

Instituto Nacional de Pesquisas da Amazônia

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Partição de recursos em assembleias de primatas neotropicais: uma
comparação entre dois tipos vegetacionais da amazônia

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Manaus, Amazonas

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comparação entre dois tipos vegetacionais da amazônia

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Sinopse:

Foi estudada a partição das principais dimensões do nicho entre as espécies de duas comunidades de primatas neotropicais. As comunidades estudadas apresentavam a mesma composição de espécies. As áreas de estudo apresentaram diferenças na produtividade de frutos e localizam-se no PARNA Viruá, RR e na REBIO Uatumã, AM.

Palavras chave: Primatologia, Platyrrhini, Amazônia, coexistência, sobreposição de nicho, estratificação vertical, padrão diário de atividade, uso do habitat, REBIO Uatumã, PARNA Viruá.

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RESUMO

A coexistência das espécies é determinada, em parte, pela forma como os recursos são particionados entre elas. A diferenciação entre espécies simpátricas se dá pela utilização de porções diferentes de determinadas dimensões do nicho, o que pode ocorrer de diversas maneiras. Acredita-se que os primatas se diferenciem, principalmente, pelo padrão diário de atividades, pelo uso do espaço, pela estratificação vertical e por características da dieta. O grande número de espécies de primatas simpátricos na Amazônia deveria levar a partição do nicho em mais de uma dimensão. Para compreender os mecanismos de coexistência entre os primatas neotropicais comparamos a estrutura das assembleias de duas áreas com a mesma composição de espécies de primatas e com produtividades diferentes. Até agora, nenhum estudo havia feito tal comparação. Não encontramos uma partição entre as espécies de primatas na utilização do habitat, no padrão de atividade diária e na estratificação vertical. Todas as espécies utilizaram os horários de forma similar. Houve uma organização da assembleia da REBIO Uatumã em função dos estratos verticais. Apesar disso, há grande sobreposição na utilização dos estratos intermediários, o que torna este um mecanismo ineficaz na separação do nicho das espécies. Apesar de não termos detectado diferenças estruturais no habitat, houve diferenças de produtividade entre os ambientes e as fisionomias, mas apenas durante a estação chuvosa. Registramos uma preferência dos primatas pelos habitats mais produtivos durante a estação chuvosa que não ocorreu durante a estação seca. Assim, o habitat é utilizado em função de sua produtividade, não contribuindo para a diferenciação do nicho das espécies. Nossos resultados sugerem que não há partição dos principais eixos do nicho dos primatas neotropicais. A diferenciação da dieta durante a estação seca pode ser o principal mecanismo de partição de recursos entre os primatas neotropicais, uma vez que durante a es-

tação chuvosa recursos alimentares não seriam limitantes. Esta hipótese ainda precisa ser testada.

ABSTRACT

Species coexistence is determined in part by the ways species partition resources. Sympatric species use different areas of niche space in several different ways. Primate species are thought to coexist primarily due to differences in daily activity patterns, the use of space, vertical stratification, and diet. The existence of many sympatric primate species in Amazonia suggests that the niche they occupy is partitioned in more than one dimension. In order to examine the mechanisms of coexistence among Neotropical primates, we carried out the first-ever comparison of primate community structure between two areas with the same primate species composition but different vegetation types. We found no evidence for partitioning of habitat use, daily activity patterns, or vertical stratification. All species showed similar daily activity patterns. While species in the REBIO Uatumã assemblage showed preferences for certain forest strata, there was significant overlap in the use of intermediate strata, making vertical stratification an inefficient mechanism for niche separation. We did not detect structural differences between habitats, but we did detect differences in the productivity of habitats and vegetation types during the rainy season. Primates were found to prefer more productive habitats, but only during the rainy season. Habitat preferences are thus driven by habitat productivity, and do not contribute to niche differentiation. Our results suggest no partitioning of the principal niche axes of the primate assemblages we studied. Our hypothesis is that differences in diet during the dry season may be the leading mechanism of resource partitioning among these primates, since food availability is not limiting during the rainy season.

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PARTIÇÃO DE RECURSOS EM COMUNIDADES DE PRIMATAS NEOTROPICAIS

INTRODUÇÃO

As formas como as espécies em uma comunidade repartem os recursos entre si determinam quais e quantas espécies podem coexistir (Pianka 1974). Se duas ou mais espécies usam um mesmo recurso escasso elas tenderão a se excluir devido à competição (MacArthur & Levins 1967). O conceito Hutchinsoniano de nicho (Hutchinson 1957) considera cada requerimento de uma espécie, biótico ou abiótico, como uma dimensão, um eixo, de um nicho hipervolumétrico n-dimensional.

Mas, se estas espécies coexistem, espera-se que os recursos sejam utilizados de maneiras diferentes, ou seja, que elas particionem as dimensões compartilhadas do nicho através de adaptações que evitem ou reduzam a competição (Gause 1934, Hutchinson 1959, Pianka 1981). Entretanto, a sobreposição na utilização dos recursos não indica necessariamente que haja competição entre as espécies, ao contrário, extensa sobreposições podem indicar ausência de competição, o que pode ocorrer quando os recursos não são limitantes (Pianka 1974).

Os primatas, podem utilizar o habitat de maneiras bastante distintas, sendo o número de espécies em uma determinada área influenciado pela forma como as espécies particionam as principais dimensões do nicho. Quanto maiores as diferenças na utilização dos recursos, ou quanto mais microhabitats um ambiente contiver, maior será o número esperado de espécies (Stevenson, Quiñones & Ahumada 2000, Lehman 2004). Os recursos podem ser particionados através de diferenças nos padrões de atividade e no uso do espaço

(Ganzhorn 1989), no método de forrageio (Yoneda 1984), ou na escolha dos tipos alimentares (Porter 2001).

Na Amazônia, as assembleias de primatas podem variar do menor ao maior número de espécies em relação a qualquer outro local nos trópicos, com um mínimo de três e um máximo de 14 espécies simpátricas (Peres 1997). Com tantas espécies simpátricas, a coexistência deve ser possível através do particionamento de mais de uma dimensão (Pianka 1974). Padrões de utilização do habitat, dieta, estratificação vertical e atividade diária têm sido considerados os eixos mais importantes para a separação das espécies de primatas (Schreier et al. 2009).

A distribuição espacial das espécies de primatas de uma comunidade tem sido relacionada às diferentes fitofisionomias de um habitat (Mittermeier & van Roosmalen 1981, Peres 1994, Kasecker 2006). Mesmo sem barreiras, ambientes contíguos como terra firme e várzea podem conter espécies diferentes ou manter densidades diferentes das mesmas espécies (Peres 1997). A utilização diferencial destes ambientes pode indicar partição do espaço entre as espécies.

Espécies que dividem o mesmo habitat podem particionar o eixo da dieta (Ganzhorn 1988), possibilitando a coexistência. Os primatas podem ser classificados em grandes categorias segundo os principais tipos alimentares que consomem, por exemplo, sendo considerados folívoros ou frugívoros, se folhas ou frutos, respectivamente, são o principal item em suas dietas (Clutton-Brock & Harvey 1977). Em geral, os primatas neotropicais de maior porte (Atelidae) tendem a consumir frutos e folhas, enquanto os de menor porte (Callitrichidae) se alimentam principalmente de insetos e exsudados (Fleagle 1988). Estas diferenças são os reflexos do balanço entre a massa corporal e os requerimentos energéticos e a capacidade do trato digestivo e as taxas de atividade (Oates 1987, Lambert 2007). Todavia, diferenças na dieta podem ser mais sutis quando consideramos a mesma classe de tamanho corporal. Os primatas podem

consumir recursos em diferentes fases fenológicas, como no caso de folhas jovens ou velhas e frutos maduros ou imaturos, bem como selecionar frutos e sementes em função do tamanho, da dureza ou da composição química (Gautier-Hion et al. 1985, Ganzhorn 1988, Ungar 1995).

Outra forma de partição entre espécies simpátricas é a estratificação vertical (Schreier et al. 2009). Mesmo espécies em associação mantêm diferenças na utilização dos estratos verticais (Yoneda 1984). A utilização de diferentes estratos seria uma forma de permitir a coexistência de espécies que compartilham outras dimensões do nicho. O tempo também pode ser considerado uma dimensão do nicho e, portanto, também pode ser utilizado de maneiras diferentes por espécies simpátricas. Primatas que vivem em um mesmo habitat e tem dietas semelhantes podem ter períodos de atividade diferentes, sendo ativos durante o dia ou durante a noite (Ganzhorn 1989).

Em geral, estudos de comunidades são realizados em apenas um local (e.g. Kasecker 2006). A falta de comparações entre comunidades pode tornar difícil a compreensão do papel do particionamento das principais dimensões do nicho na estruturação das comunidades e na manutenção da coexistência, uma vez que diferenças entre as espécies de um único local podem não estar relacionadas com a partição de recursos. A comparação entre locais com diferentes estruturas vegetais e diferentes produtividades pode nos ajudar a compreender a importância dos principais eixos do nicho na diferenciação entre espécies simpátricas.

OBJETIVOS

O objetivo deste estudo foi avaliar a importância da estratificação vertical, do período de atividade e do uso do habitat na estruturação das assembleias de primatas na Amazônia central, em duas áreas com a mesma composição de espécies, mas com estruturas vegetais diferentes.

CAPÍTULO 1

Brum, M. & Spironelo, W. R. Resource partitioning in Neotropical primate assemblages: A comparison of two Amazonian vegetation types. Manuscrito formatado para Journal of Animal Ecology.

1Running head: Resource partitioning among Neotropical primates

2

3Title: Resource partitioning in Neotropical primate assemblages: A comparison of two Ama-
4zonian vegetation types

5

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15

16

1Abstract

21. Species coexistence is determined in part by the ways species partition resources.
3Sympatric species use different areas of niche space in several different ways. Primate spe-
4cies are thought to coexist primarily due to differences in daily activity patterns, the use of
5space, vertical stratification, and diet. The existence of many sympatric primate species in
6Amazonia suggests that the niche they occupy is partitioned in more than one dimension.

72. In order to examine the mechanisms of coexistence among Neotropical primates, we
8carried out the first-ever comparison of primate community structure between two areas with
9the same primate species composition but different vegetation types.

103. We found no evidence for partitioning of habitat use, daily activity patterns, or vertical
11stratification. All species showed similar daily activity patterns. While species in the REBIO
12Uatumã assemblage showed preferences for certain forest strata, there was significant over-
13lap in the use of intermediate strata, making vertical stratification an inefficient mechanism for
14niche separation. We did not detect structural differences between habitats, but we did detect
15differences in the productivity of habitats and vegetation types during the rainy season. Pri-
16mates were found to prefer more productive habitats, but only during the rainy season. Habi-
17tat preferences are thus driven by habitat productivity, and do not contribute to niche differen-
18tiation.

194. Our results suggest no partitioning of the principal niche axes of the primate assem-
20blages we studied. Our hypothesis is that differences in diet during the dry season may be
21the leading mechanism of resource partitioning among these primates, since food availability
22is not limiting during the rainy season.

23Key-words: Amazonia, Platyrrhini, coexistence, vertical stratification, daily activity patterns,
24niche overlap, spatial use.

1Introduction

2

3The ways in which species in a community share resources determine which species and
4how many species can coexist there (Pianka 1974). Two or more species that use the same
5scarce resource will tend to exclude each other via competition (MacArthur & Levins 1967).
6The Hutchinsonian niche concept (Hutchinson 1957) considers every biotic or abiotic need of
7a species as one dimension, or axis, of an n-dimensional hypervolumetric niche.

8 If species are to coexist with limiting resources, they must use those resources in dif-
9ferent ways. This leads to the partitioning of shared niche dimensions via adaptations that
10reduce or eliminate competition (Gause 1934, Hutchinson 1959, Pianka 1981). However,
11overlap in resource use between species does not necessarily indicate competition. Indeed,
12extensive overlap may indicate an absence of competition, in situations where resources are
13not limiting (Pianka 1974).

14 It is assumed that the greater the differences in resource use, or the greater the num-
15ber of microhabitats in a given habitat, the more sympatric species can potentially coexist
16(Stevenson, Quiñones & Ahumada 2000, Lehman 2004). Primates use habitat in very differ-
17ent ways, and the number of species present at a given site is influenced by the ways in
18which they partition the most important niche dimensions. Resources can be partitioned
19through different activity patterns and uses of space (Ganzhorn 1989), different foraging
20methods (Yoneda 1984), or different diets (Porter 2001). Habitat use, diet, vertical stratifica-
21tion, and activity patterns are considered the leading axes that distinguish primate species
22(Schreier et al. 2009).

23 The spatial distribution of primate species in a given assemblage has been associated
24with the different architectural aspects of the habitat it occupies (Mittermeier & van
25Roosmalen 1981, Peres 1994, Mendes Pontes 1996, Kasecker 2006). Even when no physi-

1cal barriers separate them, contiguous habitats like terra firme and floodplain forests may
2harbor different species or different densities of the same species (Peres 1997), and this dif-
3ferential use of habitat may indicate species' partitioning of space.

4 Species that occupy the same habitat may coexist by partitioning the dietary axis
5(Ganzhorn 1988). Primates can be classified into broad guilds of feeding strategies, such as
6folivores (primarily leaf-eaters) and frugivores (primarily fruit-eaters; Clutton-Brock & Harvey
71977). In general, larger Neotropical primates (Atelidae) tend to eat fruits and leaves, while
8smaller species (Callitrichidae) primarily consume insects and plant exudates (Fleagle 1988).
9These differences reflect a trade-off between body size on the one hand and energy needs,
10digestive tract size, and activity rates on the other (Oates 1987, Lambert 2007). More subtle
11dietary differences occur among species of the same size. Primates may consume resources
12at different phenological stages (e.g., younger or older leaves, mature or immature fruits) or
13select fruits and seeds that differ in size, hardness, or taste, the latter being directly related to
14chemical composition (Gautier-Hion et al. 1985, Ganzhorn 1988, Ungar 1995).

15 Another way that sympatric species partition resources is via vertical stratification
16(Schreier et al. 2009). Even closely associated species may use forest strata differently
17(Yoneda 1984), thereby permitting the coexistence of species that share other niche axes.
18Time is another niche dimension that can be used differently by different sympatric species.
19Primates that occupy the same habitat and have similar diets may be active at different times
20of the day or night (Ganzhorn 1989).

21 Primate assemblages are typically studied at a single site (e.g., Kasecker 2006). The
22scarcity of between-assemblage comparisons hampers our understanding of the role niche-
23partitioning plays in structuring assemblages and allowing species coexistence, since the dif-
24ferences observed between species at a single site may not necessarily indicate resource
25partitioning. Comparing sites with different vegetation types and levels of productivity should
26help understand how the principal niche axes help distinguish sympatric species.

1 Primate community diversity varies strongly across the Amazon basin, with given sites
2 harboring from three to 14 sympatric species (Peres 1997). Where a large number of sym-
3 patric species coexist and resources are limiting, species coexistence must depend on the
4 partitioning of multiple niche dimensions (Pianka 1974). Under the assumption that resources
5 are limiting, we asked how Neotropical primates partition niches. The object of this study was
6 to examine the ways in which two Neotropical primate assemblages partition three specific
7 niche dimensions: vertical stratification, activity period, and habitat use.

1Materials and Methods

2

3**Study areas.** We worked at two sites that have both identical primate species compositions
4and an identical grid system of trails. These, established by the Biodiversity Research Pro-
5gram, are composed of six parallel east-west trails and six parallel north-south trails. All trails
6are 5 km in length and spaced at 1-km intervals from the adjacent trails. Trails are labeled
7every 50 m with markers indicating trail name and distance. Each grid occupies an area of 25
8km² (for more information see PPBio 2008 and Costa & Magnusson 2010). The standard trail
9layout in the grids allowed a rigorous comparison between the two areas we studied.

10 We carried out the study in two protected areas in central Amazonia: Uatumã Biologi-
11cal Reserve (hereafter REBIO Uatumã) and Viruá National Park (hereafter PARNA Viruá).
12REBIO Uatumã measures 942,786 ha and is located around the towns of Presidente-
13Figueiredo, São Sebastião do Uatumã, and Urucará (between 1°46'51" S and 1°49'36" S,
14and 59°13'45" W and 59°16'27" W) in Brazil's Amazonas state. The trail grid where we car-
15ried out fieldwork crosses a single vegetation type, Submontane Upland Forest (in Portu-
16guese, *Floresta de Terra Firme Submontana*). Topography is very hilly, as the site occupies
17the highest elevations in the region (those that remained above water following the creation
18of the Balbina dam reservoir). The steep topography generates visibly different forest types
19on slopes, terraces, and bottomlands. The tropical equatorial climate has well-defined sea-
20sons, with rainy season lasting from November to April (Machado et al. 2004, IBAMA 2008).

21 PARNA Viruá is located in the town of Caracaraí in the south-central region of Brazil's
22Roraima state (between 1°29'9" N and 1°26'28" N, and 61°0'10" W and 61°2'19" W). PARNA
23Viruá is bordered to the west by the Branco River, to the east by the BR-174 highway, and to
24the south by the Anauá River. Most of the park consists of the *campinarana* ecosystem
25(white sand vegetation), in which forest types are classified by the degree of soil saturation

1(Schaefer, Mendonça&Fernandes, unpublished data). The park covers approximately
2215,917 ha (IBAMA 2008) and protects a very heterogeneous mosaic containing white-sand
3forest (forested *campinarana*), bushy *campinarana* (white-sand brushland) and open-canopy
4rainforest, in addition to *Mauritia flexuosa* palm swamp (buritizal).The trail grid crosses all of
5the forest types described above. Topography is mostly flat and large areas are flooded, es-
6pecially in the southwestern portion of the grid. Climate is tropical equatorial with well-defined
7seasons. Rainy season is from April to August and dry season from September to March
8(ITERAMA 2005).

9 The primate assemblages of the two sites are composed of the same seven diurnal
10species: *Cebus apella* (Linnaeus 1758), *Chiropotes satanas chiropotes* (Hoffmannsegg,
111807), *Saimiris ciureus*(Linnaeus, 1758), *Saguinus midas* (Linnaeus, 1758), *Alouatta mac-*
12*connelli* (Elliot, 1910), *Ateles paniscus* (Linnaeus, 1758), and *Pithecia pithecia* (Linnaeus,
131758).

14 **Habitat structure.** Data collection on habitat structure was carried out at both sites
15during the dry season. We randomly selected four of the six north-south trails for sampling.
16At every 200 m along these trails (based on the standardized PPBio trail labels), we meas-
17ured vegetation attributes in rectangular plots of 10 x 20 m, the long axes of which were per-
18pendicular to the trail and located to the east/west of it. In each plot we recorded the number
19of trees with circumference at breast height (cbh) of ≥ 30 cm, the presence and height of each
20forest stratum (understory, lower canopy, upper canopy, and emergent trees), and the total
21number of palms in order to quantify the vegetational composition. We sampled vegetation
22structure in 98 plots at REBIO Uatumã and in 73 plots at PARNA Viruá. The different sam-
23pling intensity reflects the fact that some plots were inaccessible due to flooding or, in the
24case of PARNA Viruá, to the dense vegetation of the *campina* and dense bushy *campinara-*
25*na*. We did not sample plots that were underwater or that had very dense understory vegeta-
26tion.

1 **Fruit availability.** To quantify fruit availability in both dry and rainy seasons we used
2 a larger number of the plots described above. We established plots at 100-m intervals along
3 all six north-south trails at each site, giving a total of 300 plots for each site and season. In
4 each plot we searched for fruits both on the forest floor and in tree canopies. The number of
5 fruiting trees and the height and family of each fruiting tree were recorded. We used the
6 number of fruiting trees as a proxy for fruit abundance; according to Stevenson, Quiñones &
7 Ahumada (1998) this provides a better measure of fruit availability than basal area and dry
8 weight of fruits in the leaf litter. For the analyses described here, we only used data on fruits
9 known to be consumed by primates.

10 **Habitat classification.** Forests in the REBIO Uatumã trail grid are classified as
11 Dense Tropical Forest (*Floresta Tropical Densa*; Machado et al. 2004, IBAMA 2008). Within
12 this category we recognized five finer-scale forest types based on topography: terraces (high,
13 flat areas with well-drained soils); slopes-terraces (gently inclined areas between terraces
14 and slopes, with well-drained soils); slopes (steeply inclined areas with well-drained soils);
15 slopes-bottomlands (gently inclined areas between slopes and bottomlands, with well-
16 drained soils); and bottomlands (flat areas with streams and some flooding).

17 Forests in PARNA Viruá include *Campina*, Forested *Campinarana*, Bushy *Campi-*
18 *narana* and Open-canopy Rainforest (Machado et al. 2004), as well as large expanses of *bu-*
19 *ritizal*, generally in *campina* areas. Because most of the trail grid is in bottomlands, we decid-
20 ed not to subdivide forest types based on topography in PARNA Viruá.

21 **Zoological data.** Sampling methods were based on the PPBio spatial design
22 (Mendes-Pontes & Magnusson 2007, Costa & Magnusson 2010) and on Peres' (1999) rec-
23 ommendations for population censuses.

24 Censuses were carried out along 12-km transects composed of two parallel north-
25 south trails and two 1-km sections of the east-west trails connecting the north-south trails. At

1 each site we established three such transects, which were sampled alternatively in clockwise
2 and counterclockwise directions. Each group encountered during the surveys was observed
3 until the researchers were noticed by the animals, or for a maximum of 20 minutes. For each
4 group we recorded observations on feeding, social interactions, and the sex, age, and num-
5 ber of individuals, as well as the time of day and the height and habitat used by the group.

6 Data on primate communities were collected during two field campaigns at each site,
7 one in the dry season and one in the rainy season, between April and November 2009.
8 Sampling was exclusively diurnal. Surveys lasted 11 hours per day, from 06:30 to 17:30
9 without interruptions. A total of 813 km were surveyed in 790 hours, for a mean velocity of 1
10 km/h. We recorded 42 hours and 31 minutes' worth of ecological and behavioral data on the
11 primate species at both sites: 21 hours and 45 minutes at REBIO Uatumã and 20 hours and
12 46 minutes at PARNA Viruá.

13 **Statistical analyses.** To assess habitat structure we used correspondence analysis
14 (CA), a factorial analytical method for categorical variables. We built a contingency table with
15 the habitat structure variable data for the vegetation categories and topographic units in each
16 plot. Normality is not required and the output of the analysis is a graphical solution known as
17 a perceptual map, which helps visualize relationships between variables. The perceptual
18 map is the best representation of the data structure and was used to test *a priori* hypotheses
19 about the grouping of the topographic units and vegetation types.

20 Resource availability was compared using Student's t-tests. For each plot of a given
21 vegetation or topographic units we recorded the number of fruiting trees in dry and rainy sea-
22 son. The mean numbers of fruiting trees in each vegetation type or topographic units were
23 compared between seasons with Student's t-tests. To compare resource availability between
24 vegetational and topographic units in the same season we used analysis of variance (ANO-
25 VA).

1 To check for preferences in the use of topographic units in REBIO Uatumã and in the
2 use of phytophysionomy at PARNA Viruá, we used G-tests. These compared the proportions
3 of the sites occupied by each habitat with the frequencies with which primate species used
4 those habitats, to assess whether observed use differed from random expectations of use at
5 a given level of statistical significance (p).

6 Non-metric multidimensional scaling (NMDS) is a multivariate technique to reduce
7 dimensionality. The aim is to detect significant dimensions to explain similarities, dissimilarities,
8 or other patterns in an observation. We divided the time axis into hourly classes, and
9 looked for patterns in the primate assemblages' use of those daylight hours in each season.
10 With NMDS, we reduced the dimensionality of these data. We then carried out linear regressions
11 with the first two axes of the NMDS to test for possible relationships between species
12 and times of day.

13 Multivariate analysis of variance (MANOVA) is a technique similar to ANOVA which is
14 used when there is more than one dependent variable. It uses multiple unifactorial ANOVAs
15 and controls for error rates. We used MANOVA to test the relationships of primate species
16 with vertical forest strata. Because our sampling size was small, we used the Pillai's trace
17 test, which is considered the most robust.

18 As a graphical solution for the NMDS and MANOVA analyses we used compound
19 graphs that show the distribution of the usage frequencies of each hour or height class. To
20 make these graphs we carried out direct ordinations, obtaining an optimized organization of
21 species to the environment gradient.

1 Results

2

3 **Habitat structure.** The canopy at REBIO Uatumã was more uniform than that at PARNA
4 Viruá, with a mean height of 30.5 ± 5.2 m and emergent trees measuring 44.1 ± 3.7 m. At
5 PARNA Viruá the canopy was lower than at REBIO Uatumã, with a mean height of 22.3 ± 4
6 m and emergents measuring 32.5 ± 2.7 m. Table 1 summarizes the habitat structure variable
7 data.

8 We used the first two axes of the CA to reduce the dimensionality of the habitat struc-
9 ture data and to characterize each vegetation type and each topographic unit in two-
10 dimensional space. There was no obvious separation between the established habitat cate-
11 gories at REBIO Uatumã (Fig. 1) and the vegetation at PARNA Viruá (Fig. 2). This suggests
12 that while it is possible to subdivide these forests into topographic or plant community clas-
13 ses, at both sites the habitat used by primates is structurally homogeneous. The groupings
14 apparent in Figs. 1 and 2 do not correspond to any pre-determined categories. Further tests
15 are needed to determine whether the observed variation in habitat structure corresponds to
16 variation in other variables, such as edaphic characters.

17 **Fruit availability.** The number of fruiting trees per hectare differed between dry and
18 rainy seasons both at REBIO Uatumã and at PARNA Viruá (Table 2). ANOVA revealed dif-
19 ferences in the frequencies of fruiting trees between some habitats during rainy season. Ter-
20 races differed from slopes-bottomlands ($p < 0.05$) and bottomlands ($p < 0.01$); slopes-
21 terraces differed from slopes-bottomlands ($p < 0.05$) and bottomlands ($p < 0.01$); and slopes
22 differed from bottomlands ($p < 0.05$). We can thus sort fruiting tree frequency into three topo-
23 graphic classes: terraces + slopes-terraces, slopes, and slopes-bottomlands + bottomlands.

24 At PARNA Viruá the number of fruiting trees was significantly different between forest
25 and forested *campinarana* in rainy season ($t = 3.70$ and $p < 0.01$), but not in dry season ($t =$

11.15 and $p = 0.25$). In the bushy *campinarana* and *campina* no fruiting trees were recorded in
2either season.

3 Family composition of fruiting trees varied little between topographic units/vegetation
4types. During rainy season fruit availability is higher and fruiting trees are distributed patchily
5on the landscape. During dry season, by contrast, resources are scarcer and distributed ho-
6mogeneously in space. Since the composition of fruiting trees does not vary between topo-
7graphic units and phytophisionomy, the main difference observed between habitats is varia-
8tion in fruit availability in rainy season, as represented by the number of fruiting trees per
9hectare.

10 **Temporal partitioning.** Temporal partitioning was not important in structuring pri-
11mate assemblages. Regressions between the two primary NMDS axes for each site in both
12seasons confirmed the results of direct ordinations for REBIO Uatumã (Fig. 3) and PARNA
13Vuruá (Fig. 4). Significance levels for the REBIO Uatumã regressions were 0.1 for rainy sea-
14son and 0.8 for dry season. Likewise, at PARNA Vuruá significance levels were 0.8 for rainy
15season and 0.7 for dry season.

16 While there was no evidence of temporal partitioning among primate species, daylight
17hours were not used uniformly by the assemblages during dry season (Figs. 3 and 4, b), es-
18pecially at PARNA Vuruá. The primate assemblage used daylight hours in a homogeneous
19fashion during rainy season, but preferred early morning and late afternoon hours during the
20dry season.

21 **Vertical stratification.** When data from the two seasons were combined, patterns in
22vertical stratification were evident in the primate assemblage at REBIO Uatumã (Fig. 5.a;
23MANOVA, $p < 0.01$) but not at PARNA Vuruá (Fig. 5.b; MANOVA, $p = 0.34$). While vertical
24stratification was not significant at PARNA Vuruá, species patterns were similar to those at
25REBIO Uatumã: *S. midas* and *S. sciureus* occupied the lowest strata, *C. apella* and *C.*

1 *satanas* the intermediate strata, and *A. macconnelli* and *A. paniscus* the highest strata. *Pithe-*
2 *cia pithecia* showed the largest difference in stratum use between the two sites, probably
3 because of the low number of records of this species.

4 **Abundance ranking.** To analyze abundances we calculated sighting rates as the
5 number of groups encountered per 10 km surveyed. We detected a seasonal effect on pri-
6 mate abundance. Sightings were more frequent during rainy season, when we encountered
7 7.3 groups/10 km at REBIO Uatumã and 5.7 at PARNA Viruá. Comparable sighting rates in
8 the dry season were 3.2 and 3.0 groups/10 km. Sighting rates for PARNA Viruá may be un-
9 derestimates, however, because that site is a mosaic of vegetation types, some of which are
10 not used by primates. For example, primates were never recorded in bushy *campinaranas*
11 and *campinas*. When data from those vegetation types were excluded from the analysis,
12 sighting rates at PARNA Viruá were similar to those at REBIO Uatumã, with 7.5 and 3.8
13 groups/10 km in rainy and dry seasons respectively.

14 Species in the primate assemblages at PARNA Viruá and REBIO Uatumã showed
15 different relative abundances at the two sites. Fig. 6 shows the abundance rankings of pri-
16 mate species in rainy season. While sighting rates were lower in dry season, the patterns
17 shown in Fig. 6 are the same in both seasons. As there is no evidence of animal migrations
18 during the dry season, we consider the rainy season data to provide a more exact picture of
19 abundances.

20 *Cebus apella* was the most common species at both sites and in both seasons. *C.*
21 *apella* was more abundant at PARNA Viruá, as was *Chiropotes satanas*. By contrast, *Ateles*
22 *paniscus* and *Alouatta macconnelli* were more common at REBIO Uatumã. *Saimiri sciure-*
23 *us*, *Saguinus midas*, and *Pithecia pithecia* showed low relative abundances at both sites.

24 **Habitat use.** While the topographic units and vegetation types showed no obvious
25 structural differences (Figs. 1 and 2), some primates used certain habitats more or less than

1 expected by chance (Tables 3 and 4; G-test, $p < 0.001$). These analyses only included spe-
2 cies we recorded 10 or more times in each season, which we considered a minimum value
3 for reliable tests.

4 During rainy season at REBIO Uatumã the primate species analyzed showed prefer-
5 ences for certain topographic units. *Cebus apella* was the only species to show a preference
6 for the lowest elevations, while *A. macconnelli*, *A. paniscus*, and *S. midas* preferred higher
7 areas (terraces and slopes-terraces; Table 3). During dry season, only *A. macconnelli*
8 showed significant habitat preferences, preferring higher areas (Table 3). *Ateles paniscus*
9 and *Cebus apella* showed no significant habitat preferences in dry season.

10 Species with significant habitat preferences at PARNA Viruá consistently preferred
11 forest (Table 4). During rainy season, only *C. satanas* showed no habitat preference. During
12 dry season, neither *C. satanas* nor *S. midas* showed habitat preferences. *A. macconnelli* was
13 never recorded in forested *campinarana*, which suggests a general preference for forested
14 areas. When data from both seasons were combined, *A. paniscus* ($n = 14$) also showed a
15 preference for forested areas ($n = 12$ or 85.7%).

1 Discussion

2 Sympatric species that use the same scarce resource should differ in at least one niche di-
3 mension if they are to coexist (Gause 1934, Hutchinson 1959, Pianka 1981). Many primate
4 species occur sympatrically at sites around the world, and many of these species have very
5 similar diets and body sizes (Schreier et al. 2009), making them potential competitors. The
6 number of sympatric primate species found at a given site peaks in the Neotropics, where it
7 can reach 14 (Peres 1997). Most studies of interspecific niche overlap show differences
8 along at least one limiting niche axis, like feeding resources or habitat use (Stevenson, Qui-
9 ñones & Ahumada 2000). The greater the number of ecologically similar species occupying a
10 single site, the more axes are expected to be partitioned by the assemblage (Pianka 1974).
11 At our study sites, inhabited by seven sympatric species, we expected to find partitioning
12 mechanisms for more than one niche dimension.

13 Differences in daily activity patterns of primate species played an important role in
14 separating ecologically similar species in Madagascar, where nocturnal primates minimize
15 direct competition with diurnal species with similar diets by using the same resources at dif-
16 ferent times of day (Ganzhorn 1989). Although our study only included diurnal primates, we
17 expected to find differences in the way they use daylight hours. However, no evidence of
18 temporal partitioning among species was detected, which suggests that it is not an important
19 mechanism for the coexistence of our study species. This result corroborates Schreier et al.'s
20 (2009) finding that temporal partitioning among primates is not present on most continents.

21 Although we found no patterns of temporal activity that distinguished individual spe-
22 cies from each other, temporal activity was clumped during dry season. The entire assem-

1blage was more active during early morning and late afternoon hours, a pattern which ham-
2pers rather than promotes species separation, since all species show the same preferences.
3This pattern might be explained by a predilection for daylight hours with cooler temperatures
4(Oates 1987). Ganzhorn and Wright (1994) also noted that protein concentrations of leaves
5are higher in the mornings and evenings, which could contribute to a U-shaped pattern of
6temporal use in the dry season for species that complement their diet with leaves, e.g., *A.*
7*macconnelli* (Figs. 3.b and 4.b).

8 Many authors have noted the use of different forest strata as a niche-partitioning
9mechanism in primate assemblages (e.g., Reed & Bidner 2004, Schreier et al. 2009). Our
10study also showed that different species use different strata. While the pattern was only sta-
11tistically significant at REBIO Uatumã, the similarity of vertical stratification patterns at the
12two sites suggested that they are present at both. What is clear is that frugivorous species
13(*A. paniscus*) and frugivorous-folivorous species (*A. macconnelli*) occur preferentially in
14higher strata, generalist species (*C. apella* and *C. satanas*) prefer intermediate strata, and
15insectivorous species (*S. midas* and *S. sciureus*) are more commonly found in lower strata.
16*P. pithecia* did not show a clear preference at either site, probably due to the small number of
17records.

18 Reed and Bidner (2004) argued that using different forest strata might allow species a
19greater use of resources, even for those species which use similar resources. However, we
20observed significant overlap in the use of strata, especially intermediate elevations, which
21are used to some degree by all species. For that reason, we doubt that vertical stratification
22is an efficient mechanism for partitioning resources. It seems unreasonable to suppose that

1foraging primates would ignore abundant resources that are higher or lower than their pre-
2ferred stratum, especially during seasons when food is scarce.

3 In a study by Porter (2001), height and foraging techniques, as well as dietary choices
4during the dry season, helped differentiate three callitrichid species. Yoneda (1984) also
5found differences in foraging and locomotion strategies among callitrichids. Even so, these
6and other studies showed that multiple species consumed fruits in the same strata, which is
7not a useful partitioning of the resource. As with temporal partitioning, vertical stratification
8does not appear to contribute to niche partitioning in the assemblages we studied. On the
9contrary, different uses of vertical strata are probably related to dietary differences rather
10than preferences for certain strata.

11 The use of different forest types or microhabitats is often mentioned as an important
12factor for structuring assemblages and defining the niches of individual species (Reed & Bid-
13ner 2004, Vidal & Cintra 2006). Several studies have documented relationships between the
14spatial distribution of primates and vegetation types and/or structural attributes of habitat
15(e.g. Scharwzkopf & Rylands 1989, Peres 1997, Spironello 2001, Kasecker 2006, Vidal &
16Cintra 2007). We did not find significant structural differences between forest types at either
17of our sites, which should lead to a homogeneous use of habitat. However, we did detect a
18preferential use of certain forest types at both sites during rainy season. If species were parti-
19tioning resources by using the landscape in different ways, one would expect those differ-
20ences to be most pronounced during periods of scarcity, when competition is more intense
21(Shoener 1974). Contrary to this, however, in our study habitat preferences were more pro-
22nounced in the rainy season than in the dry season, which suggests that habitat structure *per*

1se is relatively unimportant. What is responsible, then, for the different patterns of habitat use
2observed during rainy season?

3 The answer is probably related to the different productivities of the forest types. Reed
4and Bidner (2004) argued that the key to understanding habitat effects on primate assem-
5blage structure is resource availability for members of the assemblage. In fact, food re-
6sources are available to different degrees in the forest types we studied (Table 2) and the
7preferred forest types are generally the more productive ones (Tables 3 and 4). As we did
8not detect any variation in habitat structure, it seems fair to assume that variation in resource
9availability and/or quality (especially of fruit) is more important than variation in structure *per*
10se.

11 Neotropical primates are ecologically less diverse than primate assemblages on other
12continents, characterized by medium sizes, diurnal activity patterns (with the exception of the
13genus *Aotus*), quadripedal arboreal locomotion, and frugivorous-faunivorous feeding habits
14(Fleagle & Reed 1996). This strong ecological similarity between species could lead to in-
15tense competition. For that reason, we expected to find partitioning of other niche dimen-
16sions, such as vertical stratification or habitat use, but did not. Such a lack of differentiation
17between species would appear to be in conflict with the Hutchinsonian niche concept (1959).

18 How, then, can a lack of ecological differentiation be reconciled with the high levels of
19alpha-diversity in the Neotropical region? One possible explanation is high primary productiv-
20ity. Terborgh (1986, cited in Reed & Bidner 2004) showed that during rainy season fruit pro-
21duction at Cocha Cashu, Peru, vastly exceeds frugivores' capacity to consume it. The fact
22that there are no limiting food resources during rainy season, thereby making resource parti-

1tioning unnecessary, could be the evolutionary cause of the low ecological diversity of Neo-
2tropical primates.

3 During dry season, on the other hand, fruit production is low enough to limit the abun-
4dances of several species in primate communities (Terborgh 1986, cited in Reed & Bidner
52004). Primate assemblage structure would thus be determined by the characteristics of re-
6sources available during periods of scarcity, when competition is stronger. Terborgh (1986,
7cited in Reed & Bidner 2004) suggested that the availability of a few key resources during
8periods of scarcity, such as figs (Moraceae) and palm fruits (Arecaceae), determine the car-
9rying capacity of frugivores in Neotropical assemblages. As in Peru, palm fruits are very im-
10portant at our sites, at least for *Cebus* spp., especially during the dry season (Spironello
111991). Adaptations that maximize the use of certain key resources during the dry season
12could explain the high levels of alpha-diversity in the Neotropics, allowing for coexistence via
13the use of different limiting resources (Tilman 1977).

14 We also observed differences in primate sighting rates between sites and between
15seasons. Sighting rates were lower during the dry season, which must reflect lower detecta-
16bility during that period. Lower detectability in dry season could be related to different species
17activity patterns, which, in turn, reflect resource availability. With fewer resources and higher
18daytime temperatures, animals tend to move less during the hottest hours of the day, espe-
19cially between 10:00 and 14:00. Because our sampling ran uninterrupted from morning to
20late afternoon, these lower-activity hours could be responsible for the lower sighting rates
21observed in dry season.

1 Although there were fewer resources at PARNA Viruá, primate abundance was high-
2er there than at REBIO Uatumã. This counter-intuitive result may be explained by an exami-
3nation of the relative abundance rankings. The lower relative abundances of *A. paniscus* and
4*A. macconnelli* were offset by the higher abundances of *C. apella* and *C. satanas*. Those
5changes may be related to differences in productivity and floristic composition between the
6two sites. The lower abundance of *A. paniscus*, a specialist frugivore, could be related to the
7lower productivity of PARNA Viruá. As such, dry season production at PARNA Viruá could be
8a limiting factor for populations of atelids, large-bodied animals which consume large quanti-
9ties of mature fruits.

10 With the lower abundances of these large-bodied competitors, the generalist *C.*
11*satanas* and *C. apella*, which are capable of using a broader range of habitats and food items
12(including immature fruits), showed higher relative abundances in the assemblage. Likewise,
13differences in the relative abundances of species between sites suggest that exploitation
14competition might be important, at least during the dry season. If such competition were not
15important, we would expect to see a proportional reduction in the abundances of individual
16species.

17 The exploitation competition could be important when we compare areas with differ-
18ent food resource availabilities (especially of fruit), as is the case of the two sites we studied.
19Peres (1997) showed that densities of *Saimiri* are much higher in floodplain forests than in
20upland forests. Floodplains lack other understory insectivores, such as *Saguinus*, thereby
21allowing *Saimiri* to maintain high densities. In the same fashion, sites that have low densities

1 of large frugivores (e.g., *A. paniscus* and *A. macconnelli* at PARNA Viruá), should have higher abundances of more generalist species like *Cebus* and *Chiropotes*.

3 Schreier et al. (2009) argued that all partitioning mechanisms, such as vertical stratification, may be linked to feeding. In their global-scale analysis, feeding was the primary
5 measure of separation between potential competitors, with diet separating 26% of potential
6 competitor species pairs. However, the authors emphasize that the true proportion could be
7 much higher, since the feeding categories they used were quite broad, with some categories
8 including several items that could potentially be used to separate species. Vertical stratification and the use of different forest types also helped differentiate between pairs of potential
10 competitors. However, as we have shown, these mechanisms are not necessarily important
11 when the entire assemblage is analyzed as a unit.

12 In conclusion, we believe that the most important resource-partitioning is related to
13 dietary differences during the dry season, when resources are limiting. With their varied
14 physical and chemical attributes, fruits offer various opportunities for ecological diversification
15 (Sourd & Gautier-Hion 1986). Macroscopical differences in diet alone were not capable, for
16 example, of distinguishing between the lemur species studied by Ganzhorn (1988), but physical and chemical differences of fruits were crucial. In Madagascar, however, differences go
18 far beyond diet. Species with similar diets use different habitats or partition time (Ganzhorn
19 1989). In the Neotropics, where ecological diversity is lower, dietary differences, especially
20 during times of scarcity, may be the most important mechanism for promoting coexistence.

21 We thus hypothesize that the differences lie in the selection of secondary food items
22 during this period, including leaves and insects but also sap, flowers, nectar, and seeds.

1Even less productive sites, like PARNA Viruá, appear capable of sustaining several primate
2species due to differences in secondary food items during the dry season, with differences
3occurring only in the abundances.

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5

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5 ing mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached
6 tamarins (*Saguinus labiatus*). *Primates*, 25 (4): 414–422.

7

1 Tables

2

3Table 1: Means and standard deviations of the habitat structure data for topographic units at REBIO Uatumã and phytophisionomy at PARNA Viruá.

Site	Topographic unit/ vegetation types	Stratification				Trees (ind./ha)	Palms		Mean cbh (cm)
		Understory (m)	Lower can- opy (m)	Upper can- opy (m)	Emergents (m)		Trunkless (ind./ha)	Arboreal (ind./ha)	
REBIO Uatumã	Terraces	4.5 (± 0.8)	15.1 (± 4.5)	33 (± 4.8)	26.2 (± 4)	635 (± 165)	1510 (± 650)	165 (± 135)	69.8 (± 21.8)
	Slopes-terraces	4.4 (± 0.8)	14 (± 3.6)	30.6 (± 4)	44 (± 5.5)	600 (± 235)	980 (± 730)	580 (± 615)	64.2 (± 9.5)
	Slopes	4.5 (± 1.1)	15 (± 3.7)	28.5 (± 7.6)	12.15 (± 20.2)	560 (± 180)	800 (± 910)	300 (± 285)	70.4 (± 26.6)
	Slopes-bottomlands	4.1 (± 1.6)	13.3 (± 3)	31.1 (± 4.4)	43.7 (± 2.5)	565 (± 210)	495 (± 590)	220 (± 230)	64.2 (± 11.7)
	Bottomlands	4.2 (± 1)	9.5 (± 6)	27.2 (± 4.6)	40	395 (± 155)	72 (± 690)	485 (± 600)	60.7 (± 11.7)
PARNA Viruá	Forest	5.7 (± 1)	13.3 (± 2.4)	22 (± 5.8)	33.24 (± 2.6)	670 (± 340)	90 (± 205)	1025 (± 1130)	52.7 (± 16.2)
	Forested <i>campinarana</i>	4.4 (± 1.7)	7 (± 5)	6.2 (± 9.1)	32	210 (± 300)	250 (± 305)	180 (± 240)	17.2 (± 24.2)

1Table 2: Frequencies of fruiting trees per hectare for each topographic units (REBIO Uatumã)
 2and vegetation types (PARNA Viruá) in rainy and dry seasons. Frequencies in each topographic
 3units and each vegetation type are statistically different between seasons (t-test, $p < 0.01$).

	Rainy season	Dry season
REBIO Uatumã		
Entire site	80 (± 56.5)	20 (± 31.5)
Terraces	92 (± 59)	20 (± 32.5)
Slopes-terraces	94 (± 57.5)	26.5 (± 36.5)
Slopes	77.5 (± 56)	20 (± 29.5)
Slopes-bottomlands	71.5 (± 52)	10 (± 20.5)
Bottomlands	58.5 (± 51.5)	22.5 (± 36)
PARNA Viruá		
Entire site	20 (± 41.5)	6.5 (± 17)
Forest	36.5 (± 48)	7 (± 17.5)
Forested <i>campinarana</i>	14.5 (± 29)	4.5 (± 14.5)

4

5

1Table 3: Habitat use by primate species at REBIO Uatumã, as percentages in the dry and rainy seasons.

	Terraces	Slopes-terraces	Slopes	Slopes-bottomlands	Bottomlands
Frequency at the site	20.3	15	38.6	13.3	12.6
Rainy Season					
<i>Alouatta macconnelli</i> (n= 16)*	37.5 [†]	31.25 [†]	12.5	6.25	12.5
<i>Ateles paniscus</i> (n= 23)*	52.2 [†]	34.8 [†]	8.7	0	4.3
<i>Cebus apella</i> (n= 25)*	8	20	20	24 [†]	28 [†]
<i>Saguinus midas</i> (n= 15)*	40 [†]	26.7 [†]	13.3	13.3	6.7
Dry Season					
<i>Alouatta macconnelli</i> (n= 10)*	50 [†]	10	30	0	10
<i>Ateles paniscus</i> (n= 20)	30	10	40	15	5
<i>Cebus apella</i> (n= 29)	20.7	6.9	41.4	13.8	17.2

2* Species showing differences between observed habitat use and expected use based on the relative frequency of each habitat (adjusted G-test, $p < 0.001$). [†]

3 Topographic units used more often than expected by chance.

1Table 4: Habitat use by primate species at PARNA Viruá, as percentages in the dry and rainy sea-
 2sons.

	Forest	Forested <i>campinarana</i>
Frequency at the site**	49	51
Rainy Season		
<i>Ateles paniscus</i> (n=10)*	90 [†]	10
<i>Cebus apella</i> (n=46)*	73.9 [†]	26.1
<i>Chiropotes satanas</i> (n=21)	42.9	57.1
<i>Saguinus midas</i> (n=20)*	80 [†]	20
Dry Season		
<i>Cebus apella</i> (n=37)*	75.7 [†]	24.3
<i>Chiropotes satanas</i> (n=13)	53.8	46.2
<i>Saguinus midas</i> (n=10)	40	60

3* Species showing differences between observed habitat use and expected use based on the relative
 4frequency of each habitat (adjusted G-test, $p < 0.001$). ** Percentages used in the G-test, excluding
 5the bushy *campinarana* and *campina*, where no primates were recorded. [†] Topographic units used
 6more often than expected by chance.

1Figure legends

2

3Figure 1: A perceptual map of the habitat structure variables at REBIO Uatumã showing the
4first and second axes of a correspondence analysis (CA). The variables included were num-
5ber of trees ≥ 30 cm cbh, the presence and height of each forest strata (understory, lower
6canopy, upper canopy, and emergent trees), and the total number of palms. The groupings
7apparent in the figure do not correspond with the previously defined categories based on to-
8pography, but suggest that other factors underlie variation in habitat structure. The eigenval-
9ues for the two primary CA axes are: CA 1 = 0.13868 e CA 2 = 0.082176. Legend: square =
10terraces, circle = slopes-terraces, triangle = slopes, star = slopes-bottomlands, cross = bot-
11tomlands.

12

13Figure 2: A perceptual map of the habitat structure variables at PARNA Viruá showing the
14first and second axes of a correspondence analysis (CA). The variables included were num-
15ber of trees ≥ 30 cm cbh, the presence and height of each forest strata (understory, lower
16canopy, upper canopy, and emergent trees), and the total number of palms. The groupings
17apparent in the figure are composed of multiple pre-established vegetation type categories.
18The eigenvalues for the first two CA axes for PARNA Viruá were: CA 1 = 0.19753 e CA 2 =
190.12000. Legend: fl = square; circle, forested *campinarana*; triangle, bushy *campinarana*.

20

21Figure 3: Composite chart for time utilization in the REBIO Uatumã obtained from di-
22rect species ordinations. Species order was determined by the distribution of temporal use:

1(a) Rainy season; (b) Dry season. The vertical black bars indicate the number of groups encountered per 10 km surveyed (sighting rate) in each time class.

3

4Figure 4: Composite chart for time utilization in the PARNA Viruá obtained from direct
5species ordinations. Species order was determined by the distribution of temporal use: (a)
6Rainy season; (b) Dry season. The vertical black bars indicate the number of groups encountered
7per 10 km surveyed (sighting rate) in each time class.

8

9Figure 5: Composite chart of vertical strata utilization obtained from direct species ordinations. (a) REBIO Uatumã; b) PARNA Viruá. The thick black bars indicate the number of
10groups encountered per 10 km surveyed (sighting rate) in each height class. The fine bars
11indicate height class.

13

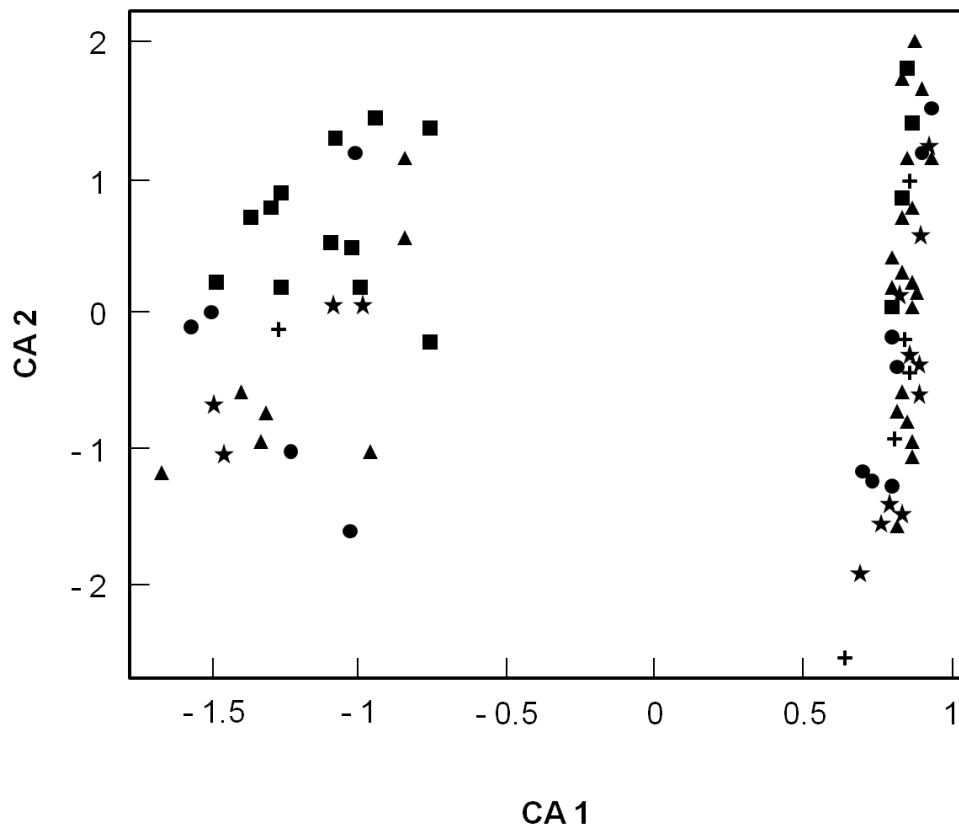
14Figure 6: Abundance ranking of primate species at both sites during the rainy season, based
15on sighting rates. Species order reflects ranking at REBIO Uatumã. Ordinal numbers refer to
16the order of relative abundance of the species. Data from PARNA Viruá do not include bushy
17*campinarana andampina*, where primates were never sighted.

18

1Figures

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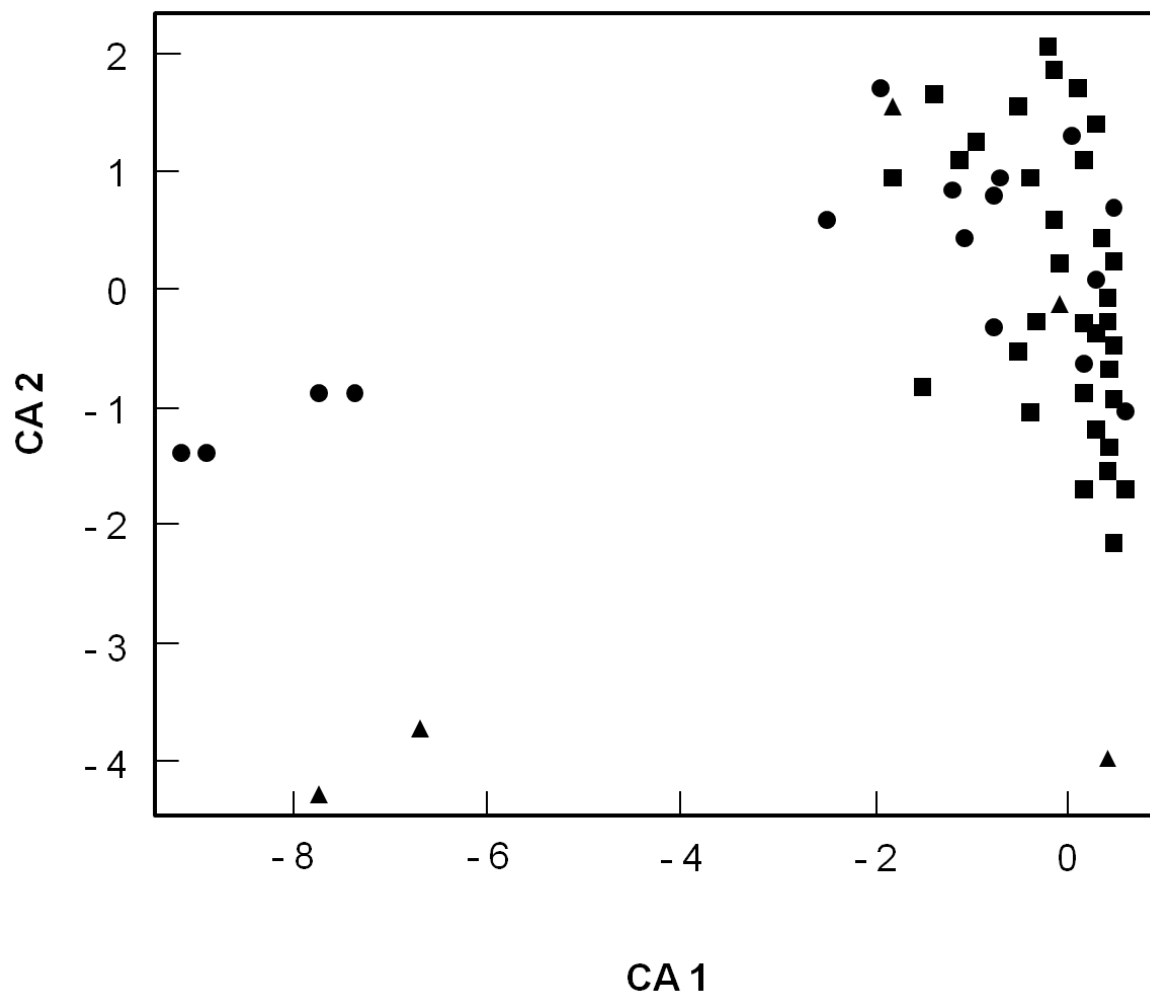
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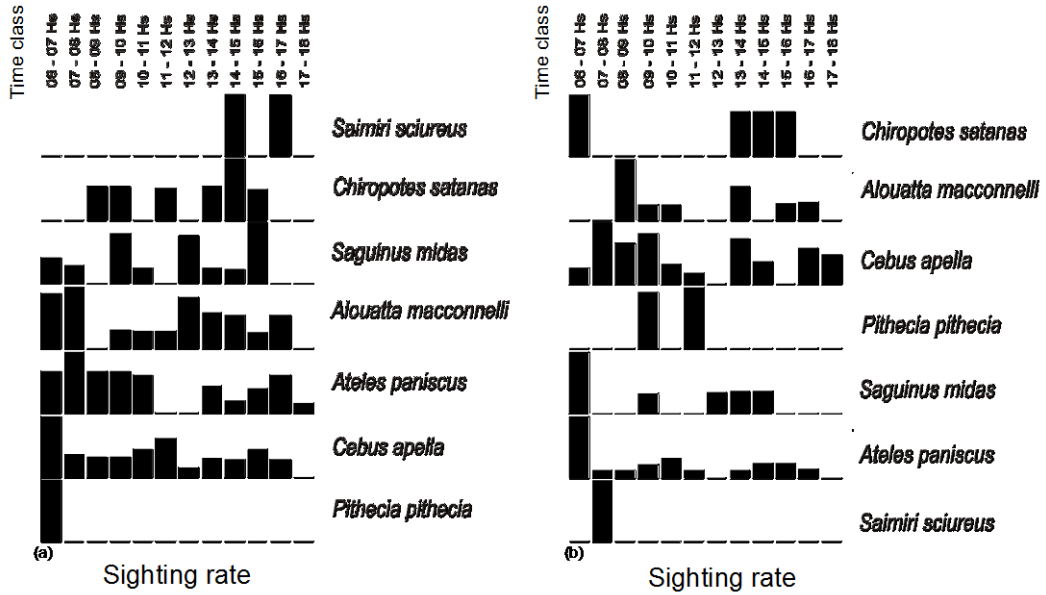
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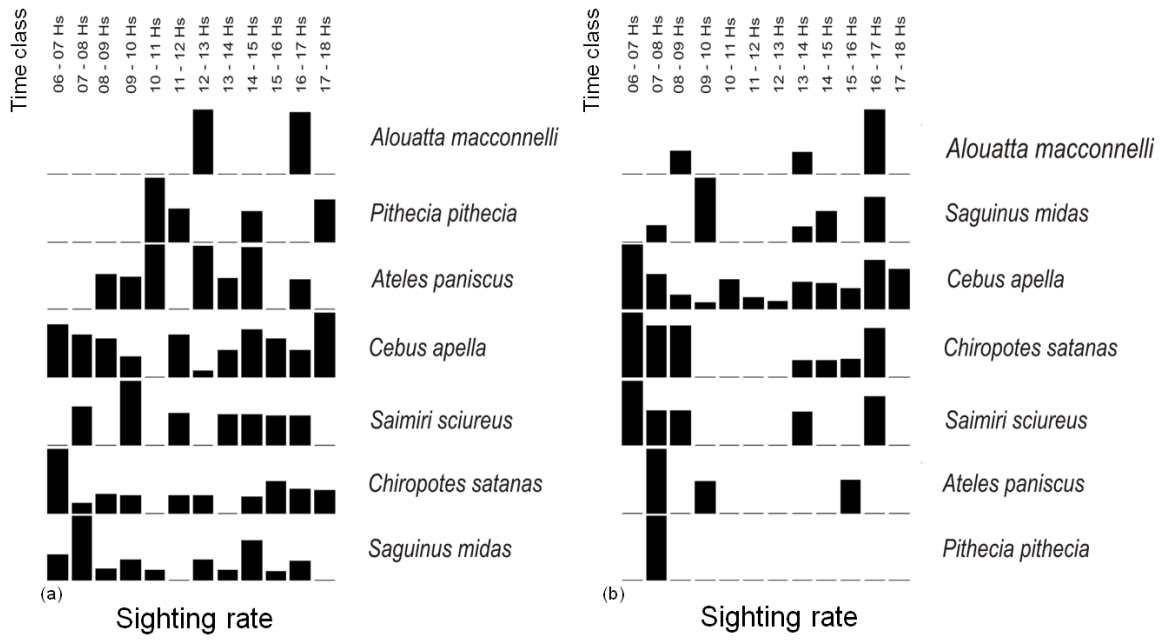


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1Figure 3



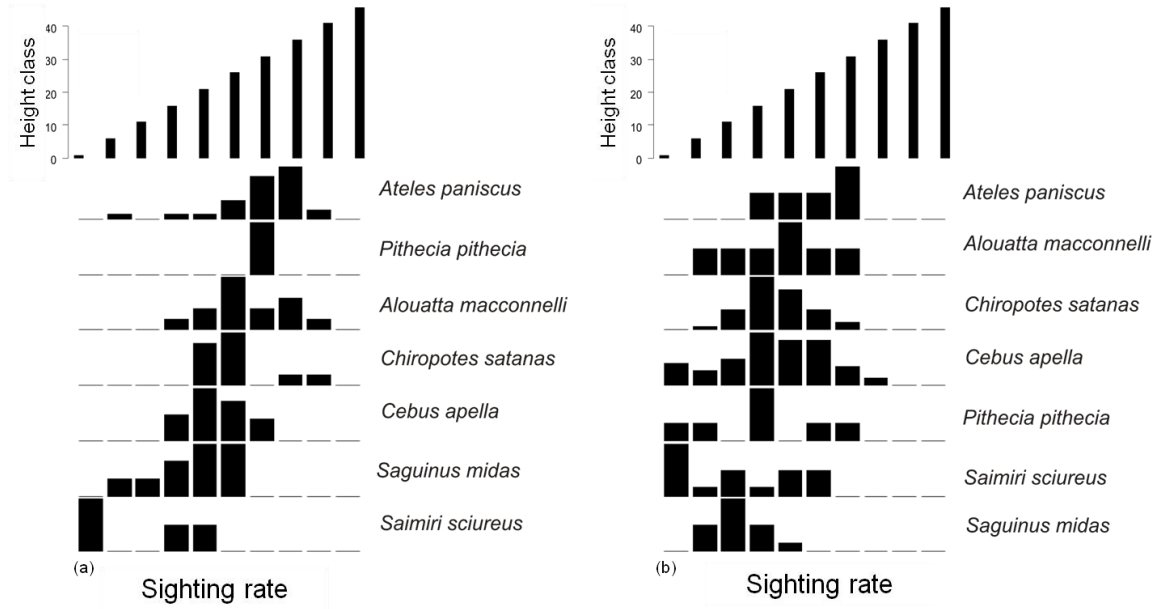
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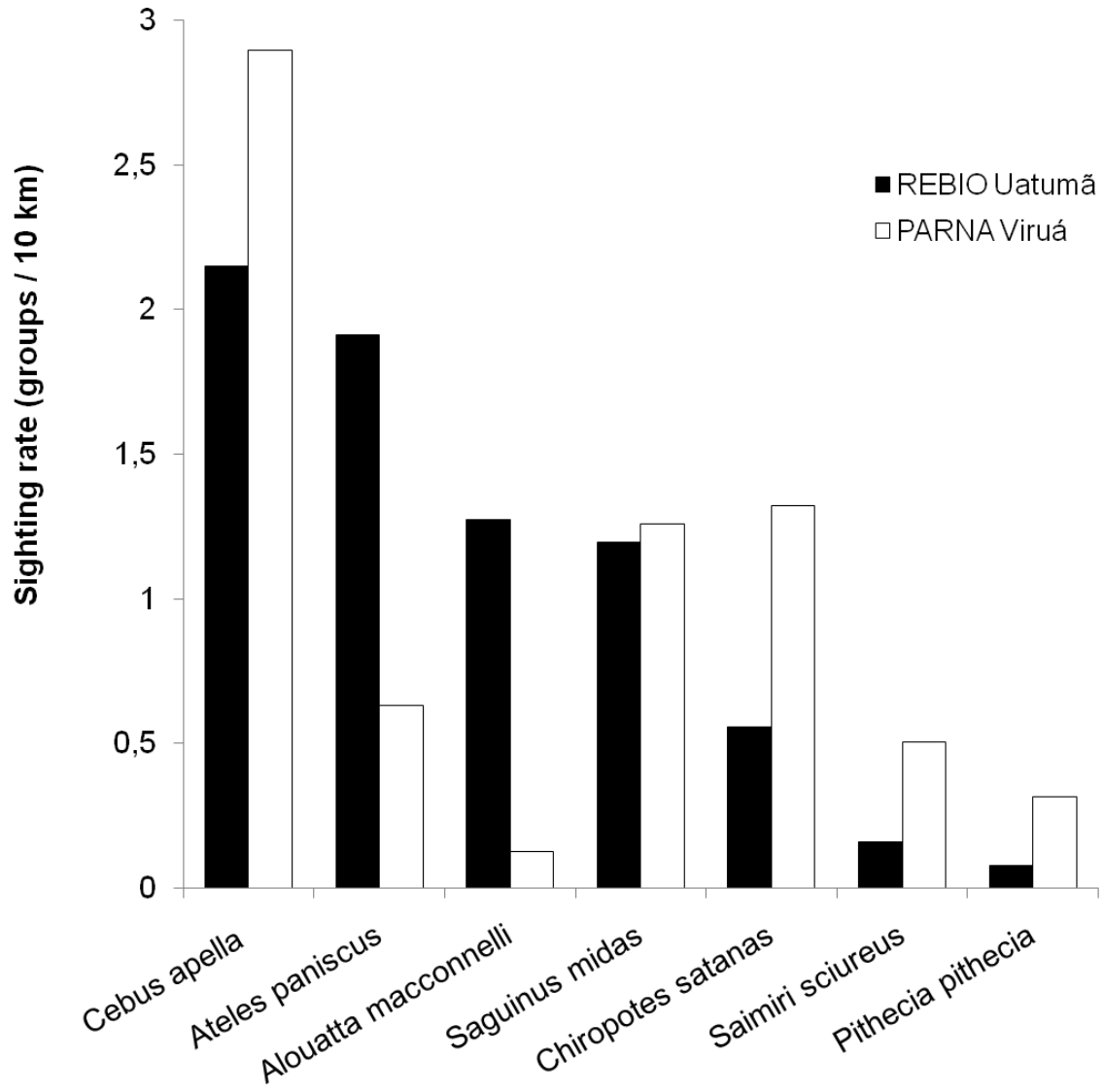
1Figure 5



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1Figure 6



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CONCLUSÃO

Não houve um claro particionamento de recursos entre os primatas durante a estação chuvosa, onde há frutos em abundância. Como esse não seria um recurso limitante não seria necessária uma segregação entre as espécies da comunidade em nenhuma das principais dimensões do nicho. A utilização do tempo, do habitat e a estratificação vertical não contribuem para a diferenciação das espécies, além de estarem relacionados com a alimentação. Para compreender como os nichos das espécies de primatas neotropicais se diferenciam é preciso focar a investigação na dieta durante a estação de escassez numa escala refinada. A escassez de alimento durante a estação seca levaria a uma diferenciação ecológica das espécies, possibilitando a coexistência. Hipotetizamos que as diferenças estejam na escolha dos itens alimentares secundários durante esse período, como folhas e insetos, mas também seiva, flores, néctar e sementes. Mesmo áreas com menores produtividades, como é o caso do PARNA Viruá, seriam capazes de sustentar várias espécies de primatas através da diferenciação dos itens alimentares secundários na estação seca, com diferenças ocorrendo praticamente só nas abundâncias.

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APÊNDICE