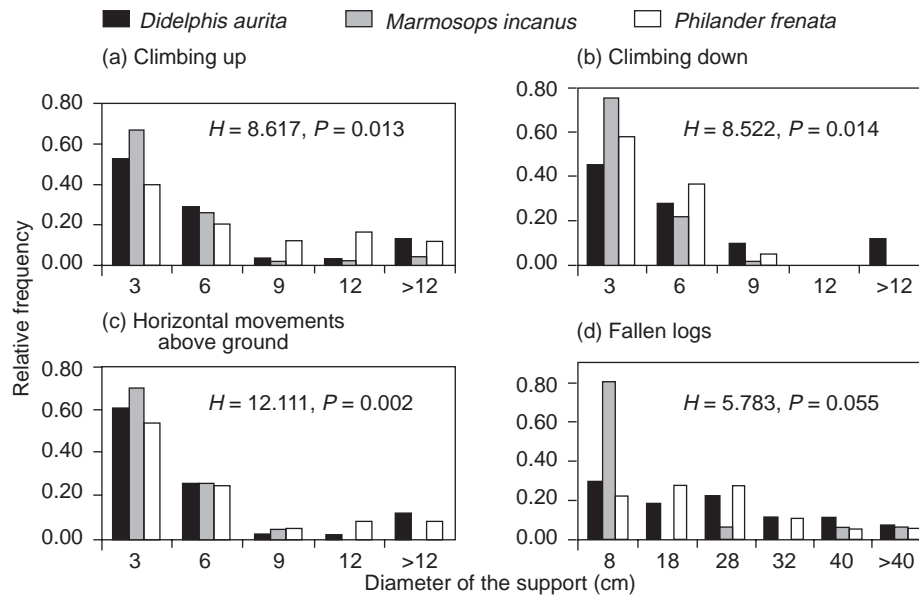


Fig. 1. Frequency distributions of diameter supports used by the three scansorial didelphids. Statistics are Kruskal–Wallis H and associated probability of differences between species.

nudicaudatus was confirmed. Miles *et al.* (1981) demonstrated the terrestrial habits of *M. nudicaudatus* using a spool-and-line device. In this study, only one above-ground movement was observed, when the thread suddenly left the ground, reached 1 m height held by a sapling, and went back to the ground level. Considering the cursorial adaptations of this species and its jumping ability (Szalay, 1994), this observation could be the result of an unusual jump.

The prevalent use of thin supports by the three scansorial didelphids accords with the specialization for grasping of this group, and probably results from their grasping hallux (Cartmill, 1974; Hildebrand, 1988; Lemelin, 1999). Arboreal or semi-terrestrial didelphids, such as species of *Marmosops* and *Didelphis*, move above ground mostly by distributing their body mass on different supports, each limb and the tail holding a different support. In this sense, the prehensile tail functions as a fifth limb (Enders, 1935; McManus, 1970; Cartmill, 1974; Lemelin, 1999). Thin supports were used more frequently even in above-ground movements, when large supports could be considered more stable. Within this major trend there were differences that follow a body size gradient. The large species, *Didelphis aurita*, used large supports more frequently than the others, and the small species, *Marmosops incanus*, used thin supports more frequently (Fig. 1 a–c). *Philander frenata* was intermediate in size and in diameter of support used. However, this positive association between diameter of support and body size was not clear in a structurally similar assemblage of didelphid marsupials in French Guiana (Charles-Dominique *et al.*, 1981).

In other variables, species differed significantly but did not follow such a body size trend. The inclines used were more related to the dominant direction of above-

ground movement. *Marmosops incanus* was the species most frequently moving above ground, as revealed by the prevalence and intensity of above-ground movements. However, it rarely reached the canopy, moving more horizontally along the understory than the other species. Accordingly, *M. incanus* used low inclines more frequently than the other species. *Didelphis aurita* did not move above ground as frequently as *M. incanus*, but when it did, it reached the canopy more frequently (Fig. 2c), using vertical supports more frequently as well (Fig. 2a, b). *Didelphis aurita* is capable of claw-climbing (*sensu* Szalay, 1994) more than the other species because of its relatively larger claws and the long forelimbs (M. V. Vieira, 1997). This could be the reason for the more frequent use of vertical supports by *D. aurita*. *Philander frenata* moved above ground as frequently as *D. aurita*, but never climbed higher than the understory. Inclines used by *P. frenata* were intermediate between the other two scansorial didelphids. Similarly, in French Guiana (Charles-Dominique *et al.*, 1981), *Philander opossum* seems to have used vertical supports more frequently than the understory species, *Marmosa murina*, which is possibly ecologically equivalent to *M. incanus* in our study site.

The hypothesis of stratification was supported, suggesting a common structure to most didelphid assemblages in the Atlantic forest and in the Amazon. *Marmosops incanus* was the species of the understory, *D. aurita* and *P. frenata* were more terrestrial, but *D. aurita* reached the canopy whereas *P. frenata* reached only the understory. In the Atlantic forest, *M. incanus* is the more common species of the understory (Fonseca & Kierulff, 1989; Stallings, 1989; Passamani, 1995; Palma, 1996; Grelle, in press). In the Amazon, other species occupy the understory, such as *Marmosa murina*, *Marmosa parvidens* and *Marmosops noctivagus*

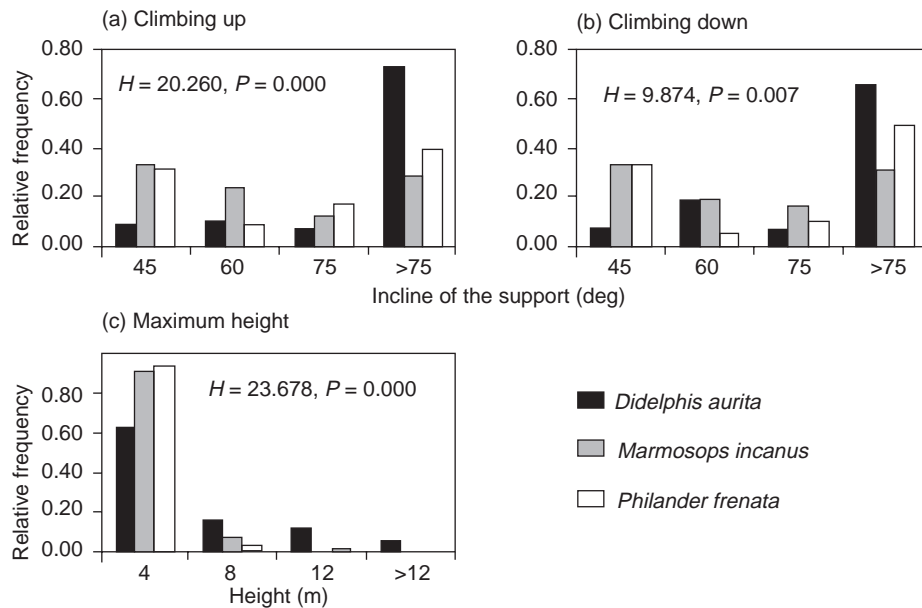


Fig. 2. Frequency distributions of incline of support and maximum height reached by the three scansorial didelphids. Statistics are Kruskal–Wallis H and associated probability of differences between species.

(Charles-Dominique *et al.*, 1981; Terborgh *et al.*, 1984; Janson & Emmons, 1991; Julien-Laferrière, 1991; Malcolm, 1991; Voss & Emmons, 1996). Although not included in our study, *Micoureus demerarae*, *Caluromys philander* and *Gracilinanus agilis* are species of the canopy present in Garrafão and in almost all assemblages of small mammals.

Partitioning of the vertical strata could be more intense when *D. aurita* and *P. frenata* occur in syntopy. *Didelphis aurita* is a potential competitor of *P. frenata* because of their overlap in food preferences (Perissé & Cerqueira, 1988), in geographic distribution (Cerqueira, 1985; Patton & Silva, 1997), and in the use of vertical strata (this study). Also, *D. aurita* may also prey occasionally on *P. frenata* (Wilson, 1970). *Didelphis aurita* used the canopy more frequently in sites where *P. frenata* was present (E. M. Vieira, 1999) than in sites where *P. frenata* did not occur (Stallings, 1989; Grelle, in press). *Philander frenata* used the understory where *D. aurita* was present, but stayed on the ground where *D. aurita* was not present (E. M. Vieira, 1999). In this study, the two species occurred in the same site. *Didelphis aurita* used the ground, the understory, and the canopy, whereas *P. frenata* used the ground and the understory as similarly observed in E. M. Vieira (1999).

Fruit consumption is also related to vertical stratification in didelphids. Species living in the canopy, such as *Caluromys philander*, are more frugivorous than species of the understory, which are more frugivorous than semi-terrestrial and terrestrial species (Charles-Dominique *et al.*, 1981; Atramentowicz, 1982; Julien-Laferrière, 1991; Malcolm, 1995). Accordingly, *D. aurita* and *M. incanus* consume fruits proportionally more than *M. nudicaudatus* and *P. frenata*, which are more insectivorous and carnivorous, respectively

(Santori, Astúa de Moraes & Cerqueira, 1995; Santori, Cerqueira & Kleske, 1995; Freitas *et al.*, 1997; Astúa de Moraes *et al.*, in press). This close association between vertical stratification and food habits further demonstrates that vertical stratification is an important mechanism of species coexistence in didelphids. The increasing complexity of vertical strata in tropical forests probably increases the richness of didelphid species.

The spool-and-line method allowed a meticulous and accurate picture of the use of vertical strata by didelphids, at least for terrestrial and scansorial species. Meticulous because the spool-and-line quantifies the proportion of movement in each stratum, the distances the animal moves continuously in strata before climbing up or down, and the characteristics of the supports used. Studies using traps at three heights generally agreed with ours, but give a much more general description. Accurate because the spool-and-line method is free from the bias inherent to studies using traps and baits, i.e. baits attract an animal away from its chosen path, support or vertical stratum. For example, a terrestrial animal might seem occasionally to use the understory, when it might in fact have climbed up only to reach a 2 m high trap. In addition, animals trapped from 6 to 15 m in the same study are all placed in the 'canopy' category (e.g. E. M. Vieira, 1998). There are drawbacks, though. One is that canopy species are difficult to track because the thread cannot be followed for very long by an observer on the forest floor, usually losing the thread close to the point of release. Another is the limited time that an animal can be followed, only a couple of nights if the animal is recaptured and equipped with a new cocoon. Miles *et al.* (1981) also reported line breakage in >30% of all observations. Line breakage is always a problem when it occurs in the first metre of line, which

occurred infrequently in our study. An alternative to spool-and-line is direct observation combined with radio-tracking (e.g. Charles-Dominique *et al.*, 1981).

Concluding, each of the four didelphids used the vertical strata uniquely, but the pattern of stratification is similar to that observed in other neotropical sites. *Marmosops incanus* moved predominantly in the understorey, occasionally on the ground, but never reached the canopy. *Didelphis aurita* was the only species using the canopy, but it moved predominantly on the ground. *Philander frenata* also moved predominantly on the ground, occasionally climbing, but never higher than the understorey. *Metachirus nudicaudatus* was the specialized terrestrial member of the group, never leaving the forest floor. All species preferred similar diameter and inclines of supports, but the diameter was positively related to body size, whereas the incline was related to dominant direction of movement (vertical vs horizontal). Classifications of didelphids as arboreal or terrestrial are too simple, precluding the visualization of differences between species in assemblages. Quantitative measures of the vertical use of the forest unravel these differences, which are likely to be important for local coexistence and species richness.

Acknowledgements

Many students of the Laboratório de Vertebrados helped in the fieldwork, capturing animals, helping in tracking and mapping their path, but we are especially grateful to Alice C. Capparelli, Ana C. Delciellos, Diogo Loretto, Fábio Pedreira, Joana Macêdo, Maíra Moura, Maycon G. Belarmino, Rosana Gentile, Sylvia M. Mendel, Vanina Z. Antunes and Vitor Rademaker. Ângela Marcondes and Nélio Pereira are thanked for their dedication in the office and laboratory work. Drs Rui Cerqueira, Carlos E. Grelle and Simone R. Freitas, and anonymous reviewers made invaluable comments on earlier versions of this manuscript. This research was funded by PROBIO (MMA-GEF), CNPq (PIBIC, PIE, PRONEX), FUJB, FAPERJ.

REFERENCES

- Astúa de Moraes, D., Santori, R. T., Finotti, R. & Cerqueira, R. (In press). Nutritional and fiber contents of laboratory-established diets of neotropical opossums (Didelphimorphia, Didelphidae). In *Predators with pouches: the biology of carnivorous marsupials*. Jones, M., Dickman, C. & Archer, M. (Eds).
- Atramentowicz, M. (1982). Influence du milieu sur l'activité locomotrice et la reproduction de *Caluromys philander* (L.). *Rev. Ecol.* **36**: 373–395.
- August, P. V. (1983). Heterogeneity in structuring tropical mammal communities. *Ecology* **64**: 1495–1507.
- Boonstra, R. & Craine, I. T. M. (1986). Natal nest location and small mammals tracking with a spool and line technique. *Can. J. Zool.* **64**: 1034–1036.
- Cartmill, M. (1974). Pads and claws in arboreal locomotion. In *Primate locomotion*: 45–83. Jenkins, F. A. Jr (Ed.). New York: Academic Press.
- Cerqueira, R. (1985). The distribution of *Didelphis* in South America (Polyprotodontia, Didelphidae). *J. Biogeogr.* **12**: 135–145.
- Charles-Dominique, P. (1983). Ecology and social adaptations in didelphid marsupials: comparison with eutherians of similar ecology. *Am. Soc. Mammal. Spec. Publ.* **7**: 395–422.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladir, C. M. & Prévost, M. F. (1981). Les memifères frugivores arboricoles nocturnes d'une forêt guyanaise: Inter-relations plantes–animaux. *Rev. Ecol.* **35**: 341–435.
- Dinerstein, E., Olson, D. M., Graham, D. J., Webster, A. L., Primm, S. A., Bookbinder, M. P. & Ledec, G. (1995). *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. Washington, DC: WWF & World Bank.
- Enders, R. K. (1935). Mammalian life histories from Barro Colorado Island, Panama. *Bull. Mus. Comp. Zool. Harvard Univ.* **78**: 383–502.
- Fonseca, G. A. B. & Kierulff, M. C. M. (1989). Biology and natural history of Brazilian Atlantic forest small mammals. *Bull. Fla State Mus. Biol. Sci.* **34**: 99–152.
- Freitas, S. R. (1998). *Variação espacial e temporal na estrutura do habitat e preferência de microhabitat por pequenos mamíferos na Mata Atlântica*. Unpubl. MSc thesis, Museu Nacional do Rio de Janeiro, Brazil.
- Freitas, S. R., Astúa de Moraes, D., Santori, R. T. & Cerqueira, R. (1997). Habitat preference and food use by *Metachirus nudicaudatus* and *Didelphis aurita* in a restinga forest at Rio de Janeiro. *Rev. Brasil. Biol.* **57**: 93–98.
- Grelle, C. E. V. (In press). Forest structure and vertical stratification of small mammals in southeast Brazil. *Stud. Neotrop. Fauna Environ.*
- Hildebrand, M. (1988). *Analysis of vertebrate structure*. 3rd edn. New York: John Wiley.
- Janson, C. H. & Emmons, L. H. (1991). Ecological structure of the nonflying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. In *Four neotropical rainforests*: 314–338. Gentry, A. (Ed.). New Haven: Yale University Press.
- Julien-Laferrrière, D. (1991). Organisation du peuplement de marsupiaux en Guyane Française. *Rev. Ecol.* **46**: 125–144.
- Leite, Y. L. R., Costa, L. P. & Stallings, J. R. (1996). Diet and vertical space use of three sympatric opossums in a Brazilian Atlantic forest reserve. *J. trop. Ecol.* **12**: 435–440.
- Lemelin, P. (1999). Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J. Zool. (Lond.)* **247**: 165–176.
- Malcolm, J. R. (1991). Comparative abundance of neotropical small mammals by trap height. *J. Mammal.* **72**: 188–192.
- Malcolm, J. R. (1995). Forest structure and the abundance and diversity of neotropical small mammals. In *Forest canopies*: 179–197. Lowman, M. D. & Nadkarni, N. M. (Eds). San Diego: Academic Press.
- McManus, J. J. (1970). Behavior of captive opossums, *Didelphis marsupialis virginiana*. *Am. Midl. Nat.* **84**: 144–169.
- Miles, M. A., Souza, A. A. de & Póvoa, M. M. (1981). Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. *J. Zool. (Lond.)* **195**: 331–347.
- Neave, H. R. & Worthington, P. L. (1988). *Distribution-free tests*. Boston: Unwin Hyman.
- Palma, A. R. T. (1996). *Separação de nichos entre pequenos mamíferos de Mata Atlântica* Unpubl. MSc thesis, Universidade Estadual de Campinas, Campinas, Brasil.
- Passamani, M. (1995). Vertical stratification of small mammals in Atlantic Hill Forest. *Mammalia* **59**: 276–279.
- Patton, J. L. & Silva, M. N. F. (1997). Definition of species of pouched four-eyed opossums (Didelphidae, *Philander*). *J. Mammal.* **78**: 90–102.

- Perissé, M. & Cerqueira, R. (1988). A alimentação na separação de nicho entre *Philander opossum* e *Didelphis aurita* (Polyprotodontia, Didelphidae). *An. Sem. Reg. Ecol.* **6**: 283–294.
- Richards, P. W. (1996). *The tropical rain forest*. 2nd edn. Cambridge: Cambridge University Press.
- Rizzini, C. T. (1979). *Tratado de Fitogeografia do Brasil: Aspectos sociológicos e florísticos*. São Paulo, Brasil: Hucitec Ltda. e Editora da Universidade de São Paulo.
- 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., Cerqueira, R. & Kleske, C. C. (1995). Anatomia e eficiência digestiva de *Philander opossum* e *Didelphis aurita* (Didelphimorphia, Didelphidae) em relação ao hábito alimentar. *Rev. Brasil. Biol.* **55**: 323–329.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. 3rd edn. New York: W. H. Freeman.
- SOS Mata Atlântica/INPE/ISA. (1998). *Atlas da Evolução dos Remanescentes Florestais e Ecossistemas Associados ao Domínio da Mata Atlântica no Período 1990–95*. SOS Mata Atlântica/INPE/ISA.
- Stallings, J. R. (1989). Small mammal inventories in an eastern Brazilian park. *Bull. Fla State Mus. Biol. Sci.* **34**: 159–200.
- Szalay, F. S. (1994). *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge: Cambridge University Press.
- Terborgh, J. W., Fitzpatrick, J. W. & Emmons, L. (1984). Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana Zool.* **21**: 1–21.
- Vieira, E. M. (1998). A technique for trapping small mammals in the forest canopy. *Mammalia* **62**: 306–310.
- Vieira, E. M. (1999). *Estudo comparativo de comunidades de pequenos mamíferos em duas áreas de Mata Atlântica situadas a diferentes altitudes no sudeste do Brasil*. Unpubl. PhD dissertation, Universidade Estadual de Campinas, Brasil.
- Vieira, M. V. (1997). Body size and form in two Neotropical marsupials, *Didelphis aurita* and *Philander opossum* (Marsupialia, Didelphidae). *Mammalia* **61**: 245–254.
- Voltolini, J. C. (1997). *Estratificação vertical de marsupiais e roedores na Floresta Atlântica do sul do Brasil*. Unpubl. MSc thesis, Universidade de São Paulo, Brasil.
- Voss, R. S. & Emmons, L. H. (1996). Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. *Am. Mus. Nat. Hist.* **230**: 1–115.
- Wilson, D. E. (1970). Opossum predation: *Didelphis* on *Philander*. *J. Mammal.* **51**: 386–387.