



Comparative Feeding Ecology of Sympatric *Microcebus berthae* and *M. murinus*

Melanie Dammhahn · Peter M. Kappeler

Received: 24 April 2008 / Accepted: 31 May 2008 /
Published online: 5 November 2008
© Springer Science + Business Media, LLC 2008

Abstract Most Malagasy primate communities harbor a diverse assemblage of omnivorous species. The mechanisms allowing the coexistence of closely related species are poorly understood, partly because only preliminary data on the feeding ecology of most species are available. We provide an exemplary feeding ecology data set to illuminate coexistence mechanisms between sympatric gray and Madame Berthe's mouse lemurs (*Microcebus murinus*, *M. berthae*). We studied their feeding ecology in Kirindy Forest/CFPF, a highly seasonal dry deciduous forest in western Madagascar. Between August 2002 and December 2007, we regularly (re-)captured, marked, and radiotracked females of both species. A combination of direct behavioral observations and fecal analyses revealed that both *Microcebus* species used fruit, arthropods, gum, insect secretions, and small vertebrates as food sources. However, *Microcebus berthae* and *M. murinus* differed in both composition and seasonal variation of their diets. Whereas the diet of *Microcebus murinus* varied seasonally and was generally more diverse, *M. berthae* relied mainly on insect secretions supplemented by animal matter. The differences were also reflected in a very narrow feeding niche of *Microcebus berthae* and a comparatively broad feeding niche of *M. murinus*. Resource use patterns of Madame Berthe's and more so of opportunistic gray mouse lemurs broadly followed resource availability within the strongly seasonal dry forest. Feeding niche overlap between the 2 sympatric species was high, indicating that food resource usage patterns did not reflect niche partitioning, but can instead be explained by constraints due to food availability.

Keywords coexistence · feeding ecology · *Microcebus* · seasonality

M. Dammhahn (✉) · P. M. Kappeler
Abteilung Verhaltensökologie & Soziobiologie, Deutsches Primatenzentrum,
Kellnerweg 4, 37077 Göttingen, Germany
e-mail: mdammha@gwdg.de

P. M. Kappeler
Abteilung Soziobiologie/Anthropologie, Universität Göttingen,
Berliner Straße 28, 37073 Göttingen, Germany

Introduction

Primates exhibit a broad range of foraging strategies and dietary preferences, including mainly folivorous, e.g., *Lepilemur*, *Colobus*, *Brachyteles*; gummivorous, e.g., *Euoticus*, *Phaner*, *Callithrix*; frugivorous, e.g. *Hylobates*, *Pongo*; insectivorous/faunivorous, e.g. *Tarsius*, *Loris*; and omnivorous feeding patterns, e.g. *Microcebus*, *Papio*, *Pan* (Clutton-Brock and Harvey 1977; Garber 1987; Gursky 2000; Nash 1986; Nekaris and Rasmussen 2003). The relationships between dietary preferences for certain food sources of highly different distribution patterns and quality are an important factor explaining inter- and intraspecific variation in ecology and behavior of primates (Clutton-Brock 1974; Clutton-Brock and Harvey 1977; van Schaik 1989; Wrangham 1980).

Classical niche theory (Chase and Leibold 2003) predicts that species coexistence is possible only if intraspecific competition is stronger than interspecific competition. The prediction requires species to differ in their partitioning of resources (Hutchinson 1957; MacArthur and Levins 1967; Tilman 1982), their temporal or spatial partitioning of one resource (Chesson 2000), or their density- or frequency-dependent predation (Holt *et al.* 1994). Researchers demonstrated niche separation among folivorous and frugivorous primates mainly by comparing their space use and food choice (Ganzhorn 1988, 1989; Nadjafzadeh and Heymann 2008; Overdorff 1993; Vasey 2000). Omnivorous species potentially exhibit a high dietary plasticity, which should offer a high potential for coexistence of several ecologically similar species and should provide them with advantages in seasonal habitats.

The Cheirogaleidae are a speciose family of small (33–500 g), nocturnal Malagasy primates with currently 23 recognized species in 5 genera (Groves 2000, 2001; Mittermeier *et al.* 2006). Cheirogaleids are distributed over nearly all remaining forest areas of Madagascar, inhabiting the evergreen forests and marsh habitats in the east and north and the dry and spiny forests in the south and west (Hapke *et al.* 2005; Hladik *et al.* 1980; Rasoloarison *et al.* 2000; Schülke and Ostner 2007). However, specific distribution patterns vary widely from a few km² in some *Microcebus* spp., e.g., *M. berthae*, *M. sambiranensis*, *M. tavaratra*, to species colonizing the entire west and south of Madagascar, e.g., *Cheirogaleus medius*, *Microcebus murinus* (Meier and Albignac 1991; Rasoloarison *et al.* 2000; Schwab and Ganzhorn 2004). Up to 5 cheirogaleid species of similar body size and ecology can coexist within some forest habitats, thereby creating a high potential for feeding competition. However, owing to a lack of detailed data on basic ecology for many cheirogaleids, the mechanisms of coexistence and niche differentiation among them remain poorly studied.

Three cheirogaleid genera exhibit different feeding specializations: *Phaner* is mainly gummivorous (Hladik *et al.* 1980; Schülke 2003), *Cheirogaleus* and some rain forest *Microcebus* are mainly frugivorous (Fietz and Ganzhorn 1999; Lahann 2007), and *Mirza* are mainly faunivorous (Hladik *et al.* 1980; Pages 1980). The most pronounced plasticity in cheirogaleid feeding patterns occurs in mouse lemurs, *Microcebus* spp., which feed on fruit, nectar, flowers, gum, insect secretions, arthropods, and small vertebrates (Kappeler and Rasoloarison 2003; Radespiel 2006). In the eastern rain forests and littoral forests they are highly frugivorous (Atsalis 1999; Lahann 2007), whereas in dry deciduous forests they feed mainly on

gum, insect secretions, and arthropods (Hladik *et al.* 1980; Radespiel *et al.* 2006). The plasticity should allow *Microcebus* spp. to coexist with several other cheirogaleid species in productive sites without clear feeding niche separation (Lahann 2007). However, in less productive areas or in those with pronounced seasons of food scarcity, distinct feeding niche differentiation between coexisting omnivorous cheirogaleids is predicted (Elton 1946; Pianka 1973). However, comparative data are available only from a few well-studied populations/species, and general mechanisms of coexistence remain obscure (Kappeler and Rasoloarison 2003; Radespiel 2006).

With our study of the feeding ecology of sympatric gray and Madame Berthe's mouse lemurs, we contribute an exemplary data set to illuminate coexistence mechanisms between mouse lemurs. Both species occur in sympatry in central western Madagascar, where they coexist with 3 other cheirogaleid species (*Phaner pallescens*, *Cheirogaleus medius*, *Mirza coquereli*), as well as *Propithecus verreauxi*, *Lepilemur ruficaudatus* and *Eulemur rufus*. In detail, we asked the following questions: 1) What are the diets of *Microcebus berthae* and *M. murinus* in the dry deciduous forest of western Madagascar? 2) What food resources are available in the different seasons of the year? 3) Does resource use vary seasonally according to resource availability? 4) Do the 2 sympatric species avoid feeding competition via niche separation?

Methods

To answer the questions we regularly (re-)captured, marked, and radiotracked females of sympatric populations of *Microcebus berthae* and *M. murinus* between August 2002 and December 2007 in Kirindy Forest/CFPF. We recorded data on feeding ecology via a combination of direct behavioral observations and fecal analyses. Based on the data we assessed overall and seasonal patterns in feeding niche partitioning. Further, we determined the statistical significance of observed niche overlap patterns by comparing them with appropriate null models. Further, we estimated seasonal fluctuations of food availability via standardized phenological monitoring of trees and arthropods.

Study Site

We conducted the study in Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar, *ca.* 60 km northeast of Morondava (44°39'E, 20°03'S, 30–60 m above sea level). The study site is within a 12,5000-ha concession of the Centre de Formation Professionnelle Forestière (CFPF) de Morondava. The climate in the area is characterized by pronounced seasonality with a hot rainy season between December and March and a cold dry season with little or no rainfall from April to November (Sorg and Rohner 1996). The forest is very dense with a comparatively low canopy; most trees ≤ 20 m in height (Sorg *et al.* 2003). We defined the study area within the concession, locally known as N5, by the boundaries of a grid system of small foot trails. Within a 500 × 500 m core area, we established a rectangular system of small trails at 25-m intervals, surrounded by additional trails at 50-m and 100-m intervals. We marked each trail intersection for orientation and used their coordinates to create a map.

Climatic Data and Phenology

We recorded weather data from January 2005 to December 2005. We collected rainfall in a rain gauge placed in an open area at the research camp (*ca.* 2 km from the study area), and measured maximum and minimum daily temperatures with a thermometer placed in the shade.

We assessed seasonal variation in food availability via vegetation and arthropod phenology data. Within the study area we established 3 transects of 500 m each, including 434 trees of 55 species [mean 8 (range 1–86) individuals/species]. We recorded presence and absence of flowering and fruit production every 2 wk. Per Bollen *et al.* (2005), we classified fruit into fleshy (22 species of transect trees) and nonfleshy fruit (33 tree species) because only fleshy fruit are potential mouse lemur food.

To assess arthropod abundance and seasonal fluctuations, we caught insects once per month (April–December 2004) and every 2 wk (April–November 2005) at constant capture sites distributed over 10 ha within the forest. We used 3 different capture methods, including attractive and quantitative sampling techniques, to cover insect groups of different guilds. We set a Malaise trap (Bioform, Germany, bidirectional surface of *ca.* 1.5 m²; Townes 1962) on a small trail within the forest for 1 wk. Malaise trap samples yielded mainly flying insects, including Diptera, Hymenoptera, and winged Isoptera (Southwood and Henderson 2000). Further, we set a light tower (Bioform, surface *ca.* 4 m²) lighted by a superactinic light (12 V, 8 W) for 6 h between 1800 and 2400 h on a small trail within the forest. We manually captured all insects >5 mm attracted by the light. Light trap samples reflect night activity only and yielded especially nocturnal flying insects, such as Lepidoptera and Coleoptera (Ozanne and Bell 2003; Southwood and Henderson 2000). In addition, we spread pitfall traps (*n*=20; diameter=18 cm) over a 200×250 m area within the forest, with 50-m distance between traps. We set traps in the late afternoon and took them down the next morning after a sampling period of *ca.* 16 h overnight. Pitfall trap samples yielded especially ground-dwelling insects (Formicidae, Coleoptera, Orthoptera, Ensifera, Collembola) and other invertebrates such as spiders, millipedes, centipedes, and crustaceans (Southwood and Henderson 2000).

We took all samples to the research station, where we identified insects to order, counted them, and assigned them to size classes (Kunz 1988). Because we kept samples in ethanol for further taxonomic classification, we calculated dry mass from length, using a power function for all adult insects as $\text{mass (mg)} = b_0 + [\text{length (mm)}]^a$ with $3.071 = \ln b_0$ and $a = 2.2968$ (Ganihar 1997). To assess intrasite and intrastudy period food availability, we calculated an index of relative resource availability as actual resource availability per average availability over the entire study period (March–December) for each year separately for arthropods (dry mass) and fruits, respectively.

Seasonality

To analyze seasonal patterns, we defined 3 time periods according to differences in rainfall and food availability (Table 1): S1, the transition between wet and dry season; S2, the dry season; and S3, the transition between dry and wet season. We did not obtain data for the core wet season (January–February) for several reasons:

Table 1 Definitions of the seasons

	Season 1 (S1)	Season 2 (S2)	Season 3 (S3)
Description	Transition between wet and dry season	Dry season	Transition between dry and wet season
Time period	March–May	June–September	October–December
Precipitation	Medium (100–450 mm) 20% of annual precipitation	Low (0–30 mm) 2% of annual precipitation	Medium (100–200 mm) 20% of annual precipitation
Resource availability	Fruits high Arthropods high	Fruits low Arthropods low	Fruits low Arthropods high

1) females of both *Microcebus* spp. are pregnant or lactating during that time and should not be stressed further by wearing radiocollars; 2) trapping success is generally very low in the wet season, which reduces the possibilities to change radiocollars; and 3) visibility is low due to full leaf cover and frequent heavy rains at night, which reduces the possibilities of quantitative behavioral observations.

Capture and Marking

We performed trapping sessions about once every month: 5 times in 2002 (August–November), 6 times in 2004 (June, August–December), 8 times in 2005 (March–July, September–November), 6 times in 2006 (March, July–November), and 6 times in 2007 (May, August–December). Each trapping session consisted of 3 consecutive nights in one half of the study area (12.5 ha) and then 3 consecutive nights in the other half of the study area (12.5 ha) (Dammhahn and Kappeler 2005). Each night we baited 200 Sherman live traps with pieces of banana at dusk, set them near trail intersections 0.5–2 m above ground, and checked and closed traps at dawn. We collected captives in the early morning and kept them at a nearby research station during the day. We briefly restrained and immobilized all newly captured individuals with 10 μ l of Ketamine 100, marked them individually with subdermally implanted microtransponders (Trovan, Usling, Germany), weighed them with a spring balance (± 0.1 g), and took a set of standard external morphometric measurements. We only identified recaptured individuals from the same trapping session; in addition, we weighed those from previous trapping sessions. We released all subjects at the site of capture shortly before dusk. We tested for seasonal variation in female body mass via Kruskal-Wallis tests and for differences between seasons via Mann-Whitney *U* tests.

Fecal Samples

We collected fecal samples from live-trapped subjects and stored them in 70% ethanol. Subsequently, we examined fecal sample contents via a dissecting microscope for presence and absence of arthropods, seeds, and other plant remains. We scored the amount of each remain type volumetrically to the next 10%. When possible, we assessed the minimum number of individual arthropods and seeds per sample and identified them further to taxon.

Behavioral Observations

We equipped 13 females of *Microcebus berthae* and 17 of *M. murinus* with radiocollars (*M. murinus*: 2 g, TW4, Biotrack, UK; *M. berthae*: 1.8 g, BD-2, Holohil, Canada). We followed focal individuals during their nocturnal activities for 1–4 h before changing to another subject. We chose the observation time opportunistically but spread it evenly between 1800 and 0100 h for every individual. Prior analyses showed that there is no qualitative difference in feeding behavior between the first and second halves of the night. We recorded the location of a focal individual every minute and took behavioral data cumulatively for 1-min observation intervals (Martin and Bateson 1993). In total we observed *Microcebus berthae* for 226 h and *M. murinus* for 340 h, respectively. Owing to low visibility at night in a dense forest, *Microcebus berthae* were in sight only in 47% of 1-min observation intervals and *M. murinus* in 70%. The species difference in visibility was due to overall higher mobility in *Microcebus berthae*. All analyses are based on 1-min observation intervals in sight. We recorded all occurrences of feeding behavior and categorized food items into arthropods, fruit, flowers, gum, homopteran secretions (a sugary secretions produced by liana-dwelling homopteran larvae), vertebrates, and unknown. Whenever possible, we determined arthropods to taxon and size classes of 5 mm and identified plant species. We measured handling time of prey items to the nearest minute. We analyzed differences in the diets of *Microcebus* via χ^2 tests and tested for seasonal variation via *G*-tests. We calculated feeding time as percentages of observation intervals in sight spent feeding.

Dietary Overlap

We calculated feeding niche overlap overall and for each season separately via Pianka's index (Krebs 1998). This symmetrical index O_{jk} ranges from 0 (no resources in common) to 1 (complete overlap) and is calculated as:

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sum p_{ij}^2 \sum p_{ik}^2}$$

wherein p_{ij} =proportion resource *i* is of the total resources used by species *j* and p_{ik} =proportion resource *i* is of the total resources used by species *k*.

We determined the statistical significance of observed niche overlap patterns by comparing them with appropriate null models calculated via the niche overlap function in EcoSim 7.72 (Gotelli and Entsminger 2006), in which we randomized the observed resource utilization data among species in 1000 simulations. We used the RA4 algorithm to calculate expected niche overlap indices. The algorithm retained both the observed niche breadth of each species and the pattern of zero resource states by reshuffling the nonzero entries for each resource, only. RA4 is the most conservative algorithm and, thus, has the greatest likelihood of revealing significant patterns of reduced niche overlap (Gotelli and Entsminger 2006; Winemiller and Pianka 1990). Subsequently, we compared mean simulated niche overlap to observed overlap. Interspecific competition (niche partitioning) should cause mean niche overlap to be less than expected by chance, whereas abiotic

constraints might cause both species having the same resource use pattern, so that observed niche overlap would be greater than expected.

We determined niche breadth overall and for each season separately via Levin's standardized index (Krebs 1998) calculated as:

$$B_s = \frac{B - 1}{n - 1}$$

wherein n =number of possible resource states and $B = \frac{1}{\sum p_j^2}$ with p_j =fraction of items in the diet that are of category j .

Results

Climate and Phenology

The climate in Kirindy in 2005 was characterized by a pronounced seasonality in rainfall and monthly temperature patterns (Fig. 1). During the cold dry season (May–September) average monthly temperature minima reached 13–17°C and maxima 32–35°C. In the warm wet season (October–April), average monthly temperatures ranged from 20 to 22°C up to 35–37°C. Total rainfall over the entire annual cycle was 783 mm and most of the annual rain fell during the wet season. Average minimum temperatures, but not maximum temperatures, correlate significantly with monthly rainfall (Spearman rank correlations, $n=12$, for minimum temperatures $r_s=0.70$, $p<0.05$; for maximum temperatures, $r_s=0.48$, $p=0.12$).

Most tree species flowered during the rainy season between October and January. However, several species bore flowers during the dry season. Thus, there were flowers available year-round but on average only 6% (range 3–10%) of all individual trees bore flowers per month. Fruit production started in December and was concentrated in the rainy season, which was reflected in unripe fruit being available mainly from January to May with decreasing abundance during the dry season. Ripe fruit were available year-round with maxima in the dry season. Nonfleshy fruit

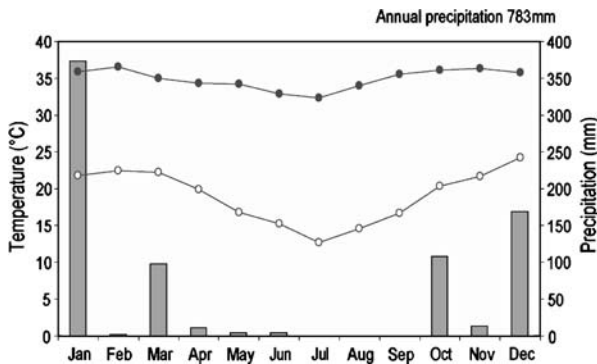


Fig. 1 Monthly rainfall (bars) and average monthly maximal (filled circles) and minimal (open circles) temperatures at Kirindy research station (44°39'E, 20°03'S, 30 m above sea level) in 2005. Note that precipitation was unusually low in February.

predominated over fleshy fruit and represented 69–100% of fruiting species and overall, the monthly proportion of trees bearing fleshy fruit was lower than expected from the proportion of tree species covered by the phenology transects ($\chi^2=41.0$, $df=11$, $p<0.001$). The relative availability of fruit varied seasonally for fleshy (Kruskal-Wallis test, $H(2; n=19)=6.88$, $p<0.05$) and nonfleshy fruit [$H(2; n=19)=14.23$, $p<0.001$; Fig. 2]. However, the patterns differed between fruit type. Both nonfleshy and fleshy fruit were maximally available during the rainy season [median (range): fleshy 1.5 (0.5–3.3); nonfleshy 1.6 (1.2–2.0)]. Whereas nonfleshy fruit availability decreased with ongoing seasons [S2: 0.9 (0.4–1.2); S3: 0.6 (0.3–0.7)], fleshy fruit availability reached a minimum during the dry season [0.3 (0–0.8)] and increased again after the first rains [S3: 0.6 (0–3.5)].

The abundance of flying insects showed pronounced seasonal variation with minima in the dry season (S2) and maxima at the beginning of the wet season (S3) [Kruskal-Wallis tests; 2005: Malaise trap, $H(2; n=19)=9.89$, $p<0.01$; light trap, $H(2; n=13)=9.00$, $p<0.05$]. Abundance of ground-dwelling insects showed a trend towards seasonal variation [Kruskal-Wallis test, 2005: pitfall trap, $H(2; n=12)=4.89$, $p=0.09$]. Dry mass followed the same seasonal pattern as for absolute numbers of individuals. Seasonal patterns in abundance and dry mass correlate with monthly rainfall for Malaise trap catches (Spearman rank correlations, 2005: monthly abundance, $r_s=0.81$, $n=8$, $p<0.05$; monthly dry mass, $r_s=0.81$, $n=8$, $p<0.05$) and light trap catches (2005: monthly abundance, $r_s=0.88$, $n=7$, $p<0.001$, monthly dry mass, $r_s=0.85$, $n=7$, $p<0.05$) but not for pitfall trap catches (2005: monthly abundance, $r_s=0.23$, $n=7$, $p=0.61$; monthly dry mass, $r_s=0.16$, $n=7$, $p=0.73$). Relative availability based on dry mass was highest in S3 and lowest in S2 in both study years and showed pronounced seasonal variation for flying insects [2004 and 2005 data combined, Kruskal-Wallis tests, Malaise trap $H(2; n=28)=15.32$, $p<0.001$; light trap, $H(2; n=19)=9.00$, $p<0.05$] but not for ground-dwelling insects [pitfall traps, $H(2; n=21)=2.37$, $p=0.31$; Fig. 3].

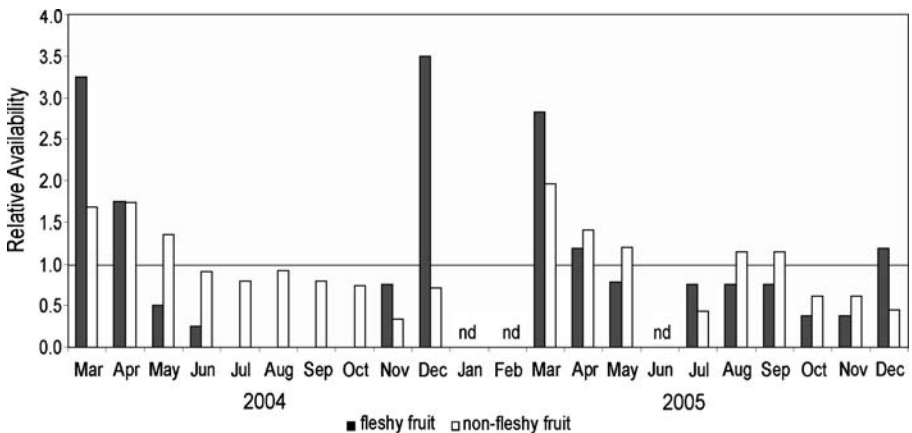


Fig. 2 Relative availability of fleshy and nonfleshy fruit in 2004 and 2005. Note that average monthly availability per year is 1.

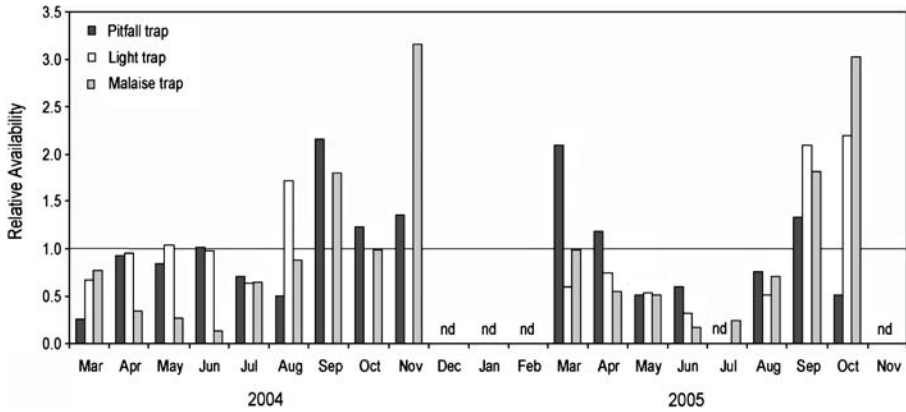


Fig. 3 Relative availability of arthropods (based on dry mass) caught with 3 different trap types in 2004 and 2005. Note that average monthly availability per year is 1.

Body Mass

Body mass of female *Microcebus berthae* and *M. murinus* exhibited significant seasonal variation [*M. berthae*: $H(9; n=164)=52.46, p<0.0001$; *M. murinus*: $H(9; n=285)=129.54, p<0.0001$; Fig. 4]. Median body mass was higher during the wet season than during the dry season (*M. berthae*: $n_{S1}=21, n_{S2}=79, z=5.85, p<0.0001$; *M. murinus*: $n_{S1}=47, n_{S2}=88, z=7.92, p<0.0001$), when female *Microcebus berthae* lost on average 23% and *M. murinus* 37% of weight.

Feeding Behavior

Both *Microcebus* spp. had an omnivorous diet and used homopteran secretions, fruit, flowers, gum, arthropods, and small vertebrates, e.g., geckos, chameleons, as food resources. However, they differed in proportions and seasonal variation of different food components (G -tests, $df=4$; S1: $G=89.4, p<0.001$, S2: $G=275.1, p<0.001$, S3: $G=8.5, p=0.0755$). *Microcebus berthae* fed mainly on homopteran secretions, which amounted to $\leq 81\%$ of their overall diet and represented higher proportions than in *M. murinus* in S1 and S2 (χ^2 tests, S1: $\chi^2=28.1, p<0.001$, S2: $\chi^2=23.5, p<0.001$; Fig. 5). This resource was supplemented further mainly by animal matter. In contrast, the diet of *Microcebus murinus* varied seasonally and was more diverse, including generally higher amounts of fruit (χ^2 tests, S1: $\chi^2=24.5, p<0.001$, S2: $\chi^2=60.7, p<0.001$, S3: $\chi^2=9.4, p<0.01$) and gum (χ^2 tests, S1: $\chi^2=8.3, p<0.01$, S2: $\chi^2=247.2, p<0.001$, S3: $\chi^2=4.1, p<0.05$) than *M. berthae*. Both species used similar amounts of animal matter in each season.

Microcebus murinus used fruit, flowers, and gum of 14 different plant species (Table 2). *Microcebus berthae* fed on fruit and flowers of only 3 plant species, one of them exclusively. *Microcebus murinus* fed on 9 different arthropod taxa, with larvae of Lepidoptera and Coleoptera being the most frequent (Table 3). *Microcebus berthae* used 6 different taxa, with Coleoptera also being the most frequent. Based on fecal analyses and behavioral observations, both species shared 7 arthropod taxa

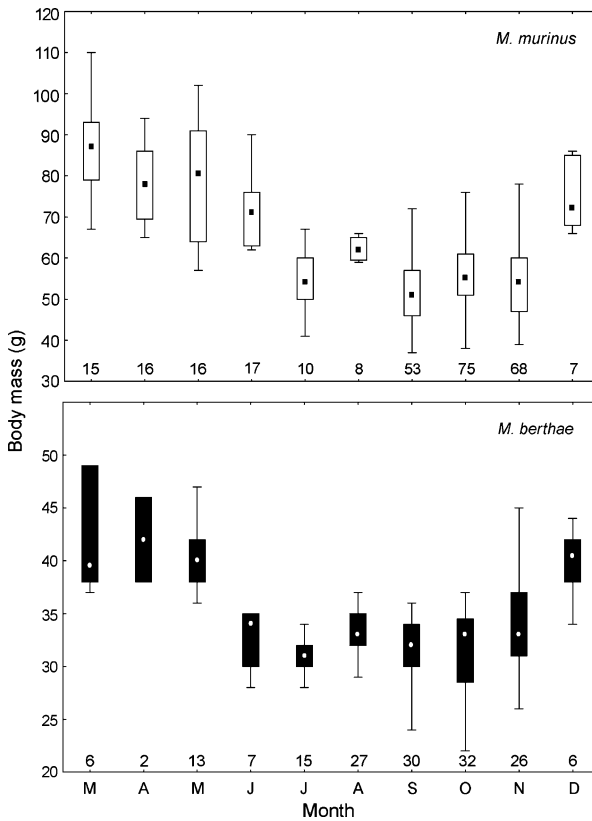


Fig. 4 Seasonal fluctuations in body mass of female *Microcebus murinus* (**above**) and *M. berthae* (**below**). Shown are medians, 25–75% quartiles (box), ranges (whiskers), and sample sizes.

in their diets (Table 3). Only *Microcebus berthae* consumed Diptera, Isoptera, and Mantida and only *M. murinus* consumed larvae of Lepidoptera, Phasmida, Heteroptera, and Diplopoda. However, subjects used most of the exclusively used taxa only rarely. *Microcebus murinus* fed on larger prey than *M. berthae* did [median and quartile ranges; *M. berthae*: 1 cm (0.5–1 cm), $n=83$; *M. murinus*: 1.5 cm (0.5–3 cm), $n=97$; Mann-Whitney U test, $z=-3.05$, $p<0.005$]. However, handling time did not differ between the species [median and quartile ranges; *M. berthae*: 1 min (1–2) per item, $n=85$; *M. murinus*: 1 min (1–2) per item, $n=97$; Mann-Whitney U test, $z=-1.30$, $p=0.19$]. In both species, handling time correlates positively with prey size (Spearman rank correlations; *M. berthae*: $r_s=0.67$, $p<0.001$, $n=83$; *M. murinus*: $r_s=0.62$, $p<0.001$, $n=97$).

Microcebus murinus spent more time feeding than *M. berthae* did in S1 (*M. berthae*: 27%, *M. murinus* 51%, $\chi^2=12.11$, $df=1$, $p<0.001$) but not in S2 (*M. berthae*: 43%, *M. murinus* 44%) and S3 (*M. berthae*: 29%, *M. murinus*: 30%). Whereas *Microcebus berthae* increased time spent feeding during the dry season, *M. murinus* spent most time feeding in S1, which corresponds to the time of seasonal fattening.

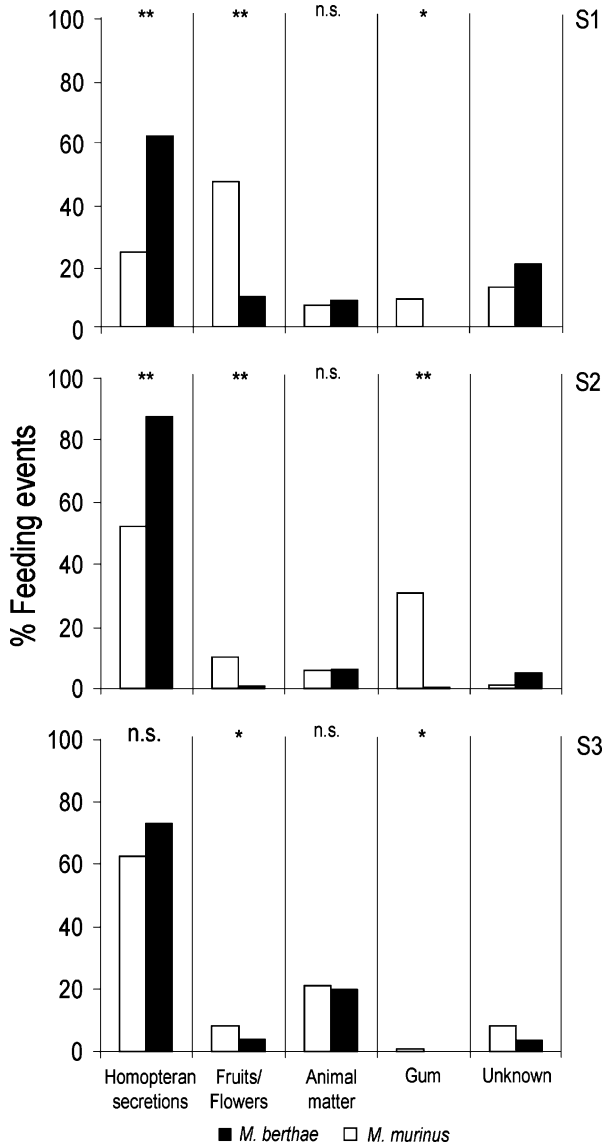


Fig. 5 Percentages of feeding events of *Microcebus berthae* and *M. murinus* on different food categories for each season. * $p < 0.05$ and ** $p < 0.001$ in χ^2 tests.

Fecal Analyses

We obtained 67 fecal samples from 42 individuals of *Microcebus berthae* and 101 samples from 65 individuals of *M. murinus*. The majority of subjects provided only 1 sample each (*M. murinus*: 67%; *M. berthae*: 71%) and only a few individuals contributed >3 samples (*M. murinus*: 5%; *M. berthae*: 7%). Biases due to individual dietary preferences should therefore be minimized. Presence-absence analyses of food remains in fecal samples revealed neither species differences nor seasonal

Table 2 Plant species and parts eaten by *Microcebus murinus* and *M. berthae* in Kirindy Forest/CFPF (March–December)

Species	Family	Local name	Consumed parts	<i>M. murinus</i>	<i>M. berthae</i>
<i>Commiphora arofy</i>	Burseraceae	Arofy	Gum	x	
<i>Terminalia</i> sp.	Combretaceae	Taly	Gum	x	
<i>Strychnus decussate</i>	Loganiaceae	Hazomy	Pulp	x	
<i>Strychnus</i> sp.	Loganiaceae	Tsivoanysao/ Hazokintoky	Pulp		x
<i>Macphersonia gracilis</i>	Mimosaceae	Tsingena	Pulp	x	
<i>Enterospermum</i> sp.	Rubiaceae	Toalakena	Pulp	x	
<i>Canthium</i> sp.	Rubiaceae	Fatekahizy	Pulp	x	
<i>Rothmannia tropophylla</i>	Rubiaceae	Piripitsokala	Pulp	x	x
<i>Grewia</i> sp.	Tiliaceae	Sely	Pulp	x	
<i>Grewia</i> sp.	Tiliaceae	Sele Sele	Pulp	x	x
<i>Grewia cyclea</i>	Tiliaceae	Latabarika	Pulp	x	
?		Lopingo	Pulp	x	
?		?	Flower	x	
?		?	Pulp	x	
?		?	Pulp	x	

variation in the number of samples with arthropods (χ^2 test, n.s.; Fig. 6). However, more samples of *Microcebus berthae* than of *M. murinus* consisted mainly of arthropod remains (>50 volume %) in S1 (χ^2 test: $\chi^2=8.54$, $df=1$, $p<0.05$) but not in S2 and S3. A higher number of samples of *Microcebus murinus* than of *M. berthae* contained seeds in season 1 (χ^2 test, $\chi^2=4.20$, $df=1$, $p<0.05$) and season 2 (χ^2 test, $\chi^2=8.26$, $df=1$, $p<0.005$) but not in season 3 (χ^2 test, n.s.). For *Microcebus*

Table 3 Arthropod taxa consumed: Quantity of fecal samples from *Microcebus berthae* (n=42) and *M. murinus* (n=33) containing arthropod remains that we identified to taxon and quantity of feeding behaviour events on different arthropod taxa

Category	Fecal samples		Feeding behavior	
	<i>M. berthae</i>	<i>M. murinus</i>	<i>M. berthae</i>	<i>M. murinus</i>
Coleoptera	9	10	41	11
Lepidoptera	8	6	6	5
Larvae		2		23
Orthoptera	6	2	1	
Ensifera	6	2	2	5
Diptera	6			
Hymenoptera	2	1		
Formicidae	5	6		
Blattaria	5	5	1	2
Aranea	2			1
Isoptera	1			
Mantida			1	
Phasmida				1
Heteroptera				1
Diplopoda				3
Unidentified larvae	1	1		

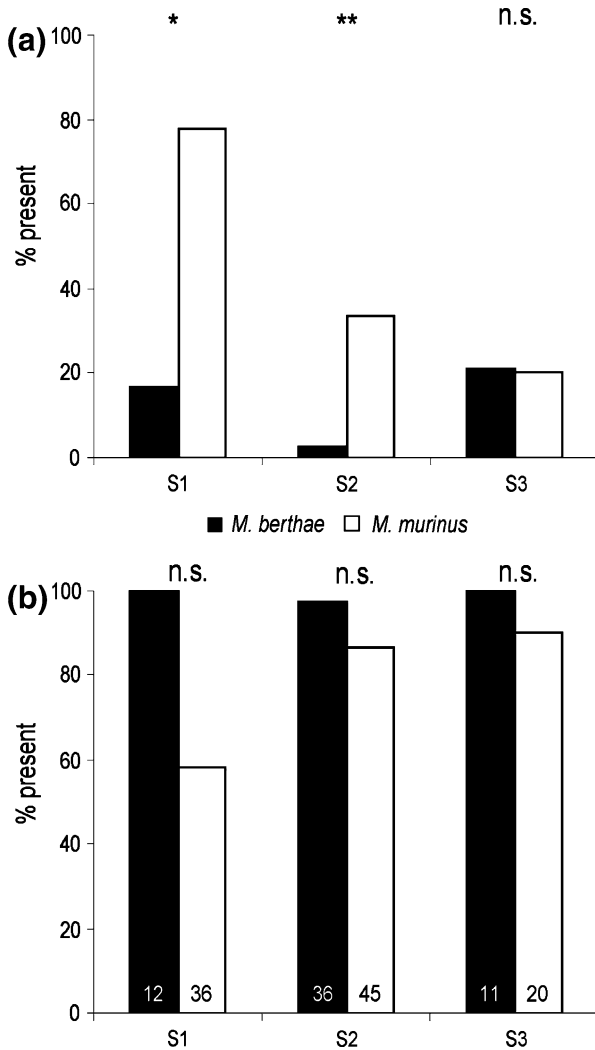


Fig. 6 Percentages of fecal samples of *Microcebus berthae* and *M. murinus* containing seed (a) and arthropod (b) remains per season. * $p < 0.05$ and ** $p < 0.001$ in χ^2 tests.

murinus there was seasonal variation in the proportion of samples containing seeds (G -test, $G=12.00$, $df=2$, $p < 0.05$) but not in the proportion of samples containing arthropods (G -test, n.s.). The proportion of fecal samples with arthropods and seeds, respectively, did not vary seasonally in *Microcebus berthae* (G -tests, n.s.).

The median minimum number of individual arthropods (MNI) per sample was 1 in both species and in all seasons (except *Microcebus murinus* S3: 2) and variation was small (min-max ranges, *M. berthae* 1–4, *M. murinus* 1–6). Feces of *Microcebus murinus* included generally higher median numbers (MNI) of seeds than feces of *M. berthae* contained [*M. murinus*: S1: 3.5 (1–18), S2: 2 (1–20), S3: 1.5 (1–2); *M. berthae*: S1: 2 (1–3), S2: 1 (1–1), S3: 1 (1–2)]. Also, seasonal variation was more pronounced in

Microcebus murinus, with highest MNI seeds at the end of the wet season and lowest at the end of the dry season.

Arthropod remains in feces of both species included Lepidoptera, Coleoptera, Blattaria, Ensifera, Orthoptera, and Hymenoptera (Table 3). Lemurs probably ingested intact small ants when they fed on fruits or homopteran secretion. Only feces of *Microcebus berthae* contained fragments of Diptera, Araneae, and Isoptera, whereas feces of *M. murinus* also included remains of lepidopteran larvae. Other material in fecal samples included hair, seed coats, whole flowers, and other plant parts, such as tiny pieces of bark and woody filaments, which lemurs probably ingested by scratching homopteran secretion from surfaces or by opening gum trees.

Feeding Niches

Feeding niche overlap increased from S1 (0.62) to S2 (0.85) with a maximum in S3 (0.99; Table 4). In S1 and S2 observed and expected overlap did not differ. However, in S3 niche overlap was higher than expected by chance [$O_{jk}(\text{obs})=0.99$, $O_{jk}(\text{exp})=0.41$, $p<0.05$]. Also, taking all seasons together, there was a trend toward a higher observed overlap [$O_{jk}(\text{obs})=0.83$, $O_{jk}(\text{exp})=0.46$, $p<0.10$]. Feeding niche breadth was narrow in *Microcebus berthae* (overall 0.12) and medium in *M. murinus* (overall 0.62; Table 5), indicating a more specialized diet in *M. berthae*. Niche breadth varied seasonally in both species. Whereas the niche breadth of *Microcebus murinus* decreased from S1 over S2 to S3, niche breadth was minimal during the dry season in *M. berthae* with an extraordinarily narrow feeding niche of 0.07, when subjects relied nearly completely on homopteran secretions.

Discussion

Phenology and Seasonal Resource Availability

The climate at Kirindy is relatively dry (800 mm rain/yr) and highly seasonal with pronounced fluctuations in rainfall and temperature (Sorg and Rohner 1996). Most rain falls in only 3 mo with virtually no rain between May and October. Most tropical dry forest trees tune their reproductive phenologies to moisture availability (van Schaik *et al.* 1993; Zimmerman *et al.* 2007). Accordingly, flowering of 68 Kirindy tree species peaked at the beginning of the wet season after the first heavy

Table 4 Observed and expected Pianka's indices of niche overlap between *Microcebus berthae* and *M. murinus*

Season	Observed index	Expected index (mean \pm SD)	p (obs \leq exp)	p (obs \geq exp)
1	0.62	0.55 \pm 0.22	0.74	0.27
2	0.85	0.37 \pm 0.30	0.82	0.18
3	0.99	0.41 \pm 0.31	1.00	0.01
All	0.83	0.46 \pm 0.22	0.90	0.10

Expected values are based on 1000 simulations using algorithm RA4 in EcoSim 7.72 Software (Gotelli and Entsminger 2006).

Table 5 Seasonal and overall feeding niche breadth based on Levins's standardized index for sympatric *Microcebus* from Kirindy and mouse lemurs from other areas of Madagascar

Season	<i>M. berthae</i> (Kirindy) ¹	<i>M. murinus</i> (Kirindy) ¹	<i>M. murinus</i> (Mandena) ²	<i>M. murinus</i> (Ampijoroa) ³	<i>M. ravelobensis</i> (Ampijoroa) ³
1	0.32	0.56			
2	0.07	0.41			
3	0.19	0.31			
Overall	0.12	0.63	0.29	0.20	0.33

¹ This study; ² Lahann (2007); ³ Reimann (2002) and Radespiel *et al.* (2006).

rains in October. Many dry deciduous forest trees produce flowers with large quantities of nectar that are pollinated by small nocturnal lemurs (Baum 1995; Wright and Martin 1995) and thus provide an important food source in austral spring (Hladik *et al.* 1980). Fruit production was maximal during the wet season with ripe fleshy fruit being available mainly between March and September and nonfleshy fruit during the whole dry season. Though fruit were available nearly year-round, most of them are not suitable food source for mouse lemurs. In the dry deciduous forest most trees produce nonfleshy, dry dehiscent capsules and indehiscent thick-husked drupes, probably as adaptations against seasonal droughts (Bollen *et al.* 2005). The fruit have hard outer layers and are fibrous with no or only very little flesh and are thus either not accessible or might not provide enough usable energy for small lemurs (Ganzhorn *et al.* 1999).

Micro- and macroclimatic patterns and seasonal variation in resource availability are the main factors triggering seasonal changes in arthropod abundance over time (Wolda 1988). In the tropics, rainfall patterns seem more important than annual temperature fluctuations, especially in areas with marked dry seasons (Basset 1991; Denlinger 1980). Therefore, arthropod abundance patterns are expected to follow the phenology patterns of the forest trees, particularly the production of flowers and new leaves (Richards and Windsor 2007). Regular standardized catches of arthropods in Kirindy Forest/CFPF revealed pronounced seasonal patterns in flying, but not in ground-dwelling, arthropods. Monthly dry mass of flying insects fluctuated up to 23 times between dry and wet season months. Also, in the eastern rain forests seasonal fluctuations in insect biomass were pronounced, with light trap catches varying *ca.* 11 times in fresh mass between dry and wet season (Atsalis 1999). Because many of the (mouse) lemur food sources contain very little protein, the availability of arthropods as a protein source might determine the carrying capacity of the dry deciduous forests for them (Hladik *et al.* 1980).

Overall and Seasonal Dietary Patterns

A combination of behavioral observations and fecal analyses revealed that both *Microcebus* spp. were omnivorous and used a variety of different food sources, including fruit and flowers of several different tree and shrub species, insect secretions, gum, arthropods, and occasionally small vertebrates such as geckos and chameleons up to their own body length. Whereas fruit were a main component of the diet of *Microcebus murinus*, particularly at the end of the wet season, *M. berthae*

exploited fruit only occasionally. The main proportions of fruit species *Microcebus murinus* consumed were shared with co-occurring *Cheirogaleus medius* (Fietz and Ganzhorn 1999). Chemical analyses revealed that the mainly frugivorous cheirogaleid preferred fruit with high amounts of sugar during prehibernation fattening (Fietz and Ganzhorn 1999), which might also be the case for *Microcebus murinus*. *Microcebus berthae* used gum only on one occasion, whereas gum of *Terminalia* and *Commiphora* amounted to $\leq 14\%$ of the diet of *M. murinus*. We could not confirm extensive gum feeding ($\leq 75\%$ of diet; Génin 2003) but the proportion of gum might vary locally with gum tree density. Further, dietary data solely based on opportunistic observations (Génin 2003) is likely to overestimate food that is obtained in long bouts and at conspicuous locations. In northwestern Madagascar, gum of a variety of different tree species was a major dietary component in both *Microcebus murinus* and *M. ravelobensis* during the dry season (Radespiel *et al.* 2006). Particularly, Taly (*Terminalia aff. diversipilosa*, Combretaceae) produces a gum that is rich in soluble sugars (88%) and has a relatively high amount of protein (5%; Hladik *et al.* 1980; Nash 1986). Mouse lemurs gouge open the bark of gum trees themselves, or feed from holes made by fork-marked lemurs.

Both species used a variety of different arthropods and spent much foraging time searching for prey. They hunted arthropods in the canopy or on the ground and often caught them manually out of the air. The proportion of animal prey in the diet did not differ between species. Further, both species utilized Coleoptera over other arthropod taxa and did not differ in taxonomic composition of prey. However, *Microcebus murinus* fed on slightly larger prey than *M. berthae* did. Fecal analyses of rain forest *Microcebus rufus* (Atsalis 1999) and opportunistic behavioral observations of *M. murinus* (Hladik *et al.* 1980) also revealed a higher utilization of beetles.

A particularly important resource for both mouse lemur species was a sugary secretion produced by liana-dwelling homopteran larvae. Larvae of endemic *Flatida coccinea* (Homoptera, Fulgoridae; Auber, 1955) are present throughout the dry season, when they form colonial aggregates and feed on the sap of vines (Hladik *et al.* 1980). Larvae of *Flatida* excrete honeydew to supply ants with food, with which they are associated in a facultative mutualistic interaction (trophobiosis) rewarding the ant's protection against predators (Hölldobler and Wilson 1990). The honeydew is produced as a white secretion that drips unto leaves and branches, where it dries. Mouse lemurs lick or scrape the white secretion from the vegetation. Nutritional analyses determined that dried secretions of *Flatida coccinea* contained relatively high amounts of sugars and carbohydrates and a low amount of protein (Hladik *et al.* 1980). This resource type seems to be particularly crucial for *Microcebus berthae*, which spent $\leq 90\%$ of its feeding time on homopteran secretions during the dry season. The importance of homopteran secretions during the dry season is underlined further by the results of a field experiment in which a female *Microcebus murinus* changed her habitat use after removal of homopteran secretion patches (Corbin and Schmid 1995). Interestingly, mouse lemurs never fed directly on the homopteran larvae, though otherwise arthropods are a highly preferred food source.

In highly seasonal habitats, food availability is not even over the year and species should not be able to rely entirely on preferred foods. Instead they are expected to include less preferred fallback foods in their diet during certain times of the year

(Marshall and Wrangham 2007). Species inhabiting the dry deciduous forests of Madagascar face high fluctuations in availability of fleshy fruit, flowers, and arthropods and a more stable provisioning from gum, homopteran secretions, and nonfleshy fruit. Therefore, it is expected that omnivorous species tune their feeding patterns to seasonal resource availability.

In *Microcebus murinus* seasonal variation in diet was clearly linked to seasonal fluctuation in food availability. During the rainy season, when unripe and ripe fleshy fruit were highly available, fruit made up about half of their diet, similar to rain forest *Microcebus rufus* (Atsalis 1999) and *M. murinus* in the littoral rain forest (Lahann 2007). Individuals that stay active during austral winter, mainly juveniles and males (Schmid 1999), changed their feeding pattern to stable (fallback) resources such as gum and homopteran secretions. At the beginning of the wet season, when insect biomass increases conspicuously, *Microcebus murinus* used large amounts of arthropods, thereby resembling rain forest *M. rufus* (Atsalis 1999). Thus, gray mouse lemurs from Kirindy Forest/CFPF opportunistically responded to seasonal changes in food availability. *Microcebus berthae* also adapted their feeding pattern to resource fluctuations, though not as pronounced as *Microcebus murinus* did. Homopteran secretions were the stable main part of their diet year-round, which was further supplemented mainly by arthropods according to their availability. Researchers have widely demonstrated such seasonal variation in feeding patterns of frugivorous and omnivorous primates for dry deciduous and even moist Malagasy forests (Atsalis 1999; Norsica *et al.* 2006; Overdorff 1993; Simmen *et al.* 2003).

Do the 2 Mouse Lemur Species Avoid Feeding Competition by Niche Partitioning?

Selection on niche partitioning as a result of interspecific competition should be further intensified by seasonal resource limitations (Elton 1946; Pianka 1973). Several lines of evidence suggest temporary food shortages for mouse lemurs in Kirindy: 1) Arthropod and plant phenology data indicated low availability during austral winter months. 2) Females of *Microcebus berthae* and *M. murinus* lost up to one-third of their wet season body mass then (Schmid and Kappeler 1998). 3) Extended periods of inactivity and torpor reduce daily energy expenditure by almost 40%, most likely as an adaptation to seasonal food and water shortages (Schmid 2001; Schmid *et al.* 2000; Schmid and Speakman 2000). Thus, interspecific resource competition should be higher in Kirindy than in more productive or diverse forest habitats, which ought to result in more pronounced niche differences between otherwise ecologically similar species.

In contrast to the expected pattern, we found high overlap between Madame Berthe's and gray mouse lemur feeding niches. Niche overlap between coexisting *Microcebus* was maximal at the end of the dry season (S3). Only then was niche overlap between the *Microcebus* spp. higher than expected by chance, and during none of the seasons was overlap smaller than expected by chance. The niche overlap pattern indicates that the food resource use of the 2 species does not reflect niche partitioning due to interspecific competition but seems instead to be due to constraints in food availability (Gotelli and Entsminger 2006). Our niche calculations are based on very coarse food categories, which theoretically might influence the results. However, we think that this is unlikely because 1) *Microcebus*

berthae relies mainly on a nonvariable resource (homopteran secretions) and 2) both species do not differ in the taxonomic composition of arthropods, which is the main supplement for *M. berthae*.

Besides food partitioning, species can also avoid competition by differentiating along 2 other main niche dimensions: habitat and time (Charles-Dominique 1975; Schoener 1974). Temporal segregation is unlikely in the 2 mouse lemur species, because both are nocturnal. Habitat separation can be achieved by either differentiation in habitat requirements or spatial separation. Though both mouse lemur species stably co-occur locally, they inhabit mainly exclusive but interdigitating habitat parts, i.e., show a checkerboard distribution (Dammhahn and Kappeler 2008; Schwab and Ganzhorn 2004). Thus, *Microcebus berthae* and *M. murinus* appear not to partition food resources but avoid competition by mutually excluding each other on a small spatial scale (Dammhahn and Kappeler 2008; Schwab and Ganzhorn 2004).

So far, detailed comparative data are available for only a few *Microcebus* spp. from 4 different regions of Madagascar (Table 6). Researchers collected the data via different combinations of methods and the data span variable parts of the year. Thus, they can be compared only with caution. However, several general patterns seem to exist:

- 1) *Microcebus murinus* is an opportunistic generalist species with a high plasticity in its feeding ecology, adjusting its diet to what is locally or temporally available in a habitat. The generalist and flexible feeding ecology might explain why the species is so widely distributed even inhabiting rural areas (M. Dammhahn,

Table 6 Results of detailed studies of feeding ecology of mouse lemurs in different forest types of Madagascar

	Kirindy	Ampijoroa	Mandena	Ranomafana
Species	<i>Microcebus murinus</i> <i>M. berthae</i>	<i>M. murinus</i> <i>M. ravelobensis</i>	<i>M. murinus</i>	<i>M. rufus</i>
Forest type	Dry deciduous forest	Dry deciduous forest	Littoral rain forest	Evergreen rain forest
Rainfall (mm)	800	1250	1680	4485
Diet (%)	<i>M. berthae</i>	<i>M. ravelobensis</i>		<i>M. rufus</i> ^a
	Fr: 4	Fr: 0		Fr: 44 (84)
	Fl: 1	Fl: 0		Fl: 0
	Ar: 13	Ar: 5		Ar: 54 (76)
	Gu: 0	Gu: 50		Gu: 2
	Hs: 82	Hs: 45		Hs: 0
	<i>M. murinus</i>	<i>M. murinus</i>	<i>M. murinus</i>	
	Fr: 24	Fr: 7	Fr: 63	
	Fl: 1	Fl: 0	Fl: 22	
	Ar: 12	Ar: 3	Ar: 11	
	Gu: 14	Gu: 11	Gu: 4	
	Hs: 50	Hs: 78	Hs: 0	
Methods	Focal observation, fecal analyses	Focal observation, fecal analyses	Focal observation, fecal analyses	Opportunistic observations, fecal analyses
Reference	This study	Radespiel <i>et al.</i> 2006 ^b	Lahann 2007	Atsalis 1999

Food categories: Fr=fruit; Fl=flowers/nectar; Ar=arthropods; Gu=gum; Hs=homopteran secretions.

^a Values in parentheses refer to % of fecal samples containing fruit or arthropod remains.

^b We corrected percentages for left out unknown food.

- pers. obs.*), degraded forests (Ganzhorn 1995; Ganzhorn and Schmid 1998), and plantations (Ganzhorn 1987).
- 2) *Microcebus berthae* is the most specialized mouse lemur with the smallest feeding niche. Because the narrow feeding niche of *Microcebus berthae* is completely included into the wider niche of *M. murinus*, specialization in *M. berthae* might not indicate feeding niche partitioning with *M. murinus* but instead might reflect a limited choice of food sources during extended periods of food scarcity. The combination of a rather inflexible and specialized diet with one of the most restricted ranges (Schwab and Ganzhorn 2004) highlights the need for conservation action to protect the smallest of all living primates (Dammhahn and Kappeler 2005).
 - 3) Feeding niche overlap between coexisting cheirogaleids is higher in areas with higher productivity and lower seasonality. At rainfall <2500 mm/yr, forest productivity increases with rainfall and declines with the number of dry months (<100 mm; Kay *et al.* 1997; van Schaik *et al.* 2005). Moreover, floristic richness of tree species increases with annual precipitation, providing greater microhabitat diversity and fostering denser ecological species packing (Ganzhorn *et al.* 1999) and increased reproductive rates (Lahann *et al.* 2006) in wet than in dry forests. Based on these general patterns, the study sites should increase in overall resource availability and microhabitat diversity and consequently decrease in feeding niche differentiation between sympatric cheirogaleid species in the following order: Kirindy > Ampijoroa > Mandena > Ranomafana (Table 6).

In Ranomafana, *Microcebus rufus* is highly frugivorous (Atsalis 1999); only very preliminary data on the feeding ecology of coexisting *Cheirogaleus major* are available (Dew and Wright 1998). In Mandena, high food availability, a low number of nonprimate competitors, together with the fact that all cheirogaleid species hibernate during the lean period have led to relaxed food competition between coexisting cheirogaleid species that resulted in the absence of feeding niche differentiation (Lahann 2007). The dry deciduous forest of Ampijoroa is less seasonal than Kirindy. Thus, competition during the dry season should be less pronounced than in Kirindy, resulting in higher feeding niche overlap and more similar body sizes of sympatric mouse lemur species. Available data indicate similar overall omnivorous diets in *Microcebus ravelobensis* and *M. murinus* and no evidence for clear feeding niche differentiation (Radespiel *et al.* 2006), though interspecific differences are larger than in Mandena. Unfortunately, researchers have not yet studied feeding ecology of coexisting *Microcebus murinus* and *M. griseorufus* inhabiting even dryer forest areas. In areas of co-occurrence, pronounced differences in feeding ecology can be predicted for the species pair, which might even have led to spatial separation as preliminary data pointed to for Beza Mahafaly (Rasoazanabary 2004) and Berenty Speciale Reserve (Yoder *et al.* 2002).

Acknowledgments We acknowledge the authorization and support of this study by Prof. O. Ramilijaona and Prof. D. Rakotondravony (Département de Biologie Animale, Université d'Antananarivo), the Commission Tripartite, and the CAFF of the Direction des Eaux et Forêts, the CFPF Morondava. We thank Rodin Rasoloarison, Léonard Razafimanantsoa, Tiana Andrianjanahary, the late Jean-Claude de Beroboka, Bruno Tsiverimana, and the Equipe Kirindy for support and assistance in the field. Roger

Andriamparany, Vanessa Mass, and Hannah McLauchlin helped with insect collection. A previous version of the manuscript benefited greatly from comments of Mia-Lana Lührs, Jörg U. Ganzhorn, and discussions in the Behavioral Ecology & Sociobiology group of the DPZ. DFG (Ka 1082/10-1&2), Margot-Marsh Biodiversity Foundation, Deutsches Primatenzentrum Göttingen, and the Christian-Vogel-Fonds (GfP) provided financial support. All research reported here is in compliance with animal care regulations and applicable national laws of Germany and Madagascar. The appropriate Animal Use and Care committees of Germany (Bundesministerium für Naturschutz, BfN) and Madagascar (Ministère de l'Environnement et des Eaux et Forêts, MINEEF) approved all research protocols.

References

- Atsalis, S. (1999). Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *20*, 193–229.
- Basset, Y. (1991). The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecological Entomology*, *16*, 265–278.
- Baum, D. A. (1995). The comparative pollination and floral biology of baobabs (*Adansonia*-*Bombacaceae*). *Annals of the Missouri Botanical Garden*, *82*, 322–348.
- Bollen, A., Donati, G., Fietz, J., Schwab, D., Ramanamanjato, J.-B., Randrihasipara, L., et al. (2005). An intersite comparison on fruit characteristics in Madagascar: evidence for selection pressure through abiotic constrains rather than through co-evolution. In J. L. Dew, & J. P. Boubli (Eds.), *Tropical fruits and frugivores: The search for strong interactors* (pp. 92–118). New York: Springer.
- Charles-Dominique, P. (1975). Nocturnality and diurnality. An ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In W. P. Luckett, & F. S. Szalay (Eds.), *Phylogeny of the primates* (pp. 69–88). New York: Plenum Press.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches. Linking classical and contemporary approaches*. Chicago: University of Chicago Press.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366.
- Clutton-Brock, T. H. (1974). Primate social organization and ecology. *Nature*, *250*, 539–542.
- Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology London*, *183*, 1–39.
- Corbin, G. D., & Schmid, J. (1995). Insect secretions determine habitat use patterns by a female lesser mouse lemur (*Microcebus murinus*). *American Journal of Primatology*, *37*, 317–324.
- Dammhahn, M., & Kappeler, P. M. (2005). Social system of *Microcebus berthae*, the world's smallest primate. *International Journal of Primatology*, *26*, 407–435.
- Dammhahn, M., & Kappeler, P. M. (2008). Small-scale coexistence of two mouse lemur species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive environment. *Oecologia*. doi:10.1007/s00442-008-1079-x
- Denlinger, D. L. (1980). Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica*, *12*, 100–106.
- Dew, J. L., & Wright, P. C. (1998). Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica*, *30*, 425–437.
- Elton, C. (1946). Competition and the structure of ecological communities. *Journal of Animal Ecology*, *15*, 54–68.
- Fietz, J., & Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat. *Oecologia*, *121*, 157–164.
- Ganihar, S. R. (1997). Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences*, *22*, 219–224.
- Ganzhorn, J. U. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology*, *12*, 205–215.
- Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia*, *75*, 436–450.
- Ganzhorn, J. U. (1989). Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia*, *79*, 279–286.
- Ganzhorn, J. U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, *76*, 2084–2096.

- Ganzhorn, J. U., & Schmid, J. (1998). Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. *International Journal of Primatology*, *19*, 785–796.
- Ganzhorn, J. U., Wright, P. C., & Ratsimbazafy, J. (1999). Primate communities: Madagascar. In J. G. Fleagle, C. H. Janson, & K. E. Reed (Eds.), *Primate communities* (pp. 75–89). Cambridge, UK: Cambridge University Press.
- Garber, P. A. (1987). Foraging strategies among living primates. *Annual Review in Anthropology*, *16*, 339–364.
- Génin, F. (2003). Female dominance in competition for gum trees in the grey mouse lemur *Microcebus murinus*. *Revue d'Écologie (Terre Vie)*, *58*, 397–410.
- Gotelli, N. J., & Entsminger, G. L. (2006). EcoSim: Null models software for ecology. Version 7. Jericho, VT 05465: Acquired Intelligence Inc. and Kelsey-Bear.
- Groves, C. P. (2000). The genus *Cheirogaleus*: unrecognized biodiversity in dwarf lemurs. *International Journal of Primatology*, *21*, 943–962.
- Groves, C. P. (2001). *Primate taxonomy*. Washington, DC: Smithsonian Institutional Press.
- Gursky, S. (2000). Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*, *21*, 477–495.
- Hapke, A., Fietz, J., Nash, S. D., Rakotondravony, D., Rakotosamimanana, B., Ramanamanjato, J.-B., et al. (2005). Biogeography of dwarf lemurs: genetic evidence for unexpected patterns in southeastern Madagascar. *International Journal of Primatology*, *26*, 873–901.
- Hladik, C. M., Charles-Dominique, P., & Petter, J. J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In P. Charles-Dominique, H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, G. F. Pariente, A. Petter-Rousseaux, & A. Schilling (Eds.), *Nocturnal Malagasy primates* (pp. 41–73). New York: Academic Press.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Belknap Press.
- Holt, R. D., Grover, J., & Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, *144*, 741–771.
- Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor Symposium. *Quantitative Biology*, *22*, 415–427.
- Kappelle, P. M., & Rasoloarison, R. M. (2003). *Microcebus*, mouse lemurs, Tsidy. In S. M. Goodman, & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1310–1315). Chicago: University of Chicago Press.
- Kay, R. F., Madden, R. H., van Schaik, C. P., & Higdon, D. (1997). Primate species richness is determined by plant productivity: implications for conservation. *Proceedings of the National Academy of Science*, *94*, 13023–13027.
- Krebs, C. J. (1998). *Ecological methodology*. Menlo Park, CA: Addison-Wesley.
- Kunz, T. H. (1988). Methods of assessing the availability of prey to insectivorous bats. In T. H. Kunz (Ed.), *Ecological and behavioral methods for the study of bats* (pp. 191–210). Washington, DC: Smithsonian Institution Press.
- Lahann, P. (2007). Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *Journal of Zoology*, *271*, 88–98.
- Lahann, P., Schmid, J., & Ganzhorn, J. U. (2006). Geographic variation in populations of *Microcebus murinus* in Madagascar: resource seasonality or Bergmann's rule. *International Journal of Primatology*, *27*, 983–999.
- MacArthur, R. H., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, *101*, 377–385.
- Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, *28*, 1219–1235.
- Martin, A., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge: Cambridge University Press.
- Meier, B., & Albignac, R. (1991). Rediscovery of *Allocebus trichotis* Günther 1875 (Primates) in northeast Madagascar. *Folia Primatologica*, *56*, 57–63.
- Mittermeier, R. A., Konstant, W. R., Hawkins, F., Louis, E. E., Langrand, O., Ratsimbazafy, J., et al. (2006). *Lemurs of Madagascar*. Washington, DC: Conservation International.
- Nadjafzadeh, M. N., & Heymann, E. W. (2008). Prey foraging of red titi monkeys, *Callicebus cupreus*, in comparison to sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Physical Anthropology*, *135*, 56–63.
- Nash, L. T. (1986). Dietary, behavioral, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology*, *29*, 113–137.

- Nekaris, K. A. I., & Rasmussen, D. T. (2003). Diet and feeding behavior of Mysore Slender Lorises. *International Journal of Primatology*, *24*, 33–46.
- Norsica, I., Carrai, V., & Borgognini-Tarli, S. M. (2006). Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*, *27*, 1001–1022.
- Overdorff, D. J. (1993). Similarities, differences, and seasonal patterns in the diet of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology*, *14*, 721–753.
- Ozanne, C. M. P., & Bell, J. R. (2003). Collecting arthropods and arthropod remains for primate studies. In J. M. Setchell, & D. J. Curtis (Eds.), *Field and laboratory methods in primatology* (pp. 214–227). Cambridge, UK: Cambridge University Press.
- Pageès, E. (1980). Ethoecology of *Microcebus coquereli* during the dry season. In P. Charles-Dominique, H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, G. F. Pariente, A. Petter-Rousseaux, J. J. Petter, & A. Schilling (Eds.), *Nocturnal Malagasy primates: Ecology, physiology and behavior* (pp. 97–116). New York: Academic Press.
- Pianka, E. R. (1973). The structure of lizard communities. *Annual Reviews in Ecology and Systematics*, *4*, 53–74.
- Radespiel, U. (2006). Ecological diversity and seasonal adaptations of mouse lemurs (*Microcebus* spp.). In L. Gould, & M. L. Sauther (Eds.), *Lemur ecology and adaptation* (pp. 211–233). New York: Springer.
- Radespiel, U., Reimann, W. E., Rahelinirina, M., & Zimmermann, E. (2006). Feeding ecology of sympatric mouse lemur species in northwestern Madagascar. *International Journal of Primatology*, *27*, 311–321.
- Rasoazanabary, E. (2004). A preliminary study of mouse lemurs in Beza Mahafaly Special Reserve, southwestern Madagascar. *Lemur News*, *9*, 4–7.
- Rasoloarison, R. M., Goodman, S. M., & Ganzhorn, J. U. (2000). Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology*, *21*, 963–1019.
- Reimann, W. E. (2002). Koexistenz und Nahrungsökologie von Weibchen des grauen und goldbraunen Mausmakis (*Microcebus murinus* und *M. ravelobensis*) in Nordwest-Madagaskar. Dissertation, University of Veterinary Medicine Hannover.
- Richards, L. A., & Windsor, D. M. (2007). Seasonal variation of arthropod abundance in gaps and the understory of a lowland moist forest in Panama. *Journal of Tropical Ecology*, *23*, 169–176.
- Schmid, J. (1999). Sex-specific differences in activity patterns and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. *Journal of Mammalogy*, *80*, 749–757.
- Schmid, J. (2001). Daily torpor in free-ranging gray mouse lemurs (*Microcebus murinus*) in Madagascar. *International Journal of Primatology*, *22*, 1021–1031.
- Schmid, J., & Kappeler, P. M. (1998). Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). *Behavioural Ecology and Sociobiology*, *43*, 125–132.
- Schmid, J., & Speakman, J. R. (2000). Daily energy expenditure of the gray mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *Journal of Comparative Physiology B*, *170*, 633–641.
- Schmid, J., Ruf, T., & Heldmaier, G. (2000). Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoximus*) in Madagascar. *Journal of Comparative Physiology B*, *170*, 59–68.
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, *185*, 27–39.
- Schülke, O. (2003). To breed or not to breed—food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur (*Phaner furcifer*). *Behavioural Ecology and Sociobiology*, *55*, 11–21.
- Schülke, O., & Ostner, J. (2007). Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. *Acta Ecologica*, *10*, 13–21.
- Schwab, D., & Ganzhorn, J. U. (2004). Distribution, population structure and habitat use of *Microcebus berthae* compared to those of other sympatric Cheirogaleids. *International Journal of Primatology*, *25*, 307–330.
- Simmen, B., Hladik, A., & Ramasirisoa, P. (2003). Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. *International Journal of Primatology*, *24*, 949–968.
- Sorg, J. P., & Rohner, U. (1996). Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. In J. U. Ganzhorn, & J. P. Sorg (Eds.), *Ecology and economy of a tropical dry forest in Madagascar* (pp. 57–80). Göttingen: Erich Goltze GmbH and Co KG.

- Sorg, J. P., Ganzhorn, J. U., & Kappeler, P. M. (2003). Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestière. In S. M. Goodman, & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1512–1519). Chicago: University of Chicago Press.
- Southwood, T. R. E., & Henderson, P. A. (2000). *Ecological methods*. Oxford: Blackwell.
- Tilman, D. (1982). *Resource competition and community structure*. Princeton: Princeton University Press.
- Townes, H. (1962). Design for a Malaise trap. *Proceedings of the Entomological Society of Washington*, 64, 253–262.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen, & R. A. Foley (Eds.), *Comparative socioecology. The behavioural ecology of humans and other mammals* (pp. 195–218). Oxford: Blackwell.
- van Schaik, C. P., Terborgh, J., & Wright, S. J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Reviews in Ecology and Systematics*, 24, 353–377.
- van Schaik, C. P., Madden, R. H., & Ganzhorn, J. U. (2005). Seasonality and primate communities. In D. K. Brockman, & C. P. van Schaik (Eds.), *Seasonality in primates. Studies of living and extinct human and non-human primates* (pp. 445–463). Cambridge, UK: Cambridge University Press.
- Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology*, 112, 411–431.
- Winemiller, K. O., & Pianka, E. R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs*, 60, 27–55.
- Wolda, H. (1988). Insect seasonality: why. *Annual Reviews in Ecology and Systematics*, 19, 1–18.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262–300.
- Wright, P. C., & Martin, L. B. (1995). Predation, pollination and torpor in two nocturnal prosimians (*Cheirogaleus major* and *Microcebus rufus*) in the eastern rain forest of Madagascar. In L. Alterman, G. A. Doyle, & M. K. Izard (Eds.), *Creatures in the dark* (pp. 45–60). New York: Plenum Press.
- Yoder, A. D., Burns M. M., & Génin, F. (2002). Molecular evidence of reproductive isolation in sympatric sibling species of mouse lemurs. *International Journal of Primatology*, 23, 1335–1343.
- Zimmerman, J. K., Wright, S. J., Calderón, O., Pagan, M. A., & Paton, S. (2007). Flowering and fruiting phenologies of seasonal neotropical forests: the role of annual changes in irradiance. *Journal of Tropical Ecology*, 23, 231–251.