Ecological determinants of social systems: Comparative and experimental feeding ecology of two mouse lemur species (*Microcebus berthae*, *M. murinus*)

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To my parents

Grey mouse lemur
(*Microcebus murinus*).

Madame Berthe's mouse lemur
(*Microcebus berthae*).

CONTENTS

GENERAL INTRODUCTION

Ecological determinants of social systems

The stunning diversity in animal societies has been a recurrent focus of behavioural ecologists (e.g. Eisenberg 1966; Smuts et al. 1987; Clutton-Brock 1989; Kappeler and van Schaik 2002; Wolff and Sherman 2007). Variation exists mainly along three main entities of social systems: (1) *social organization* referring to sex composition, spatial and grouping patterns, (2) social and genetic aspects of the *mating system* and (3) inter-individual relationships and the quality of social behaviour, the *social structure* (Kappeler and van Schaik 2002). An important aim of socio-ecological research is to understand the relative importance of bottom-up and top-down processes for the evolution and maintenance of various animal societies. This link between ecology and behaviour is provided by the socio-ecological model (SEM), which recognizes the distribution of risks and resources in the environment as the main ecological factors shaping individual behavioural interactions (Crook and Gartlan 1966; Emlen and Oring 1977; Terborgh and Janson 1986). Because female and male mammals differ in their reproductive investment, their fitness is limited by different factors (Trivers 1972; Clutton-Brock and Parker 1992). Accordingly, the SEM assumes that female distribution is mainly a function of the spatial-temporal variation of predation risk and food resources in the environment. Males, on the other hand, map their distribution primarily on that of females and go where receptive females are (Altmann 1990; Clutton-Brock 1989). Thus, a given distribution of females in space and time is the basis of a social system and fundamentally determines the potential of inter- and intra-sexual relationships. In this thesis, I therefore focus on *female* spatial and association patterns.

Solitary foragers: common but poorly understood

Both theoretical and empirical research on the evolution and maintenance of social systems has been heavily biased towards group-living species in primates and other mammals. This is partly due to solitary species being elusive or predominantly cryptic, and hence difficult to study, and partly due to their apparent lack of social complexity. Misconceptions about the differentiation between *solitary* as one form of social organization, which is distinct from *pair-* or *group-living* (Kappeler and van Schaik 2002), and *asocial* have led to much confusion in primatology (discussed e.g.

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in Bearder 1987; Müller and Thalmann 2000) and still prevail in the mammalian literature (e.g. Schwagmeyer 1988; Caro 1989). The distinctive feature of solitary species is that individuals do not synchronize their general activity and in particular their movement patterns with other individuals (Charles-Dominique 1978), and thus typically forage alone (Bearder 1987). This is, however, not synonymous with a lack of social relationships, i.e. a social structure.

Despite the difficulties in studying solitary species and in recognizing their social units, recent research has revealed an astonishing variation in the social systems of solitary foragers (e.g. reviewed in Macdonald 1983; Müller and Thalmann 2000; Kappeler and van Schaik 2002; Dalerum 2007; Lacey and Sherman 2007). Furthermore, a solitary life style is widespread in mammals and characterizes not only most of the phylogenetically basal orders (monotremes, marsupials, and insectivores) but also the majority of other large mammalian radiations, such as carnivores, rodents, chiropterans and also about one third of primates (e.g. Bekoff et al. 1984; McCracken and Wilkinson 2000; Müller and Thalmann 2000; Kappeler and van Schaik 2002; Dalerum 2007; Lacey and Sherman 2007). Therefore, including this type of social organization into comprehensive models will not only reflect variation in social systems among mammals more realistically but might also lead to a better understanding of the ecological and evolutionary processes that shape animal societies. In particular, understanding why and under which circumstances females forage solitarily but temporally associate in stable groups for communal nesting or breeding could (1) help to illuminate the adaptive basis of a solitary lifestyle (Kappeler 1997a) and (2) provide insights into the evolution of group-living (Dalerum 2007; Wagner et al. 2008).

Therefore, the main aim of this thesis was to illuminate ecological determinants of social systems in solitary foragers. As model species I used two sympatric mouse lemurs (*Microcebus* spp.), which differ in two basic characteristics of their social organization: (1) female ranging patterns and (2) sleeping associations. This overall goal was approached from three different angles: (1) by studying the feeding ecology of both species in detail as a prerequisite to link resource characteristics and behavioural consequences of different modes of intra-specific competition with differences in female association patterns, (2) by exploring consequences of inter-specific competition on female spatial patterns and population

density, and (3) by evaluating the mediating effect of different strategies to cope with seasonality on the experienced strength of competition over food.

Malagasy mouse lemurs: a test case

Mouse lemurs (*Microcebus* spp*.*) are small (30-90g) nocturnal solitary primates that forage omnivorously in the fine branch niche and are thought to resemble the ancestral primate most closely (Charles-Dominique and Martin 1970; Martin 1972b; Charles-Dominique 1974). The species-rich genus is widely distributed over nearly all remaining forest areas of Madagascar and is characterized by pronounced plasticity in feeding ecology, distribution patterns and social organization (Kappeler and Rasoloarison 2003; Schülke and Ostner 2005; Radespiel 2006) offering great potential for illuminating the effects of variable ecological conditions on social systems. In particular, comparative studies of co-existing species pairs appear to be a promising approach. First, such studies provide the possibility to identify specific determinants of variation in social systems, while controlling for ecological factors such as predation risk and seasonality. Second, several such pairs are found in different forest habitats in western Madagascar, which generally include the widely distributed grey mouse lemur (*M. murinus*) and another congeneric species with a locally restricted range (*M. berthae, M. griseorufus, M. myoxinus, M. ravelobensis*) (Schmid and Kappeler 1994; Zimmermann et al. 1998; Rasoloarison et al. 2000). Recently, several new species of mouse lemurs have been described (Kappeler et al. 2005; Louis Jr. et al. 2006; Oliveri et al. 2007) so that even more potentially co-existing congeneric species pairs exist in a variety of different habitat types, ranging from evergreen rain forest to dry spiny forest.

In this thesis, I focus on two species that co-occur in the dry deciduous forest of central western Madagascar, the 33g Madame Berthe's mouse lemur (*M. berthae*) and the 60g grey mouse lemur (*M. murinus*). Aspects of behaviour, ecology, genetics and physiology of *M. murinus* have been studied extensively in the field and the laboratory, establishing this species as one of the best known strepsirrhine primates (reviewed in Kappeler and Rasoloarison 2003; Radespiel 2006). Although much less is known about the recently discovered *M. berthae*, prior studies pointed to overall similarities in general characteristics of their ecology and life history with *M. murinus* (Schmid and Kappeler 1994; Schwab 2000; Schwab and Ganzhorn 2004). However, a detailed study of the social system of *M. berthae* revealed that both species differ in

characteristics of female spatial-temporal distribution, which might have strong implications for their social system (Dammhahn and Kappeler 2005). This variation concerns three aspects: (1) population density, (2) female spatial distribution and (3) the formation, composition and stability of female sleeping (and breeding) associations. Because this variation can theoretically be caused by multiple factors, one primary aim of this thesis was to integrate inter- and intra-specific as well as seasonal aspects of female competition in a comparative approach.

A thorough description of species-specific resource use patterns is a prerequisite for testing resource-based models of social organisation. Therefore, I first studied the feeding ecology of both mouse lemurs, using a combination of direct and indirect approaches (**chapters 1** and **2**). Further, the analysis of stable carbon and nitrogen isotopes was used to reveal proportions of animal and plant sources in omnivorous diets (**chapter 2**). In addition, understanding different forms of competition over limited food resources requires information on relative availability of food. This information is provided in **chapter 1** and is based on intensive phenological monitoring of plants and arthropods of different guilds.

Using these data on inter-specific dietary differences, I developed predictions of the SEM for solitary foragers to test whether this model, which was developed for group-living species, can explain variation in social systems of solitary species as well (**chapter 3**). In contrast to other resource-based models (reviewed in Johnson et al. 2002), the SEM makes predictions about both social organization and social structure. Hence, applying the SEM to solitary foragers goes one step beyond understanding spatial patterns, which has been the typical focus of previous studies of solitary foragers. The SEM causally links variation in ecological factors with competitive regimes and allows predictions about the consequences of these on female spatial patterns and social relationships (van Schaik 1989; Sterck et al. 1997; Koenig 2002).

Two modes of feeding competition can be distinguished: *scramble* and *contest* (Nicholson 1954). Scramble competition occurs when resources are dispersed, small, fast depleting or of low quality and each individual in the population can indirectly reduce the net energy gain of all others in the population. When resources are monopolizable by one individual or a group, i.e. medium-sized, of high quality or clumped in patches, contest competition occurs. This type of competition refers to an asymmetric partitioning of resources, in which some (dominant) individuals constrain

the net energy gain of other (subordinate) individuals but not *vice versa* (Koenig 2002). Because competition for food can take place either within groups or between groups, four different modes of competition are distinguished: *within-group scramble*, *within-group contest*, *between-group scramble* and *between-group contest* (van Schaik 1989; Koenig 2002). Combinations of these different modes of competition define the competitive regime of a given species or population.

In **chapter 3**, I argue that when females forage solitarily without defending exclusive territories, they compete over food resources with individuals that have spatially overlapping ranges, irrespective of whether they synchronize their activities or not (see also Schülke 2003 for *dispersed pairs*). Consequently, I characterized the competitive regimes of both mouse lemur species according to distinct categories developed for group-living species and tested the basic prediction of the SEM that resource distribution and the resulting competitive regimes determine distribution and association patterns of solitarily foraging females. Additionally, I tested this prediction experimentally. By manipulating resource distribution in the field, I assessed whether females adjust their ranges to actual resource distributions (**chapter 3**). Finally, predicted behavioural consequences of different competitive regimes (Koenig 2002) were examined for these solitarily foraging females.

Besides intra-specific competition, overall resource availability can also be affected by other co-existing species, in particular, when these species are ecologically very similar. Theoretically, congeneric species are expected to exhibit high resemblance in their resource and habitat requirements, susceptibility to predators, and responses to disturbances and stress (Chase and Leibold 2003). Thus, closely related species should compete more intensely, resulting in higher levels of mutual exclusion, compared to other species pairs (e.g. MacArthur 1972; Tilman 1982; Holt et al. 1994). Why some congeneric species nevertheless co-occur and which mechanisms stabilize this pattern, remains a puzzling issue in community ecology (e.g. Chesson 2000a; Chase and Leibold 2003). In order to assess the relative impact of inter-specific competition between both mouse lemur species on female spatial patterns, I studied feeding niche differentiation based on feeding behaviour (**chapter 1**) and "trophic stable isotope niches" (**chapter 2**) as well as food resource-related habitat requirements (**chapter 4**). Furthermore, using data from an intensive capture-mark-recapture study, I tested recently proposed comparative predictions for alternative classes of mechanisms that can theoretically explain

coexistence of ecologically similar species (Amarasekare 2003; Amarasekare et al. 2004) (**chapter 4**).

In mammals, female fitness is predominantly constrained by their energetic constitution because of their typically high reproductive investment in the form of gestation and lactation (Trivers 1972; Clutton-Brock et al. 1989). Thus, the main factors determining female fitness - birth rate, length of reproductive career and survival rate of offspring (van Schaik 1989) - are all directly or indirectly dependent on the amount of energy a female can allocate to reproduction. In highly seasonal environments, reproduction might be traded off against maintenance requirements during the lean part of the year (Schmid and Kappeler 2005) leading to the development of specific energy strategies to successfully survive and maximize individual reproductive success under these conditions. Depending on physiological and behavioural strategies to overcome the unfavourable part of the year, fluctuating food abundance can influence female competition differently even in species sharing the same habitat. Therefore, seasonality is a recurrent theme in most analyses presented in this thesis. In particular, **chapter 5** is focused on species-specific behavioural energy strategies and their consequences for female fitness.

CHAPTER 1

Comparative feeding ecology of sympatric mouse lemurs (*Microcebus berthae, M. murinus*)

with Peter M. Kappeler

Abstract

Malagasy primate communities harbour a diverse assemblage of omnivorous species. The mechanisms allowing the coexistence of these often closely related species remain poorly understood; partly because only preliminary data on the feeding ecology of most species are available. With this study, we contribute an exemplary feeding ecology data set to illuminate coexistence mechanisms between sympatric grey and Madame Berthe's mouse lemurs (*Microcebus murinus*, *M. berthae*). We studied the feeding ecology of these two species 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 radio-tracked females of both species. A combination of direct behavioural observations and faecal analyses revealed that both *Microcebus* species used fruit, arthropods, gum, insect secretions and small vertebrates as food sources. *M. berthae* and *M. murinus* differed, however, in both composition and seasonal variation of their diets. Whereas *M. murinus* diet varied seasonally and was generally more diverse, *M. berthae* mainly relied on insect secretions supplemented by animal matter. These differences were also reflected in a very narrow feeding niche of *M. berthae* and a comparatively broad feeding niche of *M. murinus*. Resource use patterns of Madame Berthe's and more so of opportunistic grey mouse lemurs broadly followed resource availability within the strongly seasonal dry forest. Feeding niche overlap between the two 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.

Introduction

Primates exhibit a broad range of foraging strategies and dietary preferences, including mainly folivorous (e.g. *Lepilemur*, *Colobus*, *Brachyteles*), gumnivorous (e.g. *Euoticus*, *Phaner*, *Callithrix*), frugivorous (e.g. *Hylobates, Pongo*), insectivorous (faunivorous) (e.g. *Tarsius*, *Loris*), as well as omnivorous feeding patterns (e.g. *Microcebus*, *Papio*, *Pan*) (Clutton-Brock and Harvey 1977; Nash 1986; Garber 1987; Gursky 2000a; Nekaris and Rasmussen 2003). The relationships between dietary preferences for certain food sources of highly different distribution patterns and quality have been generally recognized as an important factor explaining inter- and intra-specific variation in ecology and behaviour of primates (Clutton-Brock 1974; Clutton-Brock and Harvey 1977; Wrangham 1980). Folivores, for example, are usually larger, live in larger groups and have smaller group home ranges than comparable frugivores (Clutton-Brock and Harvey 1977). Also, the competitive regime and resulting social organization of folivores differ from those of frugivores because they usually experience weaker within-group feeding competition (Wrangham 1980; van Schaik 1989, but see the "folivore paradox" recently discussed by Snaith and Chapman 2007). Insectivores (faunivores), in contrast, are usually small, forage solitarily and have large home ranges in relation to their population group size (Clutton-Brock and Harvey 1977; Gursky 2007), a feeding pattern that has been linked to intense within-group scramble competition for small resources of high quality that cannot be shared (van Schaik 1989). However, the classification into frugivores, folivores and insectivores is not possible for numerous primate species of all large radiations, because they use food from several trophic levels.

Classical niche theory (recently reviewed by Chase and Leibold 2003) predicts that species coexistence is only possible if intra-specific competition is stronger than inter-specific competition. This 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 (e.g. Chesson 2000b) or their density- or frequency-dependent predation (e.g. Holt et al. 1994). Among folivorous and frugivorous primates, niche separation was demonstrated mainly by comparing their space use and food choice (e.g. Ganzhorn 1988, 1989; Overdorff 1993; Vasey 2000; Nadjafzadeh and Heymann 2008). 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 cheirogaleids are a specious family of small (33-500g), nocturnal Malagasy primates with currently 23 recognized species in five 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 (Hladik et al. 1980; Rasoloarison et al. 2000; Hapke et al. 2005; Schülke and Ostner 2007). Species distribution patterns, however, vary widely from a few km² in some *Microcebus* species (e.g. *M. berthae*, *M. sambiranensis*, *M. tavaratra*) to species colonizing the entire west and south of Madagascar (e.g. *Cheirogaleus medius, M. murinus*) (Rasoloarison et al. 2000; Schwab and Ganzhorn 2004). Up to five cheirogaleid species of similar body size and ecology can coexist within some forest habitats, thereby creating a high potential for feeding competition. However, due 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 specialisations: *Phaner* is mainly gumnivorous (Hladik et al. 1980; Schülke 2003), *Cheirogaleus* and some rain forest *Microcebus* mainly frugivorous (Fietz and Ganzhorn 1999; Lahann 2007), and *Mirza* mainly faunivorous (Hladik et al. 1980; Pages 1980). The most pronounced plasticity in cheirogaleid feeding patterns is found in mouse lemurs, *Microcebus* spp., which were observed feeding on fruit, nectar, flowers, gum, insect secretions, arthropods, and small vertebrates (reviewed by 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 mainly feed on gum, insect secretions and arthropods (Hladik et al. 1980; Radespiel et al. 2006). This plasticity should allow *Microcebus* species to coexist with several other cheirogaleid species in productive sites without clear feeding niche separation (e.g. Lahann 2007). In less productive areas or those with pronounced seasons of food scarcity, however, distinct feeding niche differentiation between coexisting omnivorous cheirogaleids is predicted (Elton 1946; Pianka 1973). However, comparative data are only available from a few well studied populations/species, so that general mechanisms of coexistence remain obscure (Kappeler and Rasoloarison 2003; Radespiel 2006).

With the present study of the feeding ecology of sympatric grey 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 three other cheirogaleid species (*Phaner pallescens*, *Cheirogaleus medius*, *Mirza coquereli*), as well as *Propithecus verreauxi, Lepilemur ruficaudatus* and *Eulemur rufus* (Ganzhorn and Kappeler 1996). In detail, we asked the following questions: (1) What are the diets of *M. 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 two sympatric species avoid feeding competition by niche separation?

Methods

Study site

We conducted this study between August 2002 and December 2007 in the Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar, approximately 60km northeast of Morondava (44°39'E, 20°03'S, 30-60m above sea level). The study site is located within a 12.500ha concession of the Centre de Formation Professionelle Forestière (CFPF) de Morondava. The climate in this 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 do not exceed 20m in height. For additional information on the phenology and history of the Kirindy Forest see Sorg et al. (2003). The study area within the concession (locally known as N5) was defined by the boundaries of a grid system of small foot trails. Within a 500x500m core area, a rectangular system of small trails was established at 25m intervals, surrounded by additional trails at 50 and 100m intervals. Each trail intersection was marked for orientation and their coordinates were used to create a map.

Climatic data and phenology

We recorded weather data from Januar 2005 to December 2005. We collected rainfall in a rain gauge placed in an open area at the research camp (approximately 2km 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 using vegetation and arthropod phenology data. Within the study area we established 3 transects of 500m each, including 434 trees of 55 species (mean 8 (range 1-86) individuals per species). We recorded presence and absence of flowering and fruit production every 2 weeks. Following Bollen et al. (2005), we classified fruit into fleshy (22 species of transect trees) and non-fleshy fruit (33 tree species).

In order to assess arthropod abundance and seasonal fluctuations, we caught insects once per month (Apr-Dec 2004) and every 2 weeks (Apr-Nov 2005) at constant capture sites distributed over 10ha within the forest. We used three different capture methods, including attractive as well as quantitative sampling techniques to cover insect groups of different guilds. We set a Malaise trap (Bioform, Germany, bi-directional surface of ca. $1.5m^2$) (after Townes 1962) on a small trail within the forest for one week. 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. $4m^2$) lighted by a superactinic light (12V, 8W) for 6 hours between 18:00-24:00h on a small trail within the forest. We manually captured all insects larger than 5mm attracted by the light. Light trap samples reflect night activity only and yielded especially nocturnal flighing insects, such as Lepidoptera and Coleoptera (Southwood and Henderson 2000; Ozanne and Bell 2003). In addition, we spread pitfall traps (n=20; diameter 18cm) over an area of 200x250m within the forest, with 50m distance between traps. We set traps in the late afternoon and took them down the next morning after a sampling period of approximately 16 hours over night. 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 weight from length, using a power function for all adult insects as weight[mg]=b_0+(length[mm])^a with 3.071=ln b_0 and a=2.2968 (after Ganihar 1997). To assess within site and within study period food availability, we calculated an index of relative resource availability as actual resource availability per

average availability over the entire study period (Mar–Dec) for each year separately for arthropods (dry weight) and fruits, respectively.

Seasonality

In order 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 (Jan-Feb) for several reasons: (1) females of both *Microcebus* species are pregnant or lactating during that time and should not be further stressed by wearing radio-collars, (2) trapping success is generally very low in the wet season, which reduces the possibilities to change radio-collars, (3) visibility is low due to full leaf cover and frequent heavy rains at night, which reduces the possibilities of quantitative behavioural observations.

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 (100-450mm) 20% of annual precipitation	low (0-30mm) 2% of annual precipitation	medium (100-200mm) 20% of annual precipitation
Resource availability	fruit high arthropods high	fruit low arthropods low	fruit low arthropods high

Capture and marking

We baited Sherman live traps with pieces of banana and set them near trail intersections 0.5-2m above ground for three consecutive nights in one half of the study area (12.5ha) and then three consecutive nights in the other half of the study area (12.5ha). We performed trapping about once every month: 5-times in 2002 (Aug-Nov), 6-times in 2004 (Jun, Aug-Dec), 8-times in 2005 (Mar-Jul, Sep-Nov), 6-times in 2006 (Mar, Jul-Nov), and 6-times in 2007 (May, Aug-Dec). We used a total of 200 traps per night that were opened and baited at dusk and checked and closed at dawn. We collected captured animals in the early morning and kept them at a nearby research station during the day. We briefly restrained and immobilized all newly captured animals with 10µl Ketamine 100, marked them individually with

subdermally implanted microtransponders (Trovan, Usling, Germany), weighed them with a spring balance (±0.1g), and took a set of standard external morphometric measurements. Recaptured animals from the same trapping session were only identified; those from previous trapping sessions were additionally weighed. We released all animals at the site of capture shortly before dusk. We tested for seasonal variation in female body mass using Kruskal-Wallis tests and for differences between seasons using Mann-Whitney U tests.

Faecal samples

We collected faecal samples from live-trapped subjects and stored them in 70% ethanol. Subsequently, we examined faecal sample contents with the help of 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 further identified them to taxon.

Behavioural observations

We equipped a total of 13 *M. berthae* and 17 *M. murinus* females with radio collars (*M. murinus*: 2g, TW4, Biotrack, UK; *M. berthae*: 1.8g, BD-2, Holohil, Canada). We followed focal animals during their nocturnal activity for 1-4 hours before switching to another animal. We chose the observation time opportunistically but spread it evenly between 18:00 and 1:00h for every animal (prior analyses showed that there is no qualitative difference in feeding behaviour between first and second half of the night). We recorded the location of a focal animal every minute and took behavioural data cumulatively for observation intervals of 1 minute (one-zero sampling) (Martin and Bateson 1993). In total, we observed *M. berthae* for 226 hours and *M. murinus* for 340 hours, respectively. Due to low visibility at night in a dense forest, *M. berthae* were in sight only in 47% of 1-min observation intervals, *M. murinus* in 70%. The species difference in visibility was due to overall higher mobility in *M. berthae*. All analyses are based on 1-min observation intervals in sight. We recorded all occurrences of feeding behaviour and categorized food items into arthropods, fruit, flowers, gum, homopteran secretions – sugary secretions produced by liana-dwelling homopteran larvae -, vertebrates and "unknown". Whenever possible, we determined arthropods to taxon and size classes of 5mm and identified

plant species. We measured handling time of prey items to the nearest minute. We analysed differences in *Microcebus*' diet using Chi²-tests and tested for seasonal variation using 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 using 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:

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

with 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 by the niche overlap function in EcoSim 7.72 Software (Gotelli and Entsminger 2006), in which the observed resource utilization data were randomized among species in 1000 simulations. We used the RA4 algorithm to calculate expected niche overlap indices. This algorithm retained both the observed niche breadth of each species and the pattern of zero resource states by reshuffling the non-zero entries for each resource only. RA4 is the most conservative algorithm and, thus, has the greatest chance of revealing significant patterns of reduced niche overlap (Winemiller and Pianka 1990; Gotelli and Entsminger 2006). Subsequently, we compared mean simulated niche overlap to observed overlap. Inter-specific 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 using Levin's standardized index (Krebs 1998) calculated

as: $B_s = \dfrac{B-1}{n-1}$ with *n*=number of possible resource states and $B = \dfrac{1}{\sum p_j^{\,2}}$ 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-Sep) average monthly temperature minima reached 13-17°C and maxima 32-35°C. In the warm wet season (Oct-Apr) average monthly temperatures ranged from 20-22°C up to 35-37°C. Total rainfall over the entire annual cycle was 783mm and most of the annual rain fell during the wet season. Average minimum temperatures, but not maximum temperatures, were significantly correlated 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>0.11).
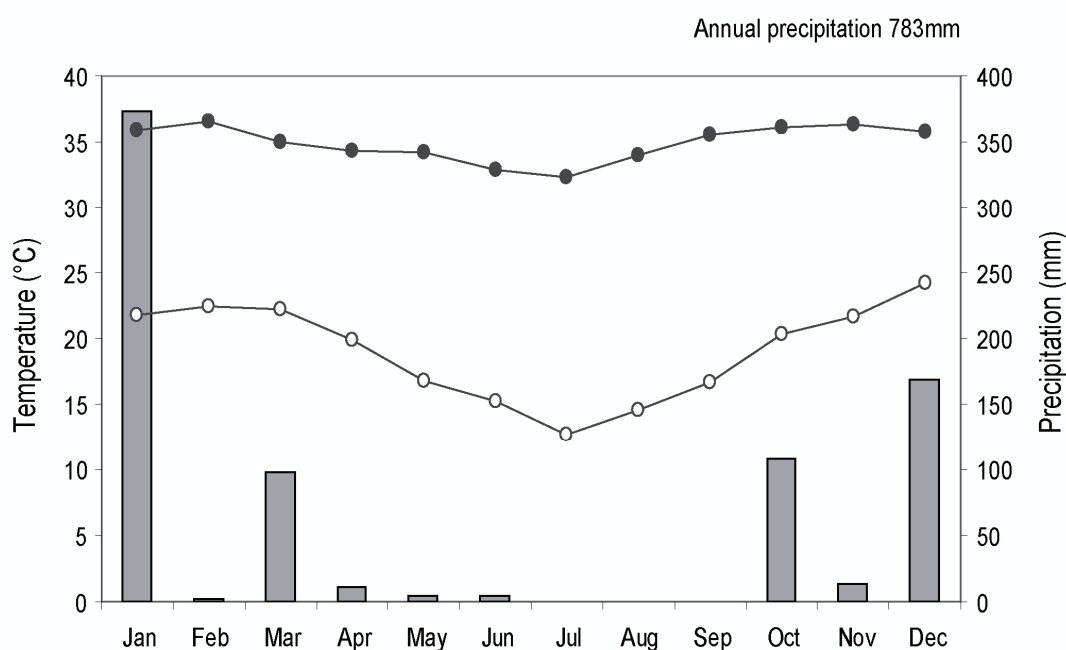
Annual precipitation 783mm

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, 30m above sea level) in 2005. Note that precipitation was unusually low in February.

Most tree species flowered during the rainy season between October and January. Several species, however, bore flowers during the dry season. Thus, there were flowers available year round but on average only 6% (range 3-10%) of all tree individuals 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 (Fig.

2). Ripe fruit were available year round with maxima in the dry season. Non-fleshy fruit 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 (χ^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 non-fleshy fruit (H(2;n=19)=14.23, p<0.001) (Fig. 2). The patterns differed, however, between fruit type. Both non-fleshy and fleshy fruit were maximal available during the rainy season (median (range): fleshy 1.5 (0.5-3.3); non-fleshy 1.6 (1.2-2.0)). Whereas non-fleshy 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) (Fig. 3). 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 weight followed the same seasonal pattern as for absolute numbers of individuals. Seasonal patterns in abundance and dry weight were correlated with monthly rainfall for Malaise trap catches (Spearman Rank Correlations, 2005: monthly abundance, r_s=0.81, n=8, p<0.05; monthly dry weight, 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 weight, 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 weight, r_s=0.16, n=7, p=0.73). Relative availability based on dry weight 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).
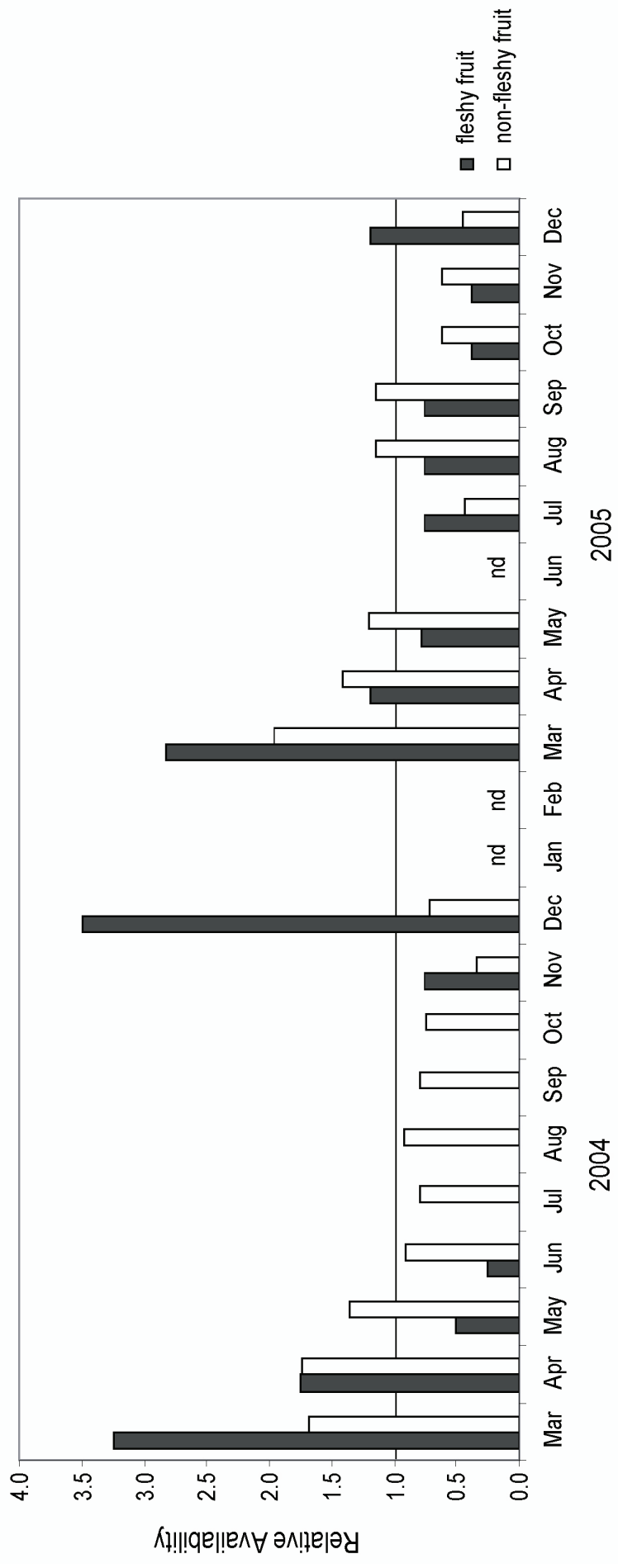
Fig. 2: Relative availability of fleshy and non-fleshy fruit in 2004 and 2005. Note that average monthly availability per year is 1.
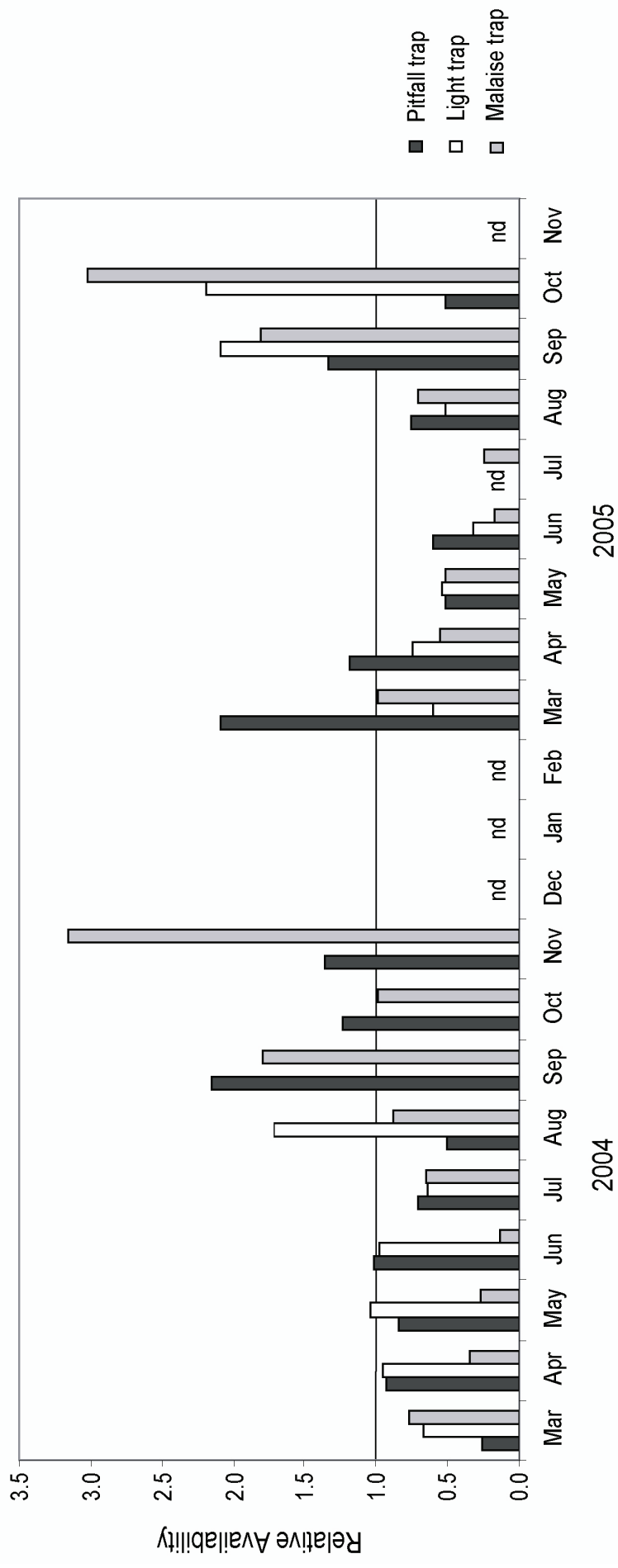
Fig. 3: Relative availability of arthropods (based on dry weight) caught with three different trap types in 2004 and 2005. Note that average monthly availability per year is 1.

Body mass

Body mass of female *M. 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 *M. berthae* lost on average 23% and *M. murinus* 37% of weight.
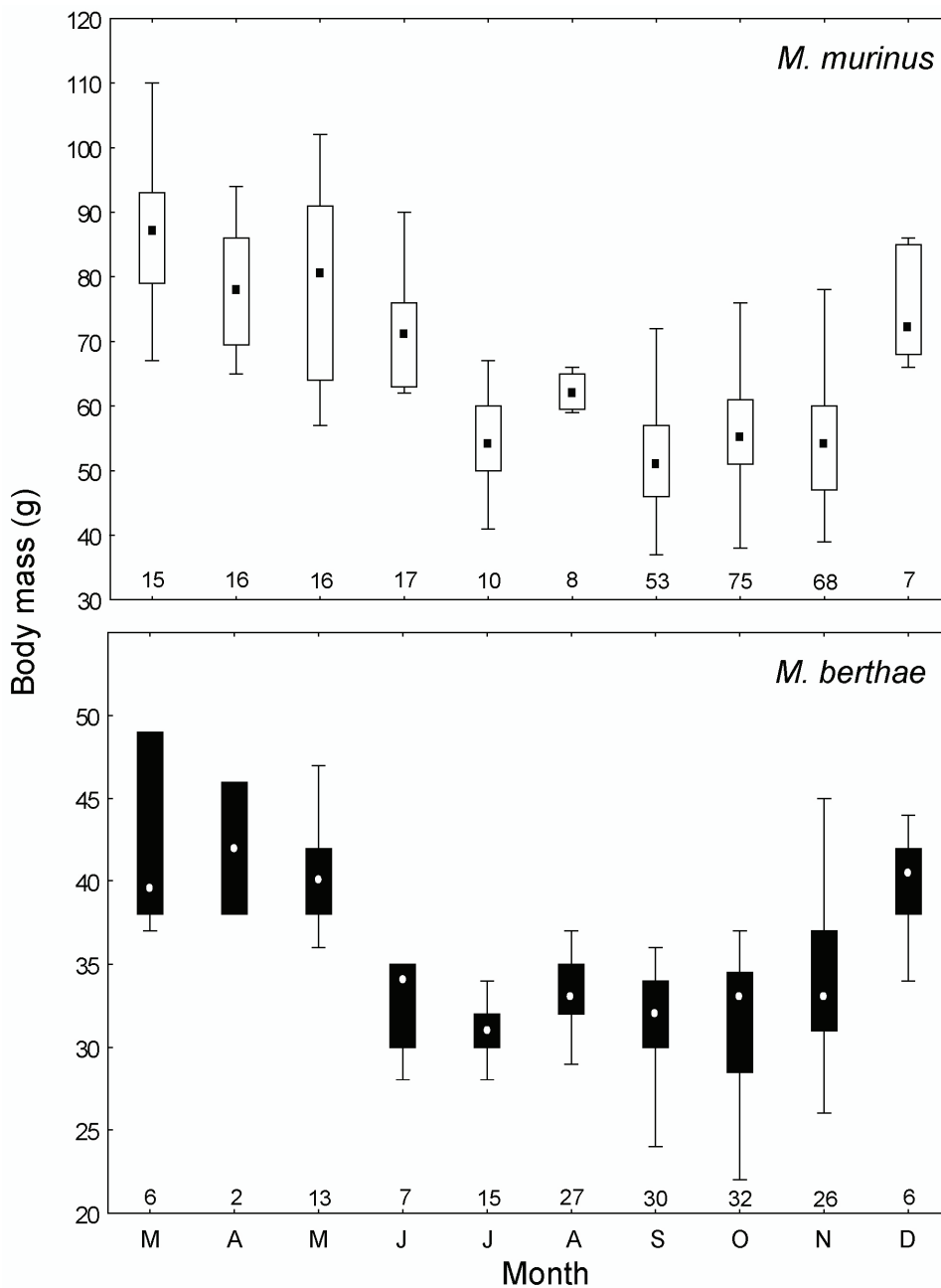

Fig. 4: Seasonal fluctuations in body mass of female *M. murinus* (above) and *M. berthae* (below). Shown are medians, 25-75% quartiles (box), range (whiskers), and sample sizes.

Feeding behaviour

Both *Microcebus* species had an omnivorous diet and used homopteran secretions, fruit, flowers, gum, arthropods and small vertebrates (e.g. geckos, chameleons) as food resources. They differed however 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=0.076). *M. berthae* mainly fed on homopteran secretions, which amounted up to 81% of their overall diet and represented higher proportions than in *M. murinus* in S1 and S2 (Chi²-tests, p<0.001) (Fig. 5). This resource was further supplemented mainly by animal matter. In contrast, *M. murinus* diet varied seasonally and was more diverse, including generally higher amounts of fruit (Chi²-tests, p<0.001 in S1 and S2, p<0.05 in S3) and gum (Chi²-tests, p<0.001 in S2 and p<0.05 in S1 and S3) than *M. berthae*. Both species used similar amounts of animal matter in each season.

M. murinus used fruit, flowers and gum of 14 different plant species (Table 2). *M. berthae* fed on fruit and flowers of only 3 plant species, one of them exclusively. *M. murinus* was observed feeding on 9 different arthropod taxa, with Lepidoptera larvae and Coleoptera being the most frequent (Table 3). *M. berthae* used 6 different taxa, with Coleoptera also being the most frequent. Based on faecal analyses and behavioural observations, both species shared 7 arthropod taxa in their diet (Table 3). Only *M. berthae* consumed Diptera, Isoptera and Mantida and only *M. murinus* consumed Lepidoptera larvae, Phasmida, Heteroptera and Diplopoda. However, most of those exclusively used taxa were used only rarely. *M. murinus* fed on larger prey then *M. berthae* (median and quartile ranges; *M. berthae*: 1cm (0.5-1cm), n=83; *M. murinus*: 1.5cm (0.5-3cm), n=97; Mann-Whitney U test, z=-3.05, p<0.005). Handling time, however, did not differ between the species (median and quartile ranges; *M. berthae*: 1min (1-2) per item, n=85; *M. murinus*: 1min (1-2) per item, n=97; Mann-Whitney U test, z=-1.30, p=0.194). In both species, handling time was positively correlated 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).

M. murinus spent more time feeding than *M. berthae* in S1 (*M. berthae*: 27%, *M. murinus* 51%, χ²=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 *M. 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.
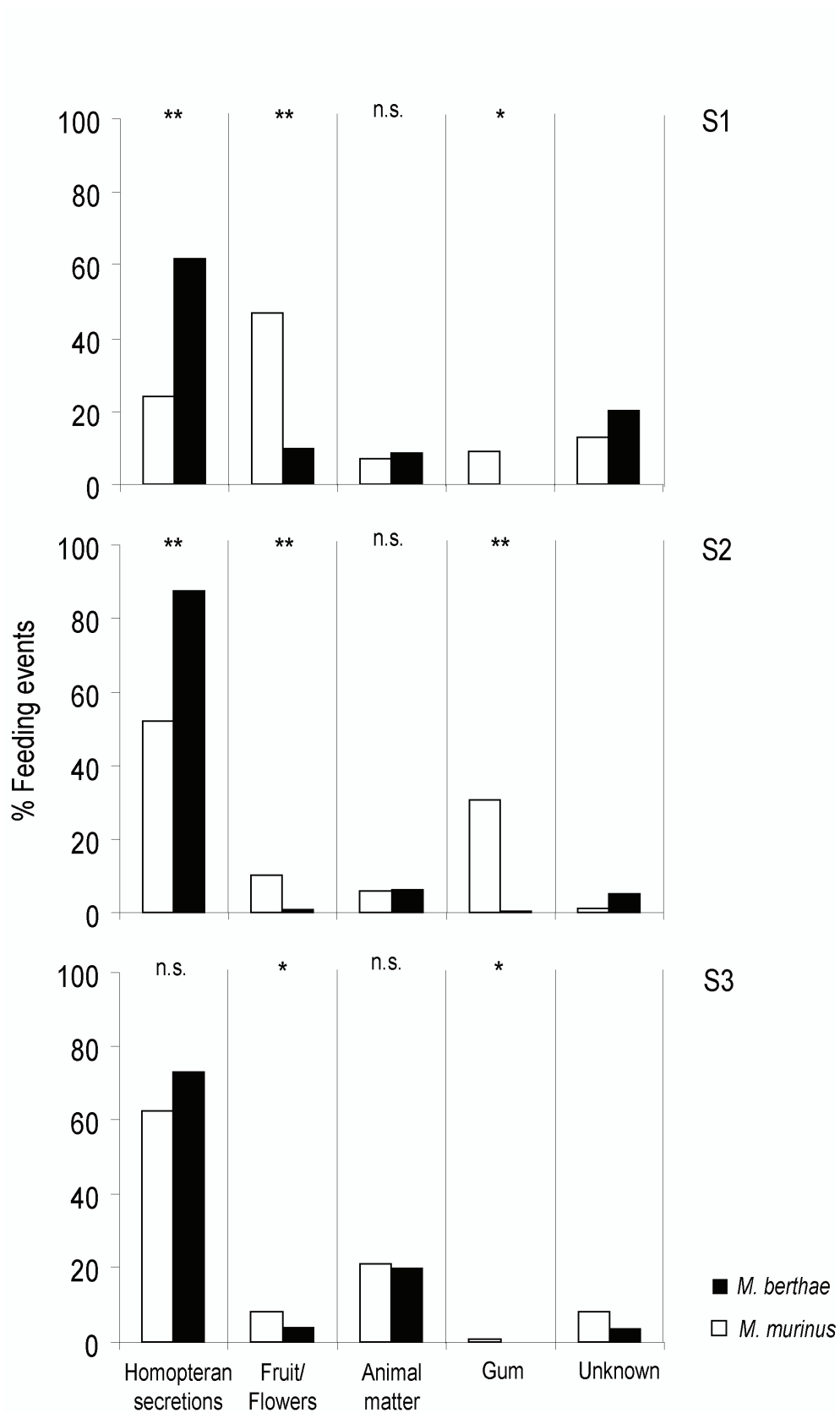
Fig. 5: Percentages of feeding events of *M. berthae* and *M. murinus* on different food categories for each season. *p<0.05 and **p<0.001 in Chi²-tests.

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

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

Faecal analyses

In total, we obtained 67 faecal samples from 42 *M. berthae* individuals and 101 samples from 65 *M. murinus* individuals. The majority of subjects provided only one 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 faecal samples revealed neither species differences, nor seasonal variation in the number of samples with arthropods (Chi²-test, n.s.) (Fig. 6). However, more *M. berthae* than *M. murinus* samples consisted mainly of arthropod remains (>50 volume %) in S1 (Chi²-test: $\chi^2=8.54$, df=1, $p<0.05$) but not in S2 and S3. A higher number of *M. murinus* than *M. berthae* samples contained seeds in season 1 (Chi²-test, $\chi^2=4.20$, df=1, $p<0.05$) and season 2 (Chi²-test, $\chi^2=8.26$, df=1, $p<0.005$) but not in season 3 (Chi²-test, n.s.). For *M. 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 faecal samples with arthropods and seeds, respectively, did not vary seasonally in *M. 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 *M. murinus* S3: 2) and variation was small (min-max ranges, *M. berthae*: 1-4, *M. murinus*: 1-6). Faeces of *M. murinus* included generally higher median numbers (MNI) of seeds than *M. berthae* faeces (*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 *M. murinus* with highest MNI seeds at the end of the wet season and lowest at the end of the dry season.

Arthropod remains in faeces of both species included Lepidoptera, Coleoptera, Blattaria, Ensifera, Orthoptera and Hymenoptera (Table 3). Intact small ants were probably ingested when the lemurs fed on fruit or homopteran secretions. Only *M. berthae* faeces contained fragments of Diptera, Araneae and Isoptera, whereas *M. murinus* faeces also included remains of Lepidopteran larvae. Other material found in faecal samples included hair, seed coats, whole flowers and other plant parts, such as tiny pieces of bark and woody filaments, which were probably ingested by scratching homopteran secretions from surfaces or by opening gum trees.
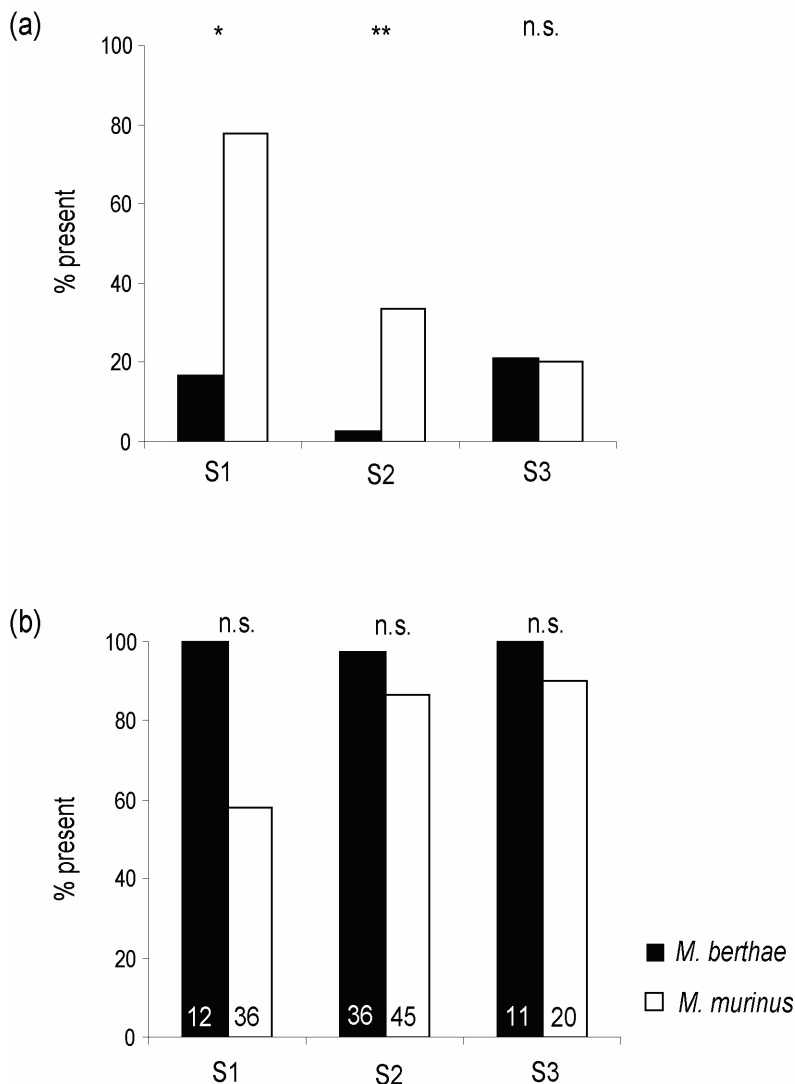

Fig. 6: Percentages of faecal samples of *M. berthae* and *M. murinus* containing seed (a) and arthropod (b) remains per season. *p<0.05 and **p<0.001 in Chi²-tests.

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

Category	Faecal samples		Feeding behaviour	
	M. berthae	*M. murinus*	*M. berthae*	*M. murinus*
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		

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. In S3 however, niche overlap was higher than expected by chance (O_{jk}(obs)=0.99, O_{jk}(exp)=0.41, p<0.05). Also, taking all seasons together, there was a trend towards a higher observed overlap (O_{jk}(obs)=0.83, O_{jk}(exp)=0.46, p<0.10). Feeding niche breadth was narrow in *M. 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 *M. murinus* niche breadth 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 animals relied nearly completely on homopteran secretions.

Table 4: Observed and expected Pianka's indices of niche overlap between *M. berthae* and *M. murinus*. Expected values are based on 1000 simulations using algorithm RA4 in EcoSim 7.72 Software (Gotelli and Entsminger 2006)

Season	Observed index	Expected index (mean ± SD)	p (obs ≤ exp)	p (obs ≥ exp)
1	0.62	0.55 ± 0.22	0.74	0.27
2	0.85	0.37 ± 0.30	0.82	0.18
3	0.99	0.41 ± 0.31	1.00	**0.01**
all	0.83	0.46 ± 0.22	0.90	0.10

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	*M. berthae* (Kirindy)*	*M. murinus* (Kirindy)*	*M. murinus* (Mandena)[1]	*M. murinus* (Ampijoroa)[2]	*M. ravelobensis* (Ampijoroa)[2]
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**

*this study, [1]Lahann (2007), [2]Reimann (2002) & Radespiel et al. (2006)

Discussion

Phenology and seasonal resource availability

The climate at Kirindy is relatively dry (800mm/year) and highly seasonal with pronounced fluctuations in rainfall and temperature (Sorg and Rohner 1996). Most rain falls in only three months 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 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 non-fleshy fruit during the whole dry season. Although fruit were available nearly year round, most of these fruit are no suitable food source for mouse lemurs. In the dry deciduous forest most trees produce non-fleshy, dry dehiscent capsules and indehiscent thick-husked drupes, probably as adaptations against seasonal droughts (Bollen et al. 2005). These 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. 1999a).

Micro- and macroclimatic patterns and seasonal variation in resource availability were described as 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 (e.g. Denlinger 1980; Basset 1991). 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 revealed pronounced seasonal patterns in flying, but not in ground-dwelling, arthropods. Monthly dry weight of flying insects fluctuated up to 23-times between dry and wet season months. Also, in the eastern rainforests seasonal fluctuations in insect biomass were pronounced with light trap catches varying about 11-times in fresh weight 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 behavioural observations and faecal analyses revealed that both *Microcebus* species 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 in size. Whereas fruit were a main component of *M. murinus* diet, particularly at the end of the wet season, *M. berthae* exploited fruit only occasionally. The main proportions of fruit species consumed by *M. murinus* were shared with co-occurring *Cheirogaleus medius* (Fietz and Ganzhorn 1999). Chemical analyses revealed that this mainly frugivorous cheirogaleid preferred fruit with high amounts of sugar during pre-hibernation fattening (Fietz and Ganzhorn 1999), which might also be the case for *M. murinus*. *M. berthae* used gum only on one occasion, whereas gum of *Terminalia* and *Commiphora* trees amounted up to 14% of *M. murinus'* diet. Extensive gum feeding (up to 75% of diet, Génin 2003) could not be confirmed in this study but the proportion of gum might vary locally with gum tree density. Further, diet data solely based on opportunistic observations (e.g. Génin 2003) is likely to overestimate food that is obtained in long bouts and at conspicuous locations. In north-western Madagascar, gum of a variety of different tree species was a major dietary component in both *M. murinus* and *M. ravelobensis* during the dry season (Radespiel et al. 2006). Particularly, Taly (*Terminalia aff. diversipilosa*, Combretaceae) was shown to produce a gum which is rich in soluble sugars (88%) and has a relatively high amount of protein (5%) (Hladik et al. 1980; Nash 1986). Mouse lemurs were observed to gouge open the bark of gum trees themselves, or to feed from holes made by fork-marked lemurs.

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

A particularly important resource for both mouse lemur species was a sugary secretion produced by liana-dwelling homopteran larvae. These 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). *Flatida* larvae excrete honeydew to supply ants with food, with whom they are associated in a facultative mutualistic interaction ("trophobiosis") rewarding the ant's protection against predators (Hölldobler and Wilson 1990). This 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 *F. coccinea* contained relatively high amounts of sugars and other carbohydrates and a low amount of protein (Hladik et al. 1980). This resource type seems to be particularly crucial for *M. berthae*, which spent up to 90% of its feeding time on homopteran secretions during the dry season. The importance of homopteran secretions during the dry season is further underlined by the results of a field experiment, in which a female *M. murinus* changed its habitat use after removal of homopteran secretion patches (Corbin and Schmid 1995). Interestingly, mouse lemurs were never observed feeding directly on the homopteran larvae, although 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 (e.g. 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 non-fleshy fruit. Therefore, it is expected that omnivorous species tune their feeding patterns to seasonal resource availability.

In *M. 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 *M. rufus* (Atsalis 1999) and *M. murinus* in the littoral rain forest (Lahann 2007). Those 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 (see also Radespiel et al. 2006). At the beginning of the wet season, when insect biomass increases conspicuously, *M. murinus* used large amounts of arthropods, resembling rain forest *M. rufus* (Atsalis 1999). Thus, grey mouse lemurs from Kirindy forest opportunistically responded to seasonal changes in food availability. *M. berthae* also adapted their feeding pattern to resource fluctuations, although not as pronounced as *M. murinus*. Homopteran secretions were the stable main part of their diet year-round, which was further supplemented mainly by arthropods according to their availability. Such seasonal variation in feeding patterns of frugivorous and omnivorous primates has been widely demonstrated for dry deciduous and even moist Malagasy forests (e.g. Atsalis 1999; Overdorff 1993; Simmen et al. 2003; Norscia *et al.* 2006).

Do the two 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) *M. berthae* and *M. murinus* females lost up to one-third of their wet season body weight during that time. (3) Extended periods of inactivity and torpor reduce daily energy expenditure by almost 40%, most likely being an adaptation to seasonal food and water shortages (Schmid et al. 2000; Schmid and Speakman 2000; Schmid 2001). Thus, inter-specific 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 grey mouse lemur feeding niches. Niche overlap between co-existing

Microcebus was maximal at the end of the dry season (S3). Only during that time of the year niche overlap between the *Microcebus* species was higher than expected by chance and during none of the seasons overlap was smaller than expected by chance. This niche overlap pattern indicates that the food resource use of the two species does not reflect niche partitioning due to inter-specific competition but seems instead be explained by constraints in food availability (Gotelli and Entsminger 2006). Our niche calculations are based on very coarse food categories, which theoretically might influence the results. We think, however, that this is unlikely because (1) *M. berthae* relies mainly on a non-variable resource (homopteran secretions) and (2) both species do not differ in the taxonomic composition of arthropods, which is the main supplement for *M. berthae*.

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

(1) *M. 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. This generalist and flexible feeding ecology might explain why this species is so widely distributed even inhabiting rural areas (M. Dammhahn, *personal observations*), degraded forests (Ganzhorn 1995; Ganzhorn and Schmid 1998) and plantations (Ganzhorn 1987).

(2) *M. berthae* is the most specialized mouse lemur with the smallest feeding niche. Because the narrow feeding niche of *M. 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 might rather reflect a limited choice of food sources during extended periods of food scarcity. The combination of a rather inflexible and specialized diet together 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.

(3) Feeding niche overlap between coexisting cheirogaleids is higher in areas with higher productivity and lower seasonality. At rainfall <2500mm/yr forest productivity increases with rainfall and declines with the number of dry months (<100mm) (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. 1999b) 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).

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

	Kirindy	Ampijoroa	Mandena	Ranomafana
Species	*M. murinus* *M. berthae*	*M. murinus* *M. ravelobensis*	*M. murinus*	*M. rufus*
Forest type	dry deciduous forest	dry deciduous forest	littoral rainforest	evergreen rainforest
Rainfall (mm)	800	1250	1680	4485
Diet (%)	*M. berthae* Fr: 4 Fl: 1 Ar: 13 Gu: 0 Hs: 82	*M. ravelobensis* Fr: 0 Fl: 0 Ar: 5 Gu: 50 Hs: 45		*M. rufus*[1] Fr: 44 (84) Fl: 0 Ar: 54 (76) Gu: 2 Hs: 0
	M. murinus Fr: 24 Fl: 1 Ar: 12 Gu: 14 Hs: 50	*M. murinus* Fr: 7 Fl: 0 Ar: 3 Gu: 11 Hs: 78	*M. murinus* Fr: 63 Fl: 22 Ar: 11 Gu: 4 Hs: 0	
Methods	focal observation, faecal analyses	focal observation, faecal analyses	focal observation, faecal analyses	opportunistic observations, faecal analyses
Reference	this study	Radespiel *et al.* 2006*	Lahann 2007	Atsalis 1999

Food categories: Fr Fruit, Fl Flowers/Nectar, Ar Arthropods, Gu Gum, Hs Homopteran secretions.
[1]values in () refer to % of faecal samples containing fruit or arthropod remains. *percentages were corrected for left out unknown food.

In Ranomafana, *M. rufus* was found to be highly frugivorous (Atsalis 1999); only very preliminary data on the feeding ecology of co-existing *Cheirogaleus major* are available (Dew and Wright 1998). In Mandena, high food availability, a low number of non-primate competitors together with the fact that all cheirogaleid species

hibernate during the lean period have led to relaxed food competition between co-existing cheirogaleid species, which resulted in the absence of 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 *M. ravelobensis* and *M. murinus* and no evidence for clear feeding niche differentiation (Radespiel et al*.* 2006), though inter-specific differences are larger than in Mandena. Unfortunately, feeding ecology of coexisting *M. murinus* and *M. griseorufus* inhabiting even dryer forest areas have not yet been studied. In areas of co-occurrence, pronounced differences in feeding ecology can be predicted for this 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).

CHAPTER 2

Scramble or contest competition over food in solitarily foraging mouse lemurs (*Microcebus* spp.): new insights from stable isotopes

with Peter M. Kappeler

Abstract

Because female reproductive success in mammals is mainly determined by access to resources, intra-specific female competition is primarily over food. The relationships between resource distribution, type of competition and consequences for social organization have been formalized in the socio-ecological model (SEM), which predicts that ecological factors are the main determinants of female distribution. Here, we aimed to test this basic prediction in two solitary primates (*Microcebus berthae*, *M. murinus*), which differ in two characteristics of female association: (1) ranging patterns and (2) sleeping associations. Using stable nitrogen and carbon isotope data of hair samples and potential food sources we quantified inter-specific differences in diet. Overall, animal source food differed from plant source food in $\delta^{13}C$ but not in $\delta^{15}N$. As predicted, $\delta^{13}C$ in *M. berthae* reflected a diet composed mainly of animal source food. Higher within-species as well as seasonal variation in $\delta^{13}C$ of *M. murinus* indicated a wider trophic niche, also including plant source food. Constantly elevated $\delta^{15}N$ in *M. murinus* most likely reflected extended torpor during the lean season. This energy-saving strategy together with the wider, more opportunistic feeding niche might reduce female competition in this species, facilitating smaller female ranges and a higher association potential. In contrast, $\delta^{15}N$ fluctuated seasonally in *M. berthae* with minima in the lean season, most likely indicating varying amounts of arthropod food in the diet. Intense scramble competition over small, dispersed resources of seasonally fluctuating availability might lead to female spatial avoidance and a reduced association potential in *M. berthae*. Thus, differences in female association patterns between these two solitary foragers are only partly due to different types of competition but seem also be influenced by the overall intensity of intra-specific competition.

for submission

Introduction

Understanding the relative importance of top-down and bottom-up processes for the evolution and maintenance of social systems is a fundamental objective of behavioural ecologists. Both components were incorporated into the socio-ecological model SEM (Crook and Gartlan 1966; Emlen and Oring 1977; Terborgh and Janson 1986), which allows predictions about the relationships between resource distribution, type of competition and consequences for social organization (van Schaik 1989). Because females invest more in each offspring than males in most mammals, female fitness is more energetically constrained and therefore mainly determined by access to food resources (Trivers 1972). Consequently, intra-specific female competition is primarily over food and ecological factors are the main determinants of female distribution in space and time (Crook and Gartlan 1966; Emlen and Oring 1977). Males, on the other hand, go where receptive females are (Altmann 1990) and distribute themselves primarily in response to female distribution (Clutton-Brock 1989).

So far, tests and further developments of the SEM were focused on group-living primates (reviewed in Sterck et al. 1997; Janson 2000; Isbell and Young 2002; Koenig 2002; Koenig and Borries 2006; Snaith and Chapman 2007). Only recently, the model has been successfully transferred to a species that is organized in dispersed pairs (*Phaner furcifer*: Schülke 2003). Variation in the social organization of solitary foragers has not been studied within the theoretical framework of the SEM, although female spatial and association patterns are also diverse in these species where individuals do not synchronize their ranging activity with other individuals (e.g. *primates*: reviewed in Müller and Thalmann 2000; *rodents*: Roberts et al. 1998; Schradin and Pillay 2005; *carnivores*: Macdonald 1983; Dalerum 2007; Wagner et al. 2008; *marsupials*: Martin and Martin 2007). Partly due to a lack of basic data on resource use and social structure, determinants of social systems of solitary foragers have remained largely elusive (Kappeler and van Schaik 2002). We aimed to narrow this informational gap by studying the feeding ecology of two sympatric solitarily foraging mouse lemur species (*Microcebus* spp.), which differ in female association patterns.

Microcebus berthae (33g) and the larger *M. murinus* (60g) co-occur in the dry deciduous forests of western Madagascar and thus experience similar overall environmental variability, such as predation pressure and seasonal fluctuations in

resource availability. In addition, both species are nocturnal solitary omnivores that use the fine branch niche (Martin 1972a; 1973; Dammhahn and Kappeler 2005) and are very similar in general characteristics of their ecology and life history. However, *M. murinus* and *M. berthae* differ in details of female spatial-temporal distribution. Whereas in *M. berthae* females use large (2.5ha), predominately exclusive ranges and overall population density is low, female *M. murinus* ranges are smaller (0.7ha) and overlap extensively with on average 10 other females in dense populations (Eberle and Kappeler 2002; Dammhahn and Kappeler 2005, in press a). Furthermore, female *M. murinus* regularly aggregate in stable sleeping groups of close female kin (Radespiel et al. 2001; Wimmer et al. 2002), which are also communal breeding units (Eberle and Kappeler 2006). In contrast, female *M. berthae* associate only opportunistically into sleeping groups of variable composition (Dammhahn and Kappeler 2005). According to predictions of the SEM, these differences in female association patterns should be caused by distinct competitive regimes resulting from differences in resource distribution. Theoretically, small, fast depleting resources that are dispersed in space lead to *scramble competition* (Nicholson 1954), resulting in female spatial avoidance and a low female association potential (van Schaik 1989). In contrast, *contest competition* over resources that are monopolizable, i.e. medium sized, of high quality or clumped in space, allows females to cluster spatially (van Schaik 1989).

A common theme of solitary foragers among primates is that they are omnivorous and nocturnal (e.g. *Daubentonia madagascariensis*: Sterling et al. 1994; *Mirza coquereli*: Hladik et al. 1980; Pagès 1980; *Microcebus* spp.: Kappeler and Rasoloarison 2003; Radespiel 2006; most Galagidae and Lorisidae: Bearder 1987). However, identifying the relative proportions of different food sources in omnivorous diets is crucial to reveal different forms of competition over limited food resources. Direct behavioural observation is notoriously difficult in small nocturnal animals living in dense forests. Additionally, this method is likely to overestimate large conspicuous food sources or those with prolonged feeding times. On the other hand, indirect methods are either invasive, e.g. stomach analysis, or limited to the detection of hard substrate material such as chitin, fibres and seeds in the case of faecal analysis. A possible approach to overcome these methodological shortcomings is the analysis of stable isotopes, which has recently become increasingly significant in ecology (Fry 2006; West et al. 2006).

The analysis of stable isotopes is based on the fact that (1) many elements have two or more naturally occurring stable isotopes that differ in mass, e.g. the abundant ^{14}N and the rare ^{15}N, (2) animals take up the stable isotope ratio of their diet, and (3) all biochemical reactions favour the lighter more abundant isotope of a particular element, which leads to an enrichment of the heavier isotope in body tissues (DeNiro and Epstein 1978, 1981; Eggers and Jones 2000). Typical are fractionations of 2-5‰, resulting in a predictable difference in the ^{15}N/^{14}N-ratio of consumers and their food sources (DeNiro and Epstein 1981; Ambrose and DeNiro 1986; McCutchan Jr et al. 2003; Vanderklift and Ponsard 2003). Consequently, within food webs there is a stepwise enrichment in ^{15}N from one trophic level to the next, which allows the analysis of complex trophic relationships (Eggers and Jones 2000; Post et al. 2000). Because enrichment is less pronounced in δ^{13}C (approximately 1‰) this isotope is often only used as an additional source of information.

Stable isotope analyses have been successfully applied in a variety of ecological studies (summarized in Fry 2006; West et al. 2006) and particularly to quantify the relative contribution of different nitrogen and carbon sources to an animal's diet, both in the past and the present (*fish:* Focken and Becker 1998; Focken 2001; Gaye-Siessegger et al. 2003, 2004; *frogs:* Araújo et al. 2007; *birds:* Hobson and Clark 1992; Hobson 1999; *mammals:* reviewed in Crawford et al. 2008). Because stable isotope analyses provide continuous measures of trophic positions, they can potentially identify relatively complex trophic strategies such as age-related trophic changes (Mendes et al. 2007), the contribution of cryptic sources to diets (Mcilwee and Johnson 1998) and intra-population variation (Clegg et al. 2003; Matthews and Mazumder 2004; Stevens et al. 2006; Loudon et al. 2007). Furthermore, this method is particularly suitable for the reconstruction of omnivorous diets (e.g. Herrera et al. 2002; Urton and Hobson 2005). Measuring isotopes in metabolically inactive keratin-based tissues such as hair and feathers has several advantages: (1) they can reveal discrete information about individual dietary histories, (2) because these tissues grow slowly and continuously, they are integrative, i.e. they preserve information of a given time period, and (3) they can be obtained non-invasively. Hair, in particular, proved to be a useful indicator of diet, because isotope turnover of mammalian tissue is high enough to resolve short-term diet changes (Macko et al. 1999; Schwertl et al. 2003), while reflecting diet composition during the growth phase of up to several months (e.g. Darimont and Reimchen 2002).

Furthermore, controlled feeding experiments demonstrated high resolution of dietary information recorded in hair (West et al. 2004).

We studied stable nitrogen and carbon in hair samples to determine proportions of plant and animal food sources in the omnivorous diets of *M. berthae* and *M. murinus*. In detail we aimed: (1) to reconstruct species-specific diet compositions as well as seasonal and intra-population dietary variation, (2) to test for ecological niche differentiation between these two congeneric species, and (3) to test the basic prediction of the SEM that resource distribution determines female distribution. Given the fact that all potential large, high quality and clumped mouse lemur food are plant sources (e.g. gum, fruit) and all potential small, dispersed sources are consumers or produced by consumers (e.g. insects, small vertebrates, and insect secretions), we made the following predictions (Table 1): (1) *M. berthae* has higher $\delta^{15}N$ and $\delta^{13}C$ than *M. murinus,* because they include larger proportions of higher trophic level food sources. (2) Within-species variation in stable $\delta^{15}N$ and $\delta^{13}C$ is higher in *M. murinus,* because this species has a wider feeding niche and mixes a higher number of trophic food levels (Dammhahn and Kappeler in press b). (3) Because both species inhabit a highly seasonal forest, which is characterized by pronounced fluctuations in temperature, rainfall and food availability, high seasonal variation in stable $\delta^{15}N$ and $\delta^{13}C$ is expected.

Table 1: Stable isotope signatures and resource characteristics of mouse lemur food sources as well as predicted modes of feeding competition and female association potentials, as based on the socio-ecological model (van Schaik 1989, Koenig 2002)

Food	Resource characteristics	Competitive mode	Female association potential	Stable Isotopes
Plant sources				
Gum	large,	contest	high	low δN^{15}
Fruit	high quality, slow depletion (monopolizable)			low δC^{13}
Animal sources				
Arthropods	small,	scramble	low	high δN^{15}
Homopteran secretions	dispersed, fast depletion			high δC^{13}

Methods

Study site

This study was conducted in the Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar, approximately 60km northeast of Morondava (44°39'E, 20°03'S, 30-60 m above sea level). The climate in this area is characterized by pronounced seasonality with a hot rainy season between December and March and little or no rainfall from April to November when most trees shed their leaves; annual precipitation averages 800mm and mean temperature is 25°C (Sorg and Rohner 1996). The forest is very dense with a canopy between 10-12m and dominated by trees <30cm DBH. Tree species richness of the Kirindy Forest/CFPF is high, including more than 200 woody species with *Commiphora* (Burseraceae), *Securinega* (Euphorbiaceae), *Poupartia* (Anacardiaceae), *Baudouinia* (Caesalpiniaceae), *Dalbergia* (Fabaceae), and *Cedrelopsis* (Ptaeroxylaceae) being the dominant tree genera (Rakotonirina 1996). For additionally information on the phenology and history of the Kirindy Forest/CFPF see (Sorg et al. 2003).

Sampling

In the course of an ongoing long-term study, members of sympatric populations of *M. berthae* and *M. murinus* have been regularly trapped and individually marked since 2002. Trapping was performed with Sherman live traps baited with pieces of banana that were set on trail intersections about every 25m within a study area of 25ha (for details see Dammhahn and Kappeler, in press a). Each individual was permanently marked with a subdermally implanted microtransponder (Trovan, Usling, Germany) under brief anaesthesia (10 µl Ketanest 100). We collected hair samples from individually known live-trapped animals (*M. murinus* n=101, *M. berthae* n=68) by cutting tail hair as close to the skin as possible with a pair of fine-tipped surgical scissors. Hair samples were stored in 70% ethanol or without any preservative. Because preservation of tissues in ethanol can alter isotope signatures (Sweeting et al. 2004), we first analysed the data for possible effects of storage method on stable carbon and nitrogen isotopes and found none. Furthermore, we collected fruit from 11 tree species and leaves from 23 tree species and dried them in the sun. Also, gum from 3 tree species, homopteran secretions and insects (Coleoptera, Orthoptera, Homoptera, Lepidoptera) were collected.

Stable isotope analysis

All samples were oven-dried at 60°C until weight was constant prior to analyses. Fruit and leave samples were grounded and homogenized with a ball mill. 1mg of the homogenized samples, of insects, or of hairs was enclosed into tin capsules for determination of carbon and nitrogen isotope ratios, respectively. Mass spectrometer analyses were carried out at the Centre for Stable Isotope Research & Analysis (KOSI) in Göttingen (Germany), using an isotope ratio mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany) in an online-system after passage through an element analyzer (NA 1110, Carlo Erba, Milan, Italy). The isotope data are presented as $\delta^{13}C$ (‰) relative to PDB standard and $\delta^{15}N$ (‰) relative to nitrogen in air and were calculated as follows: $\delta X = [(R_{sample} / R_{standard}) - 1] \times 10^3$

Where δX is $\delta^{15}N$ or $\delta^{13}C$, and R is the respective $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio. Analytical error was calculated based on the standard deviations of the external standard, acetanilide, and ranged between 0.05 – 0.08‰ for $\delta^{15}N$ and between 0.03 – 0.12‰ for $\delta^{13}C$.

Feeding experiment

In order to validate results of the stable isotope analyses, to estimate species-specific trophic shift as well as baseline values, we conducted a feeding experiment. We caught 7 *M. murinus* (3 females, 4 males) outside of the study area and kept them in 1m³ cages for 3 to 6 weeks at the field station. We took hair samples from tail hair before the experiment and re-grown hair after the experiment. Three animals were provisioned only with arthropods and four animals were fed with a fruit only diet to ensure that protein intake came from plant or animal sources only. The experiment could not be replicated with *M. berthae* because the time of fast hair growth coincided with a decrease in trapping success at the beginning of the wet season. Because sample sizes were small, we assessed differences in stable $\delta^{15}N$ and $\delta^{13}C$ values graphically and abstained from statistical testing.

Statistical analyses

Because $\delta^{15}N$ data were not normally distributed in both species (Shapiro-Wilk tests, $p < 0.05$) and variances of $\delta^{15}N$ and $\delta^{13}C$ differed between species (F-ratios, $p < 0.05$), we z-transformed all data to achieve homogeneity of variances and used transformed data in all parametrical tests. We explored within species sex-differences

and between species differences in $\delta^{15}N$ and $\delta^{13}C$ using independent t-tests and ANOVAs. Further, seasonal variation within species was assessed with Kruskal-Wallis tests because sample sizes were unbalanced. Subsequently, we compared monthly species differences using Mann-Whitney U-tests due to small sample size. In order to assess if body condition was related to $\delta^{15}N$ and $\delta^{13}C$ values we calculated Spearman Rank correlations between body weight and isotope values for male and female *M. berthae* and *M. murinus,* respectively.

We tested for within species variation to determine trophic niche width (Bearhop et al. 2004) using the Brown-Forsythe test of homogeneity of variances. Furthermore, we analysed feeding niche characteristics based on $\delta^{13}C$ - $\delta^{15}N$ bi-plots (Layman et al. 2007a, 2007b). Niche width can be characterized by the $\delta^{15}N$ and $\delta^{13}C$ ranges, calculated as the distance between the two individuals with the most enriched and most depleted $\delta^{15}N$ and $\delta^{13}C$ values, which provide measures of the degree of trophic diversity, i.e. number of trophic levels included, or the number of basal resources with varying $\delta^{13}C$ values, respectively. Also, the total area of a convex hull encompassing all $\delta^{13}C$ - $\delta^{15}N$ individual space of a species reflects trophic diversity and thus niche width. We calculated convex hull areas as minimum convex polygons (MCP) using the Animal Movement extension (Hooge et al. 1999) of ArcView GIS 3.3. (ESRI), and subsequently determined overlap between species' MCP areas. Because the area of a MCP is positively related to the number of data points included (Anderson 1982) and our data set is unbalanced, we calculate a second convex hull area based on monthly species means of $\delta^{13}C$ and $\delta^{15}N$ (n=8 months, and 11 (range 1-27) individuals per month).

The average degree of trophic diversity is also reflected in the mean Euclidian distance of each individual to the species $\delta^{13}C$ and $\delta^{15}N$ centroids. The density of individual packing can be calculated from mean same-species nearest neighbour distances, with small distances indicating high similarity in individual feeding habits. Further, we performed a discriminant function analysis to compare differences in stable carbon and nitrogen values between species and to determine whether individuals can be assigned to their species groups representing a species' "trophic isotope niche". The discriminant function analysis provides a classification procedure that is based on the discriminant function and assigns each individual isotope signature to its appropriate species (correct classification) or the other species

(incorrect classification). All statistical tests were calculated with Statistica 8.0 (StatSoft, Inc. 2007) and significance for all tests was set at alpha = 0.05.

Dietary mixing models

Dietary mixing models calculated with IsoSource 1.3.1 were used to determine the relative contributions of different food sources to *Microcebus* diet (Phillips 2001; Phillips and Gregg 2001, 2003). Because the number of potential *Microcebus* food sources exceeded n+1, with n being different isotope system tracers, no unique solution of a linear mixing model based on mass balance equations was possible (Phillips and Gregg 2003). Instead, the software IsoSource determines all possible source combinations (solutions) to an observed mixture of isotopic signatures in small increments (1%) and with a small tolerance (±0.1‰) for feasible solutions. So far, no published accurate estimate of the enrichment occurring between diet and animal tissue is available for *Microcebus* or any other primate species. Applying regression equations based on laboratory feeding experiments with rats (Caut et al. 2008) on potential *Microcebus* food sources yielded discrimination factors which were too small to be possible for δ^{15}N (-0.07 - 0.11) and relatively large for δ^{13}C (1.63 - 6.26), respectively. We therefore assumed trophic enrichment based on data of other mammalian hair (Robbins et al. 2005) and run mixing model calculations with two possible combinations of enrichment factors: (1) +5‰ for δ^{15}N and +3‰ for δ^{13}C and (2) +5‰ for δ^{15}N and +2‰ for δ^{13}C. Generally a high fractionation of nitrogen had to be assumed because differences between *Microcebus* δ^{15}N and potential food δ^{15}N were large (see results). Furthermore, we calculated enrichment as differences between mean *M. berthae* and *M. murinus* isotope signatures and food sources, as well as to leaves, which served as a primary producer habitat baseline.

Results

Within and between species variation in stable carbon and nitrogen isotopes

First, we tested for within-species sex differences. In *M. berthae* females had higher δ^{13}C mean values than males (t=2.43, p=0.018) and within-sex variation was similar (F=1.04, p=0.884), for δ^{15}N values there was a trend for females having a higher δ^{15}N mean than males (t=1.88, p=0.065) and there were no difference in within-sex variation (F=1.67, p=0.211) (Fig. 1). In *M. murinus* females had a higher δ^{15}N mean than males (t=4.04, p=0.0001) and within-sex variation was higher in

males than in females (F=2.00, p=0.016). For $\delta^{13}C$ there were no sex differences in mean (t=0.78, p=0.437) or within-sex variation (F=1.43, p=0.209).

Both *M. murinus* males and females had higher $\delta^{15}N$ than *M. berthae* males and females, respectively (males: $F(1,95)=56.56$, p<0.0001; females: $F(1,70)=67.86$, p<0.001) (Fig. 1). Carbon isotope values differed only between *M. berthae* and *M. murinus* females ($F(1,70)=4.89$, p<0.030) but not between males ($F(1,95)=2.39$, p=0.126). Subsequent 2-factorial ANOVAs revealed that species ($\delta^{15}N$, $F(1,165)=104.07$, p<0.00001; $\delta^{13}C$, $F(1,165)=7.82$, p=0.006) and sex ($\delta^{15}N$, $F(1,165)=13.18$, p<0.001; $\delta^{13}C$, $F(1,165)=4.40$, p=0.038) explained significant parts of the variation in both stable isotopes.

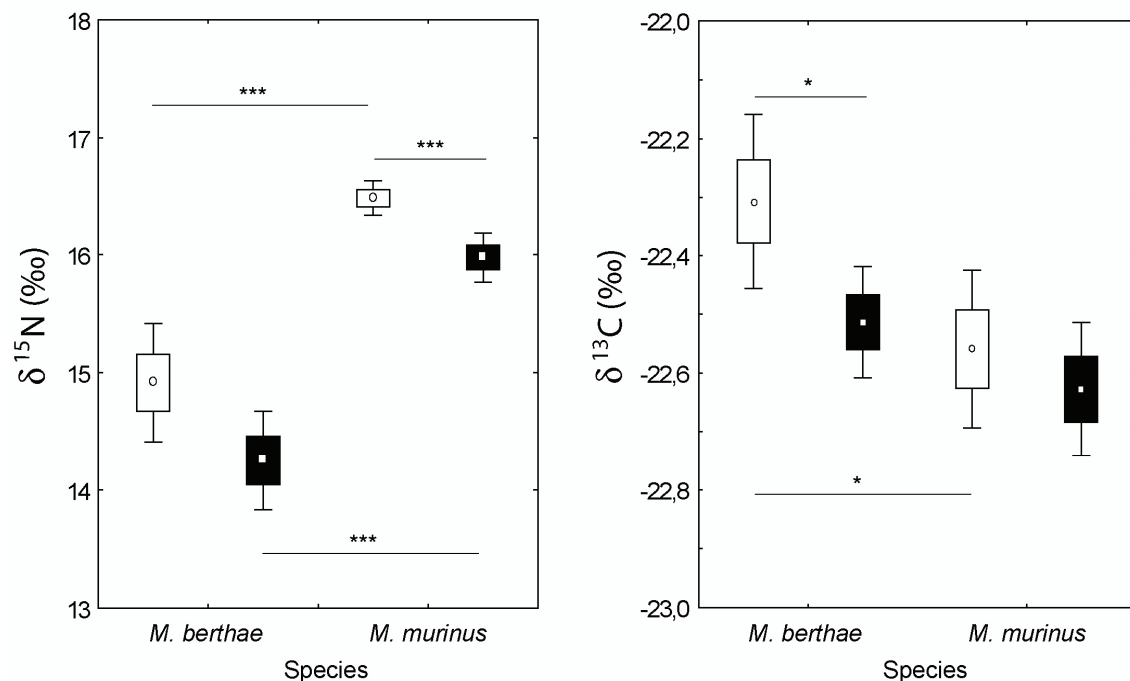**Fig. 1**: Within and between species differences in stable carbon and nitrogen isotopes: Mean (SE, 95% CI) $\delta^{15}N$ and $\delta^{13}C$ values for female (open) and male (filled) *M. berthae* and *M. murinus*. Within and between species differences are indicated by *p<0.05 and ***p<0.0001.

Stable $\delta^{15}N$ were not constant over time but varied monthly in *M. berthae* (Kruskal-Wallis test, $H(7,n=68)=17.00$, p=0.017), stable $\delta^{13}C$ showed a trend for seasonal variation ($H(7,n=68)=13.28$, p=0.066) (Fig. 2). In *M. murinus* $\delta^{15}N$ was constant (Kruskal-Wallis test, $H(7,n=102)=11.79$, p=0.108) in contrast to $\delta^{13}C$ ($H(7,n=102)=16.59$, p=0.020). Comparing data month by month using Mann-Whitney U-tests revealed higher $\delta^{15}N$ in *M. murinus* than *M. berthae* in the dry season

months, June (p<0.001), August, (p<0.05), September (p<0.001), but not in the rainy season months, March and April. δ^{13}C differed only between species in August (p<0.05). Data from May, July, October and December could not be tested due to low sample size in one or the other species.
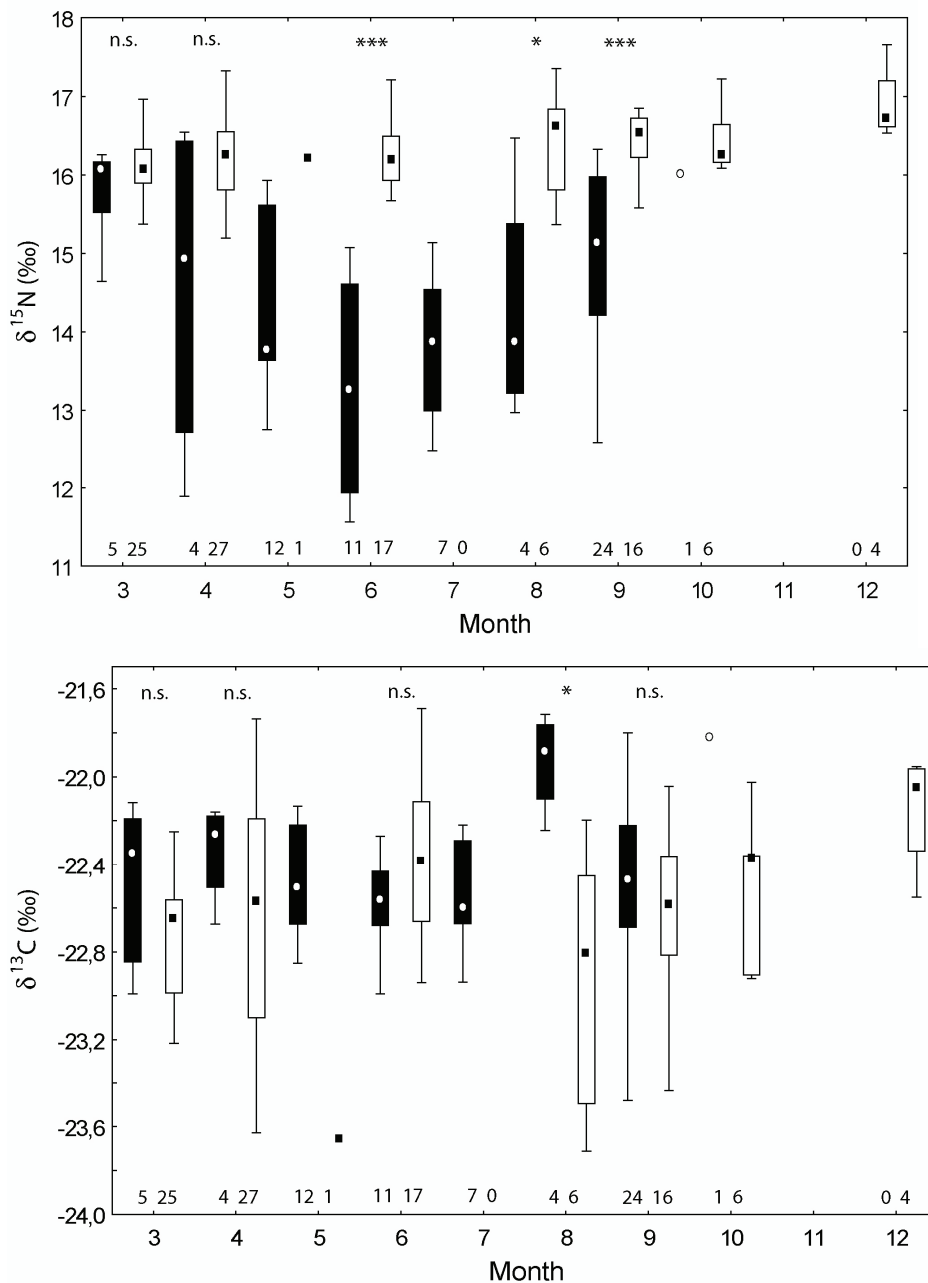

Fig. 2: Seasonal variation in stable carbon and nitrogen isotopes: (a) Stable δ^{15}N (median, 25-75% quartiles, range) showed monthly fluctuations in *M. berthae* (Kruskal-Wallis test, p<0.05) but not in *M. murinus* (Kruskal-Wallis test, p>0.1). Species differed in the dry season months (Jun, Aug, Sep) but not in the rainy season months (Mar, Apr) (Mann-Whitney U tests, *p<0.05, ***p<0.0001). (b) Stable δ^{13}C (median, 25-75% quartiles, range) showed a trend towards monthly fluctuations in *M. berthae* (Kruskal-Wallis test, p<0.07) and varied monthly in *M. murinus* (Kruskal-Wallis test, p<0.05). Species differed only in August but not in March, April, June and September (Mann-Whitney U-tests, *p<0.05). Numbers of individuals are given below.

In *M. berthae* both $\delta^{15}N$ and $\delta^{13}C$ were positively correlated with body weight in males, but only $\delta^{13}C$ was related with female body weight (Table 2). In *M. murinus* neither $\delta^{15}N$ nor $\delta^{13}C$ were correlated with body weight in either sex (Table 2).

Table 2: Results of Spearman Rank correlations between body weight and z-transformed $\delta^{15}N$ and $\delta^{13}C$ data for male and female *M. berthae* and *M. murinus,* respectively. Significant correlations are in bold.

Species		$\delta^{15}N$		$\delta^{13}C$	
	n	**R_s**	**p**	**R_s**	**p**
M. berthae					
females	21	0.23	0.307	0.46	**0.035**
males	47	0.36	**0.012**	0.37	**0.001**
M. murinus					
females	51	0.01	0.943	0.25	0.083
males	50	0.00	0.998	0.10	0.507

Stable isotope feeding niche

Trophic niche width can be assed using stable isotope values because species that consume a wide range of food types (of different isotopic signatures) will exhibit wider variation in their tissue isotopic values than those consuming a narrow range of food (Bearhop et al. 2004). We tested for differences in population variance using Brown-Forsythe test of homogeneity of variances ($\delta^{15}N$: $F(1,168)=54.13$, $p<0.0001$; $\delta^{13}C$: $F(1,168)=2.64$, $p=0.106$). Thus, intra-population $\delta^{15}N$ variation was higher in *M. berthae* (SD=1.37) than in *M. murinus* (SD=0.68), but $\delta^{13}C$ variation did not differ between species (*M. berthae,* SD=0.44; *M. murinus,* SD=0.34), indicating a wider range of different prey (food sources) and/or an inclusion of a wider range of trophic levels in the diet of *M. berthae*.

The total $\delta^{15}N$ range in *M. berthae* (5.0) was higher than in *M. murinus* (3.5), but the $\delta^{13}C$ range was smaller (*M. berthae* 1.8, *M. murinus* 2.0). Including all individual data points, *M. berthae* and *M. murinus* differed in MCP areas (*M. berthae* 5.86; *M. murinus* 4.68). The overlap of stable isotope MCP areas was 1.80 corresponding to 31% of the *M. berthae* area and 38% of the *M. murinus* area. Using monthly means, *M. berthae* total MCP area (1.31) was more than twice as large as *M. murinus* MCP area (0.56) (Fig. 3) and species areas did not overlap (Fig. 3). The average distance to the population centroid was larger in *M. berthae* (mean±SD, 1.23±0.67) than in *M. murinus* (0.64±0.42) (t-test, t=-6.94, p<0.0001). Furthermore,

M. berthae (mean±SD, 0.15±0.13, range 0.03-0.59) had significant higher nearest-neighbour distances than *M. murinus* (mean±SD, 0.12±0.092, range 0.01-0.46) (t-test, t=2.20, p<0.029). However, the evenness of individual packing, reflected by the SD of nearest-neighbour distances, did not differ between the *Microcebus* species (Brown-Forsythe test, F(1,167)=1.91, p=0.134).
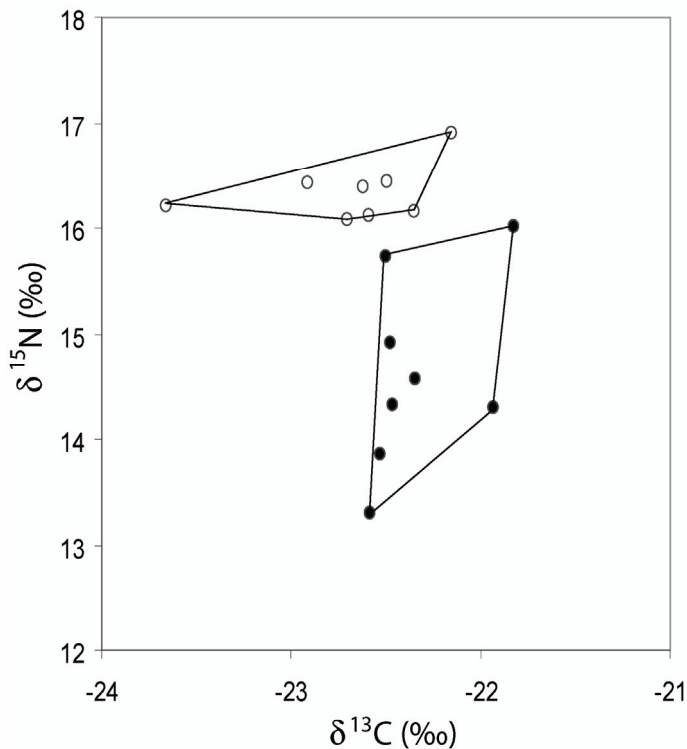

Fig. 4: Species-specific "trophic isotope niche areas": Stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) for *M. berthae* (filled circles) and *M. murinus* (open circles). Each point represents the monthly mean value for on average 11 (range 1-27) animals. Calculation of species "trophic niche area" was based on monthly means (n=8 for each species). Note complete isotope niche segregation based on monthly means.

Multivariate analysis of variance (MANOVA) showed that discrimination of the data was significantly different from random (Wilk's λ=0.51, F=80.21, p<0.0001). Using all data and classification probabilities proportional to group sizes a total of 81% classifications was correct (*M. berthae* 62%, *M. murinus* 94%). Because discriminant function analysis is sensitive to unbalanced sample sizes we ran a second analysis based on equal sample sizes for which the *M. murinus* sample was reduced by randomly drawing 68 samples. MANOVA of the balanced data set also showed that discrimination of the data was significantly different from random (Wilk's λ=0.53, F=60.69, p<0.0001) with 79% correct classifications (*M. berthae* 71%, *M. murinus* 88%).

Dietary Mixing Models

Overall, the food sources gum, arthropods and fruit differed in $\delta^{13}C$ (Kruskal-Wallis test, $H(2,n=12)=7.01$, $p<0.030$) but not in $\delta^{15}N$ ($H(2,n=30)=1.11$, $p=0.573$), and variation within food types was very pronounced (Fig. 4). Multiple pair-wise comparisons revealed differences in $\delta^{13}C$ between arthropods and fruits ($p<0.05$). Also, homopteran secretions had higher $\delta^{13}C$ (-24.1‰) than fruits (mean±95%CI, -29.1±1.6‰). Enrichment, i.e. differences between mouse lemurs and potential food sources, differed between species (Table 3). Stable nitrogen enrichment in *M. berthae* was 6.5‰ to leaves, whereas *M. murinus* hair was enriched by 8.3‰ to leaves, which we used as a primary producer habitat baseline. Stable carbon enrichment to leaves was high in both species (Table 3). During feeding observations *M. berthae* mainly fed on homopteran secretions and arthropods (Dammhahn and Kappeler in press b), to which they were enriched by 2‰ and 2.5‰ in $\delta^{13}C$ and 3.2‰ in $\delta^{15}N$, respectively. For all potential food sources, enrichment in *M. murinus* varied between 1.8-6.1‰ in $\delta^{13}C$ and 4.4-5.9‰ in $\delta^{15}N$, respectively.

Table 3: Differences between *M. berthae* and *M. murinus* mean $\delta^{15}N$ and $\delta^{13}C$ isotope signatures and potential food sources, respectively. Leaves are included as a primary producer habitat baseline although mouse lemurs do not feed on leaves.

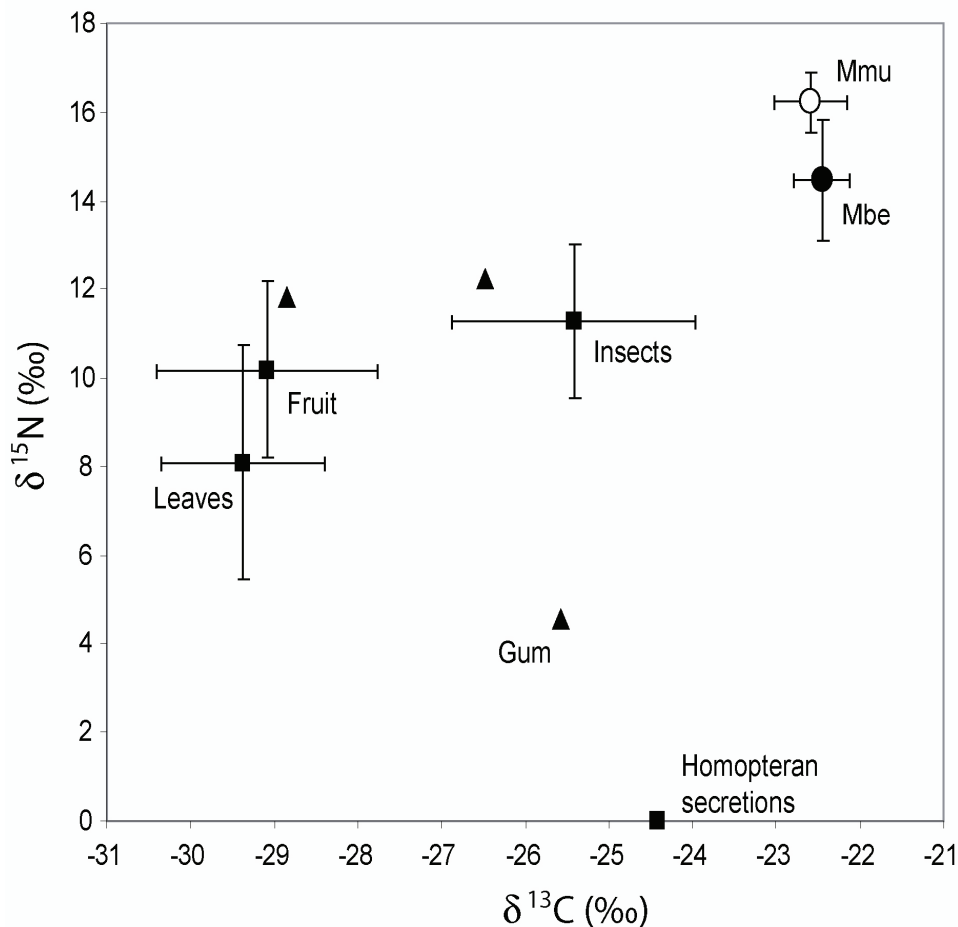| Food sources	*M. berthae*		*M. murinus*	
	$\Delta\delta^{15}N$	$\Delta\delta^{13}C$	$\Delta\delta^{15}N$	$\Delta\delta^{13}C$
Leaves	6.5	7.0	8.3	6.9
Fruit	4.1	6.3	5.9	6.1
Gum	2.6	4.0	4.4	3.9
Arthropods	3.2	2.5	5.0	2.4
Homopteran secretions		2.0		1.8

Fig. 4: Mean (±SD) stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) for *M. berthae* (filled circles), *M. murinus* (open circles) and potential food sources. Symbols without error bars indicated single samples. Leaves are included as a primary producer habitat baseline although mouse lemurs do not feed on leaves.

Because nitrogen concentration was very low in homopteran secretions, stable isotope analysis yielded no δ^{15}N value. Therefore, we first calculated a mixing-model based on one isotope (δ^{13}C) and four food sources (gum, fruit, arthropods, homopteran secretions) and a second mixing-model based on two isotopes and four sources with homopteran secretions being represented only by the δ^{13}C isotope value (Table 4). Assuming a fractionation of +2 for δ^{13}C and +5 for δ^{15}N IsoSource estimates of food contributions to *M. berthae* and *M. murinus* diets were very similar. Basing the model solely on carbon isotope values identified homopteran secretion as the main source, with on average 88% (1-99% range: 70-98%) of *M. berthae* diet and 81% (1-99% range: 56-95%) of *M. murinus* diet. Incorporating both isotopes into the model resulted in arthropods being the most important source with on average 68% (42-89%) for *M. berthae* and 73% (48-95%) for *M. murinus*. Fruit and gum were of minor importance in both mixing models. Assuming a fractionation of +3 for δ^{13}C and

+5 for δ^{15}N IsoSource estimates of food contributions to *M. berthae* and *M. murinus* diets resulted in a more mixed partitioning. The one isotope model identified again homopteran secretion as contributing high proportions to *M. berthae* (mean 33%, range 0-70%) and *M. murinus* (mean 31%, range 0-67%) diet. But gum and arthropod proportions were similarly high, whereas fruit appeared to be of minor importance. The two isotope model resulted in differently composed diets for the two mouse lemur species. Here, *M. berthae* diet was composed of arthropods (35%), homopteran secretions (33%), gum (21%) and fruit (11%) and *M. murinus* diet was dominated by arthropods (70%) supplemented by gum (21%), fruit (8%) and homopteran secretions (1%). Overall, the mixing models indicated that insect secretions and arthropods made up the main part of the diets of both species, whereas fruit and gum were of minor importance.

Table 4: Results of mixing models calculated with IsoSource for one (a and c) and two (b and d) isotope(s) and four food sources with assumed fractionation of +2 δ^{13}C and +5 δ^{15}N (a and b) and +3 δ^{13}C and +5 δ^{15}N (c and d). Shown are percent proportions of potential food sources in *M. berthae* and *M. murinus* diet as mean and 1%-99% percentile ranges, and number of feasible model solution.

Food Source	Isotope	*M. berthae* Mean	Range	n	*M. murinus* Mean	Range	n
(a)							
Gum	δ^{13}C	2	0 - 8	397	4	0 - 12	1.084
Fruit	δ^{13}C	1	0 - 4		2	0 - 6	
Arthropods	δ^{13}C	9	0 - 29		14	0 - 43	
HS	δ^{13}C	88	70 - 98		81	56 - 95	
(b)							
Gum	δ^{13}C, δ^{15}N	15	0 - 42	5.857	17	0 - 45	4.375
Fruit	δ^{13}C, δ^{15}N	6	0 - 16		6	0 - 17	
Arthropods	δ^{13}C, δ^{15}N	68	42 - 89		73	48 - 95	
HS	δ^{13}C, δ^{15}N	12	4 - 18		4	0 - 8	
(c)							
Gum	δ^{13}C	21	0 - 50	15.601	23	0 - 55	16.538
Fruit	δ^{13}C	11	0 - 24		12	0 - 26	
Arthropods	δ^{13}C	35	0 - 81		34	0 - 78	
HS	δ^{13}C	33	0 - 70		31	0 - 67	
(d)							
Gum	δ^{13}C, δ^{15}N	21	0 - 50	15.601	21	0 - 45	292
Fruit	δ^{13}C, δ^{15}N	11	0 - 24		8	0 - 17	
Arthropods	δ^{13}C, δ^{15}N	35	0 - 81		70	51 - 85	
HS	δ^{13}C, δ^{15}N	33	0 - 70		1	0 - 3	

HS: Homopteran secretions

Feeding experiment

Animals with treatment A did not differ in stable $\delta^{13}C$ and $\delta^{15}N$ values before and after the experiment (medians: $\delta^{13}C_{before}$=-22.68, $\delta^{13}C_{after}$=-22.05, $\delta^{15}N_{before}$=12.6, $\delta^{15}N_{after}$=13.5) (Fig. 5). In contrast, all treatment F animals had reduced $\delta^{15}N$ (medians: $\delta^{15}N_{before}$=12.8, $\delta^{15}N_{after}$=9.8) and elevated $\delta^{13}C$ (medians: $\delta^{13}C_{before}$=-23.18, $\delta^{13}C_{after}$=-20.20), respectively, after the experiment (Fig. 5). Furthermore, all animals of treatment A had higher $\delta^{15}N$ and $\delta^{13}C$ values than all animals with treatment F (Fig. 5).
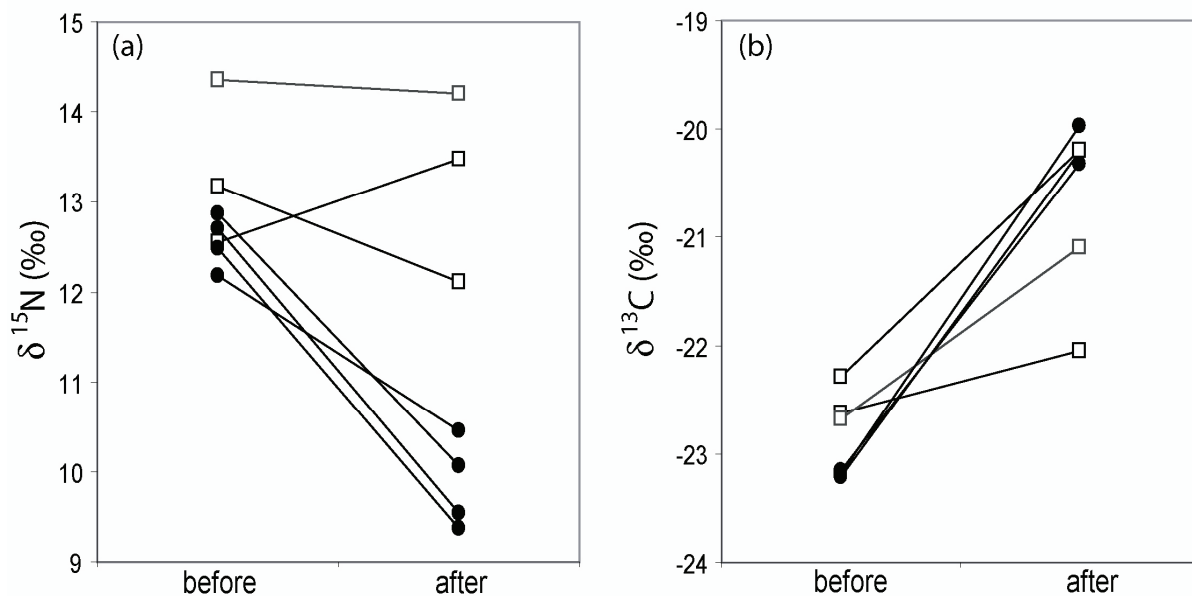

Fig 5: Results of a feeding experiment with 7 wild caught *M. murinus* individuals that were kept for several weeks under semi-natural conditions and fed exclusively insects (open squares) or fruit (black circles), respectively. Stable isotope nitrogen (a) and carbon (b) signatures of hair taken from all individuals before the onset of the experiment and re-grown hair are shown.

Discussion

Stable isotope food source characteristics

Based on the described trophic shift between food and body tissue (DeNiro and Epstein 1978, 1981), we expected mouse lemur food sources to differ by ~3‰ in $\delta^{15}N$ and ~1‰ in $\delta^{13}C$, with fruit and gum having lower stable isotope values than homopteran secretions and arthropods. Contrary to the expectation, we found no

difference in $\delta^{15}N$ between fruit, gum and arthropod samples, which was due to (1) pronounced within-food source variation and (2) enriched $\delta^{15}N$ in fruit and gum of some tree species when compared to forest tree leaves as a habitat baseline. Some tree species, e.g. *Terminalia manteliopsis* produce relative protein rich gum (Hladik et al. 1980), probably also involving $\delta^{15}N$ enrichment. High within source variation was expected for arthropods because our sample included primary and higher order consumers to reflect the wide variety of arthropod taxa in mouse lemur diet (Dammhahn and Kappeler, in press b). Although $\delta^{15}N$ values might vary among parts of plants (Marshall et al. 2007), there is no information on predictable isotopic fractionation patterns between leaves and fruit. Thus, why fruit in this dry deciduous forest are so highly enriched in $\delta^{15}N$ as compared to leaves remains unclear. The apparent lack of variation by food source $\delta^{15}N$ underlines again the necessity to directly sample food sources within the same habitat. Such additional isotope data were missing in all previous primate studies (Schoeninger et al. 1997, 1998, 1999; Sponheimer et al. 2006; Loudon et al. 2007), which largely limits the scope of interpretation. However, plant food sources differed from animal sources in $\delta^{13}C$, which allowed reconstructing mouse lemur diets based on this isotope.

Stable carbon isotopes and mouse lemur diet composition

Because food sources differed only in $\delta^{13}C$, we mainly consider $\delta^{13}C$ variation in mouse lemurs informational for diet reconstructions. Accordingly, as predicted, overall $\delta^{13}C$ was higher in *M. berthae* than in *M. murinus*. This species difference indicated higher proportions of $\delta^{13}C$ rich food sources in *M. berthae*'s diet, e.g. arthropods and homopteran secretions. Furthermore, $\delta^{13}C$ range was lower in *M. berthae*, most likely indicating a lower number of resources with different $\delta^{13}C$ signatures. Also, $\delta^{13}C$ varied seasonally in *M. murinus* but not in *M. berthae,* indicating higher seasonal variation in diet composition in *M. murinus*. Similarly, direct observations of feeding behaviour and faecal analysis revealed a diverse and seasonally varying diet in *M. murinus*, whereas *M. berthae* was found to primarily rely on homopteran secretions supplemented by animal matter (Dammhahn and Kappeler, in press b). These differences were, however, not reflected in one isotope, four source mixing-models, which yielded highly variable solutions with no clear species differences in diet composition. Nevertheless, mixing models identified homopteran secretions and arthropods as the main food sources. Dietary mixing

models are highly sensitive to the assumed enrichment factor (Phillips 2001) and currently there are no data on enrichment factors available for any primate species (Vanderklift and Ponsard 2003). Therefore, our mixing model calculations, which are based on data of other mammalian hair (Robbins et al. 2005), can only give rough estimations of diet proportions.

Two sympatric galago species (*Galago garnettii, G. zanzibaricus*) differed in $\delta^{13}C$ but not in $\delta^{15}N$, which was interpreted as indicating similar feeding patterns but separation into different forest heights (Schoeninger et al. 1998) without providing isotope data on food sources, however. Such a canopy effect of elevated $\delta^{13}C$ in animals foraging higher in the canopy was demonstrated, for example, in a mammalian community of an African tropical forest (Cerling et al. 2004). Although this pattern is well documented for leaves (Medina and Minchin 1980), little is known about systematic variation in fruit. Furthermore, when species have an omnivorous diet and mix (fallen) fruit and potentially mobile consumers such as arthropods or small vertebrates, a canopy effect might no longer be detectable (e.g. Mauffrey and Catzeflis 2003). Although vertical niche differentiation was discussed for other mainly frugivorous sympatric cheirogaleids (Lahann 2008), a canopy effect is unlikely to explain species differences in the studied mouse lemurs, because they forage at similar heights (M. Dammhahn, *unpublished data*).

Variation in stable nitrogen isotopes

Stable nitrogen isotopes values showed pronounced seasonal variation within and between species. Feeding patterns (alone) cannot explain this variation, although *M. murinus* individuals fed an arthropod diet were enriched in $\delta^{15}N$ to those that fed a fruit only diet. Furthermore, both mouse lemur species were highly enriched in $\delta^{15}N$ over their food sources and forest trees. Besides diet composition, several other factors can affect trophic enrichment, which all involve the mobilization of body substances to meet metabolic requirements of homeostasis. As a consequence of reallocation of resources during these states of reduced food intake, proteins are catabolized, resulting in elevated $\delta^{15}N$ signatures (Hobson and Clark 1992; Hobson et al. 1993).

First, it has been suggested that diet quality might influence $\delta^{15}N$ enrichment; animals feeding on poor quality food (high C:N ratio) may recycle internal nitrogen stores leading to increased enrichment values (Hobson and Clark 1992; Voigt et al.

2003; Voigt and Matt 2004; Mirón et al. 2006; but see Spence and Rosenheim 2005). Direct observations and diet reconstructions based on δ^{13}C revealed that *M. berthae* fed mainly on sugary homopteran secretions during the dry season (Dammhahn and Kappeler, in press b), which have a poor C:N ratio (Hladik et al. 1980). In contrast to the expected pattern, however, *M. berthae* had lower δ^{15}N values when including higher proportions of poor quality food in their diet.

Second, nutritional or water stress might affect enrichment in δ^{15}N and δ^{13}C mainly due to recycling of nitrogen (Ambrose and DeNiro 1986; Focken and Becker 1998; Focken 2001; Gaye-Siessegger et al. 2003, 2004; but see Kempster et al. 2007). Individuals of both mouse lemur species lose body weight during the dry season (Schmid and Kappeler 1998; Dammhahn and Kappeler, in press b), which might serve as a proxy for the degree of experienced nutritional stress. Only δ^{15}N fluctuations in *M. berthae* males were related to variation in body weight. Contrary to the expected pattern, animals that were in better body condition had elevated δ^{15}N, however.

Third, due to nitrogen recycling from urea, hibernating mammals were demonstrated to be 3‰ enriched in δ^{15}N as compared to a non-dormant physiological state (Lidén and Angerbjörn 1999). Both mouse lemur species are known for their propensity to enter torpor during the cold and food-limited dry season (Schmid et al. 2000; Schmid and Speakman 2000). Behavioural observations revealed that there are differences in the extent of inactivity between *M. berthae* and *M. murinus* (Dammhahn and Kappeler, in press c). *M. murinus* females prepare by seasonal fattening (Schmid and Kappeler 1998) for the non-productive season and remain largely inactive during the cold dry season, spending most time in energy- and water-saving torpor or even hibernating over extended periods (Schmid 1999; Schmid and Speakman 2000; Rasoazanabary 2006). In contrast, female *M. berthae* remain active throughout the dry season (Dammhahn and Kappeler, in press c) and enter spontaneous daily torpor (Schmid 1996; Schmid et al. 2000) only during the day and the colder second part of the night. Thus, species differences in overall reliance on torpor might explain elevated δ^{15}N in *M. murinus*. This is further supported by the fact that *M. murinus* females had higher δ^{15}N than males, corroborating the sex difference in activity patterns (Schmid and Kappeler 1998; Rasoazanabary 2006).

Additionally, a reduced metabolism during torpor might slow down turnover rates in tissues (Voigt et al. 2003). Accordingly, slower turnover rates due torpor might explain constantly high δ^{15}N in *M. murinus*, compared to seasonal variation of δ^{15}N in active *M. berthae*. So far, we lack detailed information about hair growth rates for *Microcebus,* but observations in the wild suggested seasonal variation with a maximum at the beginning of the austral summer (November) and a minimum growth rate during austral winter in both species (M. Dammhahn, *personal observation*). Thus, variation in δ^{15}N most likely reflected variation in the extent of torpor use between species, and between sexes in *M. murinus*. Seasonal variation in δ^{15}N in *M. berthae* most likely reflects varying amounts of arthropod food in the diet (Dammhahn and Kappeler, in press b). Because it is difficult to track seasonal changes in diet with nitrogen isotopes if they are accompanied by seasonal changes in metabolism, body mass or diet quality (Voigt and Matt 2004), only controlled experiments can reveal which factor caused δ^{15}N enrichment in these free-ranging mouse lemurs.

Food resource characteristics and female associations in solitary foragers

Based on the theoretical background of the socio-ecological model (van Schaik 1989), we predicted that differences in female spatial patterns in solitary mouse lemurs are determined by differences in intra-specific female resource competition. In detail, we expected that when females are dispersed in space they mainly use small and dispersed food resources over which they scramble. In contrast, when females are clumped in space they should rely on high quality (large) sources over which they contest. As predicted, diet reconstructions based on stable isotopes revealed that *M. berthae* mix their diet mainly of animal source food, indicated by higher δ^{13}C in hair samples as compared to *M. murinus*. These food sources are small and can be depleted within a short time, facilitating scramble competition between individuals that forage in the same area (van Schaik 1989; Koenig 2002). However, species differences were only small and dietary mixing models revealed similar diet compositions in both species. In line with results of feeding observations (Dammhahn and Kappeler, in press b), higher variation in δ^{13}C in *M. murinus* indicated a more flexible diet and a wider "trophic isotope niche".

Although not reliably reflecting food sources in our study system, nitrogen isotopes revealed differences in seasonal strategies between the two species that might also be of significance in determining intra-specific competition. Constantly

elevated $\delta^{15}N$ in *M. murinus* most likely reflected the extended use of torpor during the resource low season. This energy- and water-saving strategy (Schmid and Speakman 2000) together with the wider more opportunistic feeding niche (Dammhahn and Kappeler, in press b) might reduce intra-specific competition in this species, facilitating smaller female ranges and a higher association potential. Survival benefits of female philopatry (Lutermann et al. 2006) in combination with benefits of cooperative breeding of closely-related females (Eberle and Kappeler 2006) might lead to stable matrilineal groups (Wimmer et al. 2002, Fredsted et al. 2005), which are clumped in space (Dammhahn and Kappeler, in press a). In *M. berthae* in contrast, $\delta^{15}N$ varied seasonally with a minimum in the resource low dry season, most likely reflecting lower amounts of $\delta^{15}N$ rich arthropods in the diet (Dammhahn and Kappeler, in press b). Because *M. berthae* have a specialized feeding niche and stay active during the resource low dry season, they experience seasonally low food availability. Prolonged and predictable times of food scarcity should result in female spatial avoidance and large (exclusive) home ranges (Clutton-Brock and Harvey 1977, Eisenberg et al. 1972, Reiss 1988), which has been demonstrated empirically and experimentally for many species (e.g. Ims 1987, Roberts et al. 1998; Schradin and Pillay 2005). Thus, intense scramble competition over small, dispersed resources of seasonally fluctuating availability reduced the potential of female associations in *M. berthae*. Overall, differences in female spatio-temporal distribution between these two solitary foragers are only partly due to different types of competition over food but seem additionally be influenced by the overall strength of intra-specific competition.

CHAPTER 3

Females go where the food is. Does the socio-ecological model explain variation in social organization of solitary foragers?

with Peter M. Kappeler

Abstract

The socio-ecological model (SEM) links ecological factors with characteristics of social systems and allows predictions about the relationships between resource distribution, type of competition and consequences for social organization. It has been mainly applied to group-living species but ought to explain variation in social organization of solitary species as well. The aim of this study was to test basic predictions of the SEM in two solitary primates, which differ in two characteristics of female association patterns: (1) spatial ranging and (2) sleeping associations. Beginning in August 2002, we regularly (re-)captured and marked individuals of sympatric populations of Madame Berthe's and grey mouse lemurs (*Microcebus berthae*, *M. murinus*) in Kirindy Forest (Madagascar). We recorded data on spatial patterns, feeding and social behaviour by means of direct observation of radio-collared females. The major food sources of *M. berthae* occurred in small dispersed patches leading to strong within-group scramble competition and over-dispersed females with a low potential for female associations. In contrast, *M. murinus* additionally used patchily distributed, high quality (large) resources. Within and between-group contest competition over these monopolizable resources allowed females of this species to cluster in space. Additionally, we experimentally manipulated the spatial distribution of food sources and found that females adjusted their spatial patterns to food resource distribution. Thus, our results support basic predictions of the SEM and demonstrated that it can also explain variation in social organization of solitary foragers.

Introduction

The socio-ecological model (SEM) (Crook and Gartlan 1966; Emlen and Oring 1977; Terborgh and Janson 1986) links ecological factors with characteristics of social systems and allows predictions about the relationships between resource distribution, type of competition and consequences for social organization (van Schaik 1989). Due to the sexual differences in potential reproductive rates and the resulting sexual conflict (Clutton-Brock and Parker 1992), male and female fitness are limited by different factors. Accordingly, the SEM assumes that female distribution in space and time is mainly determined by the distribution of risks and resources in the environment. Males, on the other hand, go where receptive females are (Altmann 1990) and map their distribution primarily on that of females (Clutton-Brock 1989).

Initially, predictions of the SEM about variability in social organization were confirmed by qualitative comparisons between species (*weaver birds*: Crook 1964, *ungulates*: Jarman 1974, *primates*: Eisenberg et al. 1972; Hladik 1975; Clutton-Brock and Harvey 1977). Subsequently, primates were studied intensively with regard to variation in social structure, resulting in refined versions of the original SEM (reviewed in Janson 2000; Koenig 2002; Isbell and Young 2002; Koenig and Borries 2006). These studies focussed mainly on the consequences of variation in food resource availability, quality and distribution on the mode and strength of feeding competition and their effects on reproductive success and social behaviour of group-living females (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig 2002).

Depending on resource characteristics, two modes of feeding competition can be distinguished: *scramble* and *contest* (Nicholson 1954). Scramble competition (S) occurs when resources are dispersed, small, fast depleting or of low quality and each individual in the population can indirectly reduce the net energy gain of all others in the population. When resources are monopolizable by one individual or a group, i.e. medium-sized, of high quality or clumped in patches, contest competition (C) occurs. This type of competition refers to an asymmetric partitioning of resources, in which some (dominant) individuals constrain the net energy gain of other (subordinate) individuals but not *vice versa* (Koenig 2002). Competition for food can take place either within groups (WG) or between groups (BG) yielding four different modes of competition (WGS, WGC, BGS, BGC) (van Schaik 1989; Koenig 2002).

Combinations of these different modes of competition define the competitive regime of a given species or population.

So far the SEM has accumulated considerable support in explaining variation in group-living primates (reviewed in Sterck et al. 1997; Isbell and Young 2002; Koenig 2002; Koenig and Borries 2006; Snaith and Chapman 2007). Recently, Schülke (2003) argued that when several individuals share a territory, females compete for food with these individuals irrespective of synchronized activity. Consequently, he successfully applied the SEM to a nocturnal lemur species that is organized in dispersed pairs (*Phaner furcifer*) by demonstrating that resource distribution dictated the competitive regime (Schülke 2003). However, no rigorous attempt has been made to date to explain variation in social systems of solitary species within the theoretical framework of the SEM. Here we follow the definition of Kappeler and van Schaik (2002) with *solitary* referring to one form of social organization that is distinct from *pair-* or *group-living*. In solitary species individuals do not synchronize their general activity, and particularly, their movements about their habitat with other individuals (Charles-Dominique 1978). In contrast, in gregarious species 2 (pair-living) or >2 adult individuals (group-living) synchronize their activity in space and time (Boinski and Garber 2000).

It has been suggested that potential strong WGC over food caused avoidance of solitarily foraging females, in particular, if no further benefits, e.g. reduced predation risk, could be obtained by permanently associating with conspecifics (van Schaik 1989). However, female ranges are not exclusive in many solitary species and variation in female spatial and temporal association patterns is pronounced (e.g. reviewed for *primates*: Müller and Thalmann 2000; *rodents:* Lacey and Sherman 2007; *carnivores*: Macdonald 1983; Dalerum 2007). This variation exists in particular along two main axes: (1) extent of inter- and intra-sexual home range overlap and (2) occurrence and composition of temporal associations, such as sleeping groups (Kappeler and van Schaik 2002). When females forage solitarily without defending exclusive territories, they compete over food resources with individuals that have spatially overlapping ranges. Hence, resource distribution and resulting competitive regimes should also determine distribution and association patterns of solitarily foraging females. The main aim of this study was to test this basic prediction of the SEM for two sympatric solitarily foraging mouse lemurs, which differ in two characteristics: (1) female ranging patterns and (2) sleeping associations.

Mouse lemurs (*Microcebus* spp.) are small (30-90g) nocturnal solitary primates and are widely distributed over nearly all remaining forest areas of Madagascar (Kappeler and Rasoloarison 2003). The species-rich genus is characterized by pronounced plasticity in feeding ecology, distribution patterns and social organization (Kappeler and Rasoloarison 2003; Schülke and Ostner 2005; Radespiel 2006), offering great potential for illuminating the effects of variable ecological conditions on social systems. In particular, comparative studies of co-existing species pairs provide the possibility to identify specific factors that determine variation in social systems, while controlling ecological factors such as predation pressure and seasonality.

Here we focus on two species that co-occur in the dry deciduous forest of central western Madagascar, the Madame Berthe's mouse lemur (*Microcebus berthae*) and the grey mouse lemur (*M. murinus*). *M. berthae* is the world's smallest living primate (33g) (Schmid and Kappeler 1994; Rasoloarison et al. 2000). Within its restricted range, it is sympatric with the larger (60g) and widely distributed *M. murinus* (Schwab and Ganzhorn 2004). Both are nocturnal solitary omnivores that use the fine branch niche (Martin 1972a; 1973; Dammhahn and Kappeler 2005). Although both species are very similar in general characteristics of their ecology and life history, *M. murinus* and *M. berthae* differ in details of female spatial-temporal distribution, which might have strong implications for their social system. Within the same forest habitat, *M. berthae* occur in low population densities and females use home ranges, which are about 4-times the size of *M. murinus* female ranges and overlap with only 1-2 other females (Dammhahn and Kappeler 2005, in press a). In contrast, *M. murinus* population densities are high and female *M. murinus* use small ranges that overlap extensively with on average 10 other females (Eberle and Kappeler 2002). Furthermore, female *M. murinus* regularly aggregate in stable sleeping associations of close female kin (Radespiel et al. 2001; Wimmer et al. 2002), which are also communal breeding units (Eberle and Kappeler 2006). In contrast, female *M. berthae* associate opportunistically into sleeping groups of variable composition (Dammhahn and Kappeler 2005). The lack of stable sleeping groups of close relatives together with the apparent absence of matrilinear clusters (Dammhahn and Kappeler 2005) make communal breeding very unlikely in *M. berthae*. Hence, these two mouse lemur species differ in female association patterns, which according to the socio-ecological model should be explained by the causal

relationships between resource distribution and variation in female spatio-temporal distribution.

Predicted relationships between resource characteristics and competitive regimes as well as consequences for female energy gain, reproductive success and social structure are summarized in table 1 (Koenig 2002). Our main hypothesis was that female *M. berthae* and *M. murinus* use (food) resources, which differ in their availability and spatial distribution patterns. In detail we hypothezised: *M. berthae* use small, fast depleting resources that are dispersed in space resulting in scramble competition. Low availability of resources leads to large female ranges. High potential WGS caused avoidance of solitarily foraging individuals resulting in a low female-female association potential. In contrast, *M. murinus* mainly use larger (high quality) resources over which they contest. Higher relative resource availability leads to small female ranges. WGC or BGC over monopolizable resources allows females to spatially overlap resulting in a potential of female-female associations. Accordingly, we made the following predictions:

(1) Both mouse lemur species differ in resource use. (2) Resource availability is lower for *M. berthae* than for *M. murinus*. (3) If resource distribution is experimentally manipulated, females use smaller ranges compared to controls and range size reduction is related to resource density. (4) Home range size and distance to nearest neighbour females ("group spread") is positively related to local population size (=number of spatially overlapping individuals as a proxy for "group size") in *M. berthae* (WGS). (5) Female body condition is negatively related to local population size in *M. berthae* (WGS) and positively related (WGC+BGC) or independent (WGC) in *M. murinus*. (6) Day range is positively related to local population size in *M. berthae* (WGS) and negatively related in *M. murinus* (WGC+BGC). (7) Aggression over (food) resources is rare and unspecific in *M. berthae* (WGS), whereas aggression over (food) resources is (more) common in *M. murinus* and targeted at non-group members (BGC) or group and non-group members (WGC and BGC).

Table 1: Summary of the main predictions of the socio-ecological model (van Schaik 1989; Sterck et al. 1997) for different competitive regimes (modified after Koenig 2002) and characteristics found in *M. berthae* and *M. murinus*

	Competitive regimes				*M. berthae*	*M. murinus*
	WGS	BGC (+WGS)	WGC (+WGS)	WGC + BGC (+WGS)	WGS	WGS + WGC (+ BGC shelter)
Resource characteristics	low quality highly dispersed or very large	high quality patches > GS	high quality patches < GS	no prediction	Food: small, low quality, dispersed Shelter: low quality small or large, abundant	Food: small, low quality, dispersed & high quality, medium sized patches Shelter: high quality, large, rare
Group size ↑	↓ TEG & RS	↑ TEG & RS	TEG & RS independent	↑ TEG & RS		
Proxies						
Feeding time	↑				↑*	
Day range	↑	→		→	←	no relationship
Home range size	↑	→		→	←	←
Group spread	→				no relationship	→
F body condition	↓	↑	independent	↑	no relationship	no relationship
Aggression over (food) resources	rare	common (inter-group)	common (intra-group)	common (intra- and inter-group)	rare (inter- and intra-group)	occasionally (inter-group)
Social status ↓	TEG & RS independent	TEG & RS independent	↓ TEG & RS	↓ TEG & RS		
F dispersal	conditional	rare	rare	rare	possible[1]	rare[2]
F-F alliances	rare	common	common	common	rare	common[3]
F dominance relationships	inconsistent	inconsistent	unidirectional	unidirectional	?	unidirectional[4]

[1]Dammhahn and Kappeler 2005; [2]Wimmer et al. 2002, Radespiel et al. 2002, Radespiel et al. 2003, Fredsted et al. 2005; [3]Sleeping associations (Radespiel et al. 2001; Wimmer et al. 2002) and communal breeding units (Eberle and Kappeler 2006); [4]In captivity: Perret 1992; *Feeding time increases when resources availability decreases with constant group size (chapter 5).

Methods

Study site

We conducted this study between August 2002 and December 2007 in the Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar (for details see Sorg et al. 2003). The climate in this 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 study area was defined by the boundaries of a 500x500m grid system of small foot trails at 25m-intervals. Each trail intersection was marked for orientation and their coordinates were used to create a map. In order to analyze seasonal patterns, we defined 3 time periods according to differences in rainfall and food availability: (S1) the transition between wet and dry season (Mar-May), (S2) the dry season (Jun-Sep) and (S3) the transition between dry and wet season (Oct-Dec) (for details see Dammhahn and Kappeler, in press b).

Capture and marking

We trapped animals about once every month: 5-times in 2002 (Aug-Nov), 6-times in 2004 (Jun, Aug-Dec), 8-times in 2005 (Mar-Jul, Sep-Nov), 6-times in 2006 (Mar, Jul-Nov), and 6-times in 2007 (May, Aug-Dec). Sherman live traps baited with pieces of banana were set near trail intersections 0.5-2m above ground for 3 consecutive nights in a study area of 25ha, yielding 400 trap locations (for details see Dammhahn and Kappeler, in press a). Traps were opened and baited at dusk and checked and closed at dawn. We collected captured animals in the early morning, kept them at a nearby research station during the day and released them at the site of capture shortly before dusk. We briefly restrained and immobilized all newly captured animals with 10μl Ketamine 100, marked them individually with subdermally implanted microtransponders (Trovan, Usling, Germany), weighed them with a spring balance (±0.1g), and took a set of standard external morphometric measurements. Recaptured animals from the same trapping session were only identified; those from previous trapping sessions were also weighed.

In both mouse lemur species, female body mass fluctuates seasonally with minima at the end of the dry season (Schmid and Kappeler 1998; Dammhahn and Kappeler, in press b). We therefore based our estimates of female body condition on body mass measured at the end of the food limited dry season (September/October)

directly preceding the annual mating season. Female body condition (c) was calculated as c = body mass [g] / head width [mm].

Behavioural observations

We equipped a total of 18 *M. berthae* and 17 *M. murinus* females with radio collars (*M. murinus*: 2g, TW4, Biotrack, UK; *M. berthae*: 1.8g, BD-2, Holohil, Canada). Focal animals were followed during their nocturnal activity for 1-4 hours before switching to another animal. The observation time was chosen opportunistically but spread evenly between 18:00 and 1:00h for every animal (prior analyses showed that there is no qualitative difference in behaviour and space use between first and second half of the night). We took behavioural data cumulatively for observation intervals of 1 minute (one-zero sampling) (Martin and Bateson 1993). In total we observed *M. berthae* for 288 hours and *M. murinus* for 340 hours. Additionally, we radio-tracked female *M. berthae* sequentially for ca. 600 hours and *M. murinus* for ca. 500 hours. Due to low visibility at night in a dense forest, *M. berthae* were in sight only in 47% of 1-min observation intervals, *M. murinus* in 70%. The species difference in visibility was due to overall higher mobility in *M. berthae*. All analyses are based on 1-min observation intervals in sight. Furthermore, we searched radio-collared females during daytime about 5-times per week and determined sleeping sites by triangulation and visual inspection. Each sleeping site was marked and the composition of sleeping associations was assessed via direct observations at the onset of activity or via a transponder reading device.

All approaches to ≤5m of the focal animal were defined as social encounters. A re-entry into the 5m radius after ≥5 min was considered a new encounter. We classified all social interactions according to the behaviours shown into agonistic, affiliative and affinitive. Interactions with more agonistic, i.e. chasing or attacking each other, than affiliative behaviours, i.e. allo-grooming or huddling, were defined as agonistic. All social interactions, with more affiliative than agonistic behaviours, were defined as affiliative. All interactions, in which neither agonistic nor affiliative behaviours occurred, were defined as affinitive. Interaction partners were classified as sleeping group members, when they had shared a sleeping site ≥1 with the focal animal and as non-members, when they had never shared a sleeping site with the focal animal. We determined the context of each interaction as: "feeding" when ≥1 interaction partner was feeding directly before and/or during the interaction, as

"sleeping site" when the interaction took place directly at the sleeping site, or as "unspecific" when the context was unclear or not "feeding" or "sleeping site". We tested for differences in the frequency of agonistic, affiliative and affinitive interactions between sleeping group members and non-members using Chi²-tests.

Food resources

Detailed analyses of feeding ecology, using a combination of direct focal observation of feeding behaviour and analyses of faecal samples are reported in Dammhahn and Kappeler (in press b). Here we briefly repeat methods and main results for reasons of completeness. During focal animal observations we recorded all occurrences of feeding behaviour and categorized food items into arthropods, fruit, flowers, gum, homopteran secretions – a sugary secretions produced by liana-dwelling homopteran larvae -, vertebrates and "unknown". Differences in *Microcebus*' diet were analysed using Chi²-tests and seasonal variation was tested using G-tests. Furthermore, we collected faecal samples from live-trapped individuals (*M. berthae* n=67, *M. murinus* n=101) and examined faecal sample contents for presence and absence of arthropods, seeds and other plant remains.

In order to analyse spatial resource distribution we recorded the location and type of each resource patch that was used during focal observations. We tested spatial distribution of the main stationary food sources (homopteran secretion patches, gum trees and fruit trees) for deviation from spatial randomness within individual home ranges. To this end, we estimated actual distances between neighbouring resource patches and compared these with expected distances using nearest-neighbour analysis (Krebs 1998).

Spatial patterns

Spatial data were obtained during observations when we recorded the location of a focal animal every minute and additionally by sequential radio-tracking. Locations were estimated in reference to the nearest grid-point (<15m) and subsequently transformed into x- and y-coordinates; prior to data collection we tested observer errors in distance estimations to be <3m. Home range analyses were based on location data from focal observations that were sub-sampled at 20-min intervals and data from sequential radio-tracking. These data points were regarded as independent because individuals can cross their home range during this time interval

(Rooney et al. 1998). We calculated home ranges as 100% minimum convex polygons (MCP) (Mohr 1947) using ArcView GIS 3.3 (Esri) Animal Movement Software (Hooge et al. 1999). Because the size of MCP varies with the number of data points included in the analysis, we based MCPs always on 50 independent location data points, which were drawn randomly from all independent location points. Because we observed animals only between 18:00 and 1:00 hours, we estimated no total day range. Instead we calculated average distances covered per hour, excluding time the individual was inactive, as a measure of ranging behaviour. Furthermore, we calculated centres of activity for all individuals in the population, which were based on trapping data (range of individual trapping points per year: *M. murinus*: 1-24, *M. berthae*: 1-32) and calculated as the arithmetic means of x- and y-coordinates of the trapping points.

First, we tested for species differences in female home range size using Mann-Whitney U tests. Further, we assessed seasonal variation in subsets of independent individuals using Kruskal-Wallis tests. Finally, we tested for within-species differences in individual home range sizes between areas of inter-specific spatial overlap and areas, where only one species occurred using Mann-Whitney U tests. To assess inter-specific spatial overlap we calculated centres of activity for each individual in the population as arithmetic means of all capture locations and fitted a circular home range of mean species specific size (radius: *M. berthae* 100m, *M. murinus* 50m) around it. If the actual home range of a focal animal from species A overlapped with ≥1 of these mean ranges of an individual from species B, it was defined as being situated in the area of inter-specific spatial overlap, otherwise it was defined as being situated in the area where only one species occurred.

To determine whether relative home range size of *M. berthae* females was unusually enlarged we compiled a data set of relative home range size for 8 cheirogaleid species. Other strepsirrhines were not included to reduce phylogenetic noise. After Harvey and Clutton-Brock (1981) we calculated a Spearman Rank correlation between body weight (g) and home range area (ha) using double logarithmic scales to identify the general trend among cheirogaleid species.

Under the assumption that animals compete for food with individuals that forage in the same area, we estimated local population size (p) as the number of individuals a female overlapped with in space. Because it can be assumed that the extent of competition varies with the amount of spatial overlap, we calculated p as a

weighed index $p=2*r_1+r_2$ with r_1= number of individuals that had their centre of activity within the distance of one individual home range radius and r_2= number of individuals that had their centre of activity within the distance of twice an individual's home range radius. Individual home range radii were calculated from MCP areas assuming home ranges to be circular. Only focal females with >80% home range within the trapping area were included in this analysis. Furthermore, we calculated a measure of local female dispersion as the distance to the nearest neighbour female. Relationships between local population size (p) and day range, home range size, female condition and local female density, respectively, were tested with Spearman Rank correlations.

Experimental resource manipulation

To test predictions on female spatial patterns in relation to resource distribution we performed a controlled field experiment, in which we changed the spatial distribution of artificial food resources. These food sources were feeding platforms (ca. 30x30cm, 1.5m height) baited with syrup-water solution in a dripping bottle. Subjects were 7 *M. berthae* and 6 *M. murinus* females, which were equipped with radio collars during the course of the 8-week experiment. Prior to the experimental resource manipulation we determined individual home ranges based on 50 location points as controls by sequential radio-tracking taking 5-8 locations per night during the first 4 hours of activity. Within areas of spatial overlap between two neighbouring females we placed 7 feeding stations in 2 different setups. (1) In the "clumped" setup 7 stations were distributed over 1/10 mouse lemur home range equalling 0.25ha with ca. 30m distance between stations for *M. berthae* and 0.07ha with ca. 15m distance between stations for *M. murinus*. (2) In the "dispersed" setup 7 stations were distributed over ca. 1ha with ca. 60m distance between stations for *M. berthae* and 0.25ha with ca. 30m distance between stations for *M. murinus*. The experiment was performed in a repeated measurement design with 4(3) individuals starting with clumped and 3 with dispersed, which was then changed to dispersed and clumped, respectively. For each experimental setup we determined individual home ranges based on 50 location points by sequential radio-tracking taking 5-8 locations per night during the first 4 hours of activity. After the experiment feeding stations were removed and all radio-collars were removed. Home range sizes were estimated with ArcView GIS 3.2 Animal Movement Extension as 100% MCP. We compared home range sizes between designs and both designs with controls using

Wilcoxon tests. All tests were calculated with Statistica 8.0 (Statsoft) and significance for all tests was set at alpha=0.05.

Results

Food resources

During direct behavioural observations individuals of both *Microcebus* species used homopteran secretions, fruit, flowers, gum, arthropods and small vertebrates (e.g. geckos, chameleons) as food resources. They differed however in proportions and seasonal variation of different food components in their omnivorous diet (G-tests, df=4; S1: G=89.4, $p<0.001$, S2: G=275.1, $p<0.001$, S3: G=8.5, p=0.076) (Fig.1). *M. berthae* mainly fed on homopteran secretions, which amounted up to 81% of their overall diet and represented higher proportions than in *M. murinus* in S1 and S2 (Chi²-tests, $p<0.001$). This resource was further supplemented mainly by animal matter. In contrast, *M. murinus* diet varied seasonally and was more diverse, including generally higher amounts of fruit (Chi²-tests, S1 and S2: $p<0.001$, S3: p=0.002) and gum (Chi²-tests, S1: p=0.004, S2: $p<0.001$, S3: p=0.043) than *M. berthae*. Both species used similar amounts of animal matter in each season.
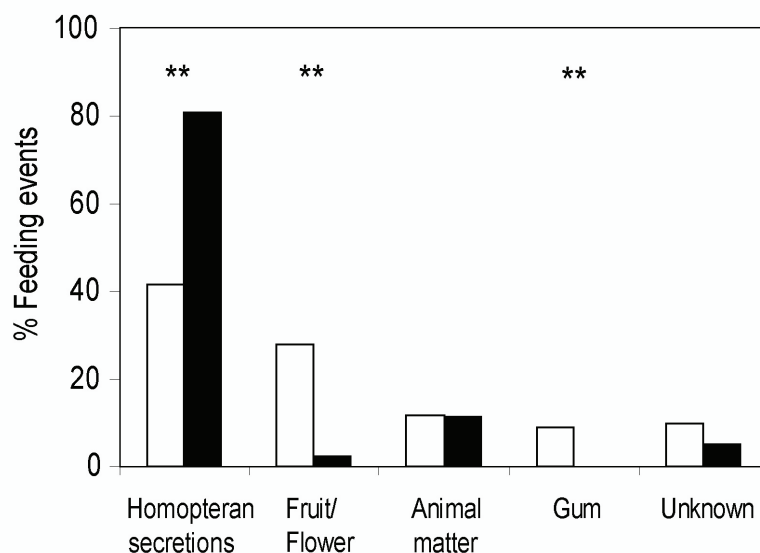

Fig. 1: Diet composition: Percentages of feeding events of *M. berthae* (n=1762) and *M. murinus* (n=2175) on different food categories over all seasons (Chi²-test, **p<0.001).

Presence-absence analyses of arthropod and fruit remains in faecal samples revealed neither species differences, nor seasonal variation in the number of samples with arthropods (Chi²-test, n.s.). However, more *M. berthae* than *M. murinus* samples consisted mainly of arthropod remains (>50 volume %) in S1 (Chi²-test: χ^2=7.64, df=1, p=0.006) but not in S2 and S3. A higher number of *M. murinus* than *M. berthae* samples contained seeds in S1 (Chi²-test, χ^2=4.20, df=1, p=0.040) and S2 (Chi²-test, χ^2=8.26, df=1, p=0.004) but not in S3 (Chi²-test, χ^2=0.01, df=1, p=0.947). For *M. 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 faecal samples with arthropods and seeds, respectively, did not vary seasonally in *M. berthae* (G tests, n.s.).

Female *M. berthae* (n=9) used on average 14 (inter-quartile range: 9-40) homopteran secretion patches, where they fed on average for 5min (inter-quartile range: 4-5min). The spatial distribution of food patches within an individuals' home range did not differ from a random pattern (p<0.01 for all individuals). This sugary secretion is renewed within a few hours and thus represents a small, dispersedly distributed resource with a short renewal time. Female *M. murinus* (n=8) used on average 16.5 (14.5-19) food patches. The average length of feeding bouts was short (median 5min, inter-quartile range 4.2-5.5min) and did not differ between fruit and homopteran secretion food patches. Because *M. murinus* used only 1-2 fruit per visit, they did not completely deplete a fruit tree. Spatial distribution of food patches in *M. murinus* female home ranges was variable (fruit patches: clumped n=1, uniform n=1, random n=3; homopteran secretions patch: clumped n=2, uniform n=1, random n=2, all p<0.01). However, the absolute density of food patches in individual home ranges was higher in *M. murinus* than in *M. berthae* (nearest-neighbour distances between food patches (m): median$_{M.\ berthae}$=14, median$_{M.\ murinus}$=7, Mann-Whitney U test, z=3.05, p<0.005; density of food patches (per ha): median$_{M.\ berthae}$=13, median$_{M.\ murinus}$=46, Mann-Whitney U test, z=-3.13, p<0.005).

Proxies of feeding competition modes

Female home ranges

Median home ranges of *M. berthae* females (2.04ha) were much larger than those of *M. murinus* females (0.26ha) (Mann-Whitney U test, z=-5.05, p<0.0001) (Fig. 2). Thus, we confirmed previously reported species differences in female spatial

patterns (Dammhahn and Kappeler 2005). Home ranges of *M. berthae* and *M. murinus* females did not vary seasonally (Kruskal-Wallis tests, *M. murinus* H(2,n=18)=1.77, p=0.414; *M. berthae* H(1,n=19)=0.38, p=0.539) (Fig. 3). However, most female *M. murinus* ceased activity during the dry season but those that stayed active had similar sized ranges as in S1 and S3. In areas of inter-specific spatial overlap both *M. berthae* and *M. murinus* females had larger ranges as compared to females that ranged in areas where only one species occurred (Mann-Whitney U tests, *M. murinus*, z=2.34, p=0.019; *M. berthae*, z=-2.16, p=0.031) (Fig. 4).

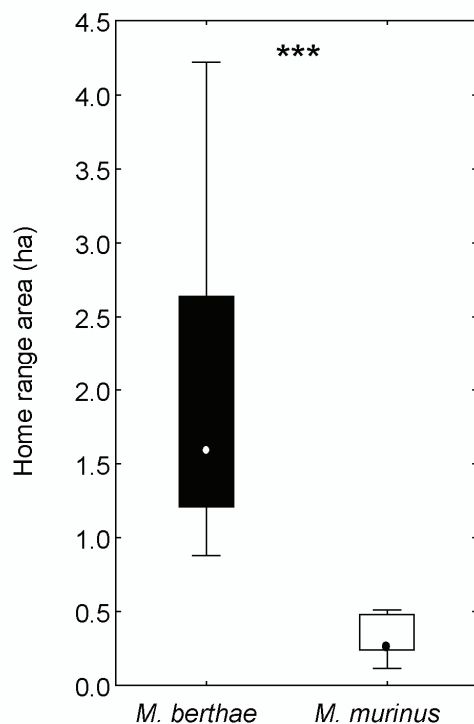**Fig. 2:** *M. berthae* females (n=18) used larger home ranges than *M. murinus* females (n=17) (Mann-Whitney U test, z=-5.05, p<0.0001). Shown are medians (25-75% quartiles, range) of 100% MCPs based on 50 independent location points.
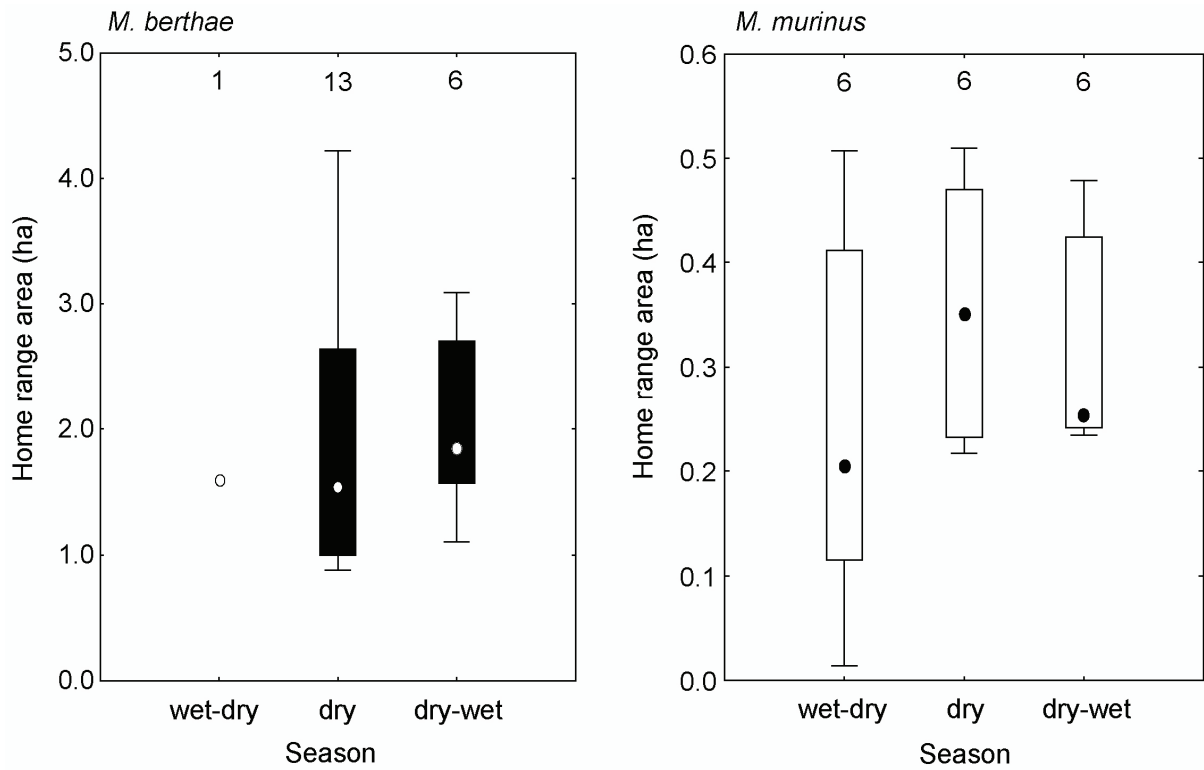
Fig. 3: Individual home range areas of *M. berthae* (left) and *M. murinus* (right) females did not vary with seasons (Kruskal-Wallis tests, n.s.). Shown are sample sizes, medians (25-75% quartiles, range) of 100% MCPs based on 50 independent location points.
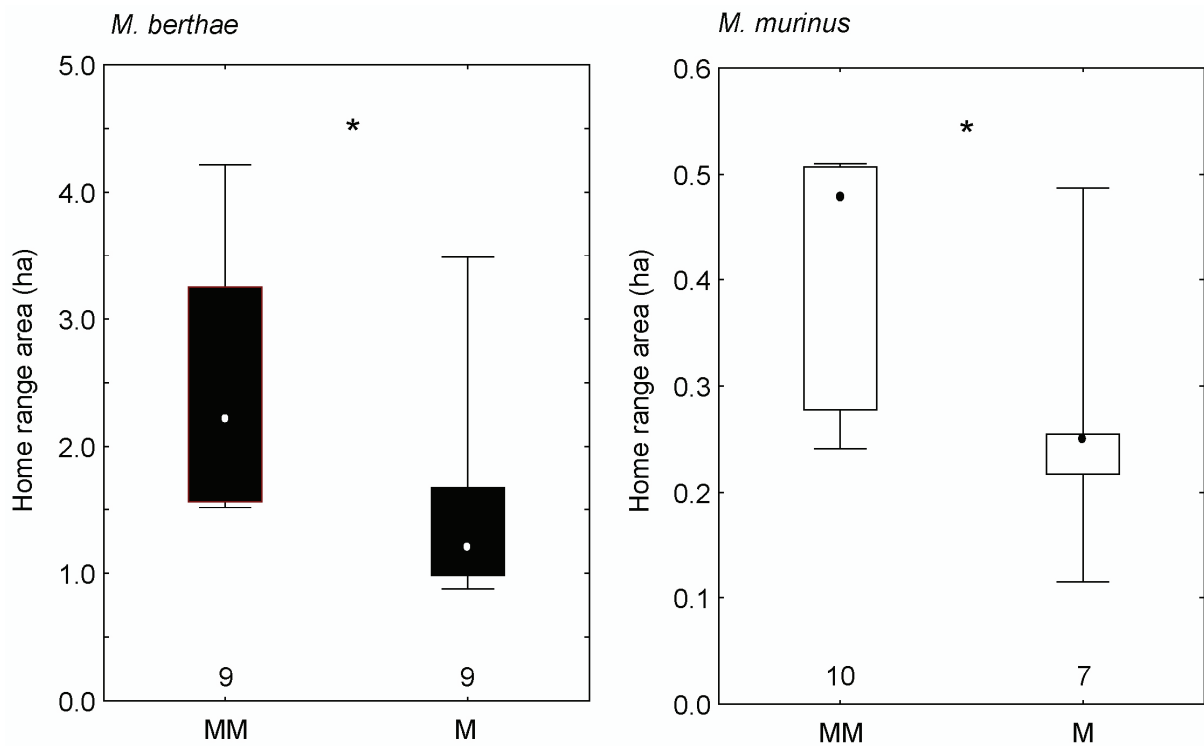

Fig. 4: In areas of inter-specific spatial overlap (MM) both *M. berthae* (left) and *M. murinus* (right) females had larger ranges as compared to individuals in areas where only one species occurred (M) (Mann-Whitney U tests, *p<0.05). Shown are sample sizes, medians (25-75% quartiles, range) of 100% MCPs based on 50 independent location points.

Female home range size and body weight were highly correlated for 8 cheirogaleid species on a double-logarithmic scale (R_s=0.86, p<0.05) (Fig. 5) confirming results for primates in general (Harvey and Clutton-Brock 1981). Calculating an expected home range size for female *M. berthae* based on the regression equation (y=0,8809*x-1,6826) yielded 0.42ha, which equals only 17% of the observed home range size. Thus, female *M. berthae* appear to have exceptionally large ranges for their body size.
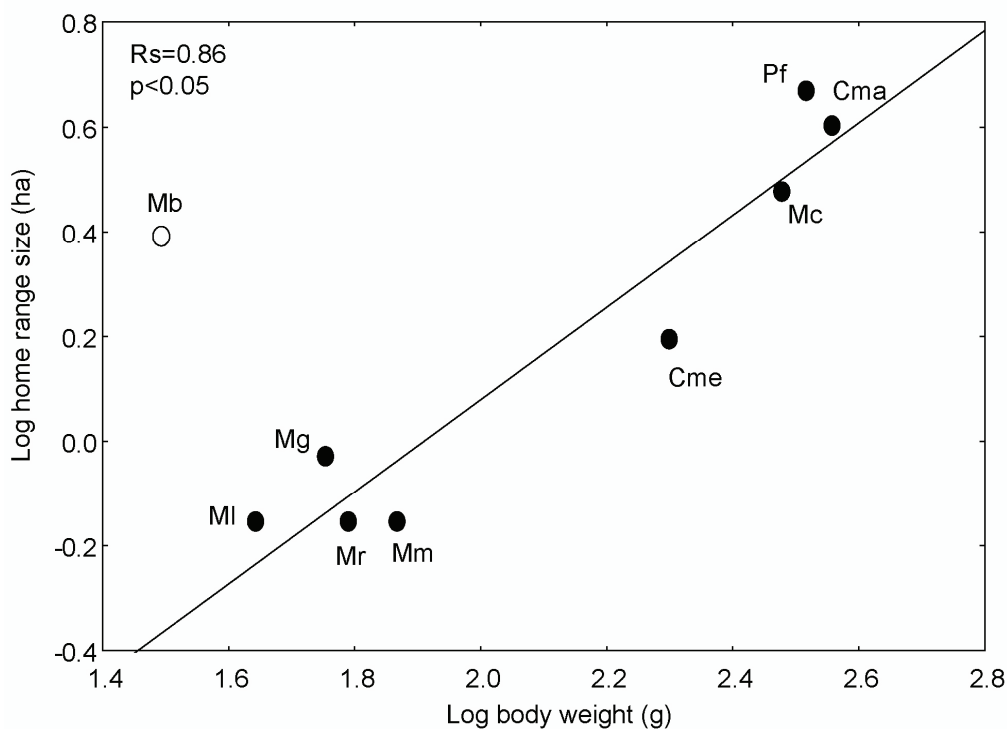

Fig. 5: Comparison of relative home range sizes of females of 8 cheirogaleid species. Trend line and regression equation are calculated without *M. berthae*. Note that observed home range area of *M. berthae* is five-times larger than expected area. Cma *Cheirogaleus major* (Lahann 2008, n=3), Cme *Cheirogaleus medius* (Fietz 1999, n=6), *M. berthae*. Mb *Microcebus berthae* (Dammhahn and Kappeler 2005, this study, n=18), Mg *Microcebus griseorufus* (Génin 2003, n=14), Ml *Microcebus lehilahytsara* (Randrianambinina 2001 cited in Radespiel 2006, n=2, species name was changed according to new taxonomy (Kappeler et al. 2005), Mm *Microcebus murinus* (Eberle and Kappeler 2004 n=56), Mr *Microcebus ravelobensis* (Weidt et al. 2004, n=16), Mc *Mirza coquereli* (Kappeler 1997b, n=10), Pf *Phaner furcifer* (Schülke and Kappeler 2003, n=8).

Relationships between local population size and proxies of competitive modes

Local population size was 13 (median, range 4-28) for *M. berthae* females (n=11) and 17 (7-37) for *M. murinus* (n=15) with no difference between species (Mann-Whitney U test, z=1.15, p=0.254). In both species home range size was positively related to local population size (Table 2). Female *M. berthae* overlapped spatially with median 2 (range 0-5) other females and 1 (0-2) of them had their activity centre within the home range of a given female. Distance to the nearest female neighbour was median 67m (range 60-133m) and was not related to the local population size (Table 2). However, home range size was positively related to the number of overlapping females (R_s=0.67, p<0.05). Female *M. murinus* overlapped spatially with median 5 (range 2-16) other females and 2 (0-4) of them had their activity centre within the home range of a given female. Distance to the nearest female neighbour was median 16m (range 0-42m) and was negatively related to the number of overlapping individuals (R_s=-0.56, p<0.05). Furthermore, home range size was positively related to the number of overlapping females (R_s=0.55, p<0.05).

Ranging distance was positively related to local population size for *M. berthae* (R_s=0.68, p<0.05, n=11) but not for *M. murinus* females (R_s=0.05, n.s., n=13). Female dispersion was not related to local population size for *M. berthae* females (R_s=0.35, n.s., n=11). Interestingly, *M. murinus* female dispersion was negatively related to local population size (R_s=-0.56, p<0.05, n=15). Finally, in both *M. berthae* and *M. murinus* female body condition was not related to the number of individuals a female spatially overlapped with (*M. murinus*: R_s=-0.11, n.s., n=13; *M. berthae*: R_s=-0.01, n.s., n=11).

Table 2: Results of Spearman Rank correlations between local population size and proxies of competitive modes for *M. murinus* (n=15, *n=13) and *M. berthae* (n=11) females

	M. murinus			*M. berthae*		
	median (range)	R_s	p	median (range)	R_s	p
Home range radius (m)	28 (19-40)	0.46	n.s.	71 (53-116	0.66	<0.05
Path length (m/h)*	128 (105-168)	0.05	n.s.	205 (108-375)	0.68	<0.05
Female NN distance (m)	16 (0-42)	-0.56	<0.05	67 (60-133)	0.35	n.s.
Body condition*	2.67 (1.96-3.17)	0.05	n.s.	1.72 (1.38-1.88)	-0.34	n.s.

Social interactions

In total we recorded 52 interactions of *M. murinus* females and 76 of *M. berthae* females, for which we could determine the identity of the interaction partner. In *M. murinus*, more interactions between non-sleeping group members than between sleeping group members were agonistic (Chi²-test, χ²=16.83, p<0.0001) (Tab. 3). On the other hand, more interactions between sleeping group members were affiliative and affinitive than between non-members (affiliative: χ²=8.29, p=0.004; affinitive: χ²=6.39, p=0.012). Agonistic interactions between non-members and female *M. murinus* occurred in unspecified (n=6) or feeding context (n=8), and some at the sleeping site (n=7). Group members, in contrast, tolerated each other in the feeding context (n=8), only once an individual was displaced from a feeding place. *M. berthae* females interacted more often affiliative with sleeping group members than with non-members (χ²=5.77, p=0.016). However, there was no difference in the frequency of agonistic and affinitive interactions between sleeping group members and non-members (agonistic: χ²=2.54, p=0.111; affinitive: χ²=0.11, p=0.744). Agonistic interactions between non-members occurred in unspecified (n=15) or feeding context (n=12), when females displaced others from feeding sites, none at a sleeping site.

Table 3: Social interactions of female *M. murinus* and *M. berthae* with sleeping group members (SG) and non-members (non SG)

Interaction	*M. murinus*				*M. berthae*			
	non SG	SG	Chi²	p	non SG	SG	Chi²	p
Agonistic	21	1	16.83	0.0001	27	3	2.54	0.111
Affiliative	0	12	8.29	0.004	8	9	5.77	0.016
Affinitive	2	16	6.39	0.012	23	6	0.11	0.744
Total	23	29			58	18		

Experimental resource manipulation and female home ranges

Female *M. berthae* reduced their home range size, when artificial feeding stations were added in a clumped pattern (Wilcoxon test, n=6, z=1.99, p=0.046); they showed a trend of range reduction, when feeding stations were added in a dispersed pattern (Wilcoxon test, n=6, z=1.78, p=0.075). However, individual home range sizes did not differ between designs (Wilcoxon test, n=7, z=0.68, p=0.499). Female *M. murinus* reduced their home range size, when artificial feeding stations were added in a dispersed pattern (Wilcoxon test, n=5, z=2.02, p=0.043); they showed a trend

towards range reduction, when feeding stations were added in a clumped pattern (Wilcoxon test, n=5, z=1.75, p=0.080). However, home range sizes did not differ between designs (Wilcoxon test, n=6, z=0.94, p=0.345).
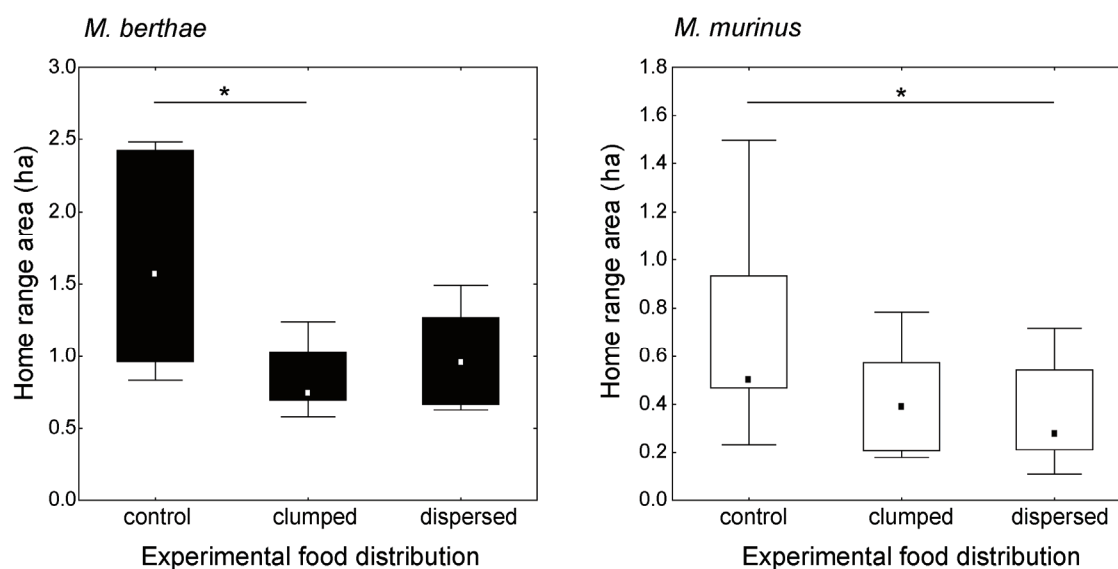

Figure 6: Results of experimental resource distribution: Female *M. berthae* (n=7, left) and *M. murinus* (n=6, right) reduced their home range sizes, when artificial feeding stations were added (Wilcoxon test, *p<0.05), irrespective of resource density (low: dispersed, high: clumped). Shown are medians (25-75% quartiles, range) of 100% MCPs based on 50 independent location points.

Discussion

Due to their predominantly cryptic life style and apparent lack of social complexity little attention has been paid to solitary foragers in theoretical models explaining social systems (e.g. Wrangham 1980; van Schaik 1989; Johnson et al. 2002). Recent research, however, revealed an astonishing variation in the social systems of solitary foragers (e.g. reviewed in Macdonald 1983; Müller and Thalmann 2000; Kappeler and van Schaik 2002; Dalerum 2007; Lacey and Sherman 2007), highlighting the need for a more comprehensive understanding of this type of social organization. Although the distribution of risks and resources in the environment have been identified as the main factors determining female spatial patterns in solitary foragers (Ostfeld 1985, 1990), existing models that link these resource characteristics to variation in social organization and structure have not been applied

to these species. Here, we studied co-existing mouse lemur species that differ in female association patterns. Our main results support basic predictions of the SEM and we demonstrated that principles of the SEM can indeed be applied to solitary foragers as well.

Food resource characteristics

Both *Microcebus* species used fruit, arthropods, gum, insect secretions and small vertebrates as food sources. *M. berthae* and *M. murinus* differed, however, in composition and seasonal variation of their diets (Dammhahn and Kappeler, in press b). *M. berthae* diet consisted mainly of a sugary secretion produced by homopteran larvae supplemented by animal matter with only little variation with season. In contrast, *M. murinus* diet varied seasonally, was more diverse and contained generally higher amounts of fruit and gum. Thus, *M. murinus* fed more opportunistically and had a wider dietary range, which completely encompassed the narrow feeding niche of *M. berthae* (Dammhahn and Kappeler, in press b). Food resources differed in size, quality, spatial and temporal distribution. On one hand, arthropods and homopteran secretions occurred in small dispersed patches, which can be depleted by an individual. Under these conditions theory predicts WGS, because animals can not avoid searching in areas for food that others just depleted (Koenig 2002). On the other hand, gum and fruit trees are usually larger, high quality resources that can be monopolized by an individual (e.g. Génin 2003) facilitating WGC. Simultaneous feeding was virtually never observed in *M. berthae*, although resource patches were not exploited exclusively. Sleeping group members tolerated each other, and occasionally fed simultaneously, in *M. murinus*. Thus, the characteristics of the main food sources predict WGS to be strong for *M. berthae* and a combination of WGS and WGC for *M. murinus* with some potential for BGC.

The competitive regimes of M. berthae *and* M. murinus

When individuals use resources that can be depleted in a short time, WGS should be facilitated (van Schaik 1989). In that case, increasing the number of individuals which exploit the same area ("group size") leads to faster depletion of resource patches. Consequently, animals may increase feeding time, day range or (group) dispersion to compensate for the declining energy gain (Koenig 2002). Using these behavioural proxies of the feeding competition mode revealed that strong WGS

predominated in *M. berthae*. Females that shared their range with many others had larger home ranges and ranged further. Female body condition and female dispersion were not negatively related to the number of spatially overlapping individuals, however. As expected in a food scramble situation, foraging-related aggression or displacement was rare and equally targeted at sleeping group members and non-members.

Because *M. murinus* used the same food sources as *M. berthae*, WGS should also occur in this species. Other dietary components, e.g. gum and fruit, should facilitate WGC because they occur in larger patches and can be monopolized by an individual (Janson and van Schaik 1988; van Schaik 1989). In line with this expected combined influence of different competition modes, we found no strong WGS and WGC in *M. murinus*. The negative effect of the number of spatially overlapping individuals did not show up for day range and female dispersion. However, female home range size increased with the number of individuals foraging in the same area. In contrast to the expected relationship under WGS, female dispersion decreased with increasing numbers of individuals that exploited the same area. Although foraging-related aggression or displacement was not particularly frequent, some individuals displaced others from high quality resource patches, such as gum trees (see also Génin 2003). Interestingly, this aggression was almost exclusively targeted at individuals, which were not part of female sleeping associations, whereas group members tolerated each other at feeding sites and occasionally fed simultaneously at large food patches, indicating BGC (van Schaik 1989; Koenig 2002).

Also other aspects of social structure, which are theoretically influenced by the mode of feeding competition (Koenig 2002), differed between the two mouse lemur species. For instance, female *M. murinus* are philopatric with closely related females (matrilines) forming spatially distinct clusters (Radespiel et al. 2001; Wimmer et al. 2002; Fredsted et al. 2005), which is expected under WGC and BGC (Koenig 2002). In contrast, preliminary genetic analyses indicated that *M. berthae* females do not cluster into matrilines and thus might disperse (Dammhahn and Kappeler 2005). Female dispersal would be expected under strong WGS to minimize feeding competition (Koenig 2002). Furthermore, several aspects of social structure in *M. murinus* are in line with predictions for BGC: (1) relatively strong bonds between group members indicated by mutual tolerance at (large) feeding sites and predominately affiliative and affinitive social interactions, (2) female alliances in

defending tree holes and (3) female associations composed of close kin, which should be the preferred allies because they provide additional indirect fitness. Main food sources used by *M. murinus*, however, are usually not large enough to feed all group members facilitating WGC. Hence, additional BGC might occur over other resources than food.

Apart from predation risk (van Schaik 1983) food resources were discussed as the main ecological determinant of female association patterns (Wrangham 1980; van Schaik 1989; Isbell 1991; Koenig 2002), but females might also compete for other resources such as shelter or nesting sites (van Schaik 1989). In particular for small mammals that face high predation risks and/or thermoregulatory expenses in temporally cold environments, shelter and nesting sites are expected to be an important resource as well (Kappeler 1998; Schmid 1998). *M. murinus* females prefer tree holes over other resting sites and stable sleeping groups occupy on average 3-7 holes (Radespiel et al. 1998; Schmid 1998; M. Dammhahn, *unpublished data*). Based on sex differences in sleeping site quality and return rates it has been suggested that safe and thermally insulated sleeping sites are a limiting high quality resource (Radespiel et al. 1998). In principle, a highly structured forest might provide abundant tree holes and, so far, no data on absolute resource densities are available. Several points, however, suggest that *M. murinus* might compete over high-quality tree holes as well, facilitating BGC: (1) close-kin groups actively defend certain holes, (2) holes are often used for several years (M. Dammhahn, *unpublished data*) and (3) they are large enough to accommodate all group members. In contrast, *M. berthae* mainly use leaf-nests and often sleep at relatively open sites (Dammhahn and Kappeler 2005), thus shelter might be a less important resource for this species.

Besides spatial-temporal distribution, overall food availability might affect female spatial patterns, because it determines the strength of intra-specific competition. Low availability, i.e. density per unit area, leads to female spatial avoidance and large (exclusive) ranges resulting in low population densities (Clutton-Brock and Harvey 1977; Eisenberg et al. 1972; Reiss 1988). All these factors reduce the potential of female associations and food limitation is indeed often discussed as the main determinant of a solitary lifestyle in general (e.g. *rodents*: Ostfeld 1985; 1990; Schradin and Pillay 2005; *primates*: Kappeler 1997; *carnivores*: Gittleman and Harvey 1982). Female *M. berthae* have unusually large home ranges, which exceed those expected for a strepsirrhine primate of that body size (Fig. 5). It has been

shown that home range size depends on a species' metabolic need (Harvey and Clutton-Brock 1981; Gittleman and Harvey 1982), but metabolism of *M. berthae* is not exceptionally increased over that of co-existing *M. murinus* (Schmid and Speakman 2000; Schmid et al. 2000).

Instead, several factors might cause high intra-specific feeding competition in *M. berthae*: (1) specialized feeding niche, (2) low seasonal food availability and (3) inter-specific competition with other co-existing lemurs (Dammhahn and Kappeler, in press a, b). *M. berthae* share their habitat with four other nocturnal omnivorous cheirogaleids, which are all larger, overlap in feeding niches and can displace *M. berthae* from feeding sites (Ganzhorn and Kappeler 1996, M. Dammhahn *personal observation*). Also supporting high food competition is the observation that females reduced their ranges when resource abundance was experimentally increased, independent of spatial resource distribution. Hence, females go where the food is and female home range size is largely a function of resource availability, which has also been demonstrated empirically (e.g. *Trichosurus cunninghami*: Martin and Martin 2007; *Rhabdomys pumilio:* Schradin and Pillay 2005) and experimentally for many rodents (e.g. *Clethrionomys glareolus*: Jonsson et al. 2002; *C. rufocanus*: Ims 1987; *Peromyscus maniculatus*: Taitt 1981; *Microtus townsendii*: Taitt and Krebs 1981; *M. californicus*: Ostfeld 1986; and reviewed in Boutin 1990; Adams 2001). Thus, low population density caused by strong feeding competition over small dispersed resources might reduce the potential for female associations in *M. berthae*. Because females are highly dispersed, close kin are not available to form stable female sleeping groups and communal breeding units (Dammhahn and Kappeler 2005; Schülke and Ostner 2005).

The SEM and variation in the social organization in other solitary foragers

First, applying the SEM to solitary foragers opens a whole new arena of test cases. A solitary social organization is widespread among mammals, e.g. about one third of primates, the majority of carnivores, rodents, marsupials and insectivores and within and between species variation in female spatial and temporal association patterns is high (e.g. Macdonald 1983; Bekoff et al. 1984; Kappeler 1997; Müller and Thalmann 2000; Lacey and Sherman 2007; Dalerum 2007). Particularly promising are rodent species with high flexibility in social organization such as the solitary foraging striped mouse (*Rhabdomys pumilio*). In this species females adapt their

range size to the temporal distribution of plant cover and the availability of (high-quality) food and consequently range solitarily in exclusive ranges or form stable sleeping groups with spatially overlapping females (Schradin and Pillay 2005, Schradin 2006). Also other rodents might, depending on food availability and distribution, live solitarily, form pairs or multi-male-multi-female groups (*Microtus ochrogaster*: Roberts et al. 1998). By experimentally manipulating food distribution, Ims (1987) demonstrated that female *Clethrionomys rufocanus* increase spatial association (e.g. range overlap) when food abundance was high.

Second, although a variety of resource-based models exists to explain variation in the social organization of solitary foragers (e.g. reviewed in Johnson et al. 2002), only few of them allow predictions on social structure as well. Thus, applying the SEM would go one step beyond understanding spatial patterns. Because most solitary species are either small and nocturnal or large and far-ranging, detailed information of their social behaviour remained often elusive. However, the development of modern field techniques such as RFID-tracking, biotelemetry, animal borne or automatic video systems is proceeding rapidly and will help to overcome these methodological shortcomings (e.g. Cooke et al. 2004; Moll et al. 2007).

Finally, it is not clear why solitary foragers should play by different rules as group-living species. Thus, by linking ecological factors with characteristics of social systems the SEM might also successfully guide research on solitary primates and other mammals. In particular, understanding why and under which circumstances solitary females temporally associate in stable groups could (1) help to illuminate the adaptive basis of a solitary lifestyle (Kappeler 1997) and (2) provide insights into the evolution of group-living (Dalerum 2007; Wagner et al. 2008).

CHAPTER 4

Small-scale coexistence of two mouse lemur species
(*Microcebus berthae* and *M. murinus*)
within a homogeneous competitive environment

with Peter M. Kappeler

Abstract

Understanding the co-occurrence of ecologically similar species remains a puzzling issue in community ecology. The species-rich mouse lemurs (*Microcebus* spp.) are distributed over nearly all remaining forest areas of Madagascar with high variability in species distribution patterns. Locally, many congeneric species pairs seem to co-occur, but only little detailed information on spatial patterns is available. Here, we present results of an intensive capture-mark-recapture study of sympatric *Microcebus berthae* and *M. murinus* populations that revealed small-scale mutual spatial exclusion. Nearest neighbour analysis indicated a spatial aggregation in *M. murinus* but not in *M. berthae*. Although the diet of both species differed in proportions of food categories, they used the same food sources and had high feeding niche overlap. Also, forest structure related to the spatial distribution of main food sources did not explain spatial segregation because parts used by each species exclusively did not differ in density of trees, dead wood and lianas. We propose that life history trade-offs that result in species aggregation and a relative increase in the strength of intra-specific over inter-specific competition best explain the observed pattern of co-occurrence of ecologically similar congeneric *Microcebus* species.

Introduction

Species spatial distribution patterns and the processes generating these patterns are of fundamental importance in population and community ecology (e.g. Diamond 1975; Pianka 1994; Bell 2000; Chesson 2000a; Amarasekare et al. 2004; Kneitel and Chase 2004). Because spatial patterns provide important insights into coexistence mechanisms of interacting species that form ecological communities, they are a crucial starting point for understanding biogeographical patterns (e.g. MacArthur 1972; Diamond 1975), species diversity (e.g. Ricklefs and Schluter 1993; Rosenzweig 1995; Huston 1999; Amarasekare 2000; Bell 2001; Mouquet and Loreau 2002) as well as the structure and stability of communities (e.g. Elton 1946; Tilman and Karieva 1997). Classical niche theory (recently reviewed by Chase and Leibold 2003) predicts that coexistence is only possible if intra-specific competition is stronger than inter-specific competition, which requires species to be different in their partitioning of resources (Hutchinson 1957; MacArthur and Levins 1967; Tilman 1982), their temporal or spatial partitioning of one resource (e.g. Chesson 2000a, 2000b) or their density- or frequency-dependent predation (e.g. Holt 1977, 1984; Holt et al. 1994).

Recently, Hubbell (2001) proposed a "unified neutral theory of biodiversity and biogeography" that challenged the classic niche-based view of community ecology. This neutral theory is based on the assumption that all species are functionally equivalent in their ecological traits; thus, species assemblages are controlled predominantly by neutral drift of species abundances (Bell 2001; Hubbell 2001). Hubbell's approach has generated much controversy (e.g. recently reviewed in Chave 2004; Alonso et al. 2006; Leibold and McPeek 2006; McGill et al. 2006). Whereas the neutral theory was particularly successful in explaining the diversity and distribution of species abundance of tropical trees (e.g. Hubbell et al. 1999; Bell 2000, 2001; Hubbell 2001), results of many other studies, particularly those focusing on mobile animals, were not consistent with predictions of the neutral model (e.g. McGill 2003; Graves and Rahbek 2005; McGill et al. 2006).

The co-occurrence of congeneric species is still a largely unresolved issue in this context (e.g. Tokeshi 1999; Chesson 2000a; Chase and Leibold 2003; Sfenthourakis et al. 2005) because it seems to contradict predictions of classical niche theory and might therefore also be of significance for discussions of classical niche vs. neutral theory (Leibold and McPeek 2006). The aim of this study was to

document small-scale spatial patterns of sympatric populations of congeneric Malagasy mouse lemurs (*Microcebus murinus* and *M. berthae,* Cheirogaleidae: Primates) and to explore possible mechanisms of their coexistence. Because of their recent common ancestry, closely related species ought to exhibit high similarities in their use of biotic and abiotic resources, susceptibility to predators, and responses to disturbances and stress. Due to these similarities, congenerics should compete more intensely and should exhibit higher levels of mutual exclusion, compared to pairs of species from different genera (e.g. MacArthur 1972; Tilman 1982; Holt et al. 1994). Thus, only few pairs of congeneric species are expected to exist within a community at any given time (Elton 1946; Pianka 1994). Moreover, current patterns of co-occurrence should provide insight into causal mechanisms that have led to higher-order structures, such as competition and niche segregation (e.g. Tokeshi 1999; Bell 2000; Chase and Leibold 2003; Sfenthourakis et al. 2005).

Recently, Amarasekare (2003) proposed a framework that allows comparative predictions for alternative classes of mechanisms that can explain coexistence of ecologically similar species, i.e. species that lack differences in (1) partitioning of resources, (2) frequency-dependent predation or (3) temporal partitioning of one resource (e.g. Tilman 1982; Chesson 2000a, 2000b; Chase and Leibold 2003). These coexistence mechanisms focus on spatial niche differences, which depend on the nature of the competitive environment experienced by the interacting species (see also Amarasekare et al. 2004). A species' competitive environment consists of biotic and abiotic factors that influence its ability to exploit space or limiting resources that vary in space. In a spatially *homogeneous competitive environment*, defined as no change of species' competitive rankings within the spatial area considered, coexistence is most likely to occur via inter-specific trade-offs between life-history attributes that influence competition (e.g. fecundity, longevity) and those that allow species to escape or minimize competition (e.g. dispersal) (Amarasekare 2003). If species coexist in a homogenous competitive environment, intra-specific clustering and inter-specific segregation at a local scale, as well as no covariance between environment and competition are expected. Alternatively, in *spatially heterogeneous environments* species competitive rankings vary with landscape variation, which leads to greater intra-specific competition than inter-specific competition in favourable areas and greater inter-specific competition than intra-specific competition in unfavourable areas (Chesson 2000a, 2000b). As a result, species are restricted to

favourable parts of the habitat and competitively excluded from unfavourable areas. In such situations source-sink dynamics can lead to stable local coexistence (e.g. Pacala and Roughgarden 1982; Mouquet and Loreau 2002, 2003; Amarasekare et al. 2004).

The species-rich genus *Microcebus* is distributed over nearly all remaining forest areas of Madagascar with a high variability in species distribution patterns. Mouse lemurs (*Microcebus* spp.) are small (30-90g) nocturnal, arboreal primates, which form a monophyletic group within the endemic primates of Madagascar (Yoder et al. 2000; Kappeler and Rasoloarison 2003). Whereas in some areas probably only one species exists, several species pairs are found in sympatry in western Madagascar. Generally, these pairs include the grey mouse lemur (*M. murinus*), which is widely distributed in the dry deciduous forest along the entire west coast of Madagascar, and another congeneric species with locally restricted ranges (e.g. NW-Madagascar: *M. ravelobensis*; W-Madagascar: *M. berthae* (Kirindy, Menabe), *M. myoxinus* (Bemaraha); S- and SW-Madagascar: *M. griseorufus*) (Schmid and Kappeler 1994; Zimmermann et al. 1998; Rasoloarison et al. 2000). Recently, several new species of mouse lemurs have been described (Kappeler et al. 2005; Louis Jr. et al. 2006; Oliveri et al. 2007) so that even more potentially co-existing congeneric species pairs exist in a variety of different habitat types, ranging from evergreen rain forest to dry spiny forest. Although niche separation to other co-existing primates has been shown in some Malagasy forests (Ganzhorn 1988, 1989), only preliminary information exists on spatial distribution patterns of *Microcebus* species pairs (see e.g. Rendigs et al. 2003; Schwab and Ganzhorn 2004), which is an important prerequisite for understanding mechanisms of coexistence (Snyder and Chesson 2003).

By documenting small-scale spatial patterns of sympatric populations of one such species pair (*M. murinus* and *M. berthae*), we aimed to explore possible mechanisms of their coexistence. In particular, we addressed the following questions: (1) Are there indications for stable coexistence or mutual spatial exclusion? (2) Are there indications for intra-specific clustering? (3) Do habitat characteristics, such as forest structure, and/or feeding niche partitioning explain species distribution on a small spatial scale? (4) Which general coexistence mechanism best explains the observed spatial pattern?

Methods

Species

Madame Berthe's mouse lemur (*M. berthae*) is the world's smallest living primate, with an average body weight of about 33g. After its discovery in 1992 in the dry deciduous forest of western Madagascar (Schmid and Kappeler 1994), it was initially thought to represent a rediscovery of *Microcebus myoxinus* (Peters 1858), but comparative morphometric and genetic studies revealed its status as a new species, *M. berthae* (Rasoloarison et al. 2000; Yoder et al. 2000). The species' currently known distribution (approximately 50 x 30km) is restricted to Kirindy Forest/CFPF, the nearby Réserve Spécial d'Andranomena and Ambadira forest in central western Madagascar. This species appears to have the most restricted range of all known *Microcebus* spp. (Rasoloarison et al. 2000; Schwab and Ganzhorn 2004). Within its range, Madame Berthe's mouse lemur is sympatric with the much more widely distributed and larger (60g) grey mouse lemur (*M. murinus*). Preliminary observations indicated that the two species are ecologically very similar (Dammhahn and Kappeler 2005). Both are nocturnal solitary foragers that use the fine branch niche and feed mainly on fruit, gum, arthropods and insect secretions (Martin 1972a, 1973; Petter 1978; Hladik et al. 1980; Corbin and Schmid 1995). However, details of the feeding ecology are not known for *M. berthae* and have been only qualitatively described for *M. murinus*.

Study site

The study was conducted in the Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar, approximately 60km northeast of Morondava (44°39'E, 20°03'S, 30-60m above sea level). The study site is located within a 12.500ha forest concession of the Centre de Formation Professionelle Forestière (CFPF) de Morondava. The climate in this area is characterized by pronounced seasonality with a hot rainy season between December and March and little or no rainfall from April to November (Sorg and Rohner 1996). The forest is very dense with a comparatively low canopy (for additional information see Sorg et al. 2003). The study area within the concession (locally known as N5) was defined by the boundaries of a grid system of small foot trails. Within a 500x500 m core area, a rectangular system of small trails was established at 25m-intervals and each trail intersection was marked for orientation and their coordinates were used to create a map. Within the Kirindy

Forest/CFPF, both *Microcebus* species stably co-occur in three different study areas covering more than 150ha, where populations have been monitored since 1994 via regular capture-mark-recapture. Also, data from line-transect trapping covering several km² further supports the generality of this co-occurrence pattern (R. Rasoloarison, L. Schäffler, D. Zinner, *unpublished data*). Thus, the area chosen for the present study is representative. Since it covers a large zone of adjacent populations of both species, it provides access to sufficiently large populations. The population densities in our study area are as high as at the other study sites and have been relatively constant since 1994.

Capture and marking

We baited a total of 200 Sherman live traps per night with pieces of banana and set them near trail intersections 0.5-2m above ground for three consecutive nights in one half of the study area (12.5ha) followed by three consecutive nights in the other half of the study area (12.5ha), covering in total 25ha with 400 trap locations at 25m intervals. Trapping locations and design were consistent across all trappings, which were performed about once every month: 5-times in 2002 (Aug-Nov), 6-times in 2004 (Jun, Aug-Dec), 8-times in 2005 (Mar-Jul, Sep-Nov) and 6-times in 2006 (Mar, Jul-Nov). Traps were opened and baited at dusk and checked and closed at dawn. Captured animals were collected in the early morning and kept at a nearby research station during the day. All newly captured animals were briefly restrained and immobilized with 10µl Ketanest 100 (Rensing 1999), marked individually with subdermally implanted microtransponders (Trovan, Usling, Germany), sexed, aged (juvenile/adults) and a set of standard morphometric measurements were taken. Recaptured animals were only identified. All animals were released at the site of capture shortly before dusk on the same day.

Spatial patterns

Using all individual trapping points (range of individual trapping points per year: *M. murinus*: 1-24, *M. berthae*: 1-32), we calculated individual mean trapping points per year as the arithmetic means of x- and y-coordinates of the trapping points and mapped them with ArcView 3.3 (ESRI). For each study year, we calculated distances to intra- and inter-specific nearest neighbours for each individual. Subsequently, we tested for species differences using independent t-tests and for

spatial randomness of species distribution within the study area using the nearest-neighbour method (Krebs 1998). Based on Clark and Evans (1954) we compared mean distance to nearest neighbour (calculated as $D=(\Sigma d_i)/n$ with n=number of individuals and d_i=distance to nearest neighbour of individual i) with expected distance to nearest neighbour (calculated as $E=1/(2\sqrt{p})$ with p=density of individuals (p=n/A with A=size of study area). Subsequently, we calculated an index of aggregation as R=D/E, with R=1 indicating a random pattern, R approaching 0 indicating a clumped pattern and R approaching 2.15 indicating a uniform pattern. We tested for significant deviation from randomness by calculating a z-test with $z=(D-E)/s$ and $s=0.2613/(\sqrt{np})$ (Krebs 1998).

Co-occurence

Analysis of co-occurrence between species was based on Diamond's (1975) hypothesis on checkerboard distributions. Two or more ecologically similar species inhabit exclusive but inter-digitating habitats. Using the co-occurrence module of EcoSim7.72 (Gotelli and Entsminger 2006) we tested for non-random patterns of species co-occurrence in a presence-absence matrix. C-scores were calculated as numbers of checkerboard units (CU) as: $CU=(r_i-S)(r_j-S)$, where S is the number of shared sites (trap locations) and r_i and r_j are the row totals for species i and species j (Stone and Roberts 1990). Based on 5000 iterations with proportional representations of species and trap stations we calculated expected C-scores (null models) and subsequently tested whether the occurrence of *M. berthae* and *M. murinus* at the trap stations deviated from randomness. C-scores larger than expected by chance indicate mutual exclusion between species (Gotelli and Entsminger 2006). We kept species representations (rows) "proportional" meaning that the probability of trapping an individual of a species was proportional to the observed number of trappings of that species, which best reflects species differences in trapping, e.g. due to differences in population size. We did not use the "fixed row" constraint which was shown to have lowest probabilities of Type I errors (Gotelli 2000) and was therefore recommended by Gotelli and Entsminger (2006) because keeping numbers of trappings per species constant is rather unrealistic. We also kept trap location representations (columns) "proportional" meaning that the probability of trapping an individual of either species at a particular trap site was proportional to the observed number of trappings at that site. This column constraint best reflects spatial

heterogeneity in trapping probability as compared to an equiprobable representation while also allowing more variation in the simulations than a fixed columns constraint.

Feeding ecology

Data on diet was obtained by means of direct focal observation (Altmann 1974) between June and December 2004-2006, a period that coincides with the dry and the beginning of the wet season in the Kirindy Forest/CFPF and is thus the time when food is most limiting (Dammhahn and Kappeler, in press b). We equipped a total of 13 *M. berthae* and 16 *M. murinus* females with radio collars (*M. murinus*: 2g, TW4, Biotrack, UK; *M. berthae*: 1,8g BD-2, Holohil, Canada). Focal animals were followed during their nocturnal activity for 1-4 hours before switching to another *M. berthae* or *M. murinus* individual. The observation time was chosen opportunistically but was spread evenly between 18:00 and 1:00h for every animal (prior analyses showed that there is no difference in feeding behaviour between first and second half of the night). We took behavioural data cumulatively for observation intervals of 1 minute (one-zero sampling) (Martin and Bateson 1993) and recorded all occurrences of feeding behaviour. Food items were categorized into arthropods, fruit, flowers, gum, homopteran secretions, vertebrates and unknown. In total we observed Madame Berthe's mouse lemurs for 213 hours and grey mouse lemurs for 171 hours. Due to low visibility in a dense forest at night, animals were in sight only in 48% of 1-min observation intervals in *M. berthae* and 71% in *M. murinus*. The species difference in visibility was due to overall higher mobility in *M. berthae*. All analyses are based on 1-min observation intervals when the animal was in sight. Differences in *Microcebus'* diet were analysed using absolute frequencies and Chi²-test.

Feeding niche overlap was calculated using Pianka's index (Pianka 1973; Krebs 1998) based on food categories. This symmetrical index O_{jk} ranges from 0 (no resources in common) to 1 (complete overlap) and is calculated as:

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

with p_{ij}=proportion resource category *i* is of the total resources used by species *j* and p_{ik}=proportion resource category *i* is of the total resources used by species *k*. We determined the statistical significance of the observed niche overlap by comparing it with an appropriate null model calculated by the niche overlap function in EcoSim

7.72 Software (Gotelli and Entsminger 2006), in which the observed resource utilization data were randomized among species in 1000 simulations. We used the RA4 algorithm to calculate expected niche overlap indices. This algorithm retained both the observed niche breadth of each species and the pattern of zero resource states by reshuffling only the non-zero entries for each resource. RA4 is the most conservative algorithm and thus has the greatest chance of revealing significant patterns of reduced niche overlap (Winemiller and Pianka 1990; Gotelli and Entsminger 2006). Mean simulated niche overlap was then compared to observed overlap. Resource niche partitioning should cause mean niche overlap to be less then expected by chance.

Vegetation plots

To estimate forest structure related to the main food sources of mouse lemurs, we measured several microhabitat variables. We estimated the density of trees, which is highly related to the density of fruit and gum sources, and the density of lianas, which determines the density of homopteran secretions because the insects (*Flatida coccinea*, Homoptera, Fulgoridae) producing these sugary secretions aggregate and feed exclusively on lianas (Hladik et al. 1980). Additionally, the density of living and dead trees provided an estimate of the availability of tree holes, another important resource (sleeping sites) for mouse lemurs. For the last two study years (2005 and 2006), species trap locations were weighted by trapping frequency with every individual counting once per location. The 8 (in 2005) and 10 (in 2006) most frequented locations per year were chosen for each species. Subsequently, quadrates of 10 x 10m were designed with the trap location representing one corner of the quadrates. We counted the total number of trees >5cm DBH, number of standing dead wood (DBH >5cm and length >1m) and number of liana stocks within every quadrate. Mann-Whitney U tests were calculated to examine differences between quadrates at *M. murinus* and *M. berthae* trapping locations. Significance for all tests was set at alpha=0.05.

Results

Capture and spatial pattern

In 30000 trap nights over 4 years we caught a total of 142 *M. berthae* individuals, between 24 and 55 per year, and 162 *M. murinus* individuals, between 49 to 71 per year (Table 1). Trapping data revealed constant small scale spatial separation between the two species (Fig. 1).

Table 1: Number of trap nights (number of nights x number of traps set), number of different individuals caught per year and number of trappings (number of trapped animals per year including recaptures) of *M. berthae* and *M. murinus* in 2002, 2004, 2005 and 2006

Year	Trap nights	*M. berthae*		*M. murinus*	
		Individuals	Trappings	Individuals	Trappings
2002	6000	39	140	55	258
2004	7200	24	33	56	164
2005	9600	55	233	71	424
2006	7200	47	420	49	265
2002-2006	**30000**	**142**	**826**	**162**	**1111**

In all 4 study years mean distances to the nearest conspecific neighbour were smaller in *M. murinus* than in *M. berthae* (t-tests, 2002: t=4.50, df=92, p<0.0001; 2004: t=-4.64, df=78, p<0.0001; 2005: t=-3.45, df=123, p<0.001; 2006: t=-4.79, df=94, p<0.0001). Moreover, *M. murinus* individuals were significantly clumped in the study area, whereas the distribution of *M. berthae* did not differ from complete spatial randomness (Table 2). Also, mean distances to the nearest inter-specific neighbour (Means and SD: 2002: 136±81; 2004: 126±100; 2005: 94±66; 2006: 103±80) were larger than to the nearest intra-specific neighbour (Table 2) (t-tests, 2002: t=4.50, df=92, p<0.0001, 2004: t=-4,64, df=78, p<0.0001, 2005: t=-3,45, df=123, p<0.001, 2006: t=-4.79, df=94, p<0.00001), indicating spatial segregation between the species.

Co-occurrence

Of the 400 possible trapping sites the two species shared only a small number in each study year (10 in 2002, 2 in 2004, 17 in 2005, 24 in 2006) and most trapping sites were exclusively occupied by one species (Table 3). For every study year, observed C-scores were higher than expected C-scores based on 5000 simulations, indicating inter-specific spatial segregation (Table 4).

Table 2: Observed (D) and expected (E) mean distances (±SD) to nearest conspecific neighbour, indices of aggregation (R) with corresponding spatial patterns and significance levels for each species and year (see methods for details)

Year	*M. berthae*					*M. murinus*				
	D	E	R	Pattern	p	D	E	R	Pattern	p
2002	39.9 ± 26.6	38.0	1.05	random	<0.01	21.3 ± 12.7	32.0	0.66	clumped	<0.01
2004	48.4 ±38.7	40.5	0.84	random	<0.01	15.4 ±8.6	31.7	0.48	clumped	<0.01
2005	32.7 ±23.1	32.0	1.02	random	<0.01	17.5 ±25.2	28.2	0.62	clumped	<0.01
2006	36.1 ±22.1	34.6	1.04	random	<0.01	17.5 ±15.4	33.9	0.51	clumped	<0.01

Table 3: Number of trapping sites (total 400) that were not occupied, occupied by one species only, and shared by both species

Year	Not occupied	Occupied by one species	Occupied by both species
2002	218	172	10
2004	304	94	2
2005	204	179	17
2006	156	220	24

Table 4: Observed and expected C-scores (mean ± SD) for each study year. Expected C-scores are based on 5000 iterations with proportional representations of species and trap stations (see methods for details)

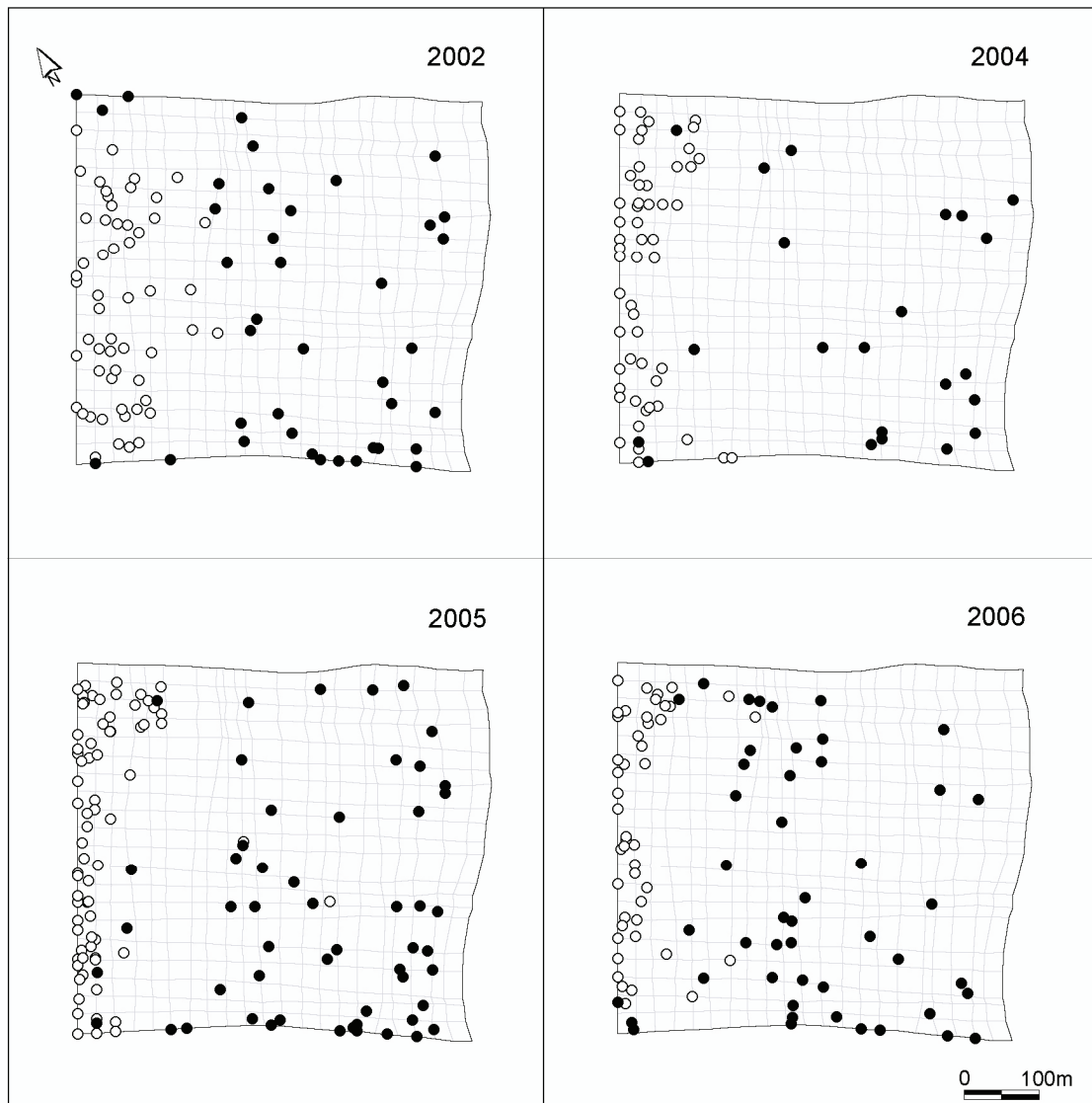| Year	C-score (obs)	C-score (exp) Null model	p
2002	7392	2007 ± 302	< 0.0001
2004	1680	443 ± 123	< 0.0001
2005	7548	2181 ± 335	< 0.0001
2006	8851	2826 ± 486	< 0.0001

Fig. 1: Spatial distribution of two *Microcebus* species. Mean coordinates of trapping points of *M. berthae* (full circles) and *M. murinus* (open circles) individuals per year.

Feeding ecology

Both *Microcebus* species had an omnivorous diet and used the same food sources, including sugary homopteran secretions, fruit, flowers, gum, arthropods and small vertebrates (e.g. geckos, chameleons). Feeding patterns of the two species differed in proportions of these food categories, however (Chi²-test, $\chi^2=265.9$, df=4, p<0.001) (Table 5). *M. berthae* mainly fed on a sugary secretion produced by homopteran larvae, which amounted up to 82% of their overall diet, which was further supplemented by animal matter. The diet of *M. murinus* was more diverse, including generally higher amounts of fruit and gum. Both species used similar amounts of

animal matter. Feeding niche overlap was high and observed overlap was higher than expected overlap (O_{jk}(obs)=0.97, O_{jk}(exp)=0.39, p<0.05).

Table 5: Percentages and total numbers of feeding events on different food sources for *M. berthae* and *M. murinus*. P values are given for Chi²-tests based on frequency data.

Food sources	*M. berthae* (n=1668)	*M. murinus* (n=1066)	p
Homopteran secretions	82.0	59.5	<0.001
Animal matter	11.4	16.6	n.s.
Fruits/Flowers	2.0	8.6	<0.001
Gum	0.2	9.2	<0.001
Unknown	4.4	6.1	n.s.

Vegetation plots

All weighted trapping points were exclusive by species. Vegetation plots at *M. berthae* and *M. murinus* trapping points did not differ in mean density of trees >5cm DBH (MWU-test, z=1.2, p=0.125), mean number of standing dead wood (MWU-test, z=-0.57, P=0.565) and mean number of lianas (MWU-test, z=0.51, p=0.609) (Fig. 2).
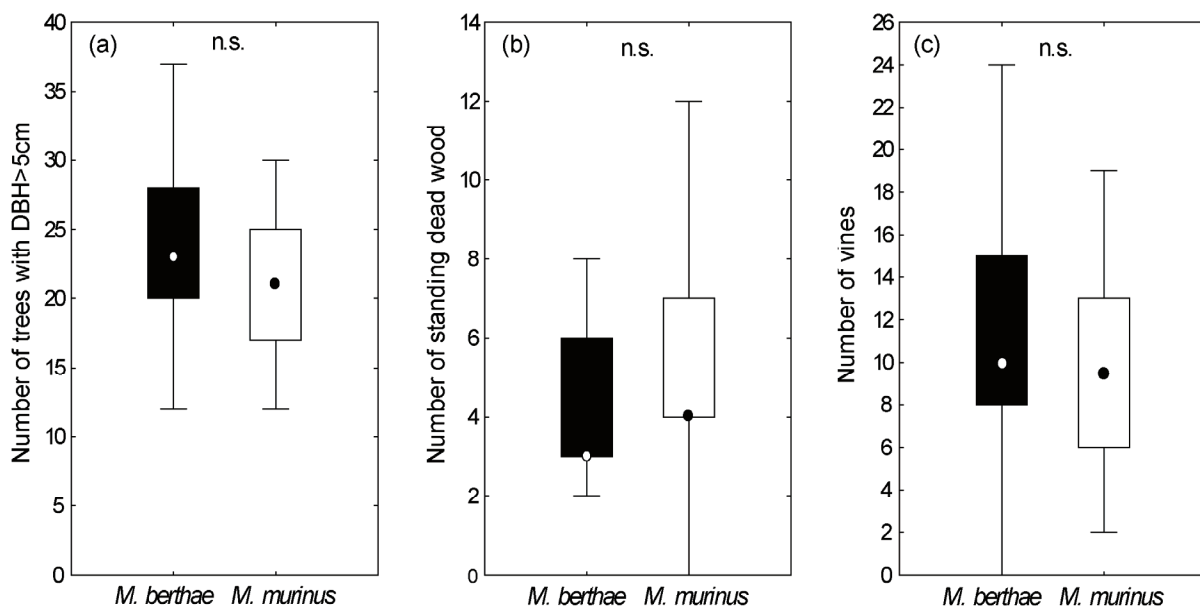
Fig. 2: Habitat characteristics. Vegetation plots at *M. berthae* (n=18) and *M. murinus* (n=18) most frequented trapping points did not differ in tree density (a), number of standing dead wood (b) and number of lianas (c) (MWU-tests). Shown are medians, inter-quartile ranges (box) and range (whiskers).

Discussion

The results of intensive trapping over a four-year period indicated mutual spatial exclusion between *M. berthae* and *M. murinus* on a small spatial scale. Within the study area, *M. murinus* individuals were spatially clumped, whereas *M. berthae* individuals were randomly spaced. Although the diet of both species differed in proportions of food categories, they used the same food source categories and had high feeding niche overlap. Thus, feeding niche partitioning most likely is not the underlying mechanism that led to the observed spatial pattern. Further, forest structure related to the spatial distribution of main food sources did not explain spatial segregation because habitat parts used by each species exclusively did not differ in mean density of trees, dead wood and lianas. Instead, we propose that life history trade-offs that result in species aggregation and a relative increase in the strength of intra-specific over inter-specific competition best explain the observed co-occurrence pattern of ecologically similar *Microcebus* species.

Although Madame Berthe's and grey mouse lemurs have been shown to co-occur regionally and have stably co-existed locally in our study area for more than 15 years (Schmid and Kappeler 1994; Rasoloarison et al. 2000; Schwab and Ganzhorn 2004), they mutually exclude each other on the smallest spatial scale (see also Schwab and Ganzhorn 2004). Both, results of co-occurrence patterns based on Diamond's (1975) hypothesis on checkerboard distributions, and relative large distances to inter- versus intra-specific nearest neighbours, indicate spatial segregation between the two *Microcebus* species. Furthermore, nearest neighbour analysis revealed that on this local scale, *M. murinus* individuals were spatially clustered, whereas *M. berthae* individuals were dispersed and randomly spaced.

Feeding niche partitioning cannot explain these spatial patterns because (1) both *Microcebus* species fed on the same food categories and their diet differed only in relative proportions, (2) the feeding niche of *M. berthae* fell completely within the wider niche of *M. murinus*, which is also reflected by the high feeding niche overlap and (3) basic characteristics of forest structure that are related to the distribution of main food resources did not correspond to the spatial distribution of the two species. Forest parts used by each species exclusively did not differ in structural characteristics. In contrast, previous studies suggested differences in microhabitat preferences to explain distribution patterns in *Microcebus* species (Rendigs et al. 2003; Schwab and Ganzhorn 2004). In co-occurring *M. murinus* and *M. ravelobensis*,

forest structure characteristics corresponded to an uneven distribution pattern with areas of coexistence and of exclusive use by one species (Rendigs et al. 2003). However, relatively high coefficients of association in a small area of sympatry imply low inter-specific spatial segregation on this spatial scale.

For *M. murinus* and *M. berthae,* Schwab and Ganzhorn (2004) discussed specific habitat requirements for *M. berthae*. However, in the same forest part also studied here (locally known as N5), differences in microhabitat structure between used and unused parts were marginal; of 6 variables measured in their study, Schwab and Ganzhorn (2004) only found a 7% difference in vegetation cover at intermediate level (30-160cm). Vegetation cover, however, was only estimated by eye to the nearest 10% and these estimates showed high variation within site categories. *M. murinus* apparently did not prefer any particular microhabitat (Schwab and Ganzhorn 2004; this study). Additionally, analyses of forest composition of the study area (C. Großheim and J.U. Ganzhorn, *unpublished data*) provided no evidence for spatial differences in the distribution of fruit and gum tree species used by mouse lemurs. Thus, spatial clumping in *M. murinus* does not appear to be explained by ecological factors. Overall, the observed spatial pattern of inter-specific segregation and intra-specific clustering within a given forest part is not likely to be explained by feeding niche partitioning and corresponding habitat characteristics, but might be based instead on mechanisms of competitive coexistence.

With 60g body mass, *M. murinus* are about twice as large as *M. berthae* and should therefore be superior in direct competition. Whereas feeding competition between the two species has not yet been demonstrated experimentally, behavioural observations of inter-specific interactions at feeding sites suggested feeding priority of *M. murinus* (M. Dammhahn, *unpublished observations*). For two reasons one can assume that the competitive rankings of the two *Microcebus* species do not change in space on small to medium scale (*homogeneous competitive environment*; Amarasekare 2003). First, the superior species (*M. murinus*) is the generalist, which inhabits even degraded, low quality forest (Ganzhorn 1995). Second, a predator-mediated change in competitive rankings is unlikely (e.g. Chesson 2000a; Chase et al. 2002) because none of the known predators (carnivores: *Cryptoprocta ferox*, *Mungotictis decemlineata*; snakes: *Ithycyphys miniatus*, *Sanzinia madagascariensis*; raptors: *Accipiter henstii*; owls: *Tyto alba*, *Asio madagascariensis*) is specialized on one of the species (Goodman et al. 1993; Rasoloarison et al. 1995; M. Dammhahn,

unpublished data) and predation pressure is higher for the inferior *M. berthae* (up to 70% mortality) than for the superior *M. murinus* (up to 50% mortality) (M. Eberle, *unpublished data*; M. Dammhahn, *unpublished data*).

Population density of the superior competitor (*M. murinus*) is higher than that of the inferior one (*M. berthae*), and mean distances to same-species nearest neighbours are smaller than between heterospecifics. Thus, coexistence via *heteromyopia*, defined as competitive interactions between heterospecific individuals occurring over shorter distances than those among same species individuals (Murrell and Law 2003), is unlikely in *Microcebus* conspecifics. Excluding heteromyopia as a mechanism, within a *homogeneous competitive environment* coexistence is most likely facilitated by inter-specific trade-offs between life history attributes that increase a species' competitive abilities, e.g. fecundity and longevity, and those that allow species to escape or minimize competition, e.g. dispersal (Amarasekare 2003). Two coexistence mechanisms are possible (1) niche succession (e.g. Pacala and Rees 1998; Bolker and Pacala 1999) and (2) competition-colonization trade-off (e.g. Pacala and Roughgarden 1982; Loreau and Mouquet 1999; Mouquet and Loreau 2002, 2003) (Amarasekare 2003; Amarasekare et al. 2004). Niche succession would require that the superior competitor lacks the ability to exploit resource-rich conditions characteristic of recently disturbed (early successional) habitats. In contrast to the prediction of niche succession, *M. murinus*, and not *M. berthae,* was shown to inhabit even degraded and secondary forest (Ganzhorn 1994, 1995; Schwab and Ganzhorn 2004).

The general mechanism underlying coexistence via competition-colonization trade-off is that superior competitors cannot exploit all the available space because they are limited in their fecundity, recruitment or dispersal and, thus, leave gaps in the landscape that inferior competitors can exploit (Amarasekare 2003; Amarasekare et al. 2004). *M. murinus* shows patchy distribution in a continuous undisturbed forest with aggregation on the smallest (i.e., several 10ha (Wimmer et al. 2002; this study)), and the next largest (several km²) spatial scale, and gaps in their distribution stretching several home range diameters within a continuous habitat without geographic barriers (Fredsted et al. 2004, 2005). Ecological constraints are unlikely to explain this spatial heterogeneity because this species seems to be ecologically very tolerant (Radespiel 2006) and has been found in various forest types, including intact primary evergreen littoral, dry deciduous and arid spiny forest (Ganzhorn 1995;

Ganzhorn et al. 1997; Ramanamanjato and Ganzhorn 2001; Rendigs et al. 2003; Rasoazanabary 2004; Schwab and Ganzhorn 2004), disturbed and secondary forest (Ganzhorn 1995; Ganzhorn and Schmid 1998) and even plantations (Ganzhorn 1987).

Female philopatry (Wimmer et al. 2002) in combination with cooperative breeding of closely related females (Eberle and Kappeler 2006) might lead to female clusters in space and thus clumped population patches in *M. murinus*. Females form stable matrilineal groups and incidences of adoption and allonursing in group-breeding females suggest that reproductive success of cooperatively breeding females is higher than that of females breeding alone (Eberle and Kappeler 2006). Also, survival benefits are obtained by the presence of close kin (Lutermann et al. 2006). A similar pattern is unlikely in *M. berthae* because females do not form permanent sleeping groups, and females that were opportunistically associated with each other were not close kin (Dammhahn and Kappeler 2005). Further, preliminary data on genetic population structure provided no evidence for the existence of spatial clusters of closely-related females (matrilines) (Dammhahn and Kappeler 2005). Benefits from limited dispersal for *M. murinus* females, in combination with limited recruitment due to high predation pressure (up to 50% mortality, M. Eberle, *unpublished data*; M. Dammhahn, *unpublished data*), might result in spatial population clusters and an increase in the strength of intra-specific competition relative to inter-specific competition, thus facilitating the coexistence of ecologically similar *Microcebus* species.

CHAPTER 5

Seasonality and energy strategies in co-existing mouse lemurs (*Microcebus berthae* and *M. murinus*)

with Peter M. Kappeler

Abstract

In highly seasonal habitats, such as the dry deciduous forests of western Madagascar, animals have to cope with thermoregulatory stress and periods of reduced food availability. To survive and successfully reproduce in such harsh environments, species are expected to have developed strategies to balance their energy budget during the lean season. One aim of this comparative study of two sympatric mouse lemur species was to illuminate species-specific energy saving strategies to cope with seasonality and to evaluate their consequences for female fitness. Since August 2002 we regularly (re-)captured and marked individuals of co-existing populations of *Microcebus berthae* and *M. murinus* in Kirindy Forest/CFPF. Data on activity were recorded through direct observation of radio-collared females. Generally, both species differed in their seasonal activity pattern: Female *M. berthae* maintained high levels of activity throughout the year, whereas female *M. murinus* nearly completely ceased activity during the cold dry season. In *M. berthae*, low survival restricted the length of female reproductive careers. Consequently, females maximized body condition with which they enter the reproductive season. In contrast, *M. murinus* females maximized survival but entered the reproductive season in poor body condition. Thus, co-existing mouse lemurs exhibited species-specific energetic strategies to cope with pronounced seasonality. These strategies affect female fitness because they alternatively allow maximizing the length of a female's reproductive career or the energetic investment in offspring in a given year.

Introduction

Endothermic animals, especially when they are small, face high energetic costs in seasonally cold or unproductive environments. Several behavioural, physiological and ecological adaptations exist to overcome these energetic constraints. For example, many mobile species, e.g. bats and birds, exhibit seasonal range shifts and migrate to more resource-rich areas (e.g. Berthold 2000; Petit and Mayer 2000). Small mammals with restricted mobility typically reduce energy expenditure during climatically or energetically most unfavourable times of the year. These species might even reduce metabolism for short (torpor) or extended periods (hibernation), with the later usually being accompanied by a preparation time, in which fat reserves are build up (Geisen and Ruf 1995).

Under highly seasonal conditions, reproduction might be traded off against maintenance requirements during the lean part of the year (Schmid and Kappeler 2005). Hence, specific energy strategies should be developed to successfully survive and maximize individual reproductive success. Because mammalian females typically invest more energy directly in each offspring than males, female fitness is highly dependent on their energetic constitution. The main factors determining female fitness - birth rate, length of reproductive career and survival rate of offspring (van Schaik 1989) - are all directly or indirectly dependent on a female's energetic make-up. For instance, the number of offspring produced per reproductive cycle as well as the number of reproductive events per lifetime is linked to the amount of energy a female can spare for reproduction. Also, offspring survival depends on how much energy a female can allocate to an offspring during gestation and lactation. Furthermore, a good body condition may also buffer females against external mortality risks, such as predation or pathogens.

Among primates, the smallest species that live in highly seasonal environments are interesting models for the study of these problems because the occurrence and use of different energy strategies seems to be highly variable (Schülke and Ostner 2007). Although physiological and behavioural strategies have been intensively studied in some species (recently reviewed by Schmid and Kappeler 2005; Schülke and Ostner 2007), the implications of these energy strategies for reproductive performance remain largely unknown. In this study, we therefore aimed (1) to illuminate species-specific behavioural energetic strategies to cope with pronounced seasonality in two small primates and (2) to evaluate the consequences

of potential species-specific behavioural strategies for female fitness. Specifically, we compared adaptations to cope with seasonality in 33g *Microcebus berthae* and 60g *M. murinus* (Cheirogaleidae). Both species live sympatrically in Kirindy Forest/CFPF, one of the larger remaining fragments of the dry deciduous forests of central western Madagascar. Mouse lemurs there have to cope with a combination of three main types of environmental stress: (1) high daily temperature fluctuations with minimum temperatures as low as 5°C during their nocturnal activity, (2) long dry seasons with up to 7 months without rain, and (3) resulting seasonal food scarcity, particularly of fruit and arthropod food (Sorg and Rohner 1996; Schmid and Kappeler 2005, Dammhahn and Kappeler, in press b).

Both mouse lemur species have tuned their reproductive schedule to the seasonality of their habitat. They are restricted to one reproductive cycle in Kirindy. The reproductive year of a *M. murinus* female starts with a short mating season in October, followed by 2 months gestation with young being born in December/January and nursed for 2 months (Eberle and Kappeler 2002, 2004). By March young are independent, leaving *M. murinus* females 4-6 weeks to acquire enough body fat to survive the largest part of the unfavourable dry season in hibernation (Schmid and Kappeler 1998). Much less is still known about the life history of *M. berthae*. They appear to follow a similar pattern with mating starting in November (Dammhahn and Kappeler 2005). Pregnant females were only caught in December (with the exception of one pregnant female caught in April (Schwab 2000)). Juvenile *M. berthae* can be caught beginning in March/April (M. Dammhahn, *unpublished data*).

Taken together, both mouse lemur species face the same environmental constraints and appear to follow similar reproductive schedules. Furthermore, both species were shown to be physiologically able to enter spontaneous daily torpor and to reduce their energy expenditure when ambient temperatures are low (Schmid et al. 2000; Schmid and Speakman 2000). Here, we wanted to explore whether both species also exhibit similar behavioural strategies to cope with seasonal energy shortages while at the same time maximizing reproductive output.

Methods

Beginning in 2002, we have regularly (re)captured and marked individuals of co-existing populations of *M. berthae* and *M. murinus* in a 25ha study area in Kirindy forest (for details see Dammhahn and Kappeler, in press a). These populations

consisted of 50 to 70 individuals of *M. murinus* and 30-55 individuals of *M. berthae*, for which we obtained data on survival and body condition. In order to get detailed information on behaviour, we equipped a total of 13 *M. berthae* and 17 *M. murinus* females with radio collars, which allowed radio-tracking and focal animal observations. We followed focal animals during their nocturnal activity for 1-4 hours before switching to another animal and choose observation times opportunistically, but evenly spread between 18:00 and 1:00h for every animal (for details see Dammhahn and Kappeler, in press b). To analyse seasonal patterns we defined 3 time periods according to differences in rainfall and food availability: transition between wet and dry season (March-May), dry season (June-September), and transition between dry and wet season (October-December).

Results

Species-specific energy strategies

Activity in *M. murinus* varied seasonal with nearly complete inactivity during the dry season (Kruskal-Wallis, $H(2, n=30)=9.55$, $p<0.01$) (Fig. 1). In contrast, *M. berthae* remained highly active throughout all seasons (Kruskal-Wallis, $H(2, n=22)=3.30$, n.s.). Instead, *M. berthae* increased locomotor activity and travelled longer path lengths during the resource poor dry season than in the subsequent beginning of the wet season (Wilcoxon-Signed Rank test, $n=8$, $z=2.38$, $p<0.05$). Due to nearly complete inactivity of *M. murinus,* female path lengths could not be analysed for this species. *M. murinus* females spent most time feeding (51%) during the end of the wet season when they acquired large fat reserves. During the dry season, *M. murinus* instead lived from their energy reserves indicated by a decrease in body mass depending on the individual activity level (Spearman Rank Correlation, $R=0.79$, $p<0.001$, $n=14$). In contrast, *M. berthae* females increased feeding time during the resource poor dry season to 43% as compared to 28% outside the dry season. Thus, females of both species used different strategies to cope with a long energetically stressful dry season. *M. murinus* reduced activity and lived from the capital of acquired fat reserves. In contrast, *M. berthae* remained highly active and actually increased locomotor and feeding activity when resources got sparse.
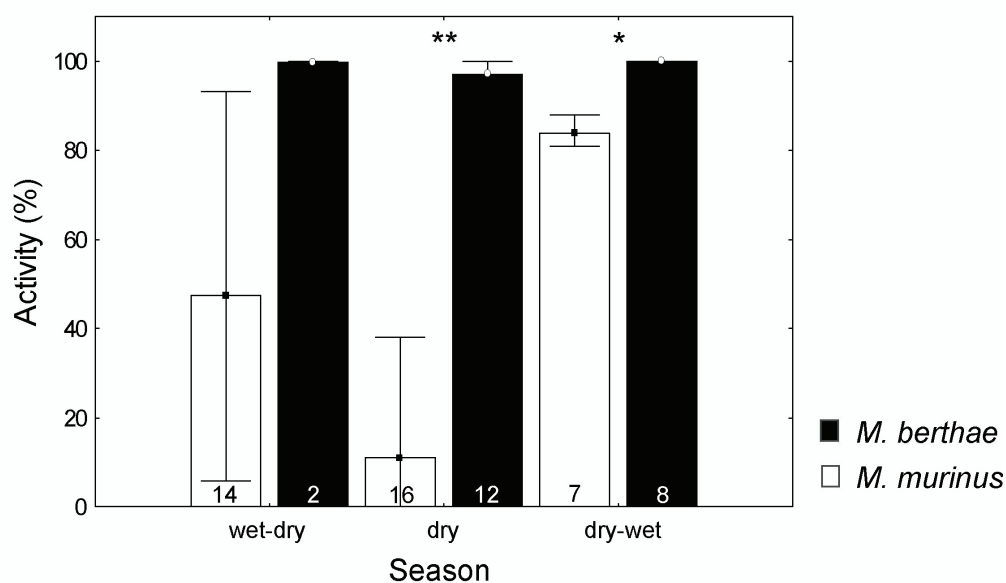
Fig. 1: Seasonal variation in activity patterns in *M. berthae* and *M. murinus*. Activity is represented as median (25-75% quartiles) percentages of active 1-min observation intervals during focal observations that were evenly spread between 18:00–1:00h. Numbers represent sample size of focal individuals, **p<0.01, *p<0.05 (Chi²-tests).

Effects of species-specific energy strategies on female reproduction

Overall, seasonal changes in body mass were similar in both species (Fig. 2): females lost weight during the dry season, showed no weight change in the transition from dry to wet season and gained weight during the wet season. In order to test the effect of the species-specific energy strategies on female reproduction, we first calculated a linear regression model over both species and all seasons with body mass as the dependent variable and head width as the independent variable to remove allometric effects. Then, we explored whether species-specific energy strategies affected two variables related to female fitness (1) body condition during the reproductive season and (2) survival until the reproductive season.
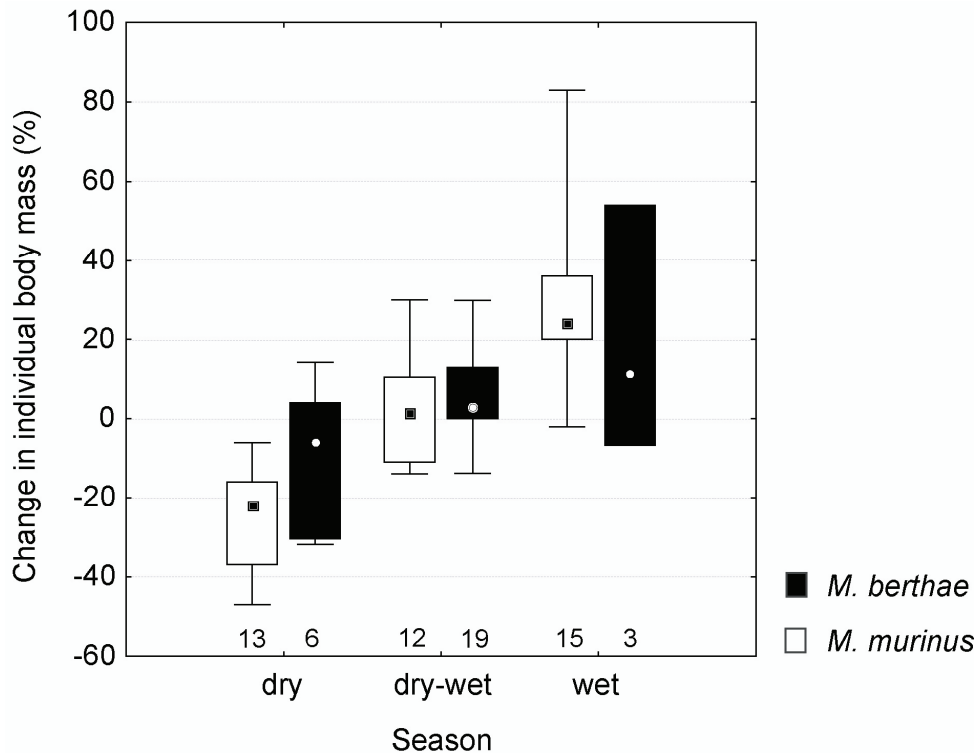
Fig. 2: Female *M. berthae* and *M. murinus* showed similar seasonal changes in individual body mass. Shown are medians (25-75% quartiles, range) of proportional differences in body mass of individuals in subsequent seasons. Numbers at the bottom represent sample sizes.

To determine in which condition females enter reproduction, we tested the residuals from the linear regression model for each season separately for species differences (Fig. 3). At the end of the wet season, *M. murinus* females were in better body condition than *M. berthae* (t-test, n_{Mbe}=7, n_{Mmu}=34, t=-3.00, p<0.01), whereas both species were in similar condition during the dry season (t-test, n_{Mbe}=69, n_{Mmu}=45, t=-0.71, n.s.). However, at the beginning of the wet season, corresponding to the mating season, the pattern was reversed and *M. berthae* were in better body condition than *M. murinus* (t-test, n_{Mbe}=36, n_{Mmu}=70, t=2.98, p<0.01).

Finally, we calculated the probability to survive from before to after the dry season based on capture-recapture data. Survival probability was higher for *M. murinus* females than *M. berthae* females (*M. murinus*: p_s=0.77, n=92; *M. berthae*, p_s=0.52, n=59; Chi²-test, χ^2=9.95, p<0.05).
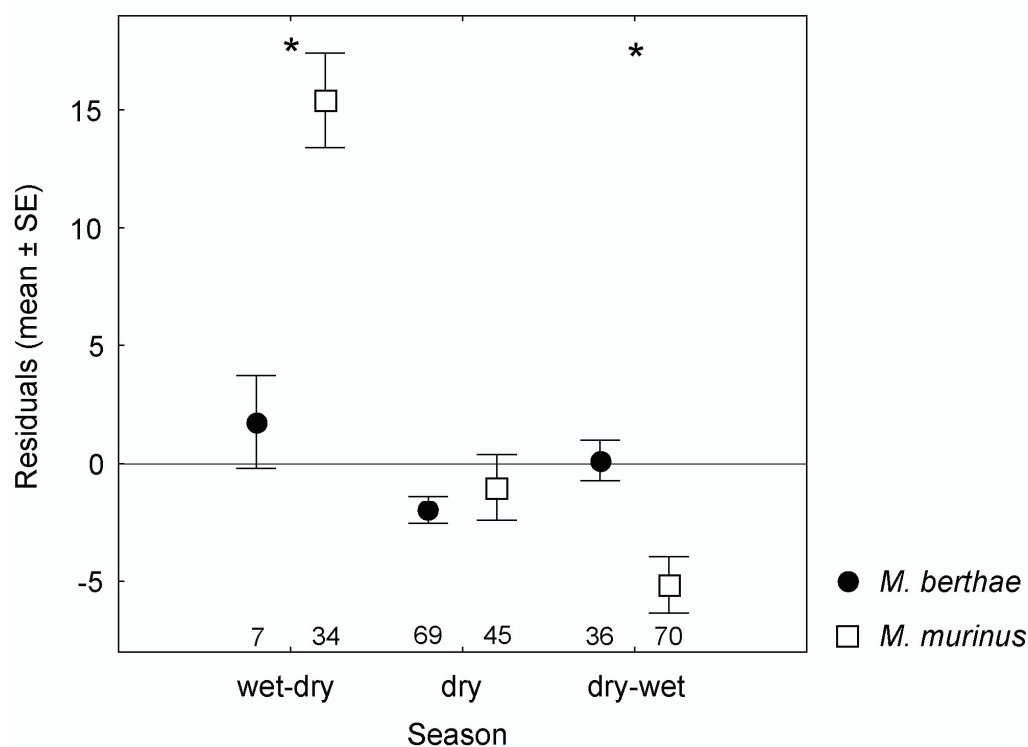
Fig. 3: Seasonal mean (±SE) residuals of a linear regression model over both species and all seasons with body mass as the dependent variable and head width as the independent variable. Numbers at the bottom represent sample sizes, *p<0.01 (t-test).

Discussion

Our study revealed that there are species-specific energy strategies to cope with pronounced seasonality in co-existing mouse lemurs. As has been described before, *M. murinus* females prepare by seasonal fattening for the non-productive season and remain largely inactive during the cold dry season, spending most time in energy-saving torpor or even hibernating over extended periods (Schmid and Kappeler 1998; Schmid 1999; Schmid and Speakman 2000; Rasoazanabary 2006). In contrast, female *M. berthae* remained active throughout the dry season and even increased feeding and ranging activity, a common strategy also used by other primates (Hemingway and Bynum 2005). Although *M. berthae* were shown to enter spontaneous daily torpor under semi-natural conditions (Schmid 1996; Schmid et al. 2000), they employed this physiological possibility only during the day and the colder second part of the night. Probably female *M. berthae* are not able to accumulate sufficiently large fat reserves during the wet season, as indicated by their poor body condition compared to *M. murinus* females. Thus, they employed an energy strategy

very similar to *M. murinus* males, which also combine activity with the use of daily torpor (Schmid and Kappeler 1998; Schmid 1999).

Low survival from one annual reproductive season to the next seems to restrict the length of a female *M. berthae* reproductive career. Consequently, females maximized body condition with which they enter the reproductive time of the year and thus appear to maximize birth rate and survival rate of offspring. A shift of the mating season towards the productive wet season (Dammhahn and Kappeler 2005) might further enhance female body condition during pregnancy. In contrast, the energy strategy used by *M. murinus* females maximized their survival, providing the opportunity for the majority of females to reproduce more than once per lifetime. Although body condition decreased with length of inactivity, female *M. murinus* extended inactivity until the onset of the mating season (October) and thus entered pregnancy in a less favourable body condition than *M. berthae* females. Breeding communally (Eberle and Kappeler 2006) might provide *M. murinus* females with an alternative mechanism to invest in offspring survival (and birth rate), however.

Data on these two *Microcebu*s species further highlight the pronounced variability in energy strategies used by members of the family Cheirogaleidae (Schülke and Ostner 2007), which largely exceed those of other groups of small primates (Lorisidae: Müller et al. 1985; Galagidae: Mzilikazi et al. 2006). *M. murinus* females behaviourally and physiologically resembled *Cheirogaleus medius,* a true hibernator (Dausmann et al. 2004), whereas *M. berthae* resembled mouse lemur species inhabiting more favourable habitats (e.g. *M. ravelobensis* and *M. murinus* in NW-Madagascar, Radespiel 2006) and co-existing *M. murinus* males. Both activity patterns are strategies to save energy and appear to be similarly successful to ensure survival and reproduction in highly seasonal environments. Actual comparisons of reproductive success have to await future genetic maternity analyses. Further comparative investigations of other members of the specious cheirogaleid family that combine behavioural and physiological data with long-term monitoring of individual reproductive success in wild populations, will provide a basis for broader comparisons of the impact of energy strategies on fitness.

GENERAL DISCUSSION

Ecological determinants of mouse lemur social systems

Due to their predominantly cryptic life style and apparent lack of social complexity, little attention has been paid to solitary species in theoretical models of social systems (e.g. Wrangham 1980; van Schaik 1989; Johnson et al. 2002). Recent empirical studies, however, revealed an astonishing diversity among solitary foragers (e.g. reviewed in Macdonald 1983; Müller and Thalmann 2000; Kappeler and van Schaik 2002; Dalerum 2007; Lacey and Sherman 2007), highlighting the need for a more comprehensive understanding of this type of social organization. Variation exists mainly in female temporal and spatial associations, i.e. the extent of range overlap and the occurrence and composition of sleeping or breeding groups (Kappeler and van Schaik 2002). Although female spatial patterns in solitary foragers have been linked to the distribution of risks and resources in the environment (e.g. Ostfeld 1985, 1990), existing models that allow testing the relationships between ecological factors and variation in social organization and structure have not been applied to these species.

This thesis provides a comparative data set of two co-occurring solitarily foraging mouse lemurs, which allowed integrating inter- and intra-specific as well as seasonal aspects of female competition. Detailed information on species-specific resource use patterns, spatial and temporal resource distribution, complemented with spatial and behavioural data of individually known females, allowed applying the SEM to solitary foragers. The main results support basic predictions of the SEM about the relationships between resource distribution, type of competition and consequences for social organization (chapters 2 and 3).

Resource characteristics and resulting competitive regimes did indeed relate to differences in female spatial patterns in these two ecologically similar mouse lemurs. As predicted, differences in competitive regimes were also reflected in behavioural consequences, such as food-related aggression, female dispersal and the occurrence of stable sleeping associations. In detail, food sources used by *M. berthae* occurred in small dispersed patches, leading to strong within-group scramble competition and over-dispersed females with a low potential for female associations. In contrast, *M. murinus* additionally used patchily distributed, high quality (large)

resources. Within and between-group contest competition over these monopolizable resources allowed females of this species to cluster in space. Additional benefits such as increased survival of philopatric females (Lutermann et al. 2006) and benefits of cooperative breeding by closely-related females (Eberle and Kappeler 2006) might lead to stable matrilineal groups (Wimmer et al. 2002; Fredsted et al. 2005), which are clumped in space (chapter 4).

Besides species differences in competitive regimes, overall resource availability was identified as a main determinant of female spatial-temporal distribution (e.g. Ostfeld 1985; 1990). This factor affected these mouse lemur species unequally, mainly due to pronounced differences in feeding niche width (chapter 1) and strategies to overcome the extended lean seasons (chapter 5). In contrast to opportunistically feeding and seasonally inactive *M. murinus*, specialized *M. berthae* females experience (seasonally) low food density, resulting in female spatial avoidance, unusually large (exclusive) ranges and low population densities (Clutton-Brock and Harvey 1977; Reiss 1988). This result was further supported by the observation that females reduced their ranges when resource abundance was experimentally increased, independent of spatial resource distribution. Thus, testing resource-based models in solitary and other mammals requires a sound understanding of seasonal variation in diet composition, food abundance and distribution, together with species-specific energy strategies, because competitive modes and female energy gain might vary seasonally (Koenig and Borries 2006).

In addition, inter-specific competition can also impact female spatial patterns in solitary foragers, in particular in communities with dense trophic species packing. This effect is likely to be asymmetric and thus influences females differently depending on the competitive rankings of interacting species and the relative strength of competitive interactions, i.e. amount of feeding niche overlap between co-existing species. This factor might add substantial variation to the relative availability and distribution of resources experienced by individuals of different species, which remains to be incorporated into the SEM or other resource-based models. Two main lines of evidence suggested food competition between *M. berthae* and *M. murinus*: (1) high feeding niche overlap together with similar habitat requirements (chapters 1, 2, 4), and (2) small-scale mutual spatial exclusion (chapter 4, see also Schwab and Ganzhorn 2004). Nevertheless, both species have been shown to stably co-occur regionally and locally (Schmid and Kappeler 1994; Rasoloarison et al. 2000; Schwab

and Ganzhorn 2004). In chapter 4, I applied a recently developed theoretical framework (Amarasekare 2003; Amarasekare et al. 2004) to explain this puzzling spatial co-existence pattern. By adopting a comparative approach, I revealed that life history trade-offs that result in species aggregation and a relative increase in the strength of intra-specific over inter-specific competition best explained the observed pattern of co-occurrence of these ecologically similar *Microcebus* species. This study adds a primate field example to the theory of spatial competitive coexistence, which is far in advance of empirical investigations (Amarasekare 2003).

In conclusion, inter-specific variation in social organization of solitary foragers is the result of the compromise to accommodate multiple ecological and social determinants. They do, however, not play by different rules as group-living species. By linking ecological factors with characteristics of social systems, the SEM might successfully guide future research on other solitary primates and mammals as well.

Why are mouse lemurs solitary?

The various ecological and social determinants of group formation have been studied in detail, resulting in a large body of comprehensive theoretical models explaining the evolution and maintenance of group-living in mammals (e.g. Alexander 1974; Jarman 1974; Wrangham 1980; van Schaik 1983; Johnson et al. 2002). However, the fundamental question why some species do not live in groups, has only been touched upon and is to date not answered satisfying (Kappeler 1997a; Kappeler and van Schaik 2003). Although a solitary life style is certainly ancestral for mammals (Martin 1972b; Müller and Thalmann 2000), it prevails in many derived mammalian groups, necessitating an explanation of the adaptive basis of this type of social organisation (Kappeler 1997a).

Factors linked to a solitary life style in primates include small body size (Clutton-Brock and Harvey 1977), nocturnal activity (van Schaik and van Hooff 1983; Bearder 1987), dietary specialisation on small resources that cannot be shared (van Schaik and van Hooff 1983; Bearder 1987; Gursky 2000a) and reduced or increased predation pressure (van Schaik and van Hooff 1983; Terborgh and Janson 1986), but none of these factors was found to have a universal explanatory power even within primates (Kappeler 1997a; Kappeler and van Schaik 2003). More generally, it could be argued that the disadvantages of group-living prevent animals from communal foraging. Apart from advantages with respect to reduced predation risk (e.g. van

Schaik 1983) or defending large food sources (e.g. Wrangham 1980; MacDonald 1983) grouping has two main disadvantages: (1) aggregated individuals are more conspicuous to predators and (2) feeding rates are decreased as a results of direct or indirect feeding competition (Clutton-Brock and Harvey 1977).

Do any of these factors explain why female mouse lemurs temporally aggregate in stable sleeping groups but forage solitarily in highly overlapping ranges? Mouse lemurs are preyed upon by a diverse assemblage of predators, including carnivores, snakes, raptors, owls and even larger lemurs (Goodman et al. 1993; Rasoloarison et al. 1995; M. Dammhahn, *unpublished data*) and predation risk is high. Mouse lemurs typically behave cryptically and avoid being detected by predators (Martin 1972a). Nevertheless, they might exhibit conspicuous anti-predator behaviour such as cooperative mobbing against snakes (Eberle and Kappeler 2007). Reducing predation risk through a solitary life style is therefore unlikely to provide a sufficient explanation for mouse lemurs. The resource-based hypothesis posits that species forage solitarily when they use small patches of food that cannot be shared (e.g. MacDonald 1983; van Schaik and van Hooff 1983; Bearder 1987). Although between- and within-species variation in the composition of omnivorous diets is pronounced (Radespiel 2006; chapter 1), most mouse lemur food sources occur in patches that can only be exploited by one individual at a time, e.g. gum trees, homopteran secretion patches and arthropods. The strongest test of the resource-based hypothesis would be increased communal foraging in mouse lemur populations/species, which are mainly frugivorous and use large patches that can be shared. To date, there are neither quantitative data on inter-individual distances in relation to resource patch size nor experiments designed to test this prediction. However, anecdotal observations of temporal foraging aggregations of *M. murinus* in large fruiting or flowering trees in Mandena (Lahann 2007) and Kirindy (M. Dammhahn, *personal observations*) point in this direction. Thus, a resource-based explanation of solitary foraging is likely for mouse lemurs but does this hold for other solitary primates?

One main argument against the resource-based hypothesis was that some solitary primates are folivorous (e.g. *Lepilemur* spp.) using a non-contestable resource (but see Snaith and Chapman 2006). However, detailed field studies revealed that many species formerly recognised as solitary foragers are actually organised in *dispersed pairs* (e.g. *Lepilemur* spp.: Zinner et al. 2003; Hilgartner 2006;

Phaner furcifer: Schülke and Kappeler 2003; *Cheirogaleus* spp.: Fietz 1999, 2003; Lahann 2008), which most likely is also the case in *Avahi* spp. (Norscia and Borgognini-Tarli 2008), *Tarsius* spp. (Gursky 2005) several Galagidae (e.g. *Galago zanzibaricus*: Harcourt and Nash 1986; Bearder 1987) and Lorisidae (e.g. *Perodicticus potto*: Pimley et al. 2005; *Nycticebus coucang*: Wiens and Zitzmann 2003). Thus, solitarily foraging primates are either faunivorous, omnivorous or frugivorous but this is also true for many group-living species. A rigorous test of the resource-based hypothesis would require detailed data on resource use patterns, spatial and temporal resource distribution and patch size relative to the body size and ranging behaviour of the species in question. Thus, although a resource-based explanation requires further testing, for the time being the adaptive basis of why some mammals do not live in groups remains in the dark.

Outlook

Based on the results of this study I encourage future research to include solitary foragers in tests and further theoretical developments of socio-ecological and other resource-based models explaining variation in animal societies. In particular, studies of species exhibiting pronounced intra-specific variation in social organization might be promising to explore the evolution of group-living and complex social structures. Further investigations are certainly needed and there are several areas where effort is required to provide theoretical clarification and direction for empirical research:

(1) Although the multiple scales along which food sources can vary are recognized (e.g. size, quality, renewal, space and time), standardized measurement methods are not well defined (Koenig and Borries 2006; Snaith and Chapman 2007). This applies in particular for any non-plant food, which might constitute significant proportions of omnivorous diets of many solitary foragers, and for assessment of resource characteristics relative to the species in question.

(2) Almost all species face seasonal variation in food availability. Primates and other mammals developed a variety of different strategies to overcome these predictable or unpredictable times of food shortage (summarized for primates Brockmann and van Schaik 2006). Because competition for food is most intense, when resources are most limiting, a species' social organization ought to be adapted to these lean seasons. Accounting for temporal variation of food quality and quantity

as a prominent factor would certainly lead to more realistic models (Koenig and Borries 2006; Snaith and Chapman 2007). Again, this particularly applies to many small- bodied solitary foragers (e.g. rodents, insectivores, chiropterans, primates: cheirogaleids), which additionally have specific energy strategies to overcome unfavourable parts of the year.

(3) Systematic experimental variation of resource distribution, density and renewal in the field can help to test predictions of resource-based models and thus contribute towards understanding causal relationships (Janson 2000). Because many solitary foragers are small and occur at relatively high densities, experimental approaches can be particularly rewarding to study the ultimate factors determining variation in social systems in these species.

(4) Disentangling the forces that initially favoured the evolution of groups from those benefit(s) that are a consequence of group-living is crucial to understand how group-living evolved (Waser 1981). Understanding why and under which circumstances solitary females temporally associate in stable groups could help to illuminate the evolution of group formation (Dalerum 2007; Wagner et al. 2008).

Summary

The socio-ecological model (SEM) integrates ecological factors with characteristics of social systems and allows predictions about the relationships between resource distribution, type of competition and consequences for social organization and structure. Both theoretical and empirical research within this framework has mainly focused on explaining the evolution and maintenance of variation among group-living primates and other mammals. The main aim of this thesis was to illuminate ecological determinants of variation in the social organization and structure of solitary species, which exhibit yet unexplained diversity in these variables. I studied two nocturnal solitary primates (*Microcebus berthae*, *M. murinus*), which differ in two characteristics of female associations: (1) ranging patterns and (2) sleeping associations. Beginning in August 2002, I monitored individuals of sympatric populations in a 25ha study area in Kirindy Forest/CFPF (Madagascar) and (re-) captured and marked a total of 177 *M. berthae* and 291 *M. murinus*. Between March 2004 and November 2007, I recorded data on spatial patterns and behaviour of 18 *M. berthae* and 17 *M. murinus* females by means of direct observation and radio-tracking in more than 1700 hours. I quantified intra-specific differences in diet based on feeding behaviour, analysis of faecal samples, and stable nitrogen and carbon isotope analysis of hair and potential food sources. Relative resource availability was assessed by year-round phenological monitoring of trees and standardized capture of arthropods from different guilds. The main results supported basic predictions of the SEM and revealed that resource characteristics and the resulting competitive regimes did indeed relate to differences in female spatial-temporal patterns and social structure of solitary foragers. The major food sources of *M. berthae* occurred in small dispersed patches, leading to strong within-group scramble competition and over-dispersed females with a low potential for female associations. In contrast, *M. murinus* also used patchily distributed, high quality (large) resources. Within and between-group contest competition over these monopolizable resources allowed females of this species to cluster in space. When food distribution was experimentally manipulated, females of both species flexibly adjusted their spatial patterns. Moreover, food availability was identified as a major determinant of female spatial-temporal patterns, which affected these mouse lemur species unequally, mainly due to pronounced differences in feeding niche width and energy strategies to survive the

lean season. In contrast to opportunistically feeding and seasonally inactive *M. murinus*, the more specialized *M. berthae* females experienced seasonally low food density, which enhanced female spatial avoidance. In addition, inter-specific competition between these ecologically similar mouse lemurs added substantial variation to the relative availability of resources for *M. berthae* and *M. murinus* females, respectively. Nevertheless, spatial competitive coexistence is possible due to life history trade-offs that result in species aggregation and a relative increase in the strength of intra-specific over inter-specific competition. In conclusion, the present study successfully applied existing socio-ecological theory to solitary foragers, tested a recent model on competitive coexistence and contributed a comparative data set to our understanding of inter-specific behavioural and ecological variation in solitary foragers.

ZUSAMMENFASSUNG

Ein grundlegendes Modell zur Evolution von Sozialsystemen ist das sozioökologische Modell (SEM), welches Vorhersagen über kausale Zusammenhänge zwischen der Variabilität in der Verteilung von Ressourcen, des resultierenden Konkurrenz-Regimes und der sozialen Organisation und Sozialstruktur macht. Die Diversität der Gesellschaftsformen von Säugetieren wurde bisher vorwiegend an gruppenlebenden Arten untersucht, wohingegen Variabilität in Sozialsystemen solitärer Arten jedoch noch wenig verstanden ist. Das generelle Ziel der vorliegenden Arbeit war es, Vorhersagen des SEM zur Evolution von Sozialsystemen vergleichend an zwei nah verwandten sympatrischen solitären Mausmaki-Arten (*Microcebus berthae* und *M. murinus*) zu überprüfen. Beide Arten weisen große Ähnlichkeiten in grundlegenden *life history*- und sozialen Merkmalen auf, unterscheiden sich aber deutlich in den räumlichen und zeitlichen Verteilungsmustern der Weibchen. Seit Beginn dieser Langzeitstudie im August 2002 habe ich in einem Untersuchungsgebiet von 25ha im Forêt de Kirindy/CFPF (West-Madagaskar) 177 *M. berthae* und 291 *M. murinus* sympatrischer Populationen regelmäßig gefangen, vermessen und markiert. In 22 Monaten Feldaufenthalt zwischen März 2004 und November 2007 wurden in über 1700h Fokustierbeobachtung und Radiotelemetrie Daten zur Raumnutzung und zum Verhalten für 18 *M. berthae* und 17 *M. murinus* Weibchen gesammelt. Die Nahrungsökologie beider Arten habe ich mit Hilfe direkten Beobachtungen, Kotanalysen und der Analyse stabiler Stickstoff- und Kohlenstoff-Isotopen untersucht. Ganzjährige regelmäßige phänologische Aufnahmen und standardisierte Fänge von Arthropoden erlaubten eine Abschätzung der relativen Ressourcenverfügbarkeit im Habitat. Die wesentlichen Ergebnisse dieser Studie entsprechen den Vorhersagen des SEM. Sie zeigen, dass die Ressourcenverteilung und daraus resultierende Konkurrenz-Regimes Unterschiede in der räumlichen und zeitlichen Verteilung und der Sozialstruktur von solitären Arten erklären können. Dies konnte zusätzlich durch ein Feldexperiment bestätigt werden, in welchem Weibchen adaptiv auf manipulierte Nahrungsverteilung reagierten. Die Hauptnahrungsquellen von *M. berthae* sind klein und dispers verteilt, was starke *Ausbeutungskonkurrenz* begünstigt und zur räumlichen Vermeidung von Weibchen führt. Im Gegensatz dazu nutzen *M. murinus* vorwiegend geklumpt verteilte, höherwertige (große) Ressourcen.

Diese Ressourcen sind monopolisierbar und begünstigen *Interferenzkonkurrenz* zwischen oder innerhalb von Gruppen, was räumliche Assoziationen von Weibchen ermöglicht. Zusätzlich hat auch die Ressourcenverfügbarkeit einen wichtigen Einfluss auf die räumliche und zeitliche Verteilung von Weibchen. Wegen großer Unterschiede in der Nahrungsnischenbreite und in der Art von Strategien, mit denen sie Zeiten von Nahrungsknappheit überstehen, sind Weibchen beider Arten davon unterschiedlich stark beeinflusst. Während *M. murinus* Weibchen saisonal inaktiv sind und vorhandene Nahrung opportunistisch nutzen, sind spezialisierte *M. berthae* Weibchen saisonaler Nahrungsknappheit stärker ausgesetzt, was die räumliche Dispersion von Weibchen weiter erhöht. Da beide Arten große Ähnlichkeiten in ihrer Nahrungsökologie und ihren Habitatansprüchen haben, besteht überdies zwischen-artliche Konkurrenz, was sich negativ auf die Nahrungsverfügbarkeit für kleinere *M. berthae* Weibchen auswirkt und kleinräumig zu gegenseitigem Ausschluss beider Arten führt. Lokale und regionale Koexistenz wird jedoch durch *life-history trade-offs* stabilisiert, die ein kleinräumiges Muster von Aggregationen der einen oder anderen Art bedingen. Zusammenfassend wurden mit dieser Arbeit vergleichende und experimentelle Daten über solitäre Primaten erhoben, die es ermöglichten existierende sozioökologische Theorien auf solitäre Arten zu übertragen und ein neueres Modell zur Koexistenz ökologisch ähnlicher Arten empirisch zu testen.

Bibliography

Adams ES (2001) Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32: 277-303

Alexander RD (1974) The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325-383

Alonso D, Etienne RS, McKane AJ (2006) The merits of neutral theory. *Trends in Ecology and Evolution* 21: 451-457

Altmann J (1974) Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267

Altmann J (1990) Primate males go where the females are. *Animal Behaviour* 39: 193-195

Amarasekare P (2000) The geometry of coexistence. *Biological Journal of the Linnean Society* 71: 1-31

Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6: 1109-1122

Amarasekare P, Hoopes MF, Mouquet N, Holyoak M (2004a) Mechanisms of coexistence in competitive metacommunities. *American Naturalist* 164: 310-326

Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69: 395-406

Anderson DJ (1982) The home range: a new nonparametric estimation technique. *Ecology* 63: 103-112

Araújo M, Bolnick DI, Machado G, Giaretta AA, dos Reis SF (2007) Using δ13C stable isotopes to quantify individual-level diet variation. *Oecologia* 152: 643-654

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 DA (1995) The comparative pollination and floral biology of baobabs (*Adansonia - Bombacaceae*). *Annals of the Missouri Botanical Garden* 82: 322-348

Bearder SK (1987) Loris, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts, BB, Cheney, DL, Seyfarth, RM, Wrangham, RW, and Struhsaker, TT (eds) *Primate societies*. The University of Chicago Press, Chicago, pp 11-24

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007-1012

Bekoff M, Daniels TJ, Gittleman JL (1984) Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics* 15: 191-232

Bell G (2000) The distribution of abundance in neutral communities. *American Naturalist* 155: 606-617

Bell G (2001) Neutral macroecology. *Science* 293: 2413-2418

Berthold P (2000) *Bird migration*. Oxford University Press, Oxford

Boinski S and Garber PA (2000) *On the move. How and why animals travel in groups*. University of Chicago Press, Chicago

Bolker BM, Pacala SW (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist* 153: 575-602

Bollen A, Donati G, Fietz J, Schwab D, Ramanamanjato J-B, Randrihasipara L, Van Elsacker L, and Ganzhorn JU (2005) An intersite comparison on fruit characteristics in Madagascar: Evidence for selection pressure through abiotic constrains rather than through co-evolution. In: Dew, JL and Boubli, JP (eds) *Tropical fruits and frugivores: the search for strong interactors*. Springer, pp 92-118

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology* 68: 203-220

Brockman DK and van Schaik CP (2005) *Seasonality in primates*. Cambridge University Press, Cambridge

Caro TM (1989) Determinants of asociality in felids. In: Standen, V and Foley, RA (eds) *Comparative socioecology. The behavioural ecology of humans and other mammals*. Blackwell, Oxford, pp 41-74

Caut S, Angulo E, Courchamp F (2008) Discrimination factors (δ^{15}N and δ^{13}C) in an omnivorous consumer: effect of diet isotopic ratio. *Functional Ecology* 22: 255-263

Cerling TE, Hart JA, Hart TB (2004) Stable isotope ecology in the Ituri Forest. *Oecologia* 138: 5-12

Charles-Dominique P (1974) Aggression and territoriality in nocturnal prosimians. In: Holloway, RL (ed) *Primate aggression, territoriality and xenophobia. A comparative perspective*. Academic Press, New York, pp 31-48

Charles-Dominique P (1978) Solitary and gregarious prosimians: evolution of social structures in primates. In: Chivers, DJ and Joysey, KA (eds) *Recent advances in primatology: Evolution*. Academic Press, London, pp 139-149

Charles-Dominique P, Martin RD (1970) Evolution of lorises and lemurs. *Nature* 227: 257-260

Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predators and competition: a review and synthesis. *Ecology Letters* 5: 302-315

Chase JM and Leibold MA (2003) *Ecological niches. Linking classical and contemporary approaches*. University of Chicago Press, Chicago

Chave J (2004) Neutral theory and community ecology. *Ecology Letters* 7: 241-253

Chesson P (2000a) General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58: 211-237

Chesson P (2000b) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366

Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35: 445-453

Clegg SM, Kelly JF, Kimura M, Smith TB (2003) Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology* 12: 819-830

Clutton-Brock TH (1974) Primate social organization and ecology. *Nature* 250: 539-542

Clutton-Brock TH (1989) Mammalian mating systems. *Proceedings of the Royal Society of London B* 236: 339-372

Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild mammals. *Nature* 337: 260-262

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. *Journal of Zoology London* 183: 1-39

Clutton-Brock TH, Harvey PH, Rudder B (1977) Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature* 269: 797-800

Clutton-Brock TH, Parker GA (1992) Potential reproductive rates and the operational sex ratio. *Quarterly Review of Biology* 67: 437-457

Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* 19: 334-343

Corbin GD, Schmid J (1995) Insect secretions determine habitat use patterns by a female lesser mouse lemur (*Microcebus murinus*). *American Journal of Primatology* 37: 317-324

Crawford K, Mcdonald RA, Bearhop S (2008) Application of stable isotope techniques to the ecology of mammals. *Mammalian Reviews* 38: 87-107

Crook JH (1964) The evolution of social organization and visual communication in the weaver birds (Ploceinae). *Behaviour Suppl.* 10: 1-178

Crook JH, Gartlan JS (1966) Evolution of primate societies. *Nature* 210: 1200-1203

Dalerum F (2007) Phylogenetic reconstruction of carnivore social organizations. *Journal of Zoology* 273: 90-97

Dalerum F, Bennett NC, Clutton-Brock TH (2007) Longitudinal differences in ^{15}N between mothers and offspring during and after weaning in a small cooperative mammal, the meerkat (*Suricata suricatta*). *Rapid Communications in Mass Spectrometry* 21: 1889-1892

Dammhahn M, Kappeler PM (2005) Social system of *Microcebus berthae*, the world's smallest primate. *International Journal of Primatology* 26: 407-435

Dammhahn M, Kappeler PM (in press a) Small-scale coexistence of two mouse lemur species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive environment. *Oecologia*

Dammhahn M, Kappeler PM (in press b) Comparative feeding ecology of sympatric mouse lemurs (*Microcebus berthae, M. murinus*). *International Journal of Primatology*

Dammhahn M, Kappeler PM (in press c) Seasonality and energy strategies in co-existing mouse lemurs (*Microcebus berthae* and *M. murinus*). In: Masters J, Gamba M, Génin F (eds) Leaping ahead: Advances in prosimian biology. *Developments in Primatology series*

Darimont CT, Reimchen TE (2002) Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80: 1638-1642

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. *Nature* 429: 825-826

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495-506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45: 341-351

Bibliography

Denlinger DL (1980) Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica* 12: 100-106

Dew JL, Wright PC (1998) Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30: 425-437

Diamond JM (1975) Assembly of species communities. In: Cody, ML and Diamond, JM (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge, pp 342-444

Eberle M, Kappeler PM (2002) Mouse lemurs in space and time: a test of the socioecological model. *Behavioural Ecology and Sociobiology* 51: 131-139

Eberle M, Kappeler PM (2004) Selected polyandry: Female choice and inter-sexual conflict in a small nocturnal solitary primate (*Microcebus murinus*). *Behavioural Ecology and Sociobiology* 57: 91-100

Eberle M, Kappeler PM (2006) Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioural Ecology and Sociobiology* 60: 582-588

Eberle M, Kappeler PM (2007) Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. *American Journal of Primatology* 69: 1-5

Eggers T, Jones TH (2000) You are what you eat...or are you? *Trends in Ecology and Evolution* 15: 265-266

Eisenberg JF (1966) The social organization of mammals. *Handbuch der Zoologie* 10: 1-92

Eisenberg JF, Muckenhirn NA, Rudran R (1972) The relation between ecology and social structure in primates. *Science* 176: 863-874

Elton C (1946) Competition and the structure of ecological communities. *Journal of Animal Ecology* 15: 54-68

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223

Fietz J (1999) Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology* 105: 259-272

Fietz J, Ganzhorn JU (1999) Feeding ecology oft the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia* 121: 157-164

Focken U (2001) Stable isotopes in animal ecology: the effect or ration size on the trophic shift of C and N isotopes between feed and carcass. *Isotopes in Environmental and Health Studies* 37: 199-211

Focken U, Becker K (1998) Metabolic fractionation of stable carbon isotopes: implications of different proximate compositions for studies of the aquatic food webs using $\delta^{13}C$ data. *Oecologia* 115: 337-343

Fredsted T, Pertoldi C, Olesen JM, Eberle M, Kappeler PM (2004) Microgeographic heterogeneity in spatial distribution and mtDNA variability of gray mouse lemurs (*Microcebus murinus*, Primates: Cheirogaleidae). *Behavioural Ecology and Sociobiology* 56: 393-403

Fredsted T, Pertoldi C, Schierup MH, Kappeler PM (2005) Microsatellite analyses reveal fine-scale genetic structure in grey mouse lemurs (*Microcebus murinus*). *Molecular Ecology* 14: 2363-2372

Fry B (2006) *Stable isotope ecology*. Springer, Berlin

Ganihar SR (1997) Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences* 22: 219-224

Ganzhorn JU (1987) A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology* 12: 205-215

Ganzhorn JU (1988) Food partitioning among Malagasy primates. *Oecologia* 75: 436-450

Ganzhorn JU (1989) Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia* 79: 279-286

Ganzhorn JU (1994) Lemurs as indicators for habitat change. In: Thierry, B, Anderson, JR, Roeder, JJ, and Herrenschmidt, N (eds) *Ecology and evolution*. Universite Louis Pasteur, Strasbourg, pp 51-56

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76: 2084-2096

Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner D (1999a) Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology* 13: 794-804

Ganzhorn JU, Kappeler PM (1996) Lemurs of the Kirindy forest. *Primate Report* 46: 257-274

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat characteristics and lemur species richness in Madagascar. *Biotropica* 29: 331-343

Ganzhorn JU, 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 JU, Wright PC, and Ratsimbazafy J (1999b) Primate communities: Madagascar. In: Fleagle, JG, Janson, CH, and Reed, KE (eds) *Primate communities*. Cambridge University Press, Cambridge, pp 75-89

Garber PA (1987) Foraging strategies among living primates. *Annual Review in Anthropology* 16: 339-364

Gaye-Siessegger J, Focken U, Abel H, Becker K (2003) Feeding level and diet quality influence trophic shift of C and N isotopes in Nile Tilapia (*Oreochromis niloticus* (L.)). *Isotopes in Environmental and Health Studies* 39: 125-134

Gaye-Siessegger J, Focken U, Muetzel S, Abel H, Becker K (2004) Feeding level and individual metabilic rate affect $\delta^{13}C$ and $\delta^{15}N$ values in carp: implications for food web studies. *Oecologia* 138: 175-183

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* 68: 935-966

Génin F (2003) Female dominance in competition for gum trees in the grey mouse lemur *Microcebus murinus*. *Revue Écologie (Terre Vie)* 58: 397-410

Génin F (2008) Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. *International Journal of Primatology* 29: 303-321

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioural Ecology and Sociobiology* 10: 57-63

Goodman SM, O'Connor S, and Langrand O (1993) A review of predation on lemurs: implications for the evolution of social behaviour in small mammals. In: Kappeler, PM and Ganzhorn, JU (eds) *Lemur social systems and their ecological basis*. Plenum Press, New York, pp 51-66

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621

Gotelli N J, Entsminger G L (2006) EcoSim: Null models software for ecology. Version 7, Acquired Intelligence Inc. & Kesey-Bear, Jericho

Graves GR, Rahbek C (2005) Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences* 102: 7871-7876

Groves CP (2000) The genus *Cheirogaleus*: unrecognized biodiversity in dwarf lemurs. *International Journal of Primatology* 21: 943-962

Groves CP (2001) *Primate taxonomy*. Smithsonian Institutional Press, Washington

Gursky S (2000a) Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology* 21: 477-495

Gursky S (2000b) Sociality in the spectral tarsier, *Tarsius spectrum*. *American Journal of Primatology* 51: 89-101

Gursky S (2005) Associations between adult spectral tarsiers. *American Journal of Physical Anthropology* 128: 74-83

Gursky S (2007) *The spectral tarsier*. Pearson Prentice Hall, New Jersey

Hapke A, Fietz J, Nash SD, Rakotondravony D, Rakotosamimanana B, Ramanamanjato J-B, Randria GFN, Zischler H (2005) Biogeography of dwarf lemurs: genetic evidence for unexpected patterns in southeastern Madagascar. *International Journal of Primatology* 26: 873-901

Harcourt C, Nash LT (1986) Social organization of galagos in Kenyan coastal forests: I. *Galago zanzibaricus*. *American Journal of Primatology* 10: 339-355

Harvey PH, Clutton-Brock TH (1981) Primate home-range size and metabolic needs. *Behavioural Ecology and Sociobiology* 8: 151-155

Hemingway CA and Bynum N (2005) The influence of seasonality on primate diet and ranging. In: Brockman, DK and van Schaik, CP (eds) *Seasonality in primates*. Cambridge University Press, Cambridge, pp 57-104

Herrera LG, Gutierrez E, Hobson KA, Altube B, Diaz WG, Sanches-Cordero V (2002) Sources of assimilated protein in five species of New World frugivorous bats. *Oecologia* 133: 280-287

Hilgartner R (2006) Living apart together: Pair-living in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). 2006. Dissertation, University of Ulm

Hladik A (1980) The dry forest of the west coast of Madagascar climate, phenology, and food availability for prosimians. In: Charles-Dominique, P, Cooper, HM, Hladik, A, Hladik, CM, Pages, E, Pariente, GF, Petter-Rousseaux, A, and Schilling, A (eds) *Nocturnal Malagasy primates. Ecology, physiology, and behavior*. Academic Press, New York, pp 3-40

Hladik CM (1975) Ecology, diet and social patterning in old and new world primates. In: Tuttle, RH (eds) *Socioecology and psychology of primates*. World Anthropology, Mouton, pp 3-35

Hladik CM, Charles-Dominique P, and Petter JJ (1980) Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique, P, Cooper, HM, Hladik, A, Hladik, CM, Pages, E, Pariente, GF, Petter-Rousseaux, A, and Schilling, A (eds) *Nocturnal Malagasy primates: Ecology, physiology, and behavior*. Academic Press, New York, pp 41-73

Hobson KA (1999) Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. *The Condor* 101: 799-805

Hobson KA, Alisaukas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *The Condor* 95: 388-394

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *The Condor* 94: 189-197

Hölldobler B and Wilson EO (1990) *The ants*. Belknap Press, Cambridge Massachusetts

Holt RD (1977) Apparent competition and the structure of prey communities. *Theoretical Population Biology* 12: 197-229

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124: 377-406

Holt RD, Grover J, Tilman D (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144: 741-771

Hooge P N, Eichenlaub W, Solomon E K (1999) The animal movement extension to Arc View Version 1.1. Alaska Science Office, U.S. Geological Survey, Anchorage

Hubbell SP (2001) *The unified neutral theory of species abundance and diversity*. Princeton University Press, Princeton

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, Loo de Lao S (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283: 554-557

Huston MA (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393-401

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposium. *Quantitative Biology* 22: 415-427

Ims RA (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology* 56: 585-596

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioural Ecology* 2: 143-155

Isbell LA, Young TP (2002) Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* 139: 177-202

Janson CH (2000) Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology* 9: 73-86

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: methods. *Behaviour* 105: 165-186

Jarman PJ (1974) The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267

Johnson DDP, Kays R, Blackwell PG, Macdonald DW (2002) Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution* 17: 563-570

Jonsson P, Hartikainen T, Koskela E, Mappes T (2002) Determinants of reproductive success in voles: space use in relation to food and litter size manipulations. *Evolutionary Ecology* 16: 455-467

Kappeler PM (1997a) Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biology Reviews* 72: 111-151

Kappeler PM (1997b) Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behavioural Ecology and Sociobiology* 45: 115-127

Kappeler PM (1998) Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology* 46: 7-33

Kappeler PM and Rasoloarison RM (2003) *Microcebus*, Mouse lemurs, Tsidy. In: Goodman, SM and Benstead, JP (eds) *The natural history of Madagascar*. University of Chicago Press, Chicago, pp 1310-1315

Kappeler PM, Rasoloarison RM, Razafimanantsoa L, Walter L, Roos C (2005) Morphology, behaviour and molecular evolution of giant mouse lemurs (*Mirza* spp.) GRAY, 1870, with description of a new species. *Primate Report* 71: 3-26

Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. *International Journal of Primatology* 23: 707-740

Kay RF, Madden RH, van Schaik CP, Higdon D (1997) Primate species richness is determined by plant productivity: implications for conservation. *Proceedings of the National Academy of Sciences* 94: 13023-13027

Kempster B, Zanette L, Longstaffe FJ, MacDougall-Shackleton SA, Wingfield JC, Clinchy M (2007) Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. *Oecologia* 151: 365-371

Kneitel JM, Chase JM (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7: 69-80

Koenig A (2002) Competition for resources and its behavioural consequences among female primates. *International Journal of Primatology* 23: 759-783

Koenig A and Borries C (2006) The predictive power of socioecological models: a reconsideration of resource characteristics, agonism, and dominance hierarchies. In: Hohmann, G, Robbins, MM, and Boesch, C (eds) *Feeding ecology in apes and other primates: Ecological, physical and behavioral aspects*. Cambridge University Press, Cambridge, pp 263-284

Krebs CJ (1998) *Ecological methodology*. Addison-Welsey Educational Publishers, Menlo Park

Kunz TH (1988) Methods of assessing the availability of prey to insectivorous bats. In: Kunz, TH (ed) *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington D.C., pp 191-210

Lacey EA and Sherman PW (2007) The ecology of sociality in rodents. In: Wolff, JO and Sherman, PW (eds) *Rodent societies: An ecological and evolutionary perspective*. University of Chicago Press, Chicago, pp 243-254

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 (2008) Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *International Journal of Primatology* 29: 117-134

Lahann P, Schmid J, Ganzhorn JU (2006) Geographic variation in populations of *Microcebus murinus* in Madagascar: Resource seasonality or Bergmann's rule? *International Journal of Primatology* 27: 983-999

Layman CA, Arrington DA, Montana CG, Post DM (2007a) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88: 42-48

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007b) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* 10: 937-944

Leibold MA, McPeek MA (2006) Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87: 1399-1410

Lidén K, Angerbjörn A (1999) Dietary change and stable isotopes: a model of growth and dormancy in cave bears. *Proceedings of the Royal Society of London B* 266: 1779-1783

Loreau M, Mouquet N (1999) Immigration and the maintenance of local species diversity. *American Naturalist* 154: 427-440

Loudon JE, Sponheimer M, Sauther ML, Cuozzo FP (2007) Intraspecific variation in hair δ^{13}C and δ^{15}N values of Ring-tailed lemurs (*Lemur catta*) with known individual histories, behavior, and feeding ecology. *American Journal of Physical Anthropology* 133: 978-985

Louis Jr. EE, Coles MS, Andriantompohavana R, Sommer JA, Engberg SE, Zaonarivelo JR, Mayor MI, Brenneman RA (2006) Revision of the mouse lemurs (*Microcebus*) of eastern Madagascar. *International Journal of Primatology* 27: 347-389

Lutermann H, Schmelting B, Radespiel U, Ehresmann P, Zimmermann E (2006) The role of survival for the evolution of female philopatry in a solitary forager, the grey mouse lemur (*Microcebus murinus*). *Proceedings of the Royal Society of London B* 273: 2527-2533

MacArthur RH (1972) *Geographical ecology.* Princeton University Press, Princeton

MacArthur RH, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377-385

Macdonald DW (1983) The ecology of carnivore social behaviour. *Nature* 301: 379-384

Macko SA, Engel MH, Andrusevich V, Lubec G, O'Connell TC, Hedges REM (1999) Documenting the diet in ancient human populations through stable isotope analysis of hair. *Philosophical Transactions of the Royal Society of London B* 354: 65-76

Marshall AJ, Wrangham RW (2007) Evolutionary consequences of fallback foods. *International Journal of Primatology* 28: 1219-1235

Marshall JD, Brooks R, and Lajtha K (2007) Sources of variation in the stable isotopic composition of plants. In: Michener, R and Lajtha, K (eds) *Stable isotopes in ecology and environmental science.* Blackwell Publishing, Malden, pp 22-60

Martin A and Bateson P (1993) *Measuring behaviour. An introductory guide.* Cambridge University Press, Cambridge

Martin JK, Martin AA (2007) Resource distribution influences mating system in the bobuck (*Trichosurus cunnighami*: Marsupialia). *Oecologia* 154: 227-236

Martin RD (1972a) A preliminary field-study of the lesser mouse lemur (*Microcebus murinus* J.F. Miller, 1977). In: Charles-Dominique, P and Martin, RD (eds) *Behaviour and ecology of nocturnal prosimians. Field studies in Gabon and Madagascar.* Paul Parey, Berlin, pp 43-85

Martin RD (1972b) Adaptive radiation and behaviour of the Malagasy lemurs. *Transactions of the Royal Society of London B* 264: 295-352

Martin RD (1973) A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J.F. Miller 1777). In: Michael, RP and Crook, JH (eds) *Comparative ecology and behaviour of primates.* Academic Press, London, pp 1-68

Matthews B, Mazumder A (2004) A critical evaluation of intrapopulation variation of δ^{13}C and isotopic evidence of individual specialization. *Oecologia* 140: 361-371

Mauffrey J-F, Catzeflis F (2003) Ecological and isotopic discrimination of syntopic rodents in a Neotropical forest of French Guiana. *Journal of Tropical Ecology* 19: 209-214

Bibliography

McCracken GF and Wilkinson GS (2000) Bat mating systems. In: Crichton, EG and Krutzsch, PH (eds) *Reproductive biology of bats*. Academic Press, London, pp 321-362

McCutchan Jr JH, Lewis Jr WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102: 378-390

McGill BJ (2003) A test of the unified neutral theory of biodiversity. *Nature* 422: 881-885

McGill BJ, Maurer BA, Weiser MD (2006) Empirical evaluation of neutral theory. *Ecology* 87: 1411-1423

Mcilwee AP, Johnson CN (1998) The contribution of fungus to the diets of three mycophagous marsupials in *Eucalyptus* forests, revealed by stable isotope analysis. *Functional Ecology* 12: 223-231

Medina E, Minchin P (1980) Stratification of $\delta^{13}C$ values of leaves in Amazonian rain forests. *Oecologia* 45: 377-378

Mendes S, Newton J, Reid RJ, Zuur AF, Pierce GJ (2007) Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* 151: 605-615

Mirón LL, Herrera LG, Ramírez N, Hobson KA (2006) Effect of diet quality on carbon and nitrogen turnover and isotopic discrimination in blood of a New World nectarivorous bat. *The Journal of Experimental Biology* 209: 541-548

Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, Rasoloarison RM, Ganzhorn JU, Rajaobelina S, Tattersall I, and Meyers DM (2006) *Lemurs of Madagascar*. Conservation International, Washington

Mohr CO (1947) Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37: 223-249

Moll RJ, Millspaugh JJ, Beringer J, Sartwell J, He Z (2007) A new "view" of ecology and conservation through animal-borne video systems. *Trends in Ecology and Evolution* 22: 660-668

Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* 159: 420-426

Mouquet N, Loreau M (2003) Community patterns in source-sink meta-communities. *American Naturalist* 162: 544-557

Müller AE, Thalmann U (2000) Origin and evolution of primate social organization: a reconstruction. *Biology Reviews* 75: 405-435

Müller EF, Nieschalk U, Meier B (1985) Thermoregulation in slender loris (*Loris tardigradus*). *Folia primatologica* 44: 216-226

Murrell DJ, Law R (2003) Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters* 6: 48-59

Mzilikazi N, Masters J, Lowe JJ (2006) Lack of torpor in free-ranging southern lesser galagos, *Galago moholi*: ecological and physiological considerations. *Folia primatologica* 77: 465-476

Nadjafzadeh MN, Heymann EW (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 LT (1986) Dietary, behavioral, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology* 29: 113-137

Nekaris KAI, Rasmussen DT (2003) Diet and feeding behavior of Mysore slender lorises. *International Journal of Primatology* 24: 33-46

Nicholson AJ (1954) On outline of the dynamics of animal populations. *Australian Journal of Zoology* 2: 9-65

Norsica I, Borgognini-Tarli SM (2008) Ranging behavior and possible correlates of pair-living in southeastern Avahis (Madagascar). *International Journal of Primatology* 29: 153-171

Norsica I, Carrai V, Borgognini-Tarli SM (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

Oliveri G, Zimmermann E, Randrianambinina B, Rasoloharijaona S, Rakotondravony D, Gutschanski K, Radespiel U (2007) The ever-increasing diversity in mouse lemurs: Three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution* 43: 309-327

Ostfeld RS (1985) Limiting resources and territoriality in microtine rodents. *American Naturalist* 126: 1-15

Ostfeld RS (1986) Territoriality and mating system of California voles. *Journal of Animal Ecology* 55: 691-706

Ostfeld RS (1990) The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* 5: 411-415

Overdorff DJ (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 CMP and Bell JR (2003) Collecting arthropods and arthropod remains for primate studies. In: Setchell, JM and Curtis, DJ (eds) *Field and laboratory methods in primatology*. Cambridge University Press, Cambridge, pp 214-227

Pacala SW, Rees M (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist* 152: 729-737

Pacala SW, Roughgarden J (1982) Spatial heterogeneity and interspecific competition. *Theoretical Population Biology* 21: 92-113

Pagès E (1980) Ethoecology of *Microcebus coquereli* during the dry season. In: Charles-Dominique, P, Cooper, HM, Hladik, A, Hladik, CM, Pages, E, Pariente, GF, Petter-Rousseaux, A, Petter, JJ, and Schilling, A (eds) *Nocturnal Malagasy primates: Ecology, physiology and behavior*. Academic Press, New York, pp 97-116

Perret M (1992) Environmental and social determinants of sexual function in the male lesser mouse lemur (*Microcebus murinus*). *Folia primatologica* 59: 1-25

Petit E, Mayer F (2000) A population genetics analysis of migration: the case of the noctule bat (*Nyctalus noctula*). *Molecular Ecology* 9: 683-690

Petter JJ (1978) Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variation in food production. In: Chivers, DJ and Herbert, J (eds) *Recent advances in primatology. Volume 1, Behaviour*. Academic Press, London, pp 211-223

Phillips DL (2001) Mixing models in analyses of diet using multiple stable isotopes: a critique. *Oecologia* 127: 166-170

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia* 127: 171-179

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136: 261-269

Pianka ER (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53-74

Pianka ER (1994) *Evolutionary ecology*. Harper-Collins College Publishers, New York

Pimley E, Bearder SK, Dixon AF (2005) Social organization of the Milne-Edward's Potto. *American Journal of Primatology* 66: 317-330

Post DM, Pace ML, Hairstone Jr NG (2000) Ecosystem size determines food-chain length in lakes. *Nature* 405: 1047-1049

Radespiel U (2006) Ecological diversity and seasonal adaptations of mouse lemurs (*Microcebus* spp.). In: Gould, L and Sauther, ML (eds) *Lemur ecology and adaptation*. Springer, New York, pp 211-233

Radespiel U, Cepok S, Zietemann V, Zimmermann E (1998) Sex-specific usage patterns of sleeping sites in grey mouse lemurs (*Microcebus murinus*) in northwestern Madagascar. *American Journal of Primatology* 46: 77-84

Radespiel U, Lutermann H, Schmelting B, Bruford MW, Zimmermann E (2003) Patterns and dynamics of sex-biased dispersal in a nocturnal primate, the grey mouse lemur, *Microcebus murinus*. *Animal Behaviour* 64: 1-11

Radespiel U, Reimann WE, Rahelinirina M, Zimmermann E (2006) Feeding ecology of sympatric mouse lemur species in northwestern Madagascar. *International Journal of Primatology* 27: 311-321

Radespiel U, Sarikaya Z, Zimmermann E (2001) Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the gray mouse lemur (*Microcebus murinus*). *Behavioural Ecology and Sociobiology* 50: 493-502

Rakotonirina G (1996) Composition and structure of the dry forest on sandy soils near Morondava. In: Ganzhorn, JU and Sorg, JP (eds) *Ecology and economy of a tropical dry forest in Madagascar*. Goltze, Göttingen, pp 81-87

Ramanamanjato J-B, Ganzhorn JU (2001) Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation* 4: 175-183

Rasoazanabary E (2004) A preliminary study of mouse lemurs in Beza Mahafaly Special Reserve, southwestern Madagascar. *Lemur News* 9: 4-7

Rasoazanabary E (2006) Male and female activity patterns in *Microcebus murinus* during the dry season at Kirindy forest, western Madagascar. *International Journal of Primatology* 27: 437-463

Rasoloarison RM, Goodman SM, Ganzhorn JU (2000) Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology* 21: 963-1019

Rasoloarison RM, Rasoloandrasana BPN, Ganzhorn JU, Goodman SM (1995) Predation on vertebrates in the Kirindy Forest, western Madagascar. *Ecotropica* 1: 59-65

Reimann WE (2002) Koexistenz und Nahrungsökologie von Weibchen des Grauen und Goldbraunen Mausmakis (*Microcebus murinus* und *M. ravelobensis*) in Nordwest-Madagaskar. Dissertation, University of Vetenary Medicine Hannover

Reiss M (1988) Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology and Evolution* 3: 85-86

Rendigs A, Radespiel U, Wrogemann D, Zimmermann E (2003) Relationship between microhabitat structure and distribution of mouse lemurs (*Microcebus spp.*) in northwest Madagascar. *International Journal of Primatology* 24: 47-64

Rensing S (1999) Immobilization and anaesthesia of nonhuman primates. *Primate Report* 55: 33-38

Richards LA, Windsor DM (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

Ricklefs RE and Schluter D (1993) *Species diversity in ecological communities: historical and geographical perspectives*. Chicago University Press, Chicago

Robbins CT, Felicetti LA, Sponheimer M (2005) The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* 144: 534-540

Roberts RL, Williams JR, Wang AK, Carter CS (1998) Cooperative breeding and monogamy in prairie voles: influence of the sire and geographic variation. *Animal Behaviour* 55: 1131-1140

Rooney SM, Wolfe A, Hayden TJ (1998) Autocorrelational data in telemetry studies: time to independence and the problem of behavioural effects. *Mammalian Reviews* 27: 89-98

Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge

Schmid J (1996) Oxygen consumption and torpor in mouse lemurs (*Microcebus murinus* and *M. myoxinus*): Preliminary results of a study in western Madagascar. In: Geiser, F, Hulbert, AJ, and Nicol, SC (eds) *Adaptations to the cold: tenth international hibernation symposium*. University of New England, Armidale, pp 47-54

Schmid J (1998) Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in Madagascar: insulation capacities and energetic consequences. *International Journal of Primatology* 19: 797-809

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 PM (1994) Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia primatologica* 63: 162-170

Schmid J, Kappeler PM (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 and Kappeler PM (2005) Physiological adaptations to seasonality in nocturnal primates. In: Brockman, DK and van Schaik, CP (eds) *Seasonality in primates. Studies of living and extinct human and non-human primates*. Cambridge University Press, Cambridge, pp 129-155

Schmid J, Ruf T, Heldmaier G (2000) Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. *Journal of Comparative Physiology B* 170: 59-68

Schmid J, Speakman JR (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

Schoeninger MJ, Iwaniec UT, Glander KE (1997) Stable isotope ratios indicate diet and habitat use in new world monkeys. *American Journal of Physical Anthropology* 103: 69-83

Schoeninger MJ, Iwaniec UT, Nash LT (1998) Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Oecologia* 113: 222-230

Schoeninger MJ, Moore J, Sept JM (1999) Subsistence strategies of two "Savanna" Chimpanzee populations: the stable isotope evidence. *American Journal of Primatology* 49: 297-314

Schradin C (2006) When to live alone and when to live in groups: ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belgian Journal of Zoology* 135: 75-80

Schradin C, Pillay N (2005) Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* 86: 99-107

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, Kappeler PM (2003) So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. *Animal Behaviour* 65: 331-343

Schülke O, Ostner J (2005) Big times for dwarfs: Social organization, sexual selection, and cooperation in the Cheirogaleidae. *Evolutionary Anthropology* 14: 170-185

Schülke O, Ostner J (2007) Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. *Acta Ethologica* 10: 13-21

Schwab D (2000) A preliminary study of spatial distribution and mating system of the pygmy mouse lemur (*Microcebus cf. myoxinus*). *American Journal of Primatology* 51: 41-60

Schwab D, Ganzhorn JU (2004) Distribution, population structure and habitat use of *Microcebus berthae* compared to those of other sympatric Cheirogaleids. *International Journal of Primatology* 25: 307-330

Schwagmeyer PL (1988) Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *American Naturalist* 131: 885-892

Schwertl M, Auerswald K, Schnyder H (2003) Reconstruction of the isotopic history of animal diets by hair segmental analysis. *Rapid Communications in Mass Spectrometry* 17: 1312-1318

Sfenthourakis S, Tzanatos E, Giokas S (2005) Species co-occurrence: the case of congeneric species and a causal approach to patterns of species associations. *Global Ecology and Biogeography* 15: 39-49

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

Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, and Struhsaker TT (1987) *Primate societies*. University of Chicago Press, Chicago

Snaith TV, Chapman CA (2007) Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology* 16: 94-106

Snyder RE, Chesson P (2003) Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology Letters* 6: 301-309

Sorg JP, Ganzhorn JU, and Kappeler PM (2003) Forestry and research in the Kirindy Forest / Centre de Formation Professionnelle Forestière. In: Goodman, SM and Benstead, JP (eds) *The natural history of Madagascar*. University of Chicago Press, Chicago, pp 1512-1519

Sorg JP and Rohner U (1996) Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. In: Ganzhorn, JU and Sorg, JP (eds) *Ecology and economy of a tropical dry forest in Madagascar*. Goltze, Göttingen, pp 57-80

Southwood TRE and Henderson PA (2000) *Ecological methods*. Blackwell Sciences Ltd., Oxford

Spence KO, Rosenheim JA (2005) Isotopic enrichment in herbivorous insects: a comparative field-based study of variation. *Oecologia* 146: 89-97

Sponheimer M, Loudon JE, Codron D, Howells ME, Pruetz JD, Codron J, De Ruiter D, Lee-Thorp JA (2006) Do "savanna" chimpanzees consume C_4 resources? *Journal of Human Evolution* 51: 128-133

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behavioural Ecology and Sociobiology* 41: 291-309

Sterling EJ, Dierenfeld ES, Ashbourne CJ, Feistner ATC (1994) Dietary intake, food composition and nutrient intake in wild and captive populations of *Daubentonia*. *Folia primatologica* 62: 115-124

Stevens RE, Lister AM, Hedges REM (2006) Predicting diet, trophic level and palaeoecology from bone stable isotope analysis: a comparative study of five red deer populations. *Oecologia* 149: 12-21

Sweeting CJ, Polunin NVC, Jennings S (2004) Tissue and fixative dependent shifts of $\delta^{13}C$ and $\delta^{15}N$ in preserved ecological material. *Rapid Communications in Mass Spectrometry* 18: 2587-2592

Taitt MJ (1981) The effect of extra food on small rodent populations: I. deermice (*Peromyscus maniculatus*). *Journal of Animal Ecology* 50: 111-124

Taitt MJ, Krebs CJ (1981) The effect of extra food on small rodent populations: II. voles (*Microtus townsendii*). *Journal of Animal Ecology* 50: 125-137

Terborgh J, Janson CH (1986) The socioecology of primate groups. *Annual Review of Ecology and Systematics* 17: 111-135

Tilman D (1982) *Resource competition and community structure*. Princeton University Press, Princeton

Tilman D and Karieva P (1997) *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton

Tokeshi M (1999) *Species coexistence. Ecological and evolutionary perspectives*. Blackwell Science Ltd, Oxford

Townes H (1962) Design for a Malaise trap. *Proceedings of the Entomological Society Washington* 64: 253-262

Trivers RL (1972) Parental investment and sexual selection. In: Campbell, B (ed) *Sexual selection and the decent of man*. Heinemann, London, pp 136-179

Urton EJM, Hobson KA (2005) Intrapopulation variation in gray wolf isotope ($\delta^{15}N$ and $\delta^{13}C$) profiles: implications for the ecology of individuals. *Oecologia* 145: 317-326

van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87: 120-140

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen, V and Foley, RA (eds) *Comparative socioecology. The behavioural ecology of humans and other mammals*. Blackwell, Oxford, pp 195-218

Bibliography

van Schaik CP, Madden RH, and Ganzhorn JU (2005) Seasonality and primate communities. In: Brockman, DK and van Schaik, CP (eds) *Seasonality in primates. Studies of living and extinct human and non-human primates*. Cambridge University Press, Cambrridge, pp 445-463

van Schaik CP, Terborgh J, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353-377

van Schaik CP, Van Hooff JARAM (1983) On the ultimate causes of primate social systems. *Behaviour* 91-117

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. *Oecologia* 136: 169-182

Vasey N (2000) Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology* 112: 411-431

Voigt CC, Matt F (2004) Nitrogen stress causes unpredictable enrichment of ^{15}N in two nectar-feeding bat species. *The Journal of Experimental Biology* 207: 1741-1748

Voigt CC, Matt F, Michener R, Kunz TH (2003) Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. *The Journal of Experimental Biology* 206: 1419-1427

Wagner AP, Frank LG, Creel S (2008) Spatial grouping in behaviourally solitary striped hyenas, *Hyaena hyaena*. *Animal Behaviour* 75: 1131-1142

Waser PM (1981) Sociality or territorial defence? The influence of resource renewal. *Behavioural Ecology and Sociobiology* 8: 231-237

Weidt A, Hagenah N, Randrianambinina B, Radespiel U, Zimmermann E (2004) Social organization of the Golden brown mouse lemur (*Microcebus ravelobensis*). *American Journal of Physical Anthropology* 123: 40-51

West AG, Ayliffe LK, Cerling CE, Robinson TF, Karren B, Dearing MD, Ehleringer JR (2004) Short-term diet changes revealed using stable carbon isotopes in horse tail-hair. *Functional Ecology* 18: 616-624

West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's ecological recorders. *Trends in Ecology and Evolution* 21: 408-414

Wiens F, Zitzmann A (2003) Social structure of the solitary slow loris *Nycticebus coucang* (Lorisidae). *Journal of Zoology London* 261: 35-46

Wimmer B, Tautz D, Kappeler PM (2002) The genetic population structure of the gray mouse lemur (*Microcebus murinus*), a basal primate from Madagascar. *Behavioural Ecology and Sociobiology* 52: 166-175

Winemiller KO, Pianka ER (1990) Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60: 27-55

Wolda H (1988) Insect seasonality: why? *Annual Review of Ecology and Systematics* 19: 1-18

Wolff JO and Sherman PW (2007) *Rodent societies: An ecological and evolutionary perspective*. University of Chicago Press, Chicago

Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300

Wright PC and Martin LB (1995) Predation, pollination and torpor in two nocturnal prosimians (*Cheirogaleus major* and *Microcebus rufus*) in the eastern rain forest of Madagascar. In: Alterman, L, Doyle, GA, and Izard, MK (eds) *Creatures in the dark*. Plenum Press, New York, pp 45-60

Yoder AD, Burns MM, Génin F (2002) Molecular evidence of reproductive isolation in sympatric sibling species of mouse lemurs. *International Journal of Primatology* 23: 1335-1343

Yoder AD, Rasoloarison RM, Goodman SM, Irwin JA, Atsalis S, Ravosa MJ, Ganzhorn JU (2000) Remarkable species diversity in Malagasy mouse lemurs (primates, *Microcebus*). *Proceedings of the National Academy of Sciences* 97: 11325-11330

Zimmerman JK, Wright SJ, Calderón O, Pagan MA, 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

Zimmermann E, Cepok S, Rakotoarison N, Zietemann V, Radespiel U (1998) Sympatric mouse lemurs in north-west Madagascar: a new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia primatologica* 69: 106-114

Zinner D, Hilgartner R, Kappeler PM, Pietsch T, Ganzhorn JU (2003) Social organization of *Lepilemur ruficaudatus*. *International Journal of Primatology* 24: 869-888

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Kapitel 1 bis 5   Koautor Peter M. Kappeler

Die vorliegende Dissertation wurde von Peter M. Kappeler angeleitet.

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