Living apart together –

Patterns, ecological basis, and reproductive consequences of

life in dispersed pairs of fork-marked lemurs

(*Phaner furcifer*, Primates)

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GENERAL INTRODUCTION

The stunning diversity of animal societies (or social systems) can be structured on three levels: species and populations may vary in their social organisation, their social relationships, and their mating system (Struhsacker 1969, Rowell 1979). Among the qualities of sociality listed by Wilson (1975) *social organisation* refers to the 'demography based factors' (Asquith 1978, p. 203): group size, demography, and cohesiveness. *Social relationships* develop between any two individuals of a social unit when they interact repeatedly with one another and each interaction may affect what happens in the subsequent ones (Hinde 1983). Because in social units of more than two animals each individual that is part of a social relationship also takes part in other relationships, a social network of relationships, called social structure, develops (Hinde 1983). *Mating systems* are usually categorised according to the number of opposite sexed individuals mating with each other during a single breeding season (Emlen & Oring 1977) and contain a genetic component that refers to the reproductive output of these matings (Kappeler & van Schaik 2002).

The three aspects of animal societies, i.e. social organisation, social structure and mating system, should be neatly teased apart if evolutionary explanations for their variation are sought (Kappeler & van Schaik 2002). Monogamy, for example, is still an ambiguous concept (Wickler & Seibt 1983), because some authors use the term to describe a form of social organisation (Fietz 1999a, Fuentes 1999), a mating system (Ribble 1991) or a mixture of both (Brotherton et al. 1997), which has led to confusion and spurious results (Sommer & Reichard 2000). However, all three aspects are tightly interrelated. Different types of social relationships (e.g. despotic/nepotistic dominance relationships cf. Sterck et al. 1997) can only be formed between individuals that live in the same social unit. Aversive relationships may even lead to exclusion of certain individuals from the social unit (e.g. through targeted aggression Vick & Pereira 1989), thus, influencing social organisation. Moreover, certain grouping patterns (i.e. social organisation) may sometimes be prerequisites for the evolution of specific mating systems (e.g. harems or one-male–multi-female groups for polygyny). Thus, as in this thesis, animal societies are best studied using an integrative approach that tackles each of the three main aspects separately without ignoring the interrelationships between them.

In this thesis, I present results of the first comprehensive study of the social system of a small, nocturnal primate: the fork-marked lemur (*Phaner furcifer*). One reason for choosing the study species was that this small (330g) lemur was long regarded as exceptional among

nocturnal prosimians, because single males and females have been described to live mainly in pairs that range in a cohesive fashion during most of their activity time (Petter et al. 1971, Charles-Dominique & Petter 1980). Charles-Dominique (1978) labelled the species 'pre-gregarious' and placed it alone on an intermediate step in his grade shift model for the evolution of gregarious group-living from a solitary life style. Several aspects of their *social organisation* remained unknown, however; e.g., how stable in time male-female pairs are, whether social boundaries exist between neighbouring pairs and how cohesive pair partners are on a metrical scale and in direct comparison to other species. These questions will be addressed in Chapter one.

Moreover, fork-marked lemurs are well known for their adaptations to gummivory (Hladik 1979, Charles-Dominique & Petter 1980, Hladik et al. 1980), the qualitative description of female agonistic dominance (Charles-Dominique 1978, Charles-Dominique & Petter 1980), and singleton births, as opposed to the regular birth of twins in all other members of the family Cheirogaleidae (Petter et al. 1971, 1975, Kappeler 1998). How fork-marked lemurs compete for their major food resources and how feeding competition has affected *social relationships* as well as differential female reproduction was unknown and will be investigated in Chapter two.

In Chapter three, I focused on the unstudied sex differences in *mating strategies,* with special emphasis on the reproductive consequences of mating between members of the same and different social units. Finally, unlike all other nocturnal prosimian primates (except *Avahi* Kappeler 1998), fork-marked lemurs have been reported to carry their young around clinging to their mother's fur during their activity period (Petter et al. 1971, 1975). Infant carrying and the associated risks (i.e. infanticide: van Schaik & Kappeler 1997) form the basis for one of seven alternative explanations for the evolution of pair-living in fork-marked lemurs that are evaluated in the General Discussion.

Integrating studies of *social organisation*, *social relationships*, and *mating system* of a single species was a primary goal of this dissertation. This goal was approached through use of innovative methods (simultaneous radio tracking of both pair partner for quantification of cohesiveness, Chapter one), application of existing theory to new areas of research ('ecological model' applied to pair-living and nocturnal primate, Chapter two), modern molecular techniques (DNA-microsatellite analyses for paternity evaluation, Chapter three), and by performing the first tests of recently formulated evolutionary models ('mate guarding hypothesis' in dispersed pairs, Chapter three). The work should increase our knowledge about

the behavioural ecology of a little studied nocturnal primate through a long-term field study. More importantly, this study opens new areas of research and contributes important comparative information to our understanding of the evolution of primate and animal societies in general.

A concise description of the social organisation of a species or population as provided in **Chapter one** is basic to most socio-ecological studies. The different categories of social organisation can be defined according to *size*, *sex composition* and *spatio-temporal cohesion* of a social unit (Kappeler & van Schaik 2002). As a necessary condition to constitute a social unit, animals that share a common range must also exchange more social interactions amongst each other than with other conspecifics (Kappeler & van Schaik 2002), i.e. the spatial boundaries have to coincide with the social boundaries. Each male and female either lives solitary or with a certain number (*size*) of other males and females (*sex composition*), yielding five types of *social organisation* (solitary, pair, one-male–multi-female group, multi-male–multi-female group, multi-male–one-female group cf. Kappeler 1999).

The types of social organisation of species and populations vary along two additional axes: social units are either cohesive or dispersed, and the organisation type is either uniform or variable. Variation in *spatio-temporal cohesion* is recognised in the distinction between *cohesive* units (cf. Müller & Thalmann 2000, *associated* sensu van Schaik & Kappeler 2003) with members travelling in closed formation, and *dispersed* units (Eisenberg et al. 1972, Martin 1981, Müller & Thalmann 2000) with members of a unit spending the main part of their activity time away from one another and meeting only rarely. If not all social units of a species or population are of the same social organisation type, this type may occur *uniformly,* where more than 90% of social units resemble one type. Alternatively a social organisation type occurs *variably,* whenever the majority, but less than 90% of social units are of one type (van Schaik & Kappeler 2003, see also Fuentes 1999).

Variation in social organisation has been studied particularly well in primates because they exhibit a wide variety of all possible types of social organisation (Janson 1992). Among primates variation between *cohesive* and *dispersed* social organisations is strongly associated with activity period in the sense that most diurnal primates live in cohesive pairs or groups (Wrangham 1987), which has been attributed to variation in predation risk (van Schaik 1983) and the risk of infanticide by males (van Schaik & Kappeler 1997). Irrespective of female group size, permanent association with at least one protector male has been interpreted as a

female counter-strategy against infanticide by males (van Schaik & Kappeler 1997) likely to succeed only if infants are associated with their mothers. The mode of infant care (i.e. association and carrying vs. parking) varies with activity period, (i.e. diurnal vs. nocturnal) in the sense that infant carrying mothers have a diurnal life style (Kappeler 1998). Nocturnal primate females are not associated with their infants, thus, do not gain benefits in terms of infanticide prevention from associating permanently with a protector male (van Schaik & Kappeler 1997, Kappeler 1998), and live solitarily or in dispersed social organisations (Müller & Thalmann 2001).

Misconceptions about the differentiation between a *solitary* life style and a *dispersed* social organisation have led to much confusion in the primate literature (Bearder 1987, Sterling 1993, Gursky 2000a, Müller & Thalmann 2000, Radespiel 2000). The consequent use of the terms *dispersed* and *cohesive* (or associated) in the classification of different types of social organisation among nocturnal primates (Müller & Thalmann 2000, van Schaik & Kappeler 2003) has clarified the issue now. Nocturnal primates are either solitary (e.g. *Mirza coquereli*: Kappeler 1997a) or live in dispersed pairs (e.g. *Cheirogaleus medius*: Müller 1998, Fietz 1999a, *Lepilemur edwardsi*: Rasoloharijoana et al. 2000, Thalmann 2001) or dispersed groups of different composition (e.g., *Galago zanzibaricus*: Harcourt & Nash 1986, *Tarsius spectrum*: Gursky 1995).

Among nocturnal primates, fork-marked lemurs are regarded as exceptional because pairs are classified as cohesive on the basis of the description that pair partners are 'in close proximity for at least half of the night' (p. 85: Charles-Dominique & Petter 1980, van Schaik & Kappeler 1997). In Chapter one I provide the first systematic quantification of this statement to evaluate the exceptional status of the fork-marked lemur. At the same time, I offer an important first reference point for future studies of the variation in cohesiveness among nocturnal primates. Moreover, this study is the first to investigate the mechanisms responsible for the maintenance of low cohesion in dispersed pairs.

Social dominance *relationships*, in general, vary in three dimensions: i) from *individualistic to nepotistic* with relatives forming alliances, ii) from *egalitarian to despotic* with dominance hierarchies forming between individuals and alliances, and iii) from *tolerant to intolerant* with dominant individuals insisting on their priority of access to resources (Sterck et al. 1997). This variation has been causally linked to the competitive regime a species is faced with (van Schaik 1989, Sterck et al. 1997). A competitive regime describes

the intensity of contest and scramble competition for food and other crucial resources within and between groups. *Contest* (Nicholson 1954) or interference competition (Begon et al. 1996) occurs between animals that compete directly over access to resources. *Scramble* (Nicholson 1954) or exploitation competition (Begon et al. 1996) will take place if individuals respond to the depression of the level of a resource by conspecifics. The competitive regime is thought to result from characteristics of the food resources used (van Schaik 1989, Sterck et al. 1997). For example, if food is of high quality and distributed in small patches that do not allow co-feeding of all group members at once, within group competition for access to these resources will take the form of a contest. Contest competition for food will promote the evolution of despotic relationships between individuals of a group with higher-ranking individuals gaining priority of access to food. If the major food resources are distributed in a fashion that does not allow monopolisation of food patches, contest competition will play a minor role and individuals will scramble for food instead. If *scramble* competition predominates relationships between individuals will be more egalitarian. This framework (the '*ecological model*' van Schaik 1989) builds upon the earlier work by Nicholson (1954) on different types of competition and by Jarman (1974) on the relation between resource characteristics and competition in antelope. It was originally conceived in order to explain the evolution of female social relationships in diurnal group living primates (van Schaik 1989, Sterck et al. 1997, Koenig 2002).

In **Chapter two** the '*ecological model*' is applied to the study of a pair-living species for the first time. Two aspects make this a promising approach. First, the 'ecological model' recognises that different types of feeding competition within and between groups will result in different patterns of differential female reproductive success, i.e., the basic currency of evolutionary change. In a situation with strong between group contest competition, for example, females living in larger groups should gain a reproductive advantage over females living in smaller groups (van Schaik 1989). Because the females of pair-living species form social units with a male partner and a varying number of offspring, these females in fact live in small groups of varying size. Thus, the principles proposed by the 'ecological model' should be applicable here as well. In Chapter two, I provide the first evaluation of the causes of differential female reproductive success in a pair-living nocturnal primate.

Secondly, the evolution of pair-living among mammals, most of which lack paternal care (Kleiman 1979), has been explained by female range exclusivity and male inability to defend access to more than one female economically (Komers & Brotherton 1997). In this

context female intrasexual avoidance is thought to result either from a serious threat of female infanticide (Wolff & Peterson 1998) or from intense feeding competition (Komers & Brotherton 1997, van Schaik & Kappeler 2003). Intense female-female feeding competition is the more likely explanation in nocturnal lemurs because vulnerability to infanticide is generally estimated to be low in nocturnal primates (van Schaik 2000a, b). Building upon the assumption that feeding competition between pair partners mirrors ancient competition patterns among females, one aim is to test the hypothesis that female range exclusivity is a precursor of pair-living in fork-marked lemurs. In doing so, I investigate the ecological basis for male-female spatial and *social relationships* in dispersed pairs in Chapter two.

Chapter three focuses on the *mating system* of fork-marked lemurs, i.e. the reproductive consequences of life in dispersed pairs. Mating systems are best perceived as the consequence of interacting reproductive strategies of individual males and females (Davies 1993). Mating systems are usually categorised according to the number of opposite sexed individuals *mating* with each other during a single breeding season (Emlen & Oring 1977). Thus, four mating systems can be distinguished: i) *monogamy*, one male and one female mate exclusively with each other, ii) *polyandry*, each female mates with several males but each male only with one female, iii) *polygyny*, each male mates with several females but each female only with one male, and iv) *promiscuity* (or polygynandry), each male and each female mates with several individuals of the opposite sex. But mating systems also contain a genetic component (Kappeler & van Schaik 2002) and recognise who finally *reproduces* with whom, which is not necessarily congruent with who mated with whom (Petrie & Kempenaers 1998). Moreover, mating may occur either within a social unit or across social units. As the latter has been first described in pair-living species these matings are referred to as *extra-pair copulations (EPCs)* and the resulting genetic consequence as *extra-pair paternity (EPP)*.

From a sexual selectionist's point of view, monogamy is the most puzzling mating system. Ever since Trivers (1972) built a theory upon Bateman's (1948) discovery that male reproductive success is limited by the number of mates, socio-ecological studies were concerned with the questions why males could forego the opportunity of polygynous matings. When socio-genetic studies yielded growing evidence for extra-pair paternity (EPP) in pair-living birds (and later in mammals, fish and invertebrates) the issue seemed to be resolved (Birkhead & Møller 1992): if one only performed sufficient numbers of genetic analyses, the lacking evidence for EPCs in many birds would be reduced to a mere observation and/or

sample size problem. More recently the pendulum swung back with genetic studies indicating the widespread occurrence of strict monogamy in birds (e.g. Haggerty et al. 2001, Masello et al. 2002, Stanback et al. 2002), fish (e.g. Jones et al. 1998), and mammals (Ribble 1991, Heller et al. 1993, Brotherton et al. 1997, Sommer & Tichy 1999). Moreover, it has been shown that mating systems are not fixed species-specific traits but that EPP varies between populations of the same species (Barber et al. 1996) or even between years in the same population (Petrie & Kempenaers 1998). Accordingly, the causes and consequences of variation in EPP among pair-living species and populations became the focus of many important mating system studies (Møller & Ninni 1998, Petrie & Kempenaers 1998, Hasselquist & Sherman 2001).

In mammals, and in primates in particular, information about paternity in pair-living species is scarce. Comparative studies of variation in EPP have therefore been impossible to date. Nevertheless, a recent model based on a phylogentic reconstruction of the evolution of pair-living in primates makes explicit and testable predictions about EPP rates in relation to the social organisation of a species (van Schaik & Kappeler 2003). Phylogentic reconstructions revealed that *uniform* pairs evolved from ancestral *variable* pairs in all primate lineages. The evolutionary transition from variable to uniform pairs involves derivation of benefits from male infanticide avoidance in combination with female territoriality or male protection of cached young against predators, which both are male services to the female and her offspring and both require a high degree of paternity certainty (van Schaik & Kappeler 2003, but see Fietz et al. 2000). EPP rates (the inverse of paternity certainty) in pair-living primates should, therefore, be high in variable and low in uniform pairs.

The vast majority of primates living in dispersed pairs has been categorised as variable pairs, which should consequently exhibit high rates of EPP (van Schaik & Kappeler 2003). Because pair partners rarely see each other during regular activities the mechanism proposed to explain high EPP rates among dispersed pairs is reduced efficiency of male mate guarding (van Schaik & Kappeler 2003). In Chapter three, the two step hypothesis that EPP rates are high in dispersed pairs and that they result from constraints on male mate guarding is investigated in fork-marked lemurs.

CHAPTER 1:

So near and yet so far: Territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*

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INTRODUCTION

The diversity of animal societies can be categorised according to size, sex composition and spatiotemporal cohesion of their members (Wilson 1975). Accordingly, an individual either lives alone or with one or several members of the same and/or the opposite sex in either transient or permanent association. Why animals form such associations or groups, and why they have a particular size and composition, remain to be some of the main questions in behavioural ecology (Pulliam & Caraco 1986; Krebs & Davies 1993; Kappeler 2000). Relevant studies suggest that gregariousness independently evolved many times in response to nonmutually exclusive selective forces that favoured decreased predation risk, improved access to mates and resources or facilitated cooperative infant care (Patterson 1965; Hoogland 1979; Wrangham 1979; van Schaik 1983; Barnard 1984; van Schaik & van Hooff 1983; van Schaik & Kappeler 1997). In contrast, the behavioural details of gregariousness and the mechanisms responsible for the maintenance of cohesiveness in nonsessile animals have only recently begun to be examined systematically (Boinski & Garber 2000).

One of the simplest forms of gregariousness is found in pair-living species, where one adult female and one adult male (and their dependent offspring) are associated and coordinate their activities and movements. The term 'social monogamy' is often used to characterize this type of social organization, but, we prefer not to confuse descriptions of social and mating arrangements for several theoretical and practical reasons (Gowaty 1996; Kappeler & van Schaik 2002). Pairs are rarely found among invertebrates (Linsenmair & Linsenmair 1971), poikilotherms (fish: Barlow 1986; amphibians: Jaeger et al. 1995) and mammals (Kleiman 1977), but in birds (Orians 1969) and primates (Kleiman 1977; but see Fuentes 1999) a relatively large proportion of species (90% of birds, 15% of primates) lives in pairs.

The degree of cohesiveness among pair partners has not been much of an issue in classifying social organization in birds and mammals, even though in birds it varies from less than 2 h per day for 2 months a year to year-round permanent spatial association (Black 1996). Among mammals, klipspringers, *Oreotragus oreotragus*, keep the distance between pair partners below 5 m for a lifetime (Dunbar 1984), whereas dik-diks, *Madoqua kirkii*, spend only about two-thirds of their time together (Brotherton & Manser 1997), giant jumping rats, *Hypogeomys antimena*, may roam synchronously one day and avoid the pair partner another day (Sommer 1997; 1998) and elephant shrews, *Rhynochocyon chrysopygus*, are rarely seen together (Rathbun 1979).

In contrast, comparative studies of primates have overemphasized the degree of cohesiveness as a distinguishing feature (Crook & Gartlan 1966; Eisenberg et al. 1972). All nocturnal primates have been grouped together as 'solitary foragers' (Bearder 1987) to distinguish them from gregarious diurnal species. Several nocturnal 'solitary foragers', however, have since been described to live in pairs (Müller 1998; Fietz 1999a; Rasoloharijoana et al. 2000; Thalmann 2001) or to show some other form of gregariousness (Harcourt & Nash 1986; Gursky 1995; Warren & Crompton 1997). Qualitative reports indicate that the degree of cohesiveness between pair partners is highly variable among species, so that introduction of the terms 'dispersed' and 'cohesive pairs' seems justified to distinguish between behaviourally very different manifestations of pair-living (Müller & Thalmann 2000; van Schaik & Kappeler, in press). In cohesive pairs, both pair partners are closely associated and coordinated, but members of dispersed pairs share a common home range but show low cohesiveness during regular activities.

The fork-marked lemur, *Phaner furcifer*, is a 330 g nocturnal pair-living prosimian primate that feeds primarily on tree exudates (Charles-Dominique & Petter 1980; Schülke, in press). The first data collected during two brief expeditions, including only 6 weeks of observations of marked individuals (Petter et al. 1971; Charles-Dominique & Petter 1980), suggested that pair partners closely associate during the night and coordinate their movements by means of vocal communication. Hence, fork-marked lemurs were regarded as exceptional among nocturnal primates which usually forage solitarily, except *Avahi* and *Aotus,* which are secondarily nocturnal (Martin 1990; Thalmann 2001). In the present study, we first investigate the fork-marked lemur's social organization. Based on data collected during simultaneous follows of both pair partners, we also present the first quantitative analysis of cohesion in a nocturnal primate and discuss its relevance for concise definitions of animal social organization. Finally, we discuss possible mechanisms for maintaining the observed degree of cohesiveness.

METHODS

Study Site and Animals

The study site at Kirindy Forest is situated at 44°39' east, 20°03' south in western Madagascar on a forest concession of the Centre de Formation Professionelle Forestière de Morondava, where the Deutsches Primatenzentrum Göttingen, Germany, operates a research station. Kirindy Forest is part of one of the largest remaining fragments of dry deciduous

forest in Madagascar. The climate is characterized by a short, hot, rainy season from December to March with an average rainfall of 800 mm and 8 months of almost no precipitation. Between June and September, temperatures may drop as low as 5° C at night (for a detailed description of the forest, see Ganzhorn & Sorg 1996).

The study took place in a 900 x 700 m grid system locally known as CS7 and started in 1998 when the capture regime for fork-marked lemurs was established during a pilot study. Between November 1998 and April 2001, 30 individuals were captured 103 times, with Tomahawk life traps, from their sleeping holes in trees. Traps were fixed to the entrance of the hollow at an average height of 8 m. Typically, the animal entered the unbaited trap 10–20 min after dusk, when neighbours and family members began loud calling in close proximity. Traps were set one at a time, and captured animals were brought to the forest camp immediately after capture. The lemurs were briefly anaesthetized (0.02 ml Ketanest) before a 2 x 12 mm microtransponder (Trovan) was implanted with an injection needle dorsally under the skin in a fashion that precluded irritation by the harness tag. Transponders were not observed to migrate beneath the skin. All adult males (M1–M10 except M8) and females (F1–F8) caught between November 1998 and April 2000 were equipped with harness-fitted radiotags (10 g) designed especially for this study by Biotrack (Wareham, U.K.). The harness tag carried two tubes at its cranial and caudal ends. A Teflon ribbon running through both tubes was tied to a flat knot on the chest of the animal. The knot was sewn tight to prevent its opening. From June 2000 onwards, females (F1–F7, F9) were fitted with brass collar tags (14 g) because many of the animals removed their harness tags. Males were not equipped with collar tags because they have a large throat gland that might be irritated by a collar. We observed no irritation of the skin due to the harness or collar tags, and we know of no long-term adverse effects (e.g. increased predation risk). Tag lifetime was approximately 1 year and tags were replaced whenever necessary. The lemurs were released at their capture site later the same night. All sleeping trees where animals were captured once were reused by the same individuals after some time. The procedures did not noticeably harm the lemurs and were carried out with permission of the Malagasy Government.

The lemurs were aged as adult or nonadult according to body length and groupmembership; that is we treated an animal that was not fullgrown when first captured but grew to full bodylength without migrating as a nonadult in all analyses. We assumed that animals not full grown when first captured were natal to the territories where they were caught. DNA microsatellite analysis of relatedness did not contradict any mother/offspring

relationship assigned on the basis of behavioural observations (O. Schülke, P.M. Kappeler & H. Zischler unpublished data).

Data Collection

We obtained the data presented here during three study periods. Between June 1999 and June 2000, O.S. collected 1038 h of behavioural and locational data during focal animal protocols (Altmann 1974) on 15 adult males (M1–M9 except M3 and M8) and females (F1–F8), which are the basis for all behavioural analyses. From July to August 2000, only locational data (120 h) on seven pairs (families 1–7) were sampled by a field assistant. Finally, simultaneous focal follows of both pair partners (162 h) were conducted with a field assistant during times roughly corresponding to premating (September 1999), gestation (December 1999) and lactation (March–April 2001). During 2-h follows, the animal's location within the grid system of 25 x 25-m squares was recorded continuously. Focal follows were conducted in the first half of the night and were evenly distributed across this time. We assumed that spatial and social relationships among adults were similar in the second half of the night. Behavioural data collected by O.S. included direct observations of all social interactions (affiliative and agonistic) that were recorded continuously (Altmann 1974) as well as instantaneous records (2.5-min intervals; Altmann 1974) of behavioural states (resting, locomotion, feeding), details of feeding behaviour (e.g. plant part and species consumed) and visual contact times. Animals were located and followed using a Telonics TR-4 receiver with a three-element yagi antenna, a headlamp and, if necessary, a strong flashlight and binoculars.

Sleeping sites of radiotagged animals were determined between April 1999 and August 2000 and again between February and April 2001 on 419 days. Demographic data were collected during biweekly patrols of sleeping sites of radiotagged animals between September 2000 and January 2001 and from May 2001 until November 2001.

Data Analyses

Locational data collected between June 1999 and August 2000 were subsampled at 5-min intervals for home range analyses. These data points are regarded as independent because this interval allows an individual to cross its home range at maximum locomotor speed (Rooney et al. 1998). Home range area estimates based on Minimum Convex Polygons (Mohr 1947) have the disadvantage of increasing with increasing sample size (Jennrich & Turner

1969; Anderson 1982). The range of data points that entered the present analysis was 160–1366 per individual ($\bar{x} \pm$ SD = 824.8 $\pm$ 423.3). A preliminary analysis for 12 individuals showed that home range size reached an asymptote after 14.9 $\pm$ 3.8 h of sampling, equivalent to 179 $\pm$ 45 data points (only two individuals had samples smaller than 179). The 95% Minimum Convex Polygon (MCP, 5% outliers removed by harmonic mean method) home range size of 15 individuals for the period June 1999 to August 2000 did not correlate with sample size (Spearman rank correlation: R_s = 0.09, n = 15, n.s.). Thus, MCP home ranges are comparable across individuals.

Home range outlines and overlap were calculated with two different home range estimation methods: 95% MCPs, as well as 95 and 50% Kernel home ranges (Worton 1989). MCPs are the most commonly used home range estimator and therefore allow comparison across studies, but they encompass areas that the animal may never have used. In contrast, 95% Kernel home ranges identify a probability area, where the chance of finding the animal is 95%; they therefore describe the pattern of range use. MCP analyses were performed with Tracker 1.1 software (Camponotus and Radio Location Systems). For Kernel home ranges and all overlap analyses we used the GIS-based Animal Movement software (Hooge & Eichenlaub 1997).

Expected rates of encounters between pair partners were calculated with a random gas model (Waser 1976): $f = (4 \times \rho \times \upsilon) / \pi \times (2d + s)$, where the expected frequency of encounter (f) is dependent on the density (ρ) of a species, the velocity of the animals (υ), the group spread (s) and the distance criterion (d). In this paper, we calculated ρ for each pair separately as the inverse of a pair's home range in square meters, including exclusive areas of both partners, υ was calculated as the average of the distances the male and the female partner covered during half a night in meters, group spread s was zero for each individual. Encounters were defined as occurring when the distance between pair partners was less than 15 m, which is close enough to allow visual contact between the animals. Interval frequencies from instantaneous samples were used in the analysis of encounter frequencies. There were nine pairs for simultaneous follows, because after one pair partner was replaced by a new animal, we treated the newly formed association as a different pair in the analysis.

We calculated the proportions of time that pair partners spent in different distance classes from 0 to 350 m (25-m intervals) for each pair. The mean proportion across pairs was then compared with data from two cohesive gregarious diurnal primates: pair-living gibbons, *Hylobates lar*, and group-living, forest-dwelling Hanuman langurs, *Semnopithecus entellus.*

Data on cohesiveness of *H. lar* pairs were obtained from Reichard (1995a, p. 69) and averaged across pairs. For *S. entellus*, the maximum distance between two individuals in the group was calculated from data on group spread, assuming the group spread out in a circle (J. Beise, unpublished data; see also Koenig et al. 1998).

Data on affiliative and agonistic interactions between pair partners were obtained between June 1999 and June 2000 from focal protocols of six families (families 2–7). Calculation of interaction rate was based on the time the observer could see the focal animal. When interactions with neighbours were of interest, all data from single or simultaneous follows, focal or ad libitum recordings were pooled, because the observation of events and identification of animals during intergroup encounters proved difficult so sample size was limited.

We used the Hinde Index (Hinde & Atkinson 1970) to determine responsibility for the maintenance of spatial proximity between pair partners in affiliative contexts. The index does not provide a reliable measure for small sample sizes (Hinde 1976) and therefore only samples with more than 16 approaches and leaves were analysed (Hill 1990). Values between –10% and 10% were regarded as uninformative, because these slight differences in responsibility may occur by chance (Hill 1987). We classified agonistic behaviour as either aggressive (charge, chase, cuff, grab, bite) or submissive (be displaced, jump to ground, flee, 'duck away' sensu Pereira and Kappeler 1997). Determination of dominance relationships among pair partners was based on decided conflicts (Hausfater 1975), defined as agonistic interactions in which one opponent showed only submissive but no aggressive behaviour, while the other showed no signs of submission. The alpha level was 0.05 for all analyses, we used two-tailed statistical tests, and report means ± SD.

RESULTS

Demographic Dynamics

Demographic change in the adult population of fork-marked lemurs occurred due to confirmed deaths of two males and one female, disappearances of two males with unknown fate of the animals, six male immigrations and the replacement of a dead adult female by her daughter (Fig. 1). At the beginning of the study, male M3 ranged over an area encompassing the home ranges of two females (F3, F8). When male M3 died in September 1999, he was immediately replaced by two newly immigrating young males. One of these males (M9) died before the breeding season in 2000, as did the female pair partner (F3), who was replaced by

her daughter (F9), who then formed a new pair with immigrant male M12. The home range of family 3 remained the same over the course of all these changes. Similarly, the immigration of male M11 into the home range of resident male M4 did not cause a change in the family's home range. The males simply divided the range in two, and female F4 continued ranging over the entire area. In families 2, 4 and 7, pair partners stayed together for at least three mating seasons, and one pair (family 5) has been stable since November 1998. Divorce with subsequent mate change, as known in many species of birds (Black 1996), may have occurred in family 1, but we have no direct evidence, because males M1 and M10 were never seen alive outside their former territories.
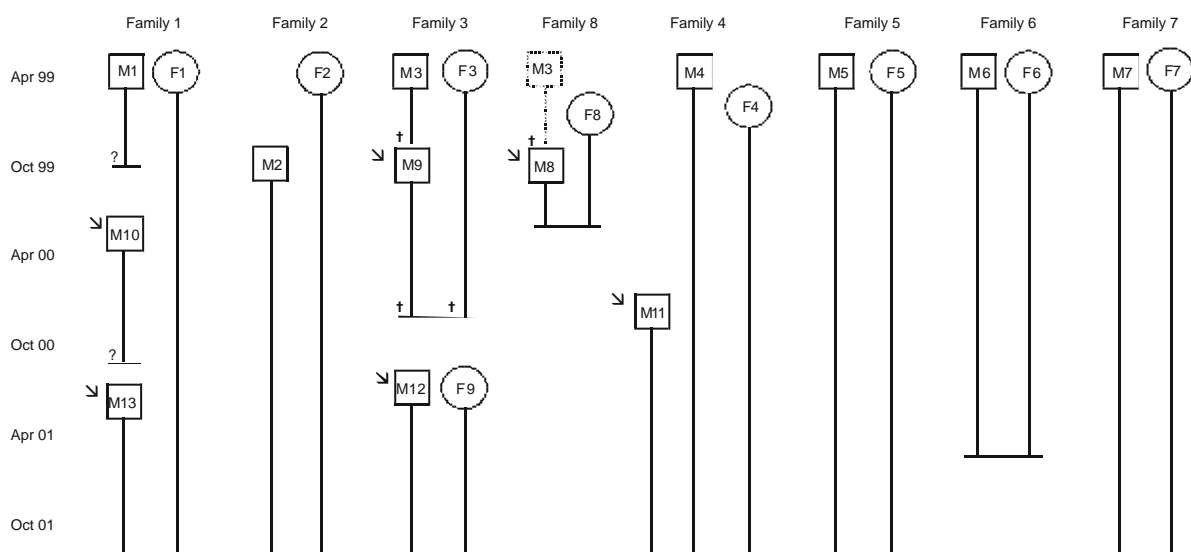

Figure 1: Demography of adult individuals from April 1999 to October 2001; infants, juveniles and subadults not shown; : males; O: females; †: death; ?: animal disappeared with unknown fate; horizontal line: no information available; ↘: animal immigrated into the study population. Animals entered the chart when they were first identified unequivocally, but are likely to have been there in April 1999.

Home Range Use and Overlap

Average home range size (MCP) was 4.65 ± 1.46 ha for females and 5.01 ± 1.91 ha for males (Fig. 2). Male home ranges plotted as 95% MCPs overlapped with those of all neighbouring males by only $13 \pm 18\%$, on average. Female-female range overlap was slightly lower ($11 \pm 16\%$). The home ranges of particular males and females overlapped extensively, and overlap was not affected by the perspective of the sex from which it is calculated (male: $82 \pm 14\%$; female: $82 \pm 12\%$). Male home ranges mirrored those of females in size and shape as indicated above. Two exceptions to this rule occurred: (1) one male (M3) temporarily ranged over the territories of two females (F3, F8) for 4 months before he died; (2) at the end of the main study period (June 2000), an unmarked male (M11) immigrated into an occupied

home range and drove the resident male (M4) to a portion of his former range, and the resident female (F4) ranged over the areas of both males.
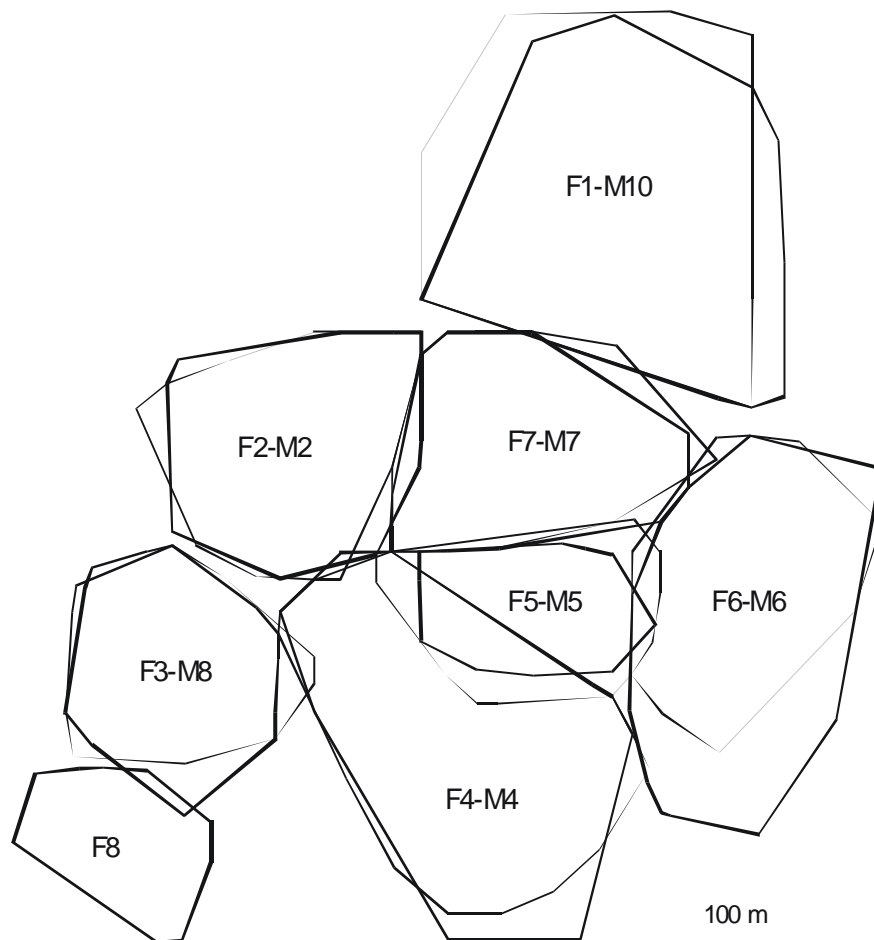

Figure 2: Minimum Convex Polygons of ranges of adult individuals from June 1999 to August 2000 (5% outliers removed by harmonic mean method). Bold outlines: female ranges; thin lines: male ranges. The male of female 8 was never captured and therefore never observed as a focal animal.

Because MCP home ranges are mere outlines of the ranging area, high MCP overlap does not imply that individuals use the area in a similar fashion. According to the 95% Kernel projection, male ranges overlapped only slightly ($11.1 \pm 8.9\%$) which is comparable to the overlap of their MCPs (Fig. 3). Female–female Kernel range overlap was virtually absent ($3.3 \pm 4.17\%$). Overlap between pair partners was much higher for females ($91.9 \pm 5.6\%$) than for males ($51.6 \pm 21.8\%$), which is because female 95% Kernel ranges were significantly smaller than those of males (Wilcoxon signed-ranks test for pair partners: $T = 0.00$, $N = 7$, $p < 0.05$).

To rule out the possibility that pair partners spent most of their time in exclusive areas of their common home range, we calculated overlap of 50% Kernel ranges. The overlap was $53.8 \pm 20.9\%$ from the males' and $78.6 \pm 29.4\%$ from the respective females' perspective.

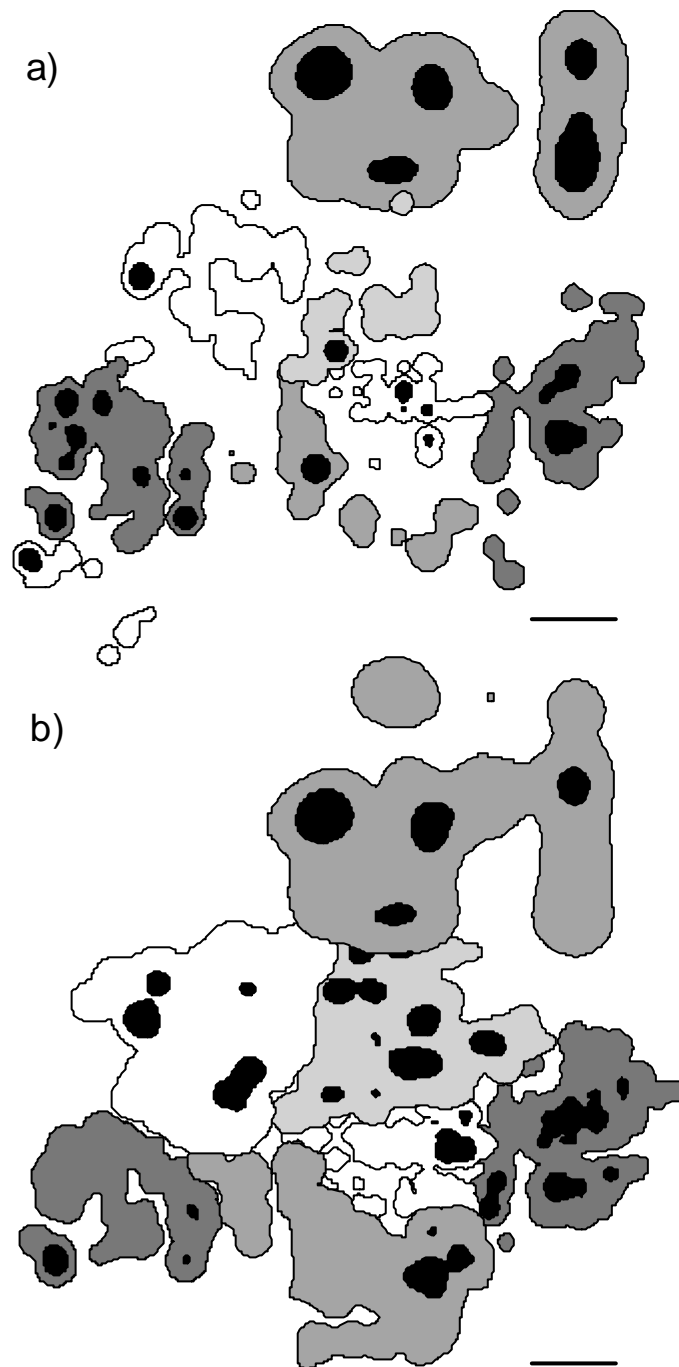**Figure 3**: Kernel home ranges (95% probability; black: 50% probability) of adult a) females b) and males from June 1999 to August 2000. Bars at lower right represent 100m.

Again, differences between male and female perspectives are due to larger areas occupied by males, although the difference fails to reach significance because of one exception (Wilcoxon signed ranks test: T = 3.00, N = 7, p = 0.06). Only static spatial

interactions were analysed, so it remains unclear whether pair partners range in a cohesive manner or independently.

Cohesiveness

According to the random gas model, two independently ranging animals behaving like gas molecules should encounter each other on average 1.1 ± 0.5 times during the first half of the night. In all pairs observed encounter rates (13.8 ± 8.9) were significantly higher than the expected values (Wilcoxon signed-ranks test: $T = 0.0$, $N = 9$, $p < 0.05$; Table 1). Pair partners spent $9.4 \pm 6.0\%$ of their activity period in close proximity (less than 15 m). During 23% of their activity period, pair partners were less than 25 m from one another (Fig. 4). However, pair partners were found in all distance categories from 50 to 150 m in almost similar proportions (range 10.4–14.6%).

Table 1: Encounter rates of pair partners (number/6 h)

Pair	F2–M2	F3–M3	F3–M9	F9–M12	F4–M4	F4–M11	F5–M5	F6–M6	F7–M7	Mean
Expected	1.29	2.23	0.51	1.03	1.07	1.13	0.92	1.12	0.65	1.11
Observed	5.72	20	3	28.08	5.56	20.13	16.01	19.62	6.04	13.8

Expected values calculated from the Gas Model (Waser 1976).

In contrast, *H. lar* pairs were found at a distance of less than 25 m more than 80% of time. The maximum distance between two individuals in a forest-dwelling multi-male–multi-female group of *S. entellus* was, on average, 47.1 m, and even these most separated individuals of a group were found less than 75 m from each other 80% of the time. Fork–marked lemurs spent only 52.6% of their time less than 75 m apart and the average distance between pair partners was 103.0 ± 24.5 m. Although simultaneous focal follows were conducted during the pre-mating season (September 1999), the gestation (December 1999) and the lactation period (April 2001), only one pair, was observed under all conditions. In all other pairs, one of the pair partners was not radiotagged at the given time or the pair constellation had changed. Mean distance between pair partners was roughly the same in all seasons (pre-mating: 108.4 ± 58.4 m; gestation 101.8 ± 59.8 m; lactation: 99.2 ± 61.8 m). However, comparisons of cohesion measures across female reproductive periods are problematic, because after the 1999 mating season only two births were observed, and only one female lactated in April 2001. Therefore, interindividual differences are probably larger than differences between seasons, but our small sample size precludes these fine-grained analyses.
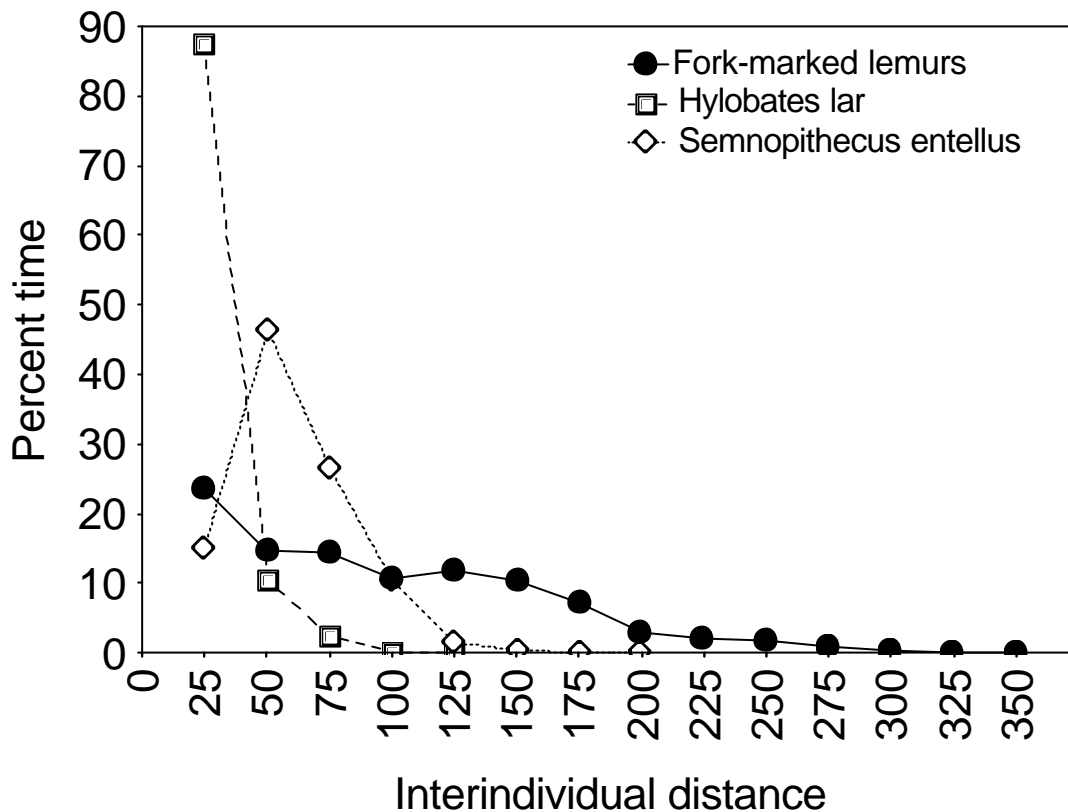
Figure 4: Cohesiveness of fork-marked lemur pairs compared to *Hylobates lar* pairs and the most distant members of a *Semnopithecus entellus* group; all distance classes contain a 25-m range (e.g. 25: 0–25 m, 50: 25–50 m).

Sleeping Associations

Fork-marked lemurs spent the day in tree holes, which were regularly shared by pair partners (Table 2). Sleeping sites were hollows in dead or live trees or leaf nests constructed by the sympatric lemur species *Mirza coquereli*. The number of sleeping sites that a single adult used was 8–38. Home ranges of families 1–7 contained 26–44 sleeping trees, as determined by the number of sites used by any family member. Although sleeping sites were obviously not limited, pair partners shared the same sleeping site about every third day (0.36 ± 0.24). When not sleeping in the same tree hole, pair partners' sleeping sites were, on average, 101 ± 60 m apart. Hence, pair partners spent more time in proximity during inactivity than during activity. Sleeping sites were never shared with neighbours, either simultaneously or consecutively (with one exception, after a territory border had been shifted slightly). We consider the influence of trapping at the sleeping site on these results minimal. Although animals avoided the tree where they were recently trapped, trapping episodes were rare: 30 individuals were trapped only a total of 104 times in 2 years. Furthermore, tree holes

were not damaged by the trapping technique, and lemurs used every trapping site again within several days or weeks.

Table 2: Sleeping associations and sleeping sites used.

Pair	Family	Number of sites	Partners together	Percentage together
F1–M1	1	42	9/22	40.9
F1–M10	1	42	0/17	0.0
F2–M2	2	31	94/140	67.1
F3–M3	3	42	33/118	28.0
F3–M9	3	42	13/168	7.7
F9–M12	3	42	39/50	78.0
F4–M4	4	44	114/228	50.0
F4–M11	4	44	28/71	39.4
F5–M5	5	39	57/230	24.8
F6–M6	6	34	120/323	37.2
F7–M7	7	26	40/225	17.8
Average		36.9		35.5

Number of sites: All sites ever used by any family member throughout the study period. Partners together: Number of days that pair partners shared sleeping sites relative to sample size.

Affiliative Interactions

We observed 102 affiliative interactions between pair partners. Affiliative behaviours included grooming interactions (80.4%), bouts of body contact (3.4%) or sitting within reaching distance (2.0%), allomarking (3.9%) and a number of interaction types that were observed only once (nose–nose contact, close following, mounting, tongue-flick). The pairs that were observed directly with sufficient visual contact (families 2–7) exchanged affiliative behaviour at an average rate of 0.22 ± 0.07 interactions/h. Pair 1 was seen less than 10% of the observation time, compared to 65 ± 10 % for the other pairs, and was therefore excluded from the analyses of interactions. The mean duration of affiliative behaviour was 116 ± 77.0s. If only grooming interactions are taken into account, variation was less pronounced, with pairs grooming, on average, 80.7 ± 14.4 s/bout.

Sex differences in responsibility for the maintenance of proximity in affiliative contexts were calculated from the distribution of approach/leave interactions. The Hinde Index could be calculated in five of the six pairs (Table 3). In pair M6–F6, the male and the female approached and left each other almost equally often and hence were equally responsible for the maintenance of proximity. In the remaining four pairs, males were clearly responsible for the maintenance of spatial proximity, and females showed little interest, as expressed by negative Hinde values.

Table 3: Hinde Index for proximity in context of affiliative interactions

Pair	Family	Approaches (%)	Leaves (%)	N	Hinde Index	Responsible
F2–M2	2	0	75	6	-75	N too small
F3–M9	3	33,33	100	16	-66,67	Male
F4–M4	4	38,89	75	34	-36,11	Male
F5–M5	5	16,67	54,55	23	-37,88	Male
F6–M6	6	54,55	46,15	24	8,39	Both
F7–M7	7	57,14	75	19	-17,86	Male

Approaches and leaves calculated from the female's perspective. *N*: Sum of all approach and leave interactions.

Agonistic Interactions

During 455 h of direct visual contact with adult focal animals, 225 agonistic interactions between identified pair partners were observed. Of these conflicts 60.4% were over access to food, 12.4% occurred during mate guarding (in the mating season), 3.1% occurred in other social contexts (resting, immigration of new male, meetings with neighbours) and 24.0% occurred for undetermined reasons (Table 4).

Table 4: Context of agonistic interactions among pair partners

	Feeding	Guarding	Meeting	Immigration	Resting	Unknown
F2–M2	10		1			
F3–M9	19			5		22
F4–M4	22	28				15
F5–M5	32				1	13
F6–M6	36					4
F7–M7	17					
Total	136	28	1	5	1	54

Guarding: Mate-guarding behaviour in mating season. Meeting: Meeting with adult neighbours. Immigration: Immigration of a new male partner.

Mate guarding was observed in pair M4–F4 on 2 days only and was characterized by very high rates of female aggressive behaviour; two-thirds of decided conflicts involved aggression by the female. Conflicts during mate guarding constituted 43.1% of all observed agonistic interactions between M4 and F4 and introduced a large bias to the overall distribution of conflicts in different contexts. The frequency of conflicts during feeding was higher than would be expected if conflicts were equally distributed over all activities ($CHI^2_6 = 14.9$, $p < 0.05$): although animals spent on average $74.6 \pm 5.1\%$ time feeding, conflicts over food accounted for 85.2 ± 21.6 % of all agonistic interactions with an identified context.

Pair partners interacted agonistically, on average, 0.48 ± 0.14 times/h (Table 5) which was frequent compared to affiliative interactions in all pairs observed (Wilcoxon matched

pairs test: T = 0.0, N = 6, p < 0.05). In 10.7% of the cases, it was not possible to observe the complete course of agonistic events, so it is unknown whether conflicts were decided. Only 5.3% of the remaining conflicts were undecided. The majority of conflicts were decided (189 of 225) and the winners in all decided cases were females. Subordinate animals showed a curious submissive behaviour: they let themselves fall from the tree where they sat, often down to the forest floor, and ran away on the ground for some metres. Each of the six males observed, fled to the ground at least once, and the behaviour was observed on 49 occasions. Hence, fleeing on the ground appears to be part of the submissive behavioural repertoire of the species. Fork-marked lemurs never touched the ground in any other context and seem to avoid the lower strata of the forest if possible. Submissive behaviour in males was evoked by female aggression (AS) or occurred spontaneously (0S) at roughly the same rates (Table 5).

Table 5: Rates and types of agonistic interactions among pair partners.

Pair	N	No./h	Decided conflicts			Undecided	Undetermined
			Total	AS	0S	A0	?
F2–M2	11	0.41	10	5	5		1
F3–M9	46	0.46	37	19	18	6	3
F4–M4	65	0.57	54	29	25	2	9
F5–M5	46	0.65	34	14	20	4	8
F6–M6	40	0.53	37	11	26		3
F7–M7	17	0.25	17	6	11		
Total	225		189	84	105	12	24
Mean		0.48	31.5	14.0	17.5	4.0	4.8

A: Aggression; S: Submission; 0: No agonistic behaviour.

Meetings Among Neighbours

Meetings involving 2–10 neighbours occurred frequently (once every 6.5 h) where the territories of different families intersected. Animals of all age-sex classes participated in these meetings. Interactions were difficult to observe, because they often involved more than two animals at a time and took place high in the forest canopy. Only qualitative data for dyadic between-pair interactions among identified individuals are reported here. Affiliative female–female interactions were observed 21 times, and all focal females had affiliative contact with neighbouring females at least once. Adult females interacted affiliatively with strange or neighbouring males in only five cases. Males were never observed to exchange affiliative behaviour with other males. Dyadic agonistic interactions between males and females were observed on 24 occasions. Again, female dominance characterized the relation between the sexes, and females won all of the 19 decided conflicts involving identified neighbours. Males

were found fighting with males 28 times. Rank reversals occurred in 10 male–male dyads that were observed at least twice. When rank reversals occurred, they took place in different grid squares, suggesting site-dependent dominance relationships. Only six female–female interactions involving agonistic behaviour were observed.

DISCUSSION

Social Organization

Adult fork-marked lemurs had almost exclusive home ranges that were shared with only one member of the opposite sex. Within the MCP borders, males used space more evenly, but females had a more patchy usage pattern. Opposite-sexed individuals that shared a home range interacted more frequently with each other than with any other adult individual. Interactions with neighbours were not quantified systematically, but such meetings were rare compared to rates of affiliative or agonistic interactions with a coresident. Thus, two animals shared a home range, the borders of which coincided with social boundaries. Across eight social units and 3 years of study (18 of 21 family years), pairs were the prevailing grouping pattern, and most pairs were stable for more than three years.

The study area was saturated with fork-marked lemur home ranges. Home ranges of different pairs overlapped only slightly and were defended against members of both sexes. During meetings at territory borders, males fought with males as well as females, but females never fought with females. Hence, home ranges may be called territories. At the same time, females were observed exchanging affiliative behaviours, which was never seen among males. Females seemed to tolerate their female neighbours and thus showed some kind of a 'dear-enemy phenomenon' observed in many animals living in territorial systems (Temeles 1994), but males were tolerated by neither male nor female neighbours.

Cohesiveness During the Night

Pair partners approached each other to within 15 m about 13 times more often than expected by chance, based on the assumption that pair partners behave as independent gas molecules (Waser 1976). Gas molecules, however, do not prefer one area over another. The nonhomogeneous and often patchy Kernel ranges of females show that this assumption is violated in fork-marked lemurs. Unfortunately, the measurable patterns of space use are already the consequence of dynamic spatial interactions between pair partners and individual preferences for certain locations (e.g. feeding sites) and therefore cannot be used to generate

predictions about encounter rates. Nevertheless, the gas model is of some heuristic value because it marks the far end of the possible distribution of interindividual spacing. If animal spacing matches expectations derived from the gas model, it appears safe to assume that animals meet rarely and have little interest in each other. In some rare cases, as orang-utan, *Pongo pygmaeus*, males (Mitani et al. 1991), encounter rates may even be lower than expected by the gas model, indicating that males avoid encounters. The encounter rate measured in this study may appear to be oversampled. Once pair partners approached one another, one encounter was counted every 5 min until they separated again. However, the fact that pair partners stayed within 15 m for 5 min or more is noteworthy, because each partner was free to move to every other point in the home range within this time interval.

Despite high encounter rates compared to gas molecules, cohesiveness between pair partners was nevertheless low compared to diurnal pair-living gibbons. Even if the two most widely separated individuals of a diurnal langur group are considered, fork-marked lemurs must be regarded as relatively dispersed. This comparison again highlights the poor applicability of the gas model for interpretations of animal spatial association. Although fork-marked lemurs are extremely dispersed, their encounter frequencies are higher than the gas model's predictions. The assumption of a circle as the geometry of langur group spread may underestimate the maximum distance between two group members, but the circle will at least be a fairly good approximation during times when langurs feed (J. Beise, personal communication). The mean distance between fork-marked lemur pair partners was about 100m, which is far considering that it constitutes almost half a home range diameter for many pairs. Thus, fork-marked lemur social organization is best classified as dispersed pairliving, which is in contrast to their widely cited categorization as cohesive (Petter et al. 1971; Charles-Dominique & Petter 1980).

Female Dominance

Diverging from patterns found in anthropoid primates, dominance relationships among the sexes in Malagasy lemurs are characterized by some form of female social precedence (Richard 1987; but see Pereira et al. 1990). Because female lemurs are not larger than males (Kappeler 1990a, 1991), this asymmetry does not rest on superior force of females, but must instead result from a leverage advantage (Kappeler 1993). Unconditional female dominance, that is the ability of females consistently to evoke submissive behaviour from all males in dyadic interactions is unique in lemurs and not found among other mammals (Kappeler 1993).

However, quantitative analyses of dominance relationships across contexts are pending for many of the 50 lemur species (but see Jolly 1966; Richard 1987; Kappeler 1990b; Pereira et al. 1990; Roeder & Fornasieri 1995; Kubzelda et al. 1992), especially for nocturnal lemurs (but see Rendall 1993; Radespiel & Zimmermann 2001). Although Charles-Dominique & Petter (1980) proposed female dominance for fork-marked lemurs on the basis of qualitative data, the data presented here provide the first quantitative demonstration of female dominance across contexts and across social units in a wild population of nocturnal lemurs. Together with evidence of unconditional female dominance in captive *Microcebus murinus* (Radespiel & Zimmermann 2001), another nocturnal lemur, our data support earlier studies proposing female dominance as the ancestral condition in lemurs (Jolly 1998).

Cohesiveness During the Day

Cohesiveness has another aspect that has been comparatively well documented in nocturnal primates, namely cohesiveness during phases of inactivity (reviewed in Kappeler 1998). During the day, fork-marked lemur pairs shared a sleeping site on average every third day. Sleeping sites are not rare in their home ranges, and even if some sites are preferred over others, meeting every third day at one of 40 sleeping sites can be interpreted as attraction between pair partners. When pair partners did not share a sleeping site, however, they were not spatially associated but slept, on average, more than 100 m apart. The degree of association at sleeping sites varies markedly among nocturnal pair-living species, from *Lepilemur ruficaudatus*, which share sleeping sites every fifth day (D. Zinner, R. Hilgartner, T. Pietsch, P.M. Kappeler & J.U. Ganzhorn in press), to *Cheirogaleus medius,* which spend 2 out of 3 days at one site together (Fietz 1999a; but see Müller 1999a), to *Tarsius spectrum*, which sleep together in the same tree every day (Gursky 2000a). Sleeping associations seem not to be directly related to cohesiveness during activity, because *T. spectrum* pairs interact, on average, only once per night (Gursky 2000a), but fork-marked lemurs interact 0.7 times/h despite sharing a sleeping site only every third day. Possible functions of association during inactivity may include improved thermoregulation (Radespiel et al. 1998, Schmid 1998, Ostner 2002), strengthening of the pair-bond, reduction of ectoparasite-borne diseases by allo-grooming (Clark 1985), exchange of information (Ward & Zahavi 1973) or dilution effects in predation risk (Schülke & Ostner 2001).

Problems with Defining Animal Societies

Animal societies can be structured on three levels. Species and populations may vary in their social organization, their mating systems and their social relationships (Struhsaker 1969; Wilson 1975; Rowell 1979). Although these aspects are clearly interrelated, for example, in the sense that social relationships can be formed only between individuals that live in the same social unit, teasing them apart is necessary if evolutionary explanations for their diversity are sought (Kappeler & van Schaik 2002, but see Müller & Thalmann 2000). Categories of social organization can be defined according to size, sex composition and spatiotemporal cohesion of a society. An animal either lives alone or with one or several members of the same or the opposite sex (Kappeler 1999), yielding five types of social organization (solitary, pair, one-male–multi-female group, multi-male–multi-female group, multi-male–one-female group). Theses categories coincide with the social organization of a species only if spatial dispersion of individuals corresponds with social boundaries (Kappeler & van Schaik 2002). Although these statements may sound trivial, the diversity among nocturnal primates demonstrates that a clarification of terminology and classification is worthwhile.

Information on nocturnal primate species is increasing, but many data necessary for a concise classification of their social organizations are still lacking. A methodological review of 27 studies of nocturnal prosimians (Sterling et al. 2000) revealed that in 34% of studies dealing with sociality, data were obtained only from trapping reports, and animals were neither located nor observed during their nightly activity period. Although early studies described social interactions at least qualitatively (e.g. Charles-Dominique 1974; Charles-Dominique & Petter 1980), many recent publications have presented only locational or mark-recapture data (e.g. Atsalis 2000; Schwab 2000), sometimes accompanied by descriptions of sleeping group composition (e.g. Müller 1998; Fietz 1999a). Quantitative assessments of affiliative and agonistic interactions among nocturnal prosimians are almost entirely lacking (but see Pagès-Feuillade 1988), precluding conclusive classification of their social organization because social boundaries are not defined. A species or population should not be classified as being groupliving on the basis of locational and sleeping site data only. Where interaction frequencies between animals with overlapping home ranges simply decrease with increasing average distance between individuals, species must be regarded as solitary or as forming networks at most. To constitute a group, animals sharing considerable space must exchange more social interaction with each other than with individuals with whom they share

only little space with. For territorial species, this means that, only if spatial boundaries coincide with social boundaries can the social unit be classified as a group.

In earlier studies of other nocturnal primates, even if individuals were observed directly and some measurement of interaction frequencies was available, only one individual was in the observer's focus and simultaneous information about the location of conspecifics was lacking. All nocturnal primates except *Avahi* and *Aotus* have been classified as solitary foragers to distinguish them from diurnal species (Bearder 1987; Müller & Thalmann 2000). The classification of social organizations given above, however, implies that degree of cohesiveness will describe only one aspect of the social organization of a species that is either organized in groups or pairs or lives a solitary life. Solitary animals will have social interactions with conspecifics, but patterns of interaction will not allow for a description of a closed social unit. Furthermore, animals can live in groups without synchronizing their activities and movements (e.g. chimpanzees *Pan troglodytes*; Wrangham 1977). Hence, each type of social unit (pair or different groups) can be either cohesive or dispersed. The usefulness of this differentiation has been recently demonstrated in a phylogenetic reconstruction of the evolution of pairliving in primates, because it led to the insight that dispersed and cohesive pairs evolved independently as adaptations to different selective pressures (van Schaik & Kappeler 2003).

Although the importance of cohesiveness as a qualifying trait of a social unit was recognized earlier (Bearder 1987), no quantitative data were given on interindividual distances during foraging activities. For example, adult diurnal *H. lar* spend about 80% of their time 5–20 m from their pair partners, which is considered a close association (Reichard 1995a). The presence of a second animal at 5–20 m distance, however, can easily escape the attention of the observer of a small nocturnal primate in a dense forest. Therefore, reliable information about the spatial association of nocturnal primates can be gathered only by simultaneous focal follows of more than one individual or by very rapid sequential radiotracking generating quasisimultaneous locations of different individuals. Unfortunately, data of this quality are so far available only for fork-marked lemurs, and this study has shown that other methods (e.g. Charles-Dominique & Petter 1980) may yield misleading results.

Mechanisms Maintaining Cohesiveness

As a first step towards understanding the mechanisms underlying cohesiveness among pair partners, we analysed the nature of their social relationships. Affiliative interactions

representing social attraction between pair partners were rare compared to agonistic interactions in all pairs observed. This parallels the situation in *T. spectrum*, where the majority of interactions between pair partners were agonistic (Gursky 2000a). When in conflict, female fork-marked lemurs were always dominant over males, and conflicts over food were overrepresented. The mainly solitary activity pattern may therefore be explained as a consequence of males avoiding meetings with females. However, males were responsible for maintaining spatial proximity in the context of affiliative interactions. Thus, males seem to be attracted to their pair partner, but they avoid feeding competition with the female.

The proximate mechanism responsible for the spatial association between fork-marked lemurs proposed by Charles-Dominique & Petter (1980) was continuous vocal communication. Most movements are indeed accompanied by contact calls ('hons': Charles-Dominique & Petter 1980) that may signal the position of the animal. These hon calls do not carry far, however, and therefore have the potential to coordinate travel only at close range. Given that the average distance between pair partners is about 100 m, a better candidate for a movement-coordinating call is the 'kiu' call (Charles-Dominique & Petter 1980), which is audible even across several home ranges. However, movements are not strictly associated with kiu calls, although they are uttered often and throughout the activity period. Furthermore, kiu calls are not always answered, and hence information about the position of the pair partner is likely to be incomplete. If a lemur lacks detailed information about its pair partner's spatial position, its movement choice will sometimes be 'wrong', and hence the distribution of affiliative and agonistic interactions cannot be expected to be a reliable reflection of the individual's interests.

Instead, high rates of conflict may result from unintended meetings at limited and highly predictable food resources. Fork-marked lemurs rely on tree exudate as major food resource year-round and concentrate more than 50% of their feeding time on one tree species (Schülke submitted). A territory contains 15–39 of these key resources, which are repeatedly visited by both pair partners; therefore the likelihood of chance meetings is rather high. Intense feeding competition, reflected by a negative correlation between female fertility and family size (Schülke submitted), may explain why meetings at food resources always lead to conflict. The common use of limited food resources may explain not only why most social interactions are agonistic but also the higher than expected frequency of encounters between pair partners.

Broader Implications

Primate pairs were thought to differ from other pair-living mammals in that they form close bonds that are reflected by highly cohesive movement patterns (Kleiman 1977; van Schaik & Dunbar 1990). With qualitative reports on the social organization of nocturnal prosimians accumulating, however, a different picture emerges. What makes pair-living primates exceptional among mammals is the variation in cohesiveness between pair partners which was first acknowledged by the introduction of the terms 'dispersed' and 'cohesive' pairs (Müller & Thalmann 2000; van Schaik & Kappeler 2003). The present study is the first that quantifies cohesion in a dispersed pair and it reveals a more mammal-like form of pairliving in a primate. Future studies should evaluate whether primates show just the two extremes of cohesiveness represented by gibbons and fork-marked lemurs, or whether this trait varies continuously between species or populations.

Quantitative assessment of the social interactions among pair partners and neighbouring adults is crucial for the classification of a species' social organization and provides a first insight into the mechanisms facilitating cohesion between individuals. The coordination of movements among gregarious animals involves not only conflicting interests between group members but also a complex evaluation of costs and benefits of close association for each individual itself (Boinski 2000). In contrast to animals living in cohesive associations, dispersed pairs have the opportunity to avoid feeding competition and to choose travel routes more independently (Garber 2000). This tendency, however, conflicts with the social needs of the pair partners that have to be fulfilled despite an individual's solitary foraging activities. These aspects make the study of cohesion in dispersed pairs even more promising, because the contrasts with cohesive species allow us to refine models predicting decisions about animal movements (e.g. Janson 2000). However, dispersed pairs have to cope with incomplete information about the movements of their partners. Since most models of animal movement decisions are optimality models (e.g. Milton 2000), lack of information should be incorporated into these models as a source of error in the choices of individuals.

General selection pressures favouring life in a cohesive group include reduction of predation risk, feeding competition, and infanticide risk, or facilitation of paternal care (van Schaik 1983). They are also thought to be responsible for the evolution of dispersed social systems (Sterling & Richard 1995; Gursky 2002). We stress, however, that variation in group cohesion directly affects the costs and benefits of life in a group. For example, an increase in overall vigilance levels by adding one member to the social unit, will not benefit other

members if they typically range 100 m apart. Dilution effects on individual predation risk will apply only if cohesion is high enough for a predator to catch sight or sound of more than one individual at a time. However, despite their dispersed association pattern, members of fork-marked lemur families inform each other about the detection of a predator via alarm calls (Schülke 2001), which may help family members to avoid surprise attacks. Other benefits of group life (e.g. male defence against infanticide) are also sensitive to the cohesiveness among individuals, but conclusive analyses of the question of exactly which selective pressures lead to the evolution of dispersed pairs in general, and the social organization of fork-marked lemurs in particular, are beyond the scope of this paper.

ABSTRACT

Among pair-living species, which represent a simple form of gregariousness, the degree of cohesion appears to be highly variable, but the mechanisms responsible for the maintenance of cohesiveness have been poorly studied. We present data from long-term behavioural observations of eight pairs of fork-marked lemurs, including year-round data on their sleeping site use and spatial data from simultaneous focal follows of both pair partners, that characterize its social organization as 'dispersed pairs'. Although pairs were stable over several years, territories of pair partners overlapped almost perfectly and interactions between them were frequent, the cohesiveness of pairs was extremely low. High rates of conflict relative to frequencies of affiliative interactions indicated that avoidance of the pair partner is the key mechanism responsible for the observed pattern of space use. The repeated use of the same predictable food resources during the night, frequent conflicts over food and patterns of vocal communication imply that avoidance of direct feeding competition, together with incomplete knowledge about the pair partner's position, lead to the observed low cohesiveness. The freedom to forage solitarily and the associated lack of information about the pair partner's position found in fork-marked lemurs are in contrast to most group-living species and qualify dispersed pairs as a focus for future studies of models on animal movement decisions.

CHAPTER 2:

To breed or not to breed – food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur, *Phaner furcifer*

OLIVER SCHÜLKE

INTRODUCTION

In species where females carry the burden of gestation and postnatal infant care (and males are virtually free from parental investment) female reproductive success is thought to be limited mainly by access to food resources (Williams 1966, Trivers 1972, Clutton-Brock et al. 1982). Apart from competition for access to mates in order to obtain good genes, marital gifts, or hired guns (review in Birkhead 2000), intra-specific female-female competition is therefore mostly concerned with food competition. Different modes of competition (scramble and contest cf. Nicholson 1954) within and between groups and variation in food resource characteristics (scarcity, clumpedness, patch size) have been successfully integrated into a model ('ecological model', van Schaik 1989) that predicts differences in female reproductive success and variation in female social structure among gregarious primates and other mammals (Jarman 1974, Sterck et al. 1997).

Accordingly, a solitary lifestyle and pair-living are thought to result from strong within group female-female contest competition for food (van Schaik 1989) that lead to avoidance between females; the absence of substantial benefits of group-life (e.g. very low predation pressure and hence no positive effects from increased vigilance or safety in numbers) may facilitate this step. However, it has been overlooked that, if females choose to live away from each other and form pairs with males, pairs resemble groups (better: families) because offspring live in their territory. Hence, females compete for food within their family and differential female net energy gain will, therefore, depend on the same principles as in gregarious females. Based on the 'ecological model' this paper investigates the competitive regime of the pair-living fork-marked lemur (*Phaner furcifer*) and consequently asks how differences in net energy gain translate into differential female fertility. In doing so, female reproductive decisions are also investigated in relation to delayed natal dispersal and the allocation of resources to current and future offspring.

The 'ecological model' (van Schaik 1989) recognizes several basic modes of competition: competition for food will take place either within groups (WG) or between groups (BG) and individuals or groups will either scramble (S) or contest (C) for food yielding four different modes of competition (WGS, WGC, BGS, BGC), each describing an effect of competition on female net energy gain. The relative strength and combination of these four components constitute the competitive regime of a species or population. Competitive regimes have been linked to food characteristics such that low quality, highly

dispersed or very large food resources promote WGS and discrete patches of high quality resources lead to WGC and to BGC if high quality patches are dispersed but large enough to feed all group members (see Koenig 2002 for review of primate evidence and Sterck et al. 1997 for other mammals).

Which competitive regime is experienced by a population can be inferred from correlation of female net energy gain and group size on the one hand and dominance status on the other hand (van Schaik 1989). Negative correlation with group size implies a strong WGS component (seen in *Gorilla gorilla berengei* van Schaik 1983, Watts 1990), whereas a positive correlation with group size results from strong BGC situations with larger groups displacing smaller ones from high quality food patches (found in *Chlorocebus aethiops* Cheney et al. 1988). If WGC is strong dominance differences between individuals translate into differential energy gain or reproductive success (seen in *Papio cynocephalus* Altmann et al. 1988). Because strong WGC is thought to be responsible for female intrasexual avoidance in pair-living species, the effect is expected to prevail and to characterize within group competition among family members. Hence, dominance status will have a significant positive influence on an individuals net energy gain; if females are dominant over other group members or if they have priority of access to resources they will gain more energy then subordinates (van Schaik 1989).

But differences in net energy gain will not always translate directly into differential reproductive success. Firstly, confounding variables may influence the relationship between group size, dominance rank and birth rates (Isbell 1991). In red howler monkeys (*Alouatta seniculus*), for example, infanticide rate is positively related to group size and overrides feeding competition borne group size effects on birth rates (Crockett and Janson 2000). Secondly, female fertility (i.e. the probability that a female reproduces in a given season) is not simply determined by a female's physical condition as determined by her access to food resources. Because lifetime reproductive success depends on both, the number of offspring produced and their survival to reproductive age, the decision to breed in a given season is often a decision against further maternal investment in the survival of current offspring (Williams 1966). Females cease lactation and indirect maternal investment such as vigilance and thermoregulation for the current offspring and allocate resources (i.e., time and energy) to future offspring (Trivers 1974, *Papio cynocephalus ursinus* Lycett et al. 1998).

While female competitive regimes (Sterck et al. 1997, Koenig 2002), determinants of female fertility (Bercovitch 1991) and allocation of maternal investment (Lee 1999, Fairbanks

2001) have been intensively studied in diurnal gregarious primates, comparative data from wild nocturnal primate populations are lacking. Although nocturnal primates (except *Avahi* and *Aotus*) forage solitarily as a rule (Bearder 1987, Müller and Thalmann 2000, Kappeler and van Schaik 2002), their social organization, nevertheless, varies form truly solitary (*Mirza coquereli* Kappeler 1997a) through dispersed and associated pairs (*Cheirogaleus medius* Müller 1999a, Fietz 1999a, *Avahi occidentalis* Thalmann 2001, *Phaner furcifer* Schülke & Kappeler 2003) and harem groups (*Galago alleni* Charles-Dominique 1977, some *Tarsius spectrum* Gursky 1995) to some form of multimale-multifemale societies (*Microcebus murinus* Martin 1972, Radespiel 2000). Increased food competition is one of the major costs of grouping (Wrangham 1979, van Schaik 1983), hence studying female competition is at the core of understanding the tremendous variation in nocturnal primate social organization (Kappeler and van Schaik 2002) and mechanisms involved in the co-ordination among group members (Schülke and Kappeler 2003).

This paper aims to investigate the applicability of the 'ecological model' for predicting the influence of food competition on female physical condition for the pair-living fork-marked lemur (*Phaner furcifer*). Moreover, I present the first data on the relationship between female physical condition and reproductive performance in a nocturnal lemur. The fork-marked lemur is a small (330g), nocturnal prosimian primate living in the dry deciduous forests along Madagascar's west coast. It is active year-round and feeds primarily on tree exudate (Hladik et al. 1980). This paper presents the first data on year-round monthly and age-sex-differential variation in the diet of fork-marked lemurs to define the resources the animals compete for. Most adults are organized in pairs that are stable for more than three years and share a common territory (Charles-Dominique and Petter 1980, Schülke and Kappeler 2003). Territories vary markedly in size (1.8 - 6.5 ha) and are defended against intruders of either sex (Schülke and Kappeler 2003). Although both pair partners use all parts of their territory and regularly share sleeping sites, they, are not cohesive during their activity period, but seem to avoid each other and forage 100 m apart from one another on average (Schülke and Kappeler 2003) – they live in 'dispersed pairs' (sensu van Schaik and Kappeler 2003). Females are dominant over males and win in all conflicts irrespective of context (Schülke and Kappeler 2003).

Comparative analysis of the evolution of pair-living among primates revealed that dispersed pairs evolved independently from cohesive pairs, as found in gibbons for example, and derived most likely from a solitary form via female-female avoidance and later

association with a male (van Schaik and Kappeler 2003). If female-female avoidance was the consequence of a strong contest situation in female feeding competition I predict WGC to be strong in the families that females live in today. Although each female shares her territory with only one adult male, group size effects may, nevertheless, play a role, because pairs live with a varying number of offspring. These offspring can represent equal competitors, if they consume similar food. Energetic requirements of young animals will be similar or even higher than those of adults, because growth poses extra costs on offspring. Where natal dispersal is not balancing the increase of group size due to birth, groups will grow. Full-grown fork-marked lemurs may delay natal dispersal for several years (as in female *Cheirogaleus medius* Müller 1999b), which opens the possibility for extreme variation in group size. The causes of delayed dispersal and effects on parents and offspring are discussed in detail.

METHODS

Study Site and Animals

The study site at Kirindy Forest is situated at 44°39' East / 20°03' South near the western coast of Madagascar about 60 km north-east of Morondava on the forest concession of the C.F.P.F. (Centre de Formation Professionelle Forestière de Morondava) and is run by the Deutsches Primatenzentrum Göttingen, Germany. Kirindy Forest is part of one of the largest remaining continuous strips of dry deciduous forest of Madagascar. The climate is characterized by a short, hot rainy season from December to March with 800 mm average rainfall and eight months of virtually no precipitation. Between June and September temperatures may drop as low as 5 °C at night (details in Ganzhorn and Sorg 1996).

The study took place within a 900 x 700 m grid system (mainly 25x25 m squares) locally known as CS7 starting in 1998 when the capture regime for fork-marked lemurs was established during a pilot study. Between November 1998 and April 2001, a total of 30 individuals were captured 103 times, using Tomahawk life-traps. Traps were fixed to the entrance of the sleeping holes in dead or live trees at an average height of 8 meters. Typically, an animal entered the unbaited trap 10-20 minutes after dusk, when neighbours and family members began loud-calling in close proximity. Animals were brought to camp immediately after capture and were briefly anesthetized (0.02 ml Ketanest©) before measurements were taken and radio tags were fitted. All adult males and females caught between April 1999 and April 2000 were equipped with harness-fitted radio tags (10 g) especially designed for this study by Biotrack (Wareham, UK). From June 2000 onwards, females were fitted with brass

collar tags (14 g) because many harness tags were removed by the animals. Males were not equipped with collar tags because they possess a large throat gland that might get irritated by a collar. Tag life-time was approximately one year and tags were replaced whenever necessary. Animals were released at their capture site later the same night. All sleeping trees where animals were captured once were reused by the same individuals after some time. All procedures caused no noticeable harm to the animals and were in compliance with current laws of the countries where they were carried out.

Animals were aged as adult or subadult according to size (body length) and group-membership, i.e. an animal that was not full-grown when first captured but grew to full body-length without migrating was treated as a subadult in all analyses. It was assumed that animals not full grown when first captured were natal to the territories they were caught in. DNA micro-satellite analysis of relatedness did not contradict any mother-offspring relationship assigned on the basis of behavioural observations (O. Schülke, P.M. Kappeler, H. Zischler unpubl. data).

Data Collection and Analysis

Between June 1999 and July 2000 seventeen adult (7 female, 7 males) and subadult (1 female, 2 males) radio-tagged individuals were observed during two hour focal animal protocols (Altmann 1974) for a total of more than 1,200 hours. During observations, a Telonics TR-4 receiver with a three element yagi antenna, a head-lamp and if necessary flashlights and binoculars were used. The focal animal's location in the grid system (i.e. the respective 25x25m square) and all social interactions (affiliative and agonistic) were recorded continuously, whereas Behavioral states (resting, locomotion, feeding), details of feeding behaviour (e.g. plant part and species consumed) were recorded in a 2.5 min instantaneous sampling procedure (Altmann 1974). If animals were out of sight at the time of instantaneous sampling, this was recorded and all calculations were related to the total number of intervals an animal was in sight. Food trees were marked and numbered during observations and identified later. Abundance of the ten most important food trees (rated by feeding time) was measured via line-transects (North to South) with a strip width of 10 m (total length 4.5 km). In each of the eight fork-marked lemur territories three transects of approximately the same length were established. Abundance of food resources was calculated as the number of trees counted in a territory per strip length times strip width (10 m) projected onto the total territory size for each female. Per capita abundance of food resources was defined as abundance in a

certain territory divided by the number of animals in the respective family. Female physical condition was calculated as the body mass index BMI = body mass [kg]/(head body length [m])².

For home range analyses locational data were sub-sampled at 5-minute intervals. These data points are regarded as independent because the interval allows an individual to cross its home range at highest locomotor speed (Rooney et al. 1998). Home range outlines and sizes were calculated by the Minimum Convex Polygon method (Mohr 1947) with 5% outliers removed by the harmonic mean method (for details of home range analysis see Schülke and Kappeler 2003).

Because the variables were not normally distributed, the allocation of feeding time to different food items or plant species were compared between seasons and age sex classes using Kolmogoroff-Smirnov-2-sample-tests (KS-tests) as implemented in StatView©4.82. Whether the distribution of main food trees within each territory was clumped vs. uniform/stochastic was tested with nearest neighbour analysis as implemented in the GIS-based Animal Movement Program (Hooge & Eichenlaub. 1997). Relationships between two variables were tested for significance with Pearson's product moment correlation (Pearson correlation, Statistica© 6.0). Differences in physical condition between males and females were tested for significance using a t-test. The multi-variate relationships between physical condition or fertility and several independent variables were analyzed using General Regression Models implemented in Statistica© 6.0 software. These multiple regression models allow for the use of categorical variables as predictors and/or dependent variables. To investigate the influence of repeated measurements animal identity was added as a predictor variable in the General Regression Model. Since this procedure did not change any of the results, the data set was treated as being free of repeated measurements. Hourly rates of interaction in parent-offspring dyads (six dyads from focal data of three offspring and either of their parents) were compared to rates among adult pair partners (six pairs) with t-tests Statistica© 6.0.

RESULTS

Demography

Family size varied from 2 to 4 individuals (Tab. 1). Changes in group composition occurred due to births, disappearances, deaths and immigrations. Natal dispersal was not observed and dispersal distances are unknown. One subadult female took over the breeding

position in her natal territory after the death of her presumed mother. Subsequent to the death or disappearance of adults, immigration of previously unknown males and take-over of the breeding position was observed 3 times (Schülke and Kappeler 2003). Subadults reached full body size and body mass prior to the mating season at the age of 1.5 years. Nevertheless, some individuals remained in their family until the age of 4.5 years, hence there is evidence for delayed dispersal of up to 3 years.

Table 1: Group composition in the breeding season and distribution of births

Family	1998/99	Birth	1999/00	Birth	2000/01	Birth
1	F M saM[1]		F M saM[1]		F M saM[1]	
2	F M	1	F M saM[2]		F M saM[2]	
3	F M saF[3]		F M saF[3]		F M saF[3]	
3a	F M saF[10]	1				
4	F M		F M	1	F M M[4]	
5	F M saM[5]		F M saM[5]		F M saM[5]	
6	F M saM[7]		F M saM[7]	1	F M saM[7]	
7	F M	1	F M sa?[9]		F M sa?[9]	1

Change in adult group composition not shown except M[4]. F adult female, M adult male, saM subadult male, saF: subadult female, ? sex undetermined, [1]born before 1997, [2]born 1999, [3]born 1998, [4]immigrated 2000, [5]born 1996, [6]born 1997, [7]born 1998, [8]born 2000, [9]born 1999, [10]born 1998.

Variation in Diet According to Season and Age-Sex Class

The diet of fork-marked lemurs consisted mainly of gums and saps (Fig. 1), which were consumed from wounds in the bark of several tree species or from small holes that fork-marked lemurs gouged themselves. Animal matter was obtained mainly by hunting moths and other nocturnal insects and by searching for insect pupae and eggs under the bark of certain tree species, which were available mainly during the dry season. This exudate-based diet was complemented by a small amount of fruit, insect secretions, flowers and nectar. The composition of the diet showed only little variation across months (Fig. 1) and differences between wet (December to mid-April) and dry season (mid-April to November) were not significant (KS-test: $N_1 = N_2 = 6$, max. diff. = -1.67, CHI² = 3.00, n.s.).

Table 2: Allocation of feeding time to different food items [% feeding time]

	Females	Males	Subadults
undetermined	3,58	4,45	5,95
Insects	0,24	0,19	13,76
Insect secretions	8,07	8,32	0,91
Fruit	0,42	0,32	0,55
Flowers and nectar	1,85	0,86	2,57
Gum and sap	85,82	85,75	76,20

The distribution of feeding time across different food items did not differ between the sexes (Tab. 2, KS-test: $N_1 = N_2 = 6$, max. diff. = 1.67, CHI² = 0.33, n.s.). Subadults were rarely observed to consume insect secretions but foraged for insect prey longer than females did. Nevertheless, exudates constituted three quarters of the subadult diet and were staple food year-round, yielding an extreme dietary overlap across age-sex classes (KS-test allocation of feeding time on different food items females vs. subadults: $N_1 = N_2 = 6$, max. diff. = -0.33, CHI² = 1.33, n.s.).
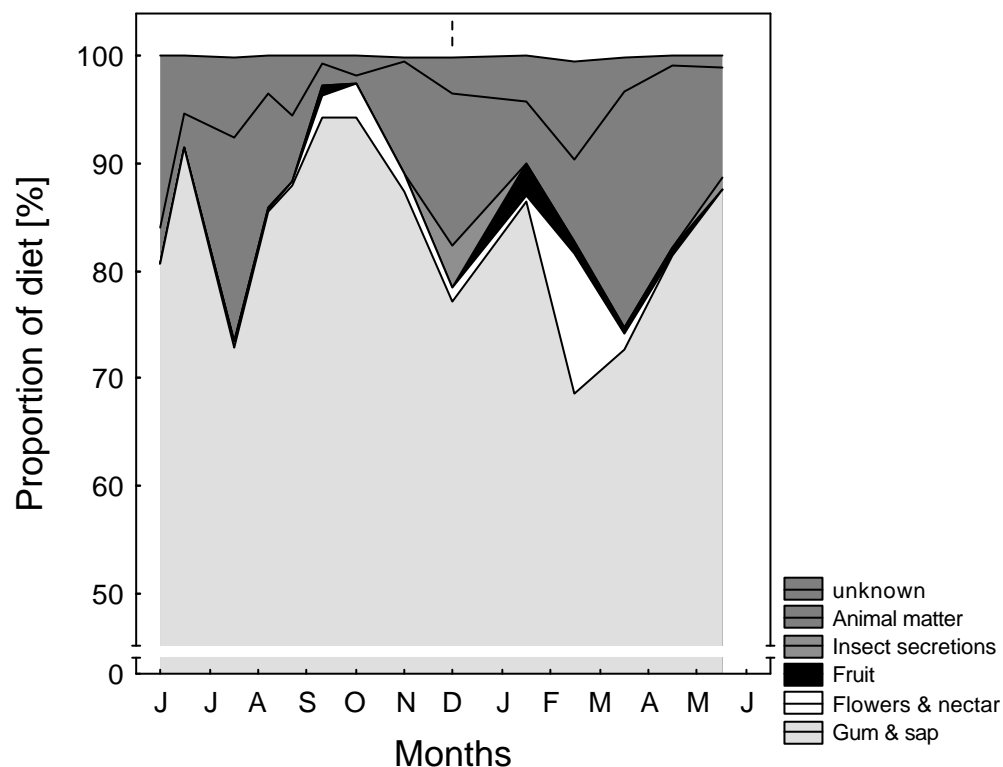
Figure 1: Diet composition of adult and full-grown subadult fork-marked lemurs across 13 months of observation. Values are weighed means across individuals for which data were available for the respective observation block. Observation blocks varied in length, hence values correspond to full months or parts of one or two months as indicated by the position of peaks relative to the x axis.

More than 90% of feeding time were allocated to 10 tree species from 8 plant families (Tab. 3). Again, seasonal variation measured as differences between the wet and the dry season was not significant (KS-test: $N_1 = N_2 = 10$, max. diff. = -0.50, CHI² = 5.00, n.s.) and the tree species selected by females were similar to the ones chosen by males (KS-test: $N_1 = N_2 = 10$, max. diff. = -0.20, CHI² = 0.80, n.s.). Subadults did not differ from females, if the usage of the top 10 food trees is considered (KS-test allocation of feeding time on top 10 species females vs. subadults: $N_1 = N_2 = 10$, max. diff. = -0.40, CHI² = 3.2, n.s.).

Table 3: Top ten plant species consumed by fork-marked lemurs ranked according to averages usage intensity [% feeding time plant matter]

Vernacular Name	Scientific name	Family	Dry	Wet	All
Taly	*Terminalia* aff*. diversipilosa* H. Perrier	Combretaceae	53,8%	44,9%	50,9%
Baobab	*Adansonia rubrostipa* Jum. & H. Perrier	Bombacaceae	15,0%	17,8%	15,9%
Sari sakoambanditse	*Operculicarya gumifera* Capuron	Anacardiaceae	4,0%	12,6%	6,8%
Arofy	*Commiphora arofy* H. Perrier	Burseraceae	7,1%	4,3%	6,2%
Sakoambanditse	*Poupartia sylvatica* H. Perrier	Anacardiaceae	2,3%	9,3%	4,6%
Taly nala	*Terminalia ombrophila* H. Perrier	Combretaceae	4,3%	1,1%	3,2%
Hompy	*Quivisianthe papinae* Baillon	Meliaceae	3,2%	0,6%	2,4%
Monongo	*Zanthoxylum tsihanimposa* H. Perrier	Rutaceae	2,7%	1,1%	2,2%
Handy	*Neobeguea mahafaliensis* J.F. Leroy	Meliaceae	1,1%	0,9%	1,0%
Malamasefoy	*Delonix floribunda* Capuron	Caesalpiniaceae	0,9%	1,1%	1,0%
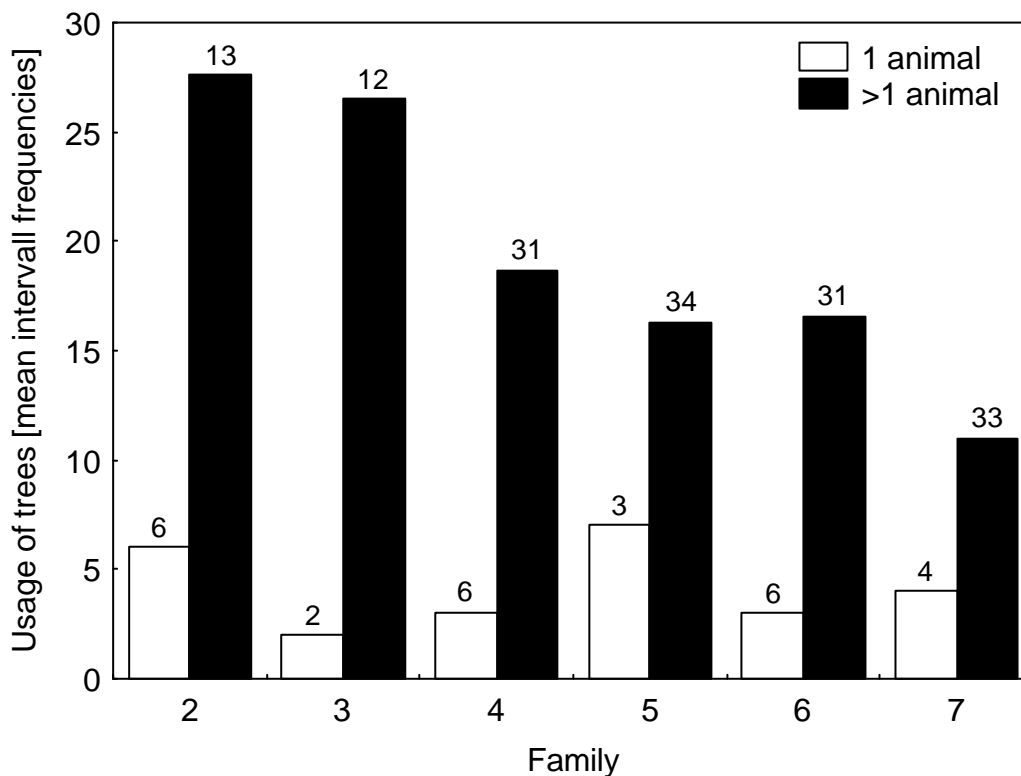
Figure 2: Usage intensity of Taly trees visited exclusively by one family member or by more than one family member. Values are averages across trees and family members. The number of trees in each category is given with each column.

Family members not only used the same type of food from the same species of trees. All known tree individuals of the most important species, the taly (*Terminalia* aff. *diversipilosa)*, were marked and numbered, making it possible to analyze whether group members used the same tree individuals. In four out of six families analyzed here, only the

two adults were focal animals, whereas in two other families focal follows were conducted on subadults (two males and one female respectively), as well.

The vast majority of individual taly trees (79.59 ± 13.25%) were used by more than one family member. Trees used exclusively by one family member were used only occasionally. The mean individual usage frequency for trees used by a single lemur was much smaller than the usage frequency of common food trees in all six families (Fig. 2). Hence, family members did not seem to reduce feeding competition by avoiding competitors in space and selecting individually exclusive or preferred feeding sites. Avoidance in time, however, seems to play a role as indicated by low cohesion between family members.

Table 4: Distribution of major food resource (*T*. aff. *diversipilosa*)

Family	z-value	r-value	Next neighbour analysis
2	14.60	1.91	n.s.
3	16.23	2.02	n.s.
4	13.94	1.74	n.s.
5	40.35	3.05	n.s.
6	6.15	1.39	n.s.
7	18.06	2.08	n.s.

The distribution of taly trees within each territory was not clumped. Nearest neighbour analyses for each family yielded only non-significant results indicative of an even or dispersed distribution of trees in space (Tab. 4)

Modes of Competition

Both WGS and BGC are modes of competition that are related to group size. In WGS situations all animals living in larger groups suffer from decreased foraging efficiency and should be in worse physical condition than animals living in smaller groups. Conversely, if BGC is strong, animals living in larger groups occupy areas with high quality food resources and defend them against smaller groups, which should lead to a positive relationship between group size and physical condition as a measure of net energy gain. Data from three consecutive years revealed a negative group size effect on female net energy gain, which is indicative of strong WGS for food (Fig. 3). The average physical condition of seven females (across three years) was significantly and negatively correlated with average group size (Pearson correlation: $r = 0.93$, $p < 0.05$).
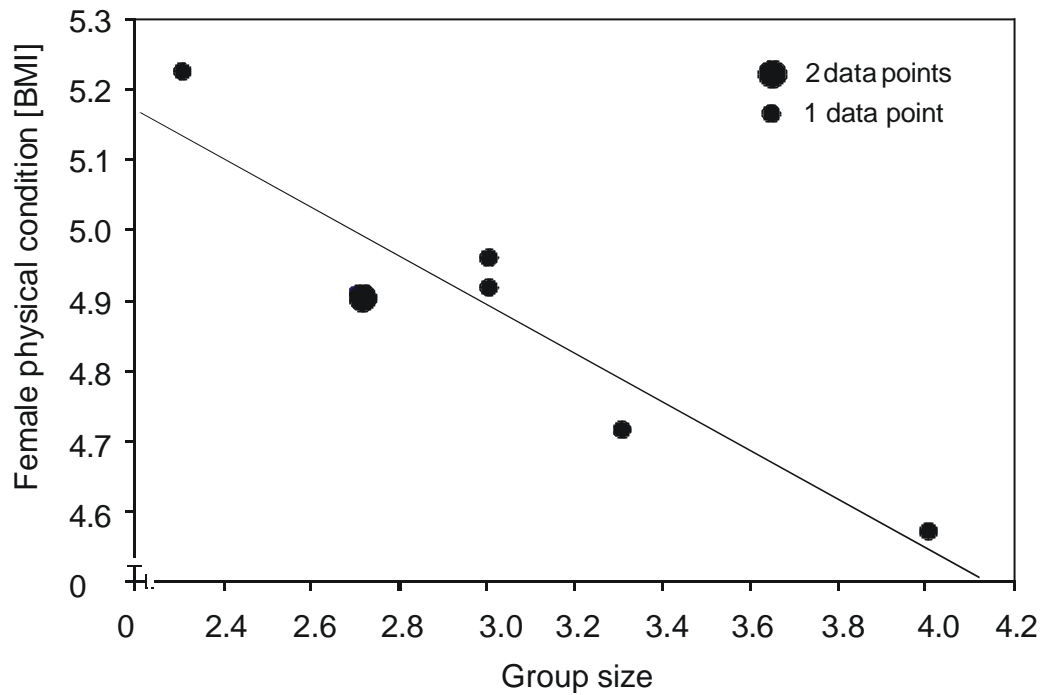
Figure 3: Group-size effect on female net energy gain measured as female physical condition (BMI). Values are averages across three years representing long term effects.

Because females are dominant in fork-marked lemurs, dominance effects on net energy gain should lead to inter-sexual differences in physical condition.
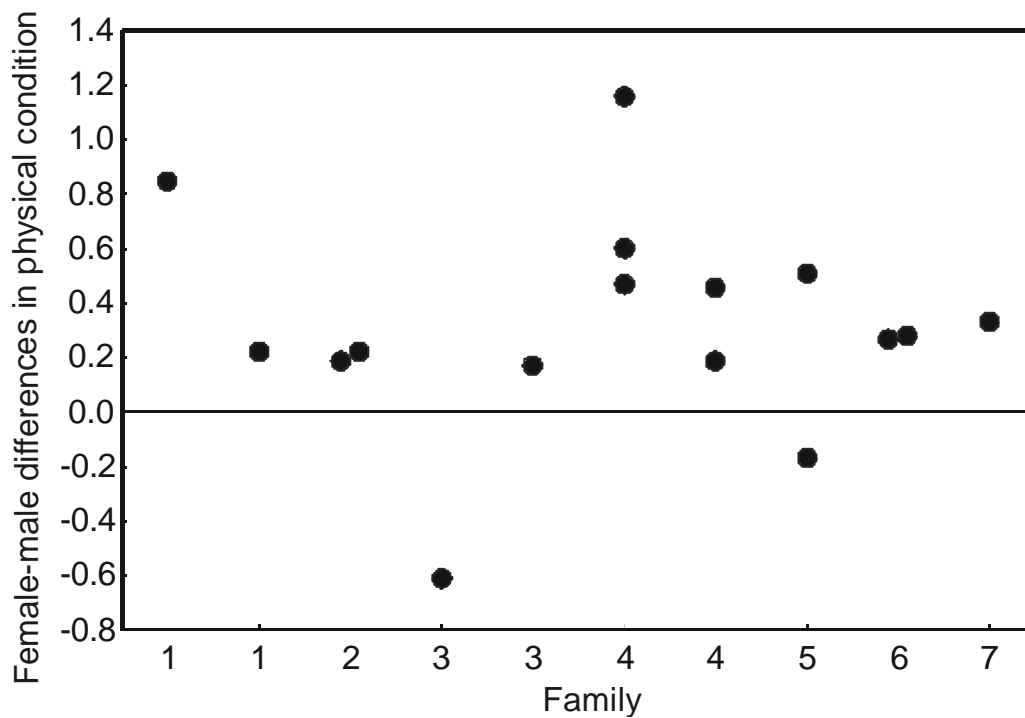

Figure 4: Physical condition (BMI) of dominant females and subordinate males. Values are given for each pair-constellation observed in a family separately (e.g., if one partner died and was displaced) and for each year of observation.

Indeed, across three years all females were almost always in better physical condition than their male pair partner (Fig. 4). The average female BMI was significantly higher than the average BMI of her mate in the ten pair-constellations observed (t-test: t = -2.11, p < 0.05).

Determinants of physical condition and fertility

The relative importance of factors determining female physical condition were analyzed in a General Regression Model (GRM) using territory size, absolute food abundance (i.e. number of trees from the top ten food species in a given territory), family size in the respective breeding season, per capita food abundance and reproductive events in the preceding breeding season as independent variables. A GRM including only per capita food abundance and previous reproductive events was selected by best fit analysis as having the largest predictive power. It explained 57% of the variance in female physical condition ($F_{2,13}$ = 8.70, p < 0.01) with per capita food abundance being the only factor with a significant effect (Fig. 5).
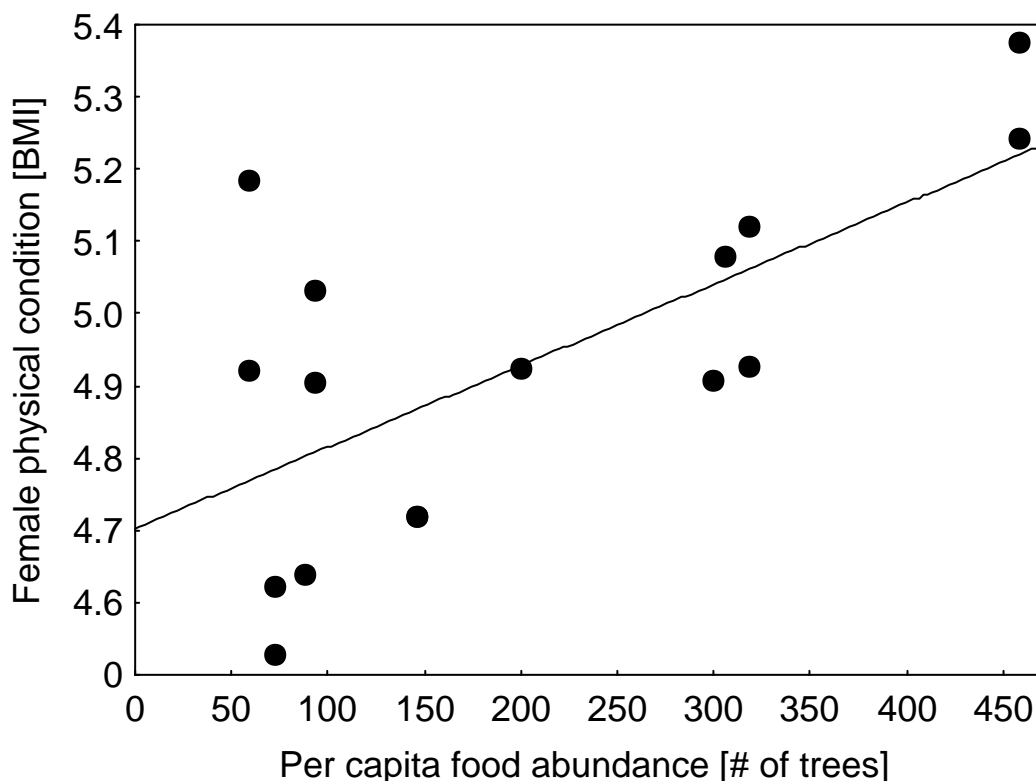

Figure 5: Correlation of per capita food abundance in a female's territory and her physical condition.

Female fertility, i.e., whether a female bred in the respective season, was determined by family size, previous reproductive events, per capita food abundance, and absolute food

abundance with factors selected by best fit analysis in a General Regression Model. In combination these factors account for 50% of the variance in female fertility ($F_{4,15} = 3.77$, $p < 0.05$), but family size was the only predictor yielding a significant effect. The influence of family size on fertility is highlighted by a comparison of the distribution of births across family sizes (2, 3 or 4) in 22 female years: births were over-represented in 2-animal families, under-represented in 3-animal families and never occurred in families with 4 members (Fig. 6).
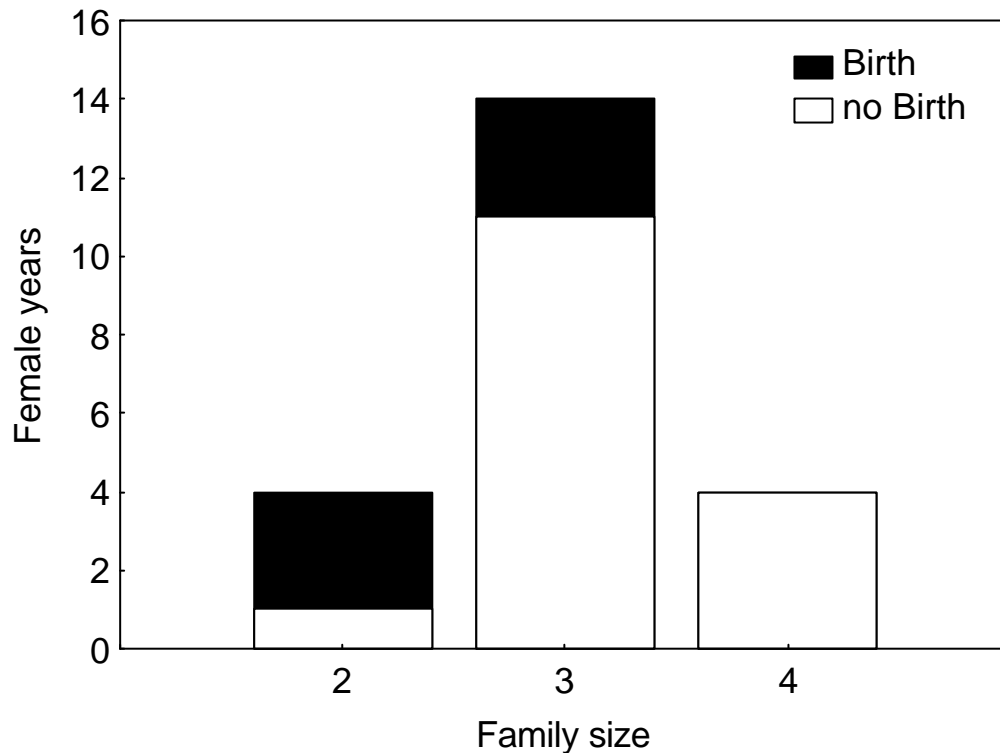

Figure 6: Distribution of births across group sizes.

DISCUSSION

Food Characteristics and Competitors for Food

The diet of fork-marked lemurs showed only little variation with season. They fed mainly on tree exudates of a small number of tree species. Although females live in separate social units they competed with their male pair partner and their offspring for food resources. Unlike animals that circumvent feeding-competition within social units by age or sex-specific feeding behaviour (e.g. birds of prey: Andersson 1994), females, males and subadults had similar diets and even used the same resources. Resources were small relative to group size, because food trees were monopolisable by single individuals and simultaneous feeding was

virtually never observed. The main food tree species *Terminalia* aff. *diversipilosa* (taly) is relatively rare with 14-37 identified trees per territory, which were used with different intensity. Resources were not clumped in the sense that a group could use different trees of the same species and still stay together in a cohesive manner. Under these condition theory predicts WGC to occur (van Schaik 1989). Food resources, however, depleted fast because once the dry exudate that closes the wound in the bark was consumed it took some time for the tree to refill it. Small, fast-depleting patches facilitate WGS, because animals can not avoid searching for food in a patch that was just depleted by another group member (Koenig 2002). The major food patches (i.e., gum trees) are renewing, however, so that the effect should be attenuated. Thus, the characteristics of the main food resources predict WGC and WGS, but not BGC to occur.

The Competitive Regime of Fork-Marked Lemurs

Using differential female physical condition as a proxy of the modes of competition characterizing feeding interference revealed that strong WGS and weak BGC predominate. Hence, short resource depletion time strongly affected the mode of competition among family members. Other resource characteristics predicted strong WGC, which was reflected by a positive relationship between dominance and net energy. Although pair partners were not foraging in a cohesive manner and important major food trees were used by males as well as females, direct contest for food occurred. The strength of this effect is also reflected by a very high rate of agonistic inter-sexual interactions, compared to rates of affiliative exchange (Schülke and Kappeler 2003); pair partners fought more than twice as often as they groomed or huddled. Although conflicts occurred in other situations as well, the vast majority was over food and food-related conflicts were over-represented relative to the time spent foraging (Schülke and Kappeler 2003). WGC may have ultimately caused females to avoid each other, but persists nevertheless because females did not change their diet consequently and continued to compete with their family members for the same resources. The competitive regime therefore is characterized by strong WGC and WGS.

Despite the negative group size effect on net energy gain, strict territoriality suggests that BGC nevertheless plays a role in female-female competition with larger groups displacing smaller ones in contest over food. But territory size did not correlate with family size (Pearson correlation: N = 21, r = -0.22, n.s.), which could be expected if larger groups gain an advantage in territorial disputes. With only one exception, the territory borders were

stable over the course of 2.5 years, although family size varied in several cases. Females often interacted friendly when meeting at the territory border but fought with neighbouring males whenever they met them. Female territoriality as opposed to female-female avoidance, which does not necessarily lead to range exclusivity but may allow some overlap, may therefore have evolved for other reasons than food competition (e.g. infanticide avoidance Wolff and Peterson 1998).

Food competition has been demonstrated in other nocturnal primates as well. Decreasing abundance of insect prey is correlated with decreased cohesion between family members in spectral tarsiers (*Tarsius spectrum*, Gursky 2002). Similarly, during the lean season, when food is demonstrably scarce, the time tarsiers allocated to travel and foraging and the frequency of territorial disputes were increased compared to the wet season. These results are interpreted as evidence for food competition within and between tarsier groups (Gursky 2000b). Strong competition for food between social units is even proposed to be responsible for the evolution of pair-living in some nocturnal primates, because females are thought to benefit from permanent association with a male by uniting forces in territorial disputes (Thalmann 2001). However, the modes of food competition and the competitive regime have not yet been studied in other nocturnal primates. However, understanding the influence of feeding interference on physical condition and reproductive success is, essential if variation in social organization among nocturnal primates is of interest. Evidence for WGC in fork-marked lemurs may explain why pair partners avoid each other and usually forage at opposite ends of their common territory. However, solitary foraging, although poorly studied (Schülke and Kappeler 2003), seems to characterize almost all nocturnal primates irrespective of their diet, suggesting that other factors than WGC may be of importance. More studies on the co-ordination of movements and the competitive regimes of nocturnal primates are needed to clarify this issue.

Female Physical Condition and Fertility

Competition for resources will lead to decreased foraging efficiency and was measured throughout the study using physical condition as a measure of net energy gain. In an attempt to analyze the relative importance of different factors determining differential female physical condition, a combined effect of group size and food abundance (per capita abundance) was identified as the best predictor. Differential female physical condition, however, did not translate directly into variation in female fertility. In as many as 22 female

years only 6 births were recorded. Over a period of three years only 5 out of 9 females gave birth at least once, and only one female bred twice. Such a low fertility is unexpected in a small primate with a supposedly fast life-history (Stearns 1976, Harvey et al. 1987, but see Kappeler 1995). The observed variation in female body mass index revealed that if a small number of fork-marked lemurs shared a large number of food trees, females were in good physical condition. Whether a female gave birth in the respective year, however, depended mainly on the number of offspring in her territory. Food abundance (absolute or per family member) did not predict female fertility reliably; only females living in small families reproduced and once family size reached 4, females did not breed at all.

The fact that food abundance predicted female physical condition but not fertility may be indicative of a decision process involved in female reproduction. Females that are in good physical condition may trade off investment in current offspring against investment in future offspring (Williams 1966, Trivers 1974). When family size grows too large, i.e. the number of current offspring grows too large, females may allocate investment to current offspring. Females did obviously not invest directly in their offspring after weaning, but restrained reproduction, i.e., the decision not to breed in a certain year, may be an investment in itself, because it may reduce the female's future reproductive success. If parents have an interest in their offspring's presence, social relationships between parents and offspring should be relaxed and reflect the parents' tolerance towards their subadult offspring. Indeed, affiliative, as well as agonistic interactions (that were limited to the feeding context), and sharing of sleeping sites occurred in parent-offspring dyads at similar rates as among adult pair partners (Tab. 5). Comparison of the duration of affiliative interactions imply that parents value their offspring even more than their pair partners; interactions involving a non-adult group member were found to be twice as long (170 ± 31 s) on average as interactions between pair partners (81 ± 14 s; t-test: $N_1 = N_2 = 6$, $t = 6{,}41$, $p<0.05$).

Table 5: Rates of interaction in parent-offspring and adult-adult dyads

	Parent-offspring	Pair partners	t-statistics
Affiliative interactions (h^{-1})	0.29 ± 0.10	0.22 ± 0.07	$t = 1.52$, n.s.
Agonistic interactions (h^{-1})	0.33 ± 0.28	0.52 ± 0.25	$t = 1.25$, n.s.
Sharing sleeping site (% days)	37.5 ± 18.3	33.0 ± 15.7	$t = -0.45$, n.s.

Female Reproductive Decisions and Delayed Natal Dispersal

Natal dispersal of at least one sex is ubiquitous among primates (Pusey 1993), and in pair-living primates both sexes usually disperse (Pusey and Packer 1987). Although not

widely recognized, dispersal has two faces: 1) the offspring's decision whether to stay or to leave and 2) the mother's problem how to allocate resources to philopatric and dispersing offspring (Murren et al. 2001). Mobil animals living in heterogeneous environments are expected to exhibit phenotypic plasticity with regard to these decisions (Murren et al 2001). Under certain conditions a female (and her mate) should allow her offspring to stay instead of evicting full-grown individuals from the natal territory. Either full-grown offspring that stay in the natal territory benefit their parents in some way (Hamilton 1964), or dispersal involves high costs for the dispersing individual that influence the parents' decisions through inclusive fitness trade-offs.

Among callithrichine new world primates delayed natal dispersal regularly occurs with helping at the nest (Tardiff et al. 1993). Full-grown offspring carry their younger siblings during group movements and provision them with food (Garber 1997). Gibbon (*Hylobates lar*) helpers are thought to benefit the adult pair through improving physical and social development of infants by playing and grooming them or through defence of resources in agonistic encounters with neighbours (Brockelman et al. 1998). In fork-marked lemurs, which park their infants during the first weeks of life until the infants begin moving independently, no such helping at the nest has been observed. Older siblings neither guard the parked infants nor do they transfer food. Even indirect allo-care via territorial defence is unlikely to play a role. During meetings at territory borders agonistic interactions between subadults (N=3) and adults (3 females, 2 males) from different families were observed on 22 occasions. Subadults were males in all cases and lost conflicts with females (N=13) as well as with males (N=9). This leaves open the possibility that high costs associated with the process of dispersal are responsible for the parents' tolerance.

The costs of dispersal generally result from higher travel costs, increased predation risk and/or decreased foraging efficiency (e.g. Ims and Hjermann 2001). In gregarious species increased vigilance, safety in numbers and co-operative defence are among benefits of group-life (reviewed in Chapman and Chapman 2000) reducing predation risk. Lack of these benefits in dispersing male baboons (*Papio cynocephalus*) may increase mortality up to a order of magnitude, compared to males living in groups (Alberts and Altmann 1995). Because fork-marked lemurs always forage alone, however, they will not lose these benefits when dispersing. Only the consequences of decreased familiarity with the area (Isbell and van Vuren 1996) remains as a cost in terms of increased predation risk, but this factor will only be strong in species that flee into hides (e.g., marmots: van Vuren and Armitage 1994).

Like all dispersing animals, fork-marked lemurs face difficulties in locating food resources while searching for a vacant territory, but they differ in two respects from most other primates. Firstly, the majority of gum holes used by fork-marked lemurs is gouged by the animals themselves in an energy- and time-consuming process. A dispersing animal may not have the time to open new gum holes and/or return to them, while roaming. Secondly, gum is a renewing resource and to a certain degree the productivity of the resource is positively related to the intensity of use. It was regularly observed that the lemurs returned to the same gum holes in the same trees during 2h focal follows. When 6 hour follows were conducted it became apparent that the lemurs moved in circles from one gum tree to the next, returning always to the same trees to collect the gum that had exuded in the meantime. Without knowledge of the location of exudate trees and the possibility to return to productive gum holes after short time periods, foraging will become extremely inefficient and certainly poses unusually high costs for dispersing animals.

That dispersal is indeed costly in terms of decreased foraging efficiency is supported by the observation of risk aversive excursions by one subadult male. Although he crossed 2-3 adjacent territories on his excursions, he never fed while roaming and always returned to his natal territory the same night. Throughout the study period he was never found absent from his natal territory during the day, when sleeping sites were checked (340 times). It seems likely that the male returned to refill his energy resources in an area with familiar food resources. The resource use of fork-marked lemurs is similar to other gum-feeding primates: *Callithrix penicillata* groups usually possess one major gum resource in their territory to which they return several times during a day (Rylands 1984). *Cebuella pygmaea* use a small number of exudate trees in a repetitive fashion until the resources are depleted and consequently the entire territory is shifted (Ramirez et al. 1978, Soini 1982). Unfortunately, information about the dispersal distances and the costs involved in dispersal is lacking for these species.

Spatially heterogeneous or patchy habitats induce an extra dispersal cost because they generally lead to poor environments for dispersers (Gandon and Michalakis 2001). Fork-marked lemurs are apparently not distributed uniformly across Kirindy forest. Census data from ten 1km² plots in Kirindy forest indicate that fork-marked lemur densities vary between 153 and 555 individuals per km² (Ganzhorn and Kappeler 1996). Moreover, density was shown to correlate with a crude measure of food availability (Ganzhorn and Kappeler 1996). During three census walks in N5, another grid system intensively used to observe nocturnal

primates in Kirindy, fork-marked lemurs were seen and heard in the northern part of the grid only, suggesting discontinuous distribution on a small scale (pers. obs.). Although all trees with a dbh larger than 10 cm are marked in N5 only 5 taly trees were counted in the southern part where no fork-marked lemurs occur. The observed variation in population density and the patchy distribution of fork-marked lemurs in one plot (N5) seem to result from spatial variation in habitat quality, which would place extra costs on dispersing animals.

A potential alternative explanation for low reproductive rates in fork-marked lemurs is based on the idiosynchracies of the Malagasy environment. Accordingly, Madagascar is an extremely unpredictable and harsh environment that promoted the evolution of several adaptations among primates (Wright 1999, but see van Schaik and Kappeler 1996) all concerned with the conservation of energy or the optimization of resource exploitation. As a reaction to unpredictable environments animals may react with bet-hedging (Stearns 1976), which refers to a set of life-history traits that facilitate longer reproductive careers with lower reproductive rates but maximum reproductive success (for *Propithecus verreauxi verreauxi*: Richard et al. 2002). In fork-marked lemurs, however, physical condition and fertility are uncoupled as shown above. Unlike other Malagasy primates (*P. verreauxi:* Richard et al. 2000, *L. ruficaudatus:* Ganzhorn 2002, *Lemur catta:* Gould et al. 1999) and anthropoids (Koenig et al. 1997), they are not capital breeders as they do not seem to conserve energy prior to conception. Unfortunately, most life-history parameters, such as age at first conception and total life-span are still unknown for fork-marked lemurs.

Conclusion

This study is the first to apply the principles of the 'ecological model' (van Schaik 1989) to either pair-living species or nocturnal primates. In general, the results support the basic prediction of the model: the characteristics of the major food resources dictate the competitive regime. Since fork-marked lemurs avoid spatial proximity during foraging, and the number of resources available is large enough for the male to find food elsewhere if one tree is occupied by the female, it was unexpected that WGC effects would be measurable. The results suggest, instead, that male foraging efficiency is effectively reduced compared to dominant females even in a species living in dispersed pairs. The repeated use of a small number of food trees in small territories, however, together with incomplete knowledge of the pair partners position lead to high rates of agonistic encounter between pair partners, which invariably lead to the retreat of the male (Schülke and Kappeler 2003).

Although the 'ecological model' was formulated to predict variation in female social relationships among gregarious primates, it has now been shown to be extendable to analyzing competition among family members in a pair-living species. Identifying the principle components of food competition in pair-living females is a first step towards understanding how differential female reproductive success is determined. The evidence for group size effects among pair-living females opens a new area for research on the costs and benefits of delayed dispersal. Conclusive analysis of the proposed hypothesis explaining delayed dispersal by costs accruing from reduced foraging efficiency has to await comparative analysis of dispersal phenomena across species without helpers at the nest.

ABSTRACT

Differential access to food resources is thought to be the main determinant of differences in female reproductive success but is poorly studied in both pair-living and nocturnal primates. The modes of food competition within and between families were investigated following the principles proposed by the 'ecological model' using three years of field data from eight fork-marked lemur (*Phaner furcifer*) families. The major food resources were identified from year-round feeding observations and the strength and mode of competition were inferred from differences in physical condition. The most important food resource of fork-marked lemurs were tree exudates that occurred in small, defendable food patches characterized by fast depletion and rapid renewal. These characteristics led to strong within-group contest and scramble competition, which were found to yield a positive dominance effect and a negative group size effect on female net energy gain. Differential physical condition, however, did not translate directly into differential reproductive success. Low female fertility was best predicted by large family size associated with delayed dispersal by previous offspring. Although there is no obvious benefit from full-grown offspring in their territory, adults tolerate delayed natal dispersal, probably because dispersal poses extraordinary costs for the offspring. These costs are likely to accrue from decreased foraging efficiency in unfamiliar habitats because exudate feeding requires very rigid feeding itineraries. Comparative analysis of dispersal patterns among (pair-living) nocturnal lemurs using different food resources but subject to the same predation pressures will facilitate evaluation of this hypothesis. In conclusion, the presented evidence for group size effects on reproductive success in pair-living females opens a new area for research on the costs and benefits of delayed dispersal.

CHAPTER 3:

Constraints on male mate guarding explain high extra-pair paternity in pair-living fork-marked lemurs, *Phaner furcifer*

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INTRODUCTION

Monogamy is a puzzling mating system for any species without substantial paternal care. Because male reproductive success is limited by the number of mates (Trivers 1972), behavioural ecologists have always tried to explain why some males apparently forego opportunities for polygynous matings and, hence, the possibility to increase their genetic representation in the next generation's gene pool. A surprising result of socio-genetic studies was the demonstration of the widespread occurrence of extra-pair paternity (EPP) among pair-living, and thus supposedly monogamous, birds (50-92% of broods in tree-swallows: Barber et al. 1996, Møller & Ninni 1998), reptiles (Bull et al. 1998), fish (DeWoody et al. 2000) and mammals (e.g. Girman et al. 1997, Goossens et al. 1998, Fietz et al. 2000, Wolff & Dunlap 2002). However, recent studies have also demonstrated the existence of strict monogamy in several non-passerine birds (e.g. Müller et al. 2001, Moreno et al. 2000, Stanback et al. 2002, Masello et al. 2002, Michalek & Winkler 2002), passerines (e.g. Haggerty et al. 2001), fish (Jones 1998), and mammals (Ribble 1991, Heller et al. 1993, Brotherton et al 1997, Sommer & Tichy 1999). Today, extra-pair paternity (EPP) is thought of as an integral part of the mating system of socially monogamous species (Gowaty 1996) and much research focuses on the causes and consequences of variation in EPP (Westneat & Sherman 1997, Petrie & Kempenaers 1998, Birkhead 2000).

Variation in EPP among pair-living primates has been attributed to differences in social organization (van Schaik & Kappeler 2003). Pair-living among primates has long been thought of as homogenous phenomenon involving long-lasting close bonds between pair partners reflected by affiliative interactions and highly cohesive movements (e.g. Mason 1974, Kleiman 1977, van Schaik & Dunbar 1990, Anzenberger 1992). Recent comparative analyses, however, have shown that pair-living primate species exhibit variation along two axes (bracketed terms refer to van Schaik & Kappeler 2003): i) Species are either strictly pair-living (uniform pairs) or some larger percentage of social units are groups of more than two adults (variable pairs). ii) They either form cohesive units (associated pairs) or they spend a significant percentage of their activity time apart from their pair partners (dispersed pairs). On the basis of phylogentic reconstructions and reasoning about the causes of character shifts it has been proposed that EPP rates are high among variable pairs and that the mechanism mediating high EPP among dispersed pairs are constraints to mate guarding (mate guarding hypothesis, van Schaik & Kappeler 2003). The only paternity data available for a pair-living

primate so far (Fietz et al. 2000) support the hypothesis by demonstrating high EPP rates in the nocturnal primate *Cheirogaleus medius* that lives in dispersed pairs. However, information regarding the mechanisms, i.e. the behavioural strategies of males and females resulting in EPP are lacking.

In the present study, we investigate male and female mating strategies and the resulting reproductive consequences in fork-marked lemurs (*Phaner furcifer*), who live in dispersed pairs, to test the mate guarding hypothesis for variation in EPP rate among pair-living primates. In nocturnal fork-marked lemurs the key factor determining year-round low cohesion between pair partners is avoidance of direct feeding competition (Schülke & Kappeler 2003, Schülke submitted). Frequent encounters at a limited number of food resources invariably led to agonistic interactions between pair partners, with females dominating males in all cases (Schülke & Kappeler 2003). Nevertheless, pairs were stable over time and represented the modal grouping pattern in 18 out of 21 group years. Pair partners used well defined territories (5ha) that overlapped only slightly between neighbouring pairs. Fork-marked lemurs spend the day in hollow trees where pair partners associated on average every third day (Schülke & Kappeler 2003). Reproduction is highly seasonal and limited to a few weeks per year. Strong limits to group size, together with constraints on juvenile dispersal, lead to low reproductive rates with only 0.3 offspring per year and female (Schülke submitted).

In this paper, we first investigate extra-pair paternity via DNA-microsatellite analyses. In addition to direct observations of mating patterns and male mate guarding behaviour, we use indirect behavioural information to test the hypothesis because restricted visibility at night hampered behavioural observations. With respect to male-female interactions, we predicted that i) if males guard their pair partners during the mating season, they should increase the rate of association at the diurnal sleeping site during the mating season. ii) If male mate guarding is against the interests of the female, changes in the quality of intersexual social relationship should reflect this conflict. iii) If males and/or females actively seek EPCs, they are expected to search for and assess additional mating partners in the vicinity of their territory. This effort should result in increased travel times and distances, an increase in the time spent in peripheral areas of the territory, and increased rates of encounters with neighbours/strange conspecifics during the mating season. iv) Finally, if EPC rate is high, sperm competition influences male reproductive success and males are expected to have

relatively large testes. We tested these predictions with behavioural, morphometric and genetic data from a wild population of 30 fork-marked lemurs.

METHODS

Study Site and Animals

The study was conducted at Kirindy Forest which is situated at 44°39' East / 20°03' South in Western Madagascar. On the forest concession of the Centre de Formation Professionelle Forestière de Morondava (C.F.P.F.) the Deutsches Primatenzentrum Göttingen, Germany operates a research station. Kirindy Forest is part of one of the largest remaining fragments of dry deciduous forest in Madagascar. The 900 x 700 m grid system (25 m squares) where the study was conducted is locally known as CS7. The region is characterised by a short, hot rainy season from December to March with an average rainfall of 800 mm and eight months of virtually no precipitation. Between June and September temperatures may drop as low as 5°C at night (for a detailed description of the forest and climate see Ganzhorn & Sorg 1996).

Between November 1998 and April 2001, a total of 30 fork-marked lemurs were captured 103 times. Tomahawk life-traps were fixed to the entrance of their sleeping site in hollow trees. Typically, animals entered the unbaited trap 10-20 minutes after dusk. Animals were brought to the forest camp immediately after capture and were briefly anesthetized (0.02 ml Ketanest©). Animals were weighed and standard field measurements were taken by O.S. (Schülke & Kappeler 2003). Until April 2000 only harness fitted radio tags (10g) especially designed for this study by Biotrack (Wareham, UK) were used because males possess a large scent gland at their throat that might get irritated by collar tags. From June 2000 onwards, females were fitted with brass collar tags (14 g) because harness tags were often removed by the animals. Tag life-time was approximately one year and tags were replaced whenever necessary. The study is ongoing and animals are still wearing tags. Animals were released at their capture site later the same night. All sleeping trees where animals were captured once were reused by the same individuals after some time. All procedures caused no noticeable harm of the animals and were in compliance with current laws of Madagascar.

Data Collection

Behavioural and spatial data were sampled between June 1999 and August 2000 and from February to April 2001. Animals were located and followed using a Telonics TR-4

receiver with a three element yagi antenna, a head-lamp and if necessary a strong flashlight and binoculars. Focal animals were all adult males and females from eight fork-marked lemur families carrying radio collars at the respective time. For most analyses below, however, a subset of only six pairs was used because of bad observation conditions in one pair and lack of observations on the male in another pair. During two hour follows, the focal animal's (Altmann 1974) spatial position within the grid system of 25 x 25 m squares was recorded continuously. Focal follows were conducted in the first half of the night and were evenly distributed across this time period. Behavioural data collected included all social interactions (affiliative and agonistic) and were recorded continuously. Instantaneous records (2.5 min intervals) of behavioural states (resting, locomotion, feeding) included details of feeding behaviour (e.g. plant part and species consumed) and visual contact times. The number of observation hours accumulated per animal varied between 12 and more than 20 and totalled 1227 hours for all adults over the entire study period. Sleeping sites of radio-tagged animals were determined between April 1999 and August 2000 and again between February and April 2001 on a total of 419 days.

Animals were aged according to body length, body mass, cranium size, teeth wear and, in the case of males, testis development and size of the sexually dimorphic throat gland. It was assumed that animals not yet fully grown when first captured were natal to the territories they were caught in. DNA microsatellite analyses of relatedness (see below) did not contradict any of these assigned mother-offspring relationships.

Data Analyses

Spatial data were sub-sampled at 5 min intervals, thereby making consecutive data points independent because 5 min are enough for an individual to reach any point in its home range at highest locomotor speed (Rooney et al. 1998). Minimum convex polygons (Mohr 1947) were calculated with Tracker 1.1 software (©Camponotus and Radio Location Systems) with 5% outlier removal by the harmonic mean method (for details of homerange analysis see Schülke & Kappeler 2003). The periphery of a homerange was defined as all grid squares that touched the border of the 95% MCP.

Testis volume was calculated from testis length (TL) and width (TW) assuming the form of a spherical ellipsoid: $V = 1/6 * \pi * (TL * TW^2)$. Values for right and left testis of each individual were averaged for these calculations. For a comparison of relative testis size with

that of other Malagasy primates, additional data on testis size were gathered from the literature and through personal communication.

In order to compare behaviour between the mating and the non-mating season, the mating season had to be defined. Despite good observation conditions in the dry season 1999, only one copulation and one case of mate guarding were observed. Hence, the mating season could not be defined using actual matings. Births occurred late in February and in early March in 2000 and in late January in 2001 (Schülke 2003). Assuming gestation to be comparable in length to that of closely related, similar-sized species (e.g. *Mirza coquereli*, Kappeler 1997a), the mating season was inferred to take place in October and/or November.

DNA Microsatellite Analysis

DNA was obtained from small (ca. 3*3mm) tissue samples taken from the animals' ears at first capture. Samples were preserved in 70% ethanol and stored at 4°C for 3 to 13 months. DNA extraction was carried out using the a QIAamp Tissue Kit (Quiagen, Hilden, Germany) following the instructions of the manufacturer and extracts were stored at -20°C. A total of 56 primer pairs originally designed for amplification of microsatellite loci in *Cheirogaleus medius* (23) and *Microcebus murinus* (33) (Fietz et al. 2000, Hapke et al. 2003, Hapke et al. unpubl. data) were tested for applicability in fork-marked lemurs. Although each primer pair was tested under several PCR conditions, products were amplified with 30 primer pairs only. All but seven loci amplified were monomorphic in the study population.

Table 1: Primers used in paternity analysis, polymorphism, PCR conditions (temerature [°C] and duration [s]), and paternity exclusion probability of each locus.

Oligo #	Locus	Origin	Alleles	Start	Denat.	Anneal.	Elong.	Final	Cycles	$P_{excl.}$
221/222	18	C.m.[1]	3	94	94	50	72	72	35	0.178
				2.00	1.00	1.00	1.00	5.00		
262/258	110	C.m.[1]	2	94	94	49	72	72	35	0.157
				2.00	1.00	1.00	1.30	5.00		
878/879	33103	C.m.[2]	4	92	92	58	72	72	35	0.371
				2.00	0.40	0.40	1.00	5.00		
901/916	33226	C.m.[3]	2	92	92	52	72	72	35	0.120
				2.00	0.40	1.00	1.00	5.00		
902/903	33228	C.m.[3]	5	92	92	58	72	72	35	0.375
				2.00	0.40	1.00	1.00	5.00		
990/991	Mm22	M.m.[2]	6	92	92	58	72	72	35	0.305
				2.00	0.40	1.00	1.00	5.00		
1149/1150	Mm58	M.m.[3]	2	92	92	54	72	72	35	0.182
				2.00	0.40	1.00	1.00	5.00		

[1] Fietz et al. 2000, [2] Hapke et al. unpubl. data, [3] Hapke et al. 2003.

Standard hot-start PCRs (2 min initial denaturation at 92-96°C) were performed using 2 µl of DNA extract and 30-35 cycles in a Peltier Thermal Cycler 200 (MJ Research) with one primer being labelled with infrared fluorescent dye (IRD 800 or IRD 700). Temperatures and duration of each PCR step are given in table 1 for all primers used for the paternity analysis. About 1/20 of the PCR products were denatured (94°C for 2 min) and subjected to a denaturing acrylamid gel electrophoresis on LI-COR 4000 or 4200 DNA laser sequencers (MWG Biotech) along with an internal, labelled standard (LI-COR STR marker). Genotypes were scored using the ONE-D scan software (MWG Biotech, Scanalytics).

Paternity Analyses

Paternity likelihood analysis was performed using Cervus 2.0 software (Marshall et al. 1998). Ten-thousand simulations were run on the genotypes of 30 individuals at 7 loci under the assumption that 50% of candidate fathers have not been sampled and that typing errors occur at a rate of 1%. The likelihood that a given male is the true father was compared to the likelihood that this male is not the true father given the observed genotypes (likelihood ratio). The product of the likelihood ratios of all genotypes were log (base e) transformed (LOD score) and compared across males. Positive LOD scores denominate males that are more likely to be the true father than an arbitrary randomly chosen male. The male with the highest LOD score is the most likely father. Confidence limits of 80% and 95% for the differences in LOD scores between the most likely and the second most likely father were calculated from the simulation to describe whether these differences are likely to occur by chance.

The time lag between the conception of the respective offspring and the first unequivocal identification of the social father varied between 0 and 24 months. According to demographic data from a three year period the average male tenure in a pair is 22.3 ± 11.8 months (N = 9), which is an underestimation because the maximum of 36 months was observed in two of the three males that were caught during the first field season and because it is unlikely that all tenures measured ended exactly when data sampling ended after three years. Although it can not be verified retrospectively, we assumed for the subsequent paternity analyses that males residing in a pair at a given time have been residents two years before and are the social father of offspring sired during that time.

Means and standard deviations are given throughout the paper and all tests are performed two-tailed with the alpha level set at 0.05. Exact p values are given to allow for a

rough estimation of the beta error in case of non-significant results. Most comparisons of measures between the mating season and the non-mating season are performed as paired tests, thus controlling for inter-individual differences.

RESULTS

Paternity Analysis

Paternity analysis was performed at 7 loci amplified with primers designed for *Cheirogaleus medius* (N=5) and *Microcebus murinus* (N=2), which were moderately polymorphic with 2 to 6 alleles (mean 3.4 alleles) in the sampled population of 30 fork-marked lemurs (Tab. 1). Where tests were appropriate, the distribution of alleles in the sample population did not differ statistically from Hardy-Weinberg Equilibrium. Informative homozygotes were genotyped at least 4 times in independent PCRs to control for allelic dropout phenomena. Mother-offspring relations were known from detailed behavioural observation (1999 to 2001) or inferred for offspring born before 1999. Inferred mother-offspring relationships were never contradicted by the genetic data.

Table 2: Paternity analysis for 7 offspring born between 1997 and 2001

Year[a]	Offspring	Mother[b]	Social father[c]	Time lag[d]	Excluded?[e]	Likely father[f]	Not excluded[g]
2001	#29	F7	M7	0	yes [1]	M6 [+]	M6
2000	#26	F6	M6	0	no	M6 [*]	none
1999	#19	F7	M7	4	yes [3]	M4 [-]	none
1999	#8	F2	M2	10	yes [1]	M5 [-]	M5
1998	#30	F6	M6	12	yes [2]	M2 [-]	none
1998	#13	F3	M3	18	no	M3 [-]	M5, M3
1997	#10	F5	M5	24	no	M5 [*]	none

[a] Refers to year of birth. [b] mother-offspring relations known from detailed behavioural observation (1999-2001) or inferred. [c] Social fathers known to have been present in mating season or captured for the first time 4 months to 2 years later. [d] time lag between conception of offspring and first identification of the potential social father. [e] Combined paternity exclusion probability 90%. [1,2,3] number of loci where male is excluded from paternity of respective offspring. [f] Cervus 2.0 likelihood analysis based on 10,000 simulations with known mother-offspring relations and under assumption of 50% potential fathers sampled and 1% of loci mistyped, confidence levels for differences in LOD scores between most likely and second most likely father: * strict confidence (95%), + relaxed confidence (80%), - most likely. [f] males not excluded except social father; all males included in analysis irrespective of date of first capture

All 12 males were included in paternity exclusion analysis (Tab. 2), irrespective of the date of first capture (November 1998 to February 2002). Exclusion power for the second parent varied between 14% and 49% between loci, combining to a total paternity exclusion probability of 90%. Paternity exclusion analysis was carried out by hand, assuming that any mismatch excludes a male from paternity. Given that mother-offspring relations were assigned correctly for births before 1999 the social father was excluded as genetic father at 1-

3 loci in 4 cases, was one of 3 males not excluded in 1 case and was the only male not excluded to be the genetic father in 2 cases.

Paternity likelihood analyses revealed that social fathers were the most likely fathers in 3 of 7 cases analyzed. In none of the 4 case where social fathers were excluded from paternity by at least one genotypic mismatch were they the most likely father among the males sampled. Thus, the paternity likelihood analysis strengthened the result of the paternity exclusion analyses that social fathers are often not the genetic fathers.

Sleeping Associations

Pair partners shared the same sleeping site at an average rate of 0.36 ± 0.24 per day, i.e. about every third day. When not sleeping in the same tree hole pair partners' sleeping sites were on average 101 ± 60 m apart from one another which is about half a territory diameter (Schülke & Kappeler 2003). The rate of association at the sleeping site did not differ between the mating season (0.34 ± 0.38 per day) and non-mating season in six pairs (0.31 ± 0.18 per day; paired t-test: $t_6 = 2.46$, $p = 0.815$).
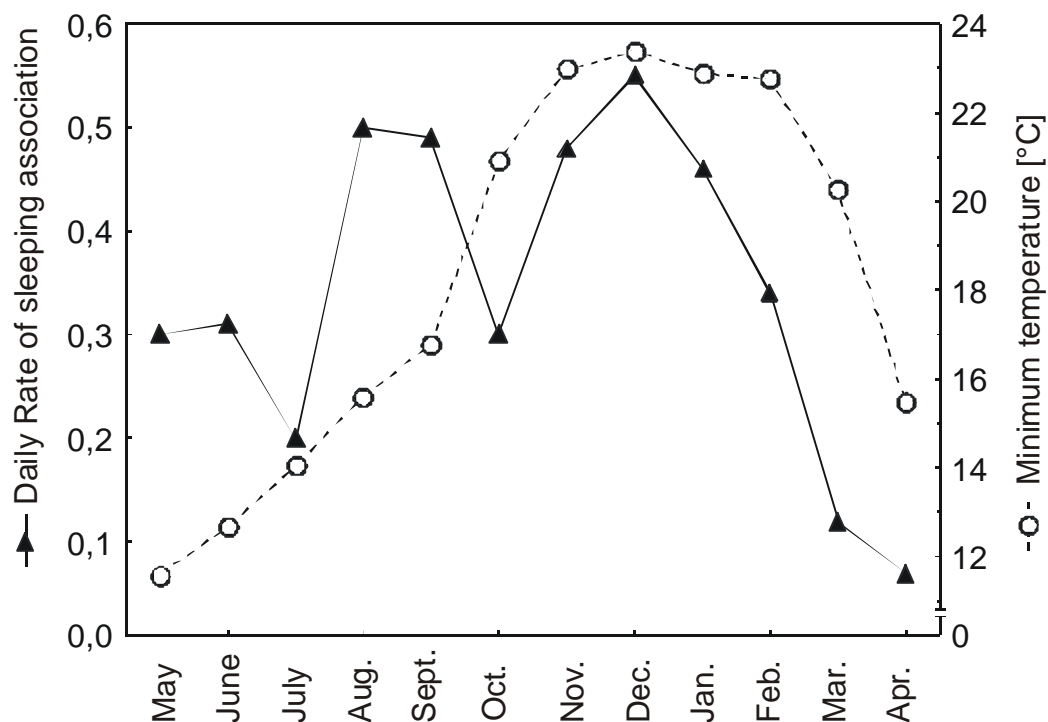
Figure1: Seasonal variation in the frequency of sleeping association between pair partners in relation to the monthly mean of the daily minimum temperature. October and November correspond to the mating season.

Mating takes place in the late dry season when temperatures are intermediate between the very cool dry season and the hot rainy season. Because many nocturnal primates associate

at sleeping sites to facilitate thermoregulation (Radespiel et al. 1998, Schmid 1998), we correlated the monthly rate of association at the sleeping site (mean of six pairs) with the monthly mean minimum ambient temperature and found an unexpected positive trend in an overall non significant relationship (Fig 1, Pearson correlation: $r_{12} = 0.38$, $p = 0.224$). Association rates were at their maximum in the hot rainy season which corresponds to the gestation period.
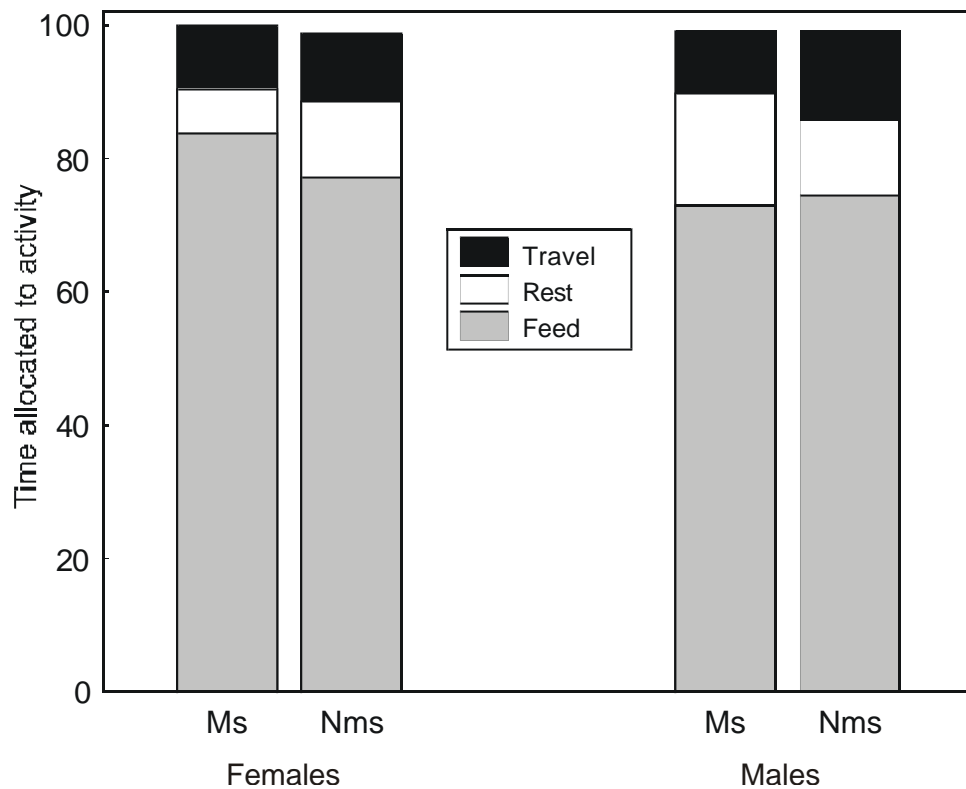

Figure 2: Time allocated to different activities by females and males during the mating season (Ms) and the non mating season (Nms).

Mobility and Space Use

Comparison of time allocation during the mating and non-mating season (Fig. 2) revealed that during the mating season females fed longer (paired t-test: $t_7 = 2.89$, $p = 0.028$) and rested less (paired t-test: $t_7 = -2.90$, $p = 0.027$; travel: $t_7 = -0.68$, $p = 0.524$) whereas males travelled longer (paired t-test: $t_6 = -2.56$, $p = 0.05$; feed: $t_6 = -0.26$, $p = 0.81$; rest: $t_6 = 1.28$, $p = 0.26$). Individual mean travel distances varied considerably (males: 1345 m - 2335 m , females: 913 m - 1578 m per 6 hs), which can be attributed to differences in territory size between pairs. The larger a female's territory, the longer her travel distance per night (Pearson correlation: $r_6 = 0.95$, $p = 0.004$). Since territories of pair partners are of similar size and travel distances are related to territory size, only males and females from the same pair can be

compared between seasons. Although males spent significantly more time travelling in the mating season than during the rest of the year this difference did not translate into longer travel distances. Throughout the year males had 25% longer travel distances than females (paired t-test: $t_6 = -3.73$, $p = 0.01$) but male travel distances were similar during and outside the mating season (paired t-test: $t_6 = -1.10$, $p = 0.322$). In contrast, 6 out of 7 females travelled further during the mating season, a difference that just failed to reach significance (Fig . 3, paired t-test: $t_7 = 1.73$, $p = 0.134$). As a result, male (1624 ± 665 m) and female (1668 ± 361 m) travel distances were similar during the mating season (paired t-test: $t_6 = 0.174$, $p = 0.869$).
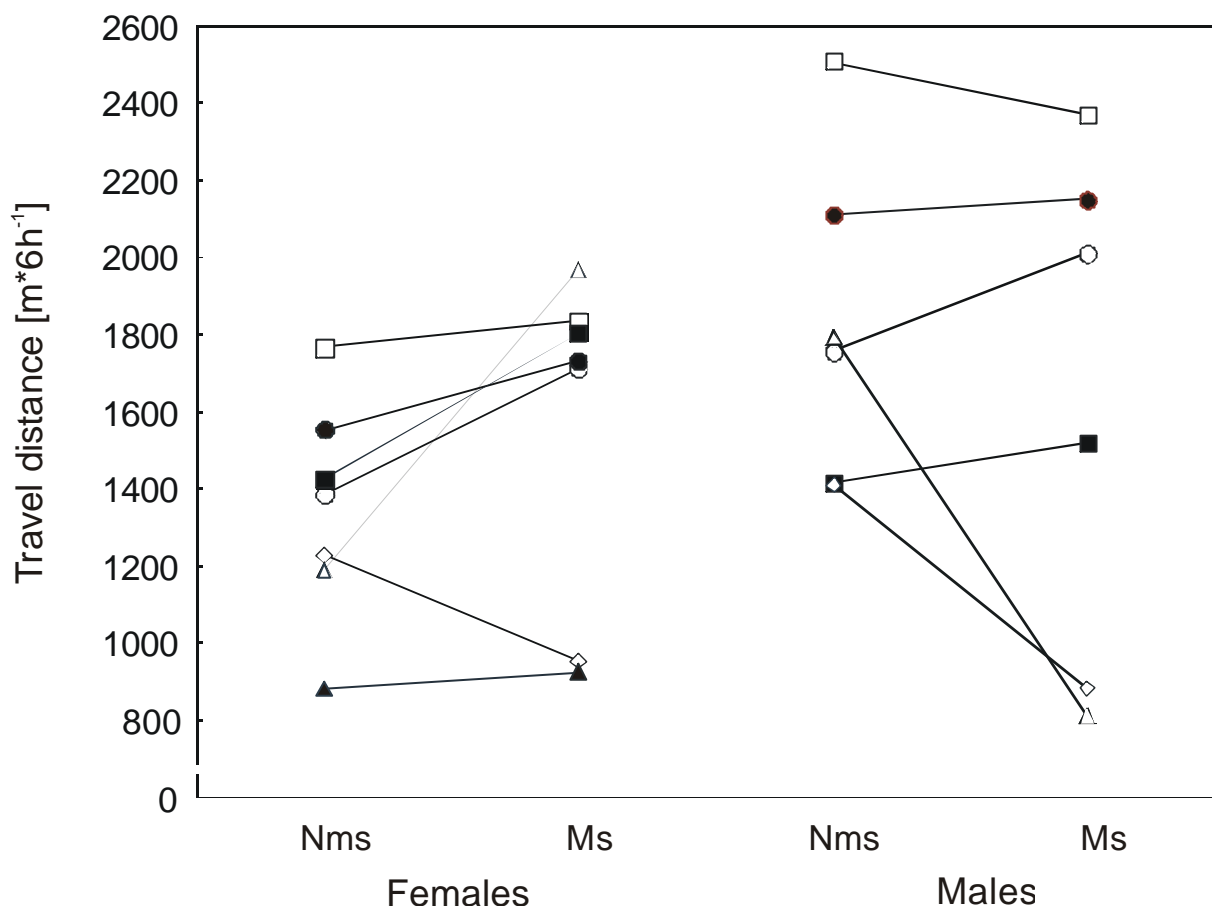
Figure 3: Mean travel distances of individual females and males during the non mating season (Nms) and the mating season (Ms). Same symbols refer to pair partners.

To test whether ecological differences may explain these effects, we compared travel distances within the mating season with those of the climatically similar two months preceding the mating season. If mating season vs. non mating season differences in female

travel distance would result form ecological changes travel distances should be similar in ecologically similar conditions. For this comparison data from only five females are available. These individuals however, travelled much further (32%) in the mating season (1811 ± 102 m) than during the two preceding months (1371 ± 152 m), indicating that social, rather than ecological reasons were responsible for this increase in locomotor activity (paired t-test: t_5 = 3.975, p = 0.016).

If EPCs were the motivation behind longer travel distances, females should not only travel further, but also spend more time in the periphery of their territory than during the rest of the year. However, for both sexes, no differences between mating and non-mating season were found in the time spent in the periphery of the homeranges (Tab. 3), even if only outlier positions are considered (i.e. the 5% locations outside the 95% MCP borders, Tab. 3).

Table 3: Time spent in peripheral territory areas and outlier locations (outside 95% MCP area) during the mating season (Ms), the non-mating season (Nms), and the months prior to the mating season (Before).

		Females	N	t^1	Males	N	t^1
Periphery	Ms	25.3 ± 13.0	5	0.36	26.0 ± 20.0	6	-0.95
	Nms	26.6 ± 10.5			19.9 ±16.3		
	Ms	26.0 ± 14.4	6	-0.10	16.9 ± 10.1	3	1.88
	Before	26.6 ± 19.0			13.1 ± 11.3		
Outliers	Ms	5.4 ± 4.8	4	0.48	5.2 ± 4.5	6	0.19
	Nms	4.5 ± 1.4			4.8 ± 1.3		
	Ms	3.7 ± 3.5	6	2.59	6.0 ± 5.3	3	1.62
	Before	2.18 ± 2.7			2.7 ± 2.4		

[1] t-value for paired t-tests, all results n.s.

Interactions Within and Between Pairs

During the mating season the rate of affiliative interaction (per hour of observation of either of the partners) between pair partners increased in some pairs and decreased in others, compared to the non-mating season (Fig. 4a, paired t-test: t_6 = 0.10, p = 0.921). In contrast, the mating season had a strong effect on the rate of agonistic interactions. In all pairs conflicts occurred at higher rates during the mating than during the non-mating season, a difference that failed to reach significance due to small sample size (Fig 4b, paired t-test: t_6 = 2.42, p = 0.06).

The mean rate of meetings between neighbours per month did not change during the mating season (0.17 ± 0.02 per hour) compared to the rest of the year (0.17 ± 0.07 per hour, t-test: N_{ms} = 2, N_{nms} = 14, t = 0.13, p = 0.90; non-mating season includes June - September 1999, December 1999 – June 2000, February-April 2001). The majority of between-pair

encounters took place in overlapping or peripheral zones of neighbouring territories. Excursions from the territory were observed several times. Most excursions involved a subadult male and were scattered across the year. Nevertheless, one adult female was observed to intrude neighbouring territories three times (October 14., 15., and 18. 1999). She was more than 100m away from the 95% MCP border of her territory when she met neighbouring males, females and subadults. Her male partner participated in only two of these meetings, all of which took place during the mating season. Throughout the study there was no evidence for the existence of non-territorial or transient males in the population.
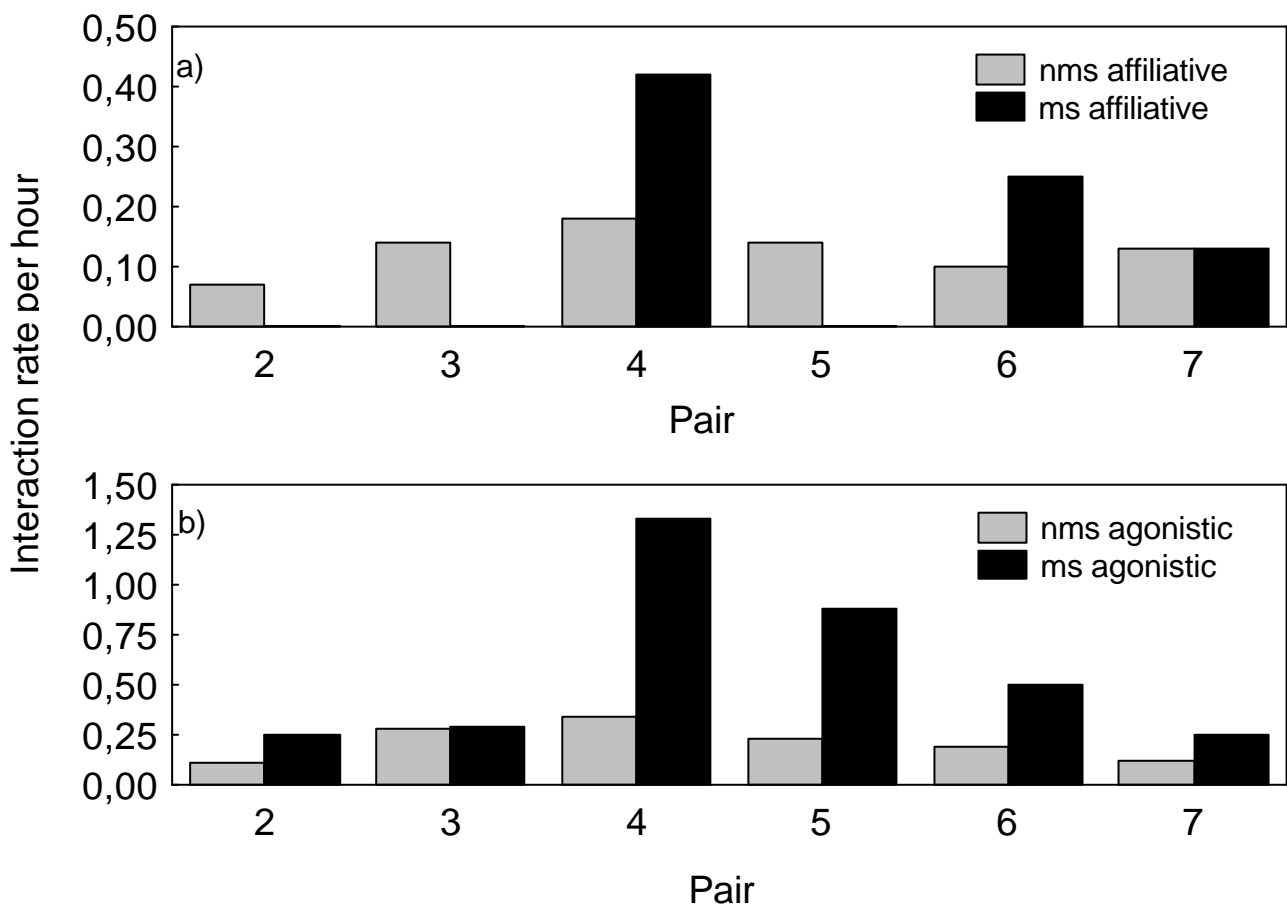
Figure 4: Social relationships between pair partners (frequency of a) affiliative and b) agonistic interactions) during the mating season (ms), compared to the non-mating season (nms).

Mate Guarding Behaviour

Very close mate guarding has been directly observed in one pair for one night. Usually male and female pair partners avoid each other and are separated by more than 100 meters during nocturnal activities (Schülke & Kappeler 2003). But that night the male stayed within

5 meters of the female and incessantly tried to make body contact. The female reacted with flight and often with aggressive behaviour to the approaches of her male partner. Agonistic interactions occurred at rate of 11.5 per hour, compared to the usual 0.5 interactions per hour. When the female guided the pair to an area of territory overlap and they met a neighbouring male, her partner left her and chased, hit and bit the neighbour in a vigorous manner.

Behaviour of Reproducing Females

The comparison of male and female behaviour across seasons may be flawed because only two females were definitely in estrus during the observed mating season because they were observed to give birth in the subsequent birth season. Other females may either not have conceived or subsequently lost their infant unnoticed. Taking only the behaviour of the two conceiving females into account, a strong tendency for polyandrous matings emerges. Both females travelled longer and rested less, passed longer distances and spent more time in the periphery of their territories during the mating season. Moreover, behavioural changes during the mating season included an increased proportion of time spent outside the MCP border of the territory in one female, as well as an increase of agonistic interaction frequency with the male partners in both pairs.

Relative Testis Size

A new comparative data set on relative testis size for Malagasy primates was compiled. In contrast to earlier studies (Kappeler 1997b), only data from wild populations were included. A regression between testes volume and body mass was calculated using double logarithmic scales to identify the general trend among prosimian primates. As in other lemurs living in (dispersed) pairs, testis size of fork-marked lemur was smaller than expected for a lemur of this body size (Fig. 5).
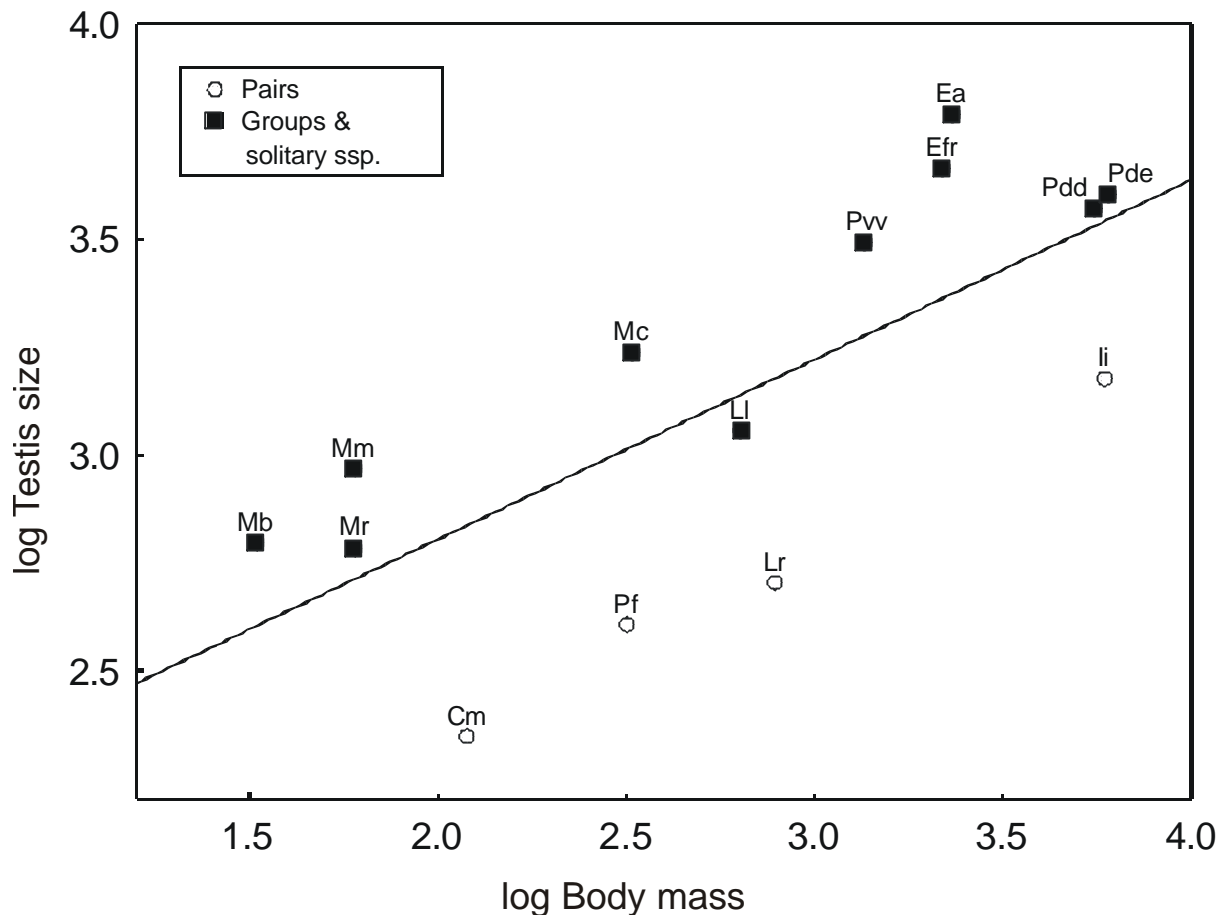
Figure 5: Comparison of relative testis size across Malagasy primates (r = 0.73, p = 0.003). Species are classified as 1) living in (dispersed) pairs or 2) as being solitary or living in (dispersed) groups. All measures taken in the mating season unless stated otherwise. Cm *Cheirogaleus medius* (Fietz 1999a), Ea *Eulemur albocollaris* (Johnson et al. 2002, S. Johnson, A. Gordon, B. Bradley & R. Kitko unpubl. data), Efr *Eulemur fulvus rufus* (Johnson et al. 2002, S. Johnson, A. Gordon, R. Stumpf, D. Overdorff & A. Merenlender unpubl. data), Ii *Indri indri* (Powzyk 1997), Ll *Lepilemur leucopus* (L. Nash unpubl. data), Lr *Lepilemur ruficaudatus* (measures closest to ms, D. Zinner & R. Hilgartner unpubl. Data), Mb *Microcebus berthae* (Schwab 2000), Mc *Mirza coquereli* (Kappeler 1997a, Kappeler unpubl. data), Mm *Microcebus murinus* (Fietz 1999b), *Mr Microcebus ravelobensis* (N. Hagenah, U. Radespiel, B. Randrianambinina, B. & Zimmermann, E unpubl. data), Pdd *Propithecus diadema diadema* (Powzyk 1997), *Pde Propithecus diadema edwardsi* (value of Pochron & Wright 2002 divided by 8), Pf *Phaner furcifer* (largest testis size per male, this study), Pvv *Propithecus verreauxi verreauxi* (Lewis & Kappeler unpubl. data).

DISCUSSION

EPP Rates in Dispersed Pairs

The hypothesis that primates living in variable pairs with low spatial cohesion between pair partners during regular activities (i.e. dispersed pairs) have high EPP rates was derived from a phylogenetic reconstruction of the evolution of pair-living among primates (van Schaik & Kappeler 2003). Dispersed pair-living is found among nocturnal primates only and was reconstructed to have evolved from the solitary ancestral state with female range exclusivity prohibiting males from monopolizing access to more than one female

economically (Komers & Brotherton 1997). Whenever female range size is small enough, however, males should exclude rivals and small onemale-multifemale groups should form (Orians 1969), resulting in variable pairs with some percentage of social units being groups instead of pairs (van Schaik & Kappeler 2003). A species will shift from the ancestral variable to the derived uniform pair-living only if some form of direct care (e.g. protection against infanticide, protection against predators) is provided by the male which requires high paternity certainty and thus low EPP. The data available to date suggest, however, that uniform pairs are rare among dispersed pairs. Thus, demonstration of high EPP rates in dispersed pairs would support the hypothesis that the transition from variable to uniform pairs at some stage involved the derivation of benefits from male parental care.

Fork-marked lemurs live in dispersed pairs and fit well into the larger model of the evolution of pair-living among primates. Females exhibit range exclusivity but daily travel distances of males were long (3.7 km per night) in relation to female territory size (4.7 ha), which enabled one male to monopolize two out of 8 females (Schülke & Kappeler 2003). Another deviation from the modal grouping pattern in pairs involved the formation of a twomale-onefemale unit, which is more difficult to explain (Schülke & Kappeler 2003). Thus, pairs are variable but not uniform in fork-marked lemurs and, as predicted from the model, we found high rates of EPP in our sample. Empirical support for this conclusion is weak, however, because the social father was observed during the respective mating or birth season in only three cases and much later in the other 5 cases. However, even if only the former three cases are considered, 2 out of 3 offspring were sired by an extra-pair male. Finding such a high incidence of EPP in such a small sample like ours would be highly improbable if the population wide EPP rate was very low. Thus, we are confident that larger samples will support our result of high EPP.

Are EPCs Sought by Males and/or Females?

Whether EPP is sought by females depends on the benefits the individual can gain from it (Birkhead 2000) which are a consequence of the mode of pair formation. In many birds the males arrive at the breeding grounds first, establish territories and/or nest sites and females can choose a male to pair (and mate) with (Orians 1969). The situation among most pair-living mammals is different because they form permanent pairs that stay together for several breeding seasons (e.g. giant jumping rats, *Hypogeomys antimena*: Sommer & Tichy 1999, klipspringers, *Oreotragus oreotragus*: Dunbar 1984, dik-diks, *Madoqua kirkii*:

Brotherton & Manser 1997*)*. Females can, therefore, choose only from a very limited number of currently unmated males.

Moreover, the female's choice of a pair partner may be even more restricted if access to females is mainly regulated via direct male-male competition (gibbons, *Hylobates lar*: Brockelman et al. 1998). In both scenarios many females will gain a lot from EPP with respect to the genetic compatibility or quality (Birkhead 2000) of their mates because many females live in pairs with less than optimal males. Unfortunately, variation in the number of potential pair partners available in a population and the degree of female control over male-male competition during pair formation have been little studied in mammals and their influence on variation in EPP remain to be tested.

Which sex seeks EPCs in fork-marked lemurs was first investigated via indirect evidence from mating season vs. non-mating season comparisons. This evidence is inconclusive with regard to our predictions. Males travelled longer but not further, whereas females travelled further but not longer during the mating season. Both male and female travel distances during the mating season were very long (3.2 km per night) in relation to the average territory size of 5.0 and 4.7 ha for males and females, respectively. Hence, males may not need to increase the distance travelled in order to meet and assess potential mates outside their social unit.

Neither males nor females increased the frequency of encounters with neighbours or the use of peripheral areas of their territory in search for mates. Despite the lack of statistical differences between mating and non-mating season the average proportion of time spent in the periphery of the homerange (26.0-16.9%) complemented by another 6.0-3.7% of time spent outside the MCP borders during the mating season was very high. Similarly, the rate of meetings with neighbours was high (one meeting every 6 hours) throughout the year. Eighty-one out of 91 meetings involved more than just two individuals (mean 4.3 individuals) and in several cases all members of all families whose territories intersected at a given place came together. It is therefore possible that every individual encounters every neighbour once a night, which may be sufficient for both sexes to sample the condition and reproductive status of several potential mates.

Alternatively, female reproductive status and male mate quality may be advertised through long distance communication signals, such as mating calls in females (Semple & McComb 2000) or high-energy loud calls in males (e.g. gibbons: Ramaekers & Ramaekers 1985, Sommer & Reichard 2000). In this case every individual would be informed about

mating opportunities in the vicinity without patrolling the overlapping areas of the home ranges. Female mating calls, although known from other nocturnal lemurs (*Microcebus murinus*: Büsching et al. 1998, *Mirza coquereli*: Stanger et al. 1995), have not yet been described for fork-marked lemurs but would be easy to miss by observers if emitted only on the single fertile day per year. The relationship between male loud call characteristics and male quality has yet to be investigated.

The observation that one female left her territory repeatedly and penetrated deeply into neighbouring territories on three consecutive observation days exclusively in the mating season implies that behavioural strategies to actively seek additional potential mates exist in the repertoire of the species but they may be realised only rarely. Notably the respective female gave birth to extra-pair young twice, although not after the mating season when the excursions were observed, perhaps because she was paired with a low quality or infertile male. Taking into account that the two females that definitely bred during the study period travelled longer, further, more in the periphery, and more outside of the MCP borders, it must be concluded that females take an active part in accomplishing EPCs through increased mobility and active mate search. Male mate guarding seems to be a viable paternity guard (Møller & Birkhead 1991) in this situation.

Does Male Mate Guarding Occur?

Indirect evidence for the occurrence of male mate guarding in fork-marked lemurs comes from the observation that in all pairs the frequency of agonistic encounters increased during the mating season whereas affiliative interactions were more frequent in three but absent in the other three pairs. As a consequence, the affiliative bonds between pair partners were, on average, weaker during the mating season, which may be attributed to the conflict of interest (Lifjeld et al. 1994) between the mate guarding male and the polyandrous female.

During the day males did not closely guard females, as reflected by the lack of increased rates of association at the sleeping site. Pair partners slept in the same tree hole every third day only. While male mate guarding during the night does not necessarily involve close proximity but can effectively be carried out from a distance of 5-10 meters, guarding against the female's interests at the sleeping site is very difficult to accomplish. Because females are dominant in all contexts (Schülke & Kappeler 2003) they can easily expel males from narrow sleeping holes which may explain why the rate of sleeping association did not increase in the mating season.

The observation of close mate guarding in one pair shows that male mate guarding is part of the species' behavioural repertoire. Males can try to fight their rivals off and prevent neighbours from approaching their female partner. It may be argued that mate guarding should only occur while the female pair partner is receptive which was the case in two pairs only. If the male's assessment of his partner's receptivity is only slightly uncertain, however, it will pay him to guard her, irrespective of her true reproductive status. Unfortunately, the degree to which males are informed about female reproductive status appears to vary widely across species (e.g. Heistermann et al. 2001).

The alternative paternity guard to male mate guarding would be frequent copulations with the partner (Møller & Birkhead 1991). Instead of competing for access to the fertile female, males could try to out-compete rivals by frequently inseminating their partner with large numbers of sperm (Parker 1970). Such a situation has been proposed to occur in lar gibbons, *Hylobates lar* (Reichard 1995a), where many EPCs but more within-pair copulations have been observed. The large testes of gibbons relative to other species living in onemale-units, such as gorillas (Harcourt et al. 1981), support this argument (Reichard 1995b). Fork-marked lemurs, however, had small testes like all other pair-living lemurs in our sample. The question why pair-living species such as fork-marked lemurs and *Cheirogaleus medius* have not developed larger testes despite high rates of EPP and thus a high potential for sperm competition needs further study.

Constraints to Mate Guarding

We have shown that female fork-marked lemurs seek EPCs. Apart from insuring fertilization (see example above, Birkhead 2000) an important direct benefit to fork-marked lemur females from polyandrous matings may be the opportunity to obtain 'good genes' (Jennions & Petrie 2000). Fork-marked lemur females are territorial in order to avoid feeding competition (Schülke submitted) and live in stable pairs for several years (Schülke & Kappeler 2003). As a consequence of high mate fidelity the majority of females lives with less than optimal males. Females could compensate this sub-optimal choice by shopping for 'good genes' in their neighbourhood which should result in a moderate EPP rate (Petrie & Kempenaers 1998).

Males, however, try to guard their mates and to limit free female choice (Gowaty 1996, Petrie & Kempenaers 1998). The mate guarding strategy, however, is constrained by several factors (Birkhead & Møller 1992). Firstly, females face only low costs when

searching and assessing potential extra-pair mates (Petrie & Kempenaers 1998). In a fork-marked lemur neighbourhood, territories are densely packed and neighbours meet regularly, a constellation that promotes EPCs (Westneat & Sherman 1997). The mode of between-pair interactions regularly observed in fork-marked lemurs even lowers the search and assessment costs for females. Neighbours meet in areas where typically more than two territories overlap. In these arenas, females that advertise their presence (e.g. by the typical 'kiu' loud call Charles-Dominique & Petter 1980) can attract all males from the intersecting territories and directly compare them. Meetings during the mating season (N = 21) involved more individuals (4.9 vs. 4.1 individuals) and the sex ratio was more male-biased (1.3 vs 1.1 male per female) than during the rest of the year (N = 70).

Secondly, male mate guarding may be more difficult than in many other pair-living primates. Fork-marked lemurs are nocturnal, which enables females to escape and hide from their guards while they are distracted by fighting off rivals.

Thirdly, female resistance has been shown in some animals to regulate male mate guarding efficiency (Jormalainen & Merilaita 1995). Female fork-marked lemurs are dominant over males and female aggression at feeding sites has led to mutual avoidance of pair partners during regular activities (Schülke & Kappeler 2003). Hence, females cannot be physically forced to restrain from EPCs (Brotherton et al. 1997) and punishment of infidelity (Clutton-Brock & Parker 1995, Gowaty 1996) is unlikely to occur, both of which decreases the efficiency of male mate guarding.

Fourthly, highly seasonal reproduction may facilitate free mate choice for females because even if female fertile periods are not perfectly synchronized, highly seasonal reproduction will produce opportunity costs (Grafen 1980) for males. Until their female pair partner has conceived, males cannot be quite sure when she will be in oestrus and thus have to guard her several days or weeks while loosing mating opportunities in the neighbourhood. The degree to which this opportunity cost reduce mate guarding efficiency or effort depends on the oestrous synchronization between females (Emlen & Oring 1977) and on the amount of information males can gain over a female's reproductive status (Reichert et al. 2002). Both factors are under female control and likely to play a role in determining male mate guarding efficiency.

Constrained Mate Guarding and Variation in EPP Among Pair-living Primates

Understanding male mate guarding always involves assumptions about the control of the situation. Studies on mate guarding in birds suggested that female are under perfect control of paternity within and outside pairs (Birkhead & Møller 1993, Davies et al. 1996). The intensity of mate guarding in birds is not significantly related to EPP (Møller & Ninni 1998). The mate guarding event as observed in the fork-marked lemur suggests at first glance that males are under control of their female partner's mating opportunities. But the more control over paternity males get, the stronger will be selection for female counter strategies (Birkhead & Møller 1991) so that the outcome of this ongoing evolutionary arms race will lie somewhere between the extremes of perfect female and perfect male control (Petrie & Kempenaers 1998). That mate guarding is indeed only partly successful in fork-marked lemurs is demonstrated by the paternity data presented above.

This study suggested that not the dispersed social organization per se, i.e. low cohesion between pair partners during regular activities outside the mating season, but other characteristics of dispersed pairs may be responsible for high EPP rates. Guarding of females is much more difficult in nocturnal species and visibility is one of the major factors determining female monopolizability (Rowell 1987, Winkler et al. 1988, Ostner & Kappeler in prep.). The influence of nocturnal activity on mate guarding efficiency and EPP, however, is not testable in primates because all dispersed pairs are nocturnal. This is in contrast to the other two factors influencing mate guarding efficiency, i.e. female dominance and high reproductive synchrony, which chracterize virtually all lemurs. (Pereira 1991, Jolly 1998, Wright 1999, Schülke & Kappeler 2003). The crucial test of the hypothesis that female dominance and seasonal reproduction act on the EPP rates via reduced mate guarding potential could be performed with *Tarsius spectrum* and *Galagoides zanzibaricus,* which live in dispersed pairs but lack strict seasonality in reproduction as well as female dominance (Nash 1983, Gursky 2000c).

ABSTRACT

Variation in extra-pair paternity (EPP) rates among pair-living primates has been attributed to differences in social organization (van Schaik & Kappeler 2003). In species with low spatial cohesion between pair partners, so-called dispersed pairs, a larger percentage of social units resembles groups instead of pairs. It has been proposed that these species did not shift to uniform pair-living because of high EPP rates that forbid the evolution of male

parental care. These high EPP rates are thought to result from constraints to mate guarding. This two step hypothesis was investigated using DNA-microsatellites for paternity analyses, more than 1200 hours of focal animal observations, and testis size measurements of fork-marked lemurs, *Phaner furcifer*, living in dispersed pairs in Kirindy Forest, Madagascar. Four out of seven offspring were most likely sired by extra-pair males. Behaviour during the mating season showed that both females and males take an active part in achieving EPP. Males tried to guard their mates as indicated by direct observation and high rates of intersexual conflict. Significant EPP suggests that mate guarding is relatively inefficient which can be attributed to several factors: 1) Low search and assessment costs for females due to**,** frequent meetings with neighbours, high population density, and possibly long distance advertisement calls, 2) nocturnal activity with low visibility that enables females to escape their guard, 3) female agonistic dominance that constraints male punishment of infidelity, and 4) strictly seasonal reproduction that may facilitate synchronisation of female fertile periods thus increasing male opportunity costs. Thus, high EPP rates in variable dispersed primate pairs can be explained by constraints to mate guarding common to all primates living in variable dispersed pairs.

GENERAL DISCUSSION

Fork-Marked Lemur idiosynchracies

This dissertation provides previously not available data on a little studied species that challenge the view that fork-marked lemur social organisation and parental care are exceptional among lemurs. On the basis of qualitative descriptions of highly co-ordinated movements, close proximity and continuous vocal contact between pair partners (Petter et al. 1971, Charles-Dominique & Petter 1980) fork-marked lemur social organisation was characterised as intermediate between a solitary and a gregarious life style (Charles-Dominique 1978). Chapter one presented the first systematic investigation of spatial relationships between fork-marked lemur pair partners. I compared cohesion in fork-marked lemurs with cohesion in diurnal gibbons and Hanuman langurs, which both live in cohesive social units and found it to be particularly low. Although quantitative reports are lacking, low cohesion, i.e., a *dispersed social organisation*, is thought to be the rule (Bearder 1987, Müller & Thalmann 2000) among nocturnal prosimians living in pairs or groups. Deviations from pair-living have been found at Marosalaza Forest in one of 6 cases (Charles-Dominique & Petter 1980) and in 3 of 21 group years at Kirindy Forest (Chapter one). In conclusion, fork-marked lemur social organisation can no longer be regarded as exceptional and is best classified as variable dispersed pair-living.

Furthermore, the 'pre-gregarious' status of fork-marked lemurs is questioned in Chapter one, because this study revealed that spatial cohesion between members of a social unit is not a step on a route to higher social complexity (Charles-Dominique 1978, see also Crook & Gartlan 1966, Eisenberg et al. 1972), but is better thought of as only one aspect among others that define a species' social organisation (Kappeler & van Schaik 2002). A dispersed social organisation is found not only among basic primates like nocturnal lemurs, but in all primate radiations and geographical regions, i.e. in African and Asian lorises (Bearder 1987), neotropical plathyrrhines (muriquis, *Brachyteles arachnoides*: Strier et al. 1989, spider monkeys, *Ateles geoffroy*: Klein & Klein 1975), and African (chimpanzees, *Pan troglodytes*: Goodall 1968 and bonobos, *Pan paniscus*: Badrian & Badrian 1984) as well as Asian catarrhines (orang-utans, *Pongo pygmaeus*: van Schaik 1999). Phylogenetic analyses reconstructed the last common ancestor of all primates as a nocturnal creature with a dispersed social organisation (Martin 2000, Müller & Thalmann 2000, van Schaik & Kappeler 2003). The evolutionary transition from dispersed to associated social organisation cannot reflect a teleological grade shift towards a more complex organisation type (Charles-Dominique 1978) because it has been reversed in anthropoid primates.

The second trait that characterised the fork-marked lemur's idiosyncratic status was its mode of infant care (Kappeler 1998, Ross 2001). Leaving very young infants unguarded in shelters or hidden in the vegetation is the infant care strategy of all nocturnal lemurs (except *Avahi*), whereas all diurnal primates carry their young with them during travel (except *Varecia*: Pereira et al. 1987). On the basis of interviews with local people, fork-marked lemurs were described to carry their infants clinging to the mother's fur during regular activities after a short initial phase of caching in tree holes (Petter et al. 1971, 1975). My observations do not support this view, however (Schülke 2003). For about the first four weeks after parturition infants were cached in the tree hole in which the mother spent the day. Later, they were parked in the vegetation at variable distance to the tree hole, before they started moving independently at approximately 7 weeks of age (Chapter two). Infants were carried in the mother's mouth from the day shelter to their parking place in the vegetation or between hiding places, but were never observed to actively cling to the mother's fur. Thus, fork-marked lemurs do not deviate with respect to the mode of infant care from the pattern observed in other nocturnal lemurs of the genera *Lepilemur*, *Microcebus*, *Mirza*, and *Cheirogaleus* (Kappeler 1998, Ross 2001).

Other peculiarities of fork-marked lemur biology have been supported by my study. Based on year-round observations of a larger number of individually marked animals it became apparent that fork-marked lemurs are indeed specialised gum feeders (Petter et al. 1971, Hladik et al. 1980) that rely on this resource even during the rainy season when other food (e.g. insects, fruit) is abundant (Chapter two). For a short period of some weeks during the dry season more than 90% of the total feeding time were devoted to the processing and consumption of tree exsudates. This effort is concentrated on a small number of tree species. The importance of these top ten exudate tree species is stressed by the observation that female physical condition varies with the abundance of these trees in the territory (Chapter two). Although found also among primates of South America and Africa, specialization on gum feeding is nevertheless rare among primates. In an extensive review of the diet of 144 primate species, Kappeler and Heymann (1996) found only 9 species whose major food resources included tree exudates, but all species except fork-marked lemurs fed also extensively on fruit and/or insects, yielding a more mixed diet. Thus, the diet of fork-marked lemurs is exceptionally specialised even among exudate feeders.

In line with earlier descriptions (Charles-Dominique & Petter 1980), fork-marked lemurs were found to exhibit female dominance (Chapter one). For the first time, I have shown that female social precedence is unconditional (sensu Kappeler 1993) in a nocturnal lemur in the wild. Finally, earlier reports of the unusual reproductive biology of the fork-marked lemur (Petter et al. 1971) have been supported by this study. Although females have two pairs of mammae, there is no indication that they deliver litters, but they appear to give birth to singletons, which is unusual among the generally litter-bearing Cheirogaleidae (Kappeler 1998).

Several other characters are combined in fork-marked lemurs that differentiate them from the other members of the family Cheirogaleidae. In addition to behavioural traits and physiological adaptations described above, fork-marked lemurs exhibit idiosyncratic morphological adaptations to their exudate based diet (i.e. a prolonged caecum, caninised upper first premolars, exceptionally strong lower incisors, finger and toe nails that resemble claws and a long and tipped tongue: Petter et al. 1971, 1975, Charles-Dominique 1980). Another idiosyncrasy is the large throat gland of adult males (Rumpler & Adriamiandra 1971). Unusual genetic traits include a unique karyotyp with 46 chromosomes instead of 66 in the other Cheirogaleidae (Rumpler 1975), a high number of karyotypic rearrangements (Dutrillaux & Rumpler 1995), and genomic divergence revealed by a unique lack of hybridisation of fork-marked lemur DNA fragments with probes of *Microcebus murinus* DNA (Rumpler et al. 1994). Consequently, the family Cheirogaleidae was divided into two subfamilies, the Phanerinae with fork-marked lemurs being the only species, and the Cheirogaleinae containing all other species of the family (Rumpler & Rakotosamimanana 1971, Rumpler et al. 1994). Based on recent mt-DNA analyses that support the notion that the phylogentic line leading to fork-marked lemurs branched off very early in the evolution of the Cheirogaleid clade, we propose that the taxon is now best recognised as the monotypical family Phaneridae (C. Roos, J. Pastorini, H. Zischler & O. Schülke in prep.).

The Evolution of Fork-Marked Lemur's Social Organisation

The evolution of particular social organisations is often difficult to disentangle from the evolution of mating systems, because benefits derived from a particular mating pattern (e.g. male mate guarding behaviour: Palombit 1999, see below) may pay beyond the mating season and facilitate the evolution of a particular social organisation. If females choose their mates mainly for their absolute genetic quality, i.e. for 'good genes' (Pomiankowski 1988),

male reproductive success will be extremely skewed and it will pay low quality males to persuade single females into monogamy via one of three sets of means (Gowaty 1996): i) Males may help females to increase their survival or the survival of their offspring (although female reproductive success will be reduced by mating with a low quality male). Males may aid females via preventing predation, preventing coercion (including infanticide) by other males or via paternal care. ii) Males may aggressively coerce females into monogamy through forced copulations, punishment of infidelity and aggressive mate guarding. These mechanisms are either neutral or decrease female survival probabilities and diminish female reproductive success even further. iii) Males that are not freely chosen by females may persuade them into mating via resource brokering (sensu Gowaty 1996). If males exhibit some (not necessarily perfect) control over resources limiting female survival and/or reproduction, males may trade these resources (e.g. a territory containing essential nutrients) against mating opportunities.

The evolutionary explanations for the occurrence of monogamous mating outlined above are summarised in the 'constrained female' hypothesis (Gowaty 1996). The degree to which free female choice is constrained by male control over both female behaviour and resources limiting female survival and reproduction determines which mating system will evolve (Gowaty 1996). Although the 'constrained female' hypothesis is an 'origin hypothesis' (cf. Gowaty 1996) and not conceived to explain the maintenance of monogamy and the evolution of pair-living, it summarises and structures all factors that have been proposed to explain the evolution of pair-living in mammals and primates in particular. Seven not mutually exclusive hypotheses (terminology cf. Fuentes 2002) can be distinguished.

Several of these hypotheses can be rejected as explanations for fork-marked lemur social organisation because female fork-marked lemurs are dominant over males in all contexts (Chapter one). The amount of control males can exert over female choice is low in female dominated species because males cannot control female behaviour and males cannot help in several situations ('infanticide prevention', 'body-guard', 'mate guarding' and 'females as a widely dispersed resource' hypothesis). Little constrained female choice results in high variability in male reproductive success and makes pair-living unlikely to evolve. Moreover, male control over essential food resources is largely constrained and makes resource brokering an unlikely path for the evolution of pair-living in fork-marked lemurs ('male defence against resource competition' hypothesis). Another important aspect for the evaluation of these hypotheses is that pair partners live dispersed in fork-marked lemurs

(Chapter one), which precludes several explanations ('infanticide prevention', 'mate guarding', 'male defence against predators' hypothesis). Although most explanations seem to be generally rejected, all hypotheses will be outlined and investigated in more detail for their applicability in the fork-marked lemur below.

Male help persuades females

Four hypotheses propose male help to be the driving factor in the evolution of pair-living. The 'infanticide prevention' hypothesis (van Schaik & Dunbar 1990, van Schaik & Kappeler 1997) proposes that females associate with one protector male to reduce the risk of infanticide by strange or neighbouring males. Infanticide is thought to be an adaptive male strategy to increase individual reproductive success by killing the unrelated dependent young of a female (Hrdy 1979, Hausfater & Hrdy 1984). Following the death of her infant the female should return to receptivity faster and, given that the male still has access to the female, become available as a mating partner sooner than without infanticide (Hanuman langurs, *Semnopithecuis entellus*: Borries et al. 1999a). Males that mated with a female when the dependent offspring was conceived should defend this offspring from infanticide by other males (*S. entellus*: Borries et al. 1999b) because they might have sired the infant. Pair-living will result if females prefer to live separately to avoid food competition (van Schaik & Dunbar 1990).

Short lactation periods relative to gestation length make most nocturnal prosimians little vulnerable to infanticide by males (van Schaik 2000a, b). But fork-marked lemurs are vulnerable to infanticide due to long inter-birth intervals and strong negative group size effects on female fertility (Chapter two). Infant parking (Schülke 2003), however, is a mode of infant care thought to be associated with a low risk of infanticide (van Schaik &Kappeler 1997) because strange or neighbouring males cannot detect the hidden infants or link them to a particular mother. Thus, there is no support for this hypothesis in fork-marked lemurs.

Secondly, the 'body guard' hypothesis (Emlen & Wrege 1986, Smuts & Smuts 1993, Mesnik 1997) extends the threat that selects females to associate with a protector male to all kinds of sexual coercion (Smuts & Smuts 1993) males may inflict upon females. Fork-marked lemur males, however, are not associated with their pair partner (Chapter one) and can, thus, not serve as body guards. Moreover, male coercion is unlikely to be a serious threat, because

males are not larger and females are dominant over males (Chapter one). This hypothesis must therefore also be rejected.

The third hypothesis proposes male help with respect to predator avoidance ('male defence against predators' hypothesis Dunbar 1988, van Schaik & Dunbar 1990). In many primates males are better in repelling predators (van Schaik & van Noordwijk 1989, van Schaik & Hörstermann 1994) and in some species also in detecting predators (Koenig 1998). Subsequently, females gain security and/or can reduce the time they allocate to vigilance and use it for some other activity, e.g. feeding or resting, which should consequently increase their survival and/or reproductive success.

Diurnal raptors hunt fork-marked lemurs during twilight (*Buteo brachypterus* and *Aviceda madagascariensis*: Goodman et al. 1993) or are likely to take their prey from tree holes during the day (*Polyboroides radiatus*: Schülke & Ostner 2001). Rasoloarison et al. (1995) found remains of fork-marked lemurs in the scats of the cathemeral carnivore *Cryptoprocta ferox*. During the night boid snakes may present a threat, as suggested by the observation of mobbing behaviour towards *Sanzinia madagascariensis* (Schülke 2001). Owls are present in Kirindy forest, but predation on fork-marked lemurs has not yet been witnessed. Despite a full set of diurnal and nocturnal predators, association with a protector male is not likely to benefit a female with respect to increased predator detection and defence. Males may inform females of the presence and position of snakes if they detect one (Schülke 2001) and they will provide safety in numbers (Hamilton 1971) when they share a sleeping site with a female (every third day on average: Chapter one). Nevertheless, it seems doubtful that these benefits will outweigh the costs of mating with a low quality male and sharing resources with him.

The last hypothesis to propose male help is the 'male parental care' hypothesis (Kleiman 1977) that assumes that male assistance is inevitable for successful rearing of the young. Some authors (e.g. van Schaik & Dunbar 1990), however, propose that this hypothesis will only explain the maintenance, but not the origin of pair-living because females that depend on male assistance for successful rearing of their young are not likely to evolve before male presence is insured.

Male fork-marked lemurs were never observed to guard their young in the tree hole or at the hiding place, as has been observed in *Cheirogaleus medius* (Fietz 1999a). Males did not

stay close to the young when infants started moving independently, e.g. to protect them from predators. Males may assist in the thermoregulation of the offspring (Gubernick & Terefi 2000) but i) males were never observed to enter the shelter of the young during the night, ii) during the day, the mother was always associated with the young, which should be sufficient to warm a single infant, and iii) the rate of male-infant association at the sleeping site was low and highly variable (6-56%) between males during the first month after birth. For the nocturnal lemur *C. medius* it has been proposed that males provide provisioning of the young through defence of a territory (Müller 1998, 1999a). This seems questionable because female agonistic dominance makes it impossible for males to protect the territory against neighbouring females. Although the crucial test of reduced reproductive success in females without male assistance is pending, the paternal care hypothesis is rejected because evidence for paternal care is lacking.

Males aggressively coerce females

The second set of explanations proposes male aggressive coercion, or at least serious constraints on female mate choice, to drive females to mate with low quality males. Accordingly, pair-living evolved because females are more or less widely dispersed and each male guards one female against all contact with other males ('mate guarding' hypothesis, Brotherton & Manser 1997, Palombit 1999). If single low quality males begin to acquire this strategy, roving males will not gain access to all potential mates and roving will consequently pay less. Extension of mate guarding beyond the period of actual mating activity is thought to benefit the male because neighbouring or roving males will not be able to assess the female's reproductive state (dik-diks, *Madoqua kirkii*: Brotherton & Manser 1997) and females are constrained in their assessment of alternative male mate quality (gibbons, *Hylobates lar*: Palombit 1999).

Several aspects of fork-marked lemur socio-ecology contradict predictions of the hypothesis. First, paternity analyses revealed that mate guarding is very ineffective as indicated by high extra-pair paternity rates (Chapter three). Secondly, assessment of male mate quality and female reproductive status is difficult to constrain by mate guarding, because frequent meetings among neighbours at territory borders and elaborate long distance acoustic communication presumably facilitate mate assessment (Chapter three). Finally the 'mate guarding' hypothesis predicts continuous or near continuous association between pair partners

(Palombit 1999) and/or the potential for males to punish infidelity (Brotherton & Manser 1997); both traits have not been found in fork-marked lemurs (Chapter one).

The 'females as a widely dispersed resource' hypothesis (Emlen & Oring 1977, Wrangham 1980, van Schaik & van Hooff 1983, Rutberg 1983) focuses on constraints to males. It is proposed that females live so widely dispersed that males are unable to defend access to more than one female against other males economically. But even if males could defend an area larger than one female range, males roving over several territories might gain fewer conceptions than a male forming a pair with only one female. The larger the area to control and the shorter female fertile periods, the lower will be the number of females impregnated by a roving male.

For evaluation of the 'females as a widely dispersed resource' hypothesis it is crucial whether home ranges are defendable or not. Home range defendability can be measured from the relation between daily travel distances and home range size, using the defendability indices D (Mitani & Rodman 1979) or M (Lowen & Dunbar 1994). Assuming that territorial species can defend their ranges, whereas non-territorial species cannot, D values larger than 0.98 and M values larger than 0.08 indicate range defendability. Accordingly, fork-marked lemur males travelling 3.7 km per night (Chapter one) could defend an area covering at least six 5 ha female ranges economically (Chapter one). Following van Schaik & Dunbar (1990), even if the fertile periods of females are assumed to last only one day, a male roving over the territories of six females would find and impregnate 1.3 females per day by chance alone, which is more than the one female a staying male will impregnate. The probability to find a fertile female will be higher than chance levels because female range use can be predicted from resource dispersion (Chapter one) and because females can sometimes be localised through their loud calls. Consequently, roving males would impregnate even more than 1.3 females. Thus, neither prediction of the 'females as a widely dispersed resource' hypothesis is supported in fork-marked lemurs.

Male resource brokering persuades females

The last pathway to pair-living which applies to many birds is through resource brokering and defence of a territory and the resources therein ('defence against resource competition' hypothesis, Wrangham 1979, Thalmann 2001, for fork-marked lemurs: Charles-Dominique & Petter 1980). The resource to defend is not necessarily food, but could be a

nesting site (Holm 1973) or a burrow instead (Linsenmair & Linsenmair 1971). If males primarily defend the resources, pairs should result as long as single males are not able to defend enough resources to feed two females ('polygyny threshold' model Orians 1969).

Fork-marked lemur males, however, cannot provide access to resources in exchange for mating privileges because they cannot defend a territory against neighbouring dominant females (Chapter one). One-male–multi-female groups have been observed in both fork-marked lemur studies (Chapter one, Charles-Dominique & Petter 1980), indicating that a polygyny threshold exists. The largest territory with the highest resource abundance at Kirindy, however, was inhabited by a multi-male–one-female group, which cannot be reconciled with the 'defence against resource competition' hypothesis.

Thalmann (2001) proposed a slightly different version of this hypothesis, postulating repetitive feeding itineraries as a constraint to male ranging abilities in *Avahi occidentalis*. This makes the hypothesis relevant for fork-marked lemurs with their highly repetitive exploitation of exudate trees (Chapter one & two). Ranging is thought to be constrained by the amount of knowledge an individual can gain of the distribution of crucial resources. It seems inconclusive, however, why a male that frequently uses two female ranges should not gain enough knowledge to range over an area twice as large and return to each resource half as often. Moreover, Thalmann's (2001) analysis is flawed and still unsupported because he contrasted the food characteristics of *Avahi* with those of *Lepilemur edwardsi. L. edwardsi*, however, depends on more evenly distributed abundant resources that are not used repetitively. Nevertheless, they also live in pairs which contradicts a basic assumption of this hypothesis. Altogether, the 'defence against resource competition' hypothesis is therefore not supported in fork-marked lemurs.

Conclusions

The lack of a priori support for any current hypothesis leaves us with no convincing explanation for the evolution of pair-living in fork-marked lemurs. It remains elusive why a female of a female-dominated species without paternal care should allow a male to share a territory with her. In Chapter two, it has been shown that female range exclusivity with regard to same-sexed individuals most likely results from strong within-group feeding competition that prevails in fork-marked lemur families. This finding supports the view that female range exclusivity is a precursor for the evolution of pairs from solitary ancestors (Komers & Brotherton 1997, van Schaik & Kappeler 2003). Strong within-group contest competition for

a limited number of food resources explains why females are not permanently associated with a male and why the two nevertheless meet more often than expected by chance (Chapter one & two). It can be argued that whatever the female may gain from high cohesion with regard to predator avoidance or prevention of sexual coercion will be overcompensated by the extreme costs of direct food competition.

Fork-marked lemurs, however, do not only contest for food, they also scramble within families (Chapter two). Female physical condition has been demonstrated to be strongly affected by family size, with females living in larger groups being in worse physical condition than females living in smaller families. This means that pair formation imposes inevitable energetic costs upon females, even if cohesion is low and direct competition avoided. Because the decision of males and females to associate in pairs involves cost-benefit analyses in both parts, variation in the costs of feeding competition is very likely to affect the final outcome, i.e. whether pairs form or not. Taking into account that the benefits of pair-living to males and females are not obvious and potentially very small, it could be argued that pairs form nevertheless because the costs are low. Unfortunately, the costs of pair-living accruing from increased food competition have never been investigated in any primate. Although few of the hypotheses for the evolution of pair-living deny these costs, they cannot be compared between species. From comparison with diurnal primate species varying in competition effects (longtailed macaques, *Macaca fascicularis*: van Schaik & van Noordwijk 1988, Thomas langurs, *Presbytis thomasi*: Sterck 1995, Hanuman langurs, *Semnopithecus entellus*: Koenig 2000) it seems unlikely, however, that fork-marked lemurs present a case of particularly low food competition effects. For the time being, it therefore remains elusive why female-dominated fork-marked lemurs live in variable dispersed pairs with high extra-pair paternity and strong within group scramble and contest competition for food.

SUMMARY

Cohesiveness between members of a social unit is a defining characteristic of animal social organization. Dispersed social organizations, where members of a social unit spend the main part of their activity period apart, have only recently been distinguished from cohesive social organizations and are still poorly understood with respect to their ecological basis and reproductive consequences. The general goal of this dissertation was to study the three components of the social system of fork-marked lemurs (*Phaner furcifer*), a small nocturnal primate from Madagascar living in dispersed pairs. First, I characterise their social organization, focusing on behavioural mechanisms of cohesion between pair partners. Second, through application of van Schaik's ecological model, I investigate predictions about the ecological basis of female intra-sexual avoidance, male-female social relationships and the determinants of differential female reproductive success. Finally, I analyse behavioural and genetic aspects of the mating system to test a recent hypothesis that proposes high extra-pair paternity in dispersed primate pairs resulting from constraints on male mate guarding.

The study was conducted in Kirindy Forest in Madagascar between September 1998 and April 2001 during three field seasons for a total of 20 months. During more than 1400 hours of focal animal protocols, I sampled year-round data on space use, feeding ecology, time budgets, and social behaviour of all adults and three subadults of 8 families, complemented by simultaneous focal follows of both pair partners, year-round information on sleeping site use, measures on food abundance in each territory, morphological measurements, and DNA-microsatellite data for seven newly discovered polymorphic loci.

Across eight social units and three breeding seasons, pairs were the prevailing grouping pattern (18 of 21 family years). Most pairs were stable for more than three mating seasons and used well defined stable territories. Although both pair partners used the same territory in a fairly similar fashion, average distance between pair partners was 100m, which was far considering that many territories measure only 200m in diameter. Pair partners spent only about 20% of activity time in less than 25m distance of each other and shared a sleeping site on average only every third day. Females were found to be dominant over their partner as well as over neighbouring males in all behavioural contexts. Most important food resources were exudates of a small number of tree species. Major food resources were distributed in small, defendable patches characterized by fast depletion and rapid renewal. In accordance with the ecological model, this led to strong within-group contest and scramble competition and weak between-group contest competition over food, as indicated by a positive dominance effect and a negative group size effect on female physical condition. Female reproductive

success was determined mainly by family size. Paternity likelihood and exclusion analyses revealed that four out of seven offspring were most likely sired by an extra-pair male. Behaviour during the mating season implied that females as well as males take an active part in obtaining extra-pair copulations and that males try to guard their mates. Dispersed social organization in itself, i.e. low cohesion between pair partners, cannot explain high extra-pair paternity. I propose instead that several other factors common to most primates living in dispersed pairs constrain mate guarding and lead to high EPP.

The ecological settings determine the mode of food competition and have shaped the social system of fork-marked lemurs in several ways. Intense within-group competition for food may have ultimately led to female intra-sexual avoidance and range exclusivity which represents an evolutionary precursor of pair-living. Although it remains elusive why females ultimately associated with single males, patterns of within-group contest competition for food explain why pair partners avoid each other during nocturnal activity. The limited number of food resources that is used in repetitive fashion and incomplete knowledge about the pair partners position explain why pair partners meet relatively often and why most encounters involve agonistic conflict. Rigid feeding itineraries characteristic of exudate feeders are likely to pose high costs to offspring dispersing to unfamiliar areas. Feeding ecology can, therefore, explain why parents tolerate delayed natal dispersal despite a negative effect on actual female reproductive success. In conclusion, the present study successfully applied existing socio-ecological theory to a new area of research, refined a recent evolutionary model and contributed important comparative data to our understanding of dispersed pairs in particular and primate and animal societies in general.

ZUSAMMENFASSUNG

Die Kohäsion zwischen Mitgliedern einer sozialen Einheit ist ein definierendes Charakteristikum der sozialen Organisation von Tieren. Disperse soziale Organisation, in der die Mitglieder einer sozialen Einheit den Großteil ihrer Aktivitätszeit allein verbringen, wurde erst kürzlich von kohäsiven sozialen Organisationsformern unterschieden und ist bisher im Hinblick auf ihre ökologische Basis und die reproduktiven Konsequenzen wenig verstanden. Das generelle Ziel der vorliegenden Arbeit war die Untersuchung der drei Komponenten des Sozialsystems des Gabelstreifenmakis (*Phaner furcifer*), eines kleinen, nachtaktiven Primaten aus Madagaskar, der in disperser sozialer Organisation lebt. Zuerst charakterisiere ich die soziale Organisation mit Fokus auf den Verhaltensmechanismen der Kohäsion zwischen Paarpartnern. Im zweiten Teil untersuche ich Vorhersagen über die ökologischen Grundlagen der Meidung unter Weibchen, der sozialen Beziehungen zwischen Männchen und Weibchen und der Determinanten des differenziellen Reproduktionserfolges der Weibchen. Zuletzt analysiere ich Verhaltens- und genetische Aspekte des Paarungs-systems. Damit wird eine neuere Hypothese getestet, die für disperse Paare eine hohe Rate von Vaterschaften außerhalb des Paares vorhersagt, welche auf Einschränkungen der Partner-bewachung zurückzuführen seien. Die Studie wurde zwischen September 1998 und April 2001 während dreier Feldaufenthalte von insgesamt 20 Monaten im Kirindy Wald in Madagasakar durchgeführt. In mehr als 1400 Stunden Fokustierprotokollen sammelte ich Informationen zur Raumnutzung, Nahrungsökologie, Zeitbudget und Sozialverhalten von allen Adulten und drei Subadulten aus 8 Familien im Jahresverlauf. Diese wurden durch simultane Beobachtung beider Paarpartner, Registrierung der Schlafbaumnutzung im Jahres-verlauf, Messungen der Nahrungsverfügbarkeit im Territorium, morphologische Messungen und DNS-Mikrosatelliten Daten von sieben neu beschriebenen polymorphen Loci ergänzt. Über acht soziale Einheiten und drei Fortpflanzungszeiten hinweg waren Paare die vorherr-schende Gruppenstruktur (18 von 21 Familien-Jahren). Die meisten Paare waren über mehr als drei Paarunsgzeiten hinweg stabil und nutzten wohl definierte Territorien. Obwohl beide Paarpartner dieselben Territorien in sehr ähnlicher Weise nutzten, war der mittlere Abstand zwischen ihnen mit 100m, was etwa einem halben Territoriumsdurchmesser entspricht, sehr groß. Paarpartner verbrachten etwa 20% ihrer Aktivitätszeit in weniger als 25m Distanz zueinander und verbrachten etwa jeden dritten Tag in derselben Schlafhöhle. Weibchen waren in allen Verhaltenskontexten über alle Männchen dominant. Die Hauptnahrung waren Exsudate von einigen wenigen Baumarten. Die wichtigsten Ressourcen waren in kleinen, verteidigbaren Einheiten verteilt, die sich durch schnelle Erschöpfung und hohe Regenera-tionsrate auszeichneten.

Entsprechend den Erwartungen des ökologischen Modells führte dies zu starker direkter und indirekter Konkurrenz innerhalb von Gruppen und zu schwacher direkter Konkurrenz zwischen Gruppen, was sich aus positiven Dominanz- und negativen Gruppengrößeneffekten auf die physische Kondition von Weibchen ablesen ließ. Weiblicher Reproduktionserfolg wurde hauptsächlich durch die Familiengröße bestimmt. Vaterschafts-ausschluß und Vaterschaftswahrscheinlichkeitsanalysen zeigten, daß vier von sieben Jung-tieren wahrscheinlich nicht von ihren sozialen Vätern gezeugt wurden. Das Verhalten während der Paarungszeit deutete darauf hin, daß sowohl Männchen als auch Weibchen eine aktive Rolle beim Zustandekommen von Paarungen außerhalb des Paares spielen, und daß Männchen versuchen ihre Partnerinnen zu bewachen. Disperse soziale Organsition an sich, also die geringe Kohäsion zwischen Paarpartnern, kann die hohe Rate von Vaterschaften außerhalb des Paarbundes nicht erklären. Ich schlage statt dessen einige Faktoren vor, die den meisten Primaten gemein sind, die in dispersen Paaren leben und die die Partnerbewachung erschweren und somit die Vaterschaften außerhalb des Paarbundes erklären können. Die ökologischen Gegebenheiten beeinflussen den Modus der Nahrungskonkurrenz und haben das Sozialsystem des Gabelstreifenmakis in mehrfacher Hinsicht geformt. Intensive Konkurrenz innerhalb von Gruppen könnten ultimat zur Meidung unter Weibchen und exklusiven Streifgebieten geführt haben, was einen evolutionären Vorläufer für das Paarleben darstellt. Obwohl es ungeklärt bleiben muß, warum sich Weibchen ursprünglich mit einem Männchen zusammenschlossen, so können doch die Muster der Konkurrenz innerhalb vor Gruppen erklären, warum Paarpartner während nächtlicher Aktivität Nähe meiden. Die begrenzte Zahl von Nahrungsressourcen und deren wiederholte Nutzung, sowie unvollständige Information über den Aufenthaltsort des Paarpartners, können erklären, warum Paarpartner sich relativ häufig treffen und warum die meisten Begegnungen zu agonistischen Auseinandersetzungen führen. Nachwuchs, der in unbekannte Areale auswandert, muß wahrscheinlich hohe Kosten in Kauf nehmen, weil Exsudatkonsumenten typischerweise ein sehr strenges Nutzungsmuster von Nahrungsressourcen aufweisen. Die Nahrungsökologie kann also erklären, warum Elterntiere ihren erwachsenen Nachwuchs im Territorium dulden, obwohl dies einen negativen Effekt auf den aktuellen Reproduktionserfolg der Weibchen hat. Zusammenfassend konnten mit dieser Arbeit existierende sozioökologische Theorien auf ein neues Forschungsgebiet angewandt, ein neueres evolutionäres Modell verfeinert und wichtige Vergleichsdaten für unser Verständnis von dispersen Paaren im besonderen und den Sozialsystemen von Primaten und Tieren im allgemeinen beigesteuert werden.

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