

Distribution and Morphological Variation of *Microcebus* spp. Along an Environmental Gradient in Southeastern Madagascar

S. Jacques Rakotondranary · Andreas Hapke · Jörg U. Ganzhorn

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Abstract The lemurs of Madagascar are known for their extraordinary levels of speciation. However, the mechanisms and environmental conditions that led to this diversity remain obscure. We used 3 species of *Microcebus* (*M. griseorufus*, *M. murinus*, *M. rufus*) occurring along an environmental gradient as a model to investigate 1) how the different species are distributed in relation to variation in environmental conditions and ecotones; 2) whether or not the morphology of a given species varies in relation to environmental conditions; and 3) whether or not there is evidence for morphological character displacement to reduce congeneric competition in sympatry vs. allopatry. The 3 species of *Microcebus* show clear associations with specific habitat types. Distributions overlap at ecotones. Nevertheless, the ecotone between dry spiny and gallery forest represents a species boundary between *Microcebus griseorufus* and *M. murinus* while the ecotone between dry spiny forest and evergreen humid forest represents the species boundary between *M. murinus* and *M. rufus*. Different ambient conditions are not reflected in changes in body measurements of *Microcebus murinus* living in different vegetation formations. There is no indication for character displacement in sympatry vs. allopatry. Thus, differences in body mass or other morphological characteristics do not contribute to species separation between *Microcebus griseorufus* and *M. murinus*. The results confirm the importance of ecotones as species boundaries as a condition postulated for the radiation of lemur and other species on Madagascar. They also demonstrate different habitat affinities of seemingly very similar lemur species and thus illustrate

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our very limited understanding of the actual selection pressures, adaptations of lemurs to their environments, and their possible response to interspecific competition.

Keywords Competition · Evolution · Lemurs · Niche · Primates · Southeastern Madagascar

Introduction

Madagascar is known for its extraordinary biodiversity and high degree of microendemic species (Goodman and Benstead 2003; Myers *et al.* 2000). Lemurs are no exception. On average, their geographical ranges are orders of magnitudes smaller than the ranges of other primate species, and the diversity of species exceeds the primate diversity in other areas of the world (Martin 1995; Mittermeier *et al.* 2008). The evolutionary processes that led to this extraordinary diversity remain enigmatic (Vences *et al.* 2009).

In other parts of the world, temperature and moisture are major factors that limit the distribution and abundance of plants and animals (Krebs 2009). In particular, the distributions of species are often confined by environmental discontinuities at ecotones (Terborgh 1971). Physical conditions (temperature) or biological resources can vary in parallel with environmental gradients. These adaptations may be reflected in intraspecific morphological variation in relation to environmental conditions (McNab 2010). Apart from adaptations to environmental conditions, interspecific competition may result in competitive exclusion or morphological or behavioral character displacements in sympatry vs. allopatry (Grant and Grant 2006, 2010).

Several hypotheses have been formulated to explain the biogeographic and phylogeographic patterns of lemurs and the evolution of microendemism (Ganzhorn *et al.* 2006; Goodman and Ganzhorn 2004a,b; Groeneveld *et al.* 2009; Martin 1972; Masters *et al.* 2007; Pastorini *et al.* 2003; Richard and Dewar 1991; Rumpler 2000; Thalmann 2000; Vences *et al.* 2009; Weisrock *et al.* 2010; Yoder *et al.* 2005). In particular, 2 recent hypotheses aim to provide a general framework for the radiations of Madagascar's biota. Both emphasize the role of ecotones in parapatric or allopatric speciation. The watershed hypothesis postulates that river catchments with sources at different altitudes produce sharp ecosystem boundaries during times of desiccation that lead to allopatric speciation (Wilmé *et al.* 2006). The current climate hypothesis postulates that species reach their distributional limits at ecotones created by climatic gradients (Dewar and Richard 2007). The 2 hypotheses thus imply the same mechanism but predict different patterns of microendemism and are supported by the distribution of different taxa (Pearson and Raxworthy 2009).

Although evolutionary scenarios are of great interest, it remains an open question how species maintain their species identity once they have evolved into different forms. Understanding the mechanisms that maintain species identities is of interest, as many of these taxa may hybridize under natural conditions in geographically restricted areas but remain morphologically and genetically distinct over the rest of their range (Gligor *et al.* 2009; Thalmann *et al.* 2002; Vasey and Tattersall 2002;

Wyner *et al.* 2002; Zaramody and Pastorini 2001). This is an issue not just for Madagascar but also for other primate radiations (de Jong and Butynski 2010; Merker *et al.* 2009) and biology in general (Arnold and Martin 2010).

Allopatric and parapatric occurrences might reflect adaptations to specific habitat characteristics. These adaptations might also have come about by interspecific competitive displacement, as interspecific competition is supposed to be aggravated between congeneric species occurring in sympatry (Houle 1997). Compared to other regions of the world, Madagascar seems particularly rich in the sympatric occurrence of congeneric species that seem to have rather similar habitat and food requirements, such as sympatric species of *Microcebus*, *Cheirogaleus*, *Hapalemur*, and *Eulemur* (Blanco *et al.* 2009; Wright 1999). On a community level, competition over the same principle resources is thought to be reduced to levels that allow coexistence if species differ in body mass by a factor of 2 and in length measurements by a factor of about 1.4 (Hutchinson 1959). This “Hutchinson’s rule” has been applied to explain body mass patterns in different animal communities, including primates (Ganzhorn 1999) as well as for sexual dimorphism in carnivores and herbivores (Dayan *et al.* 1989; Pérez-Barberia *et al.* 2008).

Among the lemurs of Madagascar, *Microcebus* has been the subject of numerous phylogeographic studies (Louis *et al.* 2008; Radespiel *et al.* 2008; Weisrock *et al.* 2010; Yoder *et al.* 2000). These studies describe sympatric species pairs (*Microcebus murinus* and *M. berthae*) that match Hutchinson’s rule, and also niche differentiation between these and other sympatric congeneric species or species turnover at ecotones (Dammhahn and Kappeler 2008; Génin 2008; Radespiel *et al.* 2006; Rendigs *et al.* 2003; Schwab and Ganzhorn 2004; Yoder *et al.* 2002). Species turnover at ecotones is of particular interest for species that have diverged rather recently, such as the sister species *Microcebus griseorufus* and *M. murinus* (Yoder and Yang 2004) that occur sympatrically in southern Madagascar. Where they occur in sympatry, *Microcebus griseorufus* seems to be restricted to drier parts of the habitat, such as dry spiny forest, while *M. murinus* occupies wetter sites, such as gallery forests (Yoder *et al.* 2002). In the case of allopatry, *Microcebus griseorufus* occupies a variety of vegetational types including gallery forests and various forms of dry spiny forests (Génin 2008; Rakotondranary *et al.* 2010; Yoder *et al.* 2002). In the evergreen humid forests, *Microcebus murinus* is replaced by *M. rufus*. *Microcebus rufus* evolved within a lineage that split off from the *M. griseorufus* and *M. murinus* group ca. 5–12 million yr ago, i.e., much earlier than the divergence between *M. griseorufus* and *M. murinus* (Yoder and Yang 2004). So far, there are no reports of hybridization between *Microcebus rufus* and *M. murinus*, while hybrids are known between *M. murinus* and *M. griseorufus* (Gligor *et al.* 2009). An investigation of the mechanisms that either maintain or generate the distinct identities of these closely related taxa may help to understand the mechanisms postulated to underlie species radiations in Madagascar (Pearson and Raxworthy 2009; Vences *et al.* 2009; Wilmé *et al.* 2006).

Andohahela National Park in the extreme southeast of Madagascar provides an ideal opportunity to investigate the various patterns and evolutionary constraints along a continuous environmental gradient ranging from evergreen humid rain forest to dry spiny forest. This gradient covers all types of forest ecosystems known from this portion of Madagascar (Andriaharimalala *et al.* in press; Goodman 1999).

Previous studies have revealed a clear separation of *Microcebus* spp. between humid rain forest (*Microcebus rufus*) in the east and dry spiny forest in the west of Andohahela (*M. cf murinus*; Feistner and Schmid 1999). At the time of these earlier studies, the different forms of *Microcebus* of the dry forest ecosystems had not been recognized as distinct species. Our own subsequent studies indicated that the dry ecosystems of the western part of Andohahela contained *Microcebus murinus* and *M. griseorufus* occurring in allopatry or sympatrically with some forms showing intermediate phenotypes (Rakotondranary *et al. unpubl. data*).

Vegetation in Andohahela forest is continuous along the environmental gradient, and all species have the opportunity to move across the different habitats. Thus the distribution of species is likely to reflect their preferred environmental conditions in concert with possible interspecific competition.

As a basis for further studies on speciation and physiological and ecological niche differentiation under the impact of congeneric competition, we addressed the following questions:

- 1) How are the different *Microcebus* spp. distributed along the environmental gradient in relation to environmental conditions and ecotones?
- 2) Can the 2 sister species *Microcebus griseorufus* and *M. murinus* be distinguished based on external morphological characteristics?
- 3) Does the morphology of a given species vary in relation to environmental conditions, reflecting the environmental/physiological constraints under different ambient conditions and possible adaptations on very small scales?
- 4) Is there evidence for morphological character displacement to reduce congeneric competition in sympatry vs. allopatry? If differences in body mass or other morphological measures reflect a mechanism to reduce competition over limited resources between the *Microcebus* spp. of Andohahela, we predict that *Microcebus griseorufus* and *M. murinus* would differ more in their morphological measures at sites where they live in sympatry than at sites where only 1 of the species occurs.

Methods

Study Sites

We conducted the study in the Andohahela National Park (Parcel 1, Parcel 2 and between Parcel 1 and 2) in southeastern Madagascar. The park is characterized by a steep rainfall gradient from 400 mm/yr in the west to 2400 mm/yr in the east with contiguous vegetation formations ranging from dry spiny forest (Parcel 2) to evergreen humid forest (Parcel 1) (Barthlott *et al.* 1996; Goodman 1999). Based on the vegetation classification of Moat and Smith (2007), we selected 7 different sites in 3 types of vegetation—rain forest, gallery forest, dry spiny forest—along 2 transects from the humid east to the dry west. The northern transect consisted of sites at Mahamavo, Ankoba, Ambatoabo, and Hazofotsy and the southern transect was composed of sites at Ebosika, Tsimelahy, and Mangatsiaka (see electronic supplement Table SI; Fig. 1). Andriaharimalala *et al.* (in press) verified the

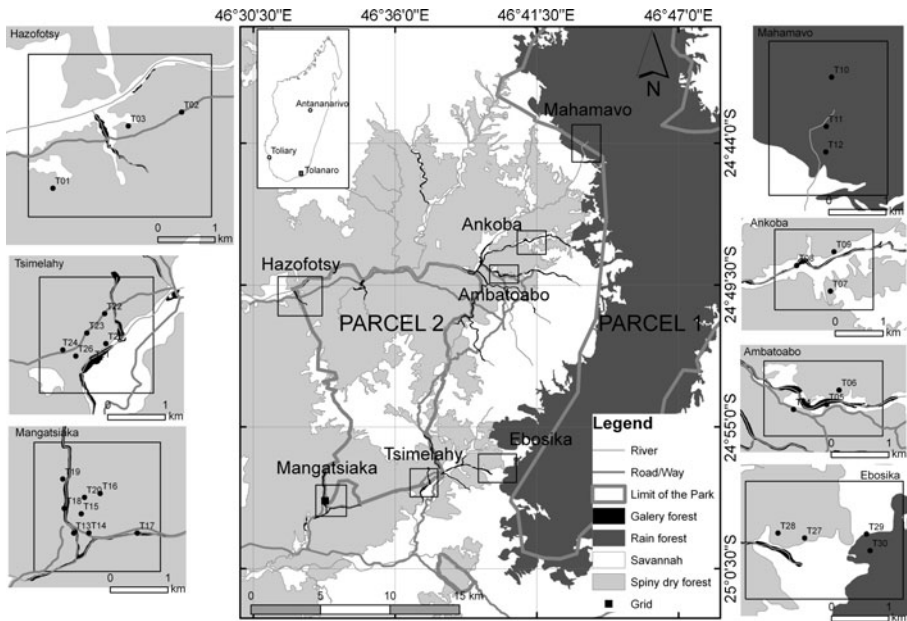


Fig. 1 Study sites in and between Parcel 1 and Parcel 2 of Andohahela National Park (modified from Google Earth).

classification of the different sites by detailed vegetation studies. We georeferenced the sites with a GPS and extracted the altitude of the site from Google Earth version 5.2.1.1588.

We measured air temperature (in °C) and relative humidity (in %) in the different habitat types with 11 data loggers (Hygrochron IButton/DS1923, Dallas Semiconductor) placed in shaded places. We programmed loggers to record data every 2 h. Temperature measurements started in October 2006, September 2007, and May 2008 in the gallery forest, dry spiny forest, and humid forest, respectively (Fig. 2).

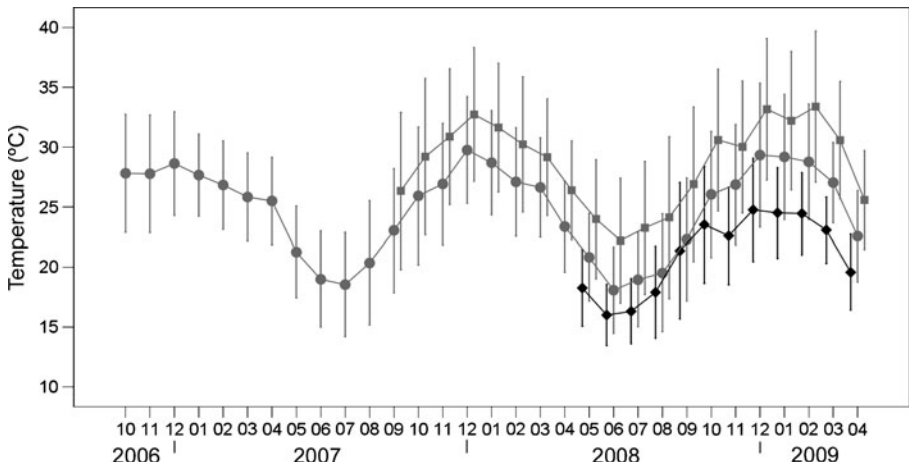


Fig. 2 Monthly temperature in different vegetation formations in Andohahela (◆, rain forest; ■, dry spiny forest; ●, gallery forest). Values are means and standard deviations.

Humidity measurements started in October 2006, September 2007, and November 2008 in the gallery, dry spiny, and humid forest, respectively (Fig. 3).

Study Period

From September 2006 to June 2009 we captured *Microcebus* spp. at the different sites during the end of the dry season (September, October, November) and after the birth season toward the end of the wet season (April, May, June).

Trapping

We captured lemurs at 30 trap lines of 475 m length within the 3 vegetation formations (see electronic supplement Table SI; Fig. 1). Each of the 30 transects was composed of 20 trapping sites, spaced at 25 m intervals. At each site, we installed 2 Sherman traps ($7.7 \times 7.7 \times 23$ cm) in a tree. In addition, we established a rectangular trapping grid at Mangatsiaka with 200 trapping stations (10×20 stations spaced at 25-m intervals), each consisting of 2 Sherman traps. The coordinates of the southwest corner of the trapping grid were ($24^{\circ}57'52.27''S$, $46^{\circ}33'17.25''E$). We added body mass and morphological measurements of the individuals caught in this grid to the samples of the trap lines. We baited traps with bananas for 4 successive nights per transect and checked the traps early in the morning. We anesthetized captured *Microcebus* with 0.01–0.03 ml of Ketanest (100 mg/ml).

We marked each mouse lemur individually using either coded ear clipping or a subcutaneous transponder (Trovan[®] Passive Transponder System, Typ ID-100). We kept the mouse lemurs in traps in the shade to recover from anesthesia and provided them with bananas and water. We released them at their trapping sites at dusk of the same day they were trapped. We identified recaptured lemurs based on the transponder and released them immediately.

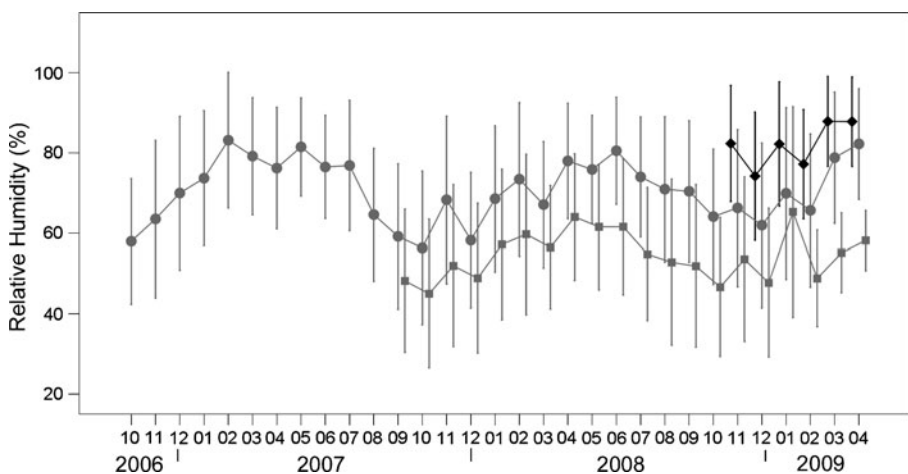


Fig. 3 Monthly relative humidity in different vegetation formations in Andohahela (◆, rain forest; ●, gallery forest; ■, dry spiny forest). Values are means and standard deviations.

Species Characterization

In the field, we identified species according to morphological measurements. Because it was unclear whether species identification based on phenotypes was reliable, A. Hapke verified the identifications by mitochondrial DNA and microsatellite analyses (A. Hapke, *personal communication*). A. Hapke used ear tissue samples stored in 90% ethanol for the genetic analyses. Except for *Microcebus rufus* (from the humid forest) that could be distinguished easily from all other forms, he genotyped all individuals considered in the present publication at 1 mitochondrial locus—the hypervariable region 1 (HV1) of the control region—and at 9 nuclear microsatellite loci. The genetic analyses and the procedures to determine hybrids and reputed backcrosses follow Gligor *et al.* (2009). The genetic analyses are presented elsewhere (A. Hapke, *personal communication*). They confirmed our field classification.

Microcebus spp. reproduce between December and March during the wet season (Wright 1999). Thus, individuals caught between April and June could be either juveniles or adults. Because *Microcebus* reach sexual maturity in their first year of life, we considered all individuals caught after the hibernation period between September and November to be sexually mature. Based on this assumption, we used the lowest body mass of an individual caught between September and November as the threshold to distinguish juveniles from adults. Because we did not capture any *Microcebus rufus* between September and November, we based our classification of juveniles on the minimum body mass of individuals trapped by Blanco (2008) in the humid forest of Ranomafana in October. Based on these criteria, we considered individuals as adults at a body mass of 47 g for *Microcebus murinus*, 42 g for *M. griseorufus*, 48 g for hybrids (*M. griseorufus* × *M. murinus*), and 34 g for *M. rufus*.

S. J. Rakotondrany took morphological measurements on the anesthetized subjects. Here, we present only measurements from adults. Tibia length represents the greatest length of the tibia. Other measurements were made according to Rasoloarison *et al.* (2000). All longitudinal measurements were taken to the nearest mm:

Ear length: from the notch at the base of the ear to the distalmost edge of the pinna

Head and body length: from the tip of the nose to the distalmost point of the body (at base of tail)

Hind foot length: from the back edge of the heel to the tip of the longest toe (not including claw)

Tail length: from the base of the tail (at right angles to the body) to the end of the distalmost vertebra, excluding terminal hair tufts

Mass: measured with Pesola spring scales to the nearest g

The following measurements follow Hafen *et al.* (1998):

Head length: distance between the nostrils and the foramen magnum

Head width: bizygomatic distance perpendicular to head length

Ear width maximum width measured perpendicular to ear length

Statistical Analysis

The morphological data do not deviate from normality according to Kolmogorov-Smirnov tests. We used a principal components analysis (PCA) on head and body length, tail length, head length, head width, ear length, ear width, tibia length, and hind foot length (see electronic supplement Table SIII) to derive a measure of the overall shape of the subjects, extracting all eigenvalues >1 .

We used parametric analysis of variance (ANOVA) and Scheffé's *post hoc* tests for the comparisons of morphological measures between species and hybrids. We used *t*-tests for pairwise comparisons. We analyzed data via SPSS 13.0. We used only morphometric measurements recorded at the first capture of each lemur, regardless of any subsequent recaptures. To compare species (*Microcebus griseorufus*, *M. murinus*, *M. rufus*), we added data from an additional 9 individuals captured outside the transect work but in the immediate vicinity of the transects and in the same vegetation formation. We considered differences significant at $p \leq 0.05$.

Results

Abiotic Factors: Temperature and Relative Humidity

Figures 2 and 3 illustrate monthly temperatures and humidity in the 3 types of vegetation in Andohahela. The dry spiny forest is characterized by the highest and the humid rain forest by the lowest temperatures. December and January are the hottest months in all vegetation types, while June and July are the coldest. Relative humidity is highest in the rain forest, followed by gallery and dry spiny forest. On a site-specific level, the principal differences remain the same, but similar vegetation formations show additional variation between sites located in the northern transect (Mahamavo – Ankoba – Ambatoabo – Hazofotsy) and in the southern transect (Ebosika – Tsimelaha – Mangatsiaka). Measurements taken during the hottest (December, January) and coldest months of the year (June, July) indicate that the rain forest, gallery, and dry spiny forests (except for Hazofotsy) have higher temperatures and lower humidity in the southern than in the northern transect. The dry spiny forest of Hazofotsy does not follow this pattern, but this dry vegetation formation is likely to represent a special form of dry spiny forest that is not matched by a site in the southern transect (see electronic supplement Table SII; Figs. 2, 3). Daily fluctuations in temperature and humidity increase in the drier habitats with less vegetation cover (Figs. 4, 5).

Distribution of *Microcebus* spp. Along the Environmental Gradient

We captured 163 different individual *Microcebus* spp. in 7040 trap-nights at the 30 standardized trap lines along the transect (44 capture sessions with 40 traps per trap line, set for 4 nights; Table I). We found *Microcebus rufus* only in the rain forest of Mahamavo, the site with the lowest temperatures and highest humidity (see electronic supplement Table SII). We caught *Microcebus griseorufus* only in the dry spiny forest, but trapped *M. murinus* in all 3 vegetation types. We captured

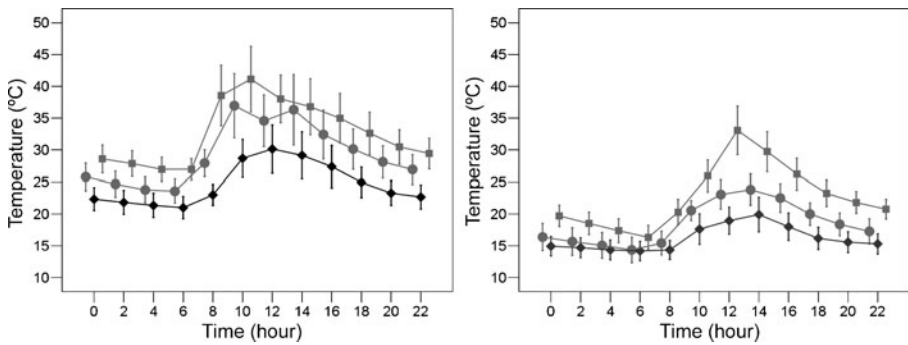


Fig. 4 Daily temperature fluctuation in different vegetation formations of Andohahela (◆, rain forest; ■, dry spiny forest; ●, gallery forest). Values are means and standard deviations of 2-h intervals in the hot season (December 2008, January 2009; left) and the cold season (June, July 2008; right).

individuals classified genetically as hybrids between *Microcebus griseorufus* and *M. murinus* in transects and the trapping grid where dry spiny forest and gallery forest were in close proximity. Thus, despite the occurrence of some hybrids, the limits of all *Microcebus* spp. were fairly well defined by ecotones.

Seasonal and Intraspecific Variation in Body Mass and Morphology

We classified 139 of the 163 individuals caught in transects and 9 individuals caught in the grid at Mangatsiaka as adults based on our body mass criteria (Fig. 1; Table I; see electronic supplement Table SI). Seasonal differences in body mass were pronounced in *Microcebus murinus*. Male body mass was lower at the end of the wet season (54.0 ± 4.4 g, $n=27$) than at the end of the dry season: (61.6 ± 6.0 g; $n=14$; $t=4.56$, $p<0.001$). However, none of the other morphological measurements differed between seasons, so we did not consider the seasonal effects separately in subsequent analyses.

Of the 3 species, only females and males of *Microcebus murinus* differed in body mass; females were heavier (65.0 ± 11.9 g; $n=41$) than males (56.6 ± 6.2 g; $n=41$; $t=4.04$, $p<0.001$). With respect to morphological measurements, sex differences were

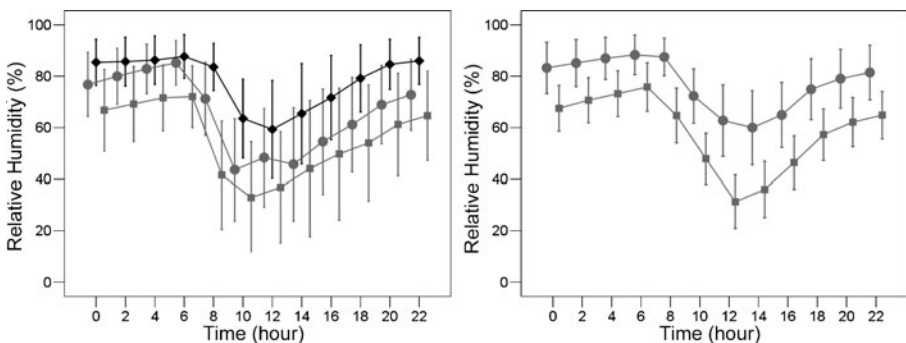


Fig. 5 Daily fluctuation in relative humidity in different vegetation formations of Andohahela (◆, rain forest; ■, dry spiny forest; ●, gallery forest). Values are means and standard deviations of 2-h intervals in the hot season (December 2008, January 2009; left) and the cold season (June, July 2008; right).

Table 1 Numbers of *Microcebus* captured per 4-night capture session at each transect

Site	Transect	September–October–November					April–May–June				
		Year	<i>M. griseorufus</i>	Hybrid	<i>M. murinus</i>	<i>M. rufus</i>	Year	<i>M. griseorufus</i>	Hybrid	<i>M. murinus</i>	<i>M. rufus</i>
Hazofotsy	T01	2007	11	0	0	0	2008	2	0	0	0
	T02	2007	2	1	0	0					
	T03						2008	0	0	0	0
Ambatoabo	T04	2007	0	0	3	0	2008	0	0	1	0
	T05	2007	0	1	6	0	2008	0	0	2	0
	T06						2008	0	0	6	0
Ankoba	T07	2007	0	0	0	0	2008	0	0	1	0
	T08	2007	0	0	0	0					
	T09	2008	0	0	0	0	2008	0	0	4	0
Mahamavo	T10	2007	0	0	0	0					
	T11						2008	0	0	0	6
	T12						2008	0	0	0	12
Mangatsiaka	T13	2006	0	1	0	0					
	T14	2006	1	1	0	0					
	T15	2006	0	0	1	0	2008	3	1	0	0
		2007	2	0	1	0					
	T16						2008	0	1	2	0
T17	2006	0	0	2	0	2008	0	0	6	0	
	2007	0	2	2	0						

T18	2007	0	0	6	0	2008	0	1	12	0
T19						2008	1	2	6	0
T20						2008	1	3	3	0
T21	2006	0	0	5	0	2008	0	0	1	0
T22	2006	0	0	4	0	2008	0	0	3	0
T23	2006	3	0	0	0					
T24	2006	7	1	0	0	2008	3	0	0	0
T25	2006	0	0	4	0	2008	0	0	1	0
T26						2008	3	0	1	0
T27	2006	0	0	2	0					
T28	2006	1	1	0	0					
T29	2006	0	0	0	0					
T30	2006	0	1	3	0					
Total		27	9	39	0		13	8	49	18

The blank cells indicate that no capture was performed in a given season. Hybrids represent crosses or backcrosses between *M. griseorufus* and *M. murinus* as characterized by microsatellites (Hapke *unpubl. data*).

apparent only in head and body length and ear width (see electronic supplement Table SIII). Female *Microcebus murinus* and *M. griseorufus* have larger head and body length than males (*M. murinus*: females: 14.3 ± 1.1 cm, $n=40$; males: 13.7 ± 0.6 cm, $n=41$; $t=2.93$, $p<0.01$; *M. griseorufus*: females: 14.0 ± 1.1 cm, $n=22$; males: 13.0 ± 1.0 cm, $n=14$; $t=2.64$, $p<0.05$). Male *Microcebus murinus* males have wider ears (1.83 ± 0.11 cm; $n=41$) than females (1.77 ± 0.11 cm; $n=41$; $t=2.65$, $p<0.01$). None of the other measures differed between the sexes (see electronic supplement Table SIII).

Intraspecific Morphological Variation in Relation to Environmental Conditions

We found no significant difference in the morphology of populations inhabiting the different vegetation formations. Females from the rain forest had very high body mass, but our sample size is too small to conclude that females have higher body mass in the humid forest than in the gallery and dry spiny forest (Table II).

Interspecific Differences in Body Mass and Morphology

Microcebus rufus was clearly distinct from *M. murinus* and *M. griseorufus* based on body mass, head body length, tail length, ear measurements, and the length of the tibia (Table III). *Microcebus griseorufus* had longer tails than *M. murinus*. Though these 2 species did not differ significantly in any other morphological measurement, *Microcebus griseorufus* leaves the impression of being smaller than *M. murinus*, with a smaller and more slender head. Combining these head measurements with the tail length and the ratios of tail length to head length and of tail length to head width provided very clear criteria separating the 2 species. Based on single morphological characteristics, hybrids resemble *Microcebus murinus* more than *M. griseorufus* in these traits (Table III; Fig. 6). A principal component analysis yielded 3 principal components (PCs; see electronic supplement Table SIV). The first reflects increasing size, the second reflects large heads, and the third represents individuals with short tails and wide heads. The first 2 PCs did not separate the different taxa, but *Microcebus griseorufus* and *M. murinus* were clearly distinct for PC3 and the hybrids were intermediate between the 2 (Table III; see electronic supplement Table SIV).

Effects of Possible Interspecific Competition on Morphology

Male *Microcebus griseorufus* were smaller with lower body mass and smaller head and body length when in sympatry with *M. murinus* than when in allopatry (Table IV). None of the other measurements indicated any difference between sympatry and allopatry, either for *Microcebus griseorufus* or for *M. murinus*.

Discussion

The ultimate goal of the study was to contribute to the understanding of the processes that led to the evolution of microendemic lemur species and the

Table II Comparison of adult *Microcebus murinus* in the different forest types

	Rain forest				Gallery forest				Dry spiny forest				ANOVA	
	<i>n</i>	Min	Max	Mean±SD	<i>n</i>	Min	Max	Mean±SD	<i>n</i>	Min	Max	Mean±SD	<i>F</i>	<i>p</i>
Body mass (female)	2	73.0	87.0	80.0±9.9	15	47.0	83.0	65.1±10.2	24	47.0	90.0	63.8±12.6	1.781	0.182
Body mass (male)	1			59.0	18	47.0	70.0	56.5±7.2	22	47.0	69.0	56.5±5.5	0.075	0.928
Head and body length (female)	2	13.0	15.0	13.9±0.9	14	11.0	16.0	14.4±1.3	24	12.0	16.0	14.2±0.9	0.238	0.790
Head and body length (male)	1			13.0	18	13.0	15.0	13.7±0.7	22	13.0	15.0	13.7±0.6	0.669	0.518
Tail length	3	14.4	15.0	14.6±0.3	32	13.0	16.6	14.5±0.9	47	12.0	16.7	14.6±1.0	0.150	0.861
Head length	3	3.5	3.9	3.7±0.2	33	2.5	3.9	3.5±0.2	47	2.5	3.9	3.5±0.2	1.494	0.231
Head width	3	2.0	2.4	2.2±0.2	33	2.0	2.8	2.2±0.1	46	2.0	2.8	2.2±0.1	0.114	0.893
Ear length	3	2.1	2.4	2.3±0.2	33	1.4	2.8	2.4±0.2	47	2.1	2.7	2.4±0.2	0.668	0.515
Ear width	3	1.7	1.8	1.8±0.1	33	1.5	2.1	1.8±0.1	47	1.6	2.0	1.8±0.1	0.359	0.700
Tibia length	3	4.0	4.2	4.1±0.1	31	3.7	4.5	4.2±0.2	46	3.8	4.5	4.1±0.2	0.812	0.448
Hind foot length	3	3.5	3.5	3.5±0.1	33	3.0	3.6	3.3±0.1	47	3.1	3.6	3.4±0.1	2.528	0.086
Tail length/head length	3	3.8	4.1	3.9±0.2	32	3.7	5.8	4.1±0.4	47	3.4	5.8	4.1±0.4	0.448	0.641
Tail length/head width	3	6.1	7.3	6.6±0.6	32	4.8	7.3	6.5±0.6	46	5.2	7.5	6.6±0.5	0.133	0.875

Body masses are in g; all other morphological measures are in cm. *n*=sample size; Min=minimum, Max=maximum, Mean±standard deviations. *F*-values indicate differences between characters according to ANOVA.

Table III Body mass and morphological measurements of *Microcebus* spp

	<i>M. griseorufus</i>				<i>M. murinus</i>				Hybrids (<i>Mg</i> × <i>Mm</i>)				<i>M. rufus</i>				ANOVA	
	<i>N</i>	Min	Max	Mean±SD	<i>n</i>	Min	Max	Mean±SD	<i>n</i>	Min	Max	Mean±SD	<i>n</i>	Min	Max	Mean±SD	<i>F</i>	<i>p</i>
Body mass (female)	22	42.0	72.0	52.9±7.4 ^{ab}	41	47.0	90.0	65.0±11.9 ^a	6	48.0	58.0	53.7±3.6 ^{ab}	9	35.9	72.9	46.7±12.8 ^b	11.55	0.001
Body mass (male)	14	42.0	60.0	52.2±4.6 ^a	41	47.0	70.0	56.6±6.2 ^a	6	50.0	65.0	56.7±5.7 ^a	8	37.9	56.9	43.3±6.3 ^b	12.43	0.001
Head and body length (female)	22	12.0	16.0	14.0±1.1 ^a	40	11.0	16.0	14.3±1.1 ^a	6	12.0	14.0	13.5±0.9 ^{ab}	9	12.9	13.9	12.5±0.5 ^b	7.542	0.001
Head and body length (male)	14	10.0	15.0	13.0±1.0 ^{ab}	41	13.0	15.0	13.7±0.6 ^a	6	11.0	15.0	13.4±1.3 ^{ab}	8	12.9	14.9	12.5±0.6 ^b	6.574	0.001
Tail length	36	13.7	17.0	15.5±0.9 ^a	82	12.0	16.7	14.6±0.9 ^b	12	12.5	16.0	14.5±1.1 ^b	17	12.0	15.0	13.2±0.8 ^c	25.459	0.001
Head length	35	3.3	3.7	3.5±0.1	83	3.3	3.9	3.5±0.2	12	3.3	3.7	3.5±0.1	17	3.3	3.7	3.5±0.1	1.834	0.144
Head width	35	1.9	2.4	2.1±0.1 ^a	82	2.0	2.8	2.2±0.1 ^a	12	2.1	2.3	2.2±0.0 ^a	17	2.0	2.3	2.2±0.1 ^a	4.980	0.003
Ear length	35	2.1	2.6	2.4±0.1 ^a	83	1.4	2.8	2.4±0.2 ^a	12	2.1	2.7	2.3±0.2 ^a	17	1.7	1.9	1.8±0.1 ^b	64.726	0.001
Ear width	35	1.5	2.0	1.8±0.1 ^a	83	1.5	2.1	1.8±0.1 ^a	12	1.5	2.1	1.7±0.2 ^a	17	1.2	1.5	1.3±0.1 ^b	99.938	0.001
Tibia length	35	3.7	4.3	4.1±0.1 ^a	80	3.7	4.5	4.1±0.2 ^a	12	3.9	4.5	4.1±0.2 ^a	17	3.6	4.1	3.8±0.1 ^b	17.630	0.001
Hind foot length	35	3.0	3.6	3.3±0.1 ^a	83	3.0	3.6	3.3±0.1 ^a	12	3.1	3.5	3.3±0.1 ^{ab}	17	3.0	3.3	3.2±0.1 ^b	6.247	0.001
Tail length/head length	35	3.9	5.0	4.5±0.3 ^a	82	3.4	5.8	4.1±0.4 ^b	12	3.6	4.6	4.1±0.3 ^b	17	3.5	4.2	3.8±0.2 ^c	20.106	0.001
Tail length/head width	35	6.1	8.5	7.3±0.5 ^a	81	4.8	7.5	6.6±0.5 ^b	12	5.8	7.5	6.6±0.5 ^b	17	5.5	6.7	6.1±0.3 ^c	25.552	0.001
PC1	35			-3.78±0.76 ^a	79			0.08±1.03 ^a	12			-0.43±1.31 ^a	Not included				1.429	0.244
PC2	35			-0.32±0.81 ^a	79			0.11±1.09 ^a	12			0.21±0.74 ^a	Not included				2.543	0.083
PC3	35			-0.56±0.89 ^a	79			0.27±0.96 ^b	12			-0.15±0.89 ^{ab}	Not included				9.548	0.001

Body masses are in g; all other morphological measures are in cm; variables with significant differences are in bold. Head width differences are not significant according to Scheffé's *post hoc* test. PC1–PC3: Principal components based on morphological measurements; *M. rufus* is not included in the calculation of these PCs. *n*=sample size; Min=minimum, Max=maximum, mean±standard deviations. *F*-values indicate overall differences between characters according to ANOVA. Different superscripts (a, b, c) indicate differences between characters with *p*<0.05 according to Scheffé's *post hoc* test. *Mg*=*Microcebus griseorufus*; *Mm*=*M. murinus*.

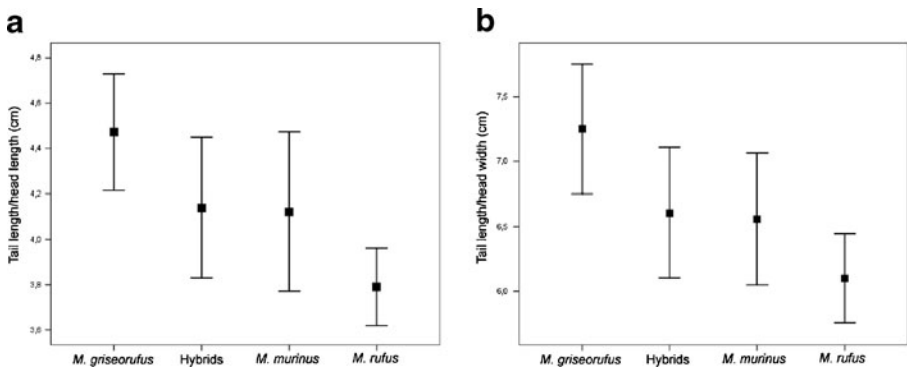


Fig. 6 Ratios of tail length/head length (**a**) and tail length/head width (**b**) of *Microcebus*. Values are means and standard deviations.

mechanisms that allow sympatric congeneric species to coexist. The region represented by the Andohahela National Park is ecologically extremely complex and had a very dynamic recent history that might represent a model for Madagascar's evolutionary history. Excavations of subfossil remains at the cave of Andrahomana a few kilometers south of Andohahela suggest that the western slopes of Andohahela have been subject to various episodes of climate changes with waxing and waning of the different ecosystems (Burney *et al.* 2004, 2008). Within the framework of these complex changes, the situation in Andohahela has components of the watershed as well as of the current climate scenario. The ecotone between the humid evergreen forest and the dry spiny forest corresponds to the current climate hypothesis where the evergreen humid forest represents the distributional limit for *Microcebus rufus*. In contrast, the distributions of *Microcebus murinus* and *M. griseorufus* resemble the watershed scenario. According to this scenario, species could retreat into mesic habitats at times of desiccation. These mesic refugia are represented by watersheds that extend from the evergreen humid forest. *Microcebus murinus* could be interpreted as such a species that is confined by the watershed. *Microcebus griseorufus* would then represent a species that has adapted to the dry conditions outside the watershed.

The distribution of *Microcebus* spp. along the environmental gradient matches the pattern found at other sites. *Microcebus murinus* is the most widespread species on Madagascar. However, along the environmental gradient represented in our study site, it is replaced by *Microcebus griseorufus* in the driest part of the study area at Hazofotsy and by *M. rufus* in the humid forest of Mahavavo. *Microcebus murinus* and *M. griseorufus* form hybrids with an intermediate morphological Gestalt, as summarized by a principal component analysis of the morphological measurements, in the dry vegetation formations inhabited by both species. In some of these vegetation formations, the 2 species occur in sympatry. In an area further west, at Tsimanampetsotsa National Park, *Microcebus griseorufus* is the only species present. There, it occupies all vegetation formations with higher densities in the more mesic formations, such as dry deciduous forest growing along the lake (Bohr *et al.* 2011; Rakotondranary *et al.* 2010). The data from Tsimanampetsotsa illustrate that *Microcebus griseorufus* can do well in mesic vegetation formations and does better there than in the drier vegetation formations such as dry spiny forest or spiny bush.

Table IV Comparison of body mass and head and body length of *Microcebus murinus* and *M. griseorufus* in allopatry and sympatry

Species	Sex	Allopatry			Sympatry			t-test				
		n	Min	Max	Mean±SD	n	Min	Max	Mean±SD	t	p	
Body mass (g)	<i>M. griseorufus</i>	Female	19	42	72	53.2±7.8	3	48	55	51.0±3.6	0.474	0.640
	Male	11	47	60	53.6±3.6	3	42	51	47.0±4.6	2.687	0.020	
<i>M. murinus</i>	Female	27	47	90	64.9±11.3	12	47	86	62.9±12.6	0.485	0.631	
	Male	28	47	70	57.5±6.5	12	47	64	54.3±5.0	1.538	0.132	
Head and body length (cm)	<i>M. griseorufus</i>	Female	19	12	16	14.1±1.2	3	13	14.7	13.7±0.9	0.466	0.646
	Male	11	12.6	15	13.4±0.6	3	10.3	12.5	11.7±1.2	3.477	0.005	
<i>M. murinus</i>	Female	26	10.6	16	14.3±1.0	12	11.5	15.5	14.3±1.2	0.039	0.969	
	Male	28	12.5	15	13.7±0.6	12	13	14.5	13.7±0.6	0.385	0.702	

n=sample size; Min=minimum, Max=maximum, mean±standard deviations. Significant differences are indicated in bold.

Thus, the absence of *Microcebus griseorufus* in the more mesic vegetation formations at Andohahela could be explained by competitive exclusion of *M. griseorufus* by *M. murinus* from the more mesic sites. *Microcebus murinus*, in turn, seems to be excluded from the humid forest by the presence of *M. rufus*. Similar to the situation of *Microcebus griseorufus* at Tsimanampetsotsa, *M. murinus* also does well in evergreen rain forests where *M. rufus* is not present. This situation is found in Mandena littoral forests, an evergreen humid forest with 1600 mm annual rain fall, where *Microcebus rufus* is absent (Lahann *et al.* 2006). The sequence of *Microcebus* spp. turnover along the gradient could therefore be due to a series of competitive exclusions: *M. griseorufus* seems best adapted to very dry vegetation formations, as conditions become more mesic, it is replaced by *M. murinus*, which in turn is substituted by *M. rufus* at the most humid end of the gradient. Thus, distinct species seem to have an evolutionary advantage within their respective vegetation type. To date, the ecological and physiological data available for these species do not provide any explanation for the selective advantage of one species over the other in the different vegetation formations. In particular, recent studies have revealed very high intraspecific variation in morphology and physiology with respect to energy metabolism and reproduction. This makes it almost impossible to draw conclusions about evolutionary advantages of species-specific life history traits from studies in different sites (*Microcebus rufus*: Atsalis 2007; *M. murinus*: Lahann *et al.* 2006; *M. griseorufus*: Génin 2008; Kobbe *et al.* 2011).

The scenario outlined in the preceding text implies strong competition between the 2 sister species of *Microcebus*: *M. griseorufus* and *M. murinus*. However, this is not reflected in changes in body measurements between populations in sympatry and allopatry as predicted by Hutchinson's rule. Among sympatric species pairs of *Microcebus* studied so far, only *M. murinus* and *M. berthae* differ in body mass by a factor of about 2 and thus match Hutchinson's rule that postulates that differences in body mass are important to allow the coexistence of congeneric species. This mechanism does not appear to be true for *Microcebus murinus* and *M. griseorufus*. We observed only minor changes in body mass and head and body length in *Microcebus griseorufus*. *Microcebus griseorufus* were smaller in sympatry than in allopatry. The direction of these changes could be interpreted as character displacement, but the degree of change was far from the difference postulated to reduce competition to the extent that would allow coexistence (Ganeshiah *et al.* 1999; Hutchinson 1959).

Conclusion

Andohahela provides an excellent opportunity to investigate the evolutionary phenomena that are thought to have led to the radiation of lemurs and other taxa. The ecotone at the interface of the evergreen humid and the dry spiny forest represents a very clear border between *Microcebus rufus* and *M. murinus* without any indication of hybridization. The lack of hybridization may also be a consequence of their long divergence some 5–12 million yr ago. This clear species separation supports the current climate hypothesis. Situations wherein the much younger sister species *Microcebus murinus* and *M. griseorufus* come into contact are more

complex. Where gallery and dry spiny forests form clear boundaries because of rivers with permanent water (such as in Ambatoabo or Tsimelahy), the 2 species are clearly separated and the incidence of hybrids is low. This indicates that processes associated with the watershed hypotheses can also produce species boundaries. At sites where vegetation formations are poorly defined and form a small-scale mosaic of different vegetation types, hybrids are more common. Thus, the evolution of distinct taxa seems to require distinct vegetation formations, regardless of whether ecotones are generated by climate zones or by edaphic phenomena. Where congeneric species occur in sympatry, competition seems to be avoided primarily by differences in food composition.

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