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Forest Structure and Vertical Stratification of Small Mammals in a Secondary Atlantic Forest, Southeastern Brazil

Carlos Eduardo Viveiros Grelle

UFMG, Belo Horizonte, MG, Brazil.

Abstract

This study investigated the differential capture rates of small mammals in different strata of a secondary forest, Minas Gerais State, Brazil. From March through October 1994 mammals were live-trapped at ground, understory and mid-story level. Five species of marsupials and six species of rodents were recorded. *Didelphis aurita*, *Marmosops incanus*, *Metachirus nudicaudatus*, and *Oryzomys* spp. were captured mostly on the ground, while *Caluromys philander*, *Micoureus demerarae*, *Rhipidomys mastacalis* and *Sciurus aestuans* were sampled mainly at 5–12 m height. Species richness was correlated with structural complexity of the forests surveyed. On the other hand, a relationship between species richness and habitat heterogeneity was not detected. These results suggest that local saturation of small mammal species, rather than regional species richness, is determined by the level of habitat complexity. The conservation of stratified forests, such as those found at the Parque Estadual do Rio Doce and the other sites in the Rio Doce valley, are therefore essential for the maintenance of local species diversity.

Keywords: Atlantic forest, habitat complexity, habitat heterogeneity, marsupials, species richness, rodents.

Introduction

The importance of canopy ecology for studies of tropical biology has recently been demonstrated (e.g. Dial & Roughgarden, 1995; Lowman & Wittman, 1996). Studies of birds (MacArthur & MacArthur, 1961), lizards (Pianka, 1967) and small mammals (Rosenzweig & Winakur, 1969) at temperate sites have established the positive relationship between more complex habitats (cf. August, 1983) and species richness. Since tropical forests are structurally more complex than temperate forests, we could expect a more significant amount of habitat complexity in tropical rainforest. This could be represented by vertical stratification of species in the tropics.

Some small mammals of the Atlantic forest (Fonseca & Kierulff, 1989; Stallings, 1989; Passamani, 1995; Leite et al., 1996), of the Amazon (Malcolm, 1991, 1995) and of the Cerrado (Fonseca & Redford, 1984; Mares et al., 1986; Nitikman & Mares, 1987) use the forest floor as much as the understory, while others explore mainly the tops of trees. Recently, Fonseca et al. (1996) pointed out that about 42% of the 209 species of Brazilian marsupials and rodents are arboreal or scansorial. Despite the relevance of traps in trees to investigate small mammal richness in Brazilian biomes, their importance for estimating the abundance of arboreal and scansorial small mammals has been rarely evaluated.

In addition to habitat complexity, habitat heterogeneity (cf. August, 1983) has also been invoked to allow the coexistence of numerous species in the Neotropics (August, 1983; Stallings et al., 1990b; Malcolm, 1995), because variation in habitat patches along the horizontal dimension would permit habitat separation between species. For instance, in the Atlantic forest of Brazil, richness and diversity of small mammals have been associated with habitat complexity (Fonseca, 1989) and heterogeneity (Stallings et al., 1990b). However, other studies in the same biome have found no relationship between habitat complexity and heterogeneity with species richness (Paglia et al., 1995; Gentile & Fernandez, 1999), suggesting that more studies are necessary to understand the relationship between these variables. These studies are most urgently needed in threatened biomes, such as the Atlantic forest. Studies on the Atlantic forest of Minas Gerais

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Correspondence: C.E.V. Grelle, Laboratório de Vertebrados, Departamento de Ecologia, UFRJ, C.P. 68020, 21941-590 Rio de Janeiro, RJ, Brazil. E-mail: grellece@biologia.ufrj.br

State indicate that less than 5% of the state still has forest cover (Fonseca, 1985).

Here I evaluate the use of traps above the ground to estimate species richness and abundances of small mammals. Another objective is to determine if the richness of small mammal species is associated with habitat complexity and heterogeneity at the scale of microhabitat, thus examining relations between these variables on a local scale.

Materials and methods

Study site

The study was undertaken at the Parque Estadual do Rio Doce, hereafter PERD (19°48′–19°29′S, and 42°38′–42°28′W), with 36,000 ha localised in the municipality of Marliéria, Minas Gerais State. The climate of the park is tropical humid with mean annual temperature averaging 22°C (Stallings, 1989). The vegetation is classified as semideciduous subtropical forest of southeastern and southern Brazil (Hueck, 1972). The sampling was performed in a forest locally known as Mata do Vinhático which was partially burned in 1967 (Stallings, 1989). As a consequence, it is a secondary forest with a mosaic of habitats, showing, in the same location, herbaceous plants in open areas, bamboos and graminoids, developed midstory vegetation, and trees of 20–25 meters in height. This is an appropriate site to test associations between species richness and habitat complexity and heterogeneity.

Sampling

Monthly periods of five nights of trapping were conducted from March to October 1994. I established a three-dimensional grid with 49 trap-stations 30 m apart, covering an area of 3.24 ha. Each trap-station had three squirrel-size Tomahawk live-traps (30 × 15 × 15 cm): one on the ground (at the centre of the station); one at an intermediate level (1.5–2.5 m above the ground) wired to a tree, branch or vine; and another on a platform (5.5–9 m in height). Platforms followed Malcolm's (1991) pulley model. All traps were placed within 5 m from the trap-station centre. Fresh pineapples, oatmeal and a cotton ball soaked with codfish oil were used as bait. For each individual captured, the following data were recorded: species, ear tag number, capture station and height of trap. Identification of the individuals of tribe Oryzomyini was not possible in the field. Thus, individuals were removed and killed for correct classification. Voucher specimens of all species were deposited in the Departamento de Zoologia of the Universidade Federal de Minas Gerais, MG; and the Museu Nacional, RJ, Brazil.

Determination of habitat parameters

The concept of habitat complexity and heterogeneity followed the studies of August (1983) and Paglia et al. (1995). At each trap-station eight habitat measurements were made. All of them were recorded within a circle of 10 m in diameter, with the observer at the centre of the trap-station. To avoid seasonal bias in foliage, habitat measurements were recorded once in the dry season. The following measurements were used to estimate habitat complexity: volume at canopy height (VC), volume of midstory (VM) and volume of herbaceous cover (VH) estimated on a scale from 0 to 3 with 0 score indicating no vegetation and 3 representing dense vegetation; number of strata (NS); superior obstruction (SO) representing degree of connectivity (0–3) of leaves and branches above 1.70 m; inferior obstruction (IS) representing degree of connectivity (0–3) of leaves and branches below 1.70 m. Measures of VC, VM and VH followed August (1983). Herbaceous covers (HC), expressed in percentages, and mean diameter at breast height (DBH) of all woody plants with DBH greater than 3.2 cm were used to estimate habitat heterogeneity.

Data analysis of habitat

The index of habitat complexity was the sum of scores of habitat variables (VC, VM, VH, NS, SO and IS) per trap-station. This kind of index has been associated with other complexity measurements (see August, 1983). To calculate the heterogeneity index, I estimated the ratio between variance and mean of HC and DBH measures. The heterogeneity index was the mean of these ratios per trap-station.

Results

Species richness and abundances

In a total of 5880 trap-nights, 63 individuals of 11 species, five marsupials and six rodents, were captured 170 times, resulting in a trap success of 2.9% (Table 1). Marsupials represented 76.6% of the first captures, with *Didelphis aurita*, *Micoureus demerarae* and *Metachirus nudicaudatus* accounting for 81.6% of individuals captured (Table 1). Of the total captures (first captures plus recaptures), marsupials represented 90.6%, with 72.4% of total captures accounting for two of the most abundant species: *D. aurita* and *M. demerarae* (Table 1).

Terrestrial traps had 46.8% of total captures, traps on platforms accounted for 34.5% of total captures, and traps in the understory represented 18.7% of total captures (Table 2). Some species, such as *M. demerarae*, *Caluromys philander*, *Rhipidomys mastacalis*, and *Sciurus aestuans*, explored mainly the higher strata above the ground (Table 2). On the other hand, individuals of *M. nudicaudatus* and *Oryzomys* spp. were captured exclusively on the ground (Table 2). *Didelphis aurita* used three strata, but showed a preference for traps on the ground (Table 2).

Table 1. Number of individuals captured and total captures by sex (males (m) and females (f)) at Parque Estadual do Rio Doce, Brazil, between March and October of 1994.

Species	Number of individuals		Total captures (first captures plus recaptures)	
	♂♂	♀♀	♂♂	♀♀
DIDELPHIMORPHIA				
Caluromys philander	2	3	3	4
Didelphis aurita	6	10	20	32
Micoureus demerarae	7	5	51	20
Marmosops incanus	3	1	3	1
Metachirus nudicaudatus	7	5	10	9
RODENTIA				
Oryzomys seuanezi	3	5	3	5
Oryzomys subflavus	1	–	1	–
Oryzomys sp.	1	–	1	–
Rhipidomys mastacalis	1	–	3	–
Echimys sp.	–	1	–	1
Sciurus aestuans	2	1	2	1

Table 2. Total captures of small mammals at different height at Parque Estadual do Rio Doce, Brazil, between March and October of 1994.

Species	Height of traps: ground 0 m	understory 1–3 m	midstory 5–12 m	Value of χ^2	P
Caluromys philander	–	–	7		
Didelphis aurita	40	11	1	47.44	<0.001
Micoureus demerarae	7	19	45	31.82	<0.001
Marmosops incanus	3	1	–		
Metachirus nudicaudatus	19	–	–	37.95	<0.001
Oryzomys seuanezi	8	–	–		
Oryzomys subflavus	1	–	–		
Oryzomys sp.	1	–	–		
Rhipidomys mastacalis	–	–	3		
Echimys sp.	–	1	–		
Sciurus aestuans	–	–	3		
Total of captures	79	32	59	19.62	<0.001

Habitat complexity and heterogeneity

Habitat complexity and number of species were positively correlated (rs = 0.38, $P < 0.005$, $n = 49$, Fig. 1). On the other hand, correlation between number of species and habitat heterogeneity was not significant (rs = –0.14, $P > 0.10$, $n = 49$, Fig. 2).

Discussion

Species richness and abundances

The captures by strata of *M. demerarae*, *C. philander* and *R. mastacalis* confirm the arboreal habits of these species, as already observed in other studies (Charles-Dominique et al., 1981; Fonseca & Kierulff, 1989; Stallings, 1989; Malcolm, 1991; Passamani, 1995; Leite et al., 1996). However, the results concerning *D. aurita* are controversial. Apparently, the scansorial *D. aurita* use the upper stratum of the forest as a result of flooding (Leite et al., 1996). In flooded sites in Venezuela, the congener *D. marsupialis* was mostly captured above the ground (O'Connell, 1979). On the other hand, studies at unflooded sites registered *D. aurita* predominantly captured on the ground (Fonseca & Kierulff, 1989; Stallings, 1989; this study).

In a total of 64,300 trap-nights, Stallings et al. (1990a) recorded 21 species of small mammals (marsupials and

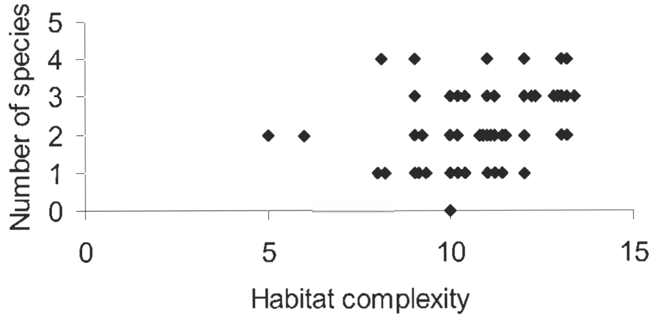

Fig. 1. Relationship between species richness of small mammals and habitat complexity at Parque Estadual do Rio Doce, Brazil, between March and October, 1994. See the text for definition of habitat complexity.

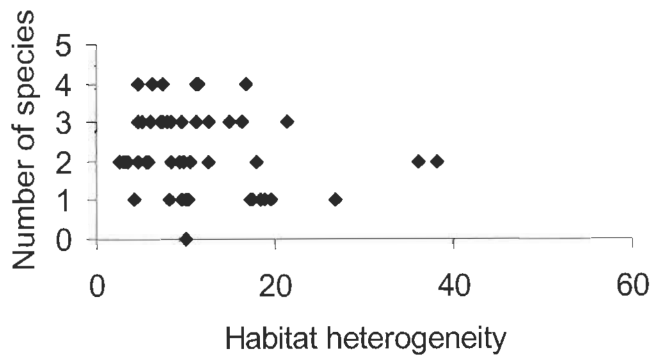

Fig. 2. Relationship between species richness of small mammals and habitat heterogeneity at Parque Estadual do Rio Doce, Brazil, between March and October, 1994. See the text for definition of habitat heterogeneity.

rodents), and 11 of them were found at the same site as the present study (Stallings, 1989). In spite of the lower sampling effort in the present study, I detected two more undetermined species (*Oryzomys* sp., and *Echimys* sp.) in addition to nine that were already reported for the study site (Stallings et al., 1990a). Notably, *Echimys* sp. is an arboreal rodent that was captured above the ground, thus reinforcing the importance of sampling understory and canopy to assess total richness of small mammals, as has been pointed out by other studies as well (e.g. Fonseca & Redford, 1984; Fonseca & Kierulff, 1989; Stallings, 1989; Malcolm, 1991; Passamani, 1995; Leite et al., 1996).

Also, differences between species recorded in the present study and by Stallings (1989; Stallings et al., 1990a) can be related to the type of traps used. In addition to Tomahawk traps, Stallings (1989) also used Sherman traps and frequently captured smaller species (<100 grams), such as *Gracilinanus microtarsus*, *Akodon cursor*, *O. trinitatis* and *Oxymycterus roberti* with them. Although he found significantly different captures rates between trap types for *A. cursor* only, the absence of some small species from my sample might be explained by the different trap type used.

My results clearly show the influence of trapping design on the capture success for different species of mammals. Aboveground sampling greatly increases the probability to capture species with arboreal habits (e.g. *M. demerarae*). If based on captures on the ground only, abundance of *M. demerarae* at PERD would be greatly underestimated. In fact, other researchers reporting high abundances of this marsupial also used traps on platforms (Charles-Dominique et al., 1981). For *D. aurita* my results revealed a higher abundance at PERD than former studies that sampled at the same and two nearby sites (Fonseca & Robinson, 1990), or in other areas of the Atlantic forest (Bergallo 1994; Cerqueira et al., 1993; Gentile et al., 2000). Similar high abundance of the congener *D. marsupialis* were observed in Venezuela using traps above the ground (August, 1984; O'Connell, 1979) and this emphasise the importance of three-dimensional sampling grids for more accurate quantitative approaches.

Habitat complexity and heterogeneity

In studies comparing other sites, in the same PERD, traplines at different successional stages (Stallings, 1988), and sites separated by ca. 200 km (Fonseca, 1989) also revealed a positive relationship between habitat complexity and species richness. Apparently, habitat complexity allows species packing, with some ecologically similar species occurring at the same site.

In contrast to my results, Stallings et al. (1990b) recorded that habitat heterogeneity explained the species richness variation among different traplines in the PERD. This relationship was not found in the present study, consisting of only one of the sites explored by Stallings et al. (1990b). According to August (1983), the lack of correlation between habitat complexity and heterogeneity with species richness could be a problem of sampling scales. Habitat heterogeneity could be important to increase species diversity among sites and traplines, from a regional perspective. On a small scale, within a site or traplines in the Atlantic forest, at least in the Rio Doce valley, habitat complexity could locally support more species at each site. Thus local habitat complexity can be as important as area size for the maintenance of species of small mammals.

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