Journal of Tropical Ecology (2003) **19**:501–507. Copyright © 2003 Cambridge University Press
DOI:10.1017/S0266467403003559 Printed in the United Kingdom

Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil

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(*Accepted 8th October 2002*)

Abstract: Patterns of vertical stratification and canopy utilization by rodents and marsupials were analysed in two contiguous Atlantic forests at different altitudes (100 m and 900 m asl). Twenty-two species were captured using live traps placed at ground level, in the understorey (1.5–2.0 m), and in the canopy (6–15 m) over 2 y; seven species (32%) were mainly or exclusively arboreal. Community composition and relative abundance of species in the different vertical strata were not similar, with a general reduction in the number of species, and in abundance in the upper layers. The following species were captured mainly or exclusively in the canopy: *Micoureus demerarae* and *Gracilinanus microtarsus* (Didelphimorphia, Didelphidae); *Wilfredomys pictipes*, *Oecomys* aff. *concolor*, and *Rhipidomys* aff. *macrurus* (Rodentia, Muridae); and *Nelomys nigrispinus* (Rodentia, Echimyidae). Our results indicated that altitudinal changes in Atlantic forest areas may alter the community composition of different forest layers but they do not seem to alter greatly specific patterns of vertical habitat utilization. Similar-sized species tended to differ in their patterns of vertical utilization of habitat with the exception of terrestrial akodontine rodents (genera *Akodon*, *Thaptomys*, *Oxymycterus* and *Brucepattersonius*). Rodents (mainly *Oryzomys russatus*) dominated captures at ground level at both sites but Akodontinii were numerous only at the highest site. Unlike other neotropical forests, marsupials did not dominate canopy captures.

Key Words: Brazilian Atlantic Forest, canopy ecology, marsupials, rodents

INTRODUCTION

Neotropical forests are heterogeneous and complex habitats with trees ranging in height from 25 to 40 m (Kricher 1997). This high vertical complexity (August 1983) helps increase diversity, as the upper strata of such forests are occupied by many wholly arboreal organisms not occurring on the ground (Lowman & Wittman 1996). Forest canopies have been poorly studied and only recently have biologists become more aware of the importance of sampling the upper forest layers (Lowman & Moffett 1993).

Three-dimensional use of habitat by small mammals has been reported by several authors (August 1983, August & Fleming 1984, Malcolm 1991, 1995; McClearn *et al*. 1994, Meserve 1977, Stallings 1989). In neotropical forests, there are many coexisting species with similar body size and morphological characteristics (Emmons & Feer 1997) in which resource partitioning could be facilitated by vertical segregation. Nevertheless, the analysis of patterns of vertical stratification and canopy utilization by small mammals has been limited by difficulties associated with studying the top layers of the forests, as is the case for other groups of organisms, e.g. ants (Tobin 1995), lizards (Reagan 1995) and birds (Munn & Loiselle 1995). A ground-based perception may lead to inaccurate generalizations and also to biased estimates of mammal richness and abundance. The abundance of the woolly opossum *Caluromys philander* (Didelphimorphia, Didelphidae) in Amazonian forest, for example, is much higher than indicated by previous estimates based only on ground and understorey trapping (Malcolm 1991).

The Brazilian Atlantic rain forest (Mata Atlântica) is a lowland wet tropical forest with closed canopy and trees reaching 30–40 m. Although now restricted to about 5% of its original area (Fonseca 1985), this forest harbours a great mammalian richness, with at least 129 non-volant mammal species (Fonseca & Kierulff 1989). In the present study, we analysed and compared the vertical stratification of small mammals from two contiguous Atlantic forest areas at different altitudes in south-eastern Brazil. We addressed the following questions: (1) Do species use the ground, understorey and canopy of the forest in a similar way? (2) What is the species composition and relative abundance of the small-mammal community in different vertical strata of each forest?

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STUDY AREA AND METHODS

Study area

We studied two locations in Parque Estadual Intervales (PEI) located in south-eastern Brazil (24°12′ to 24°25′S; 48°03′ to 48°30′W) on the Serra de Paranapiacaba massif of southern São Paulo State, which is part of the Atlantic forest domain. The PEI is comprised primarily of well-preserved forest covering approximately 490 km^2 and ranging from 70 to 1100 m asl. Together with three other parks it forms a continuous protected area of more than 1200 km^2.

We conducted the study between September 1995 and August 1997 at two locations, Saibadela (24°14′S, 48°04′W) and Barra Grande (24°17′S, 48°21′W). The Saibadela site is an area of primary forest with an altitudinal range from 70 to 350 m. The mean annual temperature is 23 °C. The climate is very wet with no marked dry period, but most of the annual rainfall (mean of 4200 mm y^{-1}) occurs between November and February. Barra Grande is a highland site (altitude of about 900 m), and is also a primary forest, but with different vegetation, including abundant bamboos (mainly *Guadua angustifolia*, *Merostachys* spp. and *Chusquea* spp.; Olmos 1996). The mean annual temperature is 17 °C. Most of the annual rainfall (mean of 1600 mm y^{-1}) also occurs between November and February. Both sites had a canopy height of about 20–30 m, with some emergent trees. For more detailed descriptions on the vegetation see Vieira & Izar (1999).

Trapping procedures

We established two trapping grids, one in Saibadela (100 m asl) and the other in Barra Grande (900 m asl). Each grid had 12 traplines with eight trap stations spaced 20 m apart (n = 96 trap stations). The lines were 10 m apart and the entire 8 × 12 grid covered about 1.5 ha. We captured the animals with Sherman trap model XLF15 (10.4 × 12 × 38 cm) and home-made wire-mesh cage traps (15 × 15 × 30 cm).

In each trapping session we randomly selected 66 trap stations where traps were placed on the ground. After capturing an animal, a trap was moved to another station to avoid recaptures at the same trap station. Thus we were able to sample the entire grid and calculate home ranges (not discussed in the present study) without concern for subsequent captures at a same trap station. Additionally we placed 41 traps in the understorey (mean height of 1.7 m, range from 1.5 to 2.0 m), and 25 traps in the canopy of the Saibadela but only 20 at canopy stations in Barra Grande. Mean height of canopy stations was 10 m (range 6 to 15 m). Rectangular wooden boards were placed on the trees to support the understorey traps as needed. We set both trap types in the same proportion on the ground and at 1.7 m height (60% Shermans and 40% wire-mesh cage traps) but only Sherman traps in the canopy stations. Previous analysis indicated that there was no significant difference in trapping success between trap types for any studied species (E. M. Vieira, unpubl. data). Thus we could directly compare trap results for all strata. We set traps in the canopy by placing them inside wooden boxes, which were used as mobile platforms, raised and placed flush to tree branches. This method was described in detail by Vieira (1998).

Although the maximum height of the forest ranged from 20 to 30 m the canopy traps were placed below this height to maintain connectivity with adjacent canopy trees. This is a common procedure in studies focusing on forest-canopy use by small mammals (Malcolm 1991, Malcolm & Ray 2000, Stallings 1989). Although we detected differences in habitat characteristics between the ground layer and the understorey and between the understorey and the ‘canopy’ (*c*. 10 m, where canopy traps were placed), we did not detect any clear differences from 10 to 20 m above ground (i.e. the ‘canopy’ that we trapped vs. the actual forest canopy). Nevertheless, we cannot fully disregard the possibility that small-mammal assemblages in the upper canopy may differ from the lower canopy and the understorey that we sampled.

The understorey and canopy stations were evenly distributed in order to cover the entire grid area. We generally selected places connected to the canopy of neighbouring trees and also with dense upper-stratum vines and branches with aroids and bromeliads. For the canopy stations, the branches had to be parallel to the ground and generally had a diameter of 10–25 cm. Since the above-ground traps were not moved after capturing an animal, to avoid bias in the analysis caused by trap-prone individuals subsequent arboreal captures of a given animal in the same trap station in the same session were not considered in any analysis. We tried to maintain a similar trapping effort for ground and arboreal traps but we were constrained by trap availability. As it took more time to revisit canopy traps we had to limit their number to 25, otherwise we could not revisit the entire grid without exposing the captured animals to the risk of death due to prolonged detention inside the traps.

Trapping sessions lasted 6–8 consecutive nights and were conducted monthly from September 1995 to August 1997 (except in October 1995) at Saibadela (total trapping effort of 9782 trap nights on the ground, 5445 trap nights in the understorey and 2134 trap nights in the canopy), and bi-monthly from August 1996 to June 1997 at Barra Grande site (2359 trap nights on the ground, 1188 in the understorey and 638 in the canopy). Traps were checked and rebaited between 08h00 and 11h00 and remained open diurnally.

Traps were baited with a mixture of peanut butter, corn meal, mashed banana, commercial cod liver oil and vanilla essence. We noted species, location, sex and mass

https://doi.org/10.1017/S0266467403003559 Published online by Cambridge University Press

of every captured animal. Newly captured animals were ear tagged and after data collection released at the point of capture. Voucher specimens of all species studied were deposited in the Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil, and in the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC), Campinas, Brazil. Nomenclature of the animal species follows Wilson & Reeder (1993).

Data analysis

To answer the first question we compared the observed number of captures of each species to the expected number of captures for each stratum (ground, understorey and canopy) based on the total trapping effort for each stratum. The null hypothesis was that animals were evenly distributed in vertical space and would be captured in proportion to the number of trap-nights per layer. When the number of captures was low (< 16) we pooled captures at 1.7-m and canopy-level traps and performed Fisher's exact tests for comparison of captures at ground level to those above ground. We performed statistical tests only when total number of captures was greater than 10.

An analysis of more than 20 studies on small mammals in Atlantic forest areas (Vieira 1999) indicated that the overall trapping effort used in this study was sufficient for a reliable estimate of community composition in each stratum of both areas. We compared the captures in different strata of distinct taxonomic groups at the Saibadela and Barra Grande sites to contrast the potential effects of altitude on species composition and arboreality. We performed a three-factor analysis of variance to analyse the effects of site, vertical stratum and taxonomic group on overall capture probability, where the dependent variable was the total number of captures in each trap station. For this analysis the original data were log-transformed after adding 0.1 to remove zeros from the dataset (Zar 1996). We compared data from Barra Grande site with data collected at the Saibadela site during the same months that the former site was sampled, thus equating trapping effort in both areas. The low capture rates in arboreal traps precluded an analysis of seasonal patterns.

RESULTS

At Saibadela site, we recorded 1269 captures of 276 individuals at ground level (trapping success of 13.0%), 112 captures of 44 individuals in the understorey (2.1%) and 34 captures of 18 individuals in the canopy (1.6%). We captured four marsupial species in the Saibadela site (Figure 1). *Metachirus nudicaudatus* was exclusively terrestrial and *Philander frenata* did not show significant difference between ground and understorey utilization (Fisher test, $P > 0.6$). *Micoureus demerarae* and *Didelphis aurita* occurred in the three strata but only the former species used the canopy significantly more often ($\chi^2 = 20.7$, $P < 0.001$) whereas *D. aurita* appeared to use the three strata similarly ($\chi^2 = 4.65$, $P > 0.09$). A fifth marsupial species, the short-tailed opossum (*Monodelphis americana*), was observed on the ground but never captured.

We captured seven species of rodent at Saibadela. Two of these, *Wilfredomys pictipes* and *Oecomys* sp., were primarily arboreal. Although *W. pictipes* apparently concentrated its activity in the canopy the difference between ground and above-ground captures for this species was not significant (Fisher's test, $P > 0.3$). The other arboreal species, *Oecomys* aff. *concolor*, also was captured in all strata, but occurred significantly more often in the understorey ($\chi^2 = 20.8$, $P < 0.001$). We also captured the rodent *Oligoryzomys nigripes* in the three strata without significant difference between ground and above-ground captures (Fisher's test, $P > 0.8$). The other four rodent species were mainly or exclusively terrestrial. We captured *Nectomys squamipes* and *Oryzomys russatus* both on the ground and in the understorey, but these species were caught significantly more often on the ground (*N. squamipes*: $\chi^2 = 80.7$, $P < 0.001$; *O. russatus*: $\chi^2 = 335$, $P < 0.001$). *Akodon serrensis* and *Trinomys iheringi* were captured exclusively on the ground (Figure 1). Additionally, we observed the squirrel *Sciurus ingrami* (Sciuridae) in both the understorey and the canopy, but this species was not captured.

At Barra Grande we recorded 152 captures of 98 individuals at ground level (trapping success of 6.4%), 14 captures of nine individuals in the understorey (1.2%) and 30 captures of 22 individuals in the canopy (4.7%). We also captured four marsupials at this site (Figure 1). *Philander frenata* and *Monodelphis americana* were captured exclusively at ground level. The other two species, *Marmosops paulensis* and *Gracilinanus microtarsus* were captured only at Barra Grande. They occurred both on the ground and in arboreal traps, but only the latter was captured significantly more in the canopy ($\chi^2 = 14.5$, $P < 0.001$). On the other hand *M. paulensis* was not captured in the canopy and did not show significant difference between ground and understorey captures (Fisher's test, $P > 0.3$).

We captured four rodent species exclusively in the canopy of the Barra Grande site, these were the murids *W. pictipes*, *Oecomys* sp., *Rhipidomys* aff. *macrurus* and the echimyid *Nelomys nigrispinus*. The other eight rodent species captured were essentially terrestrial murids (Figure 1). Only *Akodon serrensis* had one capture above ground, but it occurred in a trap placed on a trunk that could be easily accessed from the ground via a fallen log. At this area we also observed but failed to capture the squirrel (*S. ingrami*) in the arboreal strata, both in the understorey and the canopy.

Both sites showed marked differences among taxonomic groups in relation to vertical habitat utilization

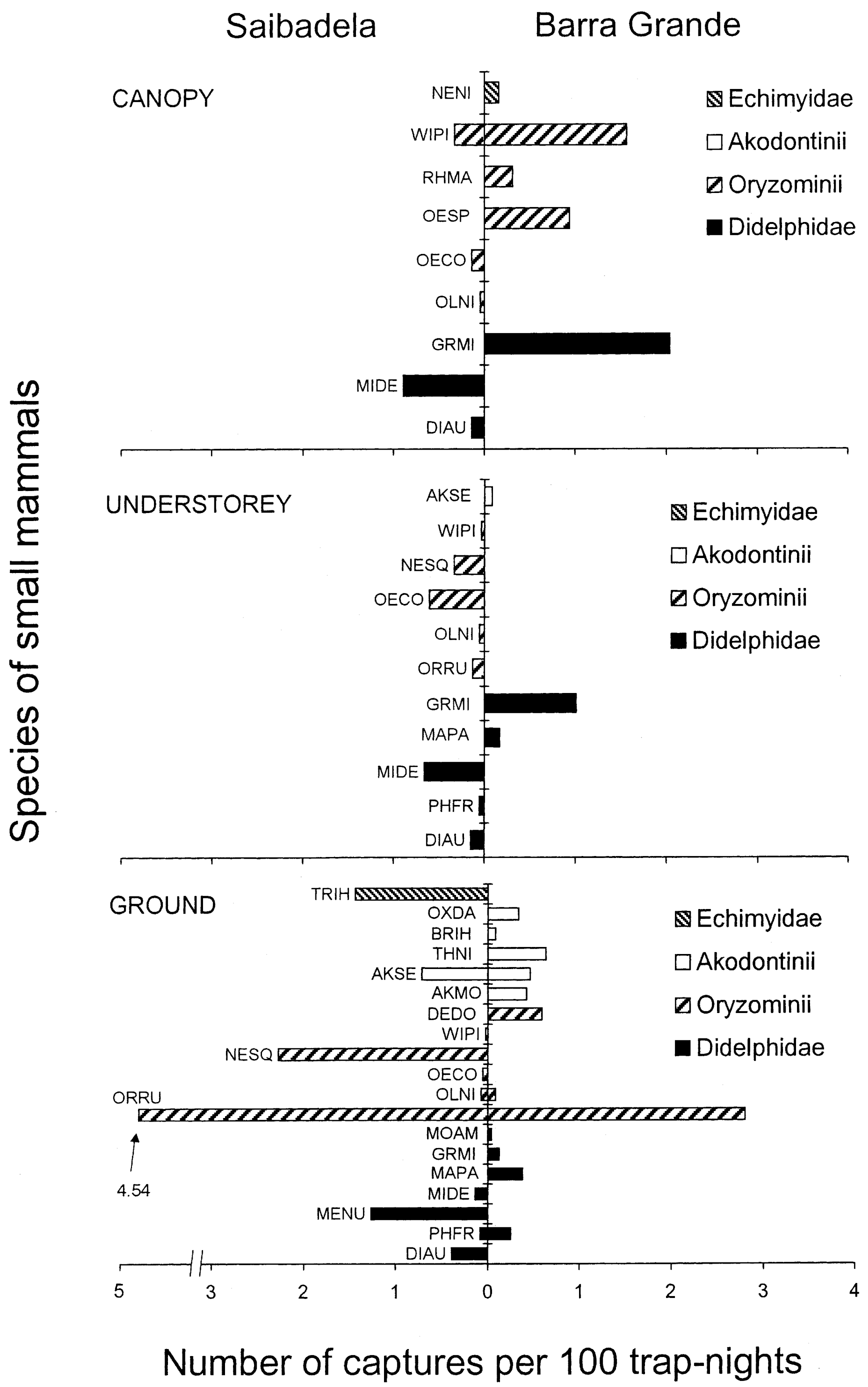

Figure 1. Patterns of utilization of three vertical strata (ground level, understorey and canopy) by small mammals in two Atlantic forest areas in south-eastern Brazil, Saibadela (SA) site (left) and Barra Grande (BG) site (right), considering all captures for each species. Species were grouped by major taxonomic groups. Species codes are as follows (number of captures and number of individuals, respectively, between parentheses). Echimyid rodents: NENI = *Nelomys nigrispinus* (Wagner, 1842) (BG: 1, 1), TRIH = *Trinomys iheringi* (Thomas, 1911) (SA: 141, 20); akodontine rodents: AKMO = *Akodon montensis* Thomas, 1902 (BG: 10, 9), AKSE = *Akodon serrensis* Thomas, 1902 (SA: 70, 25; BG: 12, 8), THNI = *Thaptomys nigrita* (Lichtenstein, 1829) (BG: 15, 13), BRIH = *Brucepattersonius* aff. *iheringi* (Thomas, 1896) (BG: 2, 2), OXDA = *Oxymycterus dasytrichus* (Schinz, 1821) (BG: 8, 7); oryzomine rodents: ORRU = *Oryzomys russatus* (Wagner, 1848) (SA: 647, 129; BG: 65, 35), OLNI = *Oligoryzomys nigripes* (Olfers, 1818) (SA: 12, 7; BG: 2, 2), OECO = *Oecomys* aff. *concolor* (Wagner, 1845) (SA: 41, 13), OESP = *Oecomys* sp. (BG: 6, 5), RHMA = *Rhipidomys* aff. *macrurus* (BG: 2, 1) , NESQ = *Nectomys squamipes* (Brants, 1827) (SA: 241, 42), WIPI = *Wilfredomys pictipes* (Osgood, 1933) (SA: 11, 7; BG: 10, 7), DEDO = *Delomys dorsalis* (Hensel, 1872) (BG: 14, 8); didelphids: DIAU = *Didelphis aurita* Wied-Neuwied, 1826 (SA: 49, 14), PHFR = *Philander frenata* (Olfers, 1818) (SA: 11, 2; BG: 6, 4), MENU = *Metachirus nudicaudatus* Illiger, 1811 (SA: 124, 31), MIDE = *Micoureus demerarae* (Thomas, 1905) (SA: 68, 9), MAPA = *Marmosops paulensis* (Tate, 1931) (BG: 11, 9), GRMI = *Gracilinanus microtarsus* (Wagner, 1842) (BG: 28, 12), MOAM = *Monodelphis americana* (Muller, 1776) (BG: 1, 1).

https://doi.org/10.1017/S0266467403003559 Published online by Cambridge University Press

(Figure 1). At Barra Grande the mean number of captures of oryzomine rodents on the ground was lower than at Saibadela. Nevertheless the main difference between both areas at ground level was the greater number of akodontine rodents (five species) and the absence of echimyids in Barra Grande. Marsupial captures were more frequent in the Barra Grande understorey but this group did not dominate in the canopy at either site (Figure 1). These differences were confirmed by the three-factor analysis of variance, which indicated that there were significant differences in the total number of captures per trap station in relation to vertical stratum and taxonomic group but not in relation to site (Table 1). However there were also significant interactions for the three factors considered together, indicating that site must have an effect even if it cannot be detected in the simple contrasts (Table 1).

DISCUSSION

Several authors have pointed out the importance of arboreal captures to the evaluation of the species composition of small-mammal communities (Bakker & Kelt 2000, Malcolm 1995, McClearn *et al.* 1994, Stallings 1989). In tropical forests from Africa, Adam (1977) captured only two rodent species (18% of the total) in arboreal traps. In Amazonian forest, Malcolm (1991) captured eight small mammal species (53% of the total) more frequently in the canopy than on the ground and four of these species were captured exclusively in arboreal traps. On the other hand, Malcolm & Ray (2000) in African tropical forests, McClearn *et al.* (1994) in Panama, and Stallings (1989) and Passamani (1995) in the Atlantic forest, did not capture any small mammal species exclusively in the canopy. Malcolm (1995) reported that only a few published studies in neotropical forests used traps at heights greater than 5 m. Among the few studies that used canopy trapping in south-eastern Brazil (see Grelle, in press; Leite *et al.* 1996, Passamani 1995, Stallings 1989) the present study is the first to analyse patterns of vertical stratification of small-mammal communities in a lowland primary forest from a continuous area of the Brazilian Atlantic rain forest.

Table 1. Results of three-way ANOVA examining the effects of taxonomic group (didelphids, Akodontinii, Oryzominii and echimyids), vertical stratum (ground, understorey and canopy), and site (Saibadela or Barra Grande) on number of captures.

Source of variation	df	F-ratio	P
Taxonomic group (TG)	3	48.2	< 0.001*
Vertical stratum (VS)	2	39.9	< 0.001*
Site	1	0.01	0.925
TG × VS	6	14.9	< 0.001*
TG × Site	3	6.45	< 0.001*
VS × Site	2	7.46	0.001*
TG × VS × Site	6	7.09	< 0.001*
Error	1256		

* Significant P values (≤ 0.001).

At Barra Grande we captured four species (25% of the total species number) exclusively in the upper forest stratum. Additionally, considering both sites, we caught seven species mainly or exclusively in above-ground traps. This number represents about 32% of the total number of small mammal species captured during the study. As in other tropical forests where canopy trapping has been conducted (Adam 1977, Grelle, in press; Malcolm 1991, Malcolm & Ray 2000, McClearn *et al.* 1994), the species composition and relative importance of different taxa changed markedly among different vertical strata at both of our study sites.

Although we detected differences between the study sites in relation to community composition at each forest layer, the vertical habitat utilization of species that occurred in Saibadela as well as in Barra Grande was similar at the two sites. Thus our results indicated that altitudinal changes in Atlantic forest areas may alter the community composition at different forest layers but do not seem to alter specific patterns of vertical habitat utilization.

Didelphid marsupials constitute generally the most common group trapped in the higher strata of neotropical forests. This group, mainly *Caluromys* spp., is dominant in forest areas from Panama (McClearn *et al.* 1994), to French Guiana (Charles-Dominique *et al.* 1981), the Amazon basin (Malcolm 1991), and other Atlantic forest areas (Grelle, in press; Leite *et al.* 1996, Passamani 1995, Stallings 1989; Vieira, in press). Our results did not follow this general pattern as rodents dominated canopy captures in both sites sampled. The relatively low frequency of didelphids in the canopy is related to the absence of *Caluromys* species in the study areas, although species of this genus do occur in other Atlantic forest areas of São Paulo state (Emmons & Feer 1997, E. M. Vieira, pers. obs.). The reasons for this absence are not clear and deserve further investigation.

Resource partitioning and habitat segregation among similar species are effective in maintaining diversity in many communities (Schoener 1974). Differences in vertical habitat utilization have been noted as one of the mechanisms that could reduce interspecific competition, thus allowing coexistence of a greater number of species (Meserve 1977, Miles *et al.* 1981). Charles-Dominique *et al.* (1981) stated that mammal species with a similar diet and comparable body size generally live in different forest layers in French Guiana. Similarly, our results indicated that, for most cases, differential vertical utilization of habitat occurred for pairs of potentially competing species of similar size. For marsupials at Saibadela site (mean adult masses for the species between parentheses, from data obtained during the present study), *M. demerarae* (113 g) was more arboreal than *P. frenata* (283 g), which in turn showed more arboreal activity than *M. nudicaudatus* (298 g). At Barra Grande, *G. microtarsus* (31 g), *M. paulensis* (42 g) and *M. americana* (21 g) are very similar in size and also used the vertical strata in different ways. The patterns of body size similarities and vertical habitat segregation detected in our study are similar to those described by Charles-Dominique *et al.* (1981) for forest didelphids in French Guiana. Charles-Dominique (1983) suggested that niche partitioning among closely related species by combining differential use of vertical strata and different body size in tropical forests is a more general pattern, which can also be observed for lorisid primates in Gabon.

We observed complementary patterns of vertical segregation for rodents. At Saibadela, *O. russatus* (90 g) and *Oecomys* aff. *concolor* (70 g) have similar adult weights and showed marked differences in their vertical habitat utilization, with *Oecomys* aff. *concolor* being predominantly arboreal, whereas *O. russatus* was terrestrial. Likewise, *W. pictipes* (26 g) is mainly arboreal while the similar sized *O. nigripes* (29 g) is relatively more terrestrial.

This pattern of vertical segregation did not hold, however, for all rodent groups. At Barra Grande two Oryzominii rodents weighing from 45 to 60 g were captured only in the canopy (*R. mastacalis* and *Oecomys* sp.) and four of the five akodontine rodents weighing 20–50 g all were terrestrial. The diet of these Akodonts appear also to be similar, as they all feed, more or less strictly, on insects and another invertebrates (Carvalho *et al.* 1999, Emmons & Feer 1997). Resource partitioning among these species, as well as mechanisms allowing for their coexistence, still needs to be better understood. The present study was not designed specifically to test vertical segregation by similar-sized species and this matter deserves further examination for the Brazilian Atlantic Forest, with appropriate null models and statistical testing.

The small mammals of the PEI might be classified into four groups in relation to their vertical activity. The group of strictly terrestrial species includes the marsupials *M. nudicaudatus* and *M. americana* and the rodents *O. russatus*, *T. nigrita*, *Oxymycterus dasytrichus*, *Brucepattersonius* aff. *iheringi*, *Akodon* spp. and *T. iheringi*. The inclusion of rare species, such as *M. americana* and *B. iheringi*, is tentative and based also on the literature (reviewed in Eisenberg & Redford 1999, Emmons & Feer 1997; Vieira, in press) and species morphology. A second group comprises scansorial species that mainly use the ground and the lower strata of the forest; this includes the marsupials *P. frenata* and *M. paulensis* and the rodent *N. squamipes*. The group of scansorial species that use the ground, the understorey and the canopy as well, includes the marsupial *D. aurita* and the rodents *S. ingrami* and *O. nigripes*.

A fourth group, formed mainly by arboreal species, may be identified. This group includes the marsupials *M. demerarae* and *G. microtarsus*, and the rodents *W. pictipes*, *Rhipidomys* aff. *macrurus*, *Oecomys* aff. *concolor*, *Oecomys* sp. and *Nelomys nigrispinus*. Some of these species were captured only once or a few times but they were rarely or never captured on the ground or in the understorey. This lack of captures at ground level despite the great trapping effort (at least 3.5 times greater trapping effort on the ground than in the canopy) strongly suggests that these are species with strictly arboreal habits.

ACKNOWLEDGEMENTS

We thank P. Charles-Dominique, D. Kelt, T. Lacher, W. Magnusson, A. R. T. Palma, W. R. Silva, and M. V. Vieira for reading earlier drafts of this paper and greatly improving it. C. R. Fonseca made helpful comments on the statistical analysis. The Fundação para a Produção e Conservação Florestal do Estado de São Paulo kindly authorized the field work and provided logistical support at the Intervales State Park. We are also grateful to D. C. Briani and many other colleagues for their help in the fieldwork. This study was supported by the Conselho Nacional de Pesquisa e Desenvolvimento Científico e Tecnológico (CNPq) through a research grant to ELAMF (nbr 400241/95-1) and a graduate scholarship to EMV.

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https://doi.org/10.1017/S0266467403003559 Published online by Cambridge University Press