

Can differences in floristic composition explain variation in the abundance of two sympatric mouse lemur species (*Microcebus*) in the Ankarafantsika National Park, northwestern Madagascar?

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Abstract

This study investigates the distribution of two mouse lemur species, *Microcebus murinus* and *M. ravelobensis*, in the Ankarafantsika National Park, to identify correlations between floristic composition of the habitat these species occupy and with the distribution and availability of food plants of the lemurs. Both aspects were studied at large and small spatial scales. The two mouse lemur species were not equally distributed in the study area: at two sites they occurred sympatrically with different relative abundances, while at the third study site, *M. ravelobensis* was the single member of this genus. Floristic composition was recorded using a transect method and compared within and between sites to detect differences in local plant species. Lemur food plants were determined using data from published studies and from a parallel study. At the large spatial scale, the general dissimilarity between the site of exclusive presence of *M. ravelobensis* and the sites at which both mouse lemur species occurred sympatrically corresponded to differences in floristic composition, but not to the distribution of food plants of the lemurs. At the smaller spatial scale, differences in habitat use could not be related to differences in floristic composition or to the distribution of food plant species. Ecological factors other than food availability

may better explain variation in lemur distribution and abundance, which may be functionally linked to structural and ecological characteristics of their habitat.

Key words: Floristic composition, *Microcebus murinus*, *Microcebus ravelobensis*, habitat selection, food plants, availability

Résumé détaillé

Cette étude a été réalisée dans la forêt sèche caducifoliée dans le Parc National d'Ankarafantsika. La forêt d'Ankarafantsika, située dans la partie Nord-Ouest de Madagascar, constitue l'une des deux plus grandes forêts sèches restantes de Madagascar. Les forêts sèches caducifoliées sont considérées comme l'un des écosystèmes majeurs à Madagascar. Elles abritent une grande diversité d'espèces endémiques végétales et animales. Cependant, elles ne sont pas floristiquement et structurellement homogènes. De même, la distribution des populations animales n'est pas homogène. Dans la présente étude, les variations des compositions floristiques dans trois habitats à différente abondance relative de deux espèces de lémuriers, *Microcebus murinus* et *M. ravelobensis* ont été analysées dans le Parc National d'Ankarafantsika. Dans le parc, les deux espèces de lémuriers sont distribuées de manière inégale. Dans un site (JBB), *M. ravelobensis* vit exclusivement. Il partage le deuxième site (JBA) avec *M. murinus*. Le troisième site (JBC) est principalement peuplé par *M. murinus*.

Trente-six transects de 50 m de long ont été installés dans les trois sites pour l'étude de la végétation. Les sites ont été comparés floristiquement afin d'identifier les relations entre la distribution des lémuriers et la composition floristique de chaque site d'une part et la distribution des lémuriers et la disponibilité de leurs plantes alimentaires d'autre part. Pour cette dernière, la liste des espèces communes recensées dans les trois sites a été comparée avec celle des plantes alimentaires des lémuriers. La liste des espèces alimentaires a été obtenue à partir des données disponibles ainsi que d'une étude effectuée parallèlement. Les deux aspects ont été étudiés à grande échelle c'est-à-dire entre les trois sites et

à petite échelle c'est-à-dire à l'intérieur du site de sympatrie (JBA).

Les résultats des analyses montrent que le site où *M. ravelobensis* vit en allopatrie (JBB) diffère clairement des deux autres sites où les deux espèces de lémuriens vivent partiellement en sympatrie (JBA et JBC). Il est floristiquement pauvre et moins diversifié et a une composition floristique très différente des deux autres sites. A grande échelle, la variation d'abondance des deux espèces de lémuriens correspond à des différences de composition floristique mais aucune relation directe avec la distribution des espèces alimentaires n'a été détectée. Au niveau local ni la composition floristique ni la distribution des plantes alimentaires n'est liée à la distribution des lémuriens dans le site JBA. Les différences d'abondance des deux espèces de lémuriens sont fonctionnellement liées à des différences structurales et floristiques de la végétation.

Mots clés : Composition floristique, *Microcebus murinus*, *Microcebus ravelobensis*, sélection de l'habitat, plantes alimentaires

Introduction

Madagascar is the fourth largest island in the world, covering an area of 587 045 km². It has an exceptionally high floristic and faunal diversity and a high rate of endemism of over 90% for most taxonomic groups (Goodman & Benstead, 2003). The island is considered to be one of the most important biodiversity hotspots in the world. One of the unique radiations in Madagascar concerns primates. Lemurs are 100% endemic to Madagascar and they occur in a wide variety of forest types, ranging, for example, from the evergreen rain forests of the east, the dry deciduous forests of the west, and the spiny bush of the south (Mittermeier *et al.*, 2010). However, it has been estimated that 90% of the original forests have already disappeared since the arrival of humans on the island about 2000 years ago (Smith, 1997). Deforestation in eastern Madagascar has been most rapid in lowland areas (Green & Sussman, 1990). Dry deciduous forests have suffered from clear-cutting at an even faster rate (Harper *et al.*, 2007). Two of the largest remaining western forest areas (Ankarafantsika and the forests of the Menabe) were recently reduced substantially by fires, illegal logging, and deforestation for agriculture (Sommer *et al.*, 2002). Similarly, the southern spiny forests have heavily suffered from slash-and-burn cultivation (Harper *et al.*, 2007). Therefore, it is unlikely that

any of these ecosystems will maintain their present biodiversity over time (Ganzhorn *et al.*, 2001).

Effective conservation planning for the unique habitats in Madagascar depends on information on the distribution and abundance of the fauna and flora (Schmid & Alonso, 2005). It is essential to know the factors determining the distribution of species and limiting their coexistence. As lemurs are among the most prominent target species for conservation in Madagascar, one of the central issues in lemur conservation is to understand the processes affecting their distribution and abundance. In general, coexistence of primate species has been linked proximately to differential habitat utilization and feeding habits (Gautier-Hion *et al.*, 1983; Terborgh, 1983).

Up to two sympatric species of mouse lemurs (*Microcebus* spp.) have been recorded in the dry deciduous forests of western Madagascar (Rendigs *et al.*, 2003; Schwab & Ganzhorn, 2004; Olivieri *et al.*, 2007). In the Mahajanga region of northwestern Madagascar, *M. murinus* and *M. ravelobensis* are known to occur (Rakotondravony & Radespiel, 2009). In some forests, these two species co-exist with varying relative abundance and in others, they are allopatric. In a previous publication, differences in general habitat characteristics between two sites where they occur in sympatry and the site with only *M. ravelobensis* were described (Sehen *et al.*, 2010). The latter site was characterized by a forest with a relatively large proportion of tall trees and a higher density of lianas, but a lower overall density and diversity of plants. The floristic composition was different from the sites where the two *Microcebus* occur in sympatry.

In this complementary study, we analyze in more detail large-scale inter-site and small-scale intra-site variation in habitat structure and floristic composition, and to relate these parameters to variation in relative abundance of both *Microcebus* spp. The following questions are addressed: 1) Can the presence/absence of both *Microcebus* spp. at a given site be related to its floristic characteristics? 2) Is the distribution of both *Microcebus* spp. related to the distribution of their specific food plants?

Methods

Study sites

The study was conducted at three sites in northwestern Madagascar in the dry deciduous forest of the Ankarafantsika National Park (Figure 1). Since 1927, the forests of Ankarafantsika have been protected as

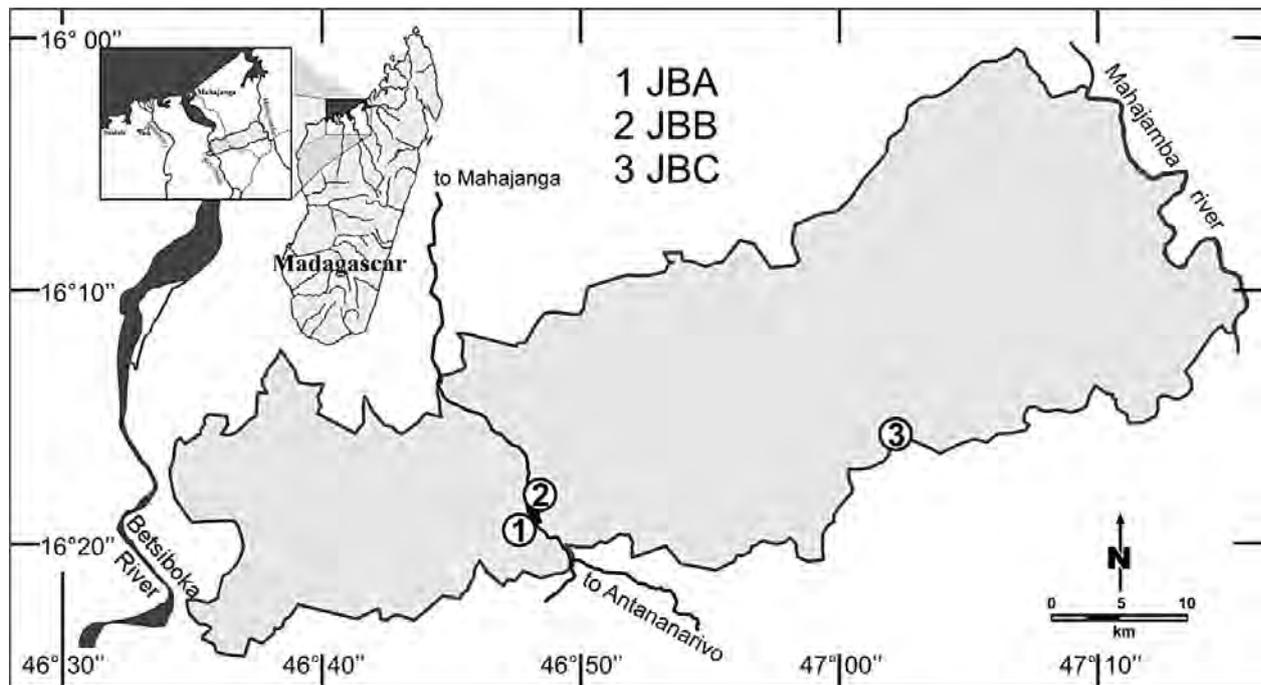


Figure 1. Map with the three study sites in the Ankarafantsika National Park (gray area). JBA: Jardin Botanique A, JBB: Jardin Botanique B, and JBC: Jardin Botanique C.

two separate components: the Strict Nature Reserve with an area of 60 000 ha towards the east and the Forestry Reserve with an area of 70 026 ha to the west. As of 1997, both zones have been protected under the status of a National Park.

The climate of Ankarafantsika is characterized by two strongly contrasting seasons, a cool and dry season from May to October and a hot and rainy season from November to April. The majority of the precipitation falls in January and February and annual rainfall varies from 1220 to 2255 mm (period: 1997–2004, Rakotondravony & Radespiel, 2009). The mean annual temperature is 27°C, with a maximum monthly mean of 37°C from October to November and a minimum monthly mean of about 16°C in June and July (Schmelting *et al.*, 2000).

The first study site, called Jardin Botanique A (JBA), is located near the park headquarters at Ampijoroa. Its vegetation consists of a dry deciduous forest growing on sandy soils. It is a relatively flat area (< 10% slopes) at 190 m above sea level (m.a.s.l.) and contains a trail system grid delineated in 50 m increments and covering an area of 30.6 ha. The second site, Jardin Botanique B (JBB), is located north of Ravelobe Lake and at 89 m a.s.l., about 3 km distant from JBA. Part of it is an alluvial forest growing on argilliferous soils partially flooded during the rainy season. It can also be accessed on a grid of trails with intersections at every 25 m covering an area of 5.1 ha. The third site, Jardin Botanique C (JBC), is located about 28 km away from JBA and JBB on a

high plateau at 343 m a.s.l. The vegetation of this latter zone is characterized by a dry deciduous forest growing on calcitic soils. JBC covers about 33.9 ha and is only accessible on a central trail (length: about 1300 m) that passes through the study site.

All three study sites are part of a large and more or less continuous forest area and were selected because of the varying relative abundances of two species of *Microcebus*. In JBA, *M. ravelobensis* and *M. murinus* are sympatric and in similar overall abundance, but individuals of both species were not trapped in equal proportions at all trap locations (Rendigs *et al.*, 2003). In JBB, *M. ravelobensis* lives exclusively, and in JBC, *M. murinus* is notable dominant in number over *M. ravelobensis* (= Ankoririka III from Rakotondravony & Radespiel, 2009).

Study period

Vegetation sampling and lemur capturing at the JBA and JBB were carried out from May to November 2007, hence during the dry season. Within this period, JBC was visited twice, from 23 June to 16 July and from 13 August to 6 September.

Capture methods

Mouse lemurs were systematically trapped during 3–4 monthly capture nights at each site with Sherman live traps (23.5 x 8 x 9 cm³). Traps were installed either at all crossings of the internal grid system (JBA, JBB) or with two traps every 20 m along the main central trail

(JBC). A total of 99, 93, and 100 traps were installed at JBA, JBB, and JBC, respectively, during each night of trapping. Each captured animal was taken to the field camp, species identity, and sex determined. The two mouse lemur species are of comparable body mass, but differ in certain aspects of their morphometry (Zimmermann *et al.*, 1998), their genetics (Pastorini *et al.*, 2001), their acoustics (Zietemann *et al.*, 2000), and their ecology and social structure (Radespiel *et al.*, 2003a, 2003b, 2009; Weidt *et al.*, 2004). All animals were marked with 1–3 systematic ear biopsies (ca. 2 mm²) that provide a unique individual mark and allow identification of more than 100 individuals per site (Rakotondravony & Radespiel, 2009).

The relative abundances of both *Microcebus* spp. were determined as the number of captured individuals of either species per site. The difference in the trapping periods between JBA/JBB on the one hand and JBC on the other hand should not cause major problems for the analyses, since this study focuses on major transitions and on small scale intra-site variation among the two *Microcebus* spp. and the trapping regime was the same within each site and for both species. We used the capture results from May to November 2007 for JBA and JBB and from June/July and August/September for JBC. During these periods, 215 trap-nights were accrued at the three sites.

Characterization of vegetation

Eighteen and nine areas of physiognomically and floristically homogenous vegetation were delimited in JBA and JBB, respectively, based on field observations. Subsequently, a 50 m transect was installed in each delimited area. Transects were placed in zones the local vegetation best represented each area. In JBC, nine 50 m transects were installed perpendicularly to the main path at a distance of about 150 m from each other, since vegetation units could not be determined due to the lack of a grid system. Along these transects, data on floristic composition and on some characteristics of the forest were recorded following the methods described in Sehen *et al.* (2010). The plant nomenclature follows Schatz (2001).

Local distribution of mouse lemurs

Local distribution of each *Microcebus* spp. was determined only for the JBA, as the level of trapping effort was large enough to establish the local distribution pattern of both species reliably, and, at the same time, it varied enough to distinguish

between areas of low and high abundance of the two species. Each individually marked *Microcebus* was counted only once at each capture location. For each trap, the number of individual captured *M. murinus* and *M. ravelobensis* was determined irrespective of their trapping frequency. This approach was used to determine transects of high and low species abundance. Transects of high abundance (H) for each lemur species were defined as being surrounded by at least three of four neighboring trap locations where two or more individuals were captured. All areas with less than three such neighboring trap locations were considered as areas of low abundance (L). It should be noted, however, that not all individual *Microcebus* spp. at a given trap station may have been captured. The chosen abundance measure therefore should not be considered as an absolute measure. From long-term capture studies in JBA, there is no evidence that both species differ in their responses to traps (Mester, 2006) and the capture data should therefore be comparable.

Treatment of capture data

The relationship between the distribution of each *Microcebus* spp. and the vegetation was analyzed within and between sites. First, the floristic dataset was compared to detect differences in plant species composition. Further, the local distribution and abundance of the *Microcebus* spp. were determined for each site and delimited area. Finally, values of relative abundance of the lemurs were superimposed on the vegetation data, with the help of the phytosociological analysis, to test for patterns of congruence.

Data analysis

Multivariate analyses

A correspondence analysis was performed in order to examine the degree of floristic similarity of the vegetation transects and was computed using PC-Ord 5 (Benzécri, 1969, 1973; Hill, 1973, 1974); all plant species were included. This method positions all vegetation transects along n axes according to their similarity in the n analyzed variables (plant species abundance). By relating the grouping pattern of the vegetation transects to variations in relative *Microcebus* spp. abundance, this method allows to identify possible parameters that may explain variations in the abundance of these animals.

Phytosociological analysis

A table of different phytosociological variables was established in order to detect plant species for which

abundance differed systematically within and between sites. The traditional technique of manual sorting was applied for grouping the vegetation transects according to their floristic composition. The columns (transects) and the rows (plant species) of the data table were moved until groups of transects with similar floristic composition appear. The aim was to identify groupings of plant species which were frequent (frequency > 60%) in certain transect groups but absent or rare in others. This method was applied to identify potential indicator species, which characterize a site or a group of transects and to find congruencies between floristic composition and abundance of the lemurs. These were then compared to the list of known food plant species of the *Microcebus* spp. to explore possible congruencies between food plant availability and variations in the relative abundance of both species. Data on food plants consumed by the *Microcebus* spp. was obtained from the literature (reviewed in Radespiel, 2006) and from a parallel study at the same three study sites (Thorén, 2011; Thorén *et al.*, 2011).

Results

Comparisons on the large spatial scale

Distribution of the Microcebus spp. at the three sites

A total of 47, 73, and three individuals of *Microcebus ravelobensis* was captured in JBA, JBB, and JBC, respectively, whereas 61, zero, and 34 individuals of *M. murinus* were trapped at these three sites. Both species were captured in about equal numbers in JBA (47:61), no *M. murinus* but many *M. ravelobensis*

were captured in JBB, and only a few *M. ravelobensis* but many *M. murinus* were trapped in JBC.

Floristic characteristics of the three sites

Diversity of plant species and families was higher in JBA/JBB than in JBC (Table 1). This applies to the complete dataset as well as to the mean values from the 50-m transects. The phytosociological information (Table 2) reveals some general floristic similarities between the three sites. Six species occurred at all three sites with > 60% frequency. These are *Rothmannia reniformis*, *Strychnos madagascariensis*, *Sapium melanostictum*, *Xylopia bemarivensis*, *Diospyros tropophylla*, and *Dalbergia greveana*. They can be considered as characteristic species of all three sites. JBA and JBC had 11 highly frequent plant species in common (> 60% frequency) that were not found in JBB. These are *Scolopia inappendiculata*, *Nesogordonia stylosa*, *Baudouinia fluggeiformis*, *Capurondendron gracilifolium*, *Rhopalocarpus similis*, *Pyrostria* sp., *Commiphora* sp. 1, *Diospyros greveana*, *Vepris arenicola*, *Peponidium velutinum*, and *Croton* sp. 2. In addition, both sites had four highly frequent species in common (*Tabernaemontana coffeoides*, *Ochna ciliata*, *Polyalthia henricii*, and *Macphersonia gracilis*) that were also found in JBB but with a frequency of < 60%. These species can be considered as associated species at JBA and JBC. At JBB and JBC two plant species were present with a frequency > 60%. These are *Molinaea retusa* and *Coptosperma madagascariensis*, both of which were also found in JBA but with < 60% frequency. No frequent plant species (> 60%) was shared only between JBA and

Table 1. Taxonomic plant diversity and number/percentage of food plant species of *Microcebus murinus* and *M. ravelobensis* at three study sites in the Ankarafantsika National Park. JBA: Jardin Botanique A, JBB: Jardin Botanique B, and JBC: Jardin Botanique C.

Site	JBA	JBB	JBC
Number of plant species	126	74	109
Number of plant families	42	31	46
Mean number of tree species per transect	52.6 ± 4.67	33.7 ± 3.32	53.9 ± 3.69
Mean number of tree families per transect	27.0 ± 1.95	18.1 ± 1.91	27.8 ± 1.86
Total number of food plant species	24 (19.0%)	16 (21.6%)	19 (17.4%)
Number and % of food plant species of <i>M. murinus</i> exclusively	3 (2.4%)	2 (2.7%)	2 (1.8%)
Number and % of food plant species of <i>M. ravelobensis</i> exclusively	10 (7 %)	11 (14.9%)	8 (7.3%)
Number and % of food plant species of both lemur species	11 (8.7%)	3 (4.1%)	9 (8.3%)

JBB. Furthermore, each site is characterized by some plant species that were exclusively present at either one site with a frequency of > 60%. Seven such plant species were found frequently only in JBA, eight in JBB, and three in JBC (Table 2). These species are considered as those that floristically distinguish each site. Furthermore, 16, eight, and 11 associated species were found at JBA, JBB, and JBC, respectively. Some of the mentioned species reached even 100% frequency at one of the three sites. These are *Rothmannia reniformis*, *Scolopia inappendiculata*, *Nesogordonia stylosa*, *Noronhia boinensis*, and *Justicia venalis* in JBA; *Sapium melanostictum*, *Xylopiya bemarivensis*, *Molinia retusa*, *Grewia ambongensis*, *Cabuccala erythrocarpa*, and *Monanthotaxis pilosa* in JBB; and *Diospyros tropophylla*, *Rhopalocarpus similis*, *Vepris arenicola*, *Tabernaemontana coffeoides*, *Coptosperma madagascariensis*, *C. clavatum*, and *Tarenna* sp. in JBC. Thus, a total of five to seven plant species reached 100% frequency at each site, but these species were not identical between sites.

The ordination diagram of the vegetation transects from JBA, JBB, and JBC illustrates differences in highly frequent plant species between the three sites (Figure 2). It shows that the vegetation transects of

each site forms three distinct clusters. Along the first axis of this figure, JBA and JBC are more similar to one another than either to JBB. This can be explained by a number of plant species common to the two sites. A corresponding tendency is also seen along the second axis between JBA and JBB.

Food plant species of the *Microcebus* spp.

Of 126 plant species found in JBA (Table 1), 24 species (19.0%) are known food plants of either *Microcebus murinus* (n = 3; 2.4%), *M. ravelobensis* (n = 10; 7.9%), or both species (n = 11; 8.7%) (Table 2) (reviewed in Radespiel 2006; Thorén *et al.*, 2011). Of 74 plant species inventoried in JBB, 16 plant species (21.6%) are consumed by either *M. murinus* (n = 2; 2.7%), *M. ravelobensis* (n = 11; 14.8%), or both species (n = 3; 4.1%). Of 109 plant species encountered in JBC, 19 (17.4%) are eaten by either *M. murinus* (n = 2; 1.8%), *M. ravelobensis* (n = 8; 7.3%), or both species (n = 9; 8.2%). These results indicate that relatively few food plant species of *M. murinus* are available in JBB, but a nearly equal number of *M. ravelobensis* food plant species occurs at all three sites. The differences in the number of food plants of *M. ravelobensis* and

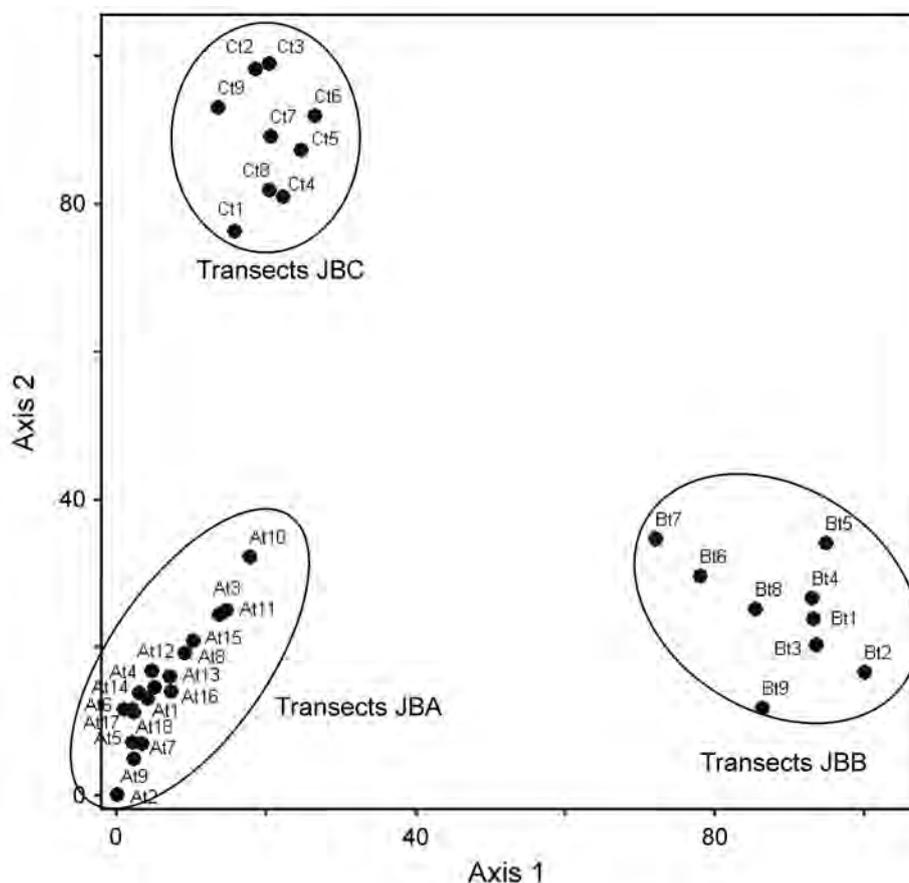


Figure 2. Correspondence analysis of the vegetation transects according to the relative abundance of plant species in JBA, JBB, and JBC. At, Bt, and Ct are the transects installed in JBA, JBB, and JBC, respectively.

Table 2. (cont.)

Parameters recorded in JBA and JBC	Food plants	Transsects JBA										Transsects JBB										Transsects JBC										Frequency																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		31	32	33	34	35	36	37	38	39	40											
Associated species in JBA and JBC		6	1	7	4	4	2	1	3	1	1	1	1	1	1	1	1	1	1	2	25	5	9	6	10	27	10	11	10	2	7	7	1	7	1	1	1	1	4	1	1	7	8	3	10	3	1		83,33	55,56	100		
<i>Tabernaemontana coffeoides</i>		1	1	2	3	2	1	3	1	1	2	1	1	1	1	1	1	1	1	1				2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	5	2	3	10	3	1		77,78	33,33	88,89	
<i>Ochna oiliata</i>		1	2	5	3	1	1	4	2	1	1	1	1	1	1	1	1	1	1	1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	1	2	2	3	1	2	1	1		61,11	44,44	88,89	
<i>Polyalthia henrici</i>		5	1	2	2	2	1	1	1	7	1	1	1	1	1	1	1	1	1	1				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	1	5	7	2	6	4	12	3		61,11	44,44	88,89	
<i>Mecherisonia gracilis</i>																																																					
Species characterizing JBB and JBC																																																					
<i>Melinaea retusa</i>	Lea., Fr.																																								11,11	88,89	66,67										
Associated species in JBB and JBC		1	1	2	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	4	2	5	1	5	2	3	1	3	1	3	3	5	1	6	1	1	2	55,56	66,67	100												
<i>Coptosperma madagascariensis</i>																																																					
Species characterizing JBA		5	6	3	4	9	1	5	1	1	2	3	2	1	2	1	3	1	3	1																					88,89	0	0										
<i>Noronhia obanceolata</i>		6	4	15	7	2	4	2	1	4	3	3	1	1	1	1	1	1	1	1																					77,78	0	0										
<i>Garcinia verrucosa</i>																																																					
<i>Malleastrum rakotozafy</i>	Fr.	10	1	1	3	1	4	1	4	3	1	2	1	1	1	1	1	1	1	1																					77,78	0	0										
<i>Mystroxydon aethiopicum</i>	Gum	4	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1																					66,67	0	0										
<i>(Cassine aethiopica)</i>																																																					
<i>Schizenterospermum rotundifolium</i>		1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1																					66,67	0	0										
<i>Astrocassine sp.</i>		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2																					61,11	0	0										
<i>Cassipourea microphylla</i>	Gum	6	4	16	12	15	13	5	12	5	12	5	12	5	12	5	12	5	12	5																					61,11	0	0										
Associated species in JBA																																																					
<i>Noronhia bohnensis</i>	Fruits	13	23	18	14	11	10	30	29	25	10	17	16	33	22	34	10	16	13	13																					100	0	55,56										
<i>Justicia venalis</i>		5	5	2	7	5	10	6	4	11	1	6	5	9	7	3	3	5	7	7																					100	0	33,33										
<i>Eugenia cloiselli</i>		1	1	1	1	1	1	2	1	2	1	2	1	1	4	1	3	1	1	1																					83,33	0	44,44										
<i>Protolus ditrimena</i>	Fr., Gum, Lea.	1	3	1	1	1	1	1	1	1	2	3	5	2	1	2	1	2	1	1																					83,33	0	33,33										
<i>Albizia mislikoronum</i>		5	2	2	1	2	2	2	1	1	1	1	3	3	1	3	6	2	3	1																					77,78	0	22,22										
<i>Mapouria sp.</i>		1	10	2	2	2	2	2	5	1	2	2	2	1	1	5	2	2	2	2																					77,78	0	55,56										
<i>Eusiphon gesy'i</i>		1	3	7	4	6	1	1	3	3	5	7	2	2	2	3	5	2	2	2																					94,44	0	22,22										
<i>Vitex pervillei</i>		1	1	1	2	1	4	1	1	1	3	6	4	4	4	3	2	1	1	1																					88,89	44,44	55,56										
<i>Erythroxylum coca</i>		9	2	5	1	2	3	5	3	4	1	1	1	11	2	2	2	2	2	2																					77,78	0	55,56										
<i>Bussea perrieri</i>	Gum	1	1	11	3	1	1	5	13	4	2	2	11	11	6	2	4	4	4	4																					72,22	0	44,44										
<i>Anaccolosa pervilleana</i>		1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1																					66,67	0	44,44										
<i>Vitex sp.</i>	Fr.	4	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1																					66,67	0	44,44										
<i>Mammea punctata</i>	Gum, Bu.	2	3	5	1	2	8	3	1	3	3	3	2	2	1	2	1	1	1	1																					66,67	44,44	11,11										
<i>Canthium sp. 1</i>		5	3	5	1	2	4	4	3	3	3	2	3	3	3	3	3	3	3	3																					72,22	0	44,44										
<i>Astrotrichia asterotricha</i>	Gum	1	1	1	1	1	3	2	1	1	2	1	1	2	1	1	1	1	1	1																					66,67	0	22,22										
<i>Mundulea sericea</i>		2	2	2	4	3	1	1	1	4	1	1	2	1	2	1	1	1	1	1																					61,11	0	33,33										

M. murinus was significant in JBB (14 vs. 5 species, Binomial test, $P < 0.05$), but not significant in the case of JBA (21 vs. 14 species) or JBC (17 vs. 11 species)

Of the six plant species common to all three sites, three species, *Rothmannia reniformis*, *Strychnos madagascariensis*, and *Sapium melanostictum* have previously been reported to be consumed by either *M. murinus* ($n = 3$) or *M. ravelobensis* ($n = 2$) (Table 2). Of the 11 plant species common to the two sites JBA and JBC, four (*Scolopia inappendiculata*, *Baudouinia fluggeiformis*, *Rhopalocarpus similis*, and *Vepris arenicola*), have previously been reported to be consumed by either *M. murinus* ($n = 3$) or *M. ravelobensis* ($n = 4$). Of the two plant species common to JBB and JBC, only one (*Molinaea retusa*) is known to be consumed by *Microcebus ravelobensis*.

Of the 21 plant species frequent only in JBA, eight are known food plants of either *M. murinus* ($n = 4$) or *M. ravelobensis* ($n = 7$) (Table 2). In JBB, four of the eight plant species, which characterize the site, are known food plants of *Microcebus* spp. but only one of these, *Calantica cerasifolia*, is a known food plant of *M. murinus*. The three other species are consumed by *M. ravelobensis*. Finally, not one of the three plant species, which characterize JBC, has been reported to be consumed by the local *Microcebus* spp.

In summary, of the 44 plant species found frequently ($> 60\%$) in JBA, 16 (36.4%) have previously been reported as food plants of either *M. murinus* ($n = 2$, 4.6%), *M. ravelobensis* ($n = 5$, 11.4%) or both ($n = 9$, 20.5%). In JBB, of the 24 frequent plant species, 11 (45.0%) have been reported as food plants of either *M.*

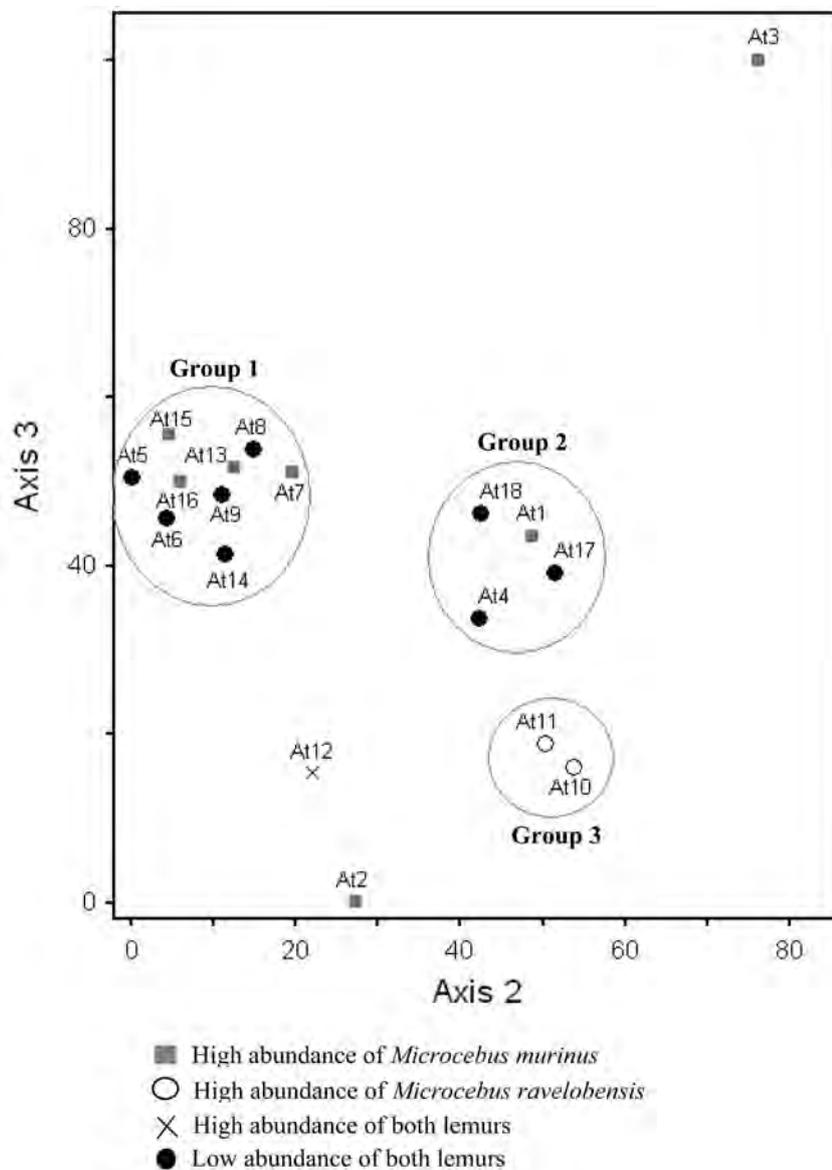


Figure 3. Correspondence analysis of the 18 vegetation transects from JBA according to the relative abundance of plant species. At₁ to At₁₈ are the transects installed within this study site.

murinus (n = 2, 8.3%), *M. ravelobensis* (n = 7, 29.2%) or both (n = 2, 8.3%). Finally, of the 37 frequent plant species in JBC, nine (24.3%) are known food plants of either *M. murinus* (n = 1, 2.7%), *M. ravelobensis* (n = 3, 8.1%) or both (n = 5, 13.5%). These results show that there were more food plant species of *M. ravelobensis* than of *M. murinus* (JBA: 14 vs. 11 species, JBB: 8 vs. 4, JBC: 8 vs. 6), at all three sites, although these differences were not significant (Binomial test, n.s.). Finally, JBB contained the lowest number of frequent food plants of *M. murinus* among the three sites.

Comparison on the small spatial scale (JBA)

Distribution of the *Microcebus* spp.

Individuals of both *Microcebus* spp. were not evenly captured across JBA. A high relative abundance of *M. ravelobensis* was found close to transects At₁₀, At₁₁, and At₁₂ (Table 3), whereas this species had a low relative abundance near the other transects. In contrast, a high relative abundance of *M. murinus* occurred in the vicinity of transects At₁, At₃, At₇, At₁₃, At₁₅, At₁₆, and At₁₂, whereas they had a lower relative abundance close to the other transects. While there was some degree of overlap between traps that captured both *Microcebus* spp. in low relative abundance, we found only one transect with high relative abundance of both species (At₁₂).

Floristic composition, distribution and food plants

JBA can generally be characterized by 44 plant taxa which were found in relatively high abundance along more than 60% of the transects (Table 3). On the basis of the ordination, 18 vegetation transects revealed the existence of three distinct groups (Figure 3). Group 1 is characterized by five plant species, which were generally frequent (> 60% frequency) at JBA (Table 3), whereas group 2 is characterized by seven plant species, and group 3 is characterized by a high abundance of *Albizia arenicola*. The transects At₂, At₃, and At₁₂ are distinct and not part of any of these groups.

When these grouping patterns are related to the *Microcebus* spp. abundances in proximity to the transects (Table 3, Figure 3), it becomes obvious that only Group 3 (At₁₀ + At₁₁) was homogenous with regard to the *Microcebus* spp. abundances. This group was characterized by a high relative abundance of *M. ravelobensis*, but low relative abundance of *M. murinus*. The transects in the other two groups

were heterogeneous in their patterns of *Microcebus* abundance. From these grouping patterns, it can be concluded that the distribution of the lemurs did not correspond closely to the transect floristic composition. This result led us to classifying the 18 vegetation transects according to the distribution of the lemurs (Table 4), in order to identify possible congruencies between the distribution of known food plants and the *Microcebus* spp. In Table 4 we show that only one plant species coincided with an exclusive high abundance of *M. murinus*. This is *Garcinia verrucosa*, not known to be consumed by either local *Microcebus* spp. Furthermore, eight plant species coincided with the exclusive high abundance of *M. ravelobensis* (*Albizia arenicola*, *Ruellia* sp., *Strychnos decussata*, *Tarenna* sp., *Polycardia lateralis*, *Carissa edulis*, *Pyrostria media*, and *Scolopia madagascariensis*), but none of them has been reported as food plant of any of the two *Microcebus* spp. Finally, two plant species, *Mapouria boenyana* and *Noronhia seyrigii*, characterize the area where both *Microcebus* spp. were in high relative abundance; neither of which is known to be consumed by these animals. Some food plants were found in the group of plants, which characterized JBA (Table 4). Of these 42 species, 16 (38%) have been reported as food plants of either *M. murinus* (n = 1, 2.4%), *M. ravelobensis* (n = 5, 11.9%) or both (n = 9, 21.4%) (Table 4).

Discussion

Can the overall abundance of *Microcebus* spp. at a given site be related to floristic characteristics?

Floristically, the site where both *Microcebus* spp. were present in about equal numbers (JBA) was comparable to the site where *M. murinus* existed predominantly (JBC). Both sites were very different from that where *M. ravelobensis* occurred exclusively (JBB). For example, both sites (JBA/JBC) contained higher numbers of plant species and families and a higher mean number of plant species per transect than JBB (Sehen *et al.*, 2010). The resemblance of JBA and JBC was also reflected in the floristic composition, which was quite different from that of JBB. JBA and JBC had several plant species in common, which was not the case between JBA and JBB or JBB and JBC. This may be explained by basic ecological conditions (soil type and elevation), which appeared to be similar in JBA and JBC, and clearly differed from those in JBB (Sehen *et al.*, 2010). In JBA and JBC, the forests are dry-deciduous, grow on sandy soils, relatively high in elevation and still part of largely undisturbed forests.

In contrast, the alluvial forest in JBB is on argilliferous soils, at a lower elevation, and partially degraded due to human activity. Several introduced plant species were found in JBB, such as *Tectona grandis* and *Mangifera indica*, further indicative of modification.

Previous studies showed that the relative population densities of the two *Microcebus* spp. were significantly and negatively correlated with each other across northwestern Madagascar (Rakotondravony & Radespiel, 2009). Whereas the relative population densities of *M. murinus* augmented with increasing elevation and were highest in dry habitats not in proximity to surface water, the population densities of *M. ravelobensis* decreased with elevation and were highest in the humid habitats close to surface water. Two of our study sites had also been included in that previous analysis (JBB, JBC; Rakotondravony & Radespiel, 2009), and the relative abundances of the two *Microcebus* spp. at our three sites correspond to the elevational predictions derived from that earlier study.

Previous studies in the JBA, also showed that both *Microcebus* spp. differ in several ecological traits, such as their choice of sleeping sites (Radespiel *et al.*, 2003a), microhabitat characteristics (Rendigs *et al.*, 2003), and some aspects of their feeding ecology (Radespiel *et al.*, 2006; Thorén *et al.*, 2011). In how far these ecological traits are directly or indirectly linked to the described floristic differences among the sites, however, waits clarification in future studies.

Interspecific differences in habitat utilization are major components for the ecological separation of possible competitors in sympatry (Schmid, 1998; Wilmé *et al.*, 2006; Pearson & Raxworthy, 2009; Vences *et al.*, 2009). In southeastern Madagascar, the sympatric *M. griseorufus* and *M. murinus* show a strict separation in habitat utilization, with *M. griseorufus* in dry spiny forest and *M. murinus* in gallery and more mesic forests (Rakotondranary & Ganzhorn, 2011). In sympatry, microhabitats used by the two species differed in the diameter of large trees. In this same region, Andriaharimalala *et al.* (2011) demonstrated differences in habitat preferences by *M. rufus* (rain forest), *M. griseorufus* (dry thicket), and *M. murinus* (gallery and "transitional" forest). Hence, the turnover of *Microcebus* spp. along a pronounced ecological gradient may be the result of competitive exclusion or of different habitat adaptation.

Taken together, our data suggest that basic ecological distinctions between the sites of exclusive and sympatric use of *Microcebus* spp. coincided with differences in the vegetation type and with specialized

floristic compositions. It cannot be excluded that the uneven distribution of the lemurs between the three sites may be functionally linked to floristic differences.

Does the large-scale distribution of *Microcebus* spp. follow the distribution of their food plants?

While the smaller number of food plants of *Microcebus murinus* in JBB could explain their absence from that site, the distribution of food plants cannot easily explain the variation in the relative abundance of *M. ravelobensis*. In contrast to our expectation, more food plants of *M. ravelobensis* than of *M. murinus* were identified at all three sites. Several aspects may explain the relatively low explanatory power of the available food plant data.

Firstly, the existing list of plants consumed by *Microcebus* spp. only provides a preliminary and qualitative picture. More quantitative studies on the feeding ecology of the two mouse lemurs are needed to provide greater insight into the relationship between the distribution and availability of essential food plants (i.e. key resources) and the distribution of *Microcebus* spp. in the Ankarafantsika National Park. Secondly, *Microcebus* are omnivorous and may feed on a variety of items, such as insect secretions, arthropods or even small vertebrates, which can constitute major dietary components for both lemurs especially during periods of low food availability (Corbin & Schmid, 1995; Radespiel *et al.*, 2006; Thorén *et al.*, 2011). For example, Corbin & Schmid (1995) showed that *Microcebus* changed their habitat usage pattern associated with the availability of insect secretions. It is also possible that other factors than food availability may determine the suitability of a given habitat for *Microcebus* spp. For example, previous studies have detected differences in microhabitat preferences and sleeping site ecology of *M. murinus* and *M. ravelobensis* (Radespiel *et al.*, 2003a; Rendigs *et al.*, 2003), indicating an ecological differentiation associated with resources.

Can the presence/absence of *Microcebus* spp. within a site be related to floristic characteristics?

The site of sympatry of the two *Microcebus* spp. (JBA) was heterogeneous with regard to its floristic composition and the relative abundance of the animals. The ordination of the vegetation transects revealed three groups of transects that differed floristically from

each other. The capture data revealed that *M. murinus* and *M. ravelobensis* were not evenly distributed across the vegetation transects. However, among the overall suite of plant species recorded in JBA, there were only few that clearly differed between transects of high or low abundance of the *Microcebus* spp. (Table 4). Therefore, no close link was found between the small-scale distribution of the lemurs, the floristic composition of the transects, and the distribution of known food plants of *Microcebus* spp.

It is possible that individuals of both species may not depend on certain tree species, but rather on aspects of habitat structure, which in turn are important for locomotion, shelter, or protection against predators (Radespiel *et al.*, 2003a). There could also be a preference sleeping tree species, an aspect not considered in the current study. For example, previous research showed that *M. murinus* is associated with microhabitats with a high abundance of trees with diameter at breast height (DBH) > 10 cm (Rendigs *et al.*, 2003) that may contain tree holes that are typically used as shelter and for rearing offspring (Ehresmann & Zimmermann, 1998; Radespiel *et al.*, 1998; Lutermann *et al.*, 2010). In contrast, *M. ravelobensis* occurs in forest with a high abundance of trees with DBH < 10 cm, as well as a higher abundance of lianas (Ehresmann & Zimmermann, 1998; Randrianambinina, 2001; Thorén *et al.*, 2009).

Conclusion

At the large spatial scale, there are differences in floristic composition between JBA and JBC, where both *Microcebus ravelobensis* and *M. murinus* occur in sympatry, and JBB, where only *M. ravelobensis* is found. A relationship to the known food plants of *M. murinus* is suggested, but needs further investigation, while in the case of *M. ravelobensis* this aspect was inconclusive. At the smaller spatial scale in JBA, neither the floristic composition nor the food plants could be linked to the distribution of the two *Microcebus* spp. Ecological factors other than food availability may better explain variation in the abundance of these animals in the Ankarafantsika National Park, these may be more closely linked to structural and ecological characteristics of their habitat. Further complementary studies on the feeding ecology of the two *Microcebus* are needed to evaluate this question in more depth.

Acknowledgements

We would like to acknowledge the CAFF/CORE, the Direction Générale des Eaux et Forêts, and the Madagascar National Parks (formerly ANGAP) for their permission to work in the Ankarafantsika National Park. We also thank all the staff of the Ankarafantsika National Park for providing logistic support, the field assistants Lalao Andriamiandrisoa, Benja Rakotonirina, Justin, Mananjara, Tôsy, Zama, Velo, Papakely for their help during the fieldwork. We are indebted to the Department of Plant Biology and Ecology/University of Antananarivo, the Institute of Zoology/University of Veterinary Medicine Hannover, and the Department of Botany/University of Rostock for their hospitality. We thank Soenke von den Berg for technical assistance and gratefully acknowledge the Deutsche Forschungsgemeinschaft (DFG) for financing this research (DFG Ra 502/9-11). For detailed comments on an earlier version of this paper we are grateful to Steven M. Goodman and Peter J. Taylor.

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