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STRUCTURAL AND FLORISTIC TRAITS OF HABITATS WITH DIFFERING RELATIVE ABUNDANCE OF THE LEMURS *MICROCEBUS MURINUS* AND *M. RAVELOBENSIS* IN NORTHWESTERN MADAGASCAR

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Abstract. We analyzed the variations in several structural and floristic parameters in three habitats with differing relative abundance of two mouse lemur species, *Microcebus murinus* and *M. ravelobensis*, in order to explore possible functional links between the vegetation parameters and relative mouse lemur abundances. In the Ankarafantsika National Park the two species live in partial sympatry but occupy different parts of the forest in different relative abundances. Nine 50-m transects and nine sampling quadrats (900 m^2 each) were installed for studying structural and schematic vegetation profiles and the spatial distribution of all woody plant individuals at the three sites. The lists of common plant species and plant species occurring along the profiles were compared with known lemur food plants. A cluster analysis based on 11 habitat characteristics revealed that the site with highest relative abundance of *M. ravelobensis* (JBB) was distinct from the two other sites (JBA/JBC). Compared with JBA/JBC, JBB comprised a relatively high forest with a higher proportion of large trees, a higher density of lianas, but a lower overall density of plant individuals. Moreover, it had lower richness in plant species and families and a floristic composition different from JBA/JBC. Finally, food plant species of both lemur species were not equally represented among the most frequent plant species. The differences in relative abundance of the two mouse lemur species may be functionally linked to structural and floristic differences in the vegetation, and these potential functional links are discussed. *Accepted 23 October 2009.*

Key words: *distribution*, *habitat choice*, *mouse lemurs*, *spatial patterns*, *vegetation*.

INTRODUCTION

Understanding the factors that regulate species distribution and abundance are of key importance in ecology. Madagascar is recognized as one of the most diverse and endangered biodiversity hotspots on Earth (Mittermeier *et al*. 2006). Despite its small size (only 2% of the African surface area), its taxonomic diversity is comparable to Africa, tropical America, and Asia. It ranks second in the world for the primate diversity and contains the third highest number of primate taxa, with 99 species and subspecies (Mittermeier *et al*. 2008). It is also renowned for its high floristic diversity, its high rate of endemism, and the presence of archaic species. It hosts 210 families, 1600 genera, and 12 000 to 14 000 species of vascular plants, 80% of which are endemics (Schatz 2000, Phillipson *et al*. 2006).

The island, with its various climatic conditions, contains a variety of ecosystems including lowland rain forest, savannas, desert-like habitats, and dry deciduous forests. The latter are well known for their importance in terms of biodiversity. They have a lower plant species diversity than the eastern forests but the level of endemism is higher (Mittermeier *et al*. 1997). Dry deciduous forests host a very diverse fauna and this exceptional richness seems to be related to their ecological heterogeneity (Du Puy & Moat 1998). However the dry forests of Madagascar have so far been rather neglected in terms of conservation, although their degradation and fragmentation have become increasingly serious (Smith 1997). Suffering from regular fires, dry forests are considered the most threatened biome in the world (Raselimanana & Goodman 2004). The dry deciduous forest of the study site Ankarafantsika is one of the two largest remaining forest areas (Conservation International 1994).

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The abundance of lemur species can vary considerably between sites, but the reasons for these variations are mostly not known. Mouse lemurs (*Microcebus* spp.), the smallest of all extant primates, are present throughout the remaining forest habitats of Madagascar (Mittermeier *et al.* 2006). The genus comprises at least 18 species island-wide (Louis *et al.* 2008, Mittermeier *et al.* 2008) but only a maximum of two species have been reported to coexist in a given region. In the Ankarafantsika National Park two species of mouse lemur, *Microcebus murinus* and *M. ravelobensis*, partially coexist but their coexistence is not equally expressed everywhere (Rakotondravony & Radespiel 2009). Whereas *M. ravelobensis* occurs exclusively at some sites, both species are present with varying relative abundance at other sites (Rakotondravony 2007). The ecological reasons for these varying patterns of coexistence are not yet understood. Previous studies have shown that these two species have a similar body size (Zimmermann *et al.* 1998) and a similar overall diet, with insect secretions and gum as the main food resources during the dry season (Radespiel *et al.* 2006). They also feed on arthropods, fruits, and nectar. Both species also show very similar patterns of overall vertical space use, utilizing the forest from the floor up to the canopy (Radespiel *et al.* 2006). They differ, however, in their choice of sleeping sites. Whereas *M. ravelobensis* often uses relatively open sleeping sites like lianas, leaf nests, or dense vegetation, *M. murinus* typically sleeps in tree holes in which females jointly rear their young (Radespiel *et al.* 2003, Eberle & Kappeler 2006). Both mouse lemur species share the forest with three other nocturnal (*Cheirogaleus medius*, *Lepilemur edwardsi*, *Avahi occidentalis*), two cathemeral (*Eulemur mongoz*, *E. fulvus*), and one diurnal lemur species (*Propithecus coquereli*). All of them are much larger than mouse lemurs and should be clearly superior in any potential direct resource competition with the two mouse lemur species. Direct interactions between mouse lemurs and other lemur genera are, however, extremely rare.

The aim of this study was to analyze the variations in several structural and floristic parameters in three habitats with differing relative abundance of the two mouse lemur species, in order to explore possible functional links between the chosen vegetation parameters and variation in relative mouse lemur abundance. Functional links could exist between structural parameters and abundance via the provision/lack of suitable sleeping sites, or between floristic parameters and abundance via the provision/lack of required food resources. Relevant parameters can be expected to show a systematic trend when comparing the sites of low, equal, and high relative abundance for either of the two species. This study compares relative abundances (the relative representation of both species in live traps) instead of species-specific population densities because the three sites differ significantly in their capture history, and capture-based population densities cannot therefore be directly compared between sites.

MATERIAL AND METHODS

Study region. The study was conducted in the Ankarafantsika National Park in northwestern Madagascar. Located between 16°10' and 16°20'S, 49°15' and 49°55'E, about 115 km southeast of Mahajanga, the National Park mainly consists of a dry multi-stratum semi-deciduous forest. The climate is characterized by an alternation of two strongly contrasting seasons: a cool dry season from May to October and a hot rainy season from November to April. Highest precipitation occurs in January and February. The average annual temperature is 27°C, with a maximum of 37°C from October to November and a minimum of 16°C in June and July (Schmelting *et al.* 2000). Annual rainfall varies from 1220 to 2255 mm (period: 1997-2004, Rakotondravony & Radespiel 2009). The National Park is located on sedimentary formations of ferruginous sandy soils (Besairie 1973). Coarse red and white sands dominate on the plateau. These soils are highly erodible especially when the vegetation cover is reduced.

Study sites. The project was conducted at three study sites called JBA, JBB and JBC (Fig. 1), all of them still being part of the continuous forest of the Ankarafantsika National Park (130 026 ha). The two former sites are separated by a paved National Road and a 3-km straight line distance, whereas the latter site lies about 28 km away from them. These three sites were selected with regard to their accessibility and to the relative abundance of both mouse lemur species, which was known from previous studies and confirmed with parallel capture sessions (Rendigs *et al.* 2003, Rakotondravony & Radespiel 2009). In the following, the term relative abundance is used to describe the different relative representation of both species in Sherman Live Traps, which are routinely used in mouse lemur field studies across Madagascar. In JBA both species enter the traps in about equal numbers (= equal relative abundance), JBB is pop-

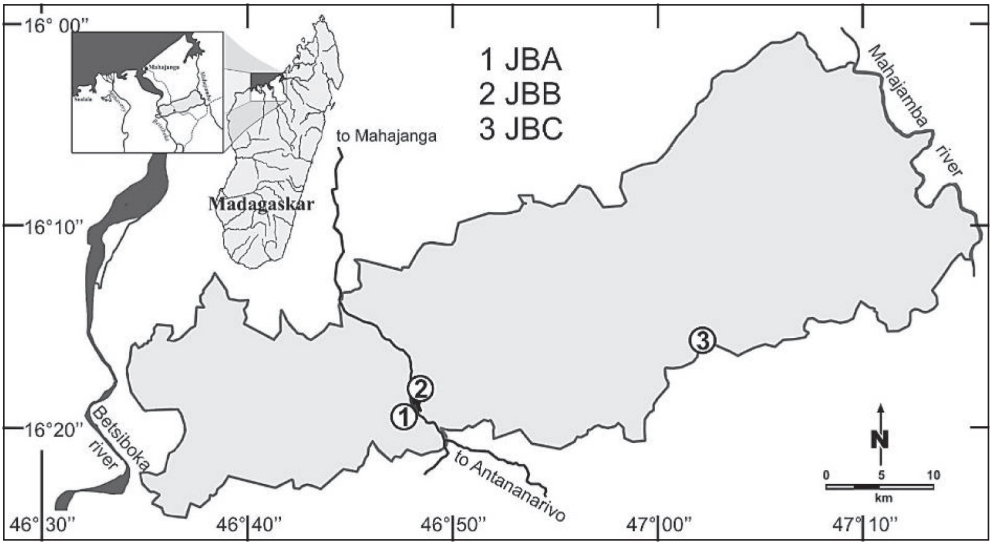


FIG. 1. Map with the three study sites in the Ankarafantsika National Park (gray area).

ulated only by *M. ravelobensis* (= high relative abundance of *M. ravelobensis* and very low relative abundance of *M. murinus*, Rendigs *et al.* 2003), while JBC contains predominantly *M. murinus* and only a few *M. ravelobensis* (= high relative abundance of *M. murinus* and low relative abundance of *M. ravelobensis*, Rakotondravony 2007).

JBA (16°19'07.2"S, 46°48'35.5"E) contains a dry deciduous forest growing on sandy soils. In this zone, the high permeability of the soil leads to some xerophytic characteristics of the vegetation. JBA is a relatively flat area (10% slope) at 190 m above sea level. The size of JBA (i.e. the surface area of the available trail grid system) is 30.6 ha and it is accessible by a trail grid system with intersections every 50 m.

JBB (16°18'02.6"S, 46°48'44.7"E) is located close to Lake Ravelobe at relatively low altitude (89 m), and parts of it belong to a gallery forest which is partly flooded during the rainy season. The forest grows on reddish argilliferous soils and is partially degraded due to previous human activities including a bushfire in 1983. It is also partly an anthropogenic forest, indicated by the existence of introduced tree species such as *Tectona grandis* and *Mangifera indica*. The trail grid system of JBB is 5.1 ha in area with intersections every 25 m.

JBC (16°15'09.0"S, 47°02'54.3"E) is located in the southern part of the Park and consists of a dry deciduous forest growing on calcitic soils on a high plateau (343 m a.s.l.) north of the village of Ankoririka. Access is possible via one central trail that passes through the study site. The site has an approximate surface area of 33.9 ha. This was estimated by adding a strip of 150 m (approximate home range diameter of mouse lemurs, Radespiel *et al.* 2003, 2009) on each side of the trail, where a parallel behavioral study was conducted on the mouse lemurs simultaneously.

Study period and determination of relative abundances. The study was carried out from May to November 2007 during the dry season. The relative abundance of mouse lemurs at the three sites was determined with six to eleven trapping sessions per site (i.e. capture nights with 90-100 traps each) that took place between June and September 2007. Capturing followed the standard routines described in Rakotondravony & Radespiel (2007). The relative abundance of both mouse lemur species was determined as the number of captured individual *M. murinus* compared with that of *M. ravelobensis*. Population densities could not be determined on the basis of these capture data because the populations in JBA and JBB were regularly captured during the previous 12 years, whereas the populations in JBC were captured only in one other year (2003). It is therefore likely that the animals from JBA/JBB and JBC had different individual knowledge of the position of traps, and it

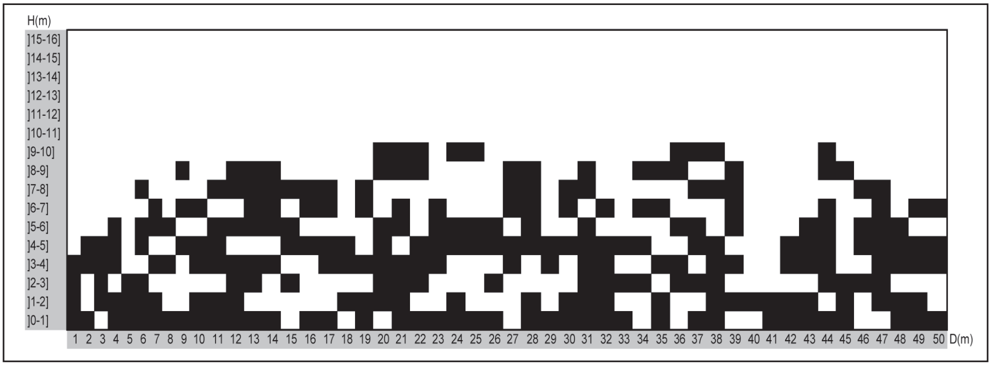


FIG. 2a. Structural profile of the vegetation in quadrat 3 in JBA (y-axis: length of the transects; x-axis: height intervals of 1 m; black squares: space occupation of the vegetation derived from contact between vegetation and measuring pole; white squares: no contact between vegetation and pole).

can be expected that trapping success is generally higher at the sites with a longer capture history. However, in a previous study across 22 different study sites it could be shown that the number of different individuals captured per site does not differ systematically between the two species (Rakotondravony & Radespiel 2009), indicating that both species show the same general trap responses. Therefore the calculation of the relative abundances (see above) for site comparisons seems to be justified.

Vegetation analyses. A total of nine sampling quadrats (30 m x 30 m) was installed at the three sites, four of which were placed in JBA, three in JBB, and two in JBC. The location of the quadrats was chosen based on the vegetation zonation within each site in order to represent all available types of vegetation. Each quadrat touched or included one or two trapping sites. In each vegetation quadrat, a structural profile (Gautier *et al*. 1994) and a schematic profile (Godron *et al*. 1983) were carried out, and the spatial

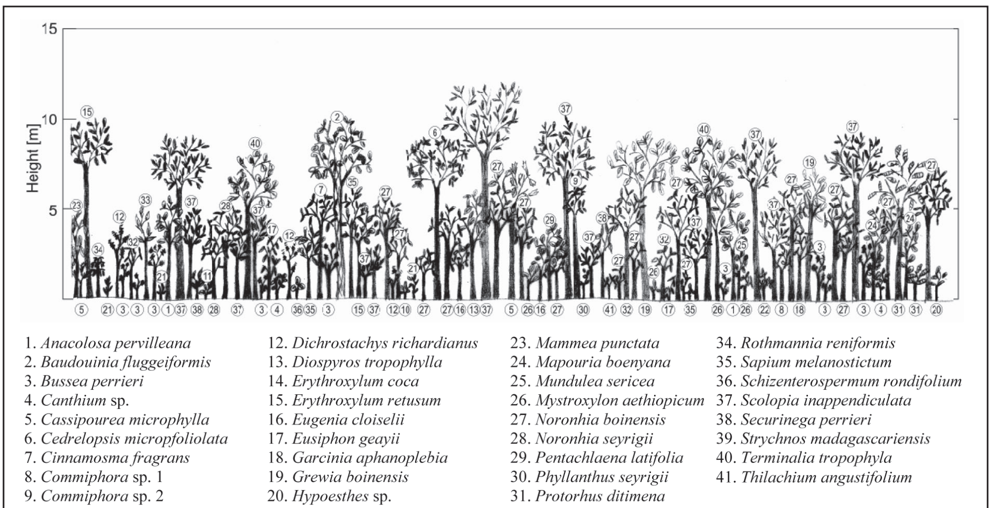


FIG. 2b. Schematic profile of the vegetation in quadrat 3 in JBA.

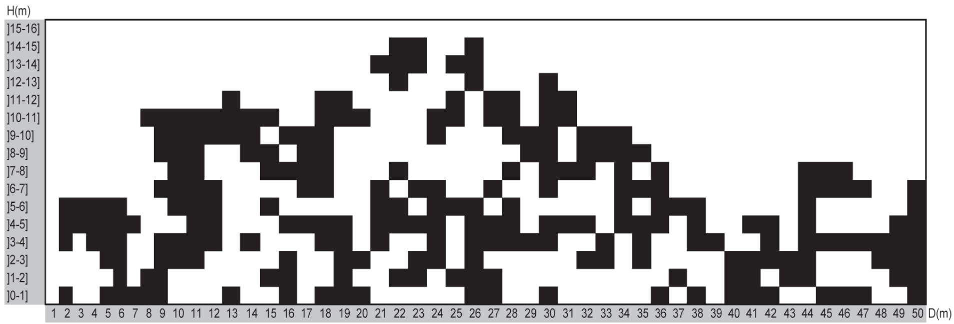


FIG. 3a. Structural profile of the vegetation in quadrat 3 in JBB (y-axis: length of the transects; x-axis: height intervals of 1 m; black squares: space occupation of the vegetation derived from contact between vegetation and measuring pole; white squares: no contact between vegetation and pole).

distribution of all individual woody plants was recorded.

Structural profile. A 50-m transect line was installed across each sampling quadrat. A 7-m long pole was used along the transect in order to determine at what height – divided into 1-m vertical intervals – the vegetation touched the transect line. This estimation was repeated at 1-m steps along the transect line. Estimates above 7 m were performed without the pole. This method was used to calculate the forest cover, to quantify the stratification of the forest, and to calculate the overall vertical occupation of space. The stratification was derived from the forest cover, which is calculated from the ratio between the numbers of occupied 1-m^2 squares and the total number of squares in each 1-m height interval (Figs. 2a, 3a, 4a, Table 1). A difference greater than 20% in the percentage tree cover between two height intervals indicates the beginning of a new layer. The total occupation of space was obtained from the ratio

1. *Alchornea alnifolia*
2. *Byttneria biloba*
3. *Dalbergia greveana*
4. *Diospyros pervillei*
5. *Diospyros tropophylla*
6. *Doranthoxylon chouxi*
7. *Drypetes madagascariensis*
8. *Fernandoa madagascariensis*
9. *Garcinia aphanoplebia*
10. *Grangeria porosa*
11. *Macphesonia gracilis*
12. *Mammea punctata*
13. *Molinaea retusa*
14. *Polyalthia henricii*
15. *Rhopalocarpus lucidus*
16. *Rinorea greveana*
17. *Rothmannia reniformis*
18. *Ruellia* sp.
19. *Sapium melanostictum*
20. *Scolopia madagascariensis*
21. *Strychnos madagascariensis*
22. *Tetrapterocarpon geayi*
23. *Trilepisium madagscariense*
24. *Vitex* sp.
25. *Xylopia bemarivensis*
26. *Zanthoxylum tsihanimposa*

FIG.3b. Schematic profile of the vegetation in quadrat 3 in JBB.

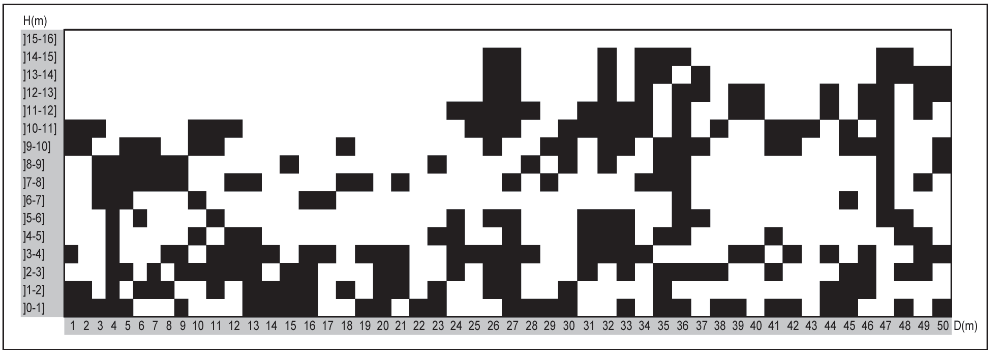


FIG. 4a. Structural profile of the vegetation in quadrat 1 in JBC (y-axis: length of the transects; x-axis: height intervals of 1 m; black squares: space occupation of the vegetation derived from contact between vegetation and measuring pole; white squares: no contact between vegetation and pole).

between the overall number of occupied squares and the total number of squares across all strata.

Schematic profile. A 50-m long rope was stretched horizontally along the 50-m transect line, and all plants touching the rope were drawn in their entirety (Figs. 2b, 3b, 4b). All individual plants within a 2-m strip on both sides of the transect line were projected onto the line. Whenever the trunks of two individual trees overlapped in the projection, only the most proximate individual tree was drawn. This method gives an overview of the typical structural elements of the vegetation.

Spatial structural analyses. The grid method was adopted for data collection. It consists of a projection of the exact position of each individual plant onto graph paper. Each vegetation quadrat of 30 x 30 m was subdivided into 36 small plots of 5 x 5 m. Each square on the paper corresponds to a plot of 25 m^2 on the ground. In each plot, maximum height (Hm), diameter at breast height (DBH) of individual plants

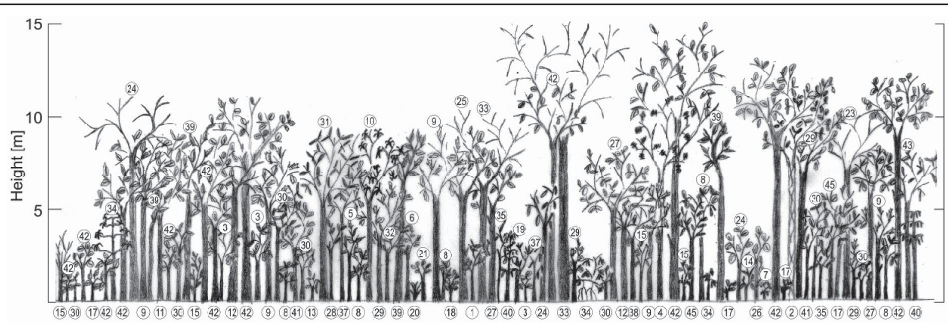


FIG. 4b. Schematic profile of the vegetation in quadrat 1 in JBC.

TABLE 1. Number and intervals of strata in each quadrat for each site.

Quadrats	Quadrat 1	Quadrat 2	Quadrat 3	Quadrat 4
SITE		JBA		
STRATA INTERVALS (m)	0-1 1-6 6-12	0-6 5-15	0-1 1-3 3-5 5-10	0-1 1-13
SITE		JBB		
STRATA INTERVALS (m)	0-1 1-15	0-2 2-14	0-5 5-12 12-15	
SITE		JBC		
STRATA INTERVALS (m)	0-4 4-7 7-15	0-12 12-15		

having a stem diameter >/= 10 cm, maximum stem diameter of those having a diameter <10 cm, and diameter of the canopy were measured for each individual plant present in the plot, excluding plantlets. Abundance and density were calculated for five diameter classes:] 0-2.5] cm,] 2.5-5] cm,] 5-10] cm,] 10-20] cm, and >20 cm. The density of these five diameter classes was plotted for one representative quadrat per site with ArcView GIS 3.3 software. These were quadrat 3 in JBA, quadrat 3 in JBB and quadrat 1 in JBC. The mean crown diameter was calculated for each stem diameter class and assigned to each individual tree of a stem diameter class. This way, the mean occupation of space was determined for each diameter class and the entire forest stand. This was graphically visualized with ArcView GIS 3.3.

Floristic analyses. All individual plants within the vegetation quadrats were determined to species level whenever possible. 96.89% of all specimens (n = 8907) in JBA, 97.12% (n = 4248) in JBB, and 99.18% (n = 4902) in JBC could be so determined. Plant nomenclature follows Schatz (2001) and the samples collected were deposited and identified in the National Herbarium in the Botanical and Zoological Park of Tsimbazaza (TAN), Antananarivo, Madagascar. The number of species and families were determined for each vegetation quadrat. The relative frequency was calculated for each species per 900-m² quadrat and all species with frequencies over 5% were listed for comparison between sites.

Comparative analysis. A cluster analysis was performed in order to test for site and quadrat similarities in vegetation structure, floristic traits, and general characteristics. For this analysis, 11 habitat characteristics were chosen (* in Table 2). The site-specific values were standardized and we used the single linkage amalgamation method together with the squared Euclidean distance as distance measure to define the clusters.

RESULTS

Relative abundance of both mouse lemur species at the three sites. We captured 32 individual *M. murinus* and 24 individual *M. ravelobensis* in JBA, giving a relative abundance of 1.3 *M. murinus* for each *M. ravelobensis* individual. At the second site (JBB) we captured 55 individual *M. ravelobensis* but no *M. murinus*, whereby the relative abundance was highly skewed towards *M. ravelobensis*. In JBC we captured 34 individual *M. murinus* and only three individual *M. ravelobensis*, resulting in a relative abundance of 8.82 *M. murinus* for each *M. ravelobensis* (i.e. high skew towards *M. murinus*). For both species we therefore have one site with high and one with low relative abundance and one site with about equal relative abundance (JBA) in our comparisons.

Habitat descriptions

JBA

The forest in JBA was a multi-stratum forest with a maximum height of about 16 m. The number of

TABLE 2. Habitat characteristics of the three sites. (* = habitat characteristics chosen for the cluster analysis).

SITES	JBA	JBB	JBC
Maximum height (m)*	16	22	16
Type of substrate*	S	A	S
Elevation (m)*	190	89	343
Mean number of species per quadrat*	113	69	105
Mean number of families per quadrat*	42	30	46
Total number of species per site	186	109	132
Total number of families per site	58	43	51
Proportion of individual plants with]0-10] cm stem diameter*	97.5	96.6	97.5
Proportion of individual plants with > 10 cm stem diameter*	2.47	3.41	2.49
Mean overall number of plants/25 m²*	59.1	38.2	67.3
Mean vertical occupation of space (%)*	32.5	32.8	34.2
Mean number of individual trees per quadrat*	2227	1416	2451
Mean density of lianas (ind./25 m²)*	9.1	11.2	8.2
Ratio of captured *M. murinus* / *M. ravelobensis*	1.3	0 : 55	6.2

S: Sandy soil, A: Argilliferous soil

forest strata varied from two to four between quadrats (Table 1). Five species were common (> 5% relative frequency) at the site: *Noronhia boinensis* (Oleaceae), *Scolopia inappendiculata* (Flacourtiaceae), *Justicia venalis* (Acanthaceae), *Acalypha reticulata* (Euphorbiaceae), and *Croton bernieri* (Euphorbiaceae) (Fig. 2b, Appendix A). Two of these species (*Noronhia boinensis* and *Scolopia inappendiculata*) have been reported to be consumed by mouse lemurs (reviewed in Radespiel 2006). Both species feed on *Noronhia boinensis*, but *M. murinus* eats the fruits whereas *M. ravelobensis* consumes the gum (Rahelinirina 2002). In addition, *M. murinus* feeds on the fruits of *Scolopia inappendiculata* (Martin 1973).

A total of 186 species belonging to 58 families was detected in JBA. Per quadrat of 900 m², a mean of 2227 individual plants belonged to a mean of 113 species and 42 families (Table 2). The forest was predominantly composed of individuals with a diameter below 2.5 cm (Table 3). The density of the individuals decreased with increasing diameter. In the highest diameter class (> 20 cm), the density was very low with only 0.21 ind./25 m². Lianas occurred with a density of 9.14 ind./25 m². The visualization

TABLE 3. Abundance and density of individual plants in the five diameter classes at the three sites.

Diameter class	]0-2,5 cm]	]2,5-5 cm]	]5-10 cm]	]10-20 cm]	> 20 cm
			JBA		
Abundance %	78.78	12.49	6.24	2.10	0.37
Density (ind./25 m²)	48.99	6.76	3.57	1.10	0.21
			JBB		
Abundance %	77.92	12.68	5.99	2.47	0.94
Density (ind./25 m²)	26.44	4.67	2.17	1.06	0.35
			JBC		
Abundance %	80.18	13.22	4.11	2.01	0.48
Density (ind./25 m²)	53.98	8.85	2.79	1.32	0.32

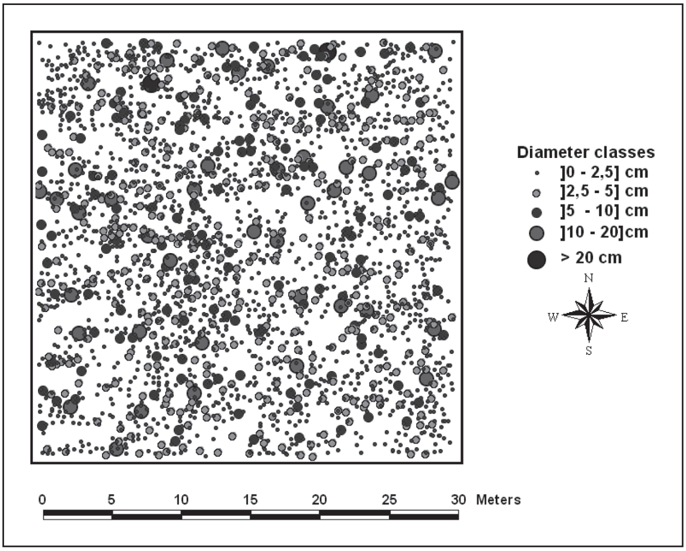


FIG. 5a. Spatial distribution of individual plants by stem diameter in quadrat 3 in JBA.

of all individual plants in the representative quadrat (quadrat 3, Fig. 5a) shows a very dense forest structure composed of many relatively small trees with small canopies (Figs. 2b, 5b). Structural and schematic profiles of the vegetation in the same quadrat are shown in Figs. 2a and 2b respectively. Of the 79 tree species recorded along the four schematic profiles, 16 species (20.25%) have previously been recorded as food plants of either *M. murinus* (n = 3; 3.8%), *M. ravelobensis* (n = 7; 8.9%), or both mouse lemur species (n = 6; 7.6%) (reviewed in Radespiel 2006).

JBB

The maximum height of the forest in JBB was about 22 m and it was composed of two to three strata (Table 1). The following 11 plant species were common: *Monanthotaxis pilosa* (Annonaceae), *Molinaea retusa* (Sapindaceae), *Malleastrum gracile* (Meliaceae),

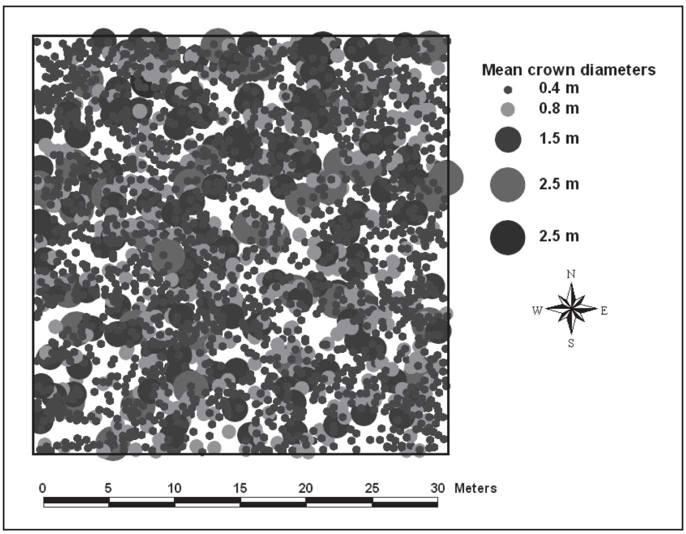


FIG. 5b. Mean occupation of space by all individual plants assigned to five stem diameter classes (cf. Fig. 5a) in quadrat 3 in JBA. Shown are the mean crown diameters calculated from the field measurements for each stem diameter class.

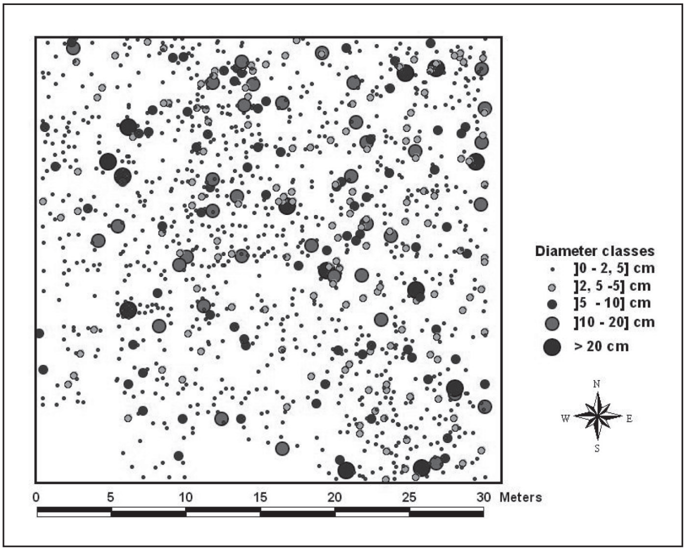


FIG. 6a. Spatial distribution of individual plants by stem diameter in quadrat 3 in JBB.

Mascarenhasia gracile (Apocynaceae), *Tricalysia cryptocalyx* (Rubiaceae), *Rinorea greveana* (Violaceae), *Strychnos madagascariensis* (Loganiaceae), *Sapium melanostictum* (Euphorbiaceae), *Grangeria porosa* (Rosaceae), *Diospyros tropophylla* (Ebenaceae), and *Doranthoxylon chouxi* (Sapindaceae) (Fig. 3b, Appendix A). They did not overlap with the common species in JBA. Four of these 11 common species (*Molinaea retusa*, *Malleastrum gracile*, *Strychnos madagascariensis* and *Grangeria porosa*) have previously been reported to be consumed by *M. ravelobensis*, but only one of them (*Sapium melanostictum*) is a known food plant of *M. murinus* (reviewed in Radespiel 2006). *M. ravelobensis* fed on leaves of these four species (Weidt 2001, Hagenah 2001) and *M. murinus* on the gum of *Sapium melanostictum* (Rahelinirina 2002).

A total of 109 plant species belonging to 43 families was detected in JBB. Per quadrat of 900 m^2, a mean of 1416 individual plants belonged to a mean of 69 species and 30 families (Table 2). As in JBA,

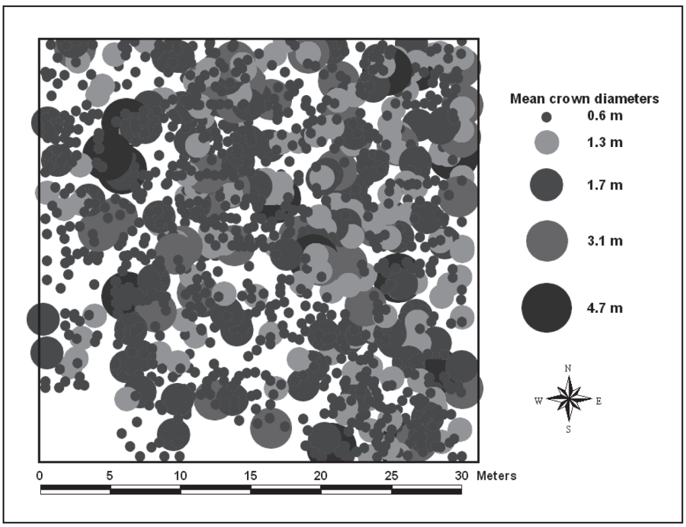


FIG. 6b. Mean occupation of space by all individual plants assigned to five stem diameter classes (cf. Fig. 6a) in quadrat 3 in JBB. Shown are the mean crown diameters calculated from the field measurements for each stem diameter class.

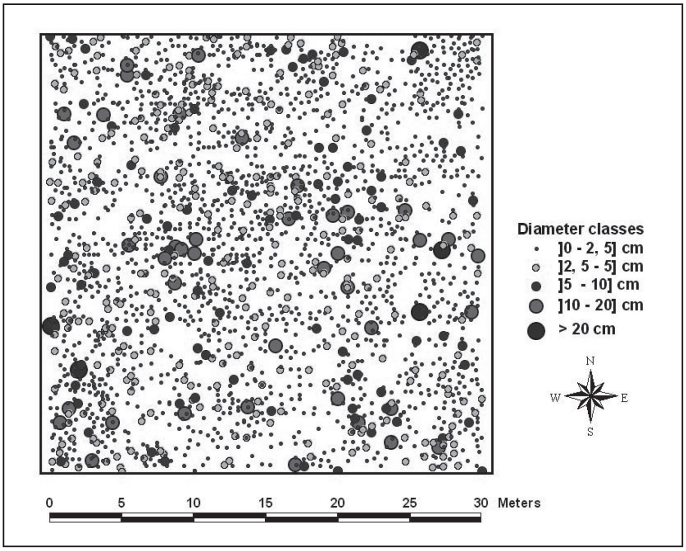


FIG. 7a. Spatial distribution of individual plants by stem diameter in quadrat 1 in JBC.

the forest was mostly composed of small individual plants with a diameter smaller than 2.5 cm (Table 3). Densities were highest in this class and decreased with increasing diameter. The mean density of lianas was 11.22 ind./25 m^2. The visualization of the individual plants in the representative quadrat (quadrat 3, Fig. 6a) reveals a greater heterogeneity in structure and a partly lower density than in JBA (see also Figs. 3b and 6b). Moreover, there was a greater number of trees with a larger crown diameter (Figs 3b, 6b). An example of the structural and schematic profile of the vegetation in the same quadrat is shown in Figs. 3a and 3b. Of the 64 tree species recorded along the three schematic profiles, 14 species (21.87 %) have previously been recorded as food plants of either *M. ravelobensis* (n = 8, 12.5 %), *M. murinus* (n = 4, 6.3 %), or both mouse lemur species (n = 2, 3.1 %) (reviewed in Radespiel 2006). Taken together, food plants of *M. ravelobensis* appear slightly more frequently than those of *M. murinus* among the com-

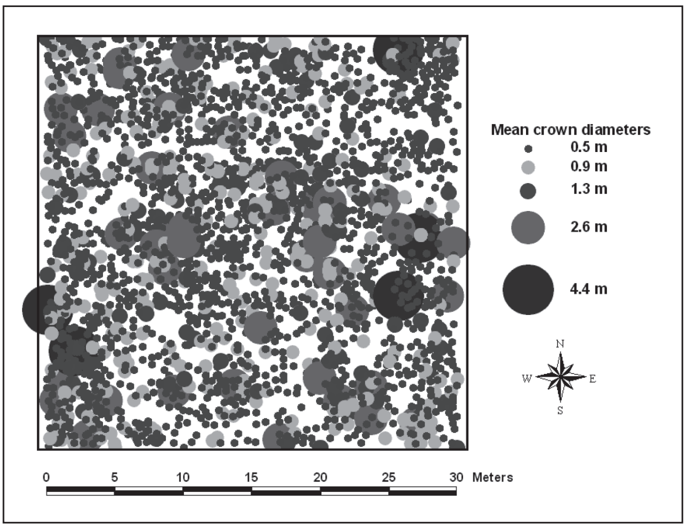


FIG. 7b. Mean occupation of space by all individual plants assigned to five stem diameter classes (cf. Fig. 7a) in quadrat 1 in JBC. Shown are the mean crown diameters calculated from the field measurements for each stem diameter class.

mon plant species and in the schematic profiles of JBA.

JBC

The forest in JBC had a maximum height of 16 m and had two strata in both vegetation quadrats (Table 1). Seven plant species were common; two of them also occurred in JBA but none in JBB (Appendix A, Fig. 4b). These are *Noronhia boinensis* (Oleaceae), *Scolopia inappendiculata* (Flacourtiaceae), *Tarenna alleizettii* (Rubiaceae), *Securinega capuronii* (Euphorbiaceae), *Coptosperma* sp. (Rubiaceae), *Coptosperma nigrescens* (Rubiaceae), and *Canthium humbertianum* (Rubiaceae). Two of these species are among the food plant species of *M. murinus*, reviewed in Radespiel (2006), *Scolopia inappendiculata* (Martin 1973) and *Tarenna alleizettii* (Génin 2003), and *M. murinus* was reported to consume the fruits of both. None of the common plant species is a known food plant of *M. ravelobensis*.

A total of 132 species belonging to 51 families was detected in JBC. Per quadrat of 900 m^2, a mean of 2451 individual plants was recorded, belonging to a mean of 105 species and 46 families (Table 2). As in the two other sites, the forest in JBC was mostly characterized by individuals of a diameter smaller than 2.5 cm and a very low density of large trees (Table 3). Lianas occurred with a mean density of 8.17 ind./25 m^2. The spatial model of the individual plants in quadrat 1 in JBC (Fig. 7a) shows a homogeneous and dense distribution of individual plants. The canopies were partly larger in JBC than in JBA (Figs. 4b, 7b). The structural and schematic profiles of the vegetation in this quadrat are shown in Figs. 4a and 4b. Of the 69 tree species recorded along the two schematic profiles, 14 species (20.28%) have previously been recorded as food plants of either *M. murinus* (n = 3, 4.3 %), *M. ravelobensis* (n = 6, 8.7 %), or both mouse lemur species (n = 5, 7.2%) (reviewed in Radespiel 2006).

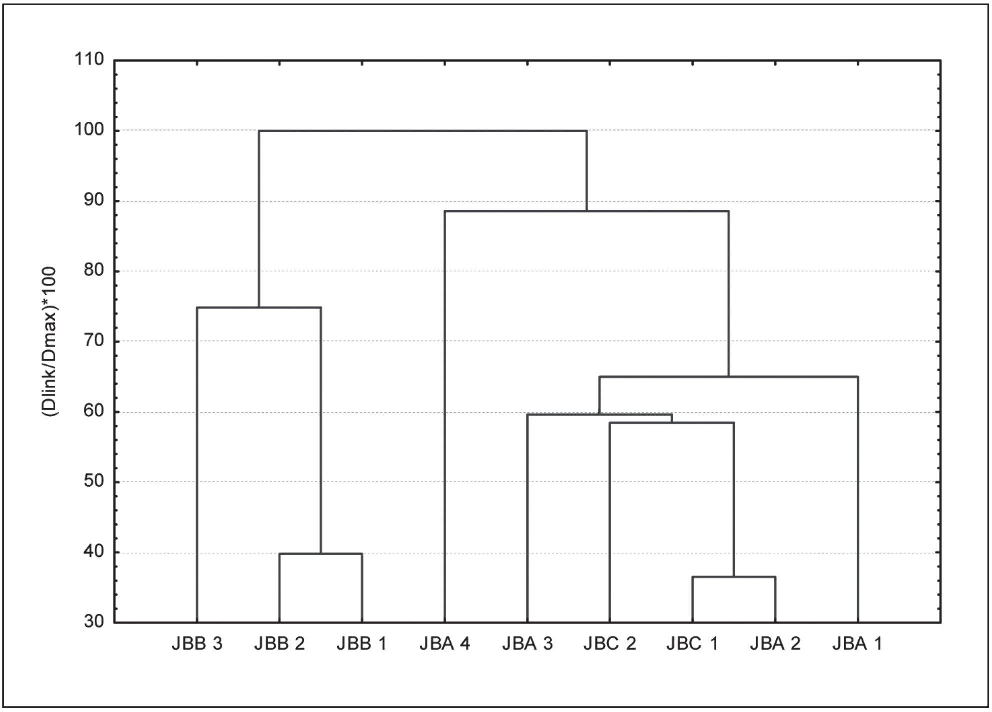
Comparison between sites. The cluster analysis revealed that the quadrats in JBA and JBC were most similar to each other and dissimilar to all three quadrats from JBB (Fig. 8). The similarities between JBA and JBC were reflected in a lower maximum height of the forest than at JBB, in the same type of soil, in a larger mean number of species and plant families per quadrat than at JBB, but also in larger overall numbers of plant families per site than at JBB, despite the fact that JBA contained the largest number of quadrats and JBC the smallest (Table 2). Moreover, JBA and JBC had both similarly high overall plant densities and low liana densities. The similarities between some quadrats of JBA and JBC were even larger than those between some quadrats of the same site, leading to one mixed cluster of the six quadrats of both sites.

Five parameters varied according to increasing or decreasing relative abundances (from JBB through JBA to JBC) of the two mouse lemur species (Table 2). These were the parameters elevation (increasing from JBB to JBC), the mean number of plant families per quadrat (increasing from JBB to JBC), the mean number of individual plants per 25 m^2 (increasing from JBB to JBC), the mean number of trees per quadrat (increasing from JBB to JBC), and the density of lianas (decreasing from JBB to JBC). In general, it seems that the relative abundance of *M. ravelobensis* decreased with increasing elevation, increasing taxonomic diversity, increasing plant and tree densities, and with decreasing liana densities. *M. murinus* showed the opposite trend.

DISCUSSION AND CONCLUSION

This study aimed to determine habitat characteristics that may coincide with, and therefore possibly explain, the varying relative abundance of two mouse lemur species in three different habitats. Parameters analyzed comprised several structural and several floristic characteristics, both of which are here discussed.

The comparison of structural characteristics revealed that the site of highest relative abundance of *M. ravelobensis* (JBB = site without *M. murinus*) differed clearly from the other sites, in which *M. murinus* occurred with increasing relative abundance. The structural differences between JBA/JBC on the one hand and JBB on the other were most prominently maximum forest height, the proportion of trees with very large stem diameter, and average plant, tree, and liana density per surface unit. Could these factors be functionally linked to the uneven representation of both mouse lemur species in the forest? Forest height has previously been related to the presence of some arboreal animals (Schunke & Hutterer 2000), and to the availability of surface water in different mouse lemur habitats (Rakotondravony & Radespiel 2009). Sufficient water supply allows single trees to grow taller and thicker and, as a consequence, overall plant density declines as the growth of smaller trees is inhibited below large tree crowns. In contrast, individual trees remain smaller and thinner under drier conditions, like those in JBA



Habitat characteristics	JBB3	JBB2	JBB1	JBA4	JBA3	JBC2	JBC1	JBA2	JBA1
Maximum tree height (m)	22	22	16	16	12	16	12	13	14
Substrate	A	A	A	S	S	S	S	S	S
Elevation (m)	89	89	89	190	190	343	343	190	190
Number of species	77	64	69	85	106	103	106	119	124
Number of families	34	28	30	35	37	47	45	50	46
% ind. with]0-10] cm stem diameter	95.94	96.75	97.09	95.88	98.29	97.11	97.91	97.97	97.91
% ind. with stem diameter > 10 cm	4.06	3.25	2.91	4.12	1.71	2.89	2.09	2.03	2.09
Mean number of indiv./25 m²	34.53	34.28	45.92	59.33	68.47	72.06	62.44	62.92	45.58
Vertical occupation of space (%)	32.8	33	31.6	31.36	32.67	32.53	35.87	36.13	32.27
Number of ind./900 m²	1298	1253	1697	2196	2559	2610	2292	2474	1678
Mean number of liana sprouts/25 m²	20.08	9.17	11.22	6.25	7.75	8. 94	7.39	12.14	10.53

FIG. 8. Cluster analysis for all nine vegetation quadrats at the three sites based on 11 habitat parameters (cf. Table 2).

and JBC, and the vegetation in total can therefore reach higher densities.

It has also been observed in a previous study that *M. ravelobensis* populations reach highest densities under humid conditions and lowest under dry conditions, whereas the opposite seems to be true for *M. murinus* (Rakotondravony & Radespiel 2009). Concerning the related structural elements in this study, it is possible that *M. ravelobensis* performs better when relatively more very large trees or more lianas are present, or when the forest is less dense. These large trees could in principle provide high-quality tree holes (i.e. high safety, good insulatory capacities) serving as shelters, but a parallel study has shown that tree holes are not used more often in JBB than in JBA for sleeping by *M. ravelobensis* (Quietzsch 2009). On the other hand, lianas have indeed previously been reported to offer important sleeping sites for *M. ravelobensis* (Radespiel *et al.* 2003) and the availability of lianas has already been suggested as being important for *M. ravelobensis* in an earlier study (Rendigs *et al.* 2003). This suggestion seems to be supported by the findings of this study.

The floristic composition of a given habitat typically has a large impact on primate feeding ecology. Animals can only consume those food items that are available at a given site in a given season, and a species may not occur, or not reach high numbers, when essential resources are missing or rare. Differences in the floristic composition can also explain differences in feeding strategies of herbivorous animals (Stevenson *et al.* 1998). Compared with the other sites, JBB is a less diverse habitat with respect to floristic composition, possessing a lower richness in plant species and plant families and a floristic composition that is remarkably different from JBA/JBC. The analysis of the floristic data suggests that the availability and abundance of certain food plant species may be functionally linked to the relative abundance of the two mouse lemur species. At all three sites the list of common plant species contained more food plants of the mouse lemur species that had the higher relative abundance. This trend could not, however, be seen in the general list of plant species along the schematic profiles. One hypothetical explanation for these discrepancies could be that it is the commonness of certain food plant species that determines the relative abundance of the two mouse lemur species. Further detailed analyses, including data on resource use and resource requirements of *M. murinus*, are urgently needed to answer this question.

The strong similarities between JBA and JBC in most vegetation parameters were somehow unexpected, since *M. ravelobensis* is only poorly represented in JBC but is rather frequently captured in JBA. Five parameters, however, varied systematically with decreasing relative abundance of *M. ravelobensis*. These were increasing altitude, a higher average number of plant families per plot, a higher overall plant and tree density, and a lower density of lianas. In a previous study, other high-altitude habitats were also shown to have lower population densities of *M. ravelobensis* than low-altitude habitats (Rakotondravony & Radespiel 2009). Lianas have already been suggested in previous studies to be important for *M. ravelobensis* (Rendigs *et al.* 2003), and they have been shown to be frequently used as sleeping sites (Radespiel *et al.* 2003). Regarding the other parameters, it is difficult to imagine how a higher taxonomic diversity or a higher density of the vegetation per se should negatively influence populations of *M. ravelobensis*, unless certain key resources may decrease under these circumstances. The floristic analysis revealed some differences between JBA and JBC that could indeed be potentially related to the question of key resources: The commonest plant species did not overlap completely between the two sites. Moreover, among the common plant species in JBC there was no *M. ravelobensis* food plant but two of *M. murinus*. Future studies should investigate more specifically the relative importance of such potential key food resources for the varying species abundance of these two partially sympatric mouse lemur species.

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APPENDIX A. Commonest plant species (> 5%) at each site (x: species exists with an abundance < 5%, -: species does not exist at this site)

JBB	Quadrats	JBA	Quadrats	JBC	Quadrats
Monanthotaxis pilosa	1,2,3	-		-	
Molinaea retusa	1,2	x		-	
Malleastrum gracile	1,2	x		-	
Mascarenhasia gracile	3	-		-	
Tricalysia cryptocalyx	2	-		-	
Rinorea greveana	3	-		-	
Strychnos madagascariensis	3	x		x	
Sapium melanostictum	1	x		x	
Grangeria porosa	1	x		-	
Diospyros tropophylla	3	x		x	
Doranthoxylon chouxi	3	x		x	
x		*Noronhia boinensis*	1,2,3,4	*Noronhia boinensis*	1,2
x		*Scolopia inappendiculata*	1,2,3,4	*Scolopia inappendiculata*	2
-		*Justicia venalis*	1,2,3,4	x	
x		*Croton bernieri*	4	x	
-		*Acalypha reticulata*	4	-	
x		x		*Tarenna alleizettii*	1,2
-		x		*Securinega capuronii*	1
-		-		*Coptosperma* sp.	1
x		x		*Coptosperma nigrescens*	1
-		x		*Canthium humbertianum*	