Male Reproductive Strategies in Verreaux's Sifaka

(*Propithecus verreauxi*)

Dissertation

zur Erlangung des Doktorgrades

der mathematisch-naturwissenschaftlichen Fakultäten

der Georg-August-Universität zu Göttingen

vorgelegt von

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Göttingen 2009

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Tag der mündlichen Prüfung:

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GENERAL INTRODUCTION

Sexual selection and male reproductive strategies

Studying the reproductive strategies employed by both male and female individuals within the framework of sexual selection theory has played a key role in our understanding of the evolution of animal social systems (Kappeler and van Schaik 2002). As sexual selection acts differently on the two sexes due to differences in potential reproductive rates (Clutton-Brock and Parker 1992), males and females pursue different strategies in order to maximize their lifetime reproductive fitness (Trivers 1972) which can lead to intersexual conflict (Parker 1979). Ultimately, the different reproductive strategies and counter-strategies of the sexes and the resulting partition of reproduction or reproductive skew within each sex, can have important ramifications for the mating system, social organization and social structure of a species (Clutton-Brock 1989b; Kappeler and van Schaik 2002).

An important step in deciphering the ultimate factors shaping animal behavior, and thus individual reproductive strategies, is to understand how ecological variables influence behavior, which has led to the development of the socioecological model. As males and females invest differently in both gamete production and infant care, their lifetime reproductive success is limited by fundamentally different factors (Trivers 1972; Emlen and Oring 1977; Clutton-Brock and Parker 1992). Environmental risks and resources set mammalian female strategies as female reproductive success is limited by the costs of internal gestation and lactation (Williams 1966; Trivers 1972). A male's reproductive success, on the other hand, is mainly limited by their access to receptive

females leading to competition with other males for available mates (Bateman 1948; Trivers 1972). The spatiotemporal distribution of females structures options for males to monopolize fertilizations via competition for receptive females and is thus the primary determinant of male sexual strategies (Emlen and Oring 1977; Wrangham 1979; Altmann 1990; van Schaik and Kappeler 2003).

Where females form groups, they become a resource that can potentially be defended by a single male. Under this scenario, contest competition between males for access to and monopolization of receptive females is predicted and generally leads to sexual dimorphism within the species, as traits that improve or advertise fighting ability are selected for (reviewed in Kappeler 2000a; Plavcan 2001). In species where small groups of females can be monopolized by a single male, sexual dimorphism is most pronounced and reproduction is highly skewed in favor of individuals with high competitive ability (Jarman 1983; Ims 1988; Plavcan 2001).

If complete monopolization of a group of females is not possible due to an increase in the absolute number of fertile females and/or an increase in their temporal overlap (Altmann 1990; Mitani et al. 1996a; Nunn 1999; Kappeler 2000a), the variance in male reproductive success is predicted to decrease as the ability for one male to monopolize all fertile females within the group and exclude rival males from group membership is greatly reduced, leading to the formation of multi-male groups (Ims 1988; van Schaik and Janson 2000). Although dominant individuals may still have priority of access to receptive females (Altmann 1962; Alberts et al. 2003), less competitive males may exploit the fact that dominant individuals are involved in mating elsewhere and secure matings for themselves (Ims 1988). Dominant males may also attempt to increase their relative reproductive success by excluding rival males from mating using

more indirect mechanisms of reproductive competition such as the behavioral and/or physiological suppression of reproduction in subordinate individuals via the use of olfactory, visual and auditory signals and/or pre- and post-copulatory mate-guarding (reviewed in Setchell and Kappeler 2003).

Subordinate males, on the other hand, are not silent bystanders to their reproductive fates and several alternative tactics used by subordinates have been documented that can reduce reproductive skew in favor of dominant individuals. Males of highly sexually dimorphic species may prolong growth and delay maturation as a means to reduce the risk of targeted aggression by conspecific males while attempting to secure low-risk sneaky copulations (Alberts and Altmann 1995b; Setchell and Kappeler 2003). Subordinate males may also form coalitions with other individuals of similar rank to force a dominant male to give up access to a receptive female (Packer 1977; Noe and Sluijter 1990; Setchell and Kappeler 2003). Finally, individuals may transfer into a group with more favorable chances of reproduction (Alberts and Altmann 1995a; van Noordwijk and van Schaik 2001). Thus dispersal decisions should also be considered as male reproductive strategies in species where females are philopatric and may be a proximate determinant of group composition (Kappeler 2000a).

Moreover, female reproductive strategies can also work in favor of subordinate males as females aim to bias and confuse paternity via mating with multiple males. Thus, female strategies, may decrease male monopolization ability which, in turn, may decrease male reproductive skew (reviewed in Setchell and Kappeler 2003). Therefore, female strategies may also affect both group composition and male reproductive success and, thus, need to be considered.

Intersexual conflict

Whether species form single-male or multi-male groups depends on both the absolute number and temporal distribution of resident females and reflects the outcome of male contest competition for mates and female counter-strategies (Altmann 1990; Mitani et al. 1996a; Kappeler 1999; Nunn 1999). Although males should prefer to live in single-male groups, where reproduction can be monopolized more easily than in multi-male groups (Kappeler 1999), group living females should prefer to live with multiple males due to certain ecological and social benefits than can be derived from living with many males, leading to sexual conflict over group composition (Hamilton 2000).

Males of some species are better at detecting and repelling predators (van Schaik and van Noordwijk 1989; Baldellou and Henzi 1992) thus decreasing the overall predation risk (van Schaik and Hörstermann 1994). Females may also benefit from decreased infanticide risk if several males jointly defend the group against takeover by infanticidal conspecifics. Several studies have shown that infanticide risk is indeed lower in multi-male groups as they are less likely to be taken over than single-male groups (Newton 1986; Robbins 1995; Koenig et al. 1998; Ostner and Kappeler 2004). Finally, female mate choice, and the opportunity for polyandrous mating as a means to confuse paternity, increases in multi-male groups. Paternity confusion may be important in species where infanticide is a sexually selected male reproductive strategy as males generally only kill infants when there is no ambiguity about their paternity. Thus, if females increase uncertainty about paternity by mating with several males, they may reduce the risk of infanticide (reviewed in Setchell and Kappeler 2003).

Females have developed several reproductive counter-strategies that decrease male monopolization ability such as receptive synchrony and lengthened receptive

periods (reviewed in Setchell and Kappeler 2003). These mechanisms limit a single male's ability to monopolize each female as she becomes receptive. In addition, unpredictable ovulation and post-conception mating may also be used by females in order to confuse paternity and decrease infanticide risk (reviewed in Setchell and Kappeler 2003). Thus, female strategies are aimed at increasing mate choice and the number of mating partners while male strategies focus on monopolization of receptive females, leading to conflict between the sexes. Male and female strategies operate on both the demographic and behavioral level as each sex struggles to control group composition and mating skew. In general, the social organization of a species must be seen as the outcome of male reproductive strategies and female counter-strategies as individuals of each sex attempts to maximize their lifetime reproductive success.

Lemur idiosyncrasies

The extant lemurs of Madagascar are the result of a single colonization event that occurred more than 50 million years ago and the subsequent spectacular adaptive radiation to fill many unoccupied ecological niches (Purvis 1995; Yoder et al. 1996). Lemurs evolved in total isolation from other primate species and deviate from predictions derived from the theoretical framework of sexual selection theory in several behavioral, demographic and morphological traits that are supported in anthropoid primates. This set of traits is collectively referred to as the "lemur syndrome" (Kappeler and Schäffler 2008). Despite the fact that many gregarious lemur species form relatively small groups with low numbers of females (Kappeler and Heymann 1996), the socionomic sex ratio tends to be even or male-biased (Kappeler 2000a; Pochron and Wright 2003). This pattern deviates markedly from what has been found for most

anthropoids where groups of up to six female individuals are generally monopolized by a single male (Andelman 1986; Mitani et al. 1996a; Nunn 1999). The tendency toward an even adult sex ratio despite small female group size implies strong intrasexual competition for mates yet sexual dimorphism in body size is not selected for (Kappeler 1990; Kappeler 1991; Kappeler 2000a; Pochron and Wright 2003). This suggests that lemur males may be resorting to alternative reproductive strategies, other than overt aggression, that enable them to monopolize paternities that de-emphasize fighting ability, and thus, relax selection on body size and weaponry. Additionally, in most primate species, adult males dominate females in dyadic interactions but among the lemurs, adult females tend to dominant males (Richard 1987; Kappeler and van Schaik 2002). The phenomenon of female dominance in lemurs may have important consequences for male reproductive strategies as female choice may override male dominance relations to determine male reproductive success (Pereira and Weiss 1991), especially if females are able to control mating opportunities or group membership (Sauther and Sussman 1993; Brockman 1999).

I studied male reproductive strategies in Verreaux's sifaka (*Propithecus verreuaxi*) in order to provide a better understanding of the mechanisms behind the unusual social organization characteristic of many gregarious lemur species. Sifakas are an ideal modal species as they exhibit all of the idiosyncratic demographic, behavioral and morphological lemur traits. Although sifakas live in small groups (2-13 individuals) where there are typically 1-3 adult females (Richard et al. 2002), males do not monopolize access to these small groups resulting in the tendency toward an even or male-biased sex ratio in group composition (Richard 1985; Lewis and van Schaik 2007; Kappeler and Schäffler 2008). Moreover, despite highly seasonal reproduction

(Brockman 1994; Brockman and Whitten 1996; Brockman 1999) and the presence of multiple males within a group, reproduction is highly skewed in favor of dominant individuals as dominant males sire almost all offspring (> 90%) (Kappeler and Schäffler 2008). Sifakas are also sexually monomorphic although intrasexual competition for mates is intense (Kappeler 1990; Richard 1992). Finally, females in this species are dominant to males (Richard 1987).

The main objective of this thesis was to illuminate the various male reproductive strategies in sifakas in light of the "lemur syndrome" (Kappeler and Schäffler 2008). More specifically, I studied (1) the mechanisms behind high reproductive skew in favor of dominant males, (2) whether dominant males and/or females benefit from the presence of supernumerary males within social groups, and (3) the reproductive strategies of subordinate males in relation to dispersal decisions.

Contents of the thesis

Given the tendency toward even or male-biased sex ratios in sifaka social organization, and especially since reproduction is extremely seasonal, the high reproductive skew in favor of dominant males (Kappeler and Schäffler 2008) is indeed surprising. In **chapter 1**, I examine the mechanisms behind the ability of dominant males to monopolize paternities (Kappeler and Schäffler 2008). Here I use non-invasive endocrine measurements to estimate the timing of ovulation and then analyze the degree of reproductive synchrony among co-resident females. I test the hypothesis that if females come into estrous asynchronously, male monopolization potential increases (Nunn 1999) and dominant males may then be able to monopolize each female as she becomes receptive via mate-guarding. In order for a male to mate-guard effectively,

information on the reproductive state of the female is necessary in order to minimize the costs of engaging in this behavior such as decreased foraging efficiency and increased levels of aggression with co-resident rival males (Bercovitch 1983; Alberts et al. 1996). As olfactory cues may be of relatively more importance in lemur species due to their retention of olfactory complexity (Schilling 1979), I examined male olfactory behavior to test the hypothesis that males are able to pick up olfactory cues as to the timing of female receptivity.

The fact that dominant males monopolize groups of females on the reproductive level but not on the demographic level begs the question of why subordinate males are tolerated within the group. In **chapter 2** I focus on possible costs and benefits associated with the presence of supernumerary males within sifaka social groups. I examine this question from both the dominant male and resident female perspective since females may play an active role in regulating group composition due to their dominant status (Richard 1987; Lewis 2008). In order to assess possible costs and benefits, I analyzed whether groups with a higher number of males had increased group productivity measured as infant survival. As infanticide has been reported for this species (Brockman and Whitten 1996; Lewis et al. 2003), I also tested wither the presence of extra males within the group decreases the risk of group takeover by extra-group males. Finally, as intergroup dominance is usually a function of group size and the number and fighting ability of adult males (Wrangham 1980; Robinson 1988), I examined whether groups with more males had a greater advantage in securing access to resources that are contested between groups. Overall, my aim was to determine whether these potential benefits outweighed the costs of increased intragroup feeding competition and intrasexual aggression (van Schaik and van Hooff 1983; Pulliam and

Caraco 1984; Janson 1988; Kappeler 1999) as a possible explanation for the presence of supernumerary males within sifaka social groups, and hence, the tendency towards even or male-biased sex ratios in group composition.

As male dispersal decisions can also influence the socionomic sex ratio of social groups and have significant consequences for individual reproductive success (Greenwood 1980; Pusey and Packer 1987; Clobert et al. 2001), in **chapter 3**, I examined the potential benefits of two subordinate male dispersal strategies; delaying dispersal to remain longer in the natal group (Kokko and Ekman 2002) and queuing as a non-breeding subordinate male in a non-natal group with the future possibility of eventually inheriting the group (Kokko and Johnstone 1999). As analysis of over 15 years of demography data revealed that older males are more successful in taking over groups (Kappeler and Mass, in prep), and thus becoming the sole breeding male member of a group, delaying dispersal, and reaping the benefits of using the natal group as a safe haven (Kokko and Ekman 2002), may indeed be a viable reproductive tactic in this species.

The questions addressed in the various chapters of this thesis aim to uncover the mechanisms behind the unusual socionomic sex ratio that characterize lemurs. By examining both dominant and subordinate male reproductive strategies and their effect on the social system, I hope to gain a better understanding of the evolution of the idiosyncratic behavioral, demographic and morphological traits unique to gregarious lemurs and provide an explanation for why these traits deviate from the predictions laid out within the framework of sexual selection theory.

Chapter 1:

Mate-guarding as a male reproductive tactic in *Propithecus verreauxi*

with P.M. Kappeler & M. Heistermann

Abstract

Sexual selection theory predicts that in group-living mammals, male reproductive tactics can lead to high reproductive skew in favor of dominant individuals. In sifakas (*Propithecus verreauxi*), a group-living primate with extremely seasonal reproduction, male reproductive success is highly skewed because dominant males sire almost all offspring despite a tendency toward an even adult group sex ratio. To understand the underlying behavioral mechanism resulting in this rank-related reproductive skew in male sifakas, we studied mate-guarding as a potential reproductive tactic. Behavioral observations of dominant males and adult females in combination with hormonal determination of timing of female receptivity in 9 groups at Kirindy Forest revealed that dominant males spent more time in proximity to females when they were receptive and were responsible for the maintenance of this proximity. Results also indicated that monopolization of receptive females was facilitated by both estrous asynchrony within groups and by the ability of dominant males to obtain olfactory cues as to the timing of female receptivity. Although dominant males engaging in mate-guarding are expected to experience various costs, there was no evidence for decreased foraging behavior and only a trend toward increased aggression between dominant and subordinate non-natal males within groups. Our results are in accordance with the hypothesis that dominant males use mate-guarding to monopolize receptive females and that it is one proximate mechanism that contributes to the high reproductive skew observed within the population of male sifakas at Kirindy.

Key words: Reproductive skew; male reproductive tactics, mate-guarding, *Propithecus verreauxi*

Introduction

The mating system of a given species is shaped by the reproductive strategies of males and females (Clutton-Brock 1989b), which in turn, reflect their respective potential rates of reproduction (Clutton-Brock and Vincent 1991). By mating with many females, males can typically increase the number of offspring that they produce. Thus, males are limited in their reproductive success by their access to and monopolization of receptive females (Bateman 1948; Trivers 1972).

An important factor influencing male monopolization ability is the spatial and temporal distribution of fertile females (Emlen and Oring 1977; Ims 1988). According to socioecological theory, where females are clumped in space, males will try to monopolize access to the group of females while at the same time trying to exclude rival males from group membership. Similarly, if the temporal distribution of receptive females is even, a male will try to monopolize each female as they become receptive. As both female group size and/or estrous synchrony increases, a male's ability to monopolize the group decreases. Thus, one of the primary determinants of whether species form single-male or multi-male groups is the number and temporal distribution of resident females (Emlen and Oring 1977; Clutton-Brock 1989b; Altmann 1990; Mitani et al. 1996a; Kappeler 1999; Nunn 1999; but see Kutsukake and Nunn 2006).

Where groups of females can potentially be monopolized by one male, contest competition between males is predicted (Clutton-Brock et al. 1977). This form of competition for access to mates can lead to the evolution of traits that improve or advertise fighting ability, such as large size and weaponry, and can result in sexual dimorphism (Plavcan 1999). Sexual dimorphism is most marked in strongly polygynous species because only a small proportion of the males in the population reproduce, and

thus, intense competition between males for access to receptive females is expected (Clutton-Brock et al. 1977; Andersson 1994; Mitani et al. 1996b; Plavcan 2001). This pattern is supported in male cercopithecoids (Plavcan and van Schaik 1997) but not in lemurs (Kappeler 1990; Kappeler 1991), even though male intrasexual competition for mates is intense.

Individual males can also increase their relative reproductive success by excluding rivals from mating (Andersson 1994; Plavcan 2001) via more indirect mechanisms of reproductive competition, such as physiological suppression or mate-guarding, or both. Huck et al. (2004) defined mate-guarding as "preventing a receptive female from copulating with other males by maintaining close proximity, and it implies that the behavior is instigated by the male" (p. 40). Although it is not the prevailing male reproductive tactic in primates (Alberts et al. 1996), mate-guarding occurs in a number of species, including moustached tamarins (Huck et al. 2004), long-tailed macaques (Engelhardt et al. 2006), and chimpanzees (Tutin 1979). Researchers have reported temporary mate-guarding in gray mouse lemurs (Eberle and Kappeler 2004) and pre- and post-copulatory mate-guarding in ringtailed lemurs (Sauther 1991; Parga 2003).

Although mate-guarding may increase a male's ability to monopolize access to a receptive female, the behavior may also incur costs. Aside from the increased risk of injury due to incursions with competing males, mate-guarding can lead to both an increase in energy expended and a decrease in energy consumed (restraints on foraging duration and foraging bout length) because mate-guarding requires active monitoring and following of a partner's movements (Bercovitch 1983; Alberts et al. 1996). In addition, mate-guarding may also carry physiological costs, such as increased glucocorticoid output as suggested from a study on sifakas (*Propithecus verreauxi*)

(Fichtel et al. 2007). Thus, males are expected to engage in this costly behavior only when a female is most likely to be fertile and receptive, and therefore, the ability to ascertain accurately when a female is in this reproductive stage is crucial (Alberts et al. 1996).

There are several cues that may serve as indicators of female reproductive status, including pheromones (Michael and Keverne 1968), sexual swellings (Setchell and Wickings 2004; Brauch et al. 2007), copulation calls (Semple 1998; van Schaik et al. 2004), and female sexual behavior (Aujard et al. 1998; Zehr et al. 2000; Engelhardt et al. 2005). Olfactory cues may be relatively more important in lemur species because they have often retained olfactory complexity, and the exchange of chemical signals plays an important role in communication (Schilling 1979). Thus, pheromones from urine, anogenital glands, and vaginal discharge may be a chemical signal communicating information about female reproductive status to both intragroup males and to extragroup males (Harrington 1974).

We studied male reproductive strategies in Verreaux's sifakas (*Propithecus verreauxi*) in an attempt to illuminate the proximate mechanism underlying male reproductive skew. Sifakas are arboreal lemurs that live in multi-male multi-female groups comprising 2–13 individuals (Richard et al. 1993) with variable adult sex ratios (Richard 1985). Female dominance and female philopatry are the norm, although females have occasionally been observed to disperse (Jolly 1966; Richard 1987; Richard et al. 1993; Kubzdela 1997; Richard et al. 2002). Females become receptive once per year (Brockman 1994; Brockman and Whitten 1996) for a period of ≤96 h (Brockman 1999) during a short mating season from January until March. Although the number of reproducing females within a group is small (1–3 individuals) (see also

Kubzdela 1997; Richard et al. 2002; Lewis 2005), dominant males do not exclude rival males from group membership, resulting in a tendency toward an even adult sex ratio. Despite the presence of multiple males within groups, according to genetic paternity analysis, reproduction in the Kirindy Forest population is highly skewed in favor of dominant individuals with dominant males siring almost all offspring (91% of 33 infants; Kappeler and Schäffler, 2008). In contrast, paternity analysis results for a population of *Propithecus verreauxi* at Beza Mahafaly revealed that extragroup fertilizations occur more frequently (Lawler 2007). Thus, although dominant males at Kirindy do not exclude rivals from group membership, they are somehow able to exclude both within and extra-group males from reproduction.

Although (Brockman 1999; Lewis and van Schaik 2007) described mate-guarding in sifakas, here we attempt to quantify this behavior for the first time. To determine whether dominant males use mate-guarding as a proximate mechanism to exclude rival males from reproduction, we tested the predictions that 1) females are receptive asynchronously within groups; 2) males increase their olfactory behavior when females are receptive; 3) dyads consisting of a female and the dominant male spend more time in proximity during the receptive period than in the mating season but there is no change in proximity between natal or non-natal subordinate males and females; 4) dominant males are responsible for both the initiation and maintenance of proximity with females; 5) in relation to the costs associated with mate-guarding, an increase in dominant male aggression rate toward rival males within the group occurs but not toward natal males, and a decrease in the total time dominant males spent feeding and their feeding bout lengths while females are receptive; and 6) if both males and females can enhance their

mating opportunities through increased contact with neighboring groups, an increase in intergroup encounter rate when females are receptive occurs.

Materials and methods

Study site and population

This study is part of an ongoing long-term study in Kirindy Forest, a dry deciduous forest in central western Madagascar, 60 km north of Morondava (Sorg et al. 2003). The site is operated by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) Morondava. The German Primate Center has established a field station with 3 study areas within the forestry concession, where ongoing research has been conducted since 1993. We studied 9 groups of well habituated sifakas living in one of these study areas. All individuals in the study population are marked with either unique nylon collars and pendants or radio collars (Kappeler and Schäffler 2008). Group size and composition varied across the 9 study groups over the 2 sampling periods (Table 1). We defined adulthood for males as 3 yr (Kraus et al. 1999) because they have been observed to mate successfully at this age (Richard et al. 1991; Rümenap 1997; Richard et al. 2002). We included only females that had previously reproduced. We determined natal and non-natal status genetically (Kappeler and Schäffler 2008).

Table 1. Composition of study groups over 2 sampling periods (excluding juvenile individuals) and observation hours.

Group	AF[a]	AM[b]	ANM[c]	OH[d]
A (A1)	1 (1)	1 (2)	0 (1)	59 (30)e
B	1	1	0–3	155
C	1–2	1	0–1	102
E	1	1	1–2	100
F	1–2	1	3	38e
G	2	1–3	0	107
H	1	1–2	0	107.5
J	1	2	0	101.5
K	2	1	0	164

The group A dominant male-female dyad of 2006 was replaced at the start of the 2007 mating season due to the death of the adult female and the subsequent takeover of the group by a new male that became dominant. Range of numbers indicates changes in group composition due to disappearances, migration, or change of status from juvenile to adult. AF = adult females; AM = adult males (dominant and non-natal subordinate males); ANM = adult natal males; OH = observation hours per study group.

eGroups observed for 1 sampling period.

General data collection

We performed observations during 2 sampling periods (January–March 2006 and 2007) encompassing 2 mating seasons. We observed dominant adult males (n = 10) and adult females (n = 12). Although there were 9 study groups, the number of dominant males observed was 10 because the dominant male in 1 group was replaced by another male at the start of the 2007 mating season. We identified the group's dominant male based on the outcome of decided agonistic interactions (Pereira and Kappeler, 1997). Eight focal individuals from 4 different groups were observed per day between 0600 and 1800 h with the help of a trained assistant (inter-observer reliability: r_s = 0.91). Each focal animal observation session lasted either 2 h (January and February) or 1.5 h (March). In total, each observer spent either 3 or 4 h with 2 groups per day resulting in a total of 547.5 observation hours over the 2 sampling periods. Although observations were equally distributed over all focal individuals and observation hours, the number of

observation hours per group is not equal (Table 1) owing to the exclusion of observations from this analysis if they fell outside the mating season, which we defined *post hoc* based on when females became receptive.

We collected behavioral data via continuous focal animal sampling (Altmann 1974). During each observation session, we continuously recorded the activity of the focal individual (foraging, resting, locomotion, and grooming). While the focal individual was engaged in an activity, we also recorded all instances of other individuals approaching (coming ≤1 m) and departing (moving out of the 1 m radius) the focal individual. In addition, we noted when the focal individual approached or departed another individual. While the focal individual was engaged in a continuous activity, we recorded aggressive, submissive, olfactory, and reproductive events simultaneously. For aggressive and submissive behaviors (sensu Brockman 1994), we recorded the context, i.e., activity the focal individual was engaged in and whether the interaction had a decided outcome, denoted by a clear submissive signal. If a series of aggressive and submissive events between the same dyad took place with no pause of >1 min between events, the series was considered one event. We recorded male olfactory behavior including place-sniffing (male sniffs the substrate where a female was resting ≤5 min after the female left), over-marking a female scent-mark (sensu Lewis 2005), anogenital sniffing (male approaches female from behind, sniffs her anogenital region, and scent marks in her urine), and general scent-marking (sensu Lewis 2005). We also noted reproductive behavior (sensu Brockman 1999). Finally, we sampled (sensu Lewis 2005) intergroup encounters *ad libitum*. We recorded the participants' location and whether the encounter was peaceful or agonistic. We conducted instantaneous focal point samples at 15-min intervals simultaneously during each focal animal observation and in addition

by 2 field assistants who rotated through all focal females, excluding continuously observed focal animals, once per day to establish the distance of the focal individual to other group members yielding a total of 2763 scans.

Fecal sample collection and analysis

To estimate day of ovulation, we collected fecal samples from the 12 focal females during both sampling periods. Frequencies of sample collection varied according to season from once per week during the pre- and post-mating season (December and March, respectively) to every second day during the mating season (January/February), yielding a total of 637 samples (19–30 samples per female per sampling period). We collected a standardized amount of feces (9 pellets) immediately after defecation and stored them in 10 ml of 70% ethanol until hormone analysis (Kraus et al. 1999). We collected all samples in the morning between 0600 and 1130 h to control for potential diurnal variation in hormone excretion. In groups with >1 adult female, we collected samples from all females within the group on the same day.

Fecal extraction and hormone analysis

Before hormone measurement, we homogenized samples in their original ethanolic solvent (Kraus et al. 1999) and subsequently extracted them twice as described by (Ziegler et al. 2000) with the modification that we vortex-mixed samples twice for 10 min on a multitube vortexer instead of shaking them overnight on a horizontal shaker. Efficiency of the extraction procedure, determined by monitoring the recovery of [^{3}H]progesterone added to a subset of samples before homogenization, was $74.1 \pm 4.5\%$ (mean $\pm$ SD, n = 12). After

extraction, we dried the remaining fecal pellets in a vacuum oven and determined the dry weight of the samples. All hormone concentrations are expressed as mass per gram of dry weight.

We measured fecal extracts for levels of immunoreactive progesterone (iP4), which has been shown to provide reliable information on female ovarian activity in sifakas (Brockman and Whitten 1996).We performed enzyme immunoassay according to the procedure described previously by (Heistermann et al. 1993). The assay used an antibody raised in sheep against progesterone-11α-hemisuccinate-BSA and progesterone-3-horseraddish peroxidase (POD) as label. We assayed 50-µl aliquots of fecal extracts (diluted 1:20-1:100 in assay buffer) along with 50 µl of standard reference solutions (range 2.5–160 pg). Sensitivity of the assay at 90% binding was 3 pg. Serial dilutions of fecal extracts from different females gave displacement curves parallel to the progesterone standard curve. Intra-and interassay coefficients of variation, calculated from replicated measurements of high- and low-value quality controls, were 7.2% (n = 16) and 12.5% (n = 21; high) and 8.1% (n = 16) and 14.3% (n = 21; low), respectively.

We used the fecal progesterone profiles to determine the presumed day of ovulation and thereby to define the period of estrus in each female. In this respect, we interpreted the significant rise in fecal iP4 levels above a threshold of the mean plus 2 standard deviations of 4–5 preceding baseline (follicular phase) values as indicating that ovulation occurred (Jeffcoate 1983). Researchers have widely used this approach to estimate the day of ovulation in various primate species, e.g., capuchins (Carosi et al. 1999), hanuman langurs (Heistermann et al. 2001), and long-tailed macaques (Engelhardt et al. 2004). We assessed the presumed day of ovulation as the day of the defined fecal iP4 increase corrected for a

time lag of 2 d to account for steroid passage time to excretion into feces (Shideler et al. 1993; Brockman and Whitten 1996). Because we collected samples every other day, estimated timing of ovulation may include an error of 1–2 d.

Data analysis

To determine whether there was a change in male behavior while females were receptive, we divided the sampling period into 2 periods: mating season (MS) and receptive period (RP). MS was the time from the onset of the first female's period of receptivity in the population to the termination of the last female's period of receptivity. We calculated the RP for each female and defined it as the presumed day of ovulation $\pm$ 7 d. This operationally defined period of female receptivity takes into account possible visual changes in female morphology that could signal the onset of receptivity (Richard 1974b; Sauther 1991; Richard 1992) and also addresses the confines of observing several study groups simultaneously. The use of this extended RP instead of the biologically true period of female receptivity for behavioral analysis is expected to dilute results and thus underestimate the true frequencies of behavior. We did not additionally include data collected during the RP of each female in the MS. Because estrous behavior, defined as female willingness to mate (Brockman and Whitten 1996), is difficult to observe at Kirindy, we defined estrus hormonally as the presumed day of ovulation ±2 d, referred to as the fertile period (Fig. 1). This definition takes into account maximum estrus (96 h) (Brockman 1999) and gut transit time (Wasser et al. 1988; Shideler et al. 1993). We used the fertile period to test for estrous synchrony within groups and within the population. Estrous synchrony refers to the complete or partial

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temporal overlap of the fertile period of individual females, whereas asynchrony is the temporal non-overlap of estrus (Brockman and Whitten 1996).
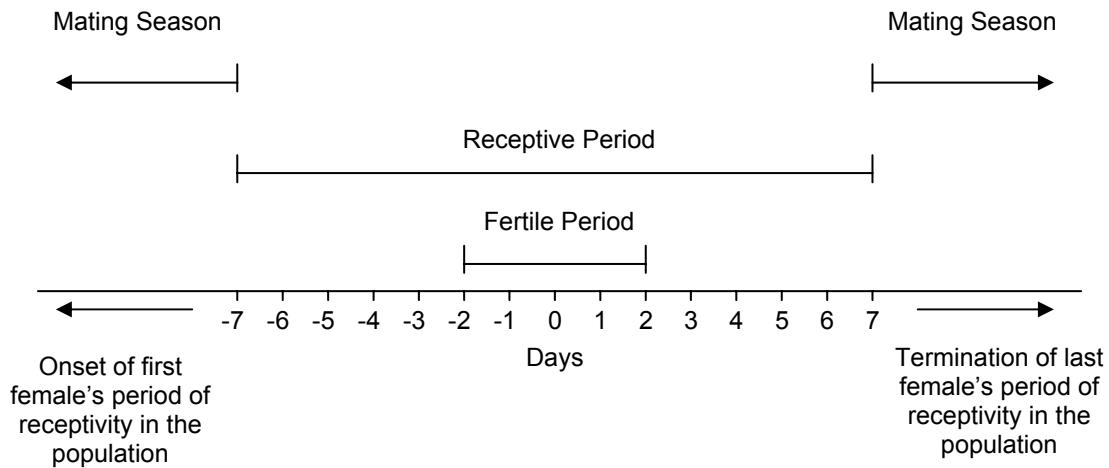
Mating Season   Mating Season

Receptive Period

Fertile Period

-7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7

Days

Onset of first female's period of receptivity in the population

Termination of last female's period of receptivity in the population

Fig. 1. Schematic representation of operational definitions used for analysis wherein 0 days indicates the presumed day of ovulation for each individual female within the study population.

To examine male olfactory behavior, we pooled all occurrences of place-sniffing, over-marking and anogenital sniffing (hereby referred to as sex-related olfactory behaviors) for each male over both sampling periods to have a sufficient sample size for analysis. We compared individual male sex-related olfactory behavior rates per hour during the RP and the MS. We also calculated male scent marking rates per hour and tested for differences between the MS and RP. For 1 male, we included only data collected during the 2006 MS in the analyses because both females present in the group did not come into estrus during the 2007 MS.

We analyzed changes in proximity for dominant, non-natal subordinate and natal male-female dyads using the distance data collected during instantaneous focal point

sampling. We divided data on each dyad into 2 distance categories: 0–5 m and >5 m. We added the total number of point samples in both the MS and divided the RP for each dyad into number of point samples dyads spent in close proximity (0–5 m) and further apart (>5 m). We tested differences in the proportion of total point samples per season that male-female dyads spent in close proximity. We then tested for differences in close proximity during the RP among the 3 types of male-female dyads. Subordinate males included were adults, although 4 natal subordinate males were between 3–4 yr of age. Although some individuals contributed to >1 dyad, i.e., groups with 2 focal females, we considered dyads as the biologically meaningful and independent unit of analysis (de Vries, 1998). We excluded 1 dyad from this analysis due to the extremely low number of point samples collected during the RP.

To determine the extent to which proximity was due to the movements of one member of the dyad rather than the other, we calculated the Hinde index (HI; (Hinde and Atkinson 1970), using counts of approaches and departs for female-dominant male dyads. The index does not provide a reliable measure for small sample sizes (Hinde 1977), and thus, we analyzed only dyads with >16 approaches and departs (Hill 1990). We regarded values between –0.1 and 0.1 as uninformative because these slight differences in responsibility may occur by chance (Hill 1987).

Finally, to ascertain which individual class (female or dominant male) was responsible for the initiation of bouts of proximity during the RP, we calculated an approach rate per hour total individual observation time for both females and dominant males and tested for differences between the 2 classes of individuals. We then compared dominant male approach rates in the MS and RP.

To test if males experience an increased risk of injury, a potential cost associated with mate-guarding behavior, we calculated aggression rates per hour for dominant males based on counts of aggressive acts toward non-natal subordinate males present in the group. We also calculated dominant male aggression rates toward group natal males for comparative purposes. We tested for differences in aggression rate between the MS and RP. We included only agonistic interactions with a decided outcome for analysis. In relation to foraging behavior, we calculated the percentage of total observation time a dominant male spent feeding in both the MS and the RP and tested for differences between the 2 periods. In addition, we calculated the average dominant male feeding bout duration length (minutes) as a direct measure of how long an individual fed without interruption. Owing to a constant need to monitor the movements of a female, a male may experience frequent interruptions while feeding, which may not be reflected in the overall time spent engaged in this activity but would result in a decrease in feeding bout duration (Alberts et al. 1996). We tested for differences in feeding bout length between the MS and the RP.

Finally, we calculated the number of intergroup encounters for each group in the MS and the RP. We then divided the total for each period by the number of hours the group was observed in each period to obtain an intergroup encounter rate per period. We then tested for differences between the RP and the MS. In addition, we tested for differences in the proportion of encounters that were peaceful or agonistic in both the MS and RP.

We used nonparametric statistics to test for differences between seasons and individual dyads. We analyzed data via STATISTICA (StatSoft Inc., version 6.0, 2001) and set the significance level at $p < 0.05$.

Results

Female estrous synchrony

We performed hormone analysis for 12 females in both sampling periods. All 12 females came into estrus in 2006 but only 10 out of 12 in 2007. The duration of the MS was 52 d (2006) and 36 d (2007), respectively. Fertile periods were more evenly distributed in 2006 and more clumped in 2007 (Fig. 2). Females residing in the same group came into estrus asynchronously, i.e., no temporal overlap, with a mean (±SD) of 13 ± 2.5 d (2006) and 10 ± 1.4 d (2007) between the fertile periods of each female within a group (Fig. 2). At the population level, most females (n = 22) were synchronous with 1 or 2 other females in the population (64% and 18%, respectively) but only 5 (28%) females were synchronous with females in neighboring groups, whereas 15 (83%) females came into estrous synchronously with non-neighboring females.

Olfactory behavior

We observed a total of 179 male sex-related olfactory behavior patterns over both sampling periods. Males increased their rate of sex-related olfactory behavior during the RP in comparison to the MS (Wilcoxon-test: T = 8, n = 10, p = 0.047, median $_{MS}$ = 1.38, range = 0.08–2.25; median $_{RP}$ = 2.14, range = 0.75–3.75; Fig. 3). There was no difference in the median rate of general male scent marking behavior between the MS and the RP (Wilcoxon-test: T = 21, n = 10, p = 0.86, median $_{MS}$ = 2.69, range = 1–6; median $_{RP}$ = 2.31, range = 1–6.25).
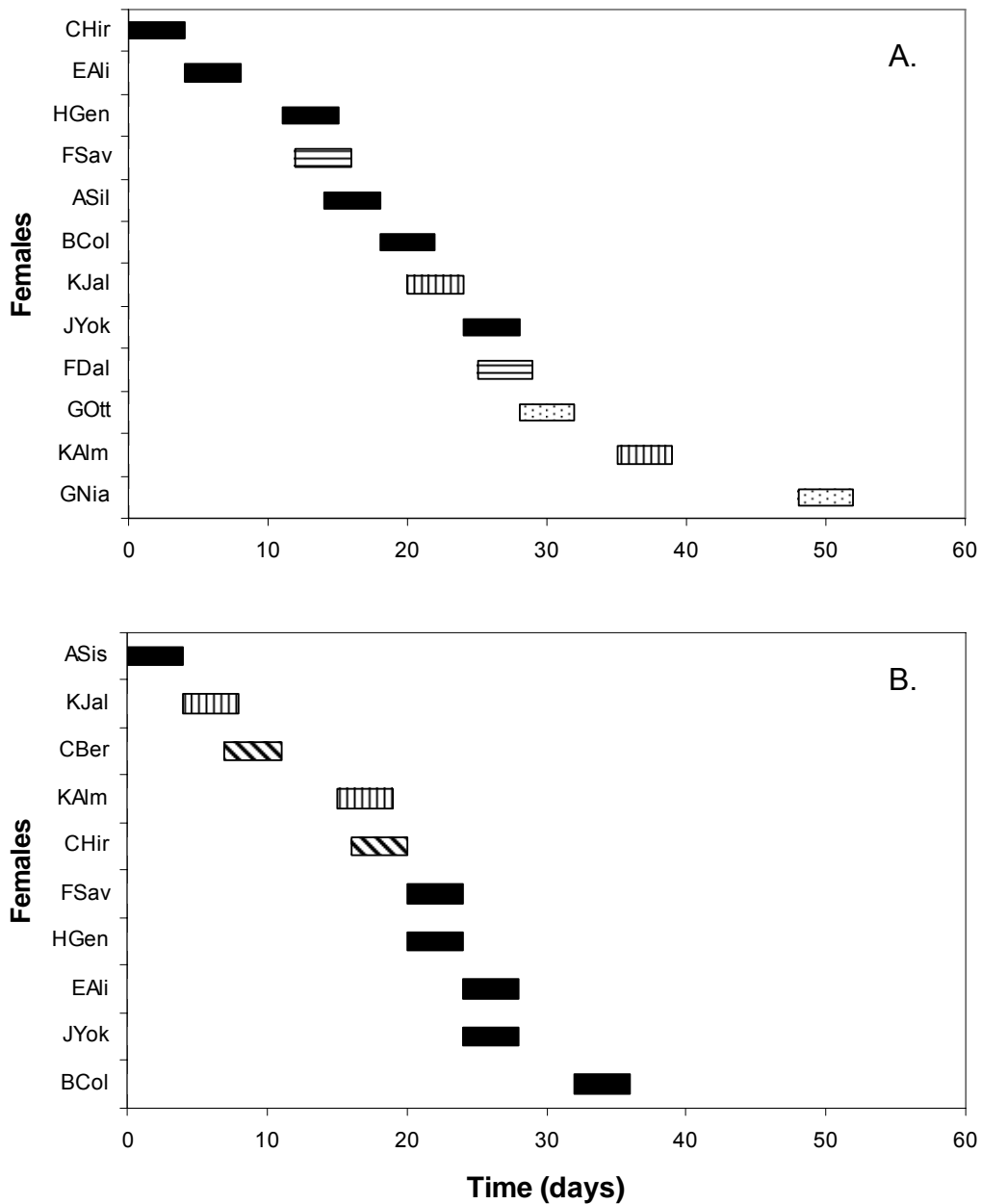
Fig. 2. Distribution of female fertile periods in the 2006 (A) and 2007 (B) mating seasons. The first letter of female identification represents the group of which the female is a member. Females in the same group share the same shading pattern. Females depicted in black are the only females present in their group (single female groups). The shorter duration of the 2007 mating season may be due to the fact that two females did not come into estrus while we collected fecal samples although 1 female may have become receptive after sampling had stopped as she had an infant late in the birth season.
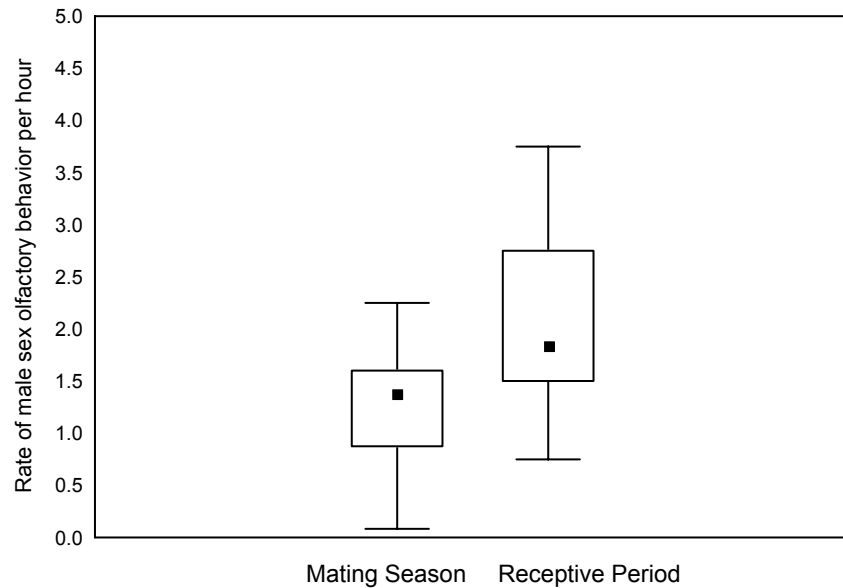
Fig. 3. Median rate per hour of male sex-related olfactory behavior in the mating season and the receptive period (n = 10). The rate is significantly higher in the receptive period (p = 0.047).

Female-dominant male dyad proximity

Dominant males spent a higher proportion of total point samples in close proximity to females in the RP in comparison to the MS (Wilcoxon-test: T = 7, n = 10, p = 0.037, median $_{MS}$ = 0.52, range = 0.34–0.76; median $_{RP}$ = 0.61, range = 0.46–0.70) but there was no such difference for either female-non-natal subordinate male dyads (Wilcoxon-test: T = 6, n = 7, p = 0.18, median $_{MS}$ = 0.14, range = 0.06–0.27; median $_{RP}$ = 0.17, range = 0–0.43) or female-natal subordinate male dyads (Wilcoxon-test: T = 4, n = 7, p = 0.09, median $_{MS}$ = 0.35, range = 0.18–0.56; median $_{RP}$ = 0.18, range = 0.11–0.53). In the RP, we found that female-dominant male dyads were in close proximity more often than both non-natal subordinate and natal male-female dyads (Kruskal-Wallis: H = 16.16, n = 24, p = 0.003; *post hoc* MWU-test dominant vs. non-natal subordinate male-female dyads: $U_{10,7}$ = 0, p = 0.0006; dominant vs. natal male-female dyads: $U_{10,7}$ = 1.5, p = 0.001; non-natal vs. natal male-female dyads: $U_{7,7}$ = 22.5, p = 0.80; Fig. 4).

Analysis of the Hinde index (HI) showed that bouts of proximity were maintained by the dominant male over both the MS (HI = 0.15) and the RP (HI = 0.29). Dominant males were not more responsible for the maintenance of proximity in the RP in comparison to the MS (Wilcoxon-test: T = 27, n = 12, p = 0.35). Finally, when analyzing approach rates per hour, we found that dominant males both initiated bouts of proximity more often than females did in the RP (MWU-test: $U_{12,12}$ = 27.5, p = 0.01, $median_{males}$ = 1.41, range = 0.31–5.17; $median_{females}$ = 0.75, range = 0.13–1.25) and that males approached females at a higher rate in the RP vs. the rest of the MS (Wilcoxon-test: T = 9, n = 12, p = 0.019, $median_{MS}$ = 0.84, range = 0.47–1.53; $median_{RP}$ = 1.41, range = 0.31–5.17).
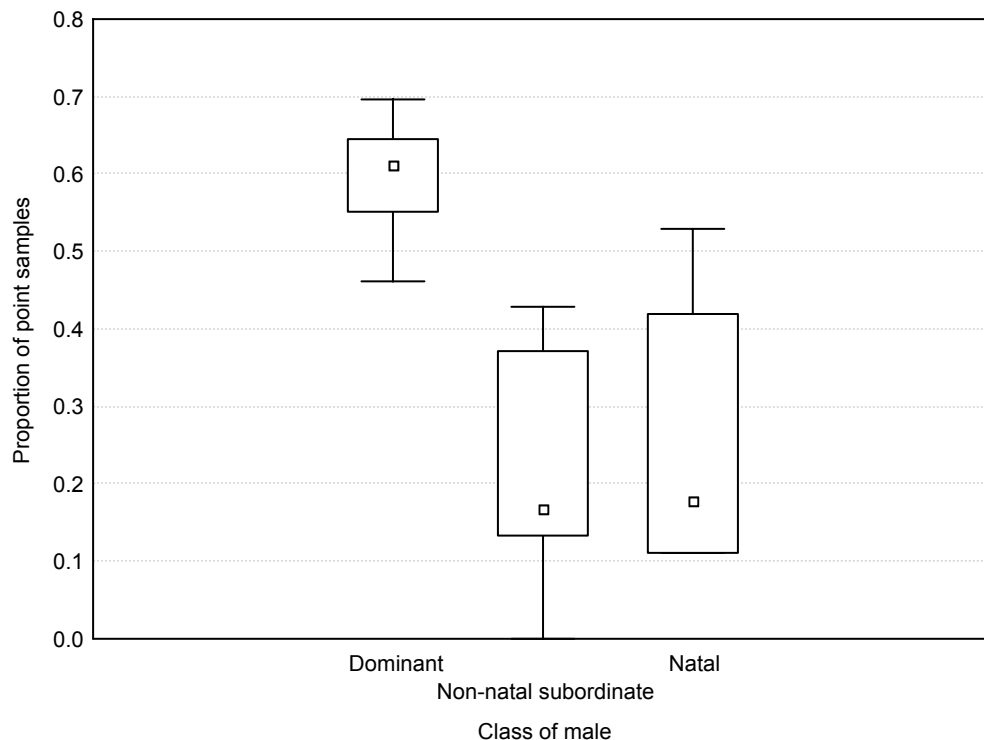

Fig. 4. Proportion of scans that dominant, non-natal subordinate and natal male-female dyads were in close proximity (0–5 m) in the receptive period. There is a highly significant difference between dominant male-female dyads (n = 10) and both non-natal subordinate (n = 7, p = 0.0006) and natal (n = 7, p = 0.001) male-female dyads but no difference in close proximity between non-natal subordinate and natal male-female dyads (p = 0.8) in the receptive period.

Costs of mate-guarding

We observed a total of 23 agonistic interactions for 5 dominant male-non-natal subordinate male dyads of which 21 were decided. All 9 interactions observed for 7 dominant male-natal male dyads were decided. Although we could not statistically compare aggression rates between the MS and the RP for dominant male-non-natal males dyads because of low sample size (n = 5), mean aggression rates were more than double during the RP (mean = 0.67 ± 0.22 aggression events/h, n = 13) when compared to the MS (mean = 0.30 ± 0.29 aggression events/h, n = 8; Fig. 5). In the RP, 85% of agonistic interactions took place in the context of resting while only 15% occurred in the context of feeding. Of the 21 interactions observed over both periods, 67% were displacements. The proportion of displacements increased to 85% (11 of 13 interactions) in the RP. The frequency of aggressive interactions by dominant males toward natal males was so low that we did not test for statistical differences between the MS (mean = 0.04 ± 0.08 aggressive events/h, n = 4) and the RP (mean = 0.06 ± 0.09 aggressive events/h, n = 5).

The foraging behavior of dominant males did not differ between the MS and the RP in either time spent feeding (Wilcoxon-test: T = 18, n = 10, p = 0.33, median $_{MS}$ = 0.45, range = 0.36–0.59; median $_{RP}$ = 0.41, range = 0.27–0.59) or average feeding bout length (minutes; Wilcoxon-test: T = 9, n = 10, p = 0.4, median $_{MS}$ = 4.5, range = 3.0–7.5; median $_{RP}$ = 4.0, range = 3.0–5.5).

Intergroup encounter rate

We observed a total of 35 intergroup encounters over the MS and RP during both sampling periods. Although the rate of intergroup encounters during the RP was higher than in the MS, the difference is not significant (Wilcoxon test: $T = 20$, $n = 10$ groups, $p = 0.44$, median $_{MS} = 0.04$, range $= 0.0–2.5$; median $_{RP} = 0.09$, range $= 0.0–0.19$). Within both the MS and RP, agonistic encounters occurred more frequently than peaceful encounters (Chi-squared $_{MS}$: $\chi^2 = 8.5$, df $= 1$, $p = 0.004$; Chi-squared $_{RP}$: $\chi^2 = 4.3$, df $= 1$, $p = 0.04$).
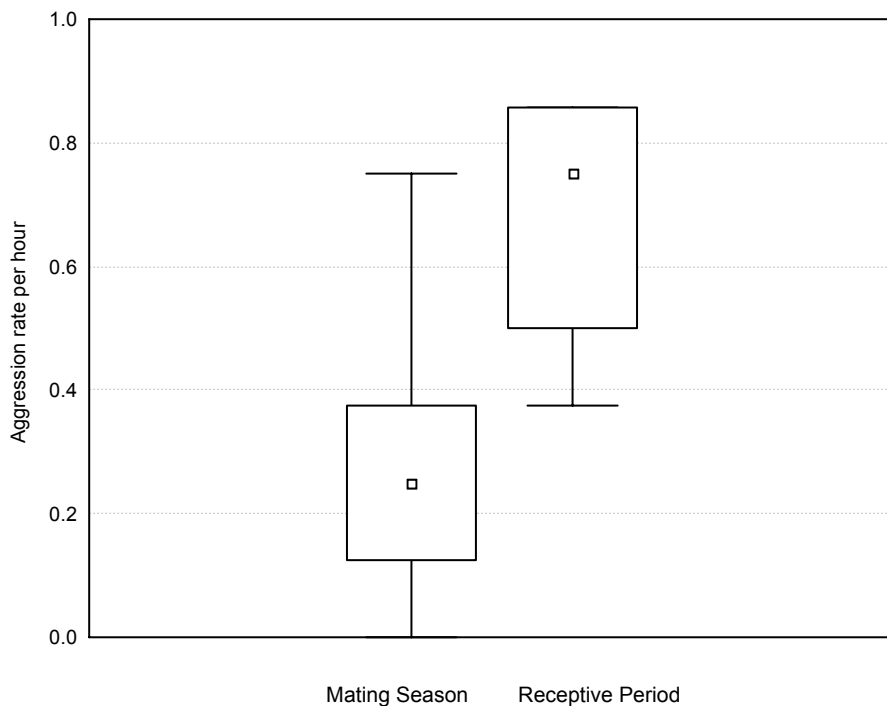

Fig. 5. Dominant male–subordinate non-natal male dyad aggression rates per hour during the mating season and the receptive period. We could not test data statistically owing to low sample size ($n = 5$).

Discussion

Our results demonstrate a quantitative change in several measures of proximity in female-dominant male dyads between the MS and the RP, which suggest the use of

mate-guarding as a reproductive tactic by dominant male sifakas. This conclusion is in concordance with previous descriptions of the behavior in sifakas of this and other populations (Brockman 1999; Lewis and van Schaik 2007). In comparison to both non-natal subordinate and natal male-female dyads, female-dominant male dyads spent more time in close proximity during the RP and these bouts of proximity were both primarily initiated and maintained by the dominant male. Although some of these measures may include behavior patterns not directly associated with mate-guarding, the changes in the different proximity measures between receptive and non-receptive periods suggest that dominant male sifakas used a form of mate-guarding.

The dominant male's ability to mate-guard may have been facilitated by female estrous asynchrony and the ability to pick up olfactory cues as to the timing of female receptivity. We predicted that males engaging in mate-guarding should face the costs associated with the behavior. Our results suggest that there is no change in dominant male foraging behavior when females are receptive, although this result could be due to our definition of RP and because feeding rates were not considered in our analysis. However, there may be an increase in aggression toward rival males within the group while a female is receptive, and thus a physiological cost could be incurred by both dominant and non-natal subordinate males because increased rates of aggression have been shown to be related to higher glucocorticoid levels, a hormonal measure of stress (Fichtel et al. 2007).

Female estrous asynchrony

When females come into estrus asynchronously, a decrease in the variance of male reproductive success in predicted (Emlen and Oring 1977; Altmann 1990; Mitani et

al. 1996a; Kappeler 1999). Although a recent cross-species comparative study found no evidence for a link between male mating skew and female estrous synchrony in primates (Kutsukake and Nunn 2006), male reproductive skew, conversely, may be linked with female estrous asynchrony, as has been shown for several species including domestic cats (Say et al. 2001) and brown lemurs (Gachot-Neveu et al. 1999). Hormone analysis results show that female sifakas living in the same group came into estrus asynchronously. Under these circumstances, the dominant male can effectively monopolize both females, which may explain the extreme reproductive skew in favor of dominant males in the Kirindy population.

Olfactory cues to female receptive state

Although general male scent marking remained constant, as Lewis (2005, 2006) found for the same population, there was an increase in male sex-related olfactory behavior during the RP. The findings are similar to those for ringtailed lemurs (Palagi et al. 2004) and moustached tamarins (Huck et al. 2004), where male olfactory investigation of female scent marks increased in the mating season. Even though our finding suggests that males may be using olfactory cues as an indicator of female receptive state, caution is warranted. If the composition of female scent marks change, and thus the information that is communicated, males do not need to increase the frequency of olfactory behavior to obtain valuable information. Studies on closely related species have shown that the volatile components of female anogenital gland secretions vary between birth and mating season in *Propithecus edwardsi* (Hayes et al. 2006) and can reveal specifics regarding reproductive status in *Propithecus verreauxi coquereli* (Hayes et al. 2004). In addition, the possibility that males may also use other cues, such

as morphological changes of the vulva (Richard 1974b; Sauther 1991; Richard 1992), cannot be excluded.

Although the function of female scent marking in *Propithecus* spp. does not appear to be to attract mates (Pochron et al. 2005; Lewis 2006) and females actually decrease the frequency of marking behavior during estrus (Brockman 1999), scent marks may nevertheless communicate information about reproductive status (Lewis 2006). Thus, although there are no data on either the composition or change in composition of female anogenital gland secretions in *Propithecus verreauxi*, males may be able to obtain some information regarding female reproductive state via olfactory cues.

If dominant males are able to ascertain the timing of female receptivity via olfactory cues, we can expect that the information conveyed in a female scent mark is public information accessible to all males. Moreover, females scent mark more in the periphery of their territories where scent marks have a higher probability of being investigated by extra-group males (Lewis 2005), making it possible for males to gain information on female receptive state without visual contact (Richard 1985). One possible tactic to limit rival male access to information on female reproductive state is for dominant males to over-mark female scent marks (Lewis, 2005). This male reproductive tactic is common in several species of vole (Ferkin et al. 2004), has been shown to occur in ringtailed lemurs (Kappeler 1998), and is suggested for owl monkeys (Wolovich and Evans 2007). In sifaka, males over-mark female scent marks more frequently in the mating season and during intergroup encounters (Lewis 2005). These findings support the use of over-marking as a male reproductive tactic in sifaka.

Costs of mate-guarding behavior

If olfactory cues are accessible to all males, including both intragroup and extra-group males, we would expect an increase in the rate of male-male aggression when females are receptive as males would compete for access to receptive females. For example, in ringtailed lemurs, male dominance hierarchies break down and intermale aggression increases in the mating season (Jolly 1966; Cavigelli and Pereira 2000; Gould and Ziegler 2007). Increases in male-male aggression rates also increase in species that have stable dominance hierarchies in the mating season, e.g., redfronted lemurs (Ostner et al. 2002). Mate-guarding males thus face an increased risk of injury owing to incursions with rival males while trying to monopolize access to receptive females (Matsubara 2003). Although we could not test statistically changes in male-male aggression rates, the data suggest that there may be an increase in aggression towards non-natal subordinate males during the RP that is not associated with feeding competition. Even so, the overall rate of aggression in the Kirindy population is low (Lewis and van Schaik 2007), which suggests that males are not physically fighting for access to females.

Low aggression rates may reflect the fact that the number of groups in our study with >1 non-natal male is low (3 groups of 9) and that the groups were stable. Thus, although aggression does exist, its importance relative to acquiring and monopolizing mates may be minimized. Moreover, the fact that aggression generally takes the form of high speed arboreal chases lends support to the idea that selection in sifakas is not operating on physiological traits that increase body mass and weaponry, which lead to sexual dimorphism, but rather on traits that improve speed and agility (Lawler et al. 2005).

If olfactory cues are available to all males, we would also expect an increase in intergroup encounter rate during the RP, especially due to both the high proportion of female estrous asynchrony in neighboring groups and a high degree (36.5–63.7%) of home range overlap (Benadi et al. 2008). One option for males to increase their reproductive success is to mate with extragroup females. For example, in banded mongooses, intergroup encounter rates increase when females are receptive as males may be actively seeking extragroup copulations in pursuit of paternity (Cant et al. 2002). Mating with extragroup males is also a beneficial strategy for females as a means to confuse paternity and thus decrease the risk of infanticide if the group is taken over by a new male (van Schaik and Janson 2000). Because (Lewis et al. 2003) documented infanticide in the Kirindy population of sifakas, mating with extragroup males would also benefit females. Although this does occur in another population of *Propithecus verreauxi* (Lawler 2007), the genetic data reveled only one extragroup paternity within the Kirindy population (Kappeler and Schäffler 2008).

The stability of the intergroup encounter rate was thus surprising but there may be several explanations for this result. If dominant males are mate-guarding effectively, attempting to mate with extragroup females during intergroup encounters may not be worth the risk of potential injury. In addition, by leaving females in their resident group in search of extragroup females, dominant males may risk losing paternity. The tradeoff between staying and searching for more females may be such that the benefits of staying in the resident group outweigh the chance of reproductive success elsewhere. Alternatively, sneaky copulations with lone males (Lewis and van Schaik 2007) and during intergroup encounters (Brockman 1999) may indeed occur but do not result in fertilizations. Thus, although reproductive skew is high (Kappeler and Schäffler 2008),

the mating skew may be more evenly distributed between males, especially because subordinate males have been observed to mate (Lewis 2004).

Intraspecific variation in male reproductive success in Verrreaux's sifaka

Although (Richard 1974a) documented intraspecific variation in the social organization and ecology of *Propithecus verreauxi*, several of our findings may help to illuminate slight variations within the mating system. Male reproductive success differs between the population at Kirindy (Kappeler and Schäffler 2008), and the population studied at Beza Mahafaly in Southwest Madagascar (Lawler et al. 2003) as reproduction is more skewed at Kirindy. This discrepancy may be due to differences between populations in female reproductive strategies, i.e., female estrous asynchrony and female choice.

In a study conducted to document intragroup estrous asynchrony at Beza, results revealed that estrus was asynchronous within 1 group but synchronous within the other (Brockman and Whitten 1996). Although the sample size was small, this result may lend insight into the differences in reproductive skew. Although resident males at Beza also sire the majority of offspring, the percentages are lower, 35–83% (Lawler et al. 2003; Lawler 2007) than for the Kirindy population (91%) (Kappeler and Schäffler 2008). This difference may be due to the inability of males to monopolize all group females if females are receptive synchronously.

In addition, Lawler et al. (2003) found that a significant fraction of offspring were sired by nonresident males at Beza when the adult sex ratio was biased toward females. At Kirindy, genetic analysis revealed only 1 extragroup paternity (Kappeler and Schäffler 2008), although group sex ratios tend to be even or male-biased (Lewis and van Schaik

2007). Finally, observations of females frequently mating with extragroup males at Beza (Richard 1992; Brockman 1994) may lend support for the decreased ability of Beza males to monopolize all females in their resident group.

Based on observations at Beza, Richard (1985) proposed that membership within a group is not necessary to mate with its females and that social group boundaries tend to break down in the mating season. In addition, females show positive mate choice toward resident and non-resident males (Brockman and Whitten 1996). Although lone males have occasionally been observed on the periphery of groups during the mating season at Kirindy, groups remain stable and females have only rarely been seen to mate with non-resident males (Mass, pers. obs.). This discrepancy is also reflected in the genetic paternity data. Thus, there appears to be some support for the use of different reproductive strategies by both males and females between the 2 sites. This may reflect differences in both group size and composition and environmental factors between Beza and Kirindy.

Mate-guarding as a mechanism underlying high reproductive skew

Although alternative reproductive strategies such as sneak copulations can reduce the effectiveness of mate-guarding (Setchell et al. 2005), the genetic data suggest that they do not result in fertilization. The low frequency of both extragroup and intragroup subordinate male paternity (Kappeler and Schäffler, 2008) imply that dominant males are able to monopolize almost all reproduction, and our results suggest that mate-guarding is one important proximate aspect in this context. Monopolization of receptive females may in addition be facilitated by small female group size, as has been

shown for langurs, wherein dominant males residing in multi-male groups also sire significantly more offspring than subordinates (Launhardt et al. 2001).

Our finding gives some insight into why, despite the small number of reproductively active females per group, some dominant males may not exclude potential rivals from group membership. Although there is a reproductive cost in having rival males present in a group as a small percentage of paternities are lost, the cost may not be high enough to risk fighting to evict them. Further, rival subordinate males may be tolerated by a dominant male if their presence benefits the group as a whole (van Hooff 2000; Ostner and Kappeler 2004). Although Lewis (2004) found that subordinate male sifakas provide services in terms of vigilance, grooming, and playing with infants, natal and non-natal subordinate males were not distinguished. However, if a dominant male is able to monopolize almost all paternities due to effective mate-guarding and if the presence of subordinate non-natal males benefits the group, this could help explain the observed tendency toward an even sex ratio in group composition. In addition, although non-natal subordinate males stay in the group with almost no reproductive success, this may be a better alternative to being a solitary male (Lewis and van Schaik 2007).

Conclusion

Achieving the position of dominant male is ultimately the best reproductive tactic for a male Verreaux's sifaka. Although dominant males do not exclude potential rivals from group membership, and subordinates have been observed to mate occasionally, dominant males are generally able to exclude rivals from successful reproduction. Results from this study show that mate-guarding is a viable dominant male reproductive tactic to monopolize receptive females. Mate-guarding is facilitated by both the temporal

distribution of estrous females within a group and due to the ability of males to obtain information on female reproductive state via olfactory cues. Within the Kirindy population, the ability to exclude rivals from paternities suggests that dominant males are mate-guarding effectively. This ability, in turn, can explain the high reproductive skew observed within the population but not why non-natal subordinate males stay with little reproductive success. Information on mating skew and the possible benefits of the presence of non-natal males within a group are essential for understanding the tendency towards adult even sex ratio despite the small number of females in sifaka groups. In understanding the interplay of the reproductive strategies of both dominant males and subordinate non-natal males, we can start to comprehend the various lemur idiosyncrasies and the evolutionary forces that shaped them.

Chapter 2:

Even adult sex ratios in lemurs: potential costs and benefits of subordinate males in Verreaux's sifaka (*Propithecus verreauxi*) in Kirindy Forest CNFEREF, Madagascar

with M. Port & P.M. Kappeler

Abstract

Optimal group size and composition are determined by both the costs and benefits of group living for the group's members. Verreaux's sifakas (*Propithecus verreauxi*) form multi-male multi-female groups with variable, but on average, even adult sex ratios despite a small average number of females per group. The unexpected presence of multiple adult males may be explained by tolerance of other group members if subordinate males provide benefits to the group that outweigh the costs associated with their presence. Results based on both demographic data collected over a 13 year period and behavioral observations suggest that subordinate males provide no benefits in terms of infant survival and defense against group takeover by outside males. Although groups with more males are more likely to win intergroup encounters, subordinate males do not participate in these encounters more often than expected. Subordinate males are not costly to other group members in terms of direct intragroup feeding competition but aggression rates between dominant and immigrated subordinate males increase in the mating season. Even though subordinate males provide very few benefits to the group, they are not very costly either, and thus, may be tolerated by resident females and dominant males. This tolerance may help to partially explain the tendency towards their unusual adult sex ratio.

Key words: Socio-ecological model, group composition, operational sex ratio, mating skew

Introduction

The size and composition of groups are among the most variable aspects of primate social organization (Strier 1994; Strum and Fedigan 2000; Kappeler and van Schaik 2002). This variability is due mainly to the different number of adult males present within a group (Hamilton and Bulger 1992; Kappeler 2000a; van Hooff 2000). Thus, within the same species and population, the formation of both single and multi-male groups is possible in some species (Cercopithecines: Andelmann (1986), Alouattinae: Eisenberg (1979), see also *Equus caballus* (Linklater 2000), *Porphyrio porphyrio* (Jamieson 1997), *Prunella modularis* (Davies 1992). Questions concerning the number of adult males found in primate social groups are of particular interest as the presence of unrelated male competitors within a group is common, is independent of phylogenetic or ecological constraints (Clutton-Brock and Harvey 1977), and has direct consequences for the fitness of group members (Hamilton and Bulger 1992; Treves 2001).

The social organization of a species is shaped by both ecological and social variables which, in turn, affect the sexes differently (Emlen and Oring 1977; Wrangham 1980; Rubenstein and Wrangham 1986). Due to differences in their respective potential rates of reproduction, males and females differ in their reproductive strategies leading to a conflict between the sexes over group composition (Clutton-Brock 1989b; Clutton-Brock and Vincent 1991). Females may gain both social and ecological benefits from the presence of several co-resident males (van Schaik and van Hooff 1983; Kappeler 1999) but the reproductive success of most mammalian males is limited by their access to and monopolization of receptive females (Bateman 1948; Trivers 1972), so that males are expected to exclude rivals from fertile females.

According to socioecological theory, the key factor that determines male monopolization ability and, thus, the number of males found in groups, is the spatiotemporal distribution of fertile females, which itself is mainly based on the distribution of risks and resources in the environment (Emlen and Oring 1977; Gaulin and Sailer 1985; Ims 1988). Where fertile females are clumped in space and become receptive asynchronously, one male will try to monopolize the group of receptive females by excluding potential rival males from group membership. As both female group size and/or estrous synchrony increases, a male's ability to monopolize the group decreases. Thus, whether species form single-male or multi-male groups depends on both the number and temporal distribution of fertile females and reflects the outcome of male contest competition for mates and female counter-strategies (Altmann 1990; Mitani et al. 1996a; Kappeler 1999; Nunn 1999).

In contrast to most group-living anthropoid species (Andelmann 1986; Cords 2000), the formation of multi-male groups in diurnal lemurs, despite small average female group size and highly seasonal breeding, is the norm, e.g. *Lemur catta*: (Pereira 1991; Sauther and Sussman 1993), *Eulemur fulvus rufus*: (Overdorff et al. 1999; Ostner and Kappeler 2004), *Propithecus verreauxi*: (Richard 1974a), *Propithecus edwardsi*: (Pochron and Wright 2003), review: (Kappeler 2000a), resulting in a tendency towards on average even adult sex-ratios. Various hypotheses have been postulated to explain this discrepancy in operational sex ratio between lemurs and other primates, focusing on either high female mortality, male transfer tactics, or fitness benefits to both females and males connected with the presence of additional males (reviews in van Schaik and Kappeler 1996; Kappeler 2000a). If benefits are provided by additional males, these benefits must more than compensate the costs associated with increased group size

(van Schaik and van Hooff 1983; Kappeler 1999), such as repressed reproduction, competition with other group members for food and mates and increased conspicuousness to predators (Alexander 1974; Bertram 1978; Pulliam and Caraco 1984; Janson 1988).

Several benefits may be derived from the presence of multiple males within a group that serve to increase the fitness of both resident females and males, including increased infant survival due to help in rearing young (Goldizen 1987; Sussman and Garber 1987; Koenig 1995; Treves 2001) and increased vigilance towards predators and potentially infanticidal conspecific males (Baldellou and Henzi 1992; Clutton-Brock and Parker 1995; Treves 2001). Males have been shown to be more vigilant than females in a number of primate species (van Schaik and van Noordwijk 1989; Isbell and Young 1993; Rose and Fedigan 1995) and several studies suggest that groups contain more males where predation risk is high (van Schaik and Hörstermann 1994; Hill and Lee 1998). In lemurs, although males contribute to group vigilance levels, there are generally no sex differences in vigilance behavior (Gould 1996b; Kappeler 2000a). Yet, their presence can serve to decrease the per capita risk of predation due to dilution effects (Pulliam 1973). In addition, the presence of now extinct large eagles (genus *Aquila*) (Goodman 1994) may have influenced social organization as multi-male groups are more common where monkey-eating eagles are found (van Schaik and Hörstermann 1994). Finally, the potential risk of infanticide is believed to be lower in multi-male groups (Newton 1986; Robbins 1995) as the presence of additional males may deter strange males from attempting to takeover the group, a major benefit to dominant males if this results in increased tenure length (Borries et al. 1999; Ortega and Arita 2002; Ostner and Kappeler 2004).

Groups with a greater number of males may also have an advantage in securing access to resources that are contested between groups. Intergroup dominance is usually a function of group size and the number and fighting ability of adult males (Wrangham 1980), as has been shown for several baboon and macaque species (Cheney 1987). Males in some species also tend to participate more frequently than females in intergroup encounters (Harcourt 1978; Robinson 1988; Rose 1994; Putland and Goldizen 1998; Majolo et al. 2005). Although male participation in intergroup encounters is generally aimed at mate defense (Cheney 1987; van Schaik et al. 1992), the outcome is the simultaneous defense of resources and territory. This is a major benefit to females as their reproductive success is limited by their access to resources (Emlen and Oring 1977; van Schaik and van Hooff 1983).

In sum, the variety of potential benefits provided by extra males in terms of vigilance, protection against takeover and intergroup dominance have both direct and indirect consequences for the reproductive success of breeding group members. Therefore, additional males may be tolerated resulting in unusual adult sex ratios.

Verreaux's sifakas (*Propithecus verreauxi*), a sexually monomorphic (Kappeler 1991) group-living lemur with female dominance (Richard 1987) and male dispersal (Richard et al. 1993), present a conundrum to research based on sexual selection theory because a small average number of adult females (1.8 at our study site) is found with several adult males (mean: 2.3; Kappeler and Schäffler, 2008). In anthropoids, this small number of females is predicted to lead to the formation of single-male groups (Andelmann 1986; Pope 2000). In addition to small female group size, sifakas are highly seasonal breeders with females becoming receptive once per year (Brockman and Whitten 1996) for a period of up to 96 hours (Brockman 1999). Moreover, females within

groups come into estrus asynchronously and therefore dominant males are able to effectively mate-guard each female as she becomes receptive (Mass et al., in press). Finally, according to genetic paternity analyses, reproduction is highly skewed as dominant males sire 9 out of 10 offspring (Kappeler and Schäffler, 2008).

Potential benefits provided by extra males in groups of sifakas such as increased vigilance and resource defense are relevant in this species for several reasons. Firstly, the Madagascar harrier hawk, *Polyboroides radiatus,* (Karpanty and Goodman 1999; Brockman 2003) and the fossa, *Cryptoprocta ferox*, (Rasoloarison 1995; Wright et al. 1997) are known to regularly prey upon sifaka. Because they have alarm calls for both predators (Fichtel and Kappeler 2002), subordinate males could provide survival benefits to their group mates by warning them. Secondly, intergroup encounters are common at feeding sites within overlapping areas of home-ranges (Lewis 2004; Benadi et al. 2008). Therefore, there is a potential for males to defend resources from other groups. Thirdly, infanticide by strange males has been observed in this species (Lewis et al. 2003), and thus, defense against group takeover and social vigilance could be important potential benefits provided by subordinate males. Indeed, subordinate males have been observed to sometimes form coalitions with the dominant male to keep extra-group males out and to prevent them from mating with resident females (Lewis and van Schaik 2007). Paternal care benefits are not relevant as male *P. verreauxi* have not been observed to engage in extensive infant care (Lewis 2004).

In this study, we examine the tendency towards even or male-biased adult sex ratios in sifakas by examining whether adult subordinate males provide benefits to the group. We test the predictions that the presence of subordinate males (1) has a positive effect on infant survival, (2) decreases the chance that a group will be taken-over by

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intruding males, (3) increases the probability of winning an intergroup encounter, and (4) does not incur costs for other group members in relation to intragroup feeding competition and inter-male aggression. In answering these questions, we hope to illuminate some of the evolutionary forces shaping the social organization of this species that could then be extrapolated to and tested in other lemur species.

Materials and methods

Study site and population

This study is part of an ongoing long-term study conducted in Kirindy Forest/CNFEREF, a dry deciduous forest located in central western Madagascar, 60km north of Morondava (Sorg et al. 2003). The site is operated by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) Morondava. The German Primate Center has established a field station with three study areas within the forestry concession, where ongoing research has been conducted since 1993. Since 1995, all individuals in the study groups have been habituated and individually marked with either nylon collars and unique pendants or radio collars (Kappeler and Schäffler 2008). This study population has been censused several times each week since 1995. All births, deaths and dispersal events were recorded and timed to within a few days. The number of groups within the study population and their size and composition (based on adult group members) varied over the years and is summarized in Table 1. From these long-term data, several demographic variables could be estimated.

Table 1. Group size, composition and sex ratio of the social groups in the study population since 1995. Group size and composition were calculated per group per month and include only adult (3+ years) individuals. The overall mean for the group is given. Male classes were determined by genetic analyses or denoted with (-) if unknown. Related males are defined as males that are related to the dominant male in a group but not to the females. Asterisks (*) denote groups sampled during the course of this study with observation hours given.

Group	Years in study population	Group size	Females	Males	Natal males	Non-natal males	Related males	Sex ratio (M : F)	Observation hours
						Male Class			
A*	12	3.69	1.60	2.09	0.80	0.29	0.00	1 : 0.77	138
B*	13	4.42	1.84	2.58	1.22	0.36	0.00	1 : 0.71	478.5
C*	13	3.10	1.23	1.87	0.15	0.56	0.15	1 : 0.66	287
D	2	3.00	1.00	2.00	0.00	1.00	0.00	1 : 0.50	-
E*	13	3.91	1.54	2.37	0.38	0.76	0.23	1 : 0.65	388
F*	13	3.63	1.74	1.89	0.81	0.08	0.15	1 : 0.92	230
F1*	2	4.96	1.43	3.46	0.25	0.00	2.21	1 : 0.45	92
G*	11	4.30	1.95	2.20	0.62	0.04	0.55	1 : 0.88	300
H*	10	2.90	1.47	1.43	0.10	0.49	0.00	1 : 1.02	200
J*	9	5.68	3.14	2.54	0.11	1.35	0.07	1 : 1.24	394.5
K*	12	3.33	2.00	1.33	0.00	0.33	0.00	1 : 1.50	300
L	8	3.48	1.48	2.00	-	-	-	1 : 0.74	-
Mean(±SD)	-	3.87±0.8	1.70±0.5	2.15±0.6	0.41±0.4	0.48±0.4	0.31±0.7	1 : 0.83	2808

Behavioral data

Behavioral data from 10 social groups were collected by V.M. and one Malagasy field assistant during three sampling periods from September to March 2005-2006, 2006-2007 and 2007-2008 using continuous focal animal sampling. Adult females who had previously reproduced (n=12) and dominant males (n=10) were observed during the first and second sampling period. Subordinate adult males (n=12) were observed during the second and third sampling period. Males were classified as dominant (D), non-natal subordinate (NN), natal subordinate (N) and related (R). R males are defined as males that are related to the D male but not the group females. Male classifications were

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established genetically (Kappeler and Schäffler 2008) and based on the outcome of decided agonistic interactions in both this and previous studies (Kraus et al. 1999; Lewis 2004). Males and females were considered adult at three years of age as males have been observed to mate successfully at this age (Richard et al. 1991; Rümenap 1997; Kraus et al. 1999; Richard et al. 2002) and females to actively participate in group defense (Mass, pers. obs.). Each focal observation session lasted 1.5 hours and four focal individuals were observed by each observer per day yielding a total of 2808 hours of focal animal observation (Table 1).

During each observation session, the activity (foraging, resting and locomotion) of the focal animal was continuously recorded. For aggressive and submissive behaviors (sensu Brockman 1994), the context (i.e. activity) the focal animal was engaged in and whether the interaction had a decided outcome, denoted by a clear submissive signal (Pereira and Kappeler 1997), were recorded. If a series of aggressive and submissive events between the same dyad took place, the series was considered one event. Aggressive intergroup encounters (sensu Cheney 1987) were sampled *ad libitum*. The participating groups, identities of participants (individuals who engaged in chasing behavior and/or aggressive approaches of members of the rival group) and whether there was a clear winner (defined by retreat of one group) or undecided outcome were recorded.

Data analyses

Although infant mortality can be due to different factors such as disease and inadequate mothering for example, the presence of non-reproductive group members may benefit the group in terms of improving infant survival via increased vigilance and

defense against infanticidal takeovers (Robinson 1988; Baldellou and Henzi 1992; van Schaik 1996; Treves 2001). This is especially the case in lemurs as this group of primates tends to suffer more losses due to predation than most other primates (Wright 1999). Therefore, we predicted that infant survival rate would be higher in groups with more adult subordinate males. Infants were operationally defined as 0-12 months of age as this is the time when they are most vulnerable to both predation and infanticide. For each group and each birth season, we calculated the proportion of infants that survived from birth to 12 months of age and defined this period as a group year. The mean adult group size and number of subordinate males were calculated for this period by averaging the group size and composition for each month. This takes into account changes in both size and number of subordinate males in the group over the year period. Infants that disappeared within the first 12 months of life can be assumed dead as sifakas less than 36 months old have never been seen to disperse voluntarily and have never been relocated in other groups after disappearing from their natal group (Richard et al. 1993, Kappeler, unpubl.data for study population). Group years in which no infants were born were not included in this analysis.

To assess whether either overall group size and/or the presence of subordinate males affects infant survival, we fit a generalized linear model (GLM) with binominal error structure to the 79 group years for which demography data were available. To test for a potential effect of overall group size on the proportion of infants that survived, we entered average group size (as defined above) as the first explanatory variable to our model and reported the difference in deviance (ΔD) to the null model. To check for an additional effect of the number of subordinate males, we then entered the average

number of subordinate males as a second explanatory variable and reported the difference in deviance to the model already containing group size. ΔD is χ^2-distributed with p-q degrees of freedom, where p and q are the numbers of parameters in the more complex and in the simple model, respectively (Dobson 1990).

A group takeover was defined as when an immigrant male comes into a group and assumes the D position and the former D male leaves within one month of this immigration event. Peaceful male immigrations were not considered takeovers as they did not result in the eviction of resident males or in the change of status of the D male. Using the demography data, we calculated an overall population takeover rate by dividing the total number of takeovers that occurred in the population by the number of years the population was censused. In order to test the prediction that groups have a lower chance of being taken-over the more adult subordinate males are present, we fit a logistic regression model. For each group year (where, in this analysis, group year was defined as the period from mating season to mating season), the occurrence or absence of a takeover was regressed against the minimum number of males present in the respective group year or against the number of males present during a takeover, if a takeover occurred.

Based on observed intergroup encounters during the study period, we used Chi-squared tests to determine whether groups with a higher proportion of males win intergroup encounters more often and if bigger groups in general win encounters more often than would be expected by chance. Only intergroup encounters including known marked groups with a clear winner were included in this analysis.

To examine the frequency of adult male and female participation in intergroup encounters, we compared observed versus expected participation using Chi-squared tests. Derived expected values take into account both the frequency of each group's participation in intergroup encounters and group composition as all groups did not participate equally nor were all participant classes equally represented within the study groups.

Finally, we measured two costs, intragroup feeding competition and inter-male aggression rates. Although feeding competition is expected to be low in small groups of folivorous primates (Isbell 1991; Janson and Goldsmith 1995), sifakas live in an environment where food availability is highly seasonal and are subject to periods of food scarcity. This is reflected in significant changes in body mass and body fat as their diet shifts from new leaves and fruit to mainly mature leaves (Lewis and Kappeler 2005). In order to determine if subordinate males increase intragroup feeding competition beyond increased scramble competition, we calculated the proportion of agonistic interactions in a feeding context (where at least one member of the dyad was either feeding or foraging) that were either won by subordinate males or females or were undecided outcomes. As a control, we also calculated proportions of agonistic interactions won by either D males or females in a feeding context. Additionally, we used Chi-squared tests to examine in which type of dyad (D male-female, subordinate male-female and female-female) the majority of aggressive interactions within a feeding context occurred. Expected values were derived that take into account the number of dyads of each type that are present within the study population.

High glucocorticoid output, a measure of stress, is a physiological cost faced by D males in the mating season (Fichtel et al. 2007) and can be influenced by aggression.

Additionally, aggression itself is a costly behavior due to risk of injury. We compared overall aggression rates between D-NN male, D-N male and D-R male dyads using a Kruskal-Wallis test. Wilcoxon matched-pairs tests were used to test the prediction that aggression rates would increase in the mating season when compared to the non-mating season in D-NN male and D-R male dyads but not in D-N male dyads. The mating season was defined as the onset of the first female's fertile phase in the study population to the termination of the last. Fertile phases were determined via hormone analysis of fecal progesterone levels as described in Mass et al. (in press).

The GLM and logistic regression were performed in R version 2.5.1. All other data analyses were preformed using STATISTICA (StatSoft Inc., version 6.0, 2001). The significance level was set at $p < 0.05$.

Results

Infant survival

Between July 1995 and June 2007, a total of 106 infants were born into the study population. Of these, only 57 survived to one year, a proportion similar to that for another population of Verreaux's sifaka at Beza Mahafaly in southwest Madagascar (Richard et al. 2002). Of the 49 infant deaths, several could be attributed to fossa predation based on the state of the remains when found. Mean(±SD) group size and number of non-natal subordinate males within groups during this period were 3.87±1.14 (range 2-9) individuals and 1.02±0.63 (range 0-3) individuals, respectively. Group size did not significantly affect the proportion of infants that survived to one year of age ($\Delta D=0.791$, df=1, $p=0.374$). When we added the number of subordinate males as an

additional explanatory variable, as compared to the model containing group size only, number of subordinate males also did not significantly reduce the deviance ($\Delta D = 0.089$, df=1, p=0.765). These results indicate that there is no effect of either group size or number of subordinate males on infant survival. A summary of the estimates (±SE) of the model is provided in Table 2.

Table 2. GLM for infant survival with group size and number of subordinate males as explanatory variables. Estimates express relationship between explanatory variables and the response variable (infant survival). There is no significant effect of either group size or number of subordinate males on infant survival.

Terms	Estimate	Standard Error	Z value	p
Intercept	-0.5482	0.7780	-0.705	0.481
Group size	0.2112	0.2522	0.837	0.402
Number subordinate males	-0.1335	0.4485	-0.298	0.766

Group takeovers

A total of eight takeovers over 12 study groups were recorded between 1995 and 2008 (n=113 group years). Seven takeovers occurred when there was one or more subordinate male present within the group and only one when there were no subordinates present. The average population takeover rate was 0.6 takeovers per year. The number of males present during a group year had no significant effect on the probability of whether a takeover occurred or not ($\beta_{males} \pm SE = 0.44 \pm 0.42$, z = 1.05, p = 0.29).

Resource defense

During the three sampling periods, a total of 134 intergroup encounters were observed. Out of this total, 81 encounters with known groups and decided outcomes could be used for the analysis of intergroup encounter winners. Bigger groups won more often (66% of encounters) than expected by chance (Chi-squared test: χ^2=5.59, df=1, p=0.018) but also groups with a higher proportion of males won (63% of encounters) significantly more often (Chi-squared test: χ^2=4.95, df=1, p=0.026).

All observed intergroup encounters (n=134) were included in the analysis of intergroup encounter participants. D males (n=10) participated in intergroup encounters more often than expected (Chi-squared test: χ^2=12.48, df= 1, p<0.0001) whereas R males (n=7) participated less often than expected by chance (Chi-squared test: χ^2=7.56, df=1, p=0.006). There was no difference between observed and expected participation frequencies for dominant females (n=10), adult females (n=9), NN males (n=4) and N males (n=10) (Fig.1.).

Intragroup feeding competition

A total of 383 agonistic interactions in a feeding context were observed over the three sampling periods between adult females and males. Females won these interactions 86% of the time. Males won agonistic interactions only 4% of the time (15 out of 383) and of these, subordinate males only won one encounter in a feeding context. The remaining 10% (38 out of 383) were interactions with an undecided outcome. Thirteen D male wins occurred during interactions with adult subordinate females. Between D and subordinate males, 67 agonistic interactions in a feeding

context were observed. As would be expected due to stable dominance hierarchies, D males won 99% of these interactions (66 out of 67). When aggressive interactions between females were included, a total of 425 interactions were observed. Aggressive interactions within a feeding context occurred more often than expected between D male-female dyads (n=18) (Chi-squared test: χ^2=115.84, df= 1, p<0.0001) and less often than expected between both subordinate male-female dyads (n=30) (Chi-squared test: χ^2=41.04, df= 1, p<0.0001) and female-female dyads (n=9) (Chi-squared test: χ^2=30.29, df= 1, p<0.0001).
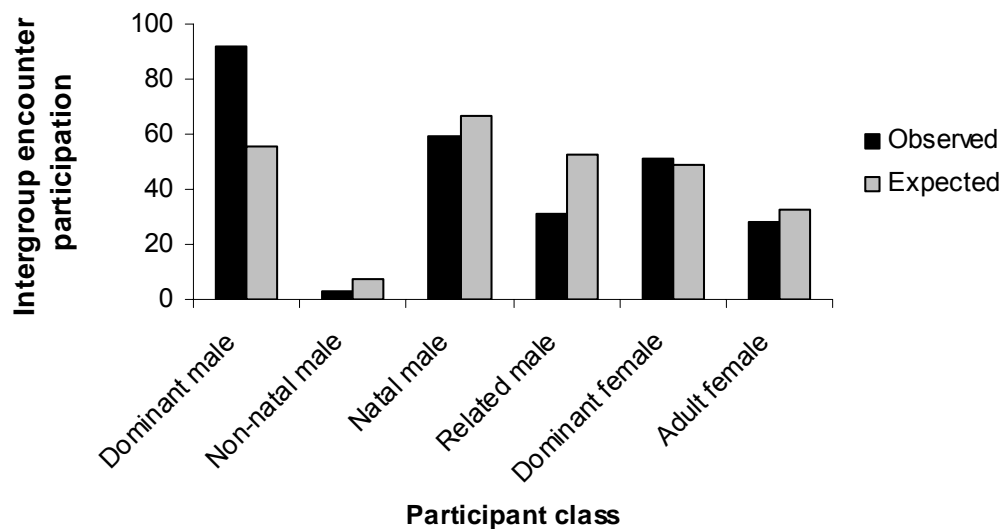

Fig. 1. Intergroup encounter participation for adult classes of individuals over three sampling periods. Dominant males participated more than expected (p = 0.0004) while related males participated less than expected (p = 0.006). All other participant classes participated as expected by chance. Expected values are weighted to take into account the different frequency of both group participation and participant classes within the population.

Inter-male aggression

There was no difference in overall aggression rates per hour between D males and all three classes of subordinate males (Kruskal-Wallis: H=2.46, n=23, p=0.29; median $_{NN}$=0.2, range=0.06-0.43; median $_N$=0.09, range=0.02-0.18; median $_R$=0.15,

range=0-0.31). Using results from hormone analyses (Mass et al. in press), we were able to divide the sampling period into mating season and non-mating season based on female fertile phases. The rate of aggression per hour increased significantly in the mating season between D-R male dyads (Wilcoxon-test: T=3, n=9, p=0.036; median $_{\text{mating season}}$=0.18, range=0-0.31; median $_{\text{non-mating season}}$=0.07, range=0-0.2) but not between D-N male dyads (Wilcoxon-test: T=15, n=10, p=0.2; median $_{\text{mating season}}$=0.04, range=0-0.3; median $_{\text{non-mating season}}$=0.1, range=0-0.21). Although we could not test for differences between the mating and non-mating season rate of aggression for D-NN male dyads due to low sample size (n=4), the data suggest an increase in aggression rate in the mating season (median $_{\text{mating season}}$=0.24, range=0.08-1.0; median $_{\text{non-mating season}}$=0.08, range=0.03-0.2) (Fig.2.).
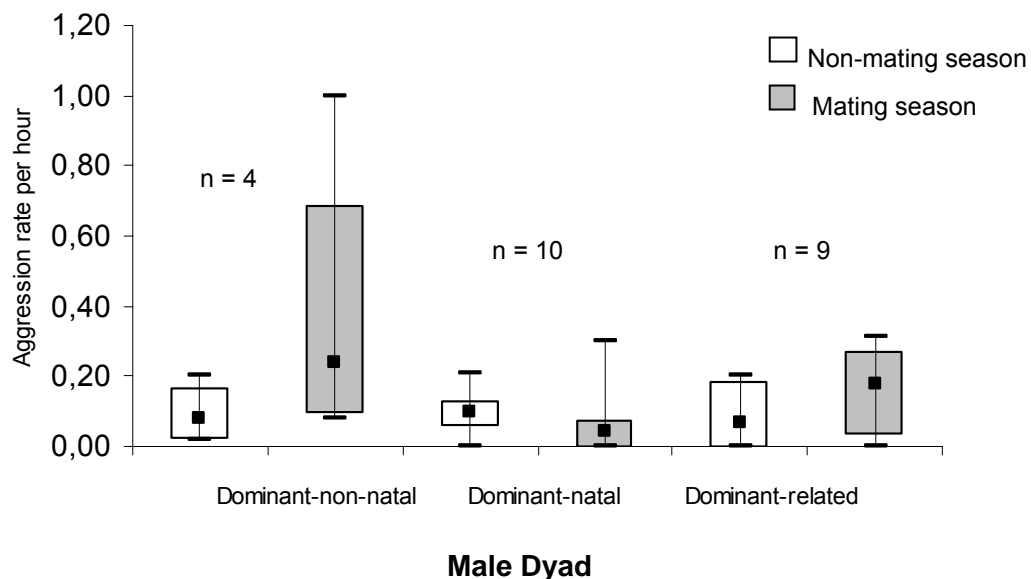

Fig. 2. Male-male aggression rates in the mating and non-mating season. There was a significant increase in aggression rate in the mating season for dominant-related male dyads (p = 0.036) but not for dominant-natal male dyads (p = 0.2). Statistical comparison of aggression rates in mating and non-mating season for dominant-non-natal male dyads could not be done due to low sample size (n = 4).

Discussion

Our results demonstrated that sifaka subordinate males provide none of the predicted benefits to the group but are also not too costly to D males or females in terms of intragroup feeding competition. Additionally, subordinate males are not very costly to the D male in terms of lost reproduction (Kappeler and Schäffler 2008). The presence of subordinate males in a group did not affect infant survival nor did it deter strange males from taking over the group. Although groups with a higher proportion of males won intergroup encounters more often, subordinate males did not participate in encounters more often than would be expected by their representation in groups. Bigger groups won intergroup encounters more frequently but group size is most often a function of the number of males in a group as the number of females tends not to vary as greatly. Although subordinate males provided almost no benefits, the D male faced some costs associated with the presence of NN and R subordinate males but not N subordinates in the form of increased mating competition as aggression rates increased when females were receptive. Thus, costs for D males in the form of increased male-male aggression may be offset by the benefits gained by females in terms of securing food resources contested between groups.

Infant survival

If males provide protection from both predators and potential infanticidal males, then groups with more males should have higher infant survival (Robinson 1988; Koenig 1995; Treves 1998; Treves 2000). Moreover, D males may benefit from the presence of subordinates if the loss in numbers of infants sired is outweighed by increased infant survival (van Schaik and Hörstermann 1994). Results from this study indicate that infant

survival in sifakas was not affected by either group size or the number of subordinate males present within the group. This result is in concordance with other group-living lemurs exhibiting even adult sex ratios, e.g. *L. catta* (Takahata et al. 2006) and *P. edwardsi* (Pochron and Wright 2003; Pochron et al. 2004) but not with *Cebus olivaceus* or *Alouatta* spp. In these species, female reproductive success and juvenile survival appear to be affected by the presence of males where females can maximize offspring survival by reproducing in a group that contains a high proportion of males (Robinson 1988; Treves 2001).

This discrepancy between lemurs and some anthropoid species could be due to differences in male vigilance effort. In both sifakas and *L. catta*, males in general were not more vigilant or likely to detect predators than females (Hussmann 1996; Gould et al. 1997) whereas males in a number of anthropoid species tend to be more vigilant than females (van Schaik and van Noordwijk 1989; Rose and Fedigan 1995). Sifaka males have been found to increase scanning behavior just prior to and during the mating season (Lewis 2004), which suggests an additional social function of male vigilance. Thus, the presence of extra subordinate males may only lower the per capita predation risk in general (Hamilton 1971), which can be a particularly important benefit in small groups.

Group takeovers

Additional males may confer fitness benefits to both D males and resident females by ensuring defense against infanticidal takeovers. Infanticide has been observed in *P. verreauxi* and *P. diadema* (Erhart and Overdorff 1998; Lewis et al. 2003). In contrast to what was reported for *E.f.rufus* (Ostner and Kappeler 2004), *Alouatta*

seniculus (Pope 1990) and *Artibeus jamaicensis* (Ortega and Arita 2002), the presence of subordinate males in Verreaux's sifaka does not deter strange males from taking over the group. Subordinate male sifakas do not face the same risk posed by potential infanticidal males in terms of decreased fitness as they are not receiving a large share of reproduction (Kappeler and Schäffler 2008) and, thus, there may be no pay off that outweighs the risks and costs of helping to defend the group from being taken over. Variable participation by subordinate males in encounters with conspecific males has also been reported for *Alouatta pigra*, a species in which infanticide after takeover also occurs (Kitchen 2004).

Thus, although groups are predicted to contain multiple males if infanticide is a serious threat (van Schaik 2000), the presence of multiple males in Verreaux's sifaka groups did not deter takeovers, and thus, this male benefit can not explain the presence of subordinate males within this species. Alternatively, the presence of multiple males may serve to reduce the risk of infanticide via paternity confusion. Although reproduction is highly skewed towards dominant individuals (Kappeler and Schäffler 2008), this may not reflect the actual mating skew. Female sifakas at Beza Mahafaly have been observed to mate with both extra-group males and within-group subordinate males (Brockman 1999). Thus, even though it is not possible to quantify the mating skew for the population of sifakas at Kirindy as mating is rarely observed, paternity confusion as a female benefit of multiple males within a group can not be ruled out.

Resource defense

Our results indicate that, in concordance with other primate species, e.g. *Eulemur macaco macaco* (Bayart and Simmen 2005) and *Cebus olivaceus* (Robinson 1988),

groups with a higher proportion of males win intergroup encounters more often, and thus, support the idea that an increased number of males within groups leads to increased intergroup dominance (Wrangham 1980). In many species of primates, males are the primary participants in encounters (Cheney and Seyfarth 1977; Harcourt 1978; Fashing 2001), which may be explained if encounters are primarily about mate defense instead of food resource defense (Cheney 1987). The fact that D male sifakas were the only individual class that participated more than expected may be explained by the fact that participating in intergroup encounters can be both costly and risky, and thus, participation may be related to greater reproductive benefits (Cheney and Seyfarth 1977; Cheney 1987). As subordinates are not receiving a large share of reproduction (Kappeler and Schäffler 2008), the fact that they do not participate more often than would be expected by chance is therefore not surprising. Alternatively, subordinate males may participate at levels that allow them to be tolerated as group members but that are not high enough to be conceded a share of reproduction.

Costs

Aggressive interactions in animals can stimulate the release of glucocorticoids (Balm 1999), which are an important component of the stress response (Munck et al. 1984). Fichtel et al. (2007) found that D male sifakas exhibit higher glucorticoid levels than subordinates during the mating season. Additionally, in several primate species including sifakas (Brockman et al. 1998; Kraus et al. 1999), males living in multi-male groups exhibit higher testosterone levels, a measure linked with heightened aggression, in the mating season due to within-group reproductive competition (Gould and Ziegler 2007; Ostner et al. 2008). Increased aggression can be costly due to an increase in the

risk of injury while engaged in aggressive interactions. Thus, although there is a cost to D males associated with the presence of males who are not related to group females, this cost may not be high enough to engage in fierce combat to evict them. Sifakas are highly seasonal breeders with females exhibiting a very short receptive period (Brockman 1999), and thus, high aggression rates should only be sustained over a short period of time.

The socioecological model and even adult sex ratios

Based on the assumptions of sexual selection theory and the socioecological model, we predicted successful monopolization of small groups of females by D male sifakas as is observed in cercopithecine primates with similar life history traits (Andelmann 1986). The fact that sifaka group composition is highly variable, even within the same population, (Richard 1985; Kubzdela 1997; Pochron and Wright 2003) but tends on average towards an even or male-biased adult sex ratio (Lewis and van Schaik 2007), shows that D males are not excluding potential rival males. This pattern has also been found for the population of Verreaux's sifaka at Beza Mahafaly (Brockman 1999). The deviation from the predictions of these two fundamental theories has been explained in several Old and New World primate species in relation to benefits provided to the group by subordinates (van Schaik and Hörstermann 1994; Mitani et al. 1996a). Additionally, it has been suggested that if D males profit in their associations with same-sex conspecifics, subordinates should receive a share of reproduction as an incentive to stay in the group (Vehrencamp 1983; Keller and Reeve 1994; Johnstone 2000).

The results of this study reveal that overall, subordinate males are not actively providing benefits to the group although their passive presence within a group does

contribute to intergroup dominance over feeding sites and a reduced per capita predation risk. Although male services have been suggested to be exchanged for mating opportunities (Duffy et al. 2007), group membership instead of reproduction could also be a commodity provided for services (van Schaik and van Noordwijk 1989; Gould 1996a). Therefore, an increase in intergroup dominance may be enough for females to tolerate the presence of subordinates and allow them group membership but may be too low for D males to provide them with a share of reproduction. This has also been shown for *Alouatta seniculus* (Pope 1990) and *Artibeus jamaicensis* (Ortega and Arita 2002).

An advantage over other groups with respect to access to feeding sites in the overlapping areas of home ranges is of relatively more importance to females (Wrangham 1980). This is especially true for a Malagasy primate living in a harsh seasonal environment where there are periods of severe food scarcity (Wright 1999). Although there is evidence to suggest that female reproductive success may be negatively affected with increasing group size due to intragroup feeding competition (Harcourt 1987; Koenig 2000; Koenig and Borries 2002), results of this study indicate that D not subordinate males are more costly to females in relation to intragroup feeding competition. Thus, the presence of subordinate males should not increase intragroup feeding competition per se for females. Moreover, Wrangham (1980) proposed that multi-male groups may have evolved as a means for females to compete more successfully for dominance over food resources with other groups.

Aside from intergroup dominance over contested food resources, female primates seem to prefer to live in groups with several males (Altmann 1990). Several benefits to females include mating with many males as a means to avoid genetic incompatibilities and to reduce the risk of infanticide through paternity confusion, enhancing parental

care, receiving good sperm and the facilitation of cryptic female choice (reviewed in Wolff and Macdonald 2004). Female Verreaux's sifaka have been observed to actively evict D males from the group but do not prevent and may even facilitate the residency and immigration of new subordinate males (Richard et al. 1993; Brockman 1999; Lewis 2004; Lewis 2008). Indeed, several studies have shown that female sifakas actively recruit subordinate males into the group (Brockman et al. 2001; Lewis 2008). Moreover, females have been observed to have facilitated copulation with both the D and subordinate males (Lewis and van Schaik 2007).Thus, female sifakas may be playing an active role in regulating group composition in favor of more males that may be facilitated by their dominant status (Richard 1987; Lewis 2008). The impact of female reproductive strategies on the evolution of even adult sex ratios in sifakas should therefore be studied in more detail.

Although variance in male mating success is generally positively correlated with dominance rank, e.g. *Cervus elaphus* (Clutton-Brock et al. 1982), *Felis catus* (Say et al. 2001), *Pan troglodytes* (Constable et al. 2001) and *Eulemur fulvus mayottensis* (Gachot-Neveu et al. 1999), a decrease in reproductive success is predicted if female group size increases as is seen in both *Alouatta palliata* (Ryan et al. 2008) and *E. fulvus rufus* (Kappeler and Port 2008). The fact that female group size in sifakas rarely exceeds four individuals and that females are receptive asynchronously within groups (Mass et al., in press) may allow D males to monopolize reproduction. Possible monopolization mechanisms include mate-guarding (Brockman 1999; Lewis and van Schaik 2007, Mass et al., in press) and physiological suppression of testosterone in subordinates by D males (Kraus et al. 1999). As a result, the presence of subordinate males is not a threat to D males in terms of lost reproduction and therefore may be tolerated by him

regardless of the lack of benefits received. Thus, D male reproductive strategies other than control of group membership can also help explain the unusual adult sex ratio in Verreaux's sifaka.

Although tolerance of subordinate males by both D males and females can lead to the evolution of even adult sex ratios in sifakas, subordinate male reproductive strategies also need to be considered as changes in group composition are mainly a result of their dispersal decisions. Thus, a combination of delayed natal dispersal and males immigrating into subordinate positions to queue for the dominant position (Kokko and Johnstone 1999; Cant and English 2006) also play a role in shaping Verreaux's sifaka social organization.

In conclusion, the tendency towards even or male-biased adult sex ratios in Verreaux's sifaka despite small female group size and estrous asynchrony within groups can be partially explained by social tolerance through benefits provided by subordinate males. These small benefits, namely dominance in intergroup competition, may be enough for females to prefer to reside in multi-male groups and for D males to tolerate subordinate males as group members but insufficient to grant them a share of reproduction. This unusual form of social organization must be seen as the outcome of the interplay of dominant male, female and subordinate male reproductive strategies. A deeper understanding of the factors that play a role in subordinate male dispersal decisions, is needed in order to fully comprehend not only why subordinate males use different reproductive strategies, but the evolutionary forces that shaped them.

CHAPTER 3:

Delayed dispersal versus social queuing: the behavioral consequences of alternative reproductive strategies in male Verreaux's sifaka (*Propithecus verreauxi*)

with P.M. Kappeler

Abstract

In group living animals, where reproduction is skewed in favor of dominant individuals, dispersal decisions can have significant consequences for an individual's lifetime reproductive fitness. In Verreaux's sifaka (*Propithecus verreauxi*), a multi-male multi-female group living lemur with a tendency toward even adult sex ratios despite low numbers of females, males are the dispersing sex while females remain philopatric. As the dominant male of a group effectively monopolizes reproduction, males should aim to attain top dominance. However, several strategies to attain top dominance exist in this species. We studied the behavioral consequences of two subordinate male strategies: delayed natal dispersal and social queuing for the dominant position in a non-natal group. Results based on >300 hours of focal observations of subordinate males in both natal and non-natal groups reveal that there are few behavioral advantages in delaying dispersal. Natal males are not groomed more often, do not spend more time feeding nor do they maintain a more spatially central position in the group when compared to non-natal males. Although there is a trend towards increased aggression for non-natal males, aggression rates were only significantly higher during the short mating season. Overall, these results suggest that there are no evident behavioral advantages in delaying dispersal, and, thus, early immigration into a non-natal group, where there is the potential to sire offspring or inherit the dominant position, may be a more beneficial strategy. Understanding the behavioral consequences of dispersal decisions may provide a deeper understanding of subordinate male reproductive strategies, which, in turn, may help shed light on relevant constraints and opportunities.

Keywords: Reproductive strategies, delayed dispersal, social queuing, *Propithecus verreauxi*

Introduction

The dispersal decisions made by group living animals can have significant consequences for both their survival and lifetime reproductive success, as well as for the genetic make-up of populations (Greenwood 1980; Pusey and Packer 1987; Clobert et al. 2001). In many species, one sex tends to disperse more frequently than the other, and the direction of this sex-bias is generally thought to reflect the mating system of the species. Whereas the majority of monogamous birds are characterized by female-biased dispersal, most polygynous mammals tend towards male-biased dispersal and female philopatry (Greenwood 1980; Dobson 1982; reviewed in Lawson Handley and Perrin 2007).

This pattern amongst mammals may be explained by the fact that in most polygynous species, male reproductive success is limited by their access to and monopolization of receptive females (Bateman 1948; Trivers 1972), whereas females, whose reproductive success is ultimately constrained by their access to resources, benefit from philopatry (Emlen and Oring 1977; Wrangham 1980; Ims 1988). Moreover, female philopatry encourages male dispersal as a means to avoid inbreeding (Pusey and Packer 1987; Lawson Handley and Perrin 2007). Cohesive groups of females constitute a resource for males that can be defended, promoting intrasexual competition (Le Boeuf 1974; Bradbury and Vehrencamp 1977; Waser and Jones 1983; Moore and Ali 1984; Voigt et al. 2001). Dispersal is therefore a mechanism that males use in an attempt to increase their reproductive success via increasing their access to potential mates (Greenwood 1980; Dobson 1982; Moore and Ali 1984; Sheilds 1987; Clutton-Brock 1989a; Alberts and Altmann 1995a).

The main proximate causes of dispersal applicable to primates are sexual attraction to extra-group individuals and eviction (Pusey and Packer 1987). In many species, males transfer into groups containing unfamiliar and/or unrelated females (Pusey and Packer 1987; Olupot and Waser 2001). If sexual attraction is the cause of dispersal, then individuals should disperse into groups with a more favorable sex ratio, as observed in baboons (Packer 1979; Alberts and Altmann 1995a), white-faced capuchins (Jack and Fedigan 2004b) and ringtailed lemurs (Sussman 1992). Dispersal may also be forced as a result of aggression by conspecifics (Pusey and Packer 1987), such as during group takeovers by strange males (Crockett and Sekulic 1984), or caused by increased levels of aggression received from resident adult males, as shown for black and white colobus monkeys (Struhsaker and Leland 1979) and gray langurs (Sugiyama 1967). In most group living primates though, there is no increase in aggression towards natal males, and, thus, the decision to disperse is generally voluntary (Henzi and Lucas 1980; Jones 1983; van Noordwijk and van Schaik 1985; Pereira and Weiss 1991).

In many primate species with a low number of adult females within groups, including mountain gorillas (Bradley et al. 2005), long-tailed macaques (van Noordwijk 1985), white-faced capuchins (Jack and Fedigan 2003) and Verreaux's sifaka (Kappeler and Schäffler 2008), reproduction is highly skewed in favor of dominant individuals, and, therefore, a male's lifetime reproductive success depends upon attaining top dominance. Dispersal is a mechanism that males can use to increase their dominance rank, and, thus, their potential reproductive success (Jack and Fedigan 2004b). Decisions concerning where to disperse should be based on knowledge of both the composition of surrounding groups and the likelihood of attaining a breeding position.

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Moreover, dispersal can be stressful (Alberts and Altmann 1995a) and risky due to increased risk of predation, lost reproductive opportunities and increased aggression from conspecifics that can result in weight loss and even death (Cheney 1983; Pusey and Packer 1987; Alberts and Altmann 1995a). Therefore, males should make decisions that increase their likelihood of moving into a breeding position.

There are two ways that males can disperse into a new group. They can either attempt to aggressively takeover the alpha position as shown for Hanuman langurs (Borries 2000) and baboons (Packer 1979), or they can enter peacefully and initially assume a lower position in the dominance hierarchy, as observed in vervet monkeys (Henzi and Lucas 1980). Aggressive takeover is a strategy more commonly used by older males, while younger males tend to immigrate into a subordinate position (Sprague 1992). Immigrating into a subordinate position in a non-natal group may be a less risky strategy in terms of limiting received aggression from resident males (van Noordwijk and van Schaik 1985; Jack and Fedigan 2004a) and may also be advantageous in terms of reproductive fitness due to both the increased probability of siring offspring, in comparison to staying in the natal group, and the possibility of eventually inheriting the dominant position within the group, a strategy referred to as social queuing (Kokko and Johnstone 1999). Queuing is a strategy used by males in several species, including mountain gorillas (Bradley et al. 2005), spotted hyenas (East and Hofer 2001) and black grouse (Kokko et al. 1998). Despite the total lack of reproduction, these males may obtain a long-term reproductive benefit by using this strategy if subordinates can eventually inherit the dominant position (Kokko and Johnstone 1999), as has been shown for Jamaican fruit-eating bats (Ortega and Arita 2002).

Delaying dispersal and remaining in the natal group past sexual maturity may also be a viable subordinate male reproductive strategy as it may allow subordinates to attain the full body size and strength needed to challenge for a dominant position (Cheney and Seyfarth 1983; van Noordwijk and van Schaik 1985; Alberts and Altmann 1995a; Sprague et al. 1998). In species where almost all reproduction is monopolized by the dominant male, the decision to delay dispersal and thus to increase the chance of obtaining a breeding position in a new group, may have significant consequences for lifetime reproductive success.

Although delaying natal dispersal past sexual maturity means that a male forgoes present reproductive opportunities (Koenig et al. 1992), a major benefit may be the ability to use the natal group as a safe haven from which to monitor or wait for breeding opportunities, especially if the chances of obtaining a breeding position elsewhere are small (Emlen 1982; Kokko and Ekman 2002). Importantly, Wolfenden and Fitzpatrick (1978) found that young individuals who remain longer in the natal group have increased fitness as they benefit from a higher probability of survival, and thus, future breeding opportunities. In the short-term, there may also be behavioral advantages in delaying dispersal that increase a male's competitive ability while remaining in a safe haven, such as minimizing conspecific aggression and predation risk, while simultaneously increasing the amount of time spent feeding.

Natal males may benefit in comparison to non-natal males by not incurring the costs associated with increased levels of aggression from conspecifics (Cheney and Seyfarth 1983; Munck et al. 1984; Dittus 1986; Pusey and Packer 1987; Balm 1999). In addition, if subordinate non-natal males are more apprehensive and therefore, more socially alert within the group due to potential aggressive interactions, the amount of

time an individual is able to spend feeding is expected to decrease as vigilance behavior is difficult to maintain while engaged in feeding and foraging activities (Ruiter 1986; Yaber and Herrera 1994). Natal males may also benefit from maintaining a more spatially central position within the group. Several studies have shown that individuals are more vigilant when they are in positions of higher predation risk, such as on the periphery of the group, or with fewer neighbors in close proximity (Hamilton 1971; van Schaik and van Noordwijk 1989; Rose and Fedigan 1995). Finally, natal males may be groomed more frequently than non-natal males, constituting a biological benefit, as removing ectoparasites and dirt from the fur enhances good health (Freeland 1976; Hutchins and Barash 1976; Barton 1985). Dispersal decisions may thus reflect the trade off between the short-term benefit of increased potential reproductive fitness in a non-natal group versus the behavioral benefits of delaying dispersal and using the natal group as a safe haven (Kokko and Ekman 2002).

The pattern of male-biased dispersal and female philopatry characterizes Verreaux's sifaka (*Propithecus verreauxi*) even though females have occasionally been observed to disperse (Jolly 1966; Richard et al. 1993; Kubzdela 1997). Although reproduction in this species is highly seasonal, with females becoming receptive once per year for a period of up to 96 hours (Brockman 1994; Brockman and Whitten 1996; Brockman 1999) during a short mating season from January to March, females come into estrus asynchronously and the dominant male of the social group is able to monopolize each female as she becomes receptive (Mass et al., in press). Indeed, genetic paternity analysis revealed that these dominant males sired almost all offspring (91% of 33 infants) (Kappeler and Schäffler 2008) despite the tendency toward an even or male-biased adult sex ratio (Richard 1985; Lewis and van Schaik 2007; Kappeler and

Schäffler 2008). Thus, the only secure route to successful breeding is to become the dominant male, yet only a few males achieve this top position within a social group. Analysis of over 15 years of demography data revealed that social queuing can pay off in terms of achieving the dominant position but that older males are more successful in taking over groups (Kappeler and Mass, in prep), suggesting that delaying dispersal and using the natal group as a safe haven (Kokko and Ekman 2002) may indeed be a viable reproductive tactic in this species. Thus, as the use of both strategies can possibly lead to long-term reproductive benefits, we examined whether there were short term behavioral benefits in delaying dispersal which could explain why some males use this strategy while others establish themselves as a subordinate in a non-natal group.

We studied the behavior of both natal and non-natal subordinate adult male sifakas to identify potential behavioral benefits of delaying dispersal. Moreover, we had the unique opportunity to assess changes in several measures of behavior in males that moved back and forth between the natal and non-natal group (roaming males). We predicted that natal males would benefit from delaying dispersal because (1) aggression rates would be lower for natal males than for non-natal males, (2) natal males would spend more time feeding than non-natal males, (3) natal males would occupy a more spatially central position within the group than non-natal males, and (4) natal males would receive more grooming than non-natal males. In quantifying how different dispersal strategies used by subordinate male sifakas may vary in terms of behavioral benefits, we hoped to gain a better understanding of the short-term costs and benefits of subordinate male dispersal decisions.

Materials and methods

Study site and population

This study is part of an ongoing long-term study conducted in Kirindy Forest, a dry deciduous forest located in central western Madagascar, 60 km north of Morondava (Sorg et al. 2003). The site is operated by the Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie (CNFEREF) Morondava. The German Primate Center (DPZ) has established a field station with three study areas within the forestry concession, where ongoing research has been conducted since 1993. Since 1995, all individuals in the sifaka study groups have been well habituated and individually marked with either nylon collars and unique pendants or radio collars (Kappeler and Schäffler 2008). We have not observed any injuries or adverse effects on behavior as a result of the capture procedure or the collars. Our research was approved by the Malagasy Ministère de l'Environnement et des Eaux et Forêt.

We studied the behavior of subordinate males residing in six of the study groups found in the 60ha study area locally referred to as CS7 (Table 1). As males disperse and are observed to mate at 3-4 years of age (Richard et al. 1991; Richard et al. 1993; Rümenap 1997; Richard et al. 2002), all males of known age included in this study were at least 3 years old. Natal and non-natal status was determined genetically using 15 nuclear microsatellite markers for parentage analysis (Kappeler and Schäffler 2008). Males were considered delayed dispersers if they were past 3 years of age, and thus sexually mature, and had not fully established themselves in a non-natal group.

Table 1. Group composition of study groups including focal individual males. (*) denotes groups in which males roam between. The number of adult males given represents the maximum number of adult males that can be present within the group at any given time.

Group	Adult Males	Adult Females	Juveniles
B*	5	1	-
C*	3	1	1
E	3	2	1
F	2	1	-
G*	5	3	1
J	3	3	1

Data collection

All subordinate males over the age of 3 years were observed and classified as either natal subordinate males (n=5) or non-natal subordinate males (n=5) (Table 2). Males residing in groups where they were unrelated to the group females were considered to be non-natal males. Three males (Bo, Ka and Ko) roamed between their natal group and a non-natal group and generally switched between groups once or twice per day. The younger males Ka and Ko locomoted between groups either solitarily or together, while the older male Bo always moved solitarily. These three males were generally found in the natal group in the early morning suggesting that they spent the night in their natal group. One male (Ma) was mostly found in the natal group but was also found on the periphery of several other study groups. Although this male attempted to disperse in 2006, he returned to his natal group in early 2007 and has since spent the majority of his time there. These four males are hereby referred to as roamers. The young natal male Ga was sighted occasionally on the periphery of another study group

in the population, generally after intergroup encounters between this group and his natal

group, but was never observed within another study group. These five males (Bo, Ka,

Ko, Ma, Ga) were classified as natal males in comparisons with non-natal males as they

still have not fully established themselves in a non-natal group. Additionally, the

observed roaming behavior while returning to the natal group may be a means to gather

information on surrounding groups to base future dispersal decisions on.

Table 2. Focal subordinate males and observation hours. Individuals denoted by (*) were observed in both their natal and non-natal groups. Observation hours are given for both groups. Age in months is based on known birth dates except for Te and To which are estimates based on dental wear.

Focal Individual	Group	Status	Age (months)	Observation Hours (natal – non-natal)
Bo*	B – G	Roam	77	4.5 – 37.5
Ka*	B – G	Roam	53	15 – 19.5
Ko*	B – G	Roam	41	7.5 – 30.0
Ma*	B – G / C	Roam	89	31.5 – 4.5
Ga	C	Natal	53	36.0
Ha	E	Non-natal	89	36.0
Me	E	Non-natal	53	36.0
Fr	F	Non-natal	65	31.5
Te	J	Non-natal	53-65	34.5
To	J	Non-natal	53-65	36.0
Total Observation Hours				**360**

Behavioral data were collected by V.M. between November 2007 and March

2008 using continuous focal animal sampling (Altmann 1974). Two focal animals were

observed per day (one morning and one afternoon session) between 6:00 and 18:00h.

Behavior was recorded using protocols based on a previously published ethogram for

the species (Brockman 1994). Each focal session lasted either 1.5 or 3 hours, yielding a total of 360 observation hours out of which 171.5 observation hours were conducted during the mating season. The discrepancy in focal protocol length was caused by dramatically increased search times if the focal animal was in transition between groups or on the periphery of a group. Sessions that were terminated before completion (i.e. focal animal out of sight for more than 10% of observation time and weather conditions) were not included in analysis. Samples were balanced across the statistical day and evenly distributed among the whole study period.

During each observation session, we continuously recorded the activity (feeding, resting, locomotion and grooming) of the focal animal. Here, feeding is defined as actively eating or reaching for the next food item. For aggressive and submissive behaviors (sensu Brockman 1994), we recorded the identity of the opponent and whether the interaction had a decided outcome, denoted by a clear submissive signal, such as a submissive vocalization, tail rolling and/or jumping away, by one opponent (Pereira and Kappeler 1997). A series of aggressive interactions between one dyad were considered a single event if less than one minute passed between consecutive interactions. Finally, we noted the distance from the focal animal to other group members via instantaneous scan sampling (Altmann 1974) at the onset of the focal protocol and at 15 minute intervals throughout the protocol, yielding a total of 1521 scans. Scans in which the focal individual moved between groups or was solitary were not included in our analyses.

Data analyses

To determine whether there are behavioral differences between natal and non-natal males, we made two types of comparisons. Firstly, we compared the behavior of roaming males in their natal group to their behavior in the non-natal group. Secondly, we compared the behavior of natal males (including roaming males in the natal group) to non-natal males. All behavioral comparisons were made using the data set that was collected during the entire sampling period, but for several analyses, we subsequently examined behavior in the mating season separately. The mating season was defined as the time between the onset of the first female's receptive period in the population until the termination of the last receptive period. Receptive periods were determined for a previous study via hormone analysis of fecal immunoreactive progesterone (iP4) levels. Fecal progesterone profiles were generated where the significant rise in fecal iP4 levels indicated that ovulation had occurred and thus we could determine the estrous period for each adult female in the population (Mass et al., in press).

All analyses were based on derived rates of behavior per hour observation time. Behavioral differences between natal males and non-natal males were tested using the Mann-Whitney U test. Due to low sample size (n=4), differences between roamers in their natal and non-natal group could not be tested statistically, and therefore, only medians and ranges are given. All data analyses were preformed using STATISTICA (StatSoft Inc., version 6.0, 2001). The significance level was set at $p \leq 0.05$ but the p-value was adjusted using the Bonferroni correction when two or more tests were conducted on the same data set.

Results

The total observation time per subordinate male ranged between 31.5-42.0 hours per individual (mean$\pm$SD=36$\pm$2.65h). There were no significant differences in the proportion of time spent feeding between natal and non-natal males over the entire observation period (MWU-test: $U_{5,5}$=11, p=0.75; median $_{natal}$=0.49, range=0.44-0.66; median $_{non-natal}$=0.54, range=0.46-0.59) or when we examined the mating season separately (MWU-test: $U_{5,5}$=10, p=0.6; median $_{natal}$=0.58, range=0.42-0.66; median $_{non-natal}$=0.62, range=0.43-0.66).

The proportion of observation time that the four roaming males spent feeding was similar in both the natal and non-natal group (median $_{natal}$=0.48, range=0.4-0.7; median $_{non-natal}$=0.43, range=0.4-0.5). Medians were also similar in the mating season and reflect those found for the whole data set, and are thus not reported here.

The proportion of time that all focal individuals were groomed by other group members was low (median=0.0027, range=0-0.009). There was no significant difference in the proportion of total observation time that natal and non-natal males were groomed by other group members (MWU-test: $U_{5,5}$=7, p=0.25; median $_{natal}$=0.0045, range=0.0004-0.0072; median $_{non-natal}$=0.0019, range=0.0012-0.0034). Roaming males were also groomed for similar proportions of time when in the natal and the non-natal group (median $_{natal}$=0.0046, range=0.0025-0.0072; median $_{non-natal}$=0.0032, range=0-0.009).

Natal and non-natal males did not differ in the proportion of total scans that they spent within 10 m of at least two group members over the entire observation period (MWU-test: $U_{5,5}$=12, p=0.92; median $_{natal}$=0.66, range=0.63-0.8; median $_{non-natal}$=0.71,

range=0.33-0.76) or during the mating season (MWU-test: $U_{5,5}$=12, p=0.92; median $_{natal}$=0.58, range=0.45-0.78; median $_{non-natal}$=0.66, range=0.3-0.71).

The proportion of scans that roaming males spent within 10m of at least two group members in the natal or non-natal group were similar over the entire observation period (median $_{natal}$=0.66, range=0.63-0.8; median $_{non-natal}$=0.52, range=0-0.52) and in the mating season (median $_{natal}$=0.59, range=0.45-0.78; median $_{non-natal}$=0.41, range=0-0.51).

Table 3. Median aggression rates per hour for natal (n=5) and non-natal subordinate males (n=5) over the entire observation period or in the mating season only. Values indicate aggression received by the subordinate male. Significant results are shown in bold.

Aggression received	Natal males (median, range)	Non-natal males (median, range)	Mann-Whitney U	
			U	$P_{adj} \leq 0.03$
All aggression				
Overall	0.25 (0.13-0.42)	0.47 (0.22-0.58)	6.5	0.21
Mating season	0.22 (0.00-0.30)	0.67 (0.13-0.87)	3.0	0.05
Male residents				
Overall	0.13 (0.11-0.22)	0.14 (0.10-0.36)	11.5	0.84
Mating season	0.15 (0.00-0.22)	0.22 (0.10-0.67)	6.0	0.18
Female residents				
Overall	0.03 (0.00-0.31)	0.13 (0.09-0.44)	7.0	0.25
Mating season	**0.00 (0.00-0.15)**	**0.20 (0.07-0.44)**	**1.0**	**0.02**

Throughout the study, we observed 148 decided aggressive interactions where subordinate males received aggression from either resident males (n=73 interactions) or resident females (n=75 interactions). Aggression rates with female opponents were higher for non-natal males in the mating season than for natal males. Although aggression rates were consistently higher for non-natal males than natal males over the

entire observation period, in the mating season and with male opponents in the mating season, these differences were not significant (Table 3). Even though we could not test for differences statistically, the rate of aggression for roaming males was also consistently higher in the non-natal group when compared to the natal group over the entire sampling period, and in the mating season only, and from both male and female opponents (Table 4).

Table 4. Median received aggression rates per hour for roaming males in the natal group (n=4) and the non-natal group (n=4) over the entire observation period or in the mating season only. Due to low sample size, differences in aggression rate could not be tested statistically.

Overall aggression received	Natal group (median, range)	Non-natal group (median, range)
All seasons	0.24 (0.13-0.27)	0.49 (0.22-0.72)
Mating season	0.11 (0.00-0.22)	0.35 (0.22-0.59)
Male residents		
All seasons	0.18 (0.13-0.22)	0.24 (0.07-0.29)
Mating season	0.11 (0.00-0.22)	0.20 (0.06-0.30)
Female residents		
All seasons	0.02 (0.00-1.30)	0.31 (0.00-0.47)
Mating season	0.00 (0.00-0.00)	0.21 (0.00-0.33)

Discussion

In our study, there were few behavioral differences between natal and non-natal subordinate males discernible. Natal males did not spend a greater proportion of time feeding, nor were there differences in the proportion of scans that they were found in proximity to other group members when compared to males in a non-natal group. Although the frequency of grooming received was low in general, natal males were not groomed more frequently than non-natal males. Finally, non-natal males may have faced a cost in terms of increased aggression when compared to natal males. Even

though there was no significant difference in the overall aggression rate, or with male opponents specifically, rates for non-natal males were still double that of natal males over the entire observation period and consistently higher than for natal males with male opponents. The trend towards increased aggression in the non-natal group was also supported when we examined aggression rates for roamers, although these results should be interpreted with caution as roaming males may incur higher aggression rates in the non-natal group as they are not group members, and there is also the possibility that residents may be resisting an immigration attempt. In addition, the overall lack of significance in aggression rates may also be due to low sample size. Nevertheless, this cost may pose a constraint on immigrating males that may contribute to delayed dispersal.

As animals are expected to be more nepotistic towards kin (Walters 1981), the fact that natal males were not groomed more than non-natal males was unexpected. This result may be due to the subordinate status of all focal individuals, regardless if natal or non-natal, as sifakas tend to groom up the hierarchy. Additionally, the fact that there were no differences in the amount of time spent feeding between natal and non-natal males was also somewhat surprising and possibly due to low sample size and/or food abundance. Nevertheless, these results are similar to what was found for blue monkeys (Ekernas and Cords 2007). Thus, although there seems to be no social or energetic benefit in delaying dispersal to remain in the natal group, queuing males may incur a cost due to the trend towards increased levels of aggression in the non-natal group.

As shown for long-tailed macaques (van Noordwijk and van Schaik 1985; IJsseldijk 1989), the rate of aggression faced by non-natal subordinate males tended to

be higher, although not significantly so, than for natal males and was consistently higher for roaming males in the non-natal group. The low to non-existent levels of aggression faced by roaming males in the natal group suggests that natal dispersal is not due to eviction, which is consistent with results for another population of sifakas at Beza Mahafaly in southwest Madagascar (Richard et al. 1993), and for several other primate species including ringtailed lemurs (Sussman 1991), white-faced capuchins (Jack and Fedigan 2004a) and long-tailed macaques (van Noordwijk and van Schaik 1985). Although most aggression in a non-natal group generally comes from same sexed individuals, immigrating individuals can also face aggression from the opposite sex (Packer 1979; Pusey and Packer 1987). In this study, the increase in aggression rate during the mating season was caused by aggression received from resident females. This sex-bias may be due to the fact that female sifakas are dominant to males, and, thus, have feeding priority (Richard 1987). Indeed, the majority of aggressive interactions occurred in a feeding context (Kappeler et al., in review). Regardless of the sex of the opponent, increased aggression can be a physiological cost associated with membership in a non-natal group.

Dispersal is primarily aimed at establishing residency in a breeding group as a means to increase mating opportunities, even though this behavior can be costly both due to increased risks while dispersing and increased rates of aggression in the target group (Alberts and Altmann 1995a). Additionally, results from a previous study revealed that the average population takeover rate for sifakas at Kirindy is low, 0.06 per year (n=113 group years, range=0.0-0.14) (Kappeler et al. in review), making the probability of entering a group in the dominant position quite low. This problem is exacerbated by the fact that dominant male tenure is around five years (Richard et al. 1993, Kappeler,

unpubl.data) with some tenures lasting more than 10 years (Kappeler, unpubl. data). Low breeding position turnover may be a major factor that contributes to delayed dispersal (Brown 1969; Koenig et al. 1992). Results based on genetic paternity analysis of over 12 years of demography data, revealed that 22% of sifaka males at Kirindy delayed dispersal (Kappeler and Schäffler 2008). This phenomenon has also been reported for the population of sifakas at Beza Mahafaly (Richard et al. 2002).

Remaining in the natal group past sexual maturity means forgoing reproductive opportunities (Koenig et al. 1992) as sifaka males have not been observed to reproduce in the natal group (Kappeler and Schäffler 2008). Yet, there may be short-term behavioral benefits associated with delaying dispersal (Kokko and Ekman 2002). Although cooperation among males is expected when living with relatives leading to inclusive fitness gains for subordinates who remain in their natal groups (van Hooff and van Schaik 1994), there are no indirect fitness benefits (Kappeler et al., in review) or behavioral benefits for subordinate male sifakas that delay dispersal. Thus, subordinate male sifakas may be using the natal group to wait for breeding opportunities in an otherwise saturated environment, and as a base to gather information on surrounding groups on which to base dispersal decisions. More specifically, males may delay dispersal until the male-female sex ratio in neighboring groups is more favorable, the female offspring of dominant males within these neighboring groups approach sexual maturity or the possibility of takeover may be more likely (Kappeler and Mass, in prep.). In addition, parallel dispersal may also help explain why some males remain longer in the natal group. As transferring groups in pairs may decrease the risks associated with dispersal, males may wait for a younger sibling to reach dispersal age so that they may leave the natal group together (Pusey and Packer 1987).

Alternatively, males can try to establish themselves as a subordinate in a breeding group with the future possibility of inheriting the dominant position (Kokko and Johnstone 1999). Queuing for the dominant position is a strategy used by at least 9% of males within the population (Kappeler and Schäffler 2008). Subordinate males may therefore decide to disperse and transfer into groups where there is a greater possibility of eventually achieving the status of dominant male, as has been shown for ringtailed lemurs (Sussman 1992). This potential future long-term benefit may be great enough to outweigh the costs associated with being a subordinate in a non-natal group such as increased aggression and giving up the natal safe haven (Kokko and Ekman 2002). Additionally, queuing for the dominant position, and, thus, the possibility of future reproductive success, can provide a strong incentive for a subordinate male to stay in the group despite no current reproductive success (Wiley and Rabenold 1984; Kokko and Johnstone 1999), as shown for many cooperative vertebrates and social insects (Emlen 1991; Monnin and Ratnieks 1999; Cant and Field 2001; East and Hofer 2001).

The stability of multi-male sifaka groups, where reproduction is monopolized by the dominant male, may be due to the fact that subordinate males may expect higher lifetime reproductive fitness by remaining in a non-reproductive position than they can by leaving in search of other reproductive opportunities (Gowaty 1981; Stacey 1982; Vehrencamp 1983). If adopting the social queuing strategy doesn't pay off, then the subordinate male still gains by being in a bisexual group in comparison to being solitary due to decreased predation risk (van Schaik and Hörstermann 1994) and the non-zero chance of siring offspring. On the other hand, failed queuers may suffer the costs of lost reproductive opportunities elsewhere while investing time in an unsuccessful group, and, thus, queuing may be a risky strategy as invested time does not necessarily guarantee

inheritance of the breeding position. Therefore, what remains to be determined is the lifetime reproductive success of males pursuing different strategies, and, thus, the long-term benefits of each strategy.

Conclusion

In Verreaux's sifaka, becoming the dominant male is ultimately the best reproductive tactic. To obtain the breeding position, males need to make informed dispersal decisions based on the probability of attaining a dominant position. Although aggressively taking over the dominant position is a viable and successful reproductive tactic, it is not a common one, as exemplified by the low population takeover rate. Subordinate males have developed additional strategies, including delaying dispersal and using the natal group as a safe haven to wait for breeding opportunities, or becoming a subordinate in a non-breeding position in a non-natal group. In this study, we had the unique opportunity to assess the behavioral costs and benefits for adult males that remained in the natal group in comparison to those that dispersed. As there were few behavioral differences between these two sets of males, the potential advantages of delaying dispersal may not be great enough to offset the costs of dispersal. Our study also highlights the importance of long-term studies for measuring the reproductive consequences of different reproductive strategies.

GENERAL DISCUSSION

Lemurs have puzzled primatologists for years due to their deviance from several predictions derived from the theoretical framework of sexual selection theory that have been supported by studies on anthropoid primates. In many anthropoids, single males are able to monopolize groups of up to 5 or 6 females (Andelman 1986; Mitani et al. 1996a; Nunn 1999), but gregarious lemurs are characterized by the presence of several males despite small female group size and extremely seasonal reproduction (van Schaik and Kappeler 1993; Kappeler and Heymann 1996; Kappeler 2000a). In most primates, the presence of several males within a group results in a high intensity of reproductive competition among males and is associated with sexual dimorphism in body size and canine length (Clutton-Brock 1985; Plavcan and van Schaik 1992). Yet, in group-living lemurs, sexual dimorphism is reduced or absent (Kappeler 1991; Kappeler 1997). Moreover, dominant males in several species are able to monopolize reproduction (Pereira and Weiss 1991; Nievergelt et al. 2002; Kappeler and Port 2008; Kappeler and Schäffler 2008). Finally, female dominance in lemurs is quite common whereas this phenomenon is rare among anthropoid primates (Richard 1987; Pereira et al. 1990; Pochron et al. 2003). Therefore, morphological, behavioral and demographic characteristics of lemurs do not follow theoretical expectations derived from both the socioecological model and sexual selection theory (Kappeler 1993; Kappeler 1997; Kappeler 2000a).

These deviations from predicted patterns lead to several fundamental questions which I attempted to address in this thesis. I used a combination of behavioral, hormonal

and long-term demographic data to examine male reproductive strategies in an attempt to illuminate the mechanisms behind high reproductive skew and the unusual sex ratios in group composition using Verreaux's sifaka (*Propithecus verreauxi*) as a model taxon. In the first part of this discussion, I will summarize the results of this present thesis on male reproductive strategies and in the second part I will then discuss how these results may help explain several lemur idiosyncrasies.

Main results

The number of females in a group and their degree of estrous synchrony are important determinants of male monopolization potential, and thus, whether species form single or multi-male groups (Andelman 1986; Ridley 1986; Altmann 1990). As female sifakas residing in the same social group become receptive asynchronously during the short breeding season and may be signaling receptivity via olfactory cues (**chapter 1**), dominant males should be able to monopolize access to each female as she becomes receptive. The ability to monopolize females at the reproductive level explains the extreme reproductive skew observed within the study population (Kappeler and Schäffler 2008).

By analyzing changes in male-female dyad proximity during periods of female receptivity, we found support for the use of mate-guarding as a male reproductive strategy in sifakas (**chapter 1**) that may underlie high male reproductive skew. In addition, although inter-male aggression increased while females were receptive, overall aggression rates were low (**chapters 1, 2 and 3**) as has been shown in another study on the same population (Lewis and van Schaik 2007). These results suggest that males may not be physically fighting over access to receptive females, and thus, traits that

increase body mass and weaponry may not be selected for. Instead, traits that increase speed and agility may be more beneficial in sifakas as most fights between males, when they do occur, take the form of high speed arboreal chases (Lawler et al. 2005). However, as the degree of reproductive skew in sifakas is similar to that of other sexually dimorphic species such as mountain gorillas (Bradley et al. 2005) and red howler monkeys (Pope 1990), the fact that sifakas are sexually monomorphic is still somewhat puzzling.

As dominant males are able to exclude subordinates from reproduction, the next logical step is to understand why groups contain an unusually high number of males (Kappeler 2000a), and thus, why subordinates are not being excluded on the demographic level. In order to examine this phenomenon, we analyzed whether there were benefits associated with the presence of subordinate males within a group as has been found for howler monkeys (Kitchen 2004; Ryan et al. 2008) and sympatric redfronted lemurs (Ostner and Kappeler 2004).

Although there was no evidence for subordinate male benefits in terms of indirect paternal care via the protection of offspring from infanticidal attacks or predators (**chapter 2**), bigger groups, with a higher proportion of male members, won intergroup conflicts over access to food resources more often (**chapter 2**). Moreover, the presence of subordinate males is not associated with increased intragroup feeding competition for females although their presence may be costly to the dominant male due to increased levels of aggression during the mating season (**chapter 2**). As reproduction is monopolized by the dominant male (**chapter 1**), reproductive concessions may be given to a subordinate if the presence of this subordinate confers certain benefits to the dominant (Keller and Reeve 1994). The fact that subordinates are not beneficial to

dominant males, and indeed somewhat costly, may explain their lack of reproductive success if indeed reproduction is controlled by dominant males. On the other hand, the presence of subordinate males may be beneficial to females as increased male group size increased the group's ability to secure access to contested resources. These results suggest that female interests may be a driving force behind the unusual social organization of this species.

As male movements between groups are one of the main proximate determinates of group composition (Kappeler 2000a), I examined two alternative male reproductive strategies in relation to dispersal decisions. I compared males who delayed dispersal and remained longer in the natal group with males who dispersed and queued as subordinates in a non-natal group. Both strategies result in male-biased sex ratios at the group level. As there were few behavioral differences between these males (**chapter 3**), there appears to be no behavioral advantage in delaying dispersal. Thus, the decision to leave the natal group and queue in a group where there is the possibility of eventually inheriting the breeding position may also be a viable alternative male reproductive strategy among sifakas.

Male reproductive strategies, intersexual conflict and lemur idiosyncrasies

Males should prefer to live in single-male groups in order to decrease intragroup competition for access to receptive females (Cowlishaw and Dunbar 1991). Although dominant males in many primate species are not able to exclude potential rivals from group membership, they are able to monopolize reproduction. Indeed, most paternity studies in cercopithecine primates have found that male social rank is highly correlated with reproductive success (Melnick 1987; de Ruiter et al. 1994; Altmann et al. 1996). In

several lemur species, where paternity data are available, dominant males residing in multi-male groups are also able to monopolize most if not all reproduction (ringtailed lemurs, Pereira and Weiss 1991; Alaotran gentle lemur, Nievergelt et al. 2002; redfronted lemurs, Kappeler and Port 2008). Therefore, although dominant males may not monopolize groups of females on the demographic level, they succeed at the reproductive level.

In Verreaux's sifakas, reproduction is also highly skewed in favor of dominant individuals (Kappeler and Schäffler 2008), and, therefore, becoming the dominant male is ultimately the best reproductive strategy. Resident females come into estrous asynchronously, despite highly seasonal reproduction, and, thus a single dominant male sifaka is able to monopolize receptive females and secure almost all paternities (Kappeler and Schäffler 2008) as has also been shown for ringtailed lemurs (Pereira 1991; Pereira and Weiss 1991) and howler monkeys (Pope 1990). High male reproductive skew despite the presence of multiple males in sifaka groups may be achieved via behavioral mechanisms such as mate-guarding and/or through physiological suppression (Kraus et al. 1999).

In order to mate-guard effectively, males may monitor the receptive state of a female (Sauther 1991). In sifakas, as in moustached tamarins (Huck et al. 2004), cotton-top tamarins (Ziegler et al. 1993) and ringtailed lemurs (Palagi et al. 2004), the timing of mate-guarding behavior may be guided by olfactory cues. While in close contact with females during pre-copulatory guarding, a male may be more likely to accurately ascertain the timing of ovulation, and, thus, increase his chances of mating while the female is most likely to be receptive (Sauther 1991). In addition to preventing rival males from mating (Alberts et al. 2003; Huck et al. 2004; Setchell et al. 2005), mate-guarding

also works to limit sexual monitoring by others (Sauther 1991). Moreover, mate-guarding may also reduce the potential for female choice even in species with female dominance (Sauther 1991). Mate-guarding is therefore a mechanism that male sifakas can use to assert control over reproduction. Thus, dominant males may tolerate the presence of subordinate males within a group as they are able to exclude these rivals from paternity and therefore, monopolize groups of females on the reproductive level.

Female reproductive strategies may also work to increase skew in favor of dominant males. Females in several gregarious lemur species are dominant to males and also roughly match males in body size and canine length insinuating that the sexes are matched in strength (Richard 1987; Kappeler 1990; Pereira et al. 1990; Kappeler 1991; Pochron et al. 2003). One assumption that can be derived based on these facts is that female choice may work either in conjunction with male reproductive tactics or may override male dominance relations to determine reproductive success among males. In female dominant spotted hyenas (East and Hofer 2001), female choice of mates was found to determine patterns of paternity and may play a more important role in limiting reproductive control by dominant males than power struggles between males (Engh et al. 2002).

Although mate-guarding and high skew in favor of certain individuals suggests that females do not control reproduction in sifakas, female choice may indeed be operating. Pereira and Weiss (1991) have attempted to explain female choice in light of dominant male reproductive monopolization in ringtailed lemurs. They proposed that females should prefer to mate with males who have displayed long-term dominance over other males as these potential fathers may be most able to deter infanticidal conspecifics. Females should therefore remain attracted to former mates that promoted

infant survival and remain dominant among males. Thus, in multi-male groups, estrous asynchrony may allow one dominant male to monopolize reproduction while a female is most fertile and female choice of this male may ensure this (Pereira and Weiss 1991). Indeed, ringtailed lemurs are known to exercise considerable mate choice and estrous asynchrony may function to maximize each female's ability to choose a preferred mate when most receptive. The order of subsequent matings reflect the dominance hierarchy and may work to decrease infanticide risk via paternity confusion (Pereira 1991; Pereira and Weiss 1991; Sauther 1991). Therefore, female choice for dominant males, in conjunction with male monopolization tactics, may also underlie the high skew observed in sifakas as it does in ringtailed lemurs.

One major difference between sifakas and ringtailed lemurs arises when monopolization by dominant males on the behavioral level is considered. Although reproductive skew in the two species may be high, this may not accurately reflect the mating skew. In ringtailed lemurs, although females may mate first, and when most receptive, with the dominant male, females generally mate with a number of males (Pereira and Weiss 1991; Sauther 1991). Mating with most or all resident males and even with extra-group males by females appears to be the norm in lemurs (Jolly 1967; Brockman and Whitten 1996; Eberle and Kappeler 2004; Ostner and Kappeler 2004). Yet, sifakas at Kirindy more closely resemble species such as howler monkeys (Glander 1980; Pope 1990) where only dominant males are observed to mate (Wright 1995). Although promiscuous female mating has been documented in another population of sifakas found at Beza Mahafaly in southwest Madagascar (Richard 1974b; Brockman 1999; Lawler et al. 2003; Lawler 2007), mating with subordinates or extra-group males was rare in Kirindy and generally due to either group instability or the presence of a

related dominant male (Lewis 2004; Kappeler and Schäffler 2008). The circumstances under which female sifakas are observed to mate with subordinate resident and extra-group males suggest mating as a means to avoid incest and/or confuse paternity in unstable groups where rank changes are likely. Therefore, as mating behavior is extremely difficult to observe in Kirindy, we can not conclude that dominant males are able to monopolize females at the behavioral level as subordinate males may mate with group females but during less receptive times of their cycle. Thus, females may indeed exert control over group membership by offering subordinate males staying incentives in the form of mating opportunities (Cant and Reeve 2002; Engh et al. 2002) but as little is known about the actual mating skew within the population, we can not confirm this hypothesis.

Alternatively, group membership in itself, instead of reproduction opportunities, could also be a commodity provided by dominant males and females to subordinates for services rendered (van Schaik and van Noordwijk 1989; Gould 1996a) as decisions over group membership may be independent from decisions over reproduction. In several species, where multiple males are found within social groups despite small female group size, dominant male tolerance of subordinates has been explained by increased benefits to the dominant associated with the presence of subordinate males. In howler monkeys (Pope 1990) and redfronted lemurs (Ostner and Kappeler 2004), for example, the presence of additional males decreases the likelihood of a group takeover. Although the presence of subordinate sifaka males did not confer benefits to the dominant male, they may benefit resident females in terms of increasing intergroup dominance over contested food resources. This discrepancy may be crucial in understanding unusual sex ratios in lemurs, as one fundamental difference between sifakas, and howlers and

redfronted lemurs, is that females are dominant over males (Richard 1987; Pereira et al. 1990).

Female reproductive success has been shown to increase with a corresponding increase in the proportion of male group members in both howler monkeys and wedge-capped capuchins (Robinson 1988; Treves 2001). As large groups are assumed to have an advantage over access to defendable resources (Wrangham 1980; Srikosamatara 1987; van Schaik and van Noordwijk 1989), females may prefer to live with more males as a means to reap the benefits of increased group size in relation to improved access to resources (Wrangham 1980) while limiting intragroup feeding competition. Due to their social dominance over males, female sifakas compete less with males than with other females over defendable food items (Kappeler 2000a). Thus, an increase in intergroup competition over resources may be enough for females to encourage subordinate group membership. Indeed, female sifakas have been observed to actively recruit subordinates into the group (Richard et al. 1993; Brockman 1999; Brockman et al. 2001; Lewis 2004; Lewis 2008). Intergroup advantage over food resources is of relatively more importance to females than males as their reproductive success is limited by their access to crucial food resources (Trivers 1972; Emlen and Oring 1977). Moreover, this benefit should be especially relevant to females living in the harsh seasonal environment of Madagascar where there are periods of severe food scarcity (Wright 1999). Hence, females may be actively regulating group composition, which may be facilitated by their dominant status, and therefore, female interests may ultimately determine the number of males within the group (van Schaik and Hörstermann 1994; Ostner and Kappeler 2004).

Even though there are no immediate costs to dominants in terms of lost reproduction, there are some physiological costs associated with the presence of subordinate males indicated by an increase in aggression rates when females are receptive. Although fighting between males during the mating season is a behavioral characteristic common in all lemurs (Jolly 1967; Richard 1992) and should lead to the evolution of sexual dimorphism in body size and weaponry (Clutton-Brock et al. 1977), lemurs are characterized by sexual monomorphism (Kappeler 1990; Kappeler 1991; Kappeler 2000a). In sifakas, highly seasonal reproduction and estrous asynchrony allow dominant males to mate-guard females as they become receptive. These characteristics should select for sexual dimorphism as subordinates should only refrain from a female which is already mate-guarded by another male if this male is superior in fighting ability. Thus, the lack of sexual dimorphism within this species does not indicate low levels of intrasexual competition and is indeed puzzling. However, selection on increased body size and weaponry may be relaxed if female choice plays an important role in regulating male reproductive opportunities in female dominant species. Moreover, the fact that dominant males are able to monopolize reproduction, may lead to tolerance of potential rivals as they are not a threat to the dominant's reproductive success. Dominant male tolerance of subordinates may therefore be a contributing factor to the unusual socionomic sex ratio observed in sifaka social organization.

Although tolerance of subordinate males by dominant males can lead to the evolution of even adult sex ratios in sifakas, subordinate male reproductive strategies also need to be considered. As sex ratios are regulated by male movements in species with male-biased dispersal, subordinate male dispersal decisions may also be a proximate determinant of group composition (Kappeler 2000a).

In sifakas, there is a low probability of a subordinate male entering a group and assuming the dominant position as evidenced by the low population takeover rate. Additionally, long dominant male tenures (Kappeler unpubl.data) exacerbate the problem for subordinate males as breeding position turnover is low. Under these conditions, a subordinate may favor group membership with no current direct or indirect fitness benefits, instead of searching for reproductive opportunities elsewhere, resulting in groups that contain more males than is optimal for the dominant male (Cant and English 2006).

Thus, one subordinate male strategy may be to enter a group as a non-breeding member and queue for the dominant position (Kokko and Johnstone 1999). If we assume that animals join groups on the basis of costs and benefits of group membership (Cant and English 2006), then it follows that the trade off of being part of a group, instead of being solitary, and the large payoff of eventually attaining the breeding position, may make up for the low probability or long wait in reaching this dominant position (Cant and English 2006) especially in species where all male bands are non-existent. As single male groups are rare (Kappeler 2000a) despite reproductive monopolization by dominants, social queuing by subordinate males may help explain the tendency towards even or male-biased sex ratios in sifakas. Multi-male groups where one male monopolizes reproduction may indeed be stable if subordinates may have a higher lifetime reproductive fitness by staying and waiting to takeover the dominant position than by leaving in search of reproductive opportunities elsewhere (Baker et al. 1993).

Alternatively, males may delay dispersal beyond sexual maturation as the attainment of better physical condition may increase the probability of a successful

takeover (Alberts and Altmann 1995a). Although there are no behavioral benefits in remaining in the natal group, older males tend to be more successful in taking over groups (Kappeler and Mass in prep.). Thus, delaying dispersal is also a viable route to reproductive success in sifakas and results in a tendency towards even or male-biased sex ratios within the species. However, in these cases, groups are effectively single-male groups (Kappeler and Schäffler 2008) as natal delayed dispersers are not expected to compete with dominants for access to receptive females who are most probably their mothers or sisters. More genetic paternity data are needed on other lemur species characterized by unusual sex ratios to see if many multi-male groups are indeed single male groups containing mature male offspring.

Lemurs have been separated on the island of Madagascar for more than 50 million years (Purvis 1995; Yoder et al. 1996) providing us with the opportunity to study convergent evolution on an evolutionary independent radiation of primates (Kappeler 2000b). Lemurs have evolved a different social organization than anthropoids (Kappeler 2000b) and one of the overall aims of this thesis was to understand the mechanisms behind unusual lemur social organization by studying male reproductive strategies. As the variation in the number of adult males present within a group is one of the most striking features of primate group composition and has drastic consequences for the behavior of the sexes (Hamilton and Bulger 1992; van Hooff 2000), I set out to explain the presence of supernumerary males in sifaka social groups as a means to discover what mechanisms are behind this social organization common among lemurs but generally absent in other anthropoid primates.

Several hypothesis have been put forth to explain the unusual number of males in gregarious lemur social groups. Firstly, multiple males may be present due to the low

monopolization potential of females (Emlen and Oring 1977; Mitani et al. 1996a). The results of this study on sifakas and of another study on ringtailed lemurs (Pereira 1991) have shown that females come into estrous asynchronously and are thus easily monopolizable, allowing us to reject this hypothesis.

Secondly, potential benefits conferred on the group by additional males have been suggested as a possible explanation for the occurrence of multi-male groups despite high monopolization potential (Kappeler 1999; van Hooff 2000). In this study, the presence of supernumerary males did not benefit the dominant male but rather the resident females. Thus, females may be playing a more active role in regulating group composition, especially in light of their dominant status, than was previously thought.

Finally, I propose that sifaka social system may more closely resemble the age-graded male groups of howler monkeys (Glander 1980; Pope 1990; Treves 2001; Ryan et al. 2008) and some langur species (Steenbeek et al. 2000; Sterck and van Hoof 2000) but with several differences due to female dominance. These systems are characterized by high skew in favor of a dominant individual and the presence of several younger subordinate males that are generally natal males. Dominant males tolerate the presence of these subordinates as they are not costly in terms of lost reproduction and their presence benefits the group (Eisenberg et al. 1972). In both howlers and langurs, the majority of subordinate males are natal males that have delayed dispersal (Pope 2000; Steenbeek et al. 2000; Sterck and van Hoof 2000). In sifakas, social groups also resemble age-graded male hierarchies but here, the presence of either subordinate natal or non-natal males primarily benefits female residents. Delayed dispersers are tolerated and non-natal males be actively recruited by females (Lewis 2008). As dominant males are not loosing a share of reproduction, non-natal males may be

tolerated despite providing no direct benefits to the dominant male. Thus, in sifakas, divergent male and female interests may place the upper and lower limits on group size and the unusual sex ratio in group composition may be the outcome of the struggle between the sexes over group membership.

In conclusion, a combination of dominant male tolerance, alternative subordinate male reproductive strategies and female strategies may explain the unusual sex ratio in group composition in sifakas. These results may increase our understanding of lemur social systems in general and how male and female reproductive strategies interplay resulting in a set of traits collectively referred to as "lemur syndrome" (Kappeler and Schäffler 2008).

Outlook

The results of this study have highlighted the need for future research on sifakas and other female dominant lemur species exhibiting unusual lemur traits. Firstly, long term data are needed in order to evaluate the potential success of alternative male reproductive strategies. In addition, more detailed observations of subordinate male strategies and dispersal decisions in other lemur species would allow us to get a better understanding of why certain males are successful in attaining the breeding position and what factors contribute to this success. Secondly, more attention needs to be paid to female reproductive strategies and how females may be regulating group composition especially in female dominant lemur species. Thirdly, the lack of sexual dimorphism is still puzzling and more work needs to be done on sifakas and other lemur species to examine if this phenomenon may be due to female dominance, ecological variables such as limited ability to feed on outer branches, or behavioral factors. Finally, this study

highlighted intraspecific variation among populations of sifakas (*Propithecus verreauxi*) found at Kirindy Forest and at Beza Mahafaly. As great intraspecific variation in group composition is rare in anthropoids but seems to be the norm in lemurs (Kappeler 2000a), cross-population comparisons are extremely important in order to discern what role different ecological factors may play in shaping the social organization, mating system and social structure of a species. In understanding variation within species, we may be able to obtain a deeper understanding of variation between species.

SUMMARY

According to sexual selection theory and the socioecological model, where groups of primates are characterized by small numbers of females and highly seasonal reproduction, single males are generally able to monopolize access to these groups of females and exclude potential rival males from group membership. The resulting high variance in male reproductive success, and thus intrasexual competition, leads to the evolution of sexual dimorphism in body size and weaponry. Lemurs deviate from expectations derived from these theoretical frameworks as single males do not exclude rivals from small groups of females leading to even or male-biased sex ratios in group composition and sexual dimorphism is virtually absent within the suborder. Thus, the main aim of this thesis was to study male reproductive strategies of sifakas (*Propithecus verreauxi*) and their effect on the social organization of the species. I studied nine groups of sifakas at Kirindy Forest CNFEREF Madagascar between 2005 and 2008 using continuous focal behavioral observations. Fecal samples were collected in order to determine the day of ovulation during the short mating season for all adult females residing in the study population. The results of this study revealed that females residing within the same social group become receptive asynchronously and may be providing an olfactory cue as to the timing of receptivity allowing dominant males to mate-guard them effectively. The presence of subordinate males did not increase infant survival nor decrease the risk of takeover by extra-group males. Subordinates may be tolerated despite the lack of benefits associated with their presence as dominant males do not loose paternities to subordinates and their presence may confer intergroup dominance

over resources, an important benefit to females. The presence of subordinate males within these groups despite little reproductive success may be explained by alternative male reproductive strategies such as delayed natal dispersal and social queuing. Overall, these results explain the high reproductive skew in favor of dominant males within the population and why subordinate males may be tolerated despite providing no discernible benefits to the dominant male. In addition, the importance of female strategies in relation to regulating group composition was highlighted in this thesis. Thus, the tendency towards even or male-biased sex ratios in sifakas may be seen as the outcome of male and female reproductive strategies and counter-strategies. By understanding how the reproductive strategies of the sexes interplay to shape social organization in lemurs, we can begin to understand why lemurs deviate from so many of the predictions tested and proven for other primate species.

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ACKNOWLEDGMENTS

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