Living apart together:

Pair-living in red-tailed sportive lemurs

(*Lepilemur ruficaudatus*)

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2006

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Summary

The amazing diversity of mammalian social systems has drawn a great degree of interest from behavioral and social scientists over decades (Clutton-Brock and Harvey 1977; Dunbar 1988; Clutton-Brock 1989; Janson 2000; Müller and Thalmann 2000; Kappeler and van Schaik 2002). Diversity in social systems is reflected in a variety of different spatial, grouping and mating patterns, which can vary among, but also within, species and populations (Richard 1978; Overdorff 1998; Ostner and Kappeler 1999; Sterck 1999). Biologists assume that social systems are mainly shaped by ecological factors, such as the distribution of resources and risks (Wrangham 1980; van Schaik and van Hooff 1983; van Schaik 1989). Moreover, different reproductive strategies among sexes and within sexes contribute significantly to the relative importance of resources and risks (Bateman 1948; Trivers 1972). Accordingly, male and female reproductive strategies should be neatly teased apart (van Schaik 1996).

Reproductive rates and costs in mammals are not equal for both sexes (Clutton-Brock and Parker 1995). Mammalian reproduction is characterized by a strong asymmetry because of internal gestation and lactation. Potential reproductive rates of females are much lower due to higher parental investment than those of males (Williams 1966). Consequently, reproductive success of females is considered to be limited mainly by resources, whereas males' reproductive success is mainly limited by the number of females they can fertilize (Bateman 1948; Williams 1966; Trivers 1972; Emlen and Oring 1977; Clutton-Brock 1989). Hence, males are not expected to limit their reproductive success by associating with only one female over more than one reproductive season. According to theoretical expectations, the majority of mammalian mating systems are indeed characterized by polygyny (males mate with several females and females mate with one male) or polygynandry (members of both sexes mate with several partners) (Wittenberger and Tilson 1980; Clutton-Brock 1989). However, monogamy is observed in about 5% of all mammalian species and it can be found in all major mammalian groups. (Wittenberger and Tilson 1980; Clutton-Brock 1989; Komers and Brotherton 1997). Especially in primates, the number of monogamous species is considerably higher with about 15% (Kleimann 1977; Fuentes 1999), and it is puzzling why males in those species restrict themselves to mate with only one female.

In the past, monogamy as a mating system has been often used in the broad sense of a social system or as synonym for pair-living (social organization) or *vice versa* (social organization: Fietz 1999, Fuentes 1999; mating system: Ribble 1991; social system: Komers and Brotherton 1997). For evaluating the evolution of pair-living it is important to distinguish between the three elements, *social organization*, *social structure* and *mating system,* that are interrelated and together form the social system (Sterling 1993; Kappeler and van Schaik 2002). *Social organization* can be considered as the key aspect of a social system as it describes group size, sexual composition and cohesion of a society (Müller and Thalmann 2000; Kappeler and van Schaik 2002). *Social structure* among members of a society describes the relationships and the pattern of social interactions among individuals. *Mating systems* contain a social component that describes mating behavior, for example number of males that females mate with during one mating season (Emlen and Oring 1977), and a genetic component, which describes the reproductive output that can be studied via genetic studies (Clutton-Brock 1989; Kappeler and van Schaik 2002).

At the behavioural level, it is only possible to describe the fact that a male and a female form a stable social unit, i.e., that they are pair-living (Kappeler and van Schaik 2002). Several studies have shown that extra-pair copulations, as well as extra-pair paternities seem to be no exception in pair-living species (Reichard 1995; Fietz et al. 2000; Sommer and Reichard 2000; Schülke et al. 2004). Hence, pair-living, as a form of social organization, should not be considered indicative of a monogamous mating system without proper paternity data (Kappeler and van Schaik 2002). Additionally, the temporal component has to be included when evaluating monogamous mating systems. Partnerships of monogamous species can be highly variable in duration, e.g. short-term partnerships, where males and females stay together only for one single breeding season (McKinney 1986; Ligon 1999). At the other side of the continuum is life-time partnership that equals life span of both partners. In several mammalian species, including humans, pair partners can be substituted either because one pair partner died or because one pair partner actively terminated the partnership while the other is still alive (Hendrichs 1975; Getz et al. 1987; Sommer 2003). These species exhibit so-called sequential monogamy (Wickler and Seibt 1983).

At the level of social organization, pair-living species can be characterized in more detail by the number of social units that consist of one adult male and one adult

female. In contrast to obligate pair-living, facultative pair-living is used for species with more than 10% of social units that do not consist of an association of one adult male with one adult female (Kleimann 1977). Pair-living species also vary in the degree of spatial association between males and females of a pair (Müller and Thalmann 2000; Kappeler and van Schaik 2002). Species are termed as cohesive pairs when pair partners are permanently spatially associated and have frequent interactions (e.g. *Hylobates lar:* Reichard 1995b; *Callicebus ssp.*: Müller and Anzenberger 2002). Characteristic attributes of cohesive pairs include frequent grooming bouts, small interindividual distance and close coordination of the behaviour of male and females (Müller and Anzenberger 2002; see Kinzey 1997 for a review). In contrast, pair partners of dispersed pairs share the same home-range but are not consistently associated during their period of activity (e.g. *Phaner furcifer:* Schülke and Kappeler 2003).

Especially in primates, the focus on pair-living has been a central aspect in studies of the evolution of primate social organization (van Schaik and Dunbar 1990; Jolly 1998; Palombit 1999; van Schaik and Kappeler 2003; Lovejoy 1981). Part of the attractiveness of pair-living can be seen in the high degree of pair-living species in primates, as well as its resemblance to typical social organization of humans in western industrialized countries (Lovejoy 1981, Pasternak et al. 1997). Theoretical considerations have shown that pair-living in primates evolved several times independently from a most likely solitary ancestor with a promiscuous mating system (van Schaik and Kappeler 2003). This contributed to the search for similar evolutionary origins and the selection pressures that drive males to mate with only one female. Consequently researchers proposed several hypotheses that aim to explain the occurrence of this puzzling social organization (reviewed in Fuentes 2002):

Paternal care hypothesis

The paternal care hypothesis assumes that female reproductive success suffers without the aid of the pair partner (Kleimann 1977; Clutton-Brock 1989). Hence, in the extreme version, females cannot raise young successfully without the help of males (Wittenberger and Tilson 1980). As a consequence, males should engage in any form of direct infant care, such as grooming, carrying behavior, predator detection or defense. To explain monogamy, several forms of male paternal care behaviours have been cited (e.g. Callitrichidae: Dunbar 1995 *Peromyscus*

californicus: Cantoni and Brown 1997; *Cheirogaleus medius*: Fietz and Dausmann 2003; *Petropseudes dabli*: Runcie 2000. However, obligate paternal care characterizes only a small minority within pair-living species (van Schaik and Dunbar 1990; Komers 1996; Komers and Brotherton 1997; Fuentes 2002). In addition, paternal care in mammals can exist in the absence of monogamy or may have evolved after species became pair-living (Wright 1990; Dunbar 1995; Buchan et al. 2003).

Female defense hypothesis

The female defense hypothesis assumes that dispersal of females is determined by the temporal and spatial distribution of resources and that males distribute themselves onto the distribution of females, defending or monopolizing as many females and/or female home-ranges as possible (van Schaik and van Hooff 1983; Altmann 1990; Komers and Brotherton 1997; Palombit 1999). Pair-living would evolve if females are so widely distributed in space or exhibit such highly synchronized estruses that economic defence of more than one female is not feasible (Emlen and Oring 1977; Nunn 1999; Dunbar 2000). Fitness gains and reproductive success of males adopting a roving strategy would have to be lower than reproductive success of males that associate with only one female (van Schaik and Dunbar 1990; Dunbar 2000).

Mate guarding hypothesis

A more refined version of the female defense hypothesis is the mate guarding hypothesis. It suggests that pair-living evolved under certain conditions, such as high costs of polygyny and/or highly exclusive female ranges. Under this scenario pair bonding is the result of prolonged mate guarding by males (Palombit 1999). Continuous male-initiated mate guarding beyond the period of actual mating activity is a strategy to avoid loss of mating partner (*Hylobates lar*: Brockelman et al. 1998), to minimize extra pair copulation and extra pair paternity and to restrict females' ability to gain information about additional mates (*Madoqua kirkii*: Brotherton et al. 1997; Brotherton and Manser 1997; *Hylobates lar*: Palombit 1999). This hypothesis does not postulate any advantages for females because females are not able to choose their mate. However females may tolerate males because this might be less costly than to attempt to expel the male from the territory (Gowaty 1996).

Resource defense hypothesis

The resource defense hypothesis assumes that only males should engage in territorial defense. Under the resource defense hypothesis, pairs should emerge when males are unable to maintain territories that can support more than one female. Resource defense should be especially favored in species where females are exposed to high energetic demands during gestation and lactation (Brockelman and Srikosamatara 1984). Without the aid of a male, females would not be able to maintain a territory, hence female reproductive success depends on the resource holding potential of respective pair partner (Parker 1974). However, high quality territories should attract and support multiple females, even if intrasexual aggression between females is high (Orians 1969; Davies 1989). The resource defense hypothesis assumes that male reproductive success is limited by the females' choice of resource access.

Infanticide hypothesis

It has been shown that infanticide by males occurs in a wide range of mammalian species (*Equs burchelli*: Pluhacek and Bartos 2000; *Panthera leo*: Packer and Pusey 1983; *Marmota marmota*: Coulon et al. 1995; *Presbytis entellus*: Sommer 1994; see van Schaik 2000 for a review). Based on these findings, the infanticide hypothesis assumes that infanticide is the primary force selecting for males associating permanently with one female (van Schaik and Dunbar 1990; van Schaik and Kappeler 1997; Palombit 2000). Under this assumption, females are not able to defend their infants against infanticidal strange males. Infanticide by new male pair partner is predicted to occur in species where females return more quickly to ovarian cycling after loss of an infant (Borries et al. 1999) and new male partners are most likely not the genetic father of the existing infants (van Schaik 2000). Following death of infants, females become earlier available as mating partner for infanticidal males. Hence, males that sire infants should associate permanently with their mating partner and defend females and their dependant infant(s) from other infanticidal males. Although infanticide is observed rarely, male and female pair bonds may be a result of infanticidal pressure in the past (van Schaik and Dunbar 1990).

Intersexual feeding competition hypothesis

The recently formulated intersexual feeding competition hypothesis assumes that food competition is high among individuals (Thalmann 2001; Schülke 2005). If females show high range exclusivity and, hence, become a widely dispersed resource, males could persuade females into pair-living by defending their territory against other males. Although males defend their territory only against other males, females still benefit because food competition by additional males is minimized. In contrast to the female defense hypothesis, the intersexual feeding competition hypothesis postulates benefits for both, males and females living in permanent association. Hence, pair-living evolved as a result of direct feeding competition and male reproductive tactics (Schülke 2005).

Aims of this study

The overall objective of this thesis was to characterize the social organization, determine basic life history traits and to test current hypotheses about the evolution

Fig. 1

of pair-living in the red-tailed sportive lemur (*Lepilemur ruficaudatus*), a nocturnal lemur species (Fig. 1). Nocturnal lemurs and other strepsirrhines provide therefore a good model to investigate the evolution of social systems in ancestral primates (Kappeler 1996; Kappeler and Heymann 1996; Kappeler 1997). Unf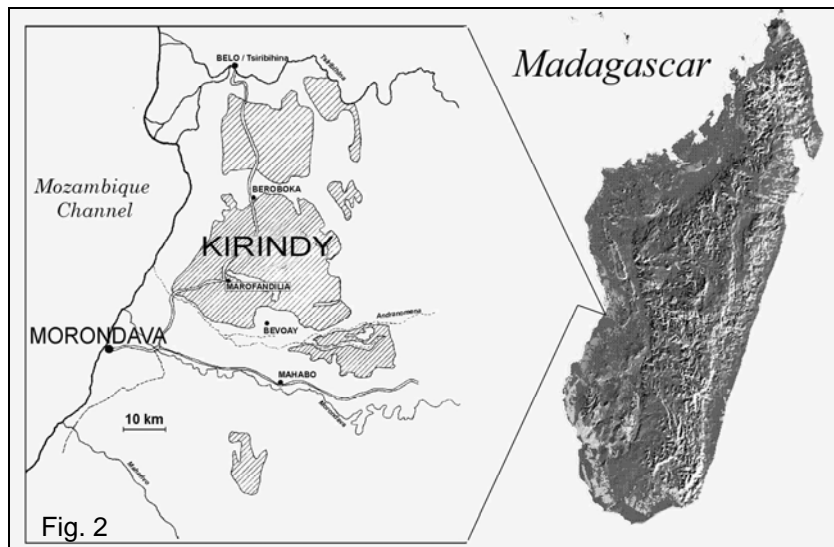ortunately, even the most basic life history traits, and behavioral aspects of mating and rearing system of many nocturnal lemur species are still unknown. However, in the last decade intensified research on nocturnal primates, particularly on nocturnal lemurs, revealed some important new insights. Several species previously thought to be solitary are in fact pair-living (*Cheirogaleus medius*: Fietz 1999; *Lepilemur edwardsi*: Thalmann 2001; *Phaner furcifer*: Petter et al. 1971; Schülke and Kappeler 2003; *Avahi occidentalis* Thalmann 2003). Moreover it seems that some nocturnal pair-living species differ in their degree of cohesiveness from diurnal pair-living primate species because males and females are only loosely

associated and were therefore termed "dispersed pairs" (Müller and Thalmann 2000; Schülke and Kappeler 2003).

Red-tailed sportive lemurs (*Lepilemur ruficaudatus*) are small (<1000g), folivorous and can be found in the dry deciduous forests in western Madagascar (Mittermeier et al. 1994; Andriaholinirina et al. 2006). Currently twelve species inhabiting all major habitats of the island are recognized within the genus of *Lepilemur* (Andriaholinirina et al. 2006, Rabarivola et al 2006). Red-tailed sportive lemurs are well known for their exceptional morphological, physiological and behavioral adaptations to their folivorous lifestyle, such as a prolonged caecum (Charles-Dominique and Hladik 1971), low resting metabolic rate (Schmid and Ganzhorn 1995; Drack et al. 1999) and prolonged resting bouts (Schmid and Ganzhorn 1995; Ganzhorn and Kappeler 1996). Based on these studies it became apparent that red-tailed sportive lemurs may be socially organized into pairs (Ganzhorn and Kappeler 1996). However, several aspects of their life history, such as paternal care, mating and birth season, as well as aspects of their social organization, such as territorial stability or cohesiveness between pair partners, remained incompletely for any member of the genus *Lepilemur*.

In **Chapter I,** I investigate the social organization of a population of red-tailed sportive lemurs. Information about spatial organization provides a fundamental framework for the characterization and evaluation of a social system (Kappeler & van Schaik 2002). In detail, I investigated the ranging behavior of individually marked red-tailed sportive lemurs. This includes home range characteristics, such as spatial and temporal stability, size and inter-individual overlap. Behavioral observations are complemented with census data and morphometric data on sexually-selected traits. To estimate home range size and stability, I used spatial data of 46 individuals (20 males; 26 females) radio-tracked at different study periods between June 1995 and November 2001 in Kirindy Forest, a dry deciduous forest in western Madagascar (44°39'E, 20°03'S), where the German Primate Center (DPZ) operates a field research station (Fig. 2 and Fig. 3). Information on home range overlap and sleeping site associations is based on data collected from 19 individuals (7males, 12 females including 2 subadults) in October 2000, February-April 2001 and October-November 2001. I found no sexual dimorphism in body size between adult males (n=15) and adult females (n=19) measured in 2000 and 2001. However, canines of males were

15% longer than canines of females. Estimation of population density ranged from 0.9 to 1.6 individuals per hectare. Long-term data from nine individuals revealed home range stability over several years. In 4 cases, I found extensive home range overlap between one adult female and one adult male. In two cases, the home range of an adult male overlapped extensively with those of one adult and one subadult female. In all cases, home range overlap between neighboring individuals was small. Individuals used on average 5.6±1.8 sleeping trees. Female and males living in the same home range shared their sleeping trees on average every fourth day. These data on home range utilization indicate that pair-living is the modal social organization of red-tailed sportive lemurs. Although I did not find males that range over home ranges of more than one adult female the observed degree of sexual canine dimorphism indicates that male-male competition for females is prominent in red-tailed sportive lemurs.

Fig. 2

Fig. 3

In **Chapter II,** I evaluate the importance of paternal care for the evolution of pair-living in red-tailed sportive lemurs. If paternal care is important for the evolution and/or maintenance of pair-living, I expected males to engage in some form of direct infant care, such as grooming, carrying behavior, baby-sitting and predator detection or defense during the birth season. Based on long-term data, I complemented

behavioral observations with data on several previously undescribed life history traits (e.g. mating and birth seasonality; litter size; gestation length; inter birth intervals, life span and predation rates). I collected data on life history traits by following marked individuals during several field seasons between October 2000 and March 2005. To quantify the degree of parental care in red-tailed sportive lemurs, I conducted simultaneous follows of pair-partners during the birth season in 2002 and 2003 together with a field assistant, using focal animal sampling (Altmann 1974). Behavioral data during the mating season were collected in 2003 and 2004. Predation rates varied between years (range: 0-40%). We identified *Cryptoprocta ferox*, *Polyboroides radiatus* and *Acranthophis cf. madagascariensis* as predators of red-tailed sportive lemurs. Mating and birth were highly seasonal. Mating was restricted to the months of May and June and indicated by conspicuous changes of vulval morphology and male mate guarding behavior. All 22 recorded births occurred between November and the first half of December in the years 2002, 2003 and 2004. In 13 cases, I was able to calculate gestation length. Singletons were born after a gestation length of on average 176 days, which is much longer than expected for a lemur of this body mass. Infants became independent of mothers after about 50 days. Females provided maternal care by lactating, warming, grooming and transporting babies in the mouth. While females foraged, infants were parked in dense vegetation. Typical parking bouts lasted 40-60 minutes. In contrast to females, males spent most of their time in distance categories between 20-30 meters from infants and were only rarely found in their proximity. Moreover, I did not find evidence for direct infant care provided by social fathers. In summary, the paternal care hypothesis cannot serve as an explanation for the evolution and/or maintenance of pair-living in red-tailed sportive lemurs.

For a more detailed evaluation of the evolution of pair-living in red-tailed sportive lemurs, I tested the female defense (FDH) and resource defense hypothesis (RDH) in **Chapter III**. For this purpose, I used a combination of behavioral and experimental data to examine specific predictions derived from FDH and RDH. I expected differences in cohesiveness of pair partners, maintenance of pair bond, home range use, travel distance, territorial defense, as well as vigilance behavior in response to simulated male and female intruders. I analyzed data obtained from 8 pairs during a long-term field stay of 24 months between 2002 and 2004. Together

with a field assistant, I collected in total >2000 hours of behavioral and spatial data during simultaneous follows of pair partners. To investigate territorial defense and vigilance behavior, I conducted 126 playback trials in total. Each of 14 individuals was exposed to playbacks of vocalizations of a strange male, a strange female, as well as a control stimuli during three consecutive seasons (mating; gestation; birth). Immediate behavioral responses were recorded for three minutes after onset of playbacks. Analysis of spatial data of eight pairs revealed that male home ranges were significantly larger than home ranges of corresponding female partners. Home ranges of pairs were exclusive and overlapped only little with home ranges of neighboring males and females. Encounter rates between pair partners were low, hence, red-tailed sportive lemurs can be considered as dispersed pairs. Only in the pre-mating and mating season pair partners met more often than expected by chance. Surprisingly no affiliative interactions during 255 encounters between pair partners were observed. More surprisingly, 47.3±7.4% of these encounters involved agonistic behavior by at least one pair partner. 76 out of 120 of these conflicts were decided; 50% of them were won by males and 50% by females. However, during the mating season, males won 87.1% of conflicts. In contrast, males lost 78.9% of the conflicts during the birth season.

I found support for the female defense hypothesis because males increased travel distances and showed high aggression towards mates or other males, as well as extensive mate guarding only during the short mating season. Moreover, males were responsible for maintenance of proximity between pair partners in this period and males defended territories mainly against other males, but not against females. Playback experiments also support the FDH because males responded strongest towards simulated male and female intruders during the mating season. Furthermore, feeding of males and females did not differ throughout the year. Based on these results, I conclude that female defense hypothesis can offer a promising explanation for pair-living in red-tailed sportive lemurs. Males defend females against other males but seem to be unable to defend more than one female. Monopolisation potential of males is certainly affected by ranging pattern of females, as well as the short mating season. However, these factors *per se* cannot fully explain evolution of pair-living in red-tailed sportive lemurs. I propose additional constraints, such as increased inter- and intrasexual aggression and a higher predation risk that prevent males from adopting a roaming strategy. Minimization of risks and, hence, of the variance in

mating success, may explain why males in red-tailed sportive lemurs focus on only one female over several reproductive cycles. However, the comparative evaluation of life-time reproductive success, as well as the relative importance of benefits and costs for males and females associated with only one partner may help to fully understand pair-living in this nocturnal primate.

Summary

In summary, in this thesis I present the first comprehensive study of the social system of red-tailed sportive lemurs (*Lepilemur ruficaudatus*). The results contribute several new data on life history traits, which are required for comparative studies that examine general patterns of primate evolution and socioecology. Moreover, I was able to clarify the social organization, social structure and mating strategy of red-tailed sportive lemurs. In particular, I was able to demonstrate that red-tailed sportive lemurs are socially organized into pairs and maintain stable territories over several years. Red-tailed sportive lemurs can be classified as dispersed pairs because pair partner meet only rarely throughout the year, except during the short mating season. I did not find evidence for direct infant care provided by the father. Hence, the paternal care hypothesis cannot serve as an explanation for the evolution and/or maintenance of pair-living in red-tailed sportive lemurs. In contrast, the results of this study emphasize the importance of female defense as a male mating strategy and offer an important contribution for the understanding of pair-living in nocturnal lemurs in particular and pair-living mammals in general.

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Zusammenfassung

Weibliche Säugetiere investieren mehr in ihren Nachwuchs als Männchen. Sie verteilen sich entsprechend der sie betreffenden Risiken und Ressourcen in Raum und Zeit um ihren Reproduktionserfolg zu maximieren. Der Reproduktionserfolg der Männchen ist dagegen durch den Zugang zu rezeptiven Weibchen limitiert. Männchen sollten folglich um Weibchen konkurrieren, wobei ihr Reproduktionserfolg primär von der Anzahl an Weibchen abhängt, die sie befruchten können. Im Bezug auf diese Grundannahme ist daher nicht zu erwarten, dass männliche Säugetiere mit nur einem Weibchen assoziiert sind und so ihren potentiellen Reproduktionserfolg einschränken. Der Anteil paarlebender Säugetierarten, bei denen zwischen einem adulten Männchen und einem adulten Weibchen eine individuelle und exklusive Bindung besteht, liegt trotzdem bei ca. 5%. Außerdem findet man diese Form der zwischengeschlechtlichen Assoziation, trotz ihrer Seltenheit, in fast allen größeren Säugerordnungen, wobei der Anteil paarlebender Primaten mit ca. 15% außergewöhnlich hoch ist.

Neuere theoretische Analysen haben ergeben, dass diese für Säugetiere seltene Kategorie der sozialen Organisation, heterogene Phänomene zusammenfasst. Je nach Häufigkeit des Vorkommens von Paaren innerhalb einer Population, kann man zwischen obligatem und fakultativem Paarleben unterscheiden. Die Unterscheidung wird mit Hilfe eines arbiträren Anteils (meist ≥ 10%) sozialer Einheiten, die nicht aus Paaren bestehen (sondern meist aus einem Männchen und mehrere Weibchen) gemacht. Außerdem erscheint es sinnvoll, zwischen so genannten kohäsiven und dispersen Paaren zu unterscheiden, da sich bei ihnen die Paarbindung auf der Verhaltensebene sehr unterschiedlich manifestiert. Bei kohäsiven Paaren sind Männchen und Weibchen permanent assoziiert und koordinieren und synchronisieren ihre Aktivitäten. Bei dispersen Paaren nutzen Männchen und Weibchen dagegen nur das gleiche, von beiden verteidigte Territorium, indem sie sich mehr oder weniger unabhängig bewegen und nur selten direkt interagieren.

Diese verschiedenen Formen des Paarlebens, die auf der Ebene der sozialen Organisation beschrieben werden können, müssen außerdem getrennt vom jeweiligen Paarungssystem betrachtet werden. Zwar werden paarlebend und monogam oft synonym verwendet, aber die genetischen Untersuchungen des

genetischen Fortpflanzungserfolgs bei paarlebenden Vögeln haben gezeigt, dass Monogamie nur bei einem Bruchteil der Paare und Arten vorkommt. Erste vergleichbare Untersuchungen an paarlebenden Primaten und anderen Säugern weisen in dieselbe Richtung. Wenn keine Daten über das genetische Paarungssystem vorhanden sind, ist es angebracht von paarlebenden anstatt von monogamen Arten zu sprechen.

Da Paarleben bei Säugetieren mehrfach unabhängig, zumeist ausgehend von solitären Vorfahren entstanden ist, kann man nach gemeinsamen Ursachen dieses Sozialsystems suchen. Primaten haben bei Untersuchungen über die Evolution von Paarleben schon immer eine zentrale Rolle gespielt. Vermutlich deshalb, weil der Anteil paarlebender Arten ungewöhnlich hoch ist und weil diese Form des Zusammenlebens auch für *Homo sapiens* als typisch angesehen wird. Um die Frage nach den selektiven Zwängen, die ein Leben in Paaren begünstigen, zu beantworten wurden insgesamt sechs verschiedene Hypothesen postuliert:

Väterliche Fürsorge

Als offensichtlichster Grund warum sich bei einigen Säugetierarten Männchen auf nur eine Sozial- bzw. Paarungspartnerin beschränken wird angenommen, dass die direkte Fürsorge beider Paarpartner für das Überleben des Nachwuchses essentiell ist. Das Männchen beteiligt sich direkt an der Jungenaufzucht, indem es z. B. Jungtiere trägt, groomt, wärmt und verteidigt oder ihnen Zugang zu Futter ermöglicht. Bei Verlust eines Paarpartners sollte deshalb die Überlebenswahrscheinlichkeit des Nachwuchses reduziert sein. Bei Primaten wird mit dieser Hypothese das Vorkommen von Paaren bei Callitrichiden und bei *Cheirogaleus medius* erklärt. Allerdings existiert bei vielen Primaten Paarleben, ohne dass die Männchen sich erkennbar an der Jungenaufzucht beteiligen.

Weibchenverteidigung

Als weitere Ursache des Paarlebens wird die, aus Sicht der Männchen, ungünstige Verteilung rezeptiver Weibchen in Raum und Zeit angesehen. Die Weibchen sind dabei räumlich so weit verteilt, dass ein Männchen aufgrund des ungünstigen „Kosten-Nutzen Verhältnis" nicht die Möglichkeit hat, das Streifgebiet von mehr als einem Weibchen zu verteidigen. Außerdem soll der Reproduktionserfolg von Männchen, die unter diesen Bedingungen eine Strategie

des Umherstreifens (roving) verfolgen, ebenfalls im Durchschnitt geringer sein, als der von Männchen, die sich mit einem Weibchen assoziieren. Dies wäre bei starker Synchronität der Fortpflanzungsaktivität der Weibchen der Fall.

Mate guarding

Diese Hypothese geht davon aus, dass die Paarbindung dadurch zustande kommt, dass ein Männchen sich einem Weibchen anschließt und dieses gegen Rivalen verteidigt. Voraussetzung dazu ist eine bestimmte Ressourcenlage und die daraus resultierende Verteilung der Weibchen. Bei einer verstreuten Weibchenverteilung und geklumpten Nahrungsressourcen, sollte die Monopolisierung eines Weibchens die beste Strategie zur Maximierung des männlichen Reproduktionserfolges sein oder zumindest zur Minimierung der Varianz des Reproduktionserfolges beitragen. Insbesondere bei einem Geschlechterverhältnis zu Gunsten der Männchen, könnten diese so *extra pair*-Kopulationen der Weibchen verhindern oder zumindest die Möglichkeit der Weibchen, Informationen über fremde Männchen zu erhalten, vermindern. Diese Hypothese postuliert keine Vorteile für die Weibchen. Es wird stattdessen angenommen, dass Weibchen die Präsenz der Männchen tolerieren, weil dies weniger Energie kostet, als Männchen andauernd zu vertreiben.

Ressourcenverteidigung

Die Ressourcenverteidigungs-Hypothese geht davon aus, dass Männchen indirekt zur Überlebenschance der Nachkommen beitragen, indem sie maßgeblich ein Territorium und die darin enthaltenen Ressourcen für den Nachwuchs und die Paarpartnerin verteidigen. Grundlage dieser Hypothese ist die Annahme, dass reproduktive Weibchen unter vergleichsweise höherem Nahrungsstress stehen als Männchen und deshalb ein hohes Maß an intrasexueller Aggressivität besteht, so dass Männchen eher in der Lage sind, größere Wanderstrecken zur Verteidigung des Territoriums zurückzulegen. Männchen sollten folglich im Vergleich zu den Weibchen größere Strecken zurücklegen und sich häufiger an territorialen Konflikten beteiligen. In Abwesenheit oder Tod der Männchen würde man erwarten, dass Weibchen nicht in der Lage sind, das Territorium weiter aufrecht zu erhalten, zumindest nicht in der bestehenden Größe. Außerdem sollten Männchen eine hohe Aggressivität gegen Eindringlinge beider Geschlechter zeigen.

Infantizid

Die Infantizidhypothese postuliert, dass sich Männchen permanent mit einzelnen Weibchen assoziieren, um den gemeinsamen Nachwuchs vor Infantizid durch fremde Männchen zu schützen. Diese Hypothese basiert auf den inzwischen bestätigten Annahmen, dass Weibchen nach einem Infantizid schneller wieder empfängnisbereit werden, und dass infantizidiale Männchen keine eigenen Jungen umbringen und außerdem mit hoher Wahrscheinlichkeit den nächsten Nachwuchs zeugen. Für Männchen kann die Strategie, bei einem Weibchen zu bleiben und deren abhängigen Nachwuchs zu verteidigen, bei einer hohen Vaterschaftswahrscheinlichkeit, durchaus vorteilhaft sein.

***Intersexual feeding competition* Hypothese**

Diese Hypothese geht von einer hohen Nahrungskonkurrenz zwischen den Individuen einer Art aus. Ähnlich wie bei der Weibchenverteidigungshypothese und *mate guarding* Hypothese, wird postuliert, dass Männchen versuchen, Weibchen und deren Territorien gegenüber männlichen Eindringlingen zu verteidigen. Man kann annehmen, dass eine hohe Exklusivität der weiblichen Territorien und die somit zerstreute Verteilung der Weibchen, das Entstehen von Paarleben begünstigt. Obwohl Männchen die Territorien nur gegen andere Männchen verteidigen, profitieren auch die Weibchen, da die Nahrungskonkurrenz durch den Ausschluss zusätzlicher Männchen vermindert ist.

Als zentrales Thema der vorliegenden Arbeit überprüfte ich am madagassischen, nachtaktiven Braunen Wieselmaki (*Lepilemur ruficaudatus*) Annahmen und Vorhersagen der existierenden Hypothesen zur Evolution von Paarleben bei Säugetieren. Neben Verhaltensdaten aus parallelen Beobachtungen der Paarpartner wurden akustische Playback-Experimente zur Simulation der Präsenz fremder und bekannter Männchen und Weibchen zu verschiedenen Fortpflanzungsphasen eingesetzt, um zu entscheiden, ob Paarleben bei dieser Art am besten durch väterliche Jungenfürsorge, Weibchenverteidigung oder Ressourcenverteidigung zu erklären ist. Die Datenaufnahme erfolgte während mehrerer Feldphasen im Westen Madagaskars zwischen 2001 und 2004 einschließlich eines 24-monatigen Langzeitaufenthalts und umfasst mehr als 2000

Beobachtungsstunden. Als Grundlage zur Charakterisierung und Evaluierung des Sozialsystems des Braunen Wieselmakis untersuchte ich in **Kapitel I** die soziale Organisation anhand der räumlichen Verteilung von 19 Individuen (7 Männchen; 12 Weibchen einschließlich 2 Subadulten). Die räumlichen Daten wurden ergänzt mit Daten zur Populationsdichte, sowie morphometrischen Daten. Um die zeitliche Stabilität der *home ranges* abzuschätzen, konnte ich die räumlichen Daten, die in vorherigen Studien zwischen 1995 und 1997 aufgenommen wurden in meine Analysen einbeziehen. Ich fand keinen Sexualdimorphismus zwischen männlichen (n=15) und weiblichen Wieselmakis (n=19). Allerdings waren die Eckzähne der Männchen im Mittel 15% länger als die Eckzähne der Weibchen. Ich ermittelte Populationsdichten von 0,9 bis 1,6 Individuen pro Hektar. Für neun Individuen lagen räumliche Daten über mehrere Jahre vor. Es zeigte sich, dass die *home ranges* über mehrere Jahre stabil sind. In vier Fällen überlappte das *home range* jeweils eines adulten Männchens extensiv mit dem *home range* von einem adulten Weibchen. In zwei Fällen überlappte das *home range* jeweils eines Männchens extensiv mit dem *home range* von einem adulten und subadulten Weibchen. In allen Fällen überlappten die *home ranges* nur geringfügig mit denen benachbarter Tiere. Zum Übertagen nutzten Wieselmakis im Durchschnitt 5,6±1,8 Schlafbäume (Schlafhöhlen). Männchen und Weibchen die sich jeweils das gleiche *home range* teilten, übertagten im Schnitt jeden vierten Tag gemeinsam in der Schlafhöhle. Die Schlafhöhlennutzung sowie die räumlichen Daten weisen darauf hin, dass Braune Wieselmakis in Paaren organisiert sind. Allerdings weist der Unterschied in der Eckzahnlänge zwischen Männchen und Weibchen auf eine mögliche Konkurrenz der Männchen um limitierende Ressourcen (z.B. Weibchen) hin.

Als offensichtlichster Grund für Paarleben wird die obligate väterliche Fürsorge angesehen. Um diese Hypothese am Braunen Wieselmaki zu überprüfen, analysierte ich in **Kapitel II** Daten zur *life history* und Jungenfürsorge. Die Paarungszeit bei Wieselmakis war auf nur wenige Wochen im Mai/Juni beschränkt. Nach einer außergewöhnlich langen Tragzeit von im Durchschnitt 176 Tagen gebärten die Weibchen jeweils ein Baby. Jungtiere wurden von den Müttern im Mund transportiert und während der Nahrungssuche in dichter Vegetation geparkt (n=22). Die parallele Beobachtung der Paarpartner mit Jungtieren ergab, dass sich die Männchen nur selten in räumlicher Nähe zum Jungtier aufhielten. Entsprechend zeigten Männchen keine direkte Jungenfürsorge wie z.B. Tragen, Fellpflege oder

Raubfeindverteidigung. Ich schloss daraus, dass direkte Jungenfürsorge keine Erklärung für die Evolution und/oder Aufrechterhaltung des Paarlebens beim Braunen Wieselmaki liefert. Entsprechend überprüfte ich in **Kapitel III** Vorhersagen zur Ressourcenverteidigungshypothese und Weibchenverteidigungshypothese. Ich analysierte Daten von acht Paaren, die ich über einen kontinuierlichen Zeitraum von 24 Monaten, mittels simultaner Beobachtung der Paarpartner, zusammen mit einem Feldassistenten aufgenommen habe. Zusätzlich führte ich insgesamt 126 Playbackexperimente durch, wobei ich jedem Paarpartner in der Paarungs-, Nichtpaarungs- und Geburtszeit jeweils typische Laute von fremden Männchen, Weibchen und Kontrolllaute vorspielte und anschließend die entsprechenden Verhaltensreaktionen aufnahm. Mit Ausnahme der Vorpaarungs- und Paarungszeit trafen sich Paarpartner nur selten während der nächtlichen Aktivität. Deshalb klassifiziere ich Braune Wieselmakis als disperse Paare. Überraschenderweise waren 47.3±7.4% aller Treffen zwischen den Paarpartnern von Aggressivität mindestens eines Paarpartners geprägt. Außergewöhnlich war auch, dass die Paarpartner kein soziopositives Verhalten, wie zum Beispiel Fellpflege austauschten. Die Analyse der räumlichen Daten sowie die Playbackdaten stützen die Weibchenverteidigungshypothese. Männchen legten größere Wegstreckenlängen während der Paarungszeit zurück. Bei allen acht Paaren waren jeweils die Männchen für die Aufrechterhaltung der räumlichen Nähe zum Paarpartner verantwortlich. Außerdem zeigten Männchen nur in der kurzen Paarungszeit *mate guarding* Verhalten und hohe Aggressivität gegenüber benachbarten Männchen. Männchen verteidigten das Territorium nur gegenüber anderen Männchen, nicht jedoch gegen fremde Weibchen. Männchen und Weibchen reagierten am stärksten gegenüber männlichen und weiblichen Lauten während der Paarungszeit. Diese Ergebnisse stützen die Weibchenverteidigungshypothese, wohingegen keine der Vorhersagen für die Ressourcenverteidigungshypothese bestätigt wurde.

Fazit und Ausblick: Zusammenfassend stellt diese Arbeit die erste umfassende Studie zum Sozialsystem des Braunen Wieselmakis (*Lepilemur ruficaudatus*) dar. Die Studie beinhaltet einige neue bis dato unbekannte Aspekte zur *life history* von Wieselmakis, die insbesondere für vergleichende evolutionsbiologische und sozioökologische Studien eine unverzichtbare Grundlage liefern. Ich konnte zeigen, dass Wieselmakis in Paaren organisiert sind und die Territorien über mehrere Jahre

hinweg stabil sind. Da sich die Paarpartner während ihrer nächtlichen Aktivität nur selten treffen, handelt es sich bei Wieselmakis um disperse Paare. Unter den vorgeschlagenen Hypothesen zur Evolution des Paarlebens weisen die Ergebnisse dieser Arbeit auf die Bedeutung der Weibchenverteidigungshypothese hin. Ich schlage vier Faktoren vor, die das Paarleben bei Braunen Wieselmakis begünstigen: (1) Die hohe Exklusivität der weiblichen Territorien trägt zu einer für Männchen ungünstigen Verteilung der Weibchen bei. (2) Die hohe Aggressivität zwischen den Geschlechtern, (3) die kurze Paarungszeit und (4) eine gesteigerte Raubfeindgefahr diskutiere ich als weitere Gründe, weshalb es Männchen nicht schaffen mehr als ein Weibchen zu monopolisieren. Die genaue Überprüfung des *life time* Reproduktionserfolgs und insbesondere die Ermittlung der Kosten und Nutzen für Weibchen und Männchen die mit nur einem Paarpartner assoziiert sind, können sicherlich zu einem tieferen Verständnis hinsichtlich der Evolution von Paarleben beim Braunen Wieselmaki beitragen.

CHAPTER 1

Social organization of *Lepilemur ruficaudatus*

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Abstract

The aim of this study was to characterize the spatial organization of red-tailed sportive lemurs (*Lepilemur ruficaudatus*) as a key aspect of their social organization and social system. Sportive lemurs are small (< 1000 g), nocturnal and folivorous primates endemic to Madagascar. We studied a population of 57 individually-marked animals in Kirindy Forest, western Madagascar, between 1995 and 2001. Twenty males and 26 females of the marked population were radio-tracked to obtain detailed information on the size and location of their home-ranges. Census data and morphometric measurements provided complementary data sets. We found that males and females occupied small (< 1 ha) home-ranges. Long-term records from 9 individuals revealed home-range stability over several years. In four cases home-ranges overlapped extensively with that of one member of the opposite sex, in two cases, we found a spatial association of one male and two females. However, home-ranges overlapped very little with neighboring individuals of both sexes. During the study period spatially associated individuals used on average 5.6 sleeping trees within 117 days, but they spent on average only about every fourth night together. These data suggest that home-ranges in red-tailed sportive lemurs are exclusively used by pairs or trios and that the modal social organization of red-tailed sportive lemurs is pair-living.

Key Words: *Lepilemur ruficaudatus*; home-range; social organization; pair-living

Introduction

The last decade of intensified research on nocturnal primates (reviewed in Sterling *et al.* 2000) has generated two new important insights. First, some species previously thought to be solitary were found to be pair-living (Fietz, 1999; Müller, 1998; Rasoloharijaona *et al.*, 2000) or to exhibit even more complex social organizations (e.g., Gursky, 2000). Second, within both solitary and pair-living taxa, an unexpected diversity of variation around the respective underlying categories has emerged. For example, solitary mouse and dwarf lemurs (*Microcebus murinus* and *Mirza coquereli*) were found to exhibit different higher-order levels of organization (Wimmer *et al.*, 2002; Kappeler *et al.*, 2002) and some pair-living species (e.g. *Phaner furcifer*) were found to be only loosely associated as so-called dispersed pairs (Schülke and Kappeler, 2003). As field studies of nocturnal primates continue to be initiated and intensified, documentation of additional variation is to be expected (Sterling *et al.*, 2000; Kappeler and van Schaik, 2002).

In this paper, we report on the spatial organization of a population of red-tailed sportive lemurs (*Lepilemur ruficaudatus*), focusing on home-range characteristics, such as temporal stability, size and overlap. Spatial organization is regarded as a key component of the social organization and social system (Kappeler and van Schaik, 2002) so that our data allow a first characterization of the social system of this species.

The genus *Lepilemur* (Sportive Lemurs) includes seven species of small (< 1 kg) folivores that inhabit different habitats throughout Madagascar, ranging from rain forest to spiny desert forest (Thalmann and Ganzhorn, 2003) and whose taxonomic status and relationships remain controversial (Ishak *et al.*, 1988, 1992; Bachmann *et al.*, 2000; Montagnon *et al.*, 2001; Groves, 2001). Information about the social systems of sportive lemurs is still fragmentary, but nonetheless indicative of variation both within and between taxa.

In *Lepilemur leucopus*, adult females defend a territory of about 0.18 ha, which they may share with their juvenile female offspring. Adult males defend territories (average size 0.30 ha) that are superimposed on those of 1-5 females. *Lepilemur leucopus* is very vocal and some of its calls may have a function in territorial advertisement. During the day, white-footed sportive lemurs can be found in tree holes and forks or liana tangles, where they rest alone (Charles-Dominique and

Hladik, 1971; Hladik and Charles-Dominique, 1974). In a subsequent study of the same population, however, Russell (1977) observed male-female and female-female pairs resting together during the day and duos and trios of adults feeding together at night.

Similarly, Petter *et al.* (1977) reported never seeing more than two animals (mother-offspring pairs) together in *Lepilemur edwardsi*, whereas Albignac (1981) saw 2-3 individuals (males and females) in the same diurnal refuge very frequently and noted extensive range overlap between neighbors. A later study of this species (Warren, 1994) revealed that 2-3 animals regularly form sleeping groups in tree holes. At night, individuals also moved together for several hours and engaged in long grooming sessions. Several (3-4) animals were regularly seen feeding without aggression in the same tree, especially during the dry season. The mean home-range size (of females) was 1.1 ha, with considerable overlap among them. Unfortunately, adult males have not yet been radio-collared, so that patterns of inter-sexual spacing are not known. Rasoloharijaona *et al.* (2000) and Thalmann (1998, 2001) report that certain individuals show large range overlaps. They observed one male and one female which had extensively overlapping home-ranges and another, possibly young male was present within this territory. Based on these observations, these authors proposed that *Lepilemur edwardsi* live in dispersed family groups.

Information on the social system of other sportive lemur taxa is mostly anecdotal. *Lepilemur mustelinus* was reported to occupy territories of about 1.5 ha, but sex differences in home-range size and the spatial organization of territories are not known. Grooming interactions between adults were never observed, suggesting that mother and dependent offspring may form the only permanent associations. Compared to other sportive lemurs, this species is not very vocal and rather cryptic (Ratsirarson and Rumpler, 1988). In *Lepilemur dorsalis*, there is little contact among adults, who apparently also spend the day alone in either tree holes or in dense vegetation (Petter *et al.*, 1977; Andrews *et al.*, 1998). *Lepilemur septentrionalis* defends territories of about 1 ha in size, but the spatial organization of individuals is not known. Individuals use more than one tree hole or liana tangle as sleeping sites (Ratsirarson and Rumpler, 1988). The social systems of *Lepilemur microdon* and *L. ruficaudatus* have not yet been studied in any detail (Porter, 1998; Ganzhorn, 1993; 2002).

Our study of the social system of *Lepilemur ruficaudatus* was prompted by partly conflicting incomplete and indirect observations. During studies of the feeding ecology (Ganzhorn, 1993; Ganzhorn and Kappeler, 1996; Pietsch, 1998; Ganzhorn 2002) and physiological adaptations (Schmid and Ganzhorn, 1996; Drack *et al.*, 1999) of this species in the dry deciduous forests of Western Madagascar, it became apparent that red-tailed sportive lemurs have relatively small home-ranges of about 1 ha that may overlap between males and females. These observations led us (Ganzhorn and Kappeler, 1996) to propose that *Lepilemur ruficaudatus* may live in pairs. On the other hand home-range overlap and defense were not quantified and the size and composition of sleeping associations was unknown. Moreover, male-biased sexual dimorphism in canine size (Kappeler, 1996), which is unusual for lemurs in general (Kappeler, 1993), indicated that a polygynous mating system, and thus a solitary social organization (Plavcan and van Schaik, 1994), is likely in some sportive lemur taxa.

The aim of our study was therefore to address these questions by characterizing basic aspects of the social system (*sensu* Kappeler and van Schaik, 2002) of *Lepilemur ruficaudatus*. Specifically, we studied the ranging behavior of individually marked red-tailed sportive lemurs to determine home-range parameters, such as size, spatial and temporal stability and inter-individual overlap, and we complement these behavioral observations with morphometric data that characterize sexually-selected traits and help to infer the mating system.

Methods

Study site and climate

This study was carried out in Kirindy Forest/CFPF, a dry deciduous forest in western Madagascar 60 km northeast of Morondava (44°39'E, 20°03'S) where the German Primate Center (DPZ) operates a research station. The study area (N5) is located within the 12,500 ha concession of the Centre de Formation Professionnelle Forestière (CFPF) de Morondava in this forest. The climate is characterized by pronounced seasonality with little or no rain from April to November, followed by a rainy season from December to February (Ganzhorn, 1995; Sorg and Rohner, 1996; Schmid and Kappeler, 1998). The forest is dense and most tree species do not

exceed 20m in height. For a detailed description of forest structure and phenology see Ganzhorn (1995) and Ganzhorn and Sorg (1996). Red-tailed sportive lemurs occur sympatrically with seven other lemurs species at Kirindy/CFPF, among them only one other folivore, the diurnal *Propithecus verreauxi verreauxi* (Ganzhorn and Kappeler, 1996).

The study area is defined by the boundaries of a systematic grid system. Within a 500 x 500 m core area, small trails were established every 25 m in both north-south and east-west directions, surrounded by additional trails at 50 m and 100 m intervals. Each intersection was marked with a plastic tag for orientation. The entire grid system was mapped and co-ordinates of each intersection were calculated.

Census data

To estimate the density of red-tailed sportive lemurs, we conducted several censuses. For one census, two of us (DZ and RH) walked along 29 trails within the grid system at about 1km/h. Each of the trials was 500 m long. We tried to avoid double-counting animals by patrolling up to 6 adjacent trails simultaneously with the help of some field assistants. Transect walks were performed on 3 subsequent nights between 19.00 h and 22.00 h in October and November. During earlier censuses (Ganzhorn 1992, 1995) no difference was found between pre- and post midnight counting. Individuals were detected by eye-shine, which could be seen at a distance of up to 20 m, by their vocalization or other noise from their leaps in the trees. Once detected, species identity of every individual was verified with the help of a strong flashlight. We counted individuals in a conservative manner and included only individuals that were detected visually. We recorded the position and encounter time of all detected *Lepilemur ruficaudatus*. Furthermore, we estimated the perpendicular distance between the animal and the path. We calculated the lower and upper limit of *Lepilemur ruficaudatus* density as follows. For the upper limit we used:

$$Ind/(l * 2 d) * 10.000 = Ind/ha \text{ (Ganzhorn, 1992)}$$

Ind = number of individuals seen

l = length of the transect (m)

d = mean distance of individuals from transect on both sides (m)

For calculating the lower limit, we assumed that the detected subjects represent all *Lepilemur ruficaudatus* within the study area.

We entered the encounter positions into a map of the grid system and tested possible clumping of individuals within the surveyed area by a 'Nearest Neighbor Analysis' (Animal Movement extension for ArcView®, Hooge and Eichenlaub, 1997) for both sets of transect walks in October and November.

Capture and Marking

Sportive lemurs were directly captured from their sleeping sites in hollow trees. Potential sleeping trees were located by transect walks and animals were caught by hand or by placing a live-trap at the tree hole entrance. Animals were then briefly anaesthetized with GM2 (Rensing, 1999) and marked with a unique subcutaneously injected transponder (Trovan; Usling, Germany). Most animals were equipped with 9g radio collars (Biotrack, Wareham Dorset, UK), which is less than 3% of body mass. Radio collars were fixed around the neck and could be easily removed after a maximum period of 10 months. Other animals were marked by shaving parts of their tail. During several study periods between April 1995 and November 2001, a total of 57 individuals were caught and 46 of them were fitted with radio collars for different periods of time (Table 1).

Table 1: Number of radio-tracked males and females per study period, mean number of observation days per individual and mean number of observation minutes per individual per observation day.

year	males	females	days/ind	minutes/ind/day
1995	6	6	9.0	135
1996	2	4	11.5	100
1998	5	4	20.8	120
2001	7*	12*	12.4	120
total	20	26		

* of each sex, one individual of each sex had less 600 g = subadult

Bodily measurements

For each individual captured in 2000 and 2001 DZ and RH took standard body measurements, including body mass, head-body length, skull width, skull length and canine height (Schmid and Kappeler, 1994). Morphometric data from earlier field seasons were discarded to minimize measurement error resulting from variation among researchers. For the estimation of sexual size dimorphism we used only data

from adult individuals. According to Ganzhorn (2002), we only considered individuals with more than 600 g body mass as adults but also took tooth wear into account when aging questionable individuals (see Richard *et al.*, 1993). A maxillary canine of one male was broken and those of one old female were heavily worn. We excluded these two animals from the comparison of canine size.

Data collection and analysis

To determine home-range size, radio-tagged animals were followed with radio-tracking equipment from Telonics (Mesa, AZ, USA). Observations were made with the aid of a headlamp and occasional use of a strong flashlight. In 1995, 1996, 1998 and 2001 we observed the animals mainly in the first half of the night. The number of radio-tracked and observed males and females for each year is given in Table 1. We used two different observation methods, scan sampling and focal animal sampling (Altmann, 1974). During scan sampling, we determined the location of each radio-tagged animal repeatedly in the same sequence by estimating the distance and bearing from the nearest marked intersection within the grid system. Within six hours, we conducted at least three rounds and obtained at least three data points on the location of up to 19 radio-tagged individuals. During focal observations we followed an animal usually for 2 hours at a time before switching to another individual. In 15-minute intervals, the exact location as well as the activity of the focal animal (foraging; resting; locomotion) was recorded. Social interactions were recorded in an all-occurrence manner. Subsequently we determined the x and y coordinates within the grid system for all recorded spatial positions. Centers of activity for each individual were calculated as harmonic means of the respective x and y coordinates of the spatial positions. Additionally, sleeping sites of *Lepilemur ruficaudatus* were marked and members of sleeping associations were identified during the day by radio signal or transponder identification (Fig. 1).

Analyses of spatial data, such as determination of home-range position, shape, size and overlap were performed with the Animal Movement (Hooge and Eichenlaub, 1997) extension for ArcView®.

Home-range analyses

Spatial data collected during radio-tracking were used to determine home-range position, shape and size. For an estimation of home-range size we calculated

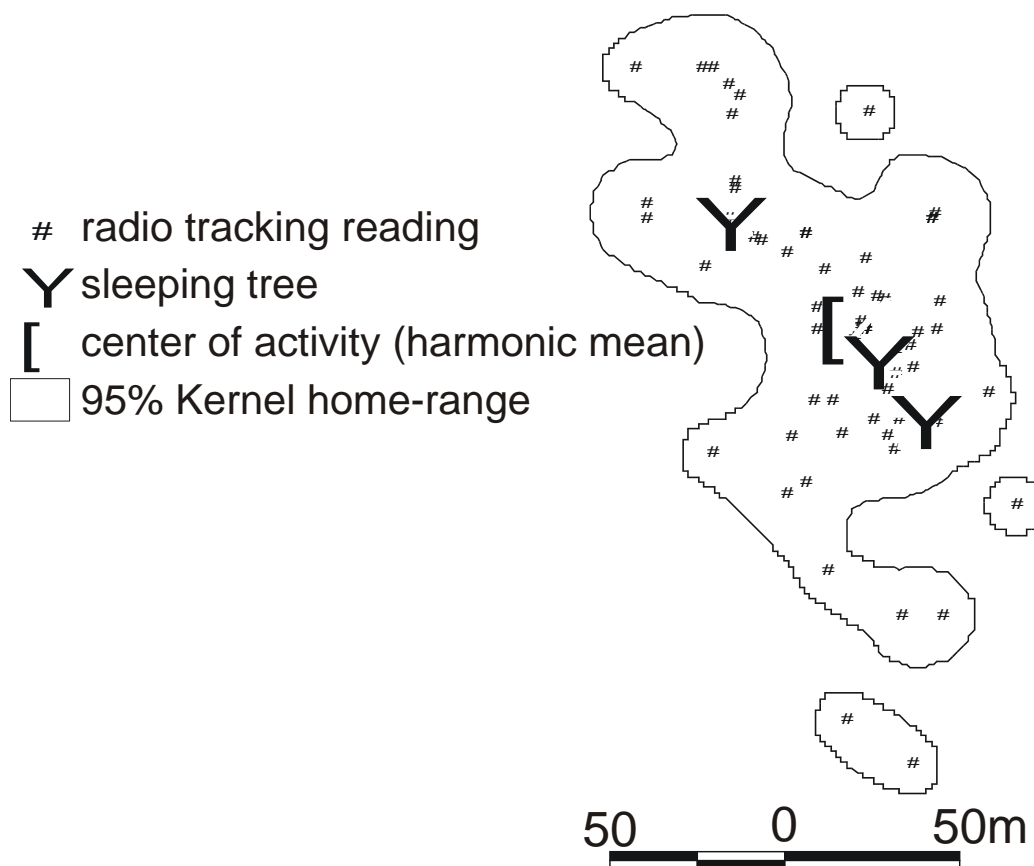95% Kernel probability plots (Harris *et al.*, 1990) (Fig. 1). Estimated home-range size

Fig. 1: Exemplary analysis of spatial data. For one individual, various radio-tracking bearings and the position of its sleeping trees are depicted. These data were combined to calculate a center of activity and the outline of its home-range, using the 95% Kernel method.

for the 19 individuals of the 2001 study period approached saturation (87.5% ±
8.5%) of true or maximum home-range size after sampling on average 50 data
points. In only 11 out of 46 cases our sample size was less than 50. In 20 cases we
had a sample size of more than 100 data points. For the calculation of home-range
size, we used spatial data of 46 individuals (20 males; 26 females) radio-tracked at
different study periods between June 1995 and November 2001.

Home-range overlap

To estimate home-range overlap we used radio-tracking data of 19 individuals
(7 males, 12 females, including 2 subadults) observed in 2001. An analysis of their
ranging data revealed a shift of the center of activity between the two observation
periods by only 30.2% (± 22.7%, corresponding to a mean of 91.6 m) of the
maximum home-range diameter. None of the animals' activity centers in October-
November 2001 were found outside the corresponding home-range determined in
February-April 2001. We therefore pooled the spatial data from both observation

periods to analyze overlap. To compare home-range overlap of individuals with potential pair-partners and adjacent individuals we used the "Exact Permutation Test" of means with 10,000 permutations (Manley, 1997).

To test home-range stability over years, we used data from nine individuals observed over up to six consecutive years (1995–2001). For each individual and year we determined the respective individual centers of activity and calculated the distance between the centers from the first and last year of observation. To evaluate the shift of activity centers, we compared the distance with the maximum diameter of the respective home-range as reference value for each individual.

Sleeping sites and associations

Data on the location of sleeping trees and the composition of sleeping associations were recorded in October 2000, February-April 2001 and October-November 2001 on a total of 117 days (control days). We determined the identity of the animals through their unique radio collar while the animals were in the sleeping tree. Additionally, we observed them when leaving the sleeping hole. We used the composition of sleeping associations and the common or exclusive use of shelters to identify potential pair-partners.

Ethical note

In all cases animal handling caused no remarkable impairment of the individuals. All procedures in our study were carried out with the permission of the Government of Madagascar and were in accordance with current laws of Madagascar.

Results

Morphometrics

In 2000 and 2001 we obtained morphometric data from 19 adult females and 15 adult males. In general, we found no sexual dimorphism in any variable related to body size (Table 2). However, male canines were on average almost 15% longer than those of females.

Table 2: Body size and canine length of adult (> 600 g) male and female *Lepilemur ruficaudatus*. (Data from October-November 2000 and February–April 2001)

sex	mean	N	SD	range	t	p
body mass (g)						
f	779.63	19	102.30	630 - 896	-0.06	0.9505
m	781.60	15	73.99	610 - 930		
head-body length (cm)						
f	30.51	19	1.34	28.01 – 33.00	-0.30	0.7638
m	30.66	15	1.59	28.14 – 34.37		
skull length (cm)						
f	6.15	19	0.20	5.78 – 6.51	-1.09	0.2827
m	6.23	15	0.22	5.67 – 6.58		
skull width (cm)						
f	3.86	19	0.09	3.64 – 4.05	-1.59	0.1218
m	3.91	15	0.11	3.66 – 4.10		
left upper canine (cm)						
f	0.61	18	0.06	0.53 – 0.76	-3.48	0.0016
m	0.70	14	0.08	0.55 – 0.83		

Population density

We estimated population density twice, in October and November 2001. Places where sportive lemurs were encountered during each census are depicted in Fig. 2. The mean encounter rate was 41.5 individuals on a total transect length of 14,500 m within the study area (975 x 500 m). For the density we calculated a minimum of 87.5 individuals/km² (0.9 ind/ha) and a maximum number of 159.8 individuals/km² (1.6 ind/ha). Nearest neighbor analysis revealed that located individuals were not patchily distributed within the study area (October: n = 43, R = 0.91, z = 1.2 n.s.; November n = 40, R = 1.0, z = 0.40, n.s.).
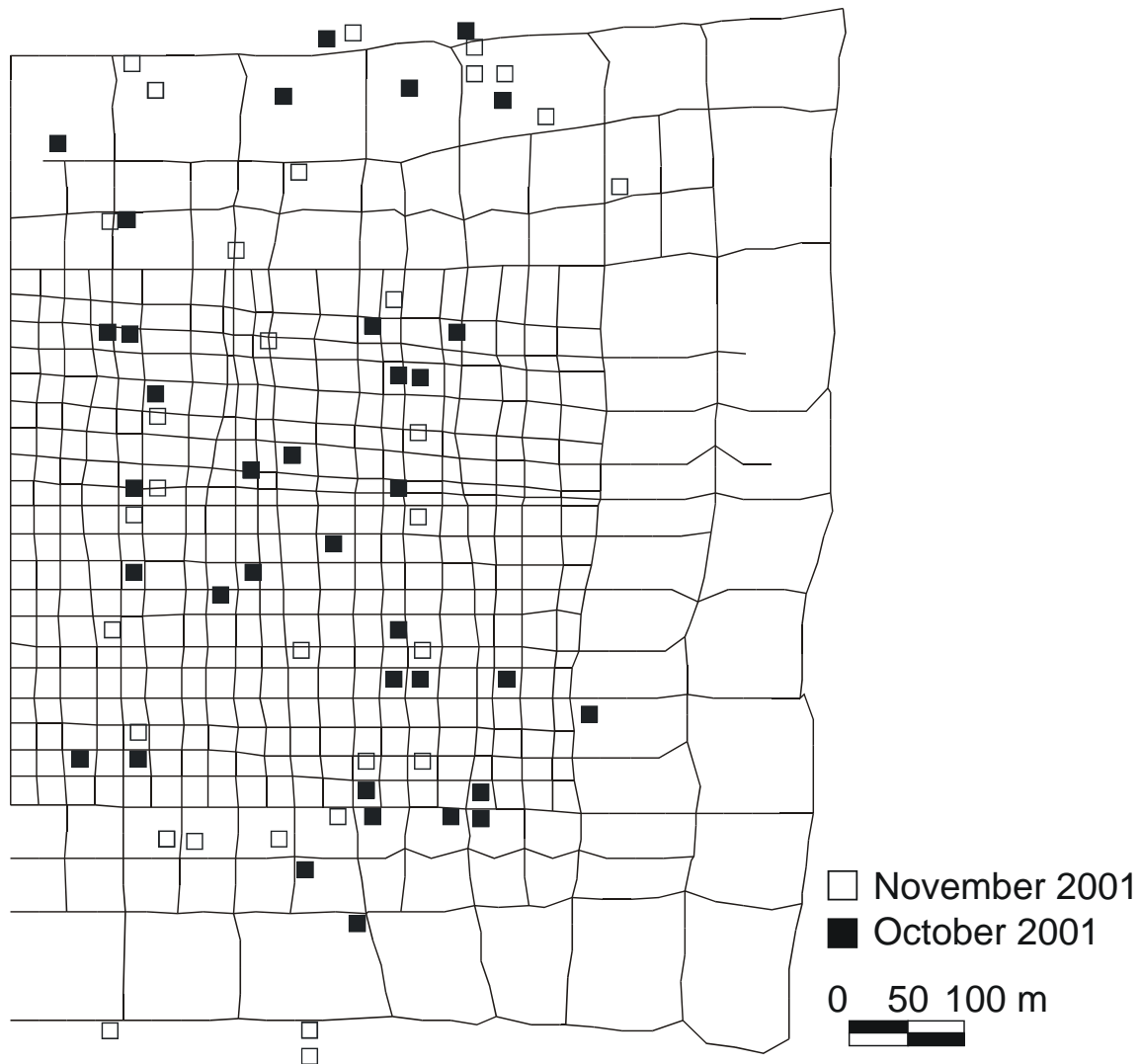
Fig. 2: Population density of *Lepilemur ruficaudatus*. Each square represents a sighting of one individual during transect walks in October and November 2001, respectively.

Home-range size

The mean home-range size of all 46 *Lepilemur ruficaudatus* was 7977 m^2 (SD = 3895 m^2). Size did not differ between sexes and among subsequent years (Fig. 3).

Home-range stability

From 9 individuals we had home-range information from more than one study period, between 1995 and 2001. We analyzed home-range stability of these individuals over a minimum period of 223 days and a maximum period of 2080 days by comparing the positions of the respective centers of activity (Fig. 4). Overall, we found no correlation between shift of activity centers and length of time intervals between subsequent observations (n = 9, r = 0.36, p = 0.395). However, excluding one data point from the analysis (case * identified statistically as an outlier in Fig. 4), we found a positive correlation between distance of activity center shift and time

interval (n = 8, r = 0.74, p = 0.035). Nonetheless, in eight out of nine cases the shift of activity center was considerably below the maximum diameter of the respective home-ranges. On average home-range shift was 53.04% (SD = 50.96%) of the maximum home-range diameter, suggesting that *Lepilemur ruficaudatus* are able to maintain stable home-ranges over several years.
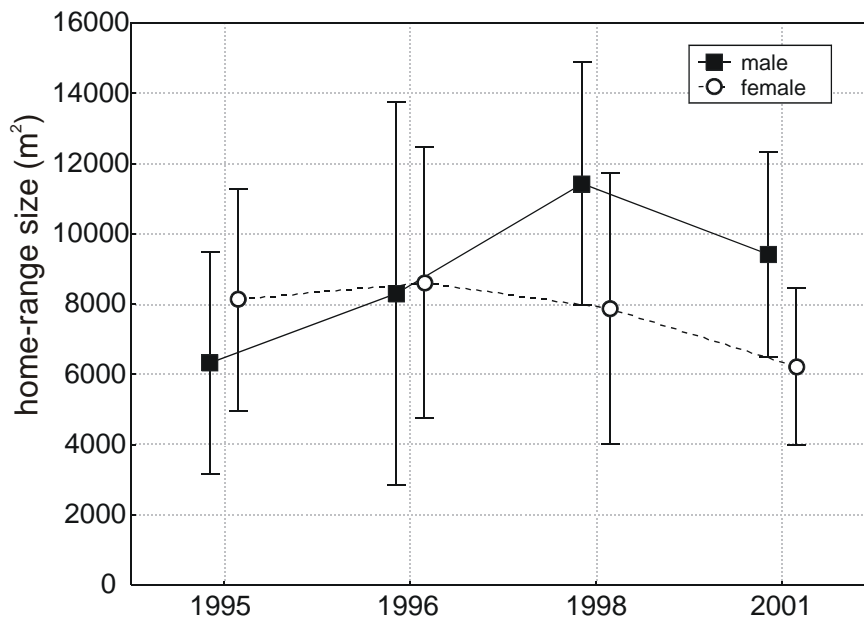

Fig. 3: Mean home-range size (m²) of male and female *Lepilemur ruficaudatus* (95% Kernel home-ranges). 2-way ANOVA: year: $F_{3,38} = 0.75$, p = 0.5309; sex: $F_{1,38} = 0.84$, p = 0.3656; year x sex: $F_{3,38} = 1.35$, p = 0.2741; (means ± 95% confidence intervals).
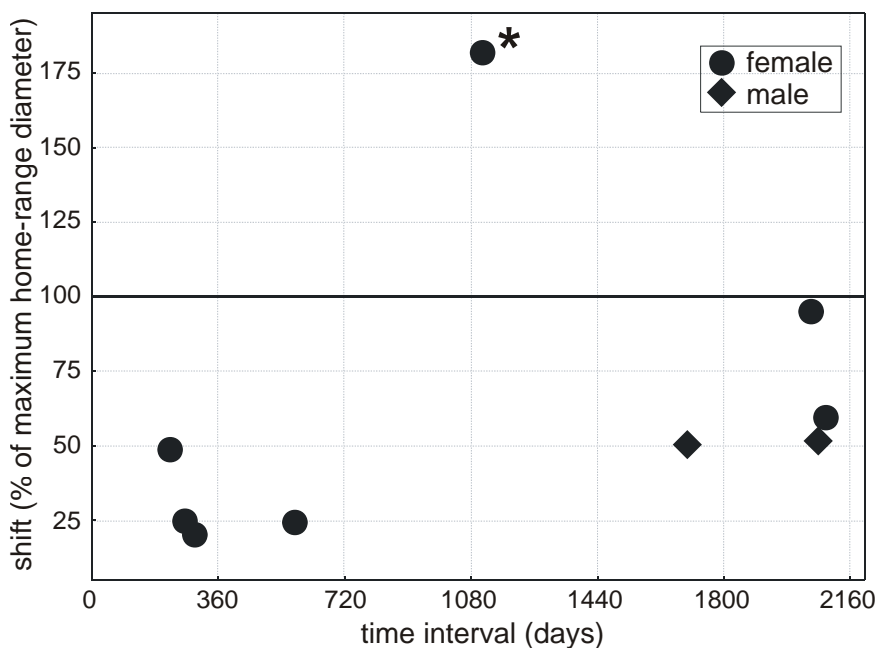
Fig. 4: Shift of centers of activity of *Lepilemur ruficaudatus* over time (7 months to 6 years) in relation to the respective maximum home-range diameter.

Home-range overlap

We estimated home-range overlap with data from 19 animals studied in 2001. In four cases we found extensively overlapping home-ranges between one adult male and one adult female, respectively, and in two cases home-ranges of a male overlapped extensively with that of two females (Fig. 5). In one of the latter two
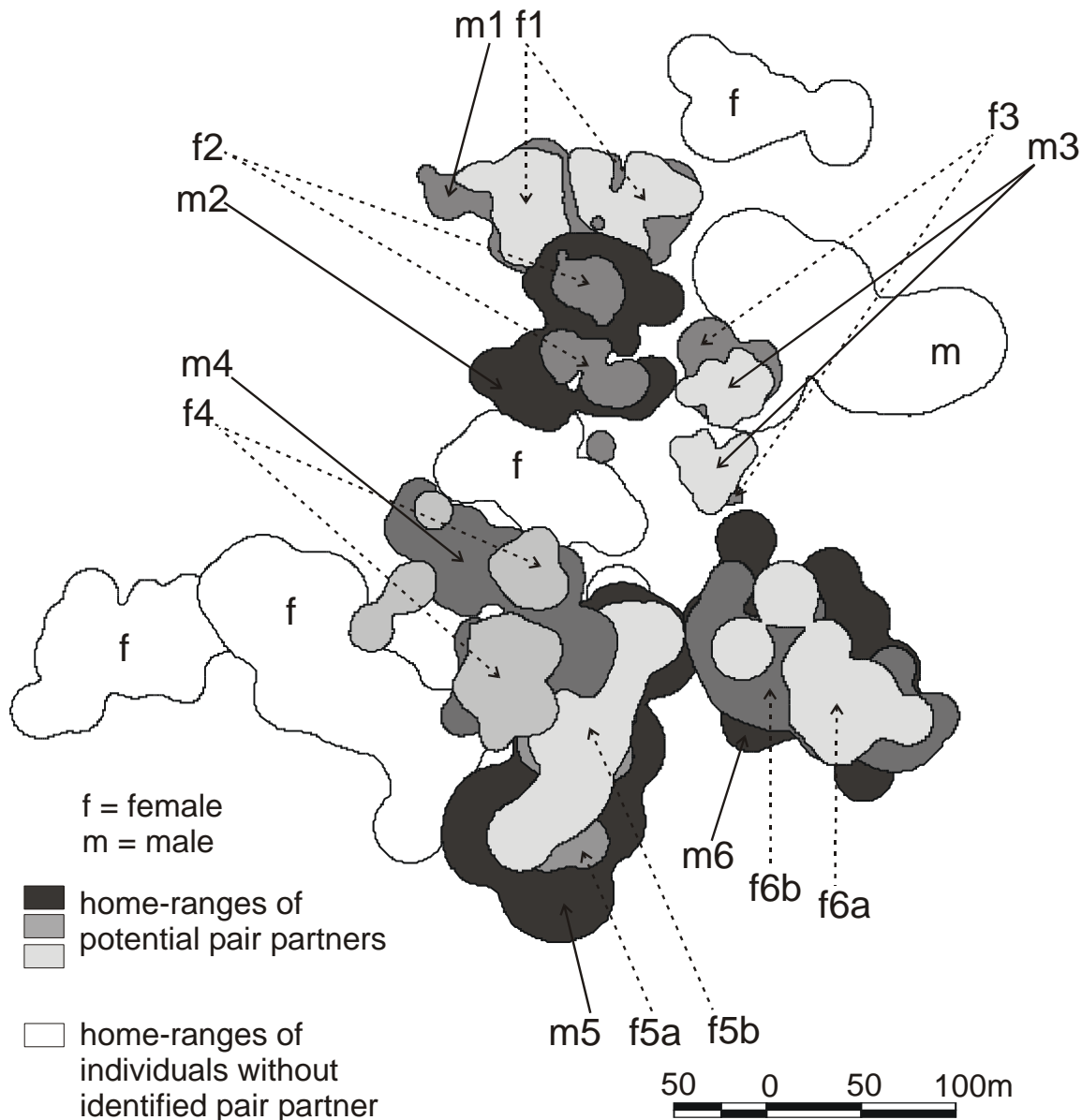

Fig. 5: 95% Kernel home-ranges of 19 *Lepilemur ruficaudatus* in 2001. Overlapping home-ranges of potential pair-partners are shaded.

cases, one of the two females (f6b) was classified as subadult at the date of capture in October 2000 (body mass 475 g) but was considered adult in October 2001. In the second case, both females were adult. Average degree of home-range overlap between these pair partners was 80.5% $\pm$ 19.3% from the females' and 49.1% $\pm$ 19.3% from the males' perspective. Home-range overlap between them was

significantly higher than overlap with other neighbors (overlap = 7.21% $\pm$ 3.62%; number of neighbors = 2 - 6; Exact Permutation Test, p < 0.001).

Shelter utilization and sleeping associations

Between October 2000 and November 2001 we detected a total of 97 sleeping sites of 19 *Lepilemur ruficaudatus*. The sleeping sites were in all cases hollow trees, with a maximum of three entrances per tree. Individuals spent most of the day inside these tree holes or close to the hole. Four times individuals were observed feeding on leaves or fruits next to their sleeping hole during daytime. In 2001 the 19 individuals used on average 5.6 ± 1.8 (range 2 - 9) sleeping trees, all located within their respective home-ranges. We found no difference in number of sleeping trees used by the sexes (Exact Permutation Test, p = 0.584).

Table 3: Number of sleeping holes shared with pair partner, used exclusively or shared with neighbors (n = 14).

pair	# sleeping trees		
	shared with pair-partner	exclusively used F / M	shared with neighbors F / M
f1/m1	5	2 / 3	0 / 0
f2/m2	3	0 / 1	0 / 0
f3/m3	5	2 / 1	0 / 0
f4/m4	5	0 / 2	0 / 0
f5a/m5	2	1 / 4	0 / 0
f5b/m5	3	5 / 4	0 / 0
f6a/m6	1	1 / 4	0 / 0
f6b/m6	4	5 / 4	0 / 0
mean	3.5	2.0 / 2.9	0 / 0
f5a/f5b	3		
f6a/f6b*	0		

* subadult

On average potential pair-partners shared 3.5 sleeping holes (Table 3), either simultaneous or successively. Female pair-partners used on average 2.0 holes exclusively; corresponding males used 2.8 holes. In those groups where two females shared a home-range with a male, we found in one case that both females shared three sleeping holes, whereas in the second case we found no evidence for

sharing sleeping holes. Sleeping holes were never shared among neighbors, neither simultaneously nor successively.

On an average of 37 days (range 6 – 66 days), we controlled the sleeping sites of both pair-partners and on an average of 8 days (26.3%) we found both of them in the same sleeping tree (Table 4). The frequency of simultaneous use of sleeping trees varied considerably among pairs (1.7% - 83.3%). In one trio (1 male, 2 females) both females slept on 85.0% of the 40 control days in the same tree. In the second case both females were never observed together in the same sleeping hole on 21 control days.

Table 4: Frequency of simultaneous use of sleeping tree by potential pair partners. (control days = number of days both pair-partners were controlled in their sleeping hole; days simultan = number of days when pair-partners were detected in the same sleeping tree).

pair	control days	days simultan	frequency [%]
f1/m1	66	22	33.3
f2/m2	48	24	50.0
f3/m3	59	1	1.7
f4/m4	32	3	9.4
f5a/m5	19	4	21.1
f5b/m5	38	3	7.9
f6a/m6	28	1	3.6
f6b/m6	6	5	83.3
mean $\pm$ SD	37 $\pm$ 20	8 $\pm$ 9	26.3 $\pm$ 28.4
f5a/f5b	40	34	85.0
f6a/f6b	21	0	0.0

Discussion

Our study produced the first quantitative data on the social organization of *Lepilemur ruficaudatus*. We found that most males and females live in mutually overlapping home-ranges, some of which were occupied by the same individuals for several years. Members of such pairs spent only every 3rd or 4th day together in the same sleeping shelter, however. Other stable constellations consisted of one male and two females. Below, we discuss these key findings in a comparative context.

Home-range and population characteristics

Average home-range size in our study area was 0.8 ha, and there was no difference between males and females. Furthermore, home-range size did not differ among subsequent years and between seasons. A similar home-range size (1 ha) was reported for *Lepilemur edwardsi* in Ampijoroa, (Warren and Crompton, 1997; Albignac, 1981), but there samples were too small to test possible sex differences. In contrast, home-ranges of *Lepilemur leucopus* at Berenty were considerably smaller (0.15 ha and 0.30 ha, Hladik and Charles Dominique, 1974; Russell, 1977), yielding a higher population density. In the Berenty population males had 80% larger home-ranges than females (Russell, 1977). We estimated population density of *Lepilemur ruficaudatus* to vary between 87.5 and 159.8 individuals/km². The lower value probably underestimates true population density, because it is likely that we did not detect all of these rather cryptic individuals during our transect walks. However, our estimate supports population densities reported by Ganzhorn and Kappeler (1996) of 144 individuals/km² in the same study area between 1988 and 1992. This population density, however, is surpassed by the population density of *Lepilemur leucopus* in the xerophyte spiny forest in Berenty (200 – 350 per km^2, up to 810 individuals per km^2 in gallery forest, Charles-Dominique and Hladik, 1971; Hladik and Charles-Dominique, 1974). Ecological factors, such as habitat quality may account for these differences in home-range size and population density.

For nine individuals, we were able to compare the spatial position of home-ranges over a maximum time period of 6 years by examining the shift of their activity centers. In eight of these individuals, the shift was considerably below the respective maximum home-range diameter, demonstrating that *Lepilemur ruficaudatus* maintain stable home-ranges over years. Home-range stability, and thus presumably settled relations with known neighbors, may be of particularly advantageous for sportive lemurs because energy conservation appears to be of paramount importance to them (Schmid and Ganzhorn, 1996; Drack *et al.*, 1999; Ganzhorn, 2002). The consequences of such home-range stability for dispersal options of maturing individuals remain to be studied.

Social organization

The spatial distribution of individuals defines important aspects of social organization (Kummer and Kurt, 1963; Sterling *et al.*, 2000; Kappeler and van

Schaik, 2002). First, we emphasize that we have evidence from census walks and direct observations that no other animals lived within the home-ranges of our focal individuals. We found that home-ranges of adult males overlapped extensively with those of at least one adult female. In addition, there was very little overlap with same-sexed neighbors. Two out of six adult males occupied home-ranges that overlapped extensively with those of two females. In both cases both females exhibited sleeping associations with the respective male. In one case, one of the females was caught in the male's home-range as a juvenile (475 g) in October 2000 and stayed there throughout 2001. The second female was clearly adult (794 g). It is possible that these female-female associations within one home-range constitute mother-daughter dyads. Ongoing genetic analyses will resolve individual relationships among members of these trios. Pattern of (joint) sleeping site use corresponded to the spatial distribution of individuals.

Our data on home-range distribution and utilization indicate that pair-living is the modal social organization of this population, but that there is possibly a tendency by males to associate with more than one female. Such variation is commonly observed in most pair-living primates (Fuentes, 1999, 2002; van Schaik and Kappeler, 2003).

Similarly, within the genus *Lepilemur* different types of social organization have been described. For example, both pair-living (Thalmann, 2001) and a dispersed harem system (Warren and Crompton, 1997) have been suggested for the same population of *Lepilemur edwardsi*. Because of our current lack of sufficient data on interactions and communication, we are unable to characterize the closeness and permanence of the association between pair-partners as either dispersed or cohesive (van Schaik and Kappeler, 2003; Schülke and Kappeler, 2003). The relative low frequency with which pair partners share sleeping sites indicates, however, that these red-tailed sportive lemurs may provide another example for dispersed pairs, which are characterized by rare direct interactions and infrequent association.

Furthermore, we can not confidently characterize the mating system of this population with the currently available data. First, as demonstrated by a study of sympatric fat-tailed dwarf lemurs (*Cheirogaleus medius*), behavioral evidence for pair-living cannot be used to infer a monogamous mating system. In *Cheirogaleus medius*, males and females are also organized into stable pairs, but several infants

were not sired by their social father (Fietz *et al.* 2000). Second, the observed degree of sexual canine dimorphism indicates that male *Lepilemur ruficaudatus* compete for important resources, such as access to females. In contrast to the "typical" pattern of home-range overlap in many solitary primates, in which male ranges overlap those of several females (Müller and Thalmann, 2000), we found that only a minority of males shared their range with more than one female, possibly offspring of the pair.

With the preliminary data currently available we can not decide whether the social organization of *Lepilemur ruficaudatus* reflects a primary response to ecological constraints, such as resource distribution, or social and reproductive constraints, such as infanticide prevention or mate guarding by males (Fuentes, 2002). Direct observations of social interactions, mechanisms of home-range defense, estimates of resource distribution and utilization combined with acoustic playback experiments are underway to illuminate the causes of pair living in *Lepilemur ruficaudatus.*

Acknowledgments

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CHAPTER 2:

Life history traits and parental care in *Lepilemur ruficaudatus*

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Abstract

In this study we investigated the importance of bi-parental care for the evolution and/or maintenance of pair-living in red-tailed sportive lemurs (*Lepilemur ruficaudatus*), a nocturnal folivorous lemur. Between 2000 and 2005, we collected data on life history traits from a total of 14 radio-collared pairs of adults and their offspring in Kirindy forest, western Madagascar. Patterns of parental care were quantified during simultaneous focal observations of both pair partners in 2003 and 2004. Mating activity was limited to the months of May and June, as indicated by conspicuous changes of vulval morphology and male mate guarding behavior After a gestation length of about five months, which is much longer than expected for a lemur of this body mass, single infants were born in November. Lactation lasted for about 50 days. Apart from lactation, females provided infant care by warming, grooming and transporting infants orally. Infants were parked in dense vegetation while females foraged. Males were seen only rarely in proximity to infants and we found no evidence for direct infant care provided by social fathers. We conclude that the necessity of direct infant care cannot explain the evolution and/or maintenance of pair-living in *Lepilemur ruficaudatus*.

Keywords: life history; pair-living; parental care; *Lepilemur ruficaudatus*

Introduction

Life history traits are products of evolution [Charnov, 1993; Charnov, 1991; Promislow and Harvey, 1990] that are closely related to ecological and social aspects of an animal's behavior. The relationships among primate life history traits and behavior have only recently begun to be explored in detail [Charnov and Berrigan, 1993; Clutton-Brock et al., 1996; Kappeler et al., 2003]. For example, litter size and mode of infant care influence behavior of adult males and females and may facilitate the evolution of a particular social organization [van Schaik and Kappeler, 1997]. However, theoretical considerations and phylogenetic analyses suggest that some life history traits may have evolved after the adoption of a certain social organization [Dunbar 1995; Komers and Brotherton 1997]. For example, the evolution of pair-living and biparental infant care in New World primates could be the result of twinning, or vice versa [Dunbar, 1995].

Information about life history traits is required for comparative studies that examine general patterns in primate evolution and socioecology [Clutton-Brock and Harvey, 1977; Lee, 1999; Lee, 1997; Ross, 1998]. Unfortunately, even the most basic life history traits, such as body mass or gestation length, remain unknown for many primate species [Kappeler and Pereira, 2003]. This is especially true for nocturnal strepsirrhines, even though they exhibit some of the most striking variation in life history traits, including litter size and infant care pattern [Gursky and Nekaris, 2003; Kappeler, 1996; Kappeler and Heymann, 1996; Kappeler, 1998; Ross, 2001]. Similarly, behavioral aspects of the mating and rearing system of nocturnal primates, many of which have functional life history correlates, are still lacking for many species in the wild [but see Gursky and Nekaris, 2003; Nekaris, 2003; Eberle and Kappeler, 2006]. Among pair-living nocturnal lemurs, for example, observations on parental care are only available for *Cheirogaleus medius.* In this species, twinning is typical and baby-sitting in the form of nest guarding, infant warming and guided excursions of infants is provided by the male and female [Fietz and Dausmann, 2003]. Because of the thermoregulatory demands of newborns and high predation pressure, obligate paternal care has been invoked as the ultimate cause for the evolution of pair-living in this species [Fietz, 1999].

The red-tailed sportive lemur (*Lepilemur ruficaudatus)* is a small (780 g) nocturnal folivorous lemur living sympatrically with *Cheirogaleus medius, Microcebus*

murinus, *Microcebus berthae*, *Mirza coquereli*, *Phaner furcifer*, *Eulemur fulvus rufus* and *Propithecus verreauxi verreauxi* in the dry deciduous forest in western Madagascar. *Lepilemur ruficaudatus* is socially organized in pairs, which maintain small (about 1ha) stable territories for several years [Ganzhorn and Kappeler, 1996; Zinner et al., 2003]. It has been reported that *Lepilemur* parks its single infants in dense vegetation [Petter, 1962; Petter Rousseaux, 1964], but detailed observations on parental care and data on basal life history traits are lacking, as for all other members of the genus [cf. Nash , 1998]. As with most lemurs, *L. ruficaudatus* is considered to be a seasonal breeder. Even though the temporal pattern of matings and births was only inferred indirectly, several influential studies of the ecology and sociobiology of *L. ruficaudatus* were based on these preliminary data [Ganzhorn, 2002; Ganzhorn et al., 2004; Pietsch, 1998].

The most prominent hypothesis that aims to explain the evolution/maintenance of pair-living is the paternal care hypothesis, which assumes that male infant care is essential for the survival of newborns [Kleimann 1977; Gubernick, 1994; Møller and Cuervo, 2000]. However, quantitative data on paternal care are limited and often insufficient to evaluate this hypothesis in pair-living lemurs (cf. Frederick 1988; Nekaris 2003; Wright, 1990). Hence, the aim of our study was (1) to detail patterns of parental care to examine its potential importance in the evolution and/or maintenance of pair-living red-tailed sportive lemurs. If paternal care occurs, we expect that males engage in some form of direct infant care, such as grooming, carrying behavior, baby-sitting and predator detection or defense (Wright, 1990), and (2) to contribute quantitative data on several life history traits of *L. ruficaudatus* based on long-term observations. During a field study spanning five consecutive years, we determined mating and birth seasonality, gestation length, lactation length, inter-birth intervals and predation rates in a population of individually-marked animals.

Methods

Study site

The study was carried out in Kirindy Forest (20°03'S, 44°39'E) in western Madagascar, 60km northeast of Morondava, where the German Primate Center

(DPZ) operates a research station within a 12,500ha forest concession of the C.F.P.F. (Centre de Formation Professionnelle Forestière). The climate is characterized by pronounced seasonality with a short and hot rainy season from December to February, followed by a cooler dry season with little or no rain from April to November [Sorg and Rohner, 1996]. The mean annual temperature is 24.7°C, with a mean minimum of 19°C and a mean maximum of 30.7°C. Temperature in the dry season can drop at night to 4°C, whereas in the rainy season temperatures do not drop below 20°C at night. The forest is dense and most tree species do not exceed 20m in height [Ganzhorn and Sorg, 1996; Sorg et al., 2003].

The study area (locally known as N5) was defined by the boundaries of a systematic grid system. Within a 500 x 500m core area, small foot trails were established every 25m in both north-south and east-west directions, surrounded by additional trails at 50m and 100m intervals along three edges of the core area. Along its western border, former logging trails (200m long at 100m intervals) were also used for radio-tracking. Each intersection was marked with a plastic tag for orientation. The entire grid system was mapped and co-ordinates of each intersection were calculated.

Capture and marking

Red-tailed sportive lemurs were directly captured from their sleeping sites in hollow trees. Potential sleeping trees were located by transect walks and animals were caught by hand or by placing a live-trap at the tree hole entrance. Individuals use up to 9 different sleeping sites [Zinner et al 2003]. In some cases sleeping sites were avoided for a few days subsequently to a capture. Captured animals were briefly anaesthetized with GM2 [Rensing, 1999] and individually marked with a subcutaneously injected transponder (Trovan; Usling, Germany). Between 1995 and 2004, a total of 87 individuals were captured and marked. Between 2000 and 2005, 28 adults were fitted with 9g radio collars (Biotrack, Wareham Dorset, UK), which weigh less than 3% of body mass (mean body mass: 780g; range 610-930g) [Zinner et al; 2003], including five individuals where only one pair partner was captured. Radio collars were fixed around the neck and could be easily replaced after a maximum period of battery life of 10 months. Infants and subadults were marked by shaving parts of their tail in a unique fashion.

Radio-tracking and behavioral observations

We followed radio-tagged animals with radio-tracking equipment from Telonics (Mesa, AZ, USA) during several study periods between October 2000 and December 2004. Behavioral data were collected during the birth seasons in 2002 and 2003. In 2004, only data on birth dates were collected. Behavioral data during the mating season were collected for the years 2003 and 2004. We observed the animals mainly during the first half of the night (18.00-02.00h) with the aid of a headlamp and occasional use of a strong flashlight. We attempted to observe all adult animals for equal periods of time. Together with a Malagasy field assistant, R.H. followed both pair-partners simultaneously [Schülke and Kappeler, 2003], using focal animal sampling [Altmann, 1974] for 3 consecutive hours. In 5-minute intervals, the exact location, as well as the activity of the focal animal (foraging, resting or locomotion) were recorded. Social interactions were recorded in an all-occurrence manner. Additionally, sleeping sites of *L. ruficaudatus* were located during the day, and members of sleeping associations were identified via their radio signal or their transponder code was read with a hand-held reading device through the tree trunk.

Mating season

To delineate the mating season, we used a combination of behavioral observations and morphological data. Reproductive state of females was determined by external examination of vulval morphology. As for example in *Microcebus murinus* [Eberle and Kappeler, 2002], female *L. ruficaudatus* show a marked swelling and reddening of the vulva during estrus. In May and June, the external genitalia of these vertical clingers and leapers were examined from close range with the aid of a strong flashlight and binoculars without capturing animals. Each marked female was examined at least once per night. We recorded whether the vulva was swollen and reddish or flat and inconspicuous.

Gestation and lactation length

We estimated gestation length for five females in 2003 and eight females in 2004 as the time interval between observed mate guarding and birth. Birth dates were determined directly by daily controls of females in their sleeping holes. We used mate guarding as the most conservative method to identify the brief time window during which conception was most likely. Observations of copulations and swollen

vulvas of females coincided with phases of mate guarding (range: 1-5 days). However, a margin of error of about 5 days around the exact date of conception was unavoidable. Data on gestation lengths for other lemur species were extracted from the literature for comparative purposes. Lactation length was calculated from date of birth until independence of infants. Independence of infants was operationally defined as (1) leaving the sleeping hole alone, (2) not being transported in mother's mouth, (3) not getting parked during nocturnal activity, and (4) independent foraging.

Infant care

Data on infant care derive from 13 infants born between 2002 and 2004, for which both pair-partner were marked. The exact infant parking location was noted for distance estimation between the mother and the infant, as well as the respective social father and the infant. Percentage of time the offspring stayed in physical contact with the mother was calculated. Our spatial analyses are based on radio-tracking data of 13 infants and respective pair partners and included 75-245 data points or fixes per individual. To test for differences in inter-individual distances between pair partners and infants, values were arcsin-transformed. The adult male pair partner that shared a home-range with the mother during mating and birth season was called social father.

Predation

Calculation of predation rates were based on observed or inferred predation events of marked individuals (n=45). Predators were identified by direct observations, predator-specific characteristics of the leftover carcasses or predator-typical bite marks on radio collars. Age estimates of predated individuals are based on a combination of body size, dental wear and date of first capture. Aging based on body mass alone was not possible due to seasonal fluctuations of body mass [Ganzhorn 2002]. We considered males as adult if body mass was >700g and testes were fully descended. Females were considered as adults if body mass was >700g and teats were fully developed and showed signs of use (e.g. lack of hairs around teats). All variables were calibrated with individuals of known age. Certain adult individuals within our study population have been known for 10 years. Because we do not have complete data sets for all individuals, samples sizes on which particular analyses are based may vary.

Ethical note

In all cases animal handling had no noticeable adverse effects on the behavior of individuals. All procedures in our study were carried out with the permission of the government of Madagascar and were in accordance with current laws of Madagascar.

Results

Mating season

Duration of mate guarding varied between one and five nights (mean: 3.0; SD: 1.3; n=14). Mating was highly seasonal and limited to only a few weeks in May and June in both 2003 and 2004. In all other months no mating or mating attempt were observed. During most of the year, the vulval area was flat and inconspicuous, but during May and June 2003 a conspicuous change, including swelling, reddening and opening, was observed in five out of nine adult females. In May 2004, all nine adult females under observation exhibited these morphological changes. Moreover, observations of mate guarding of females, defined by males staying significantly closer to their pair partner than during the rest of the year [Hilgartner et al., submitted], contributed to the delineation of the mating season. In all cases mate guarding overlapped with time of female vulval changes. Mate guarding was observed in five pairs in 2003 and in nine pairs in 2004. Mating was observed four times in three pairs (31.05.2003; 31.05.2003; 18.05.2004, 29.05.2004). In three cases mating occurred within a social pair; in one case an extra-pair copulation was observed. In all four cases mating was initiated by the female approaching the nearby male. Duration of mating varied between 3min and 9min 35s. Although mate guarding was observed for several days, we never observed females mating on two different nights.

Gestation length and inter-birth interval

We determined gestation length for five females in 2003 and eight females in 2004. Gestation took place during the dry season and lasted on average 176 days (range:

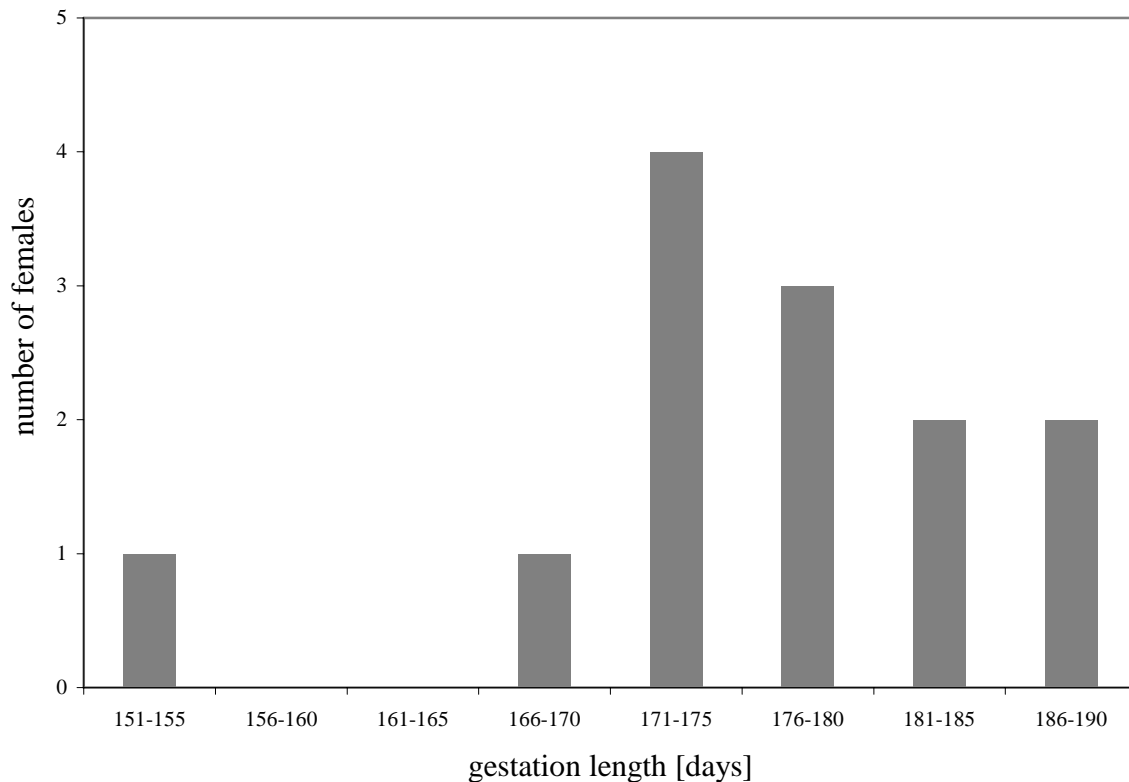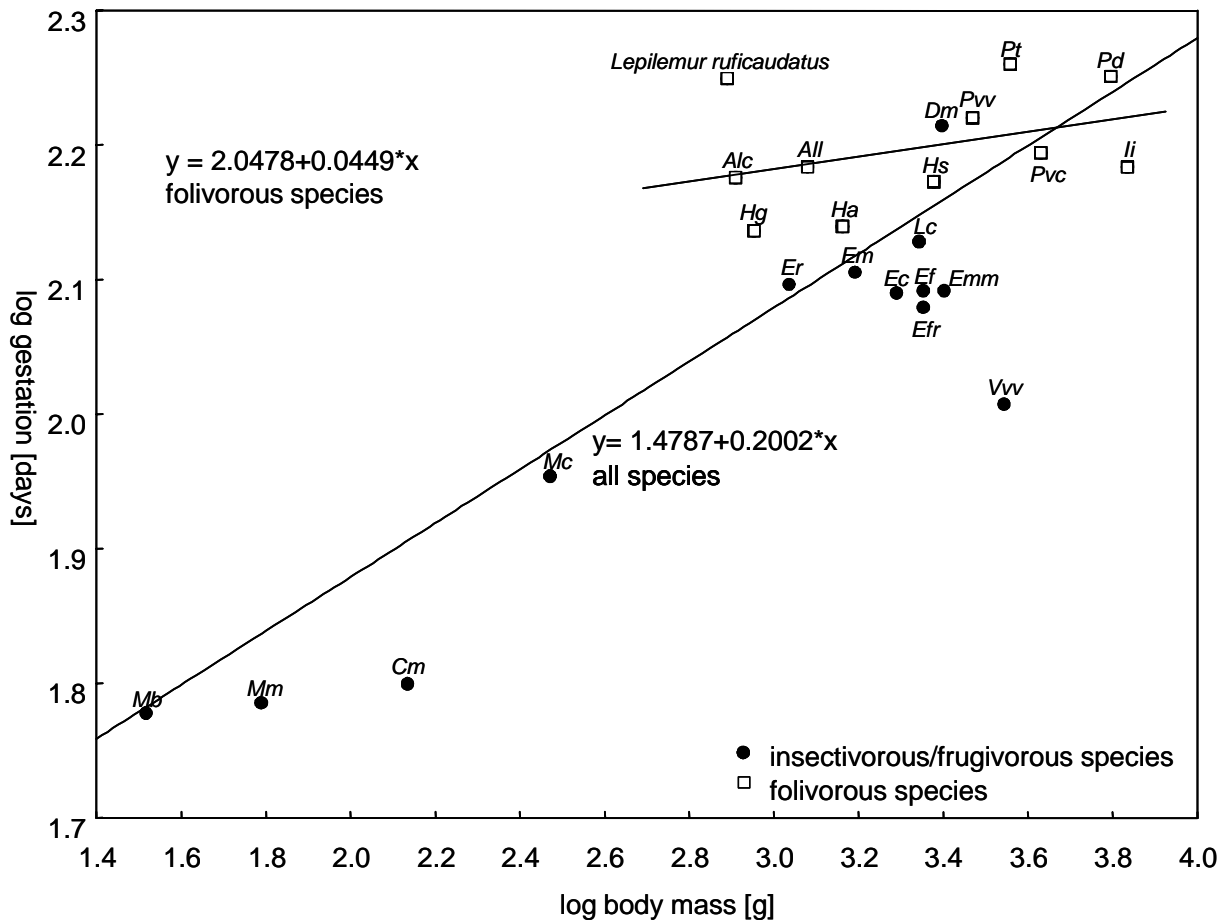151-188; Fig. 1). In 13 cases females had an inter-birth interval of one year; five times it was ≥2 years.

Fig. 1: Distribution of gestation length of *L. ruficaudatus* (n=13)

A comparative data set on gestation lengths of Malagasy primates was compiled to compare gestation lengths of Malagasy primates with *L. ruficaudatus*. Using double logarithmic scales to identify a general trend among species, a linear regression between gestation length as dependent and body mass as independent variable was calculated (Fig. 2). In contrast to frugivorous or insectivorous species, all predominantly folivorous lemur species, except *Propithecus v. coquereli* and *Indri indri* have longer gestation lengths than predicted. Within frugivorous and insectivorous species, *Daubentonia madagascariensis* is the only species which has a considerably longer gestation than expected based on its body mass. The gestation length of *Lepilemur ruficaudatus* is much longer than expected for a lemur of this body mass. It exhibited the highest positive residuals, irrespective of whether one compares all lemurs or only folivorous species.

Fig. 2: Gestation length in relation to body mass across Malagasy primates with different dietary adaptations. Species are considered as folivorous if they devote more than 34% of their feeding time to foliage. Alc *Avahi laniger occidentalis* [Thalmann, 2003], All *Avahi laniger laniger* [Tattersall, 1982; Thalmann, 2003], Cm *Cheirogaleus medius* [Fietz, 1999; Fietz and Dausmann, 2003; Foerg, 1982], Dm *Daubentonia madagascariensis* [Kappeler and Pereira, 2003; Sterling, 2003], Ec *Eulemur coronatus* [Kappeler and Pereira, 2003], Ef *Eulemur fulvus* [Glander et al., 1992], Efr *Eulemur fulvus rufus* [Boskoff, 1978; Klopfer and Boskoff, 1979], Em *Eulemur mongoz* [Terranova and Coffman, 1997; Wright, 1990], Emm *Eulemur macaco macaco* [Smith and Jungers, 1997], Er *Eulemur rubriventer* [Kappeler and Pereira, 2003], Ha *Hapalemur aureus* [Mutschler and Tan, 2003; Tan, 2000], Hg *Hapalemur griseus* [Mutschler and Tan, 2003], Hs *Hapalemur simus* [Mutschler and Tan, 2003; Tan, 2000], Ii *Indri Indri* [Pollock, 1975; Pollock, 1977], Lc *Lemur catta* [Sussman, 1991], Lr *Lepilemur ruficaudatus* (this study), Mb *Microcebus berthae* [Dammhahn and Kappeler, 2005; Schwab, 2000]; Mm *Microcebus murinus* (Eberle; unpublished data), Mc *Mirza coquereli* [Kappeler, 1997], Pd *Propithecus diadema* [Glander et al., 1992; Meyers and Wright, 1993; Wright, 1995]), Pt *Propithecus tattersalli* [Meyers and Wright, 1993], Pvv *Propithecus verreauxi verreauxi* [Kappeler and Ganzhorn, 1993; Richard, 2003], Pvc *Propithecus verreauxi coquereli* [Godfrey et al., 2004], Vvv *Varecia variegata variegata* [Rasmussen, 1985; Vasey, 2003].

Birth seasonality and litter size

For all 22 births that occurred in 2002, 2003 and 2004, we were able to obtain the exact parturition dates. Births occurred from November until the first half of December in all three years. Five out of nine potential mothers gave birth in 2002. In 2003 all nine females under observation gave birth, and in 2004 eight out of nine potential mothers gave birth. No births were observed during the first half of the night.

Infants were therefore born either during the second half of the night or during the day within the day shelter. In all 22 cases singletons were born.

Parental care and inter-individual distances between pair partner and infant

From the first day on, mothers left their sleeping holes together with their infants by carrying them in the mouth. Infants were parked in trees at a height of between 5 and 15m. Typical parking bouts lasted 40-60min. During the first two weeks after birth, parked infants remained motionless at their parking sites until their mothers' return. After two weeks, they started to explore nearby branches, but remained in the same tree. During daytime, infants stayed with their mothers in tree holes. Social fathers never shared a sleeping site with the mother, nor did they establish any physical contact with infants. This is in contrast to other seasons where males share sleeping trees with respective pair partner on average every fourth night (Zinner et al., 2003). Interaction between fathers and infants were very rare within the infant's first two months of life. In only one out of 13 cases we observed physical contact between the infant and the social father living in the same home range. However, in this case the social father had physical contact for several seconds with the infant during an aggressive encounter with the mother.

For 12 infants, data on inter-individual distances between infant and mother and infant and social father, respectively, were available. Females spent more time in
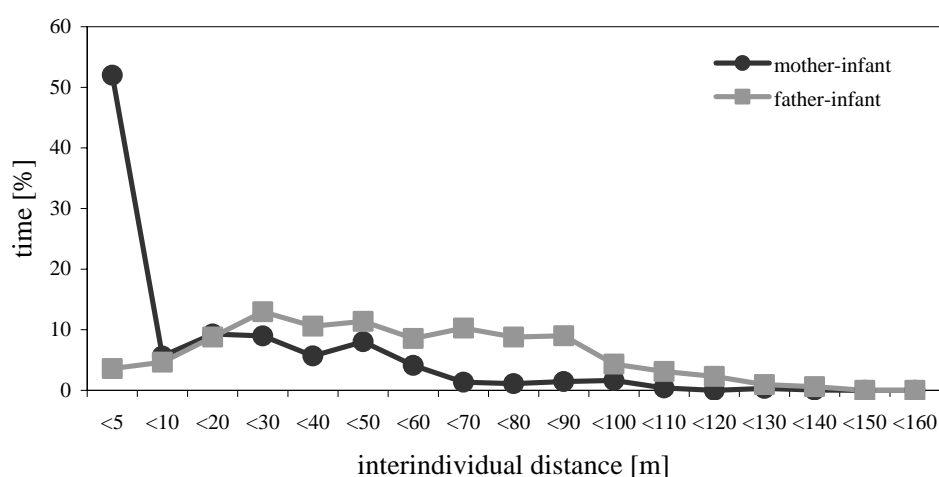
Fig. 3: Interindividual distances between mother-infant and social father-infant dyads during lactation (n=12 pairs).

close proximity to the infant (<5m) than males (t-test dependent samples t=-13.2; p<0.001 n=12). Mothers stayed within 5m of their infant on average more than 50% of their time within the first 6 weeks after birth. In contrast, males were found in this distance category only 3.6% of the time. Males spent most of their time (13%) in distance categories between 20-30m away from the infant (Fig. 3).

Infant development

Infants started to forage and leave their sleeping sites independently at an age of about 50 days. With increasing age, physical contact between mothers and infants decreased (Fig 4; r=-0.60; p<0.001; n=13). Notably, in the first week mothers spent more than 50% of their active time in physical contact with their infants, in addition to the time they spent together in the day shelter.
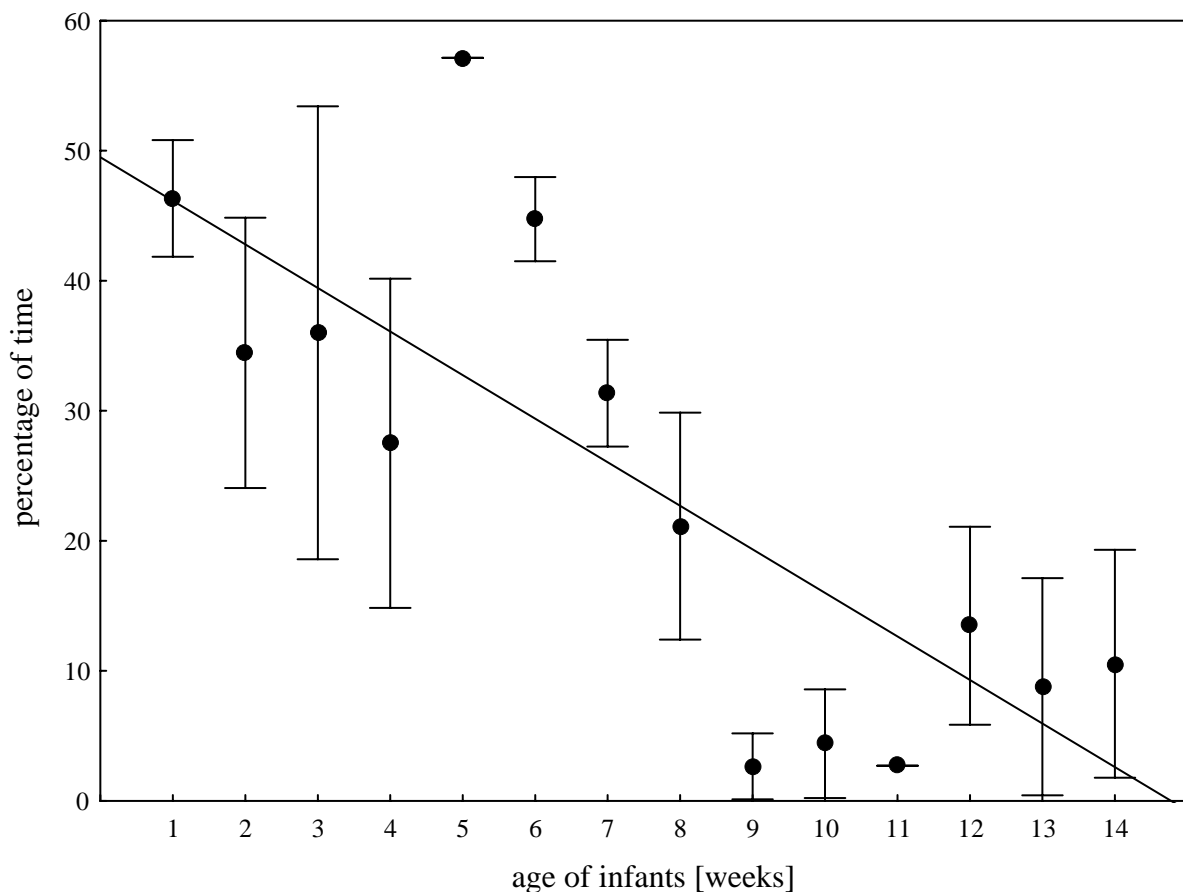
Fig. 4: Age of infants and percentage of active time mothers stayed in physical contact with their infants. Pooled data of 1-13 different litters (r=-0.78; p<0.001). Values are means and SEs

Predation

Over the course of four years, 16 out of 45 marked adult individuals became most likely victims of predation. For 10 of these 16 individuals we were able to confirm predation and determine the predator species. Predation rate of adult

Lepilemur ruficaudatus at the study site varied considerably among different years. Annual predation rate was 8.3% (year 2001), 21.7% (year 2002), 0% (year 2003) and 40% (year 2004). Mortality rate of infants could be estimated for 2002 and 2003. In 2002 three out of five (60%) infants disappeared within the first four weeks after birth, in 2003 only one out of nine (11%) infants disappeared. For infants we were not able to determine causes of mortality. In ten cases the predator species were determined due to predator-specific leftovers or bite marks on radio collars of adult victims (Tab. 1). Seven individuals were killed by the fossa (*Cryptoprocta ferox*). In these cases the collars had bite and chew marks as the fossa kills its prey with a neck bite. The Madagascar harrier hawk (*Polyboroides radiatus*) was assumed to have preyed on one individual. The collar showed beak marks and the harrier hawk sat next to the freshly-killed individual. Two individuals were killed by a boa (*Acranthophis sp.*). In both cases the radio collars were located in the resting hole of a boa. For two adult individuals we were not able to specify the cause of disappearance. Predation pressure was higher during the dry season, when ten out of twelve incidents happened.

Table 1: Disappearances of and predation on *Lepilemur ruficaudatus* between 2001 and 2004.

ID	estimated age (years)	sex	date of predation/disappearence	season	predator species
1995_04	≥8	m	May–Sept. 2001	d	?
1995_07	≥9	f	10.09.2002	d	*Cryptoprocta ferox*
1995_09	≥8	f	May-Sept. 2001	d	?
1996_03	≥10	m	27.07.2004	d	*Cryptoprocta ferox*
2000_07	≥6	m	June 2002	d	*Cryptoprocta ferox*
2000_08	≥6	f	23.06.2004	d	*Acranthophis sp.*
2001_02	≥3	f	03.09.2002	d	*Cryptoprocta ferox*
2001_07	≥5	m	22.06.2004	d	*Cryptoprocta ferox*
2001_09	≥4	m	23.01.2004	r	*Acranthophis sp.*
2001_14	≥3	m	15.12.2002	r	*Polyboroides radiatus*
2002_01	≥2	m	18.08.2002	d	*Cryptoprocta ferox*
2002_06	≥4	m	29.06.2004	d	*Cryptoprocta ferox*
2002_InfB	≤1month	?	Nov.-Dec. 2002	r	?
2002_InfF	≤1month	?	Nov.-Dec. 2002	r	?
2002_InfP	≤1month	?	December 2002	r	?
2003_InfG	≤1month	?	December 2003	r	?

d, dry season; r, rainy season

Discussion

In this study we demonstrated that direct paternal care does not occur in pair-living *Lepilemur ruficaudatus*. We documented the degree of parental care and described previously unknown aspects of life history traits, such as mating and birth seasonality, litter size, gestation and lactation length, inter-birth intervals, and predation rates. Our discussion focuses on potential causes of certain life history traits and examines the importance of paternal care for the evolution of pair-living in *L. ruficaudatus* and related species.

Mating seasonality, birth seasonality and inter-birth intervals

Mating of *L. ruficaudatus* was highly seasonal and restricted to only two weeks in May/June at the beginning of the dry season. Not surprisingly, we also found strong birth seasonality in *L. ruficaudatus*. In all three years all births were recorded within a time span of four weeks in November/December. Seasonality of reproduction and a short mating season are generally found in lemurs, with *Daubentonia madagascariensis* as the only known exception [Petter Rousseaux, 1964; Rasmussen, 1985; Sterling and Richard, 1995]. In other folivorous species, such as *Propithecus,* lactation and weaning coincides with periods of highest availability of preferred resources [Meyers and Wright, 1993; Wright, 1999; Wright et al., 2005]. We found a similar pattern in *L. ruficaudatus.* Timing of lactation, as well as weaning, coincided with the period of highest availability of young leaves during the rainy season [Ganzhorn, 2002; Sorg and Rohner, 1996], an annual schedule that may allow females to replenish energy stocks before the following reproductive season [Richard et al., 2000]. Strict breeding seasonality in lemurs has been discussed to be a mechanism for optimizing timing for reproducing females with respect to resource availability [Lewis and Kappeler, 2005; Meyers and Wright, 1993; Rasmussen, 1985; Richard et al., 2000]. However, timing of lactation and weaning may also be considered as the outcome of an evolutionary trade-off between energetic demands of infants and needs of mothers with respect to future reproduction [Crespi and Semeniuk, 2004; Trivers, 1972].

The majority of females of *L. ruficaudatus* had an inter-birth interval of one year. In *Propithecus verreauxi verreauxi*, on average of 44% of females gave birth each year [Richard et al., 1991]. However, reproductive success of females in

Propithecus v. verreauxi varied considerably and was influenced by age, body mass and infant survival of the previous year. A comparable trend was observed in *Eulemur fulvus rufus* and *Propithecus diadema edwardsi* [Overdorff et al., 1999; Pochron et al., 2004]. Inter-birth intervals were one year but inter-birth interval between surviving infants were around two years in both studies. Although we documented high infant mortality in *L. ruficaudatus* in some years (e.g. 2002) our limited data do not allow a more refined analysis of causes, such as female age or condition. Additional long-term data on births, body mass and infant survival are needed to investigate inter-birth intervals of surviving infants and variation of reproductive success of females in *L. ruficaudatus*.

Gestation length

Gestation length of *L. ruficaudatus* was on average 176 days. When comparing this value with corresponding data on other lemur species, the gestation length of *L. ruficaudatus* was found to be much longer than expected for a lemur of comparable body mass. Several authors emphasized the importance of basal metabolic rate as an important variable for the explanation of life history variation [Kappeler, 1996; McNab, 1980; Rasmussen and Izard, 1988]. Drack et al. [1999] recorded one of the lowest resting metabolic rates for mammals of comparable size in *L. ruficaudatus* during the dry season [see also Schmid and Ganzhorn 1996]. Several lorisids, such as *Nycticebus coucang* and *Loris tardigradus,* also show a long gestation length with respect to their body mass [Rasmussen and Izard, 1988]. The low resting metabolic rate of these species is interpreted as an essential variable when explaining their low growth rates and long gestation lengths [Mueller, 1979; Rasmussen and Izard, 1988]. Hence, the low basal metabolic rate could contribute to the prolonged gestation length in *L. ruficaudatus,* as well.

Most of the folivorous lemur species had a longer gestation length than expected. Our results are consistent with the findings of Godfrey et al. [2004] that more folivorous prosimians have slow prenatal growth rates. But even when taking only the folivorous lemur species into account, gestation length of *L. ruficaudatus* is exceptionally long. McNab [1983] proposed that certain classes of diet require low basal metabolic rates [but see Ross, 1992]. A diet high in toxic components is seen as one possible factor favoring certain life history adaptations, such as a prolonged gestation [Rasmussen and Izard, 1988]. Higher concentration of certain toxic

components in the diet of *Lepilemur,* compared to the diet of other folivorous species, may therefore account for part of its relatively long gestation [Ganzhorn, 1995; Ganzhorn et al., 2003]. This may also explain similarities between certain life history variables of species with different dietary regimes such as *L. ruficaudatus* and some lorisid species [Charles-Dominique, 1974; Charles-Dominique, 1977; Pietsch, 1998].

Parental care and evolution of pair-living

In several pair-living species paternal care is considered to be one, if not the, major reason for the evolution of this rare type of social organization [Clutton-Brock, 1989; Fietz and Dausmann, 2003; Kleimann, 1977]. The paternal care hypothesis assumes that reproductive success of both, males and females would be lowered if males would not engage in infant care. *Lepilemur ruficaudatus* females provided infant care in terms of lactation, warming, grooming and oral transport. However, we found no evidence for direct infant care by social fathers. We never observed males grooming, warming, carrying or baby-sitting infants. Males never had affiliative contact with infants and were only rarely found at a distance of less than 10m from them. The lack of paternal care leads us to conclude that obligate paternal care cannot provide an ultimate explanation for pair-living in *L. ruficaudatus*.

To date, detailed comparative data on infant care are lacking for many nocturnal primates in the wild [but see Gursky & Nekaris 2003]. Infant parking in dense vegetation or nests have been reported for several nocturnal lemurs (e.g. *Microcebus murinus*: [Martin, 1972]; *Phaner furcifer*: [Schülke, 2005]; *Lepilemur mustelinus*: [Klopfer and Boskoff, 1979]; *Lepilemur edwardsi*: [Rasoloharijaona et al., 2000; Thalmann and Ganzhorn, 2003]. In pair-living *Avahi occidentalis,* which occupy a similar ecological niche as *L. ruficaudatus* [Thalmann, 2001], females carry newborn infants continuously during active periods and individuals of a family group feed mostly as a cohesive group [Thalmann, 2003; Wright, 1990]. It has been suggested that *Avahi* as the only nocturnal species within the family of Indriids is secondarily nocturnal [Müller and Thalmann, 2000]. This may explain why *A. occidentalis* retained its cohesive lifestyle and may contribute to the differences of parental care between females of *A. occidentalis* and *L. ruficaudatus* or other nocturnal lemurs. However, it is still unclear to what extent males in *A. occidentalis* contribute to infant care.

In sympatric *Cheirogaleus medius,* infant care was provided by females and males [Fietz and Dausmann, 2003]. In contrast to *L. ruficaudatus, C. medius* males were observed to warm infants, to guard nests of infants as a mean of predator defense and to coordinate their activity with females. However, no quantitative data on male infant care were provided. Fietz and Dausmann [2003] hypothesized that the evolution of pair-living in *C. medius* was favored by the need of parental care of both sexes due to high predation pressure. Our study population and the population of *C. medius* studied by Fietz and Daussmann are sympatric. They are both arboreal, nocturnal and use tree holes as day shelters. They share many of the same predators and are expected to face similar predation risks [Fietz and Dausmann, 2003]. Hence, if predation defense is the main function of paternal care in *C. medius*, why can female *L. ruficaudatus* cope with predation without the help of the male?

Maternal care of *L. ruficaudatus* and *C. medius* differs in the mode of infant parking. Newborns of *Lepilemur* are parked in dense vegetation, whereas *Cheirogaleus* infants are left in tree holes (nest parking) [Fietz and Dausmann, 2003; Foerg, 1982]. Van Schaik and Kappeler [1993] consider infant parking as an evolutionary transitional stage between leaving infants in the nest and infant carrying on the fur. Most cheirogaleid species leave their infants in nests and show a tendency towards litters. Nest parking is explained as a consequence of infants that are probably less developed [Kappeler, 1996; Rasmussen, 1986]. Differences in neonatal body mass and infant development may contribute to differences in thermoregulatory demands of newborns. Care provided by both parents could therefore be advantageous for infant development in species such as *C. medius*. To test if strict thermoregulatory demand of newborns contributed to the need for paternal help [Fietz and Dausmann, 2003], comparative examination of neonatal mass, infant development and parental care would be a helpful first step.

In summary, differences in the degree of paternal care between both species living sympatrically in the same habitat and showing a similar social organization remain surprising. It remains unclear whether paternal care is the ultimate cause or a consequence of pair-living. Especially in species with a high degree of extra-pair paternity and floating males, such as *C. medius* [Fietz et al., 2000], we would expect additional or alternative constraints that favored pair-living [Birkhead and Moller, 1996; Gowaty, 1996]. In nocturnal lemur species, pair-living seems to be exceptionally common (e.g. *Cheirogaleus medius*: [Fietz, 1999]; *Avahi occidentalis*:

[Thalmann, 2001]; *Phaner furcifer*: [Charles-Dominique and Petter, 1980; Schülke, 2003]; *Lepilemur edwardsi*: [Rasoloharijaona et al 2003]; *Lepilemur ruficaudatus*: [Zinner et al., 2003]). Other hypotheses, such as female defense or resource defense, may offer promising alternative explanations for evolution of pair-living in these primates [Brotherton and Manser, 1997; Emlen and Oring, 1977; Palombit, 1999; Wrangham, 1979].

Acknowledgements

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CHAPTER 3

Why males live with only one female:

pair-living in a nocturnal lemur (*Lepilemur ruficaudatus*)

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Abstract

Pair-living and a monogamous mating strategy are rare and theoretically unexpected among mammals. Nevertheless, about 10% of primate species exhibit such a social system, which is difficult to explain in the absence of paternal care. In this study we tested the two major hypotheses proposed to explain the evolution of monogamy in mammals, the female defence hypothesis (FDH) and the resource defence hypothesis (RDH), in red-tailed sportive lemurs (*Lepilemur ruficaudatus*), a nocturnal pair-living primate from Madagascar. We combined data from behavioural observations and acoustic playback experiments on eight male-female pairs during a 24-months field study to test contrasting predictions of these hypotheses. Male and female *L. ruficaudatus* were found to live in dispersed pairs, which are characterised by low cohesion and low encounter rates within a common home-range. Social interactions between pair partners were mainly agonistic and characterised by a complete absence of affiliative interactions - body contact was only observed during mating. During the short mating season, males exhibited elevated levels of aggression towards mates, as well as extensive mate guarding and increased locomotor activity. In addition, males were exclusively responsible for the maintenance of proximity between pair partners during this period and they defended their territories against neighbouring males but not against females. Males also exhibited the strongest response towards simulated male and female intruders during the mating season. Together, these results provide unequivocal support for the female defence hypothesis, whereas none of the predictions of the resource defence hypothesis was supported. We discuss the spatial and temporal distribution of receptive females in relation to the female defence strategies of males and suggest possible costs that prevent male red-tailed sportive lemurs from defending more than one female.

Key words: monogamy, pair-living, female defence, resource defence, *Lepilemur*

Introduction

Ultimately, social and mating systems represent the outcome of conflicting male and female reproductive strategies (Parker 1979; Holland and Rice 1998; Davies 2000). A particular outcome can therefore be analysed from the perspective of both sexes. Because of the physiological constraints of internal gestation and lactation, mammalian mating strategies evolved under a particularly strong asymmetry between the sexes (Williams 1966). Because female mammals generally have lower potential reproductive rates and make a much higher parental investment than males, male mammals can maximise their reproductive success by mating polygynously (Trivers 1972; Clutton-Brock 1991). Most mammals have indeed a mating system characterised by either polygyny (successful males mating with several females and females only with one male) or polygynandry (members of both sexes mating with multiple partners) (Wittenberger and Tilson 1980; Clutton-Brock 1989). In about 5% of mammals, however, individuals mate with only one partner over one or several reproductive cycles (Kleimann 1977; Clutton-Brock 1989), i.e., they are monogamous. From the male perspective it is, therefore, puzzling, why some male mammals restrict themselves to living and or mating with a single female. As an important conceptual and operational caveat, it must be emphasised that it is only possible to describe the fact that, at the behavioural level, a male and a female form a stable social unit, i.e., that they are pair-living (Kappeler and van Schaik 2002); monogamy can only be established unequivocally by genetic methods.

Whenever biparental care is obligate or paternal care improves male reproductive success, pair-living and monogamy can be explained adaptively from the male perspective (Trivers 1972; Mock and Fujioka 1990; Gubernick 1994; Iwasa and Harada 1998; Møller and Cuervo 2000). Females may also choose particular males because of the direct benefits they provide to either themselves or their offspring in the form of protection from predation, infanticide or harassment (Gowaty 1996). Various forms of such male paternal care behaviours have been cited to explain monogamy in a few mammals (e.g. Callitrichidae: Dunbar 1995 *Peromyscus californicus*: Cantoni and Brown 1997; *Cheirogaleus medius*: Fietz 1999; *Petropseudes dabli*: Runcie 2000), which, however, apparently represent only a small minority of species (van Schaik and Dunbar 1990; Komers 1996; Komers and

Brotherton 1997; Fuentes 2002). In addition, paternal care in mammals can exist in the absence of monogamy (Wright 1990; Buchan et al. 2003).

Several alternative hypotheses have therefore been proposed to explain the evolution and/or maintenance of monogamy in mammals (see Fuentes 2002; Reichard 2003; van Schaik and Kappeler 2003; Schülke 2005 for recent reviews). The female defence hypothesis (FDH) assumes that dispersal of females is determined by the temporal and spatial distribution of resources and that males distribute themselves onto the distribution of females, defending or monopolising as many females and/or female home-ranges as possible (van Schaik and van Hooff 1983; Altmann 1990; Komers and Brotherton 1997; Palombit 1999). Female defence is the optimal male strategy if females are so widely distributed in space, or exhibit such highly synchronized estruses, that economic defence of more than one female at a time is not feasible (Emlen and Oring 1977; Nunn 1999; Dunbar 2000). Males adopting a roving strategy would not achieve higher reproductive success than males focusing on only one mate (van Schaik and Dunbar 1990; Dunbar 2000). Here we also consider mate guarding or aggressive coercion of males towards their mates as an indirect form of female defence because females are not able to choose their mates freely (Brotherton and Manser 1997; Palombit 1999; Schülke 2005).

Under the resource defence hypothesis (RDH), males monopolise resources important to females by defending a territory instead of defending females directly (Emlen and Oring 1977; Wrangham 1979; van Schaik and Dunbar 1990). Hence, male reproductive success is limited by the females' choice of resource access. If males pursue resource defence as a mating strategy, pairs should emerge whenever males are unable to maintain territories that can support more than one female. Resource defence should be especially likely in species where females are subject to high energetic demands during gestation and lactation (Brockelman and Srikosamatara 1984). Territorial defence by males decreases food competition among females and makes female reproductive success dependent on male resource holding potential (Parker 1974). However, high quality territories should attract and support multiple females, even if intrasexual aggression between females is high (Orians 1969; Davies 1989).

It has also been hypothesised that males are permanently associated with one female to protect infants against infanticidal attacks by strange males (Cockburn

1988; van Schaik and Dunbar 1990; van Schaik and Kappeler 1997; Palombit 2000; van Schaik 2000).

The recently postulated intersexual feeding competition hypothesis assumes that food competition is high among individuals (Thalmann 2001; Schülke 2005). If females live apart from each other, males could persuade females into pair-living by defending their territory against other males. A close association between males and females could help females to minimize food competition by additional males. Hence, pair-living evolved as a result of direct intra- and intersexual feeding competition and male reproductive tactics (Schülke 2005).

Among mammals, the number of monogamous species is particularly high in primates, exceeding 10% (Reichard 2003). Because of their prevalence, and perhaps because we have a particular interest in a mating system that characterises some human populations (Low 2003), monogamy has been studied in more detail in primates than in other taxa. Phylogenetic reconstructions revealed that monogamy in primates evolved several times independently in all major radiations - most likely from ancestors with a promiscuous mating system (van Schaik and Kappeler 2003). Among pair-living primate species, there seems to exist considerable variation in the degree of spatial cohesiveness between pair partners (Müller and Thalmann 2000; Kappeler and van Schaik 2002). Hence, species are classified as dispersed pairs when pair partners share a home-range but are not consistently associated during their period of activity (e.g *Phaner furcifer:* Schülke and Kappeler 2003). In contrast, species are considered as cohesive pairs whenever pair partners are permanently spatially associated and have frequent interactions (e.g. *Hylobates lar:* Reichard 1995).

The red-tailed sportive lemur, *Lepilemur ruficaudatus,* is a small (780g), nocturnal folivorous lemur restricted to the dry deciduous forests of central western Madagascar. Pairs maintain stable territories of around 1ha for several years (Ganzhorn and Kappeler 1996; Zinner et al. 2003). Their mating season is limited to only a few weeks in late May. Extra-pair copulations and extra-pair paternities occur at very low rates (Platner et al. unpublished data). Singletons are born at the beginning of the rainy season in late November and weaned about two months later. Males do not exhibit any direct paternal care (Hilgartner et al. in press). In the present study, we therefore investigated predictions of the female defence and resource defence hypotheses as possible explanations for the evolution of pair-living

and monogamy in *Lepilemur ruficaudatus* with observational and experimental data on social and territorial behaviour of eight pairs. Specific predictions of these hypotheses are summarised in Table 1 and spelled out in the proper context in the results section.

Table 1: Predictions and tests for female defence and resource defence hypotheses

Female defence	Resource defence	Test
Males responsible for pair bonding	Neither males nor females responsible for pair bonding	Hinde index for proximity
Proximity of pair partner only during premating and mating season (mate guarding)	Proximity of pair partners does not differ between different reproductive seasons	Comparison of cohesiveness and distances between pair partners during pre-mating/mating and non-mating season
Territory use and travel distance differ between mating and non-mating season	Territory use and travel distance do not differ between mating and non-mating season	Comparison of territory use and travel distances during mating and non-mating season
Males are only aggressive against strange males not against strange females	Males are aggressive against strange males and females	Analysis of observed encounters between neighbours
Males are most vigilant to simulated male and female intruders during the mating season	Males' vigilance against simulated intruders does not vary between seasons but is higher than vigilance of females	Playback experiments: acoustic simulation of male and female intruders

Methods

Study site

This study was carried out in Kirindy Forest, western Madagascar (44°39'E, 20°03'S), where the German Primate Center (DPZ) operates a field research station. The local climate is characterized by pronounced seasonality with a short rainy season from December to February, followed by a longer dry season with little or no rain from April to November (Sorg et al. 2003). The forest is dense and most tree species do not exceed 20m in height (Ganzhorn and Sorg 1996).

The study area (locally known as N5) is located within a 12,500ha forest concession of the C.F.P.F (Centre de Formation Professionnelle Forestière, Morondava) within Kirindy Forest. The study area was defined by the boundaries of a systematic grid system. Within a 500 x 500m core area, small trails were established

every 25m in both north-south and east-west directions, surrounded by additional trails at 50m and 100m intervals along three edges of the core area. Along its western border, former logging trails (200m long at 100m intervals) were used for radio-tracking whenever necessary. Each trail intersection is marked with a plastic tag for orientation. The entire grid system was mapped and coordinates of each intersection were determined.

Capture and marking

Between 1995 and 2004, a total of 87 individuals were captured from their sleeping sites in hollow trees during the day. Potential sleeping trees were initially located by transect walks, and animals were caught by hand or by placing a live-trap at the tree hole entrance. Animals were briefly anaesthetised with GM2 (Rensing 1999) and marked with a unique subcutaneously injected transponder (Trovan; Usling, Germany). Adult animals captured within the core area of our study site were equipped with 9g radio collars (Biotrack, Wareham Dorset, UK), which is less than 3% of the animal's body mass. Radio collars with unique frequencies were fitted around the neck. Radio collars were replaced after about 10 months, when battery lifespan had expired. All radio collars were removed after the end of the study. Infants and subadults were marked with unique visual cues by shaving parts of their tail. Adult males and females forming 14 pairs were fitted with radio collars between 2000 and 2005.

Data collection

Data presented here were obtained from 8 pairs that were observed continuously for 24 months between 2002 and 2004, totalling > 2000 observation hours. Each pair was observed for at least one reproductive cycle, including pre-mating (February-April), mating (May-June), gestation (June-October), and birth/weaning period (November-January) (Hilgartner et al. in press). We followed radio-tagged animals with radio-tracking equipment from Telonics (Mesa, AZ, USA). We observed the animals mainly during the first half of the night (1800-0200h) with the aid of a headlamp and occasional use of a strong flashlight and binoculars. We attempted to observe all 16 adult individuals for equal periods of time. Together with a Malagasy field assistant, R.H. followed both pair partners simultaneously for 2 hours, using focal animal sampling (Altmann 1974). At 5-minute intervals, the exact

location, as well as the behavioural state (feeding; resting; locomotion) of each focal animal was recorded (instantaneous sampling, Altmann 1974). Observer distance from the focal animals was between 1 and 15 m. We recorded if animals were out of sight at the time of instantaneous sampling of behaviour. Analyses and calculation on feeding time was based on the number of intervals animals were in sight. Social interactions between pair-partners and among neighbours were recorded by all-occurrence. Additionally, sleeping sites of *L. ruficaudatus* were marked and members of sleeping associations were identified during the day by detecting their radio or transponder signal.

Data analyses

Analyses of spatial data were performed with the Animal Movement extension for ArcView® (Hooge & Eichenlaub 1997). We used both kernel home-ranges (KHR; Worton 1989) and minimum convex polygons (MCP) to describe the overall home-range size and to calculate home-range overlap. Home-range overlap was calculated for both, pair partners and same-sexed neighbours. We used the MCP method, which tends to overestimate home-range size, only to enable comparisons with published data for other species. Our spatial analyses are based on 873-1452 data points or fixes for each of 16 individuals. For a detailed description of the calculation of home-range saturation and centres, see Zinner et al. (2003).

To estimate cohesiveness between pair partners, we calculated the percentage of time pair partners spent in various distance categories, ranging from 0-180m. We used an intra-pair distance of less than 10 m as the criterion for cohesiveness. We chose this distance because it most likely permits visual contact between partners. Cohesiveness was compared across the annual reproductive cycle, pooling data for the pre-mating and mating seasons, as well as for gestation and birth seasons (non-mating).

We compared observed encounter rates of pair partners with expected encounter rates calculated with a random gas model (Waser 1976).

$$F = (4 \times p \times v)/\pi \times (2d_m + s)$$

Generally, the expected encounter rate (F) depends on the population density (p; individuals/area), velocity of the animals (v; m/h), group spread (s; maximal

distance among group members in meters) and the distance criterion (d_m). In our analysis, we calculated (p) for each pair separately as the inverse of the home-range, including also exclusively used areas of pair partners (additive home-range). Velocity (v) of animals was the average distance male and female travelled per night. We defined encounters (distance criterion d) as situations in which pair partners approached to within 10m. We calculated encounter rates separately for each reproductive season and compared them with observed encounter rates in the respective other seasons. Hinde indices were calculated to investigate responsibility for maintenance of spatial proximity within pairs (Hinde and Atkinson 1970). Values range between 1 and -1, with values between -0.1 and 0.1 indicating equal responsibility for maintenance of spatial proximity.

To compare observed encounter rates between neighbouring males with expected encounter rates we modified the original gas model:

$$F = w \times (4 \times p \times v)/\pi \times (2d+s)$$

We calculated (p) for each male-male dyad separately as the inverse of the overlapping home-range area. Velocity (v) of animals was the average distance both males travelled per night. We used the same distance criterion as for pairs. Because both males ranged also in their exclusive areas, we corrected the model for the probability (w) that both males were within the overlapping area at the same time. We calculated encounter rates (per half night; 6h) separately for each reproductive season and compared them with observed encounter rates.

We classified social encounters between individuals into three categories: agonistic, neutral and affiliative. Affiliative behaviour included huddling and grooming. Agonistic behaviour was either aggressive (chase, charge, bite, grab) or submissive (flee, be displaced or jump away) *sensu* Pereira and Kappeler (1997). To determine dominance relationship between pair partners, we only used decided conflicts where one partner showed only submissive behaviour and no aggression and the opponent no submissive behaviour, but aggression.

We operationally defined periods of oestrus by two criteria: presence of a swollen vulva and mate guarding (Hilgartner et al. in press). To estimate oestrous synchrony, we calculated days of overlap of oestrus (as defined above) for all female dyads. To test whether neighbouring females were more synchronous than females

with more distant home-ranges, we correlated distances among females' home-range centres and days of oestrous overlap among females.

Playback experiments

Males and females of *L. ruficaudatus* have similar, but also some distinctive call types in their vocal repertoire (Hilgartner, unpubl. data). Therefore, we used typical male and female calls that were recorded during nightly activity as playback stimuli (Fig. 1). In order to simulate the presence of an intruder in the owner's home-range we used vocalisations of (1) a strange male and (2) a strange female. As a control, we used a territorial call of a sympatric nocturnal lemur (*Phaner furcifer*). We defined strange vocalisations as calls of males and females that lived more than one home-range diameter away from the respective focal animal. All three stimuli bouts were of comparable length (3-4s) and were presented six times in a row with silent intervals of 4s in between. To avoid pseudo-replication and habituation (Kroodsma 1998; Wiley 2003), we used stimuli from a different individual for each experiment and each season.

All playbacks were conducted during the first half of the night (1800-0200h). Vocalisations were broadcast at a distance of approximately 10m with a Sony Professional Walkman WM 06 DC SSV1846 and a DMS Nagra amplifier hidden behind the vegetation. The peak pressure in front of the speaker (3m) was 83 dB, comparable to natural vocalizations of *Lepilemur*. Playbacks were only started when individuals were engaged in quiet activities (foraging, resting) and engaged in no social interaction with other adult individuals. Playback experiments were conducted in the core area of the subject's home-range. For a more detailed description of the playback setup see Fichtel and Kappeler (2002).

Playback experiments were conducted with seven pairs between 2003 and 2004. Each individual (n=14) was tested with three playback stimuli (strange male, strange female, control) in each reproductive season (mating, gestation and birth seasons), resulting in 9 playback trials per individual and 126 playback trials in total. Playback experiments were conducted once per individual and per night. R.H. documented the behaviour of the experimental animal continuously 3 minutes after onset of the playback experiment with a tape recorder. We recorded movement with respect to the location of the loudspeaker, vocalisation (yes/no and type) and number of scans (head movements of more than 45°) as a measure of individual vigilance.

To compare vigilance behaviour between seasons, as well as a function of focal animal sex and stimulus type, we performed a two way ANOVA with repeated measurements on the total number of scans per individual.
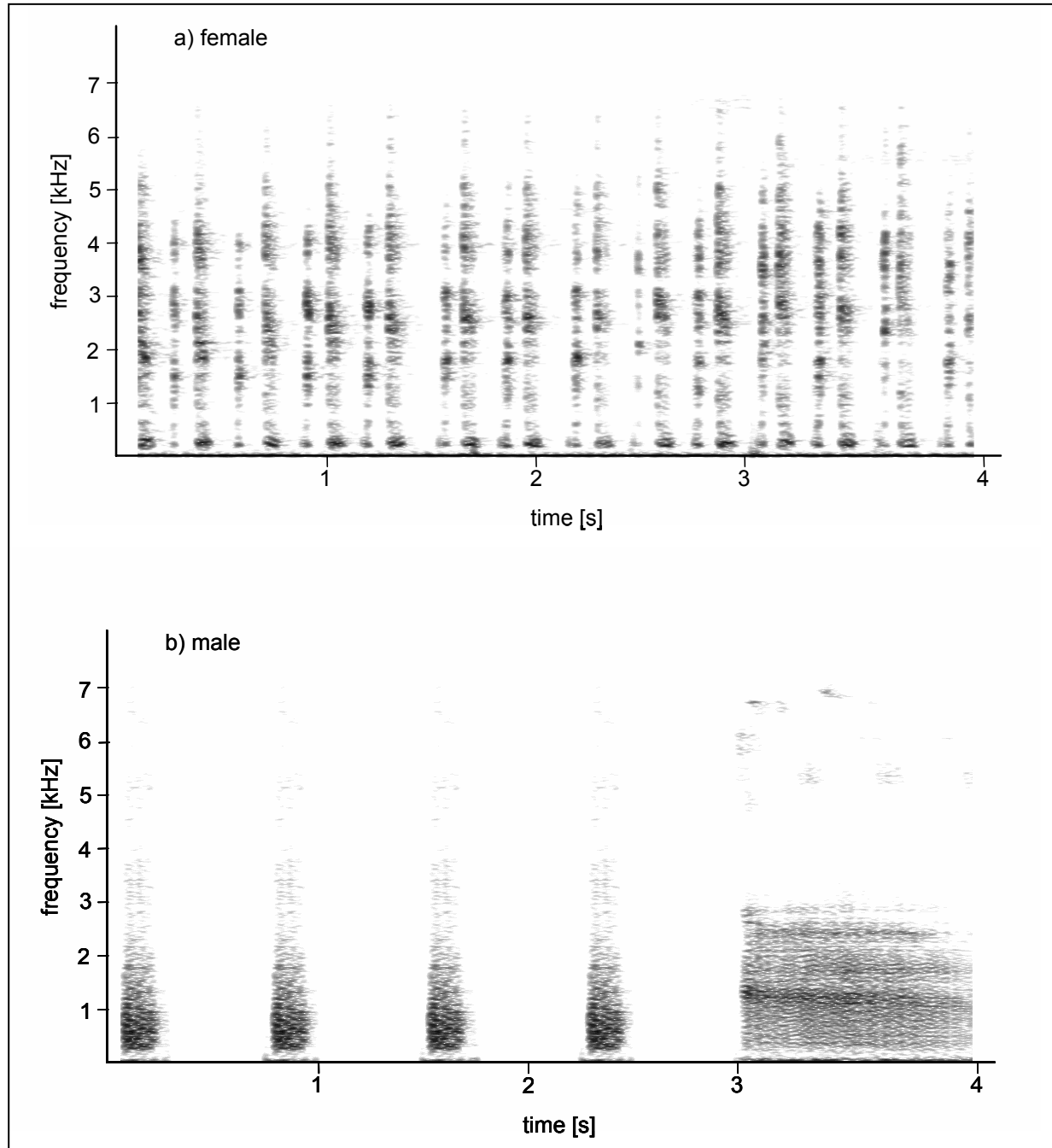
Fig.1: Spectrogram of typical a) female and b) male calls used for playback experiments.

Whenever appropriate we applied two-tailed parametric tests with α = 0.05. Statistical analyses were done with Statistica 5, Statsoft.

Results

1. Home-range Size and Overlap

Average male home-range size was significantly larger than that of the corresponding female pair partner (95% kernels: males $9912\pm5962m^2$; females $6581\pm3773m^2$; t-test dependent samples: t=2.9; p<0.05; n=8; MCP: males $15946\pm6373m^2$; females $11773\pm3095m^2$; t=3.1; p<0.05; n=8). Average maximum home-range diameter based on 95% kernels was $175\pm31m$. Based on 95% kernels, average home-range overlap between pair partners was $61.3\pm13.6\%$ from the male's perspective and $89.4\pm8.3\%$ from the female's perspective (Fig 2.).
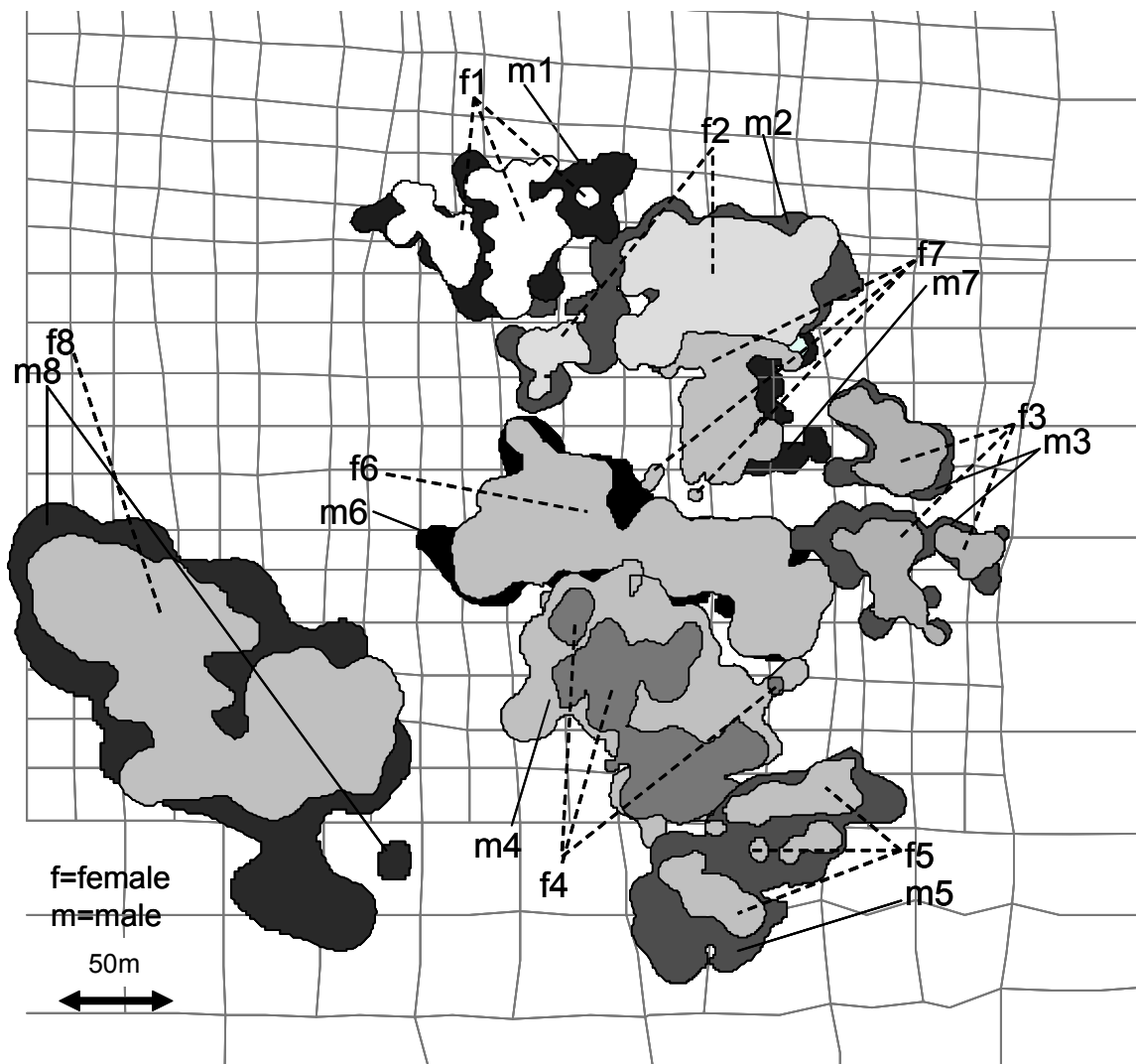
Fig. 2: Home-ranges of 8 pairs in *Lepilemur ruficaudatus* 2002-2004. Shown are Kernel 95% probability areas.

Overlap based on MCPs was 67.6±10.6% (males' perspective) and 89.0±9.5% (females' perspective). Differences between male and female perspectives are due to larger male home-ranges. Average home-range overlap between neighbouring males was 17±11% based on MCPs and 2±1% based on 95% kernels. Overlap between neighbouring females was 12±13% for MCPs and 1±1% for 95% kernels. Overlap between neighbouring males was slightly larger than overlap between neighbouring females but this difference failed to be statistically significant.

2. Cohesiveness between pair partners

Prediction from FDH: *During the pre-mating and mating season, males are more often in close proximity to their pair partner than in other seasons and show mate guarding during oestrus.*

Prediction from RDH: *Proximity between pair partners does not vary as a function of reproductive season.*

Pair partners were found in distance categories from 0m up to a maximum of 180m. Average distance between pair partners was 43.5±5.9m. However, the percentage of time pair partners spent in certain distance categories was dependent on the females' reproductive phase (Fig 3). During the pre-mating and mating
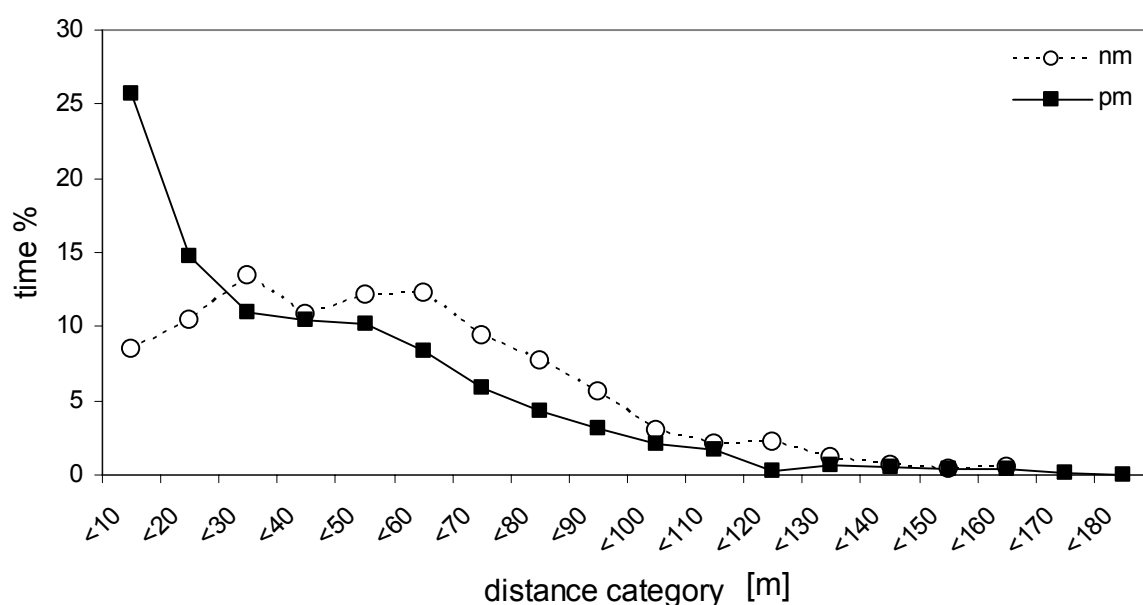
Fig. 3: Inter-individual distances between pair partners during premating/mating (pm) and non-mating (nm) season (n=8 pairs).

seasons, males spent on average 25.7±7.9% of the time at a distance of less than 10m from the female, but during the non-mating season only 8.8±2% of the time (t-

test dependent samples: t=7.2, p<0.01 n=8). Observed encounter rates (3.5±0.6/6h) between pair partners were significantly higher than expected by chance during pre-mating and mating seasons (t-test dependent samples: t=-7.06 p<0.001, n=8). Observed encounter rates in all other seasons (birth 2.5±1,2/6h and gestation 0.7±0.5/6h) did not deviate from random encounter rates (t-test dependent samples: n.s. n=8).

3. Maintenance of proximity

Prediction from FDH: *Males are responsible for maintaining proximity to the female and, hence, for maintaining pair bonds.*

Prediction from RDH: *Neither males nor females are responsible for maintenance of pair bonds.*

For sex-specific responsibility of proximity, we calculated Hinde indices on the basis of approach/leave interactions independent from the behavioural context (Tab. 2). In all eight pairs, males were responsible for the maintenance of proximity (sign test: p < 0.05).

Table 2. Hinde index for proximity calculated from the male's perspective.

pair	approach [%]	leave [%]	N	Hinde	mop
867	92	32	25	0.60	male
905	87.5	43.8	16	0.44	male
773	83.3	46.7	30	0.37	male
767	79.2	20.8	24	0.58	male
858	92.0	28.0	25	0.64	male
725	96.3	33.3	27	0.63	male
995	78.6	50.0	28	0.29	male
797	85.0	55.0	20	0.30	male
mean	86.7	38.7	24.4	0.48	

N sum of all approach and leave interactions; *mop* responsible for **m**aintenance **o**f **p**roximity.

4. Type of encounter and dominance relationship within pairs

In total, we observed 255 social encounters between pair partners. 47.3±7.4% of these encounters involved agonistic behaviour by at least one individual. 76 out of 120 of these conflicts were decided; 50% of them were won by males and 50% by females. However, during the mating season, males won 87.1% of conflicts (27 out of 31). In contrast, males lost most of the conflicts (78.9%; 30 out of 38) during the birth

season. During the rest of the non-mating season, agonistic encounters between pair partner were rare and wins were equally distributed between pair partners (total conflicts 7: winner male 3; winner female 4). No affiliative interactions, such as grooming, were observed throughout the study. The only non-agonistic situation in which males and females had body contact was mating.

5. Encounter rates and type of encounters among neighbours

Prediction from FDH: *During encounters with neighbours, males react primarily aggressively against male intruders.*

Prediction from RDH: *During encounters with neighbours, males react aggressively against males and females.*

Males met neighbours on average once every two nights (every 19.6h), but females met neighbours significantly less often (once every five nights or every 52.6h; t-test dependent samples: t=2.56; p<0.05; n=8). However, observed encounter rates between neighbouring males did not differ from expected random encounter rates (Wilcoxon matched pairs: n.s. n=7). In 95% (21 out of 23) of encounters between neighbouring males, aggression was involved. Encounters between neighbouring females and males involved aggression in only 23% (5 out of 22). Encounters between neighbouring females were only rarely observed, and in one out of three encounters aggression was observed. Sex of the opponent therefore has a significant effect of the probability of agonistic behaviour (Chi^2=4.96, 1df, p < 0.05).

6. Behavioural response of pair partners towards simulated male and female intruders

Prediction from FDH: *Males are most vigilant in response to simulated male and female intruders during the mating season when male-male competition and opportunities for extra pair copulations are highest.*

Prediction from RDH: *Males' vigilance in response to simulated male and female intruders does not vary throughout the year and is expected to be higher than vigilance of females.*

In response to simulated intruders (playback experiments), vocalisations and movements towards the speaker occurred too infrequently for statistical analysis. However, individuals scanned the environment more often after the presentation of

strange male and female calls (17.3+2.7/3min, t-test dependent samples: t=-9.90; p<0.001; n=14) than after the presentation of the control (5.3+3.3/3min)

Effects of season, type of playback stimuli (call type) and sex on scan rates of individuals are summarized in Figure 4. Season had a strong effect on scan rates of focal animals (two way ANOVA with repeated measurement: $F_{2.24}=25.57$; p<0.001). Males and females scanned significantly more often the environment after the broadcasting of strange males and females during the mating season (Fisher *Post hoc*). In contrast, reactions of males and females were lowest during gestation. Sex and call type (playback stimuli) had no effect on scan rates.
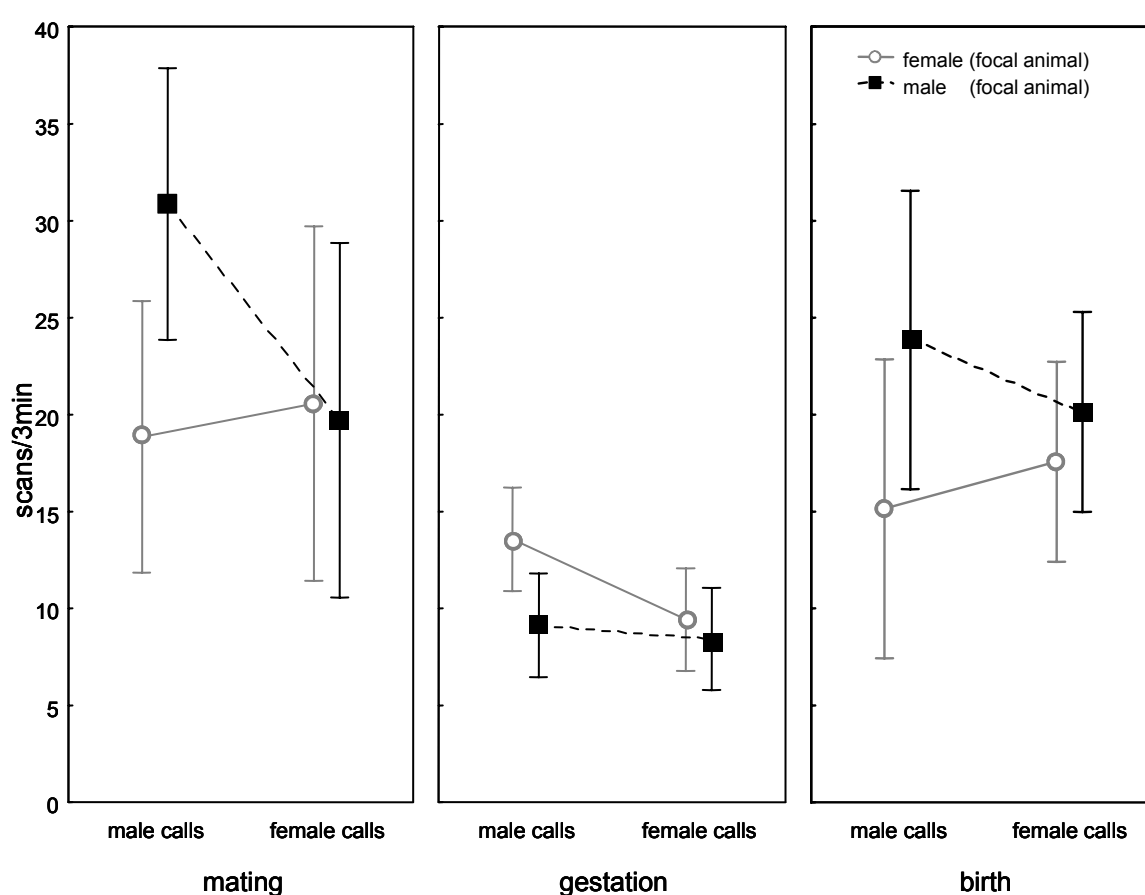
Effects	F	df	p
sex	0.717	1,12	0.414
season	25.571	2,24	<0.000
season*sex	1.244	2,24	0.306
call type	1.958	1,12	0.187
call type*sex	0.463	1,12	0.509
season*call type	0.311	2,24	0.735
season*call type*sex	0.080	2,24	0.923

Fig. 4: Comparison of scans/3min in different reproductive phases between males and females in response to playbacks with strange male and female calls. Values are means and SEs.

7. Comparison of travel distance and space use between pair partners

Prediction from FDH: *Travel distances and/or home-range use of males differ between mating and non-mating season, irrespective of resource distribution.*

Prediction from RDH: *Travel distances and home-range use of males does not differ between mating and non-mating season.*

Males travelled throughout the year on average 32.0±12.0% longer distances than their female partners (t-test dependent samples: t=6.46, p<0.001; n=8). To examine changes of travel distances between mating and non-mating season, we controlled for potentially confounding ecological factors, such as availability of young or adult leaves and abiotic factors, such as rainfall and temperature. Travel distances in the mating season were compared with travel distances during three weeks (June) following the mating season. All ecological factors remain fairly constant within these two time periods (Sorg and Rohner 1996; Ganzhorn 2002). Therefore, travel differences should be best explained by social factors, such as reproductive phase.

We found that males travelled longer distances during the mating season (t-test dependent samples: t=3.573; p<0.01; n=8). In contrast, female travel distances did not differ across seasons (t-test dependent samples: t=1.986, n.s.; n=8 Fig. 5).
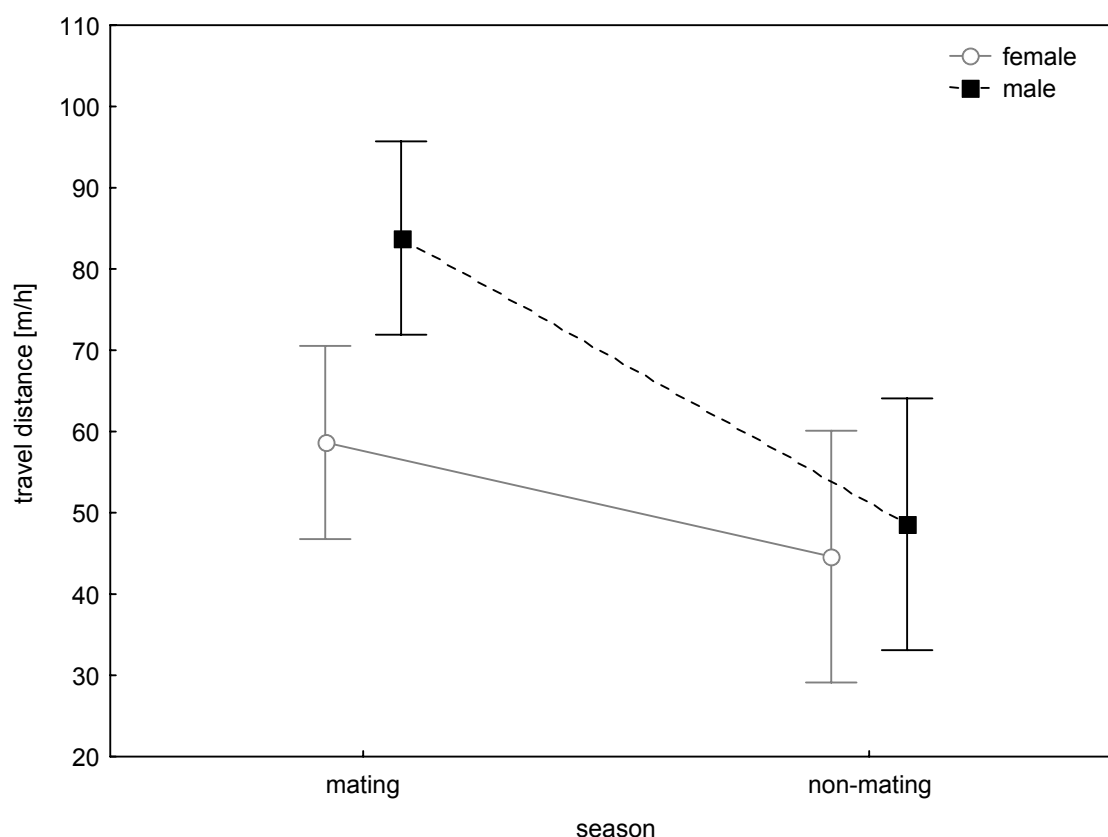
Fig. 5: Travel distances of males and females during the mating and non-mating season. Shown are means and SEs.

To investigate whether males and females spent more time in the periphery of their home-range during the mating season, we calculated the average time focal animals spent in certain distance categories from the centre of their home-range as a measure of space use. If individuals spent more time in the periphery during the mating season, the average distance from their home-range centres should be larger than during the non-mating season. However, males and females did not show differences in their distribution of space use among seasons (Fig 6; Kolmogorov-Smirnov; n.s).
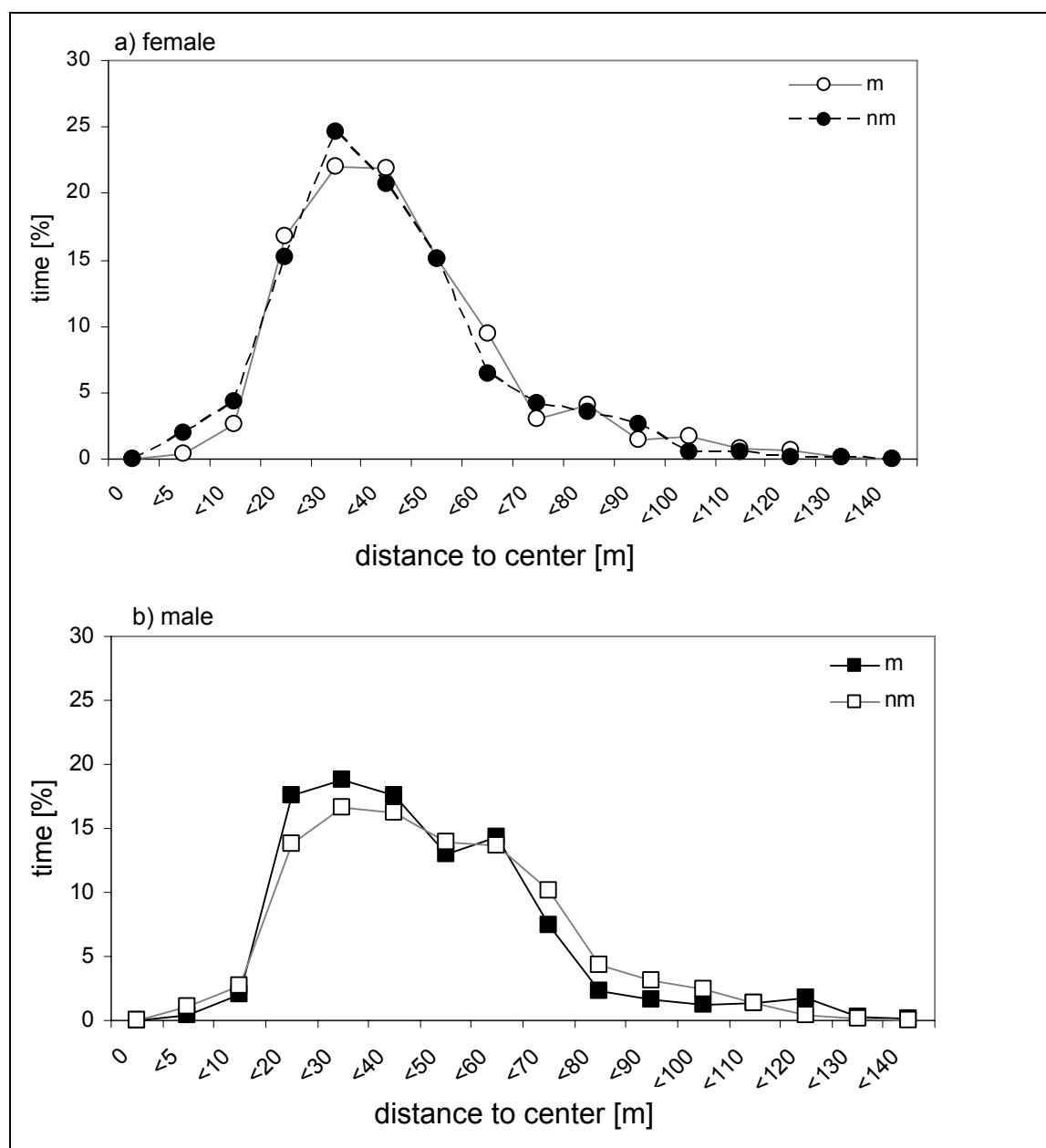
Fig. 6: Mean percentage of time a) females and b) males spent in certain distance categories to home-range centre of their respective home-range during mating (m) and non-mating (nm) season (males n=8; females n=8).

8. Monopolisation potential and defendability in relation to home-range size, travel distance and oestrous synchrony

Prediction from FDH: *Males are not able to defend more than one home-range of a female and/or females' oestruses are highly synchronized.*

Prediction from RDH: *No prediction.*

To examine home-range defendability, we calculated the D (Mitani and Rodman 1979) and M indices (Lowen and Dunbar 1994). With an average nightly travel length of 909$\pm$146m and an average home-range size of 9912m^2, we calculated 8.1 for D and 0.72 for M. Species with D values >0.98 and M values >0.08 are considered to be able to defend territories. Therefore, we conclude that territories of *Lepilemur ruficaudatus* are defendable. The threshold of M>0.08 is reached when males have to defend more than eight female territories. Under the assumption that males rove over their maximal defendable home-range, encompassing home-ranges of eight females, and females' oestrus lasting one night and being perfectly synchronised, the expected number of females impregnated would be 1.6. Average time difference of behavioural oestrus among the eight observed females was two days. Moreover, we did not find evidence for neighbouring females to experience a more synchronous behavioural oestrus than females living in more distant home-ranges (Pearson correlation: r=0.12, n=8, n.s.).

9. Comparison of foraging time between pair partners

Prediction from FDH: *No prediction*

Prediction from RDH: *Females feed more than males because of higher energetic demands.*

On average, both sexes spent more than half of their "active" time resting (59$\pm$10%). To test for differences in time spent feeding between sexes in the different reproductive phases, we arcsin-transformed data on proportion of feeding time and performed a two-way ANOVA with repeated measurement. Males and females did not differ in the time spent foraging (Fig 7. $F_{2.28}$=0.46; n=16; n.s). However, season had a significant effect on foraging behaviour of both males and females ($F_{2.28}$=12.88; n=16; p<0,001; n.s), with both sexes feeding most during birth season (Fisher *Post hoc*).
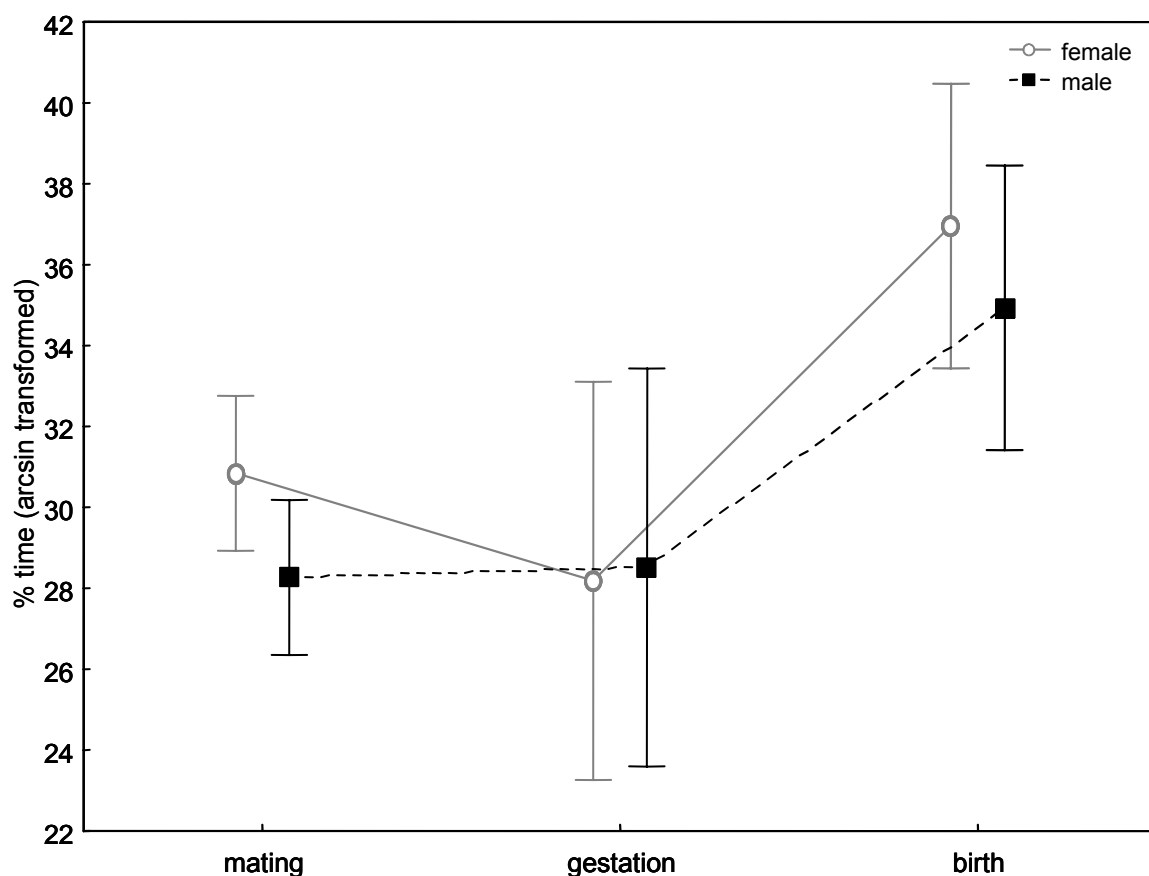
Fig. 7: Mean percentage of time and SEs of males and females spent foraging during different reproductive phases.

Discussion

The main results of our study revealed that the behaviour of male *L. ruficaudatus* changed dramatically during the short annual mating season. At this time, males increased their travel distances, exhibited extensive mate guarding, as well as elevated levels of aggression towards mates and other males. Males were also responsible for maintaining proximity between pair partners during this period. Males also defended territories mainly against other males but not against females, as also indicated by playback experiments, in which males responded strongest towards simulated male and female intruders during the mating season. Moreover, males did not feed less than females throughout the year. These results provide cumulative support for predictions of the female defence hypothesis and not the resource defence hypothesis. Below, we discuss these findings in more detail, as well as new questions that arise from this conclusion.

Proximate mechanisms of pair-living

Cohesiveness between *Lepilemur* pair partners was low during the non-mating season. Males were only rarely found at a distance of less than 10m from their female partners, and encounter rates between pair partners were low during nocturnal activity. Furthermore, they do not use their day shelters simultaneously, but successively. Similar data with comparable detail about cohesiveness are only available for fork-marked lemurs, *Phaner furcifer* (Schülke and Kappeler 2003). Both nocturnal lemurs differ from other pair-living primates and mammals in that pair-partners are rarely in close spatial proximity and rarely interact (Schülke and Kappeler 2003). Hence, their type of pair-living has been classified as dispersed (van Schaik & Kappeler 2003). Despite these similarities, there are remarkable differences in the degree of cohesiveness and encounter rates of pair partners between these two species. For example, encounter rates in *P. furcifer* were higher during the non-mating season than expected by the gas model, whereas encounter rates in *Lepilemur* did not deviate from expected values. Assuming that the gas model describes the far end of inter-individual spacing within pairs, and encounter rates of *P. furcifer* are interpreted as being rare (Schülke and Kappeler 2003), the even lower encounter rates in *Lepilemur* suggest active avoidance of pair partners.

Avoidance of pair partners can be explained as a consequence of feeding competition (Schülke and Kappeler 2003) Differences in the degree of avoidance between *P. furcifer* and *L. ruficaudatus* may be a result of the different dietary regimes. *P. furcifer* is a specialized gum feeder exploiting only a small number of tree species (Schülke 2003b). Males and females exploit the same small number of tree individual with their common home-range, which may lead to a higher encounter frequency. Hence avoidance of pair partners in such a specialized feeder may be more difficult than in folivorous *L. ruficaudatus* who feed on a broad range of tree species (Pietsch 1998; Hilgartner unpublished data). Besides feeding competition, predation pressure could be an additional factor that contributes to different degrees of pair partner avoidance. Solitariness and cryptic lifestyle are considered to represent an anti-predator strategy of nocturnal mammals (Clutton-Brock and Harvey 1977). Therefore sociality within nocturnal species may be also constrained by predation pressure. Annual predation rate for *L. ruficaudatus* was high with up to 40% (Hilgartner et al. in press). However, to examine the relationship between

predation pressure and sociality in *L. ruficaudatus*, comparable long-term data on predation rates of different nocturnal pair-living species are needed.

The quality of inter-sexual encounters is also highly variable among pair-living primates. To our knowledge *L. ruficaudatus* is the first pair-living primate species where pair partners do not show any form of affiliative interactions, such as grooming or huddling. The only affiliative body contact takes place during mating! This pattern differs strikingly from diurnal pair-living and other nocturnal primates. In gibbons, pairs coordinate their activities, and grooming bouts between males and females reach up to 15% of their daily activity (Brockelman and Srikosamatara 1984; Cowlishaw 1992; Reichard 1995b). Attributes of the relationship in pair-living titi monkey (*Callicebus ssp.*) include frequent grooming bouts small interindividual distance and close coordination of the behaviour of male and females (Müller and Anzenberger 2002; Kinzey 1997). In closely-related nocturnal lemurs, such as *Cheirogaleus medius* or *P. furcifer,* affiliative interactions are also frequently observed (Fietz and Dausmann 2003; Schülke 2003a). In *P. furcifer,* affiliative interactions have been observed on average twice per night.

Equally strikingly is the fact that about half of all encounters between pair partners in *L. ruficaudatus* were of an aggressive nature. The other half of encounters was neutral with no observable interactions between pair partners. The quality of these interactions resembles those of solitary species, such as *Mirza coquereli* or *Microcebus murinus,* with pronounced intra-sexual home-range overlap and males ranges encompassing those of several females. For *M. coquereli,* Kappeler (1997b) reported few affilliative interactions among individuals in general and disproportionately many aggressive encounters between adult males and females. A similar pattern was observed in *M. murinus,* where encounters between male and females were mainly aggressive and grooming was only observed between female dyads or adults and subadults (Eberle and Kappeler 2004; Eberle pers. comm.).

In primates, current theory and phylogenetic reconstructions suggest that monogamy as a mating system and pair-living as a type of social organization evolved from a solitary ancestor with a promiscuous mating system (Müller and Thalmann 2000; Low 2003). The different pattern of cohesiveness, encounter rates and qualities among pair-living species may represent different evolutionary stages in the transition from a solitary to a pair-living life style. Avoidance of pair partners, as

well as high levels of aggression between the sexes in *L. ruficaudatus* may reflect a very early evolutionary stage of pair-living. Observed patterns of mate guarding as well as some morphological traits point in the same direction. Male *L. ruficaudatus* have significantly longer canines than females and their testes volume increases on average by a factor of 2.3 during the mating season (Zinner et al. 2003). These traits are not predicted for pair-living species (Darwin 1871; Harcourt et al. 1981; Kappeler 1997a) and may suggest that pair-living in *L. ruficaudatus* is a recently acquired or locally labile trait.

Why defend only one female?

The results of our study clearly support the female defence hypothesis, which reflects a male mating strategy. Male *L. ruficaudatus* defended their territories mainly against other males, but not against neighbouring females. Males travelled more during the mating season, compared to the non-mating season. Furthermore, males and females responded strongest to playback experiments with strange male and female calls during the mating season, when the intensity of intrasexual competition and the possibility for extra-pair copulation were highest. Male *L. ruficaudatus* are clearly able to defend a single female, but it remains unclear which factors and constraints prevent males from defending more than one female.

Socio-ecological theory (Emlen & Oring 1977) suggests that unfavourable distributions of females in either time (i.e., oestrus is highly synchronized; Dunbar 1988) or space are the main constraints on male monopolisation. Although mating was highly seasonal, we did not find evidence for females synchronising their oestruses. Instead, *Lepilemur* females showed a high degree of home-range exclusivity, which is even more pronounced than in other pair-living primates (cf. Fietz 1999; Schülke 2003a). In fact, home-range overlap of 95% kernels among females was virtually absent, indicating high intra-sexual avoidance or resource competition among females. This notion is further supported by observed low encounter rates between neighbouring females. Thus, a certain degree and combination of home-range size, home-range overlap and intra- and intersexual aggression may represent a fundamental threshold for *Lepilemur* males in their ability to monopolise or roam over territories of several females (Emlen and Oring 1977; Komers and Brotherton 1997; Komers et al. 1997). Comparative analysis of home-range size in mammals has indeed shown that female space use is a fundamental

predictor for pair-living (Komers & Brotherton 1997). Moreover, in several other pair-living mammals high intrasexual aggression (gibbons: Brokelmann & Srikosamatra 1984, Mitani 1984; golden lion tamarins: Baker and Dietz 1996) or dispersion of females (elephant shrews: Rathbun 1979; beavers: Sun 2003) are considered as typical traits that favour evolution of pair-living.

To determine whether females are too widely distributed in space for males to monopolise several of them, it is important to consider the defendability of territories. Defendability can be measured by comparing travel distances and home-range size of a species. Defendability indices calculated for *L. ruficaudatus* (Mitani and Rodman 1979; Lowen and Dunbar 1994) did not indicate that females are over-dispersed. Theoretically, *L. ruficaudatus* males should be able to defend territories of up to eight females. This value is comparable to defendability indices calculated for P. *furcifer* or several gibbon species, where males could defend areas large enough to include the range of 4-7 females (van Schaik and Dunbar 1990; Schülke 2005). But these theoretical values are still an order of magnitude lower compared to solitary species, such as *Microcebus murinus* or *Mirza coquereli,* where males range over territories of up to 20 females (Kappeler 1997b; Eberle and Kappeler 2004). Hence, the defendability threshold has to be considered with caution. The model is based on the relation between travel distance and home-range size of males that should already reflect the consequence of mate competition. The model does not include possible additional costs and constraints males have to face if they would defend the range of more females or adopt a roaming strategy (Promislow 1992).

We propose several additional costs that could prevent males of *L. ruficaudatus* to monopolise more than one female or to adopt a roaming strategy. First, behavioural oestrus of females is short and mating is probably restricted to only one night per year (Petter-Rousseaux 1964; Eberle and Kappeler 2002; Hilgartner et al. in press). Therefore, information about female reproductive state is crucial for males. We assume that male *L. ruficaudatus* seek and gain information about the reproductive state of their pair partner because encounter rates within pairs increased during pre-mating and mating season and vigilance towards female playback calls was high during the mating season. Moreover, males were responsible for maintenance of proximity and showed intense mate guarding during behavioural oestrus. However, obtaining this information seems costly for males due to high aggression between pair partners. Hence, monopolising more than one

female would increase energetic costs of males considerably due to aggression from several females and may lead to less exclusive and precise information about female reproductive status (Ribble 2003).

Second, mate competition in *L. ruficaudatus* seems to be already intense for males defending only one female. Males encountered neighbouring males every second night and in about 95% of encounters aggression, such as chasing, biting or fighting, was observed. Moreover, we witnessed one extra-pair copulation and found evidence for a few extra-pair paternities (Platner et al. unpublished data). Although extra-pair paternity rate was low compared to other pair-living primates/mammals (Fietz et al. 2000; Schülke et al. 2004), it underlines the importance of mate competition and the resulting constraints on mate control. Hence, a roaming strategy or the control of more than one female could lead to higher encounter rates among males and therefore increase the risk of injuries as well as energy demand of males, in particular if one considers the energy saving lifestyle of Lepilemur in general (Drack et al 1999).

Third, *L. ruficaudatus* is vulnerable to a range of terrestrial and aerial predators (Rasoloarison et al. 1995). Several successful predation attempts by predators such as a large viverrid (*Cryptoprocta ferox)* and the Madagascar Harrier-hawk (*Polyboroides radiatus*) have been observed during the day when *L. ruficaudatus* sleeps in tree hollows (Hilgartner et al. in press; Schülke and Ostner 2001; Dammhahn pers. comm.). The quality of tree hollows is considered to play an important role for minimization predation risk (Schülke and Ostner 2001). Predation risk may be higher for males that roam or have to defend a larger area because risk of predation is likely to increase when being in less familiar areas with reduced knowledge about suitable, safe and unoccupied day shelters.

In summary, advantages of defending more females or adopting a roaming strategy may not outweigh the costs even for the most competitive males in *L. ruficaudatus*. Rather than fighting repeatedly over access to several females, a strategy of avoiding conflicts and minimizing costs by defending one female over several reproductive cycles could result in a higher reproductive success in the long term. This risk-averse strategy was first proposed for several other pair-living mammal species (McNamara and Houston 1992). In Kirk's dik dik (*Madoqua kirkii*) high costs of roaming were proposed as the primary reason for the evolution of pair-living (Brotherton and Manser 1997; Brotherton & Komers 2003). Studies of male

elephant shrews pointed in the same direction (FitzGibbon 1997; Ribble 2003). Defence of more than one female was temporarily limited and resulted in weight loss of males (FitzGibbon 1997). Thus, consequences of pair-living for life-time reproductive success have to be considered when evaluating different reproductive strategies of males.

Does pair-living represent a dilemma for *Lepilemur* females?

Given that an observed mating system or type of social organisation may represent the outcome of a compromise between male and female strategies, it is of interest to consider the females' perspective in this context, as well. Although increased vigilance of females following playback calls of strange males is indicative of potential female interest in extra-pair copulations, we assume that the options for female choice in *L. ruficaudatus* are restricted. First, unpaired females (following predation of mates) stayed within their home-range until new males immigrated (n=4). In these cases, we did not find evidence that females tried to repel new males from their home-range. Second, territories, as well as pair composition, remained stable for several years (Zinner et al. 2003). Third, mate guarding of males is intense and males dominate females during the short mating season. Fourth, extra pair copulations are rare and extra-pair paternity rate seems to be low (Platner et al. unpublished data). Thus, females may have only limited control over which male they live and mate with. Risks of ending up with a male which carries only low quality or incompatible genes (Birkhead and Møller 1992; Johnsen et al. 2000) or even with an infertile mate (Sheldon 1994) are considered as major disadvantages of reduced female choice.

However, females may also reap benefits from being paired with a male. First, females may face lower sexual harassment by strange males, which has been shown to be costly to oestrous females in promiscuous species (Wrangham 1980; Clutton-Brock and Parker 1995; Gowaty 1996). Moreover, females are likely to benefit indirectly from reduced feeding competition because additional males are excluded from their home-range (Schülke 2005). In addition, serial pair-living seems to be not uncommon in *L. ruficaudatus.* Although some females were paired with one male over a period of at least four years, others (n=4) lived with two males successively within four years. In all observed cases death of the previous pair partner was responsible for the appearance of a new male. Hence, serial pair-living could at least

compensate for a reduced genetic variability of the offspring, if not for a reduced female choice.

In summary, this study underlines the value of the female defence hypothesis when investigating the evolution of pair-living. Ranging pattern of females as well as a short mating season certainly affect monopolisation potential of males. However, these factors *per se* cannot fully explain the evolution of pair-living in *L. ruficaudatus*. In addition to these constraints we conclude that increased inter- and intrasexual aggression as well as a higher predation risk may prevent males to adopt a roaming strategy. Minimization of risks and hence a minimization of the variance in mating success may explain why males focus on only one female in *L. ruficaudatus*. The comparative evaluation of life time reproductive success as well as the relative importance of benefits and costs for males and females associated with only one partner may help to fully understand pair-living in this nocturnal primate.

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1998-1999 Wissenschaftliche Hilfskraft für die Insektenzucht, Universität Ulm;
Abteilung Neurobiologie

1999 Wissenschaftliche Hilfskraft für das ökologische Anfängerpraktikum, Universität
Ulm; Abteilung Systematische Botanik und Ökologie

2000 Wissenschaftliche Hilfskraft für das Praktikum Tierbestimmungsübungen
(Arthropoda), Universität Ulm; Abteilung Ökologie und Morphologie der Tiere

2000 Wissenschaftliche Hilfskraft für das botanisch-ökologische Anfängerpraktikum,
Universität Ulm; Abteilung Systematische Botanik und Ökologie

2000 Seminarleitung im Rahmen des ökologischen Anfängerpraktikums, Universität
Ulm; Abteilung Systematische Botanik und Ökologie

2003 Wissenschaftlicher Berater für die Naturdokumentation „In den Wäldern der Lemuren" ein Film von Telse und Dirk Blumenberg im Auftrag des NDR

2006 Wissenschaftlicher Berater für die BBC Filmproduktion Planet Earth „Forests"

Auslandsaufenthalte

1997 Studienreise nach Sumatra und Borneo (Indonesien). Besuch der Forschungsstationen Ketambe und Suaq (Provinz Aceh, Sumatra)

1999 Studienreise nach Sumatra und West Papua (Indonesien). Expedition ins Stammesgebiet der Keuw (Provinz Nabire; West Papua)

1999 Verhaltensökologisches Praktikum an der Forschungsstation Kirindy im Westen Madagaskars

1999-2000 Forschungsaufenthalt im Rahmen der Diplomarbeit an der Forschungsstation Kirindy im Westen Madagaskars

2002 Studienreise nach West Papua (Indonesien)

2003 Forschungsaufenthalt im Rahmen eines Naturschutzprojektes (Rapid Assesment) in Kollaboration mit der NGO Mitsinjo (Andasibe) im Osten Madagaskars

2001-2005 Forschungsaufenthalt im Rahmen der Dissertation an der Forschungsstation Kirindy im Westen Madagaskars im Zeitraum 2/2001 bis 4/2005 (26-monatiger Langzeitaufenthalt, drei Kurzzeitaufenthalte je 3 Monate)

Kongressbeiträge und Poster

Hilgartner R.; Zinner D.; Kappeler P.M. (2005) „Life history traits and infant care in red-tailed sportive lemurs (*Lepilemur ruficaudatus)*" *Primate report*. (Sp iss 72), 47-48.

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Hilgartner R., Raoilison M., Büttiker W., Lees D.C. & Krenn H.W. (subm.) Malagasy bird species as hosts for eye-frequenting Lepidoptera. *Proceedings of the Royal Society B: Biology Letters.*

Hilgartner R., Zinner D., & Kappeler P.M. (accepted) Life history traits and parental care in *Lepilemur ruficaudatus. American Journal of Primatology.*

Hilgartner R. & Raoilison M. (accepted) Hoffnung für den Erhalt der Flachrückenschildkröte *Pyxis planicauda* (Grandidier 1867) im natürlichen Habitat? *Marginata*.

Hilgartner R. & Raoilison M. (2006) Freilandbeobachtungen an *Uroplatus guentheri* einem Plattschwanzgecko aus Madagaskar. *DATZ 8*. 24-27.

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Dolch R.; Hilgartner R., Ndriamiary J-N., Randriamahazo H. (2004) The grandmother of all bamboo lemurs – evidence for the occurrence of *Hapalemur simus* in fragmented rainforest surrounding the Torotorofotsy marshes, Central Eastern Madagascar. *Lemur News* Volume 9, 20-24.

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Schülke O., Hilgartner R., Zinner D. (2002) Das nächtliche Leben zweier wenig bekannter Lemurenarten Westmadagaskars. *Zeitschrift des Kölner Zoo* 4*,* 179-194.

Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Arbeit selbstständig angefertigt und keine anderen als die in der Arbeit aufgeführten Hilfsmittel verwandt zu haben. Wörtlich oder inhaltlich übernommene Stellen sind als solche gekennzeichnet.

Ulm den 1. Oktober 2006