

UNIVERSITY OF CALGARY

Social Structure and Female Foraging Strategies
in White-Collared Lemurs (*Eulemur cinereiceps*)

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

CALGARY, ALBERTA

SEPTEMBER, 2009

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Abstract

This thesis examines the nature of male-female affiliation in *Eulemur cinereiceps*, specifically whether it consists of special relationships or a central male social structure. A special relationship includes an unrelated male and female adult who preferentially associate and affiliate with each other over all other individuals within the group. I also examine the flexibility of female foraging strategies in response to changes in resource availability and energy requirements. I tested the resource defence hypothesis, which proposes that reproductive females form special relationships with males to improve foraging success and offset the energetic costs of reproduction. Data were collected on two small groups in Mahabo forest, on the southeastern coast of Madagascar. Analysis of social structure data suggested central male structure when resources were scarce and central female structure during the period of relative resource abundance. The resource defence hypothesis was not supported by foraging data.

Acknowledgements

I would like to thank the Institute for the Conservation of Tropical Environments (ICTE), the Madagascar Institute pour la Conservation des Environnements Tropicaux (MICET), the Ministère des Eaux et Forêts (MEF), and Missouri Botanical Gardens (MOBOT) for granting permission to conduct my M.A. thesis research in Madagascar. I would also like to express my gratitude to Conservation International (PAF0708) and the University of Calgary Research Services (Grant No. 1009811) for funding the research conducted in Madagascar. For their generous support throughout the second and third year of my M.A. thesis I would like to acknowledge the University of Calgary Queen Elizabeth II Scholarship program.

Research at Mahabo would not have been possible without the help of Reza Ludovic (MBG), who introduced me to the officials and residents of Mahabo village and shared an abundance of information about Mahabo forest ecology and local traditions; Hubert St. Emilien Andriamaharoa (MBG and the Université de Madagascar), who provided generous assistance with field training, data collection, and offered a wealth of information about the lemur study groups and Mahabo ecology; Aba ny' Papita (MBG), who managed the assistants and cooks; Ranarison, who cooked delicious and healthy meals for the guides; Christina Ingraldi, who helped with data collection. I would like to extend a very special thank you to my assistants, Aba ny' Balaza and Aba ny' Seraphin for their invaluable help with group tracking and data collection and for their grace and patience while I learned to speak Malagasy and gradually gained my forest legs.

I would like to thank my thesis supervisor, Dr. Steig Johnson, for his unlimited patience, his unerring support, and his advice both in the field and during the multiple

revisions of this thesis. I would like to thank Dr. Pascale Sicotte and Dr. Mary Pavelka for their help with and support of my thesis. I would also like to acknowledge Mackenzie Bergstrom, Greg Bridgett, Sarah Carnegie, Dr. Tak Fung, Barbara Kowalzik, Amanda Melin, Heather Peacock, Tania Saj, Julie Teichroeb, and Tracy Wyman for help with statistics, maps, and the logistics of both proposal and thesis writing.

I would like to thank my parents, Regula Brunies and Pierre Ménard, for their priceless support during this endeavour and their beautiful love. I would like to show appreciation to Kerry Martens, Martha Evans, Megan St. Goddard, Jen Wilcox, Kerry Tannahill, and Lisa Scharf for their wise words and the confidence they inspire in me.

I would like to acknowledge Gordon Kelter for the million-and-one ways he has helped with this thesis, namely dropping everything and coming to live with me in Madagascar. My thanks to him for his love, his belief in me, and the special way he can lift my chin and remind me that I can do anything I set my mind to because my heart is strong and true.

Finally, I thank my Higher Power for the endless possibility that is my life, the hope that burns bright within me, and most of all for granting me serenity.

Dedication

This M.A. thesis is dedicated to the members of my family: Regula, Pierre, Gordon, Cadence, Smarties, and Simba, whose loving support and patience made it all possible.

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Chapter One: Introductory Chapter

1.1 Introduction

Mammalian social systems are inherently complex and varied due to the different interests of the individual members that create the system, and the ecological and biological constraints that influence the interests of individuals. Social systems are primarily defined by the quality and intensity of interactions between individuals (Hinde 1976), which in turn are influenced by the distribution of risk and resources, as delineated in socioecological models (Crook 1970; Emlen and Oring 1977; Wrangham 1980; Terborgh and Janson 1986; Sterck *et al.* 1997; Isbell and Young 2002).

The goal of this study is to present data on aspects of the three fundamental components of social systems (social organization, social structure, and mating system) (Struhsaker 1969; Rowell 1979, 1993) for a little known and critically endangered species of brown lemur: the white-collared lemur (WCL) (*Eulemur cinereiceps* Grandidier and Milne-Edwards 1890). I will also present data on the availability and use of food resources to evaluate whether their patterns conform to aspects of predictions derived from the social system.

In this chapter I describe the evolutionary history of WCL and the current taxonomic classification of this species. I will also be describing the geographic distribution, habitat use, activity patterns, and diet of WCL. Because WCL belongs to the brown lemur species complex, and because relatively little is known about the components of WCL social systems, comparisons will be made to related species. These components consist of the mating system (including aspects such as sexual dimorphism/dichromatism, female reproductive strategies, male reproductive strategies,

and female reproductive biology), aspects of social organization (group size, sex ratio, and fission-fusion dynamics), and features of social structure (female dominance and quality of male-female relationships).

1.2 Evolutionary history and distribution of white-collared lemurs

Eulemur cinereiceps belongs to the Suborder Strepsirrhini (E. Geoffroy Saint-Hilaire 1812) within the Order Primates (Linnaeus 1758). Within the Suborder Strepsirrhini are the Infraorders Lemuriformes (Gray 1821), Chiromyiformes (Anthony and Coupin 1931), and Lorisiformes (Gray 1821). The geographical distribution of Lorisiformes includes Central Africa, Sri Lanka, India, and Southern Asia, while Lemuriformes and Chiromyiformes are found exclusively on the island of Madagascar (Gray 2005). The Infraorder Lemuriformes contains four families: Cheirogalidae (Gray 1873), Lepilemuridae (Gray 1870), Indriidae (Burnett 1828), and Lemuridae (Gray 1821). The Family Lemuridae is composed of five genera: *Haplemur* (I. Geoffroy 1851), *Lemur* (Linnaeus 1758), *Prolemur* (Gray 1871), *Varecia* (Gray 1863), and *Eulemur* (Simons and Rumpler 1988). The number of species and subspecies within the genus *Eulemur* has varied substantially over time (Mittermeier *et al.* 1994; Goodman *et al.* 2003; Groves 2005; Mittermeier *et al.* 2008) and at present is still being debated (Groves 2001; Mittermeier *et al.* 2008; Johnson *et al.* 2008). A lengthy discussion and debate regarding the taxonomy of *Eulemur* is beyond the scope of this research; discussion will thus be limited to a subset of species within the genus.

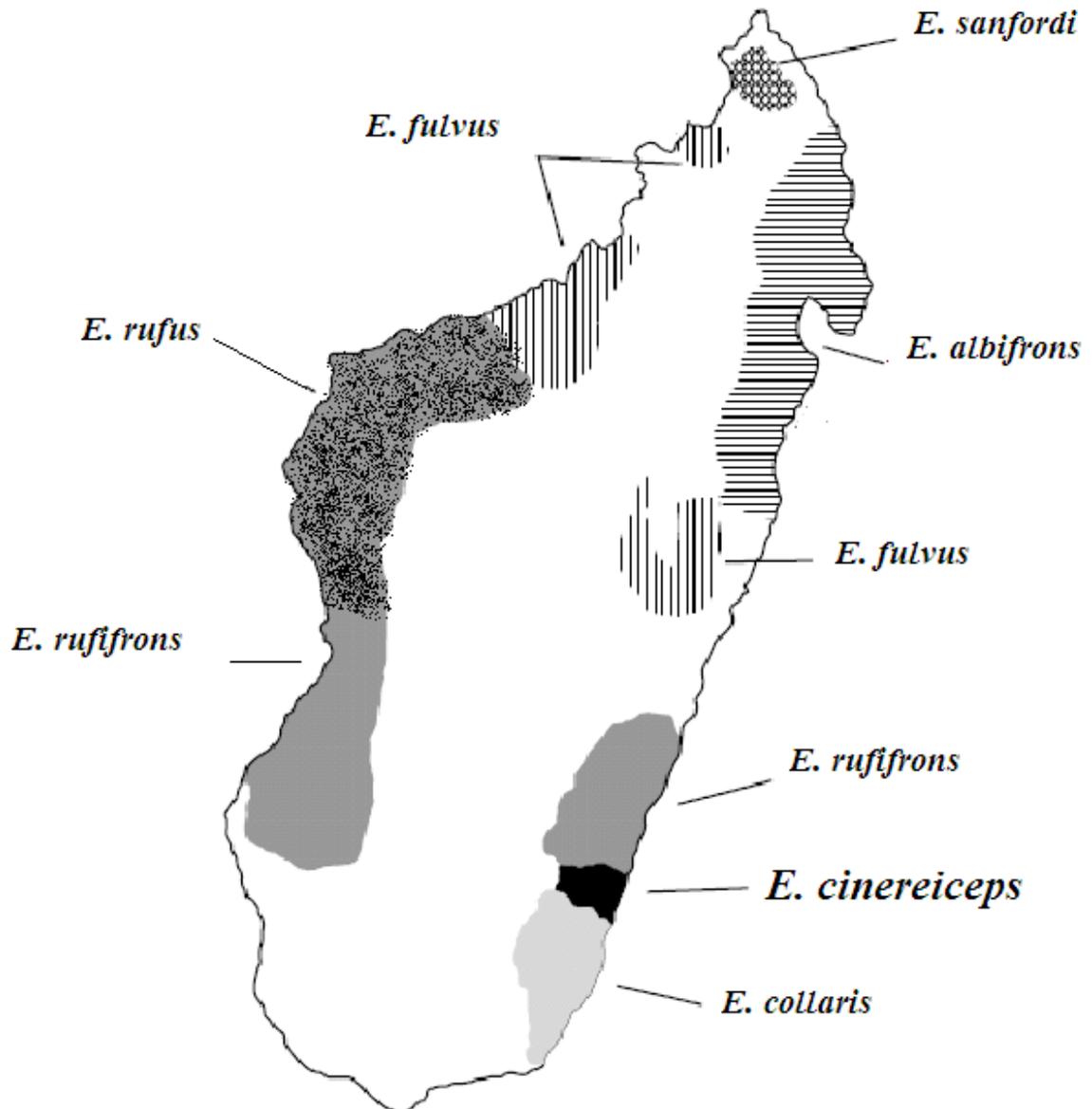
E. cinereiceps (white-collared lemur (WCL) = grey-headed lemur) belongs to the brown lemur species complex, which also includes the brown lemur (*E. fulvus*) and the collared lemur (*E. collaris*) (Johnson 2006). Some researchers held that *E. fulvus* includes

several subspecies, although the number of subspecies varies between three and six (Wyner *et al* 1999; Pastorini *et al* 2000; Groves 2001; Mittermeier *et al* 2008). *E. cinereiceps* and *E. collaris* are grouped in a clade which is thought to have recently diverged from *E. fulvus* and then split into two separate species (Hamilton *et al.* 1980; Rumpler 1989; Djelati *et al.* 1997). Prior to diversification, brown lemurs are believed to have originated in the humid forests of central-north Madagascar (Meyers and Absher 1994, in Tattersall and Sussman 1998; Tattersall and Sussman 1998). Diversification may then have led to a northern clade and to the southern brown lemur species complex (Tattersall 1992). *Eulemur cinereiceps* and *E. collaris* were traditionally classified as subspecies of *E. fulvus*, but hybrid zone field studies and genetic analysis supported their establishment as full species apart from *E. fulvus*, at least according to the biological species concept and the phylogenetic species concept (Djelati *et al.* 1997; Wyner *et al.* 1999; Johnson and Wyner 2000; Wyner *et al.* 2002; Mittermeier *et al.* 2006). The biological species concept contends that two species must be reproductively isolated from one another in order to be considered distinct (Mayr 1963). *E. cinereiceps* and *E. collaris* satisfy the previous condition in that they cannot produce fertile hybrids (Dutrillaux and Rumpler 1977; Johnson and Wyner 2000; Johnson 2002; Wyner *et al.* 2002). When either *E. cinereiceps* or *E. collaris* are crossed with *E. f. fulvus*, however, fertile hybrids are produced (Buettner-Janusch and Hamilton 1979; Rumpler 1975). The phylogenetic species concept considers the evolutionary ancestry and relatedness of species (Cracraft 1989); cladistic analysis supported the separation of *E. cinereiceps* and *E. collaris* as these taxa have diagnostic traits not shared by *E. fulvus* (Wyner *et al.* 1999).

WCL have been observed in the interior corridor and forest fragments along the southeastern coast of Madagascar (Johnson 2002; Ratsimbazafy 2002; Irwin *et al.* 2005) (Fig 1-1). WCL are found in lowland or montane rain forest (Johnson and Overdorff 1999), and a small population resides in the littoral forest (this study). *E. collaris* is also found in southeastern Madagascar, their range beginning where WCL ends (at the Mananara River) and extending to the southern tip (Fort Dauphin) (Fig 1-1) in habitats similar to *E. cinereiceps*. *E. fulvus* occurs in the northwest, northern, western and eastern regions of Madagascar in both moist montane forests and dry deciduous forests (Tattersall 1982) (Fig 1-1).

Like all lemurs, *Eulemur* species bear a significant conservation risk due to the human activities of logging, farming, mining, and hunting in Madagascar. *E. cinereiceps* has been included in the list of the world's 25 most endangered primates since 2004 (Mittermeier *et al.* 2006; Mittermeier *et al.* 2007). Of all the brown lemurs in Madagascar, it is the species with one of the lowest population densities, residing in the most severely fragmented habitat (Johnson and Overdorff 1999; Irwin *et al.* 2005). WCL population density and habitat quality surveys were conducted in 1995, 1997, 2000, 2007, and indicated consistently low population densities and habitat quality (Johnson and Overdorff 1999; Johnson 2002; C. Ingraldi, unpublished data). In addition, WCL groups at Mahabo live in critically degraded fragments of littoral forest. Mahabo forest includes some of the few remaining littoral forest fragments, which are among the most degraded animal habitats in Madagascar (Johnson 2006).

Figure 1-1 Geographic distributions of species within the genus *Eulemur*.



From Tattersall (1982) and Johnson (2006), with modified nomenclature

(Mittermeier *et al.* 2008). (*E. rufifrons* = *E. fulvus rufus*).

Preliminary studies on the diet, habitat, population density, social organization and behaviour of WCL have been conducted (Johnson 2006), but relatively little is known about the social structure of this species. Given the close evolutionary relationship of *E. cinereiceps*, *E. fulvus*, and *E. collaris* (Johnson 2006), data collected on *E. fulvus* and *E. collaris* may provide useful background information for the formulation of predictions regarding WCL behaviour.

1.3 Habitat use

Brown lemurs are primarily arboreal, and rarely travel on the ground unless travelling between open patches (Sussman 1974, 1977; Dagosto 1995). Several researchers have reported that brown lemurs are found higher in the canopy than sympatric competitors, due perhaps to niche separation (Sussman 1974, 1977; Freed 1996). Overdorff (1996) did not find any evidence, however, of vertical stratification among sympatric species (*E. fulvus rufus* and *E. rubriventer*) with similar diets. Johnson (2002), who observed differences in vertical habitat use among non-sympatric brown lemur populations, theorized that variation may be due to differences in forest structure more so than niche separation.

1.4 Activity pattern

Mammalian activity patterns, also known as circadian locomotor activity (Kappeler and Erkert 2003), are regulated by the 24-hour day-night cycle (Aschoff 1960; Reppert and Weaver 2002). Within primates, three types of activity pattern are observed. Most haplorhines are diurnal, meaning that they are active during the day, while many strepsirhine species are nocturnal (active at night) (Martin 1990; Kappeler and Heymann 1996). If an animal is cathemeral, on the other hand, its activities are distributed over the

entire 24-hour cycle (Tattersall 1987). Cathemerality has been observed in several mammalian species including some rodents (Flowerdew 2000; Halle 2000), shrews (Merritt and Vessey 2000), mustelids (Zielinski 2000), eastern grey kangaroos (Clarke *et al.* 1995), Przewalski horses (Berger *et al.* 1999), populations of howler monkeys (*Alouatta palliata*) (Dahl and Hemingway 1988), populations of owl monkeys (*Aotus azarai boliviensis*) (Wright 1989), and species within the lemur genera *Hapalemur* and *Eulemur* (Curtis *et al.* 2006). Cathemerality, although pervasive among other mammalian groups, is quite rare among primates (Curtis and Rasmussen 2006). WCL, like all *Eulemur* species, are cathemeral.

1.5 Diet

Species within the brown lemur complex, with the exception of western *E. fulvus rufus* (Sussman 1977), are primarily frugivorous, though dietary flexibility is exhibited in the context of resource scarcity. The production of fruit in Malagasy rain forests is highly seasonal and peaks in availability and scarcity may differ from one year to the next (Morland 1993; Overdorff 1996). Lemurs may adapt to unpredictable fruit availability by adjusting their diet. Ripe fruit is the primary food source when available, and flowers and leaves comprise significant secondary sources of nutrition (Johnson 2006). The proportion of these items in the diet of WCL at Vevembe closely resembles that of brown lemur populations elsewhere: fruit (approximately 66%), leaves (2-26%), flowers (4-13%) (Tattersall 1977; Overdorff 1991, 1993; Freed 1996; Vasey 1997, 2000; Rasmussen 1999; Johnson 2002, 2006; Ralainasolo *et al.* 2008). In times of fruit scarcity *Pandanus* flowers serve as a potential fall-back resource for WCL at Vevembe, a resource poor environment (Johnson 2002, 2006).

1.6 Social Systems

Animal social systems are a complex network of relationships between individuals (Hinde 1976). The diversity in social systems is determined by the level and intensity of interactions between group members, differences in mating systems and spatio-temporal cohesiveness (Hinde 1976; Gray 1985). How one individual interacts with another individual, however, is strongly influenced by extrinsic factors such as resource availability and environmental risk (Crook 1970; Emlen and Oring 1977; Wrangham 1980; Terborgh and Janson 1986; Sterck *et al.* 1997; Isbell and Young 2002). The basic premise of socioecological models is that females are organized based on the distribution of food resources and predation and/or infanticide risk, because these factors limit their reproductive success, while males are organized based on the distribution of receptive females (Emlen and Oring 1977), since the main determinant of male reproductive success is a male's access and ability to monopolize access to receptive females (Bateman 1948; Trivers 1972; Kappeler 1999).

The three fundamental components of social systems are social organization, mating system and social structure (Struhsaker 1969; Rowell 1979, 1993). Social organization is characterized by the number of individuals within a group, the male-female sex ratio, and the spatiotemporal cohesion of that group. The mating system is determined by the pattern of interactions between individuals that relate to reproduction. Social structure describes the pattern and quality of interactions between individuals and the types of relationships that can arise from specific patterns (Kappeler and van Schaik 2002).

1.6.1 Social organization

1.6.1.1 Group size

Why do some animal species opt to live in groups? One explanation is that group-living reduces the risk of predation (Terborgh and Janson 1986). Alexander (1974) goes so far as to state that the only reason group-living has evolved is because of predation pressure, while Wrangham (1980) asserts that an increase in feeding opportunities is the main advantage conferred by group-living due to increased success in inter-group contests. The connection between predation pressure and group size has been confirmed in that larger groups demonstrate higher levels of predator detection and hence have a lower predation risk (van Schaik *et al.* 1983). In addition, species in habitats with less predation pressure tend to have smaller group sizes (van Schaik and van Hooff 1983). An increased feeding opportunity in larger groups has not been supported in primates, however. Individuals obtain more food and expend less energy foraging when they are part of a small group than a large group (Janson 1998). There is thus a trade-off between predation risk and feeding competition where group size is considered.

van Schaik (1983) proposes the ‘predation – intra-group feeding competition theory’ which postulates that group-living exists due to predation pressure, but incurs costs of food competition within the group. If the disadvantages of intra-group competition are greater than the potential advantages of a larger group size for inter-group competition, van Schaik (1983) predicts that larger groups will fission. Group size is thus determined by both the level of predation pressure and food availability.

Social structure is also closely correlated with activity pattern: species active at night are mostly solitary, diurnal species live in groups (Terborgh and Janson 1986;

Clarke *et al.* 1995). Recent anthropogenic ecological changes in Madagascar have caused a cascading effect consisting of the extinction of large diurnal raptors *Aquila* and *Stephanoetus* (Goodman 1994a, 1994b) and perhaps the adaptation of formerly nocturnal strepsirhines to a diurnal or cathemeral activity pattern (van Schaik and Kappeler 1993, 1996). In the 'evolutionary disequilibrium hypothesis' (EVDH), van Schaik and Kappeler (1996) propose that formerly nocturnal lemur species, which had adapted to pair-living rather than being solitary to reduce nocturnal predation risk, experienced an incompatibility with their new diurnal activity pattern. This shaped several facets of their social system, including a group-living social structure and oestrous synchronization. It bears noting that predation risk is not eliminated as predators may also be cathemeral, *Cryptoprocta ferox* for example (Colquhoun 2006).

Brown lemur groups range in size from 4-17 individuals (Johnson 2002). Brown lemur populations inhabiting higher quality habitats such as Ranomafana National Park, where food is more abundant, tend to live in larger cohesive groups (6-12 adult individuals) (Overdorff *et al.* 1999), whereas those living in relatively resource poor habitats such as Mahabo, live in smaller groups (3-6 adult individuals) that have a fission-fusion social organization (see below) (H.E. Andriamaharoa, pers. comm.; this study). It is worth noting that during a year of resource scarcity in Ranomafana National Park a formerly cohesive group fissioned (Overdorff *et al.* 1999; D. Overdorff, pers. comm., cited in Johnson 2006). The difference in group sizes between Ranomafana populations and Mahabo populations may also be due to species specific group sizes, or because of differences in predation pressure between the two locations. The brown lemur's primary terrestrial predator, the fossa (*C. ferox*) (Johnson 2002), is found at

Ranomafana National Park (Hawkins and Racey 2005) but not at Mahabo (S.E. Johnson, pers. comm.).

1.6.1.2 Sex ratio

Brown lemur groups are multi-male multi-female, with an even or a male bias in sex ratio (Johnson 2002). Although a male bias in infant sex ratio is not uncommon among primates (Clutton-Brock and Iason 1986), high male mortality usually results in a female biased adult sex ratio (Caughley 1977; Clutton-Brock *et al.* 1977; Dunbar 1987; Small and Smith 1986). Male-biased infant and adult sex ratios are found in several lemur species however: *Lemur catta* (Sussman 1991), *Propithecus verreauxi* (Richard *et al.* 1991), *Varecia variegata variegata* (Balko 1996), and *Eulemur fulvus rufus* (Overdorff *et al.* 1999), to name a few. This adult sex ratio is an unusual trait and an exception to the predictions of the socioecological model given that males' reproductive success is determined by the number of reproductive females within a group (Trivers 1972). Males would thus have lower reproductive success if fewer females are available to mate and intrasexual competition is higher. Unlike group-living anthropoids, there is a relative lack of sexual dimorphism among group-living lemurs with even or male-biased sex ratios, indicating that males are not attempting to control access to a group of females (Kappeler 1997). It is thus theorized that female brown lemurs influence the number of males in a group via mechanisms such as oestrous synchrony (Pereira 1991; van Schaik and Kappeler 1993) and tolerate potentially increased feeding competition in favour of the possible benefits of a male-biased sex ratio: predator detection and increased paternal care (van Schaik and van Noordwijk 1989; O'Brien 1991; Kappeler 1993), although

these possible benefits have yet to be shown for species within the brown lemur species complex.

1.6.1.3 Fission-fusion dynamics

The spatiotemporal cohesion of a group is another component of social organization which refines distinctions among multi-male multi-female groups (Kappeler and van Schaik 2002). Fission-fusion is characterized by a temporal variation in social grouping patterns: a parent group separates into smaller sub-groups (fission) and reunites (fusion) a few hours to weeks after the fission has occurred (Kummer 1971; Terborgh and Janson 1986; White and Burgman 1990). Fission-fusion networks have also been described as the loose amalgamation of two or more closely knit and temporally cohesive units, or sub-groups (Ramos-Fernandez *et al.* 2006). The recently proposed fission-fusion dynamics framework outlines three dimensions for the characterization of spatiotemporal cohesion: variation in spatial cohesion of a group over time, variation in group size over time, and variation in group composition over time (Aureli *et al.* 2008). There are two types of variation in spatiotemporal cohesion: molecular and atomistic (Rodseth *et al.* 1991). In molecular, or multilevel societies, smaller one-male groups with fixed membership aggregate into large groups at night but split apart again during the day to forage. This type of organization is typical of geladas (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*), and snub-nosed monkeys (*Rhinopithecus* spp.) (Kummer 1968; Stambach 1987; Grüter and Zinner 2004). In atomistic, or fission-fusion societies, the groups frequently split into subgroups and come together again, and subgroups have variable composition. This organization is typical of chimpanzees (*Pan troglodytes*), bonobos (*P. paniscus*) (Nishida and Hiraiwa-Haegawa 1987), and black

spider monkeys (*Ateles paniscus chamek*) (Symington 1990). A further division of the atomistic type is individual-based fission-fusion vs. group-based fission-fusion (van Schaik 1999). Individual-based fission-fusion is difficult to identify as groups may be very small, possibly consisting of solitary individuals, and fusion of the entire parent group is rare. A potential example of individual-based fission-fusion is the orangutan (*Pongo pygmaeus*) (Delgado and van Schaik 2000). Group-based fission-fusion describes groups with stable membership that fission into sub-groups, potentially to decrease resource competition, and fuse after a short delay. This behaviour has been observed in long-tailed macaques (*Macaca fascicularis*) (van Schaik and van Noordwijk 1988) and a population of mantled howler monkeys (*Alouatta palliata*) (Chapman 1989).

Temporal variation in group composition differs according to the motivation for fission-fusion behaviour. Species where individuals fission for foraging activities and fuse at sleeping sites include the lesser bushbaby (*Galago* spp.) (Bearder 1987), lorises (*Loris* spp.), and mouse lemurs (*Microcebus* spp.) (Müller and Thalmann 2000; Schülke and Ostner 2005), big brown bats (*Eptesicus fuscus*) (Willis and Brigham 2004), and Bechstein's bats (*Myotis bechsteinii*) (Kerth and König 1999). Species in which some degree of sexual segregation in fissioning is witnessed include red deer (*Cervus elaphus*) (Conradt 1998), bighorn sheep (*Ovis canadensis*) (Ruckstuhl 1998), and bottlenose dolphins (*Tursiops* spp.) (Connor *et al.* 2000). Sexual segregation in these cases would be due to differences in the activity budgets of each sex, fissioning would thus result in increased efficiency in coordination of activities among male sub-groups and female sub-groups (Conradt 1998; Ruckstuhl 1998). In some species, individuals may alter their fission-fusion behaviour at certain times of the year. Parrotlets (*Forpus conspicillatus*)

usually maintain a molecular social organization. During the breeding season, however, individuals fission into breeding pair units with limited inter-pair contact (Wanker 2002). Ruffed lemurs (*Varecia variegata*) normally maintain distinct groups whose ranges do not overlap. During the warm season, when food is more plentiful, groups fission and fuse with sub-groups from other groups (Morland 1991; Vasey 1997). In some species, individuals form sub-groups or congregate based on food availability: spider monkey (*Ateles* spp.) groups split into foraging sub-groups (Asensio *et al.* 2008), and spotted hyenas (*Crocuta crocuta*) assemble to feed on carcasses (Smith *et al.* 2008).

Brown lemurs typically maintain cohesive social groups (Vasey 1997; Overdorff and Johnson 2003; Johnson 2006). Fission-fusion social organization occurs in WCL, however (Johnson 2002). It has also been observed in one *E. fulvus rufus* population during a period of change in food availability (D. Overdorff, pers. comm., cited in Johnson 2006). This variation in social organization across species within the brown lemur complex, and even across populations within the same species, may be indicative of *Eulemur* spp.'s flexible social grouping patterns in response to southeastern Madagascar's ecological stochasticity (Johnson 2002, 2006; Ratsimbazafy 2002). The newly refined perspective on fission-fusion dynamics allows for temporal flexibility of spatial cohesion patterns within a social group. It is conceivable that species within the brown lemur species complex are exhibiting a gradual shift from a low level of temporal variation in spatial cohesion (more cohesive) to a higher level, and that *E. cinereiceps* and the population of *E. fulvus rufus* mentioned above are the first to engage in this shift. Conversely, it is also plausible that fission-fusion behaviour is an artefact from an earlier

stage of transition, when species within the genus *Eulemur* converted from a nocturnal activity pattern to a cathemeral activity pattern (as proposed by the EVDH).

Fission-fusion in WCL has only been described qualitatively (S.E. Johnson, pers. comm.) although analysis of spacing patterns in WCL groups has shown that they do indeed undergo fission-fusion events (Johnson 2002). There have not been any assessments as to the causes of this lax group cohesion (Overdorff and Johnson 2003).

1.6.2 Mating Systems

Reproduction in brown lemurs is highly seasonal, with only 25-50% of females in a group successfully reproducing per year (Overdorff *et al.* 1999). Brown lemur females have a high degree of oestrous synchrony and also mate promiscuously (Overdorff 1998; Ostner and Kappeler 1999). The onset of oestrus is triggered by the pituitary gland in response to a change in photoperiodicity (daily sunlight totals) (van Horn and Resko 1977; Petter-Rousseaux 1980), which is determined by latitude. In Ranomafana National Park *E. fulvus rufus* reproduction occurs in early May (Overdorff 1998; Overdorff *et al.* 1999; Wright 1999). Gestation length, on average, is 120 days (Overdorff *et al.* 1999). Strepsirhines are characterized by short gestation lengths, epitheliochorial placentation (maternal and foetal epithelium are in contact, rather than connected, which may reduce the diffusion of energy resources from mother to foetus), and basal metabolic rates that rise and fall depending on reproductive state (Rasmussen 1985; Richard and Nicoll 1987; Young *et al.* 1990; Tilden and Oftedal 1995; Kappeler 1996; Overdorff *et al.* 1999). *E. f. rufus* give birth to one offspring in early August, and infants are weaned at approximately 6 months of age (Overdorff *et al.* 1999). These characteristics, combined with the ecological stress of seasonal variation in food availability, cause reproduction to be more

energetically expensive for strepsirhines than anthropoids of similar size. The energy required is increased due to raised basal metabolic rates during reproduction and reduced energy diffusion from mother to foetus. The energy acquired may potentially be decreased due to food scarcity and the resulting competition over resources (Richard and Nicoll 1987; Young *et al.* 1990; Kappeler and Heymann 1996; Tilden 1997; Overdorff *et al.* 1999).

WCL are sexually dichromatic, as are other brown lemur species (Tattersall 1982). The male's body pelage varies from dark grey to brown, while the head and tail are dark. WCL earn their name from the male's thick white collar or beard. The female's torso pelage is reddish-brown dorsally and slightly lighter ventrally, while the head is a dark grey. The female does not have a white collar (Mittermeier *et al.* 1994) (Fig 1-2). Sexual dimorphism in body mass appears to be absent among brown lemurs, with the exception of *E. f. rufus* in which female-biased size dimorphism is present (Johnson *et al.* 2005). WCL exhibit size monomorphism but do exhibit male-biased canine dimorphism (Johnson 2002; Johnson *et al.* 2005). Male-biased canine dimorphism is also present in *E. f. albifrons* (Kappeler 1996) and in some populations of *E. f. rufus* (Gerson 1999, 2000; but see Johnson *et al.* 2005). The presence of canine sexual dimorphism may suggest male-male direct competition. Aggression is rare among WCL (Johnson 2002), however, and females should not be monopolizable by one male due to oestrous synchrony (Pereira 1991; van Schaik and Kappeler 1993). Canine sexual dimorphism may thus be a vestigial characteristic. Earlier studies have indicated that WCL display strong sperm competition, evidenced by large testes size relative to body size (Johnson 2002; Johnson *et al.* 2005).

Figure 1-2 Female and male *E. cinereiceps*.



Females are in top row, males are in bottom row.

Large testes size and sperm competition correspond with females' propensity towards promiscuous mating (Harcourt 1991, 1994; Harcourt *et al.* 1981; Jolly and Phillips-Conroy 2003; Møller 1988). Both *E. cinereiceps* and *E. f. rufus* live in multi-male multi-female groups and employ oestrous synchrony (Overdorff 1998; Overdorff *et al.* 1999; Wright 1999; Johnson 2002), but *E. cinereiceps* males' testes are larger (Johnson *et al.* 2005). Because females' oestrous periods are synchronized and females mate with all

males within the group (Overdorff *et al.* 1999), a male's reproductive success is determined indirectly via sperm competition. Among lemurid species, those with the largest testes size are characterized by promiscuous breeding and/or low group cohesion, traits that increase the need for indirect male-male competition due to the low monopolizability of females (*Lemur catta*: Sauther 1991; Sussman 1992; *E. macaco*: Colquhoun 1997; *Varecia variegata*: Morland 1991; Vasey 2000; *E. cinereiceps* and *E. f. rufus*: Johnson *et al.* 2005).

1.6.3 Social structure

1.6.3.1 Absence of female dominance

Female dominance is characterized by the occurrence of male submissive signals directed towards females, and the absence of submissive signals from females to males (Pereira *et al.* 1990; Kappeler 1993; Overdorff *et al.* 2005). Female dominance is rare in primates, but is found in the majority of lemurs (see Wright 1999 for a detailed list of species). A possible function of female dominance in lemur species is that it gives females feeding priority in times of food scarcity and during gestation and/or lactation periods, both of which are times of elevated intragroup competition (Jolly 1966, 1984, 1998; Richard and Nicoll 1987; Kappeler 1990, 1993; Young *et al.* 1990; Wright 1993, 1999; Overdorff *et al.* 2005).

Unlike other lemur species, brown lemurs do not exhibit female dominance over males (Pereira *et al.* 1990; Pereira and Kappeler 1997; Pereira and McGlynn 1997; Overdorff and Erhart 2001). Episodic targeted aggression (Vick and Pereira 1989; Pereira 1993) is exhibited by some populations of *E. fulvus rufus*, however. During mating season, males and females target particular individuals (either male or female) within the

group and attack them, without notice or provocation. Though this behaviour provides some evidence of dominance relations in a brown lemur species, this behaviour is not sex-specific (Vick 1977; Colquhoun 1987; Vick and Pereira 1989; Pereira 1993; Pereira, unpubl. data, cited in Pereira and Kappeler 1997).

Despite the lack of data on aggression and dominance relations in brown lemur species, theories derived from the function of female dominance suggest that intrinsic factors should predict intersexual dominance relations. Young *et al.* (1990) propose that strepsirhine species that demonstrate female dominance have higher rates of prenatal maternal investment and lower basal metabolic rates (BMR), the elevation of which during gestation and lactation incurs an energetic cost (Richard and Nicoll 1987). According to their maternal investment calculations, *E. fulvus* should be female dominant. Tilden and Oftedal (1995) suggest that low quality milk in *E. fulvus*, an indicator of low parental investment, offsets the costs of prenatal investment and low BMR. Determining the energetics of parental investment, however, is more complicated than considering a single factor as it consists of a balance of numerous components such as rate of milk delivery, length of lactation, or potential for combined maternal and paternal care (Buss *et al.* 1976; Wright 1999; Fietz and Dausmann 2003). Prenatal maternal investment by WCL has not been investigated. Given the purported lack of female dominance as a counter strategy to increases in resource competition concurrent with the increased energetic requirements of reproduction, WCL females may rely on fission-fusion to decrease competition. Females may form all-female subgroups if males decrease females' energy consumption, or male-female dyadic subgroups if males help females, as per the resource defence hypothesis (see below). If the latter is true for male-

female relationships, dyadic subgroups would be most likely during females' lactation season, when their energy requirements are the highest, but primarily if a female's lactation season coincides with a season of low food availability. The preliminary evidence of group fission in *E. fulvus rufus* groups (D. Overdorff, pers. comm., cited in Johnson 2006), also characterized by a lack of female dominance (Pereira *et al.* 1990), is noteworthy as support for the proposition that females may rely on fission-fusion to decrease competition with conspecifics.

1.6.3.2 Male-female affiliation and association

Eulemur spp.'s multi-male multi-female groups have been proposed to be aggregations of several adult male and female dyads or 'pair-bonds' (van Schaik and Kappeler 1993, 1996). A pair-bond is typically formed between one adult male and one adult female of a monogamously breeding species and is qualified as persisting beyond the reproductive period (van Hooff and van Schaik 1992; Gubernick 1994). Animals that live in multi-male multi-female groups, such as WCL, have the opportunity to form male-female pairs. A bond between individuals is said to exist if agonistic support and affiliative interactions occur at a higher frequency than what is considered the norm (Wrangham 1980; van Hooff and van Schaik 1992), and if they maintain close spatial proximity with one another (Smuts 1985; van Schaik and Kappeler 1993). A pair-bond can be either sexual or social, though both should be long-term, persisting for longer than a year or seasonal cycle (Fuentes 2002). The sexual pair-bond consists of non-kin adults who preferentially mate with one another over all other individuals in the group, and the pair is usually described as monogamous (Fuentes 1999, 2002). The social pair-bond consists of two unrelated adults who preferentially associate and direct affiliative

behaviour towards each other over all other individuals within the group (Mesnick 1997; Smuts 1985; Fuentes 2002). The ‘special relationship’ is another term for the social pair-bond, derived from research conducted on multi-male anthropoid societies (Takahata 1982; Smuts 1985; Hill 1990). Pereira and McGlynn (1997) noted that the longevity of the special relationship can be as short as months (the number of months was undefined). According to this definition, it is plausible that a special relationship may begin and end in one seasonal cycle.

There are three primary hypotheses as to the function of pair-bonds: the ‘resource defence’ hypothesis (Fuentes 2002, Overdorff and Tecot 2006), which is investigated in this thesis, the ‘infanticide prevention’ hypothesis (van Schaik and Kappeler 1993, 1997; Palombit 1999, 2000), and the ‘predator avoidance’ hypothesis (Dunbar 1988; van Schaik and Dunbar 1990; Gould 1996a, 1996b). The resource defence hypothesis proposes that pair-bonding arises due to a female’s increased energetic requirements during gestation and lactation, and her need to receive assistance in the defence of food resources against conspecifics. The male thus defends the pair’s feeding site and the female’s reproductive success is not diminished by the energetic costs of resource defence (Fuentes 2002; Overdorff and Tecot 2006). It is also hypothesized that for lemur species in which female dominance does not exist females form pair-bonds with males in order to improve their foraging success (Pereira and Kappeler 1997; Pereira and McGlynn 1997).

The infanticide prevention hypothesis proposes that within a pair-bond males serve to decrease the risk of harm to or death of an infant by an outsider male (van Schaik and Kappeler 1993, 1997; Palombit 1999, 2000). Females that carry their young and are consequently more vulnerable to infanticide (van Schaik and Kappeler 1997) should thus

form close bonds with a protector adult male (Hrdy 1974; Wrangham 1979; van Schaik and Kappeler 1996, 1997), particularly in species that do not benefit from the protection of female dominance (Pereira and Weiss 1991; van Schaik and Kappeler 1993; Kappeler 1997). Males are hypothesized to commit infanticide to create breeding prospects (Hrdy 1974). The interbirth interval for *E. fulvus rufus* averages two years for surviving infants, but only one year if the infant does not survive (Overdorff *et al.* 1999). Hence a male who has not sired a female's offspring, and as a result does not have a genetic investment in the infant, may benefit from committing infanticide if he succeeds in subsequently mating with the female. A male who may have a genetic investment in a female's offspring would benefit from defending the female and her offspring from potentially infanticidal males (Hrdy 1974; Wrangham 1979). Alternate female counterstrategies against infanticide include oestrus synchrony and paternity confusion via promiscuous mating (Ostner and Kappeler 1999), both of which have been observed in *Eulemur* spp. (Overdorff 1998). To date, infanticidal threat has not been documented for wild groups of *E. fulvus rufus* or any other brown lemur species (Overdorff 1998).

The predator avoidance hypothesis suggests that within male-female dyads, the male provides an infant-carrying female with the service of predator detection. Male vigilance thus increases female and infant protection from predators (Dunbar 1988; van Schaik and Dunbar 1990; Gould 1996a, 1996b; Overdorff 1998). In her study of *E. fulvus rufus* social organization, Overdorff (1998) found that females, not males, were primarily responsible for scanning the environment and alarm calling. It was not specified whether all females participated in vigilance behaviours or whether it was just those with or without infants. If non-reproductive females, or even all females, perform vigilance

behaviours it would better serve a reproductive female to associate with another female rather than a male to reduce predation risk.

Another potential explanation for the occurrence of pair-bonding is male mate guarding. Contrary to the previously mentioned hypotheses, male mate guarding is not female solicited. By increasing time spent in close proximity with a receptive female a male may prevent her from copulating with extra-pair males (Beecher and Beecher 1979; Birkhead 1979; Møller and Birkhead 1991; Huck *et al.* 2004). In seasonal breeders, this behaviour by definition would only occur during the mating season, and would thus explain a seasonal pair-bond. Among primates mate guarding has been observed in moustached tamarins (*Saguinus mystax*) (Huck *et al.* 2004), long-tailed macaques (*Macaca fascicularis*) (Engelhardt *et al.* 2006), chimpanzees (*Pan troglodytes schweinfurthii*) (Tutin 1979), grey mouse lemurs (*Microcebus murinus*) (Eberle and Kappeler 2004), ring-tailed lemurs (*Lemur catta*) (Sauther 1991; Parga 2003), and Verreaux's Sifaka (*Propithecus verreauxi*) (Mass *et al.* 2009). Research on birds has indicated that the intensity of mate guarding behaviour is positively correlated with breeding synchrony (Hammers *et al.* 2009). Given that *E. cinereiceps* females exhibit a high degree of oestrous synchrony and promiscuous breeding, and males have not been observed to exhibit direct intra-sexual competition, mate guarding could be a beneficial male reproductive strategy.

1.6.3.3 Pair bonds vs. central males

Kappeler (1993) found evidence of male-female pairing among *E. fulvus* groups within associative (huddling and proximity) and grooming contexts. Pereira and McGlynn (1997) had different results for each of their study groups: evidence of two

male-female pair-bonds was found in one study group, whereas one male sustained bonds with two females in the other study group thereby creating a central-male dynamic (see below). Overdorff (1998) also found evidence of pair-bonds, but only within feeding contexts and again only during a period of food scarcity. While studying the social organization of black and white ruffed lemurs (*Varecia variegata variegata*) in Nosy Mangabe, Morland (1991a, b) noted that this species exhibited fission-fusion behaviour and that their multi-male multi-female sub-groups were composed of male-female dyads. White (1991) found the same results for groups in Ranomafana National Park. Rigamonti (1993), while studying red ruffed lemurs (*V. variegata rubra*) on the Masoala Peninsula, found that sub-groups were composed of both dyads and non-bonded individuals. Given the similarity in the social organization of WCL and *Varecia* spp. and some evidence from other brown lemur species, it is plausible that fission-fusion bisexual groups of WCL may be composed of several male-female dyads or pair-bonds.

It has also been suggested that brown lemur social organization may, at least in some populations, consist of the association of several females around a central male (Ostner and Kappeler 1999). Pereira and McGlynn (1997) described the social organization of one of their *E. fulvus rufus* study groups not as pair-bonded, but as the close bonds between a single male and two resident females. This result was also observed by Ostner and Kappeler (1999) in two wild groups of *E. fulvus rufus*. Females in both of their study groups associated and copulated at a significantly higher rate with a single male. In each study group that male was the same for all females within the group, thus the term central male. The central male was also documented as the dominant male in the group due to his consistent success in aggressive conflicts with peripheral males.

In non-female-bonded species such as *Eulemur* spp. (Overdorff *et al.* 1999) there is a potential for stronger bonds between females and a central male (Harcourt 1979; Watts 1990). It is thus plausible that the social structure of WCL may conform to the central male hypothesis.

1.7 Current research goals

The goal of this research is to find preliminary answers to two groups of questions:

1. What is the nature of male-female affiliation in *E. cinereiceps*? Is there evidence for pair-bonds or a central male social structure, or are associations random?
2. Do females employ flexible foraging strategies in response to changes in food availability and energy requirements? Do their association patterns change in response to extrinsic and intrinsic factors? In particular, do the results support the resource defence hypothesis?

To answer the first question, I investigate the components of social structure (affiliation, association, and spatial cohesion patterns). To address the second question, I study the temporal variation in diet composition of *E. cinereiceps* in response to extrinsic factors (seasonal variation in food availability) and intrinsic factors (females' reproductive phase). The validity of the resource defence hypothesis for *E. cinereiceps* is verified by gauging the potential variation in females' foraging success in response to their association with males.

By providing a preliminary answer to these two questions, I hope to provide much needed information regarding the social structure, diet, and reproductive strategies of this little-known and critically endangered species. This information should provide guidance

for future in-depth research of *E. cinereiceps* and help to generate adequate conservation plans in response to the dietary and social requirements for the successful reproduction and survival of this species.

Chapter Two: Methods

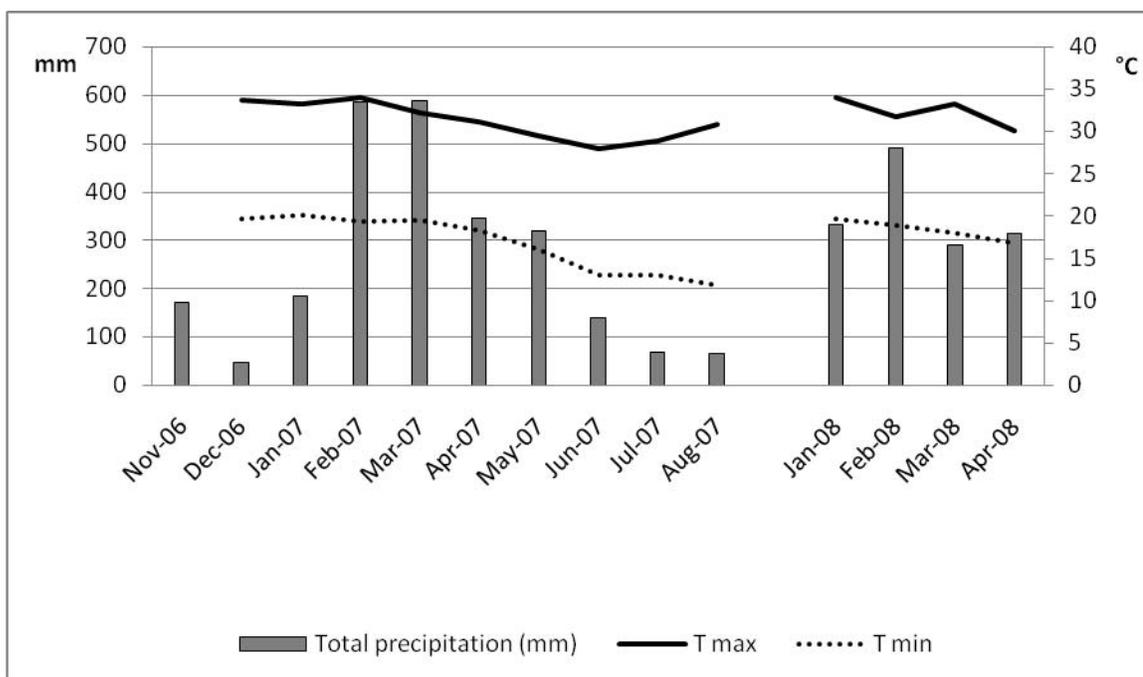
2.1 Study site

This study was conducted in Mahabo Forest, on Madagascar's southeastern coast. Mahabo Forest is located at 23°11'12"S, 47°42'56"E. It is a littoral forest composed of two fragments: inland and coastal, 900 ha and 600 ha respectively. The forest is managed by the Missouri Botanical Garden in collaboration with local communities (S.E. Johnson, pers. comm.). A concurrent and ongoing botanical study run by Reza Ludovic (Missouri Botanical Garden – Madagascar) qualifies the four types of forest in the Mahabo Forest inland fragment as sand, sand disturbed, swamp, and swamp disturbed.

Lemur species inhabiting this site include the eastern woolly lemur (*Avahi laniger*), greater dwarf lemur (*Cheirogaleus major*), mouse lemur (*Microcebus rufus*), grey gentle lemur (*Hapalemur griseus*), and the white-collared lemur (*Eulemur cinereiceps*) (Ratsimbazafy 2002; Mittermeier *et al.* 2006, H.E. Andriamaharoa, pers. comm.). Potential predators, including snakes and raptors, also inhabit the area (Ratsimbazafy 2002).

Elevation in this area ranges between 0 and 20 m above sea level. Average yearly rainfall is 2500 mm and average temperature is 23°C, with the highest temperatures from January to February and the lowest from June to July (Figure 2-1) (Ratsimbazafy, 2002; H.E. Andriamaharoa and R. Ludovic, unpublished data). Highest precipitation occurs from January to March (the hot-wet season) while the least occurs from June to November (the cold-dry and warm-dry seasons respectively) (Figure 2-1) (Ratsimbazafy 2002; Johnson 2002; H.E. Andriamaharoa and R. Ludovic, unpublished data).

Figure 2-1 Total monthly precipitation and average maximum and minimum temperatures at Mahabo from November 2006 to April 2008.

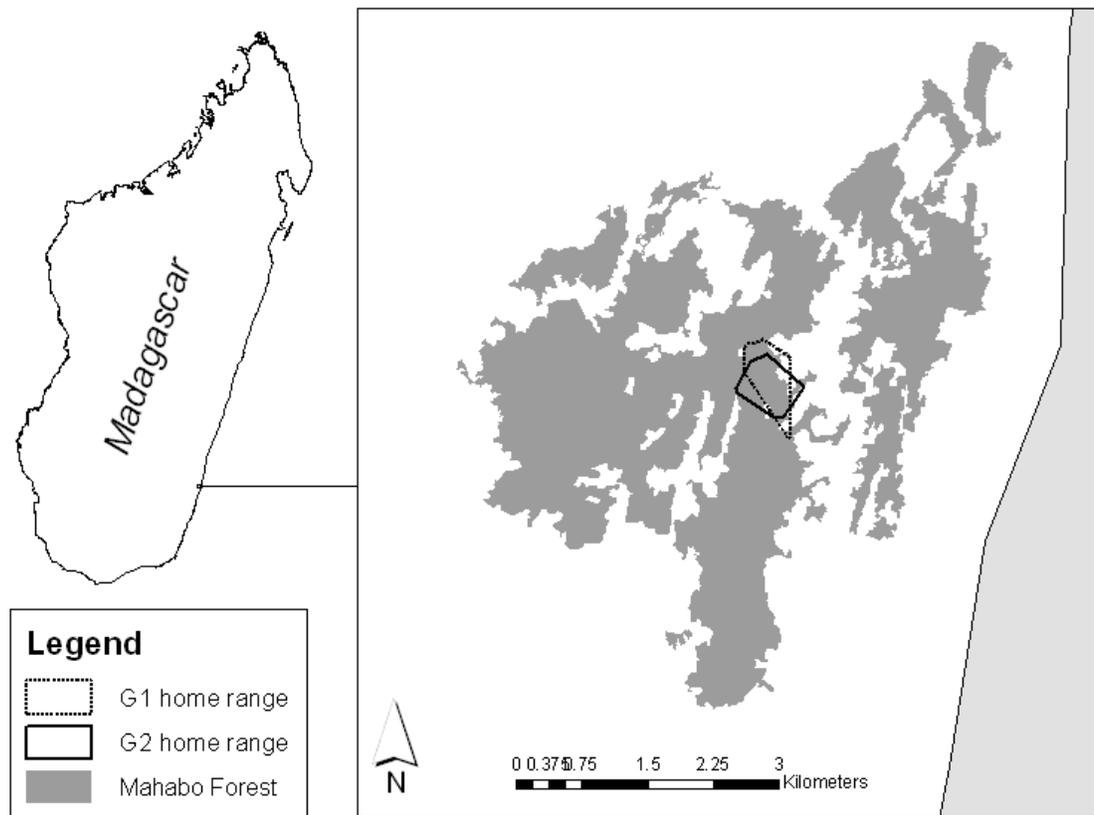


Data missing from September 2007 to December 2007

2.2 Study subjects

Two *Eulemur cinereiceps* groups were studied (Table 2-1) in the inland fragment of Mahabo forest (Figure 2-2). The male composition of Group 1 has varied from 2006 to 2007, with males leaving the group and new males entering the group during the mating season (H.E. Andriamaharoa, pers. comm.). The composition of Group 2 has remained stable over the last three years (H.E. Andriamaharoa, pers. comm.) (Table 2-1 and Table 2-2).

Figure 2-2 Map of Mahabo Forest with home ranges of study groups.



Research was conducted in the inland fragment.

Table 2-1 Composition of Study Groups

	# Adult Males	# Adult Females	# Juvenile Males	# Juvenile Females
Group 1	2	2	2	-
Group 2	2	1	1	1

Table 2-2 Individual Members of Study Groups

	Individual ^a	Name	Comment
Group 1	<i>FRA1</i>	Radio 1	
	<i>FVM</i>	Vavy Mena	
	<i>Mpl</i>	Purple	Joined group in May 2007
	<i>Mlm</i>	Lahy Mena	Joined group in May 2007
	<i>mzr</i>	Zanaky Radio	Born Sep/Oct 2006
	<i>mzm</i>	Zanaky Vavy Mena	Born Sep/Oct 2006
Group 2	<i>FRA2</i>	Radio 2	
	<i>Mtu</i>	Turquoise	
	<i>Mbb</i>	Black blue	
	<i>fZV</i>	Zanan vavy	Born Sep 25 2006
	<i>mzl</i>	Zanan lahy	Born Sep/Oct 2005

^a **F = adult female, M = adult male, f = juvenile female, m = juvenile male.**

2.3 Data collection

Data were collected from June 18 to October 22 2007, resulting in 63 days of data collection. I conducted focal animal sampling (Altmann 1974) during daylight hours. Individual study subjects were identified by a combination of coloured nylon collars and metal tags. Each day, three individuals (males and females) were selected as focal subjects and observed for two hours consecutively. During focal follows, point samples (Altmann 1974) were conducted at 10 minute intervals. A total of 174.5 hours of data

were collected for Group 1 and 134.5 hours for Group 2. The numbers of complete and incomplete focal periods per subject are listed in Table 2-3. Incomplete focal samples that were less than 1 hour in duration were not used.

Table 2-3 Number of focals and total hours of observation per individual.

Individual	# Complete Focal Samples	# Incomplete Focal Samples			Total hours of observation
	2 hours	1.5 hours	1.0 hour	< 1.0 hour ^a	
FRA1	19	3	1		43.5
FVM	19	3	1		43.5
Mpl	19	2	0		41.0
Mlm	19	5	1		46.5
FRA2	22	2	0		47.0
Mtu	21	1	1		44.5
Mbb	20	1	1	1	42.5
Total	139 (x2 hrs)	17 (x1.5 hrs)	5 (x1 hr)		308.5

^a**Incomplete focals less than 1 hr in duration were not retained for data analysis**

Two assistants (Aba ny' Balaza and Aba ny' Seraphin) accompanied me on all focal follows. They aided in locating focal individuals, identifying tree species, and confirming distance or height estimates.

2.3.1 Behavioural data collection

During focal follows I recorded social interactions involving the focal animal and other individuals. The actor and receiver of social interactions were noted. The behaviours recorded included feeding and social behaviours (allo-grooming, mutual grooming, contact, displacement, aggression, and all approaches and leaves). Approaches (and leaves) were recorded when one individual moved to within 1m (or more than 1m

away) from a stationary individual (adapted from Pereira and McGlynn 1997). Aggressive behaviour included the following categories: lunges, charges, cuffs, grabs, bites, and chases; submissive behaviour included displacement, cowers, jumps away, and flees (Pereira and Kappeler 1997). *Ad libitum* sampling was used to record rare behaviours such as inter-group agonistic interactions, group fission, group fusion, and copulatory behaviour that happened outside of focal periods, or involving individuals other than the focal. When group fission or fusion events were observed, the members of each subgroup were noted (all definitions are listed in Table 2-4).

Table 2-4 List of terms and definitions

Term	Definition
Approach	Movement of one individual towards another, crossing a 1m proximity “boundary” (Palombit 1995). At least 1 minute must have elapsed between two consecutive approaches by the same individual for them to be counted as two separate events.
Break contact	When an individual moves away from another individual whom he was physically touching. The individual may or may not remain within 1m of the target individual.
Displacement	An individual moves toward the target individual, who within the following 2 seconds physically removes itself from the location and away from the acting individual (adapted from McCowan <i>et al.</i> 2008).
Establish contact	When an individual moves towards another individual so that they are physically touching.
Feeding bout	The onset of a feeding bout was when the focal individual was observed placing a food item in its mouth. The feeding bout was considered terminated when the focal was not observed placing a food item in its mouth for at least 15 seconds (Overdorff 1998).

Feeding rate	The number of food items (fruit only) eaten per minute of feeding bout (adapted from Overdorff 1998).
Fission event	Closest members of the group are 30m or further apart, and are thus no longer in visual or close auditory contact (Johnson 2002).
Fusion event	When sub-groups move to within 30m of each other and do not move more than 30m away from each other (Johnson 2002) within the following 30 minutes (an arbitrary time criterion which I selected to control for sub-groups coming in temporary proximity with one another but not fusing. This criterion was not applied to fission events).
Grooming	Upward scraping of procumbent toothcomb (lower incisors) through hair to dislodge particles, combined with tongue licks to remove particles (Buettner-Janusch and Andrew 1962; Vick and Conley 1976).
Group spread	The greatest horizontal and vertical distance (in meters) separating the two furthest individuals within the group (Waser 1974; Olupot <i>et al.</i> 1997). Measured by visual estimation.
Leave	When an individual, within 1m of the target individual, but not in contact, moves away from the target individual and may or may not cross the 1m proximity boundary. At least 1 minute must have elapsed between two consecutive leaves by the same individual for them to be considered two separate events.
Nearest neighbour while feeding	The individual closest to the focal individual during a feeding bout, within a 5 meter radius (Overdorff 1998).
Proximity	Two individuals are considered in proximity when they are within 1m or less of each other.
Sub-group	A sub-unit of the original social group, the result of group fission.

All instances of feeding were recorded and timed during focal observations. The focal animals' nearest neighbour(s) within 5m was recorded at the onset of the feeding bout. Displacements of the focal animal from its feeding site were noted, as was the identity of the other individual involved. The species, the plant part selected, and the pick frequency were recorded when conditions permitted. The pick frequency was defined as the number of food items (fruit only) removed from the tree by the focal individual while feeding. When the focal was observed feeding on fruit, a specimen was collected and the length and width were measured, as well as the shape of the fruit (ovoid or spheroid) to calculate the volume of the fruit. Fruit was classified into small ($0.0-1.9\text{cm}^3$), medium ($2.0-29.9\text{cm}^3$), and large ($>30.0\text{cm}^3$) classes based both on volume and on common name. Some fruit have both small and large types (i.e. *Vitex oscitans*, common names of fruit: 'Sarivatoa kely' and 'Sarivatoa be', where 'kely' translates to small and 'be' means big), and thus were not included in the same size class (Table 2-5).

Point samples (Altmann 1974) were conducted at 10 minute intervals within focal observations during which I recorded sub-group composition and group spread as measures of group cohesion. Changes in sub-group composition served as an additional indication of fission and fusion events.

Table 2-5 Food species size classes: small, medium, and large.

Food Species	N	Mean length (cm)	Mean width (cm)	Mean volume (cm³)	Size Class
<i>Leptolaena</i> sp	13	0.69	0.59	0.26	small
<i>Vitex oscitans</i>	8	0.85	0.78	0.55	small
Spec. Indet. #1: Sari Kafe	4	1.25	1.18	1.86	small
<i>Noronhia emarginata</i>	13	1.78	1.02	1.94	small
<i>Vitex oscitans</i>	3	2.10	1.47	4.74	medium
<i>Noronhia emarginata</i>	21	2.55	1.81	9.12	medium
<i>Uapaca</i> sp	23	2.50	2.20	12.93	medium
Spec. Indet. #2: Vonitra	1	3.00	2.90	26.42	medium
<i>Pandanus</i> sp	2	5.80	5.65	197.68	large
<i>Garcinia madagascariensis</i>	1	8.00	5.60	262.72	large

2.3.2 Botanical data collection

Data on food availability were collected every two weeks from a pre-existing 1 ha plot in the Mahabo Forest inland fragment. This plot was not in the home range of either study group but is representative of the sand type and swamp type of forest found in the inland fragment and in the groups' home ranges.

All adult trees with a DBH (diameter at 1.3m) >10cm (N=732) were typed to species level and given a presence/absence score for fruit on a bi-weekly basis. Fruit was of interest as it is the primary food resource for *E cinereiceps*, has the highest energy content of common primate foods (Wasserman and Chapman 2003), and yet is unpredictably distributed over time and space (Overdorff 1996).

2.4 Data Analysis

2.4.1 *Seasonal variation of fruit availability*

Seasons of fruit abundance or scarcity were determined based on variation in the index of food availability. The tree species that were part of the diet of the two study groups were determined from feeding observations. The number of food trees bearing fruit per phenological survey was divided by the total number of trees in the botanical plot, and multiplied by 100, resulting in the index of food availability. The mean index and standard deviation were calculated. A difference greater than one standard deviation between two chronologically consecutive indices indicated a change in season. This analysis delineates 3 seasons during the period of June 18 to October 28: Low 1 (June 18 – August 22: 31 days of observation), the first season of fruit scarcity; High (August 23 – September 30: 20 days of observation), the season of fruit abundance; and Low 2 (October 01 – October 28: 12 days of observation), the second season of fruit scarcity (Table 2-6).

Table 2-6 Index of fruit availability based on percentage of trees bearing fruit

Date	Total # trees	# Trees bearing fruit	% fruit availability	Fruit Season
Jul 06	734	32	4.36	Low 1
Jul 30	734	31	4.22	Low 1
Aug 14	734	33	4.50	Low 1
Aug 31	734	45	6.13	High
Sep 14	733	54	7.37	High
Sep 28	733	47	6.41	High
Oct 11	733	32	4.37	Low 2

2.4.2 Reproductive seasons

Reproductive seasons are defined as Mating, Early Gestation, Late Gestation, and Lactation. The Mating season is defined as beginning when a female first copulates with a male, and ending on the day of conception. Conception was determined *a posteriori*, after parturition was observed by counting back 120 days, the average gestation length for brown lemurs (Izard *et al.* 1993, 1995; Ostner and Heistermann 2003). Early Gestation is defined as beginning on the date of conception and ending 40 days later. This definition is based on two factors: the change in hormone levels occurring at day 41 of gestation as observed in *E. fulvus rufus* (Ostner and Heistermann 2003), and the abrupt rise in energy requirements after the first trimester as observed in humans (Hyttén and Chamberlain 1980; Butte and King 2005). Late Gestation is defined as beginning on the 41st day of gestation and ending at parturition. Lactation is defined as beginning at parturition, and for the purposes of this study, ending on the last day of observations because weaning did not occur within the study period.

Reproductive seasons of the females in this study were not tightly synchronized; one female gave birth nearly two months after the other females (Table 2-1). Females with an infant delivery date at least 7 days apart are not considered to be oestrus synchronized (Pereira and McGlynn 1997). It should be noted that such a delayed (mid-July to mid-November) and asynchronous gestation period is unusual in brown lemurs.

Table 2-7 Female reproductive seasons

	FRA1	FVM	FRA2
Mating	Jun 18 – Jul 17 (11)	-	-
Early Gestation	Jul 18 – Aug 26 (10)	May 28 – Jul 06 (9)	Jun 04 – Jul 13 (3)
Late Gestation	Aug 27 – Nov 14 (18)	Jul 07 – Sep 24 (20)	Jul 14 – Oct 01 (20)
Lactation	-	Sep 25 – Oct 28 (10)	Oct 02 – Oct 28 (6)

***Number of contact days with female's group during respective reproductive season in parentheses.**

2.4.3 Affiliation between adults

For each focal individual, the frequency of grooming bouts during which the focal gave grooming to another individual was calculated. The frequency of grooming received was not considered. The frequency of grooming bouts between the focal and its adult partner were divided by the focal's total hours of observation, resulting in a grooming rate per focal individual toward the other adult in the group. Grooming rates were calculated overall, by season of fruit availability, and by female reproductive season. For reproductive seasons, grooming rates between males or between females were not calculated because females' reproductive seasons were not perfectly synchronized (i.e. different reproductive seasons occurred on the same dates and results could not be attributed to a particular reproductive period).

2.4.4 Association

2.4.4.1 Time spent in proximity and contact

Two separate measures of association were calculated: proximity score and contact score. Each score represented the percentage of a focal individual's observation time spent in proximity (or in contact) with a specific adult partner. In addition, these scores were combined for a total association score. For each focal individual, the total amount of time spent in proximity, in contact, or in total association with another individual was calculated. The total amount of time spent in proximity, contact, or total association (in minutes) between the focal and every potential adult partner were divided by the focal's total minutes of observation, and then multiplied by 100, resulting in a proximity score, contact score, and total association score per focal individual with every other adult in the group. Scores were calculated overall, by season of fruit availability, and by female reproductive season. It should be noted that for reproductive seasons, scores between males or between females were not calculated.

2.4.4.2 Maintenance of proximity

In order to determine which individual within a dyad was responsible for maintaining proximity Hinde Index values were generated by approach and leave frequencies (which also included establish contact and break contact) (Table 2-4) at the dyad level using the following equation:

$$[UA / (UA + UB)] - [SA / (SA + SB)]$$

where UA is the number of approaches noted for A towards B and UB is the number of approaches noted for B towards A, SA is the number of leaves noted for A away from B and SB is the number of leaves noted for B away from A. A value of +1.0 indicates that

A is wholly responsible for maintaining proximity with B, whereas a value of -1.0 indicates that B is wholly responsible for maintaining proximity with A. Values around 0 indicated that both individuals were mutually attracted or mutually indifferent to each other (Hinde and Atkinson 1970). Here, I choose an arbitrary threshold of between -0.29 and +0.29 as corresponding to this situation. Hinde index values were calculated only for those dyads whose sum of observed approaches and leaves was at least 10 (Hinde and Atkinson 1970).

2.4.5 Feeding

2.4.5.1 Seasonal variation in diet composition

Co-variation of seasonal changes in fruit availability with females' diets (% of ripe fruit) and association patterns was examined. I also examined female diets according to reproductive seasons.

2.4.5.2 Nearest neighbour when feeding

In nearest neighbour analyses, feeding data were not broken down by food type since nearly all feeding involved fruit (see Ch. 3). Data from focal individuals' point samples were used to calculate the number of feeding bouts during which the focal was alone, with a male, or with a female. These numbers were then divided by the total number of scan samples during which the focal individual was observed feeding. Results were compared between males and females within and across seasons of fruit availability. Females' results were compared within and across reproductive seasons.

2.4.5.3 Feeding Rate

Foraging rate can be recorded as the number of bites per minute of feeding bout (Overdorff 1998). The density of the foliage at the study site made it difficult to

accurately count the number of bites, however, and pick rate (a coarser measure) was used instead. For this study feeding rate is calculated as the number of items (fruit) eaten divided by the feeding bout length. Due to visibility conditions, pick rate could not be recorded consistently and a subset of the data was used for analyses. Mean feeding rates were compared between males and females, across seasons of food availability, and across reproductive seasons. Inferential statistics were not employed due to the low number of individuals in this study.

2.4.5.4 Foraging Success

For the purposes of this study, time spent traveling was considered a proxy measure of energy output. If time spent feeding is considered a proxy for energy intake, then time spent feeding divided by travel time (input/output) results in an indication of foraging success. Data from focal individuals' continuous focal samples were extracted for feeding and travel behaviours. Time spent travelling, time spent feeding, and foraging success were compared across sexes within and across seasons of fruit availability. Females' results were compared across reproductive seasons.

2.4.6 Cohesion

Due to poor visibility conditions it was not always possible to determine group spread and hence whether the focal individual's group had fissioned. Thus, as a measure of group cohesion, only point samples where group spread and composition were known were used to calculate the percentage of sub-group point samples. The mean group spread of the fused group was compared to the mean group spread of sub-groups. As with the previous results, the composition of subgroups and the mean duration of separation (time

between a fission and fusion event) were compared across seasons of fruit availability and reproductive seasons.

2.4.7 Overall male-female association and affiliation

Results for nearest neighbour when resting, feeding, and grooming, were compared for each adult. I calculated the number of point samples during which male or female focal individuals were at rest/feeding/giving grooming alone, with a male, or with a female, and divided these by the total number of point samples during which the male or female focal individuals were observed resting/feeding/giving grooming. Males and females were compared based on these three behaviour categories within and across seasons of fruit availability.

2.4.8 Relationship strength

Based on affiliative results, total association scores, and percentage of fissions in which a dyad was in the same sub-group, dyads were ranked on each measure from highest to lowest. In Group 1, dyads were given a score from 1 to 6 for each measure, with 6 being given to the highest ranked dyad; dyads in Group 2 were given a score from 1 to 3 for each measure. If dyads had similar results (within two percentage points) they were given equal ranking. If dyads did not associate, affiliate, or form a sub-group together they were given a rank of 0. Scores for each measure were then totalled per dyad to determine whether there was a marked difference between any dyad.

Chapter Three: Results

3.1 Introduction

The goal of this research is twofold: to determine the social structure (specifically the nature of male-female relationships) and group cohesion of *E. cinereiceps*, and to investigate female foraging strategies (variation in diet composition, choice of feeding partner, and foraging success with changes in food availability or female reproductive phase). For both lines of inquiry I establish whether food availability (low vs. high) and/or female energetic requirements (as per reproductive phase) correlate with male and female behaviours. Detailed descriptions of rarely observed behaviours such as intergroup agonism, copulation, and parturition are also provided.

3.2 Social structure and group cohesion

Social structure describes the pattern and quality of interactions between individuals and the types of relationships that are typified by specific patterns (Kappeler and van Schaik 2002). To determine the nature of male-female relationships I analysed data on affiliation, association, and sub-grouping patterns, and whether the pattern and quality of these interactions are affected by food availability or female reproductive status.

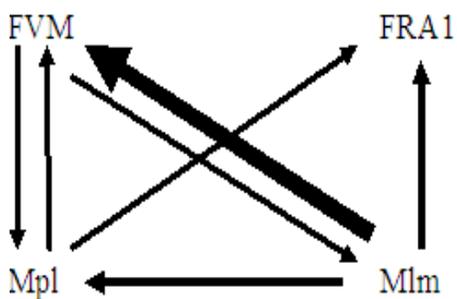
3.2.1 Grooming

Grooming rates were calculated for each focal and its adult partners as a directional measure of affiliation. Grooming rates between adults were low in the two study groups (Group 1: (mean \pm SD) 0.16 ± 0.14 bouts/hr; Group 2: 0.09 ± 0.07 bouts/hr) (Fig 3-1). Grooming rates did not vary according to food availability in either group (Fig.

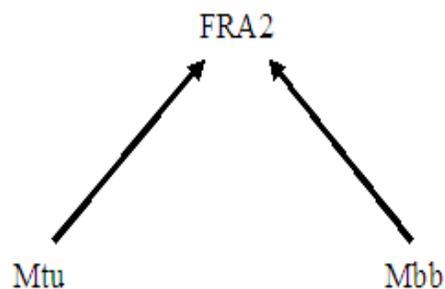
3-2). When grooming rates were calculated by reproductive season, rates remained the same except during Lactation (Mlm towards FVM: 1.55 bouts/hr) (Fig. 3-3).

Figure 3-1 Grooming rate sociograms for Group 1 and Group 2 (Overall)

Group 1



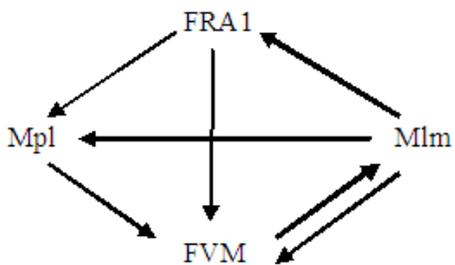
Group 2



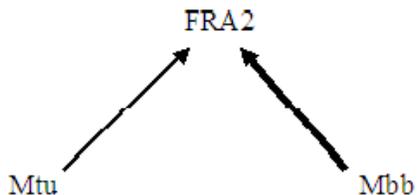
The tail of an arrow indicates the focal individual, while the head of the corresponding arrow indicates whom the focal individual groomed. The thickness of the arrows represents the value of the grooming rate (# of bouts per hour) where thickness is directly proportional to grooming rate.

Figure 3-2 Grooming rate sociograms for Group 1 and Group 2 by season of fruit availability.

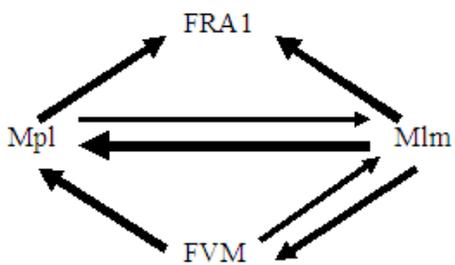
Group 1 – Low 1



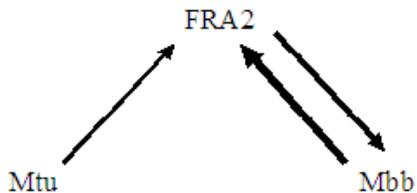
Group 2 – Low 1



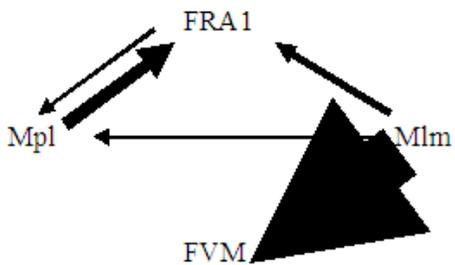
Group 1 – High



Group 2 – High



Group 1 – Low 2



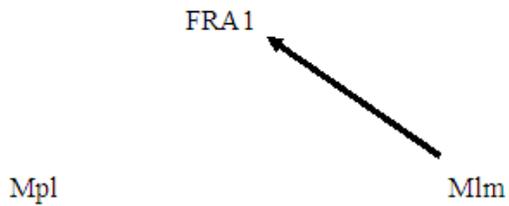
Group 2 – Low 2



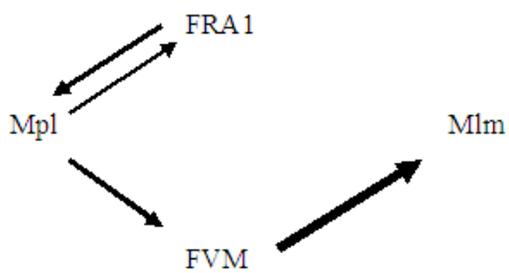
Legend as in previous figure.

Figure 3-3 Grooming rate sociograms for Group 1 and Group 2 by reproductive season.

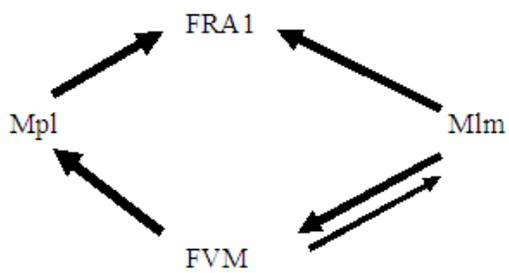
Group 1 – M season (RA1)



Group 1 – G1 season (RA1 + VM)



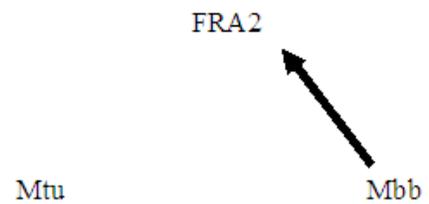
Group 1 – G2 season (RA1 + VM)



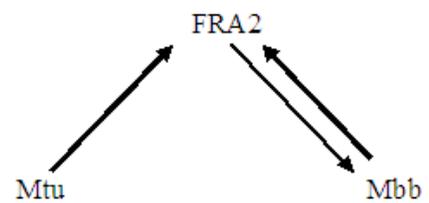
Group 1 – VM's L season



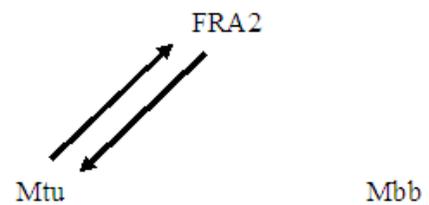
Group 2 – G1



Group 2 – G2



Group 2 – L



Legend as in previous figure.

3.2.2 Association

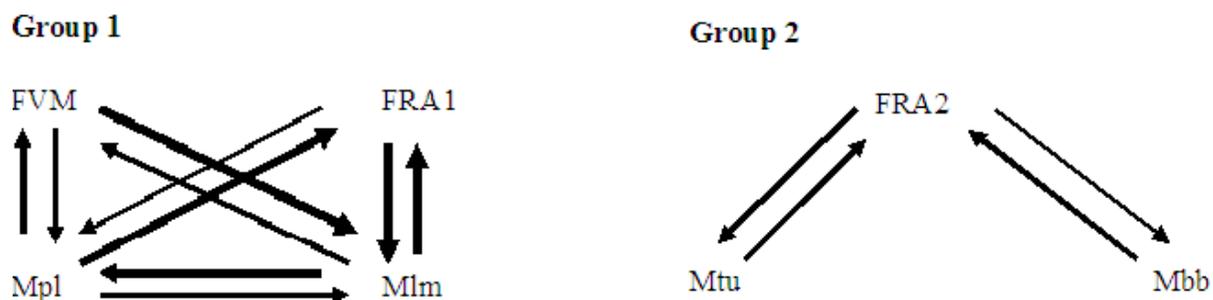
3.2.2.1 Time spent in proximity and contact

As a measure of association, the proportion of time spent in proximity (< 1m), in contact, and the sum of these proportions (total association), were calculated for each focal individual with an adult partner. The magnitude of association between individuals is used to qualify the relationship.

Focal individuals in both groups spent a low percentage of time in proximity with adult partners (below 6.1%). Individuals spent a greater percentage of time in contact with one another (Group 1: $17.0 \pm 9.3\%$; Group 2: $12.9 \pm 6.7\%$), reaching 82.0% in one case. The total percentage of time spent in association was higher (Group 1: $20.1 \pm 10.7\%$; Group 2: $14.8 \pm 7.6\%$) (Appendix A: Table A.1a for Group 1; Table A.1b for Group 2).

The percentage of time spent in total association between females was low (below 3.0%). Both females in Group 1 spent a greater total percentage of time in association with Mlm (FRA1: 30.7%; FVM: 30.6%) than with Mpl (FRA1: 17.3%; FVM: 18.0%). Both males in Group 1 spent a greater total percentage of time in association with FRA1 (Mpl: 28.8%; Mlm: 32.7%), and equally favoured FVM and each other. In Group 2, FRA2 spent a slightly greater total percentage of time in association with Mtu (Mtu: 21.9% vs. Mbb: 16.4%). Both males spent a greater total percentage of time in association with FRA2 than with each other (Mtu: 21.1% > 5.0%; Mbb: 18.9% > 5.4%) (Fig 3-4).

Figure 3-4 Total association sociograms for Group 1 and Group 2 (Overall).



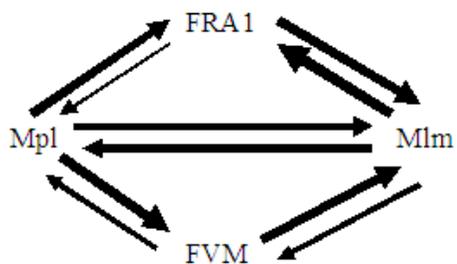
The tail of an arrow indicates the focal individual, while the head of the corresponding arrow indicates whom the focal individual associated with. The thickness of the arrows represents the value of association (% of focal's observation time spent in contact + proximity with adult individual) where thickness is directly proportional to value of association.

In Group 1, a seasonal relationship of food availability with association existed for FVM only. FVM spent a greater total percentage of time in association with Mlm during the seasons of low food availability (Low 1: Mlm: 34.6% > Mpl: 16.8%; Low 2: Mlm: 95.4% > Mpl: 19.0%), but favoured Mpl during the season of food abundance (Mpl: 19.3% > Mlm: 13.7%) (Fig 3-5). A seasonal relationship of food availability with association was not found in Group 2.

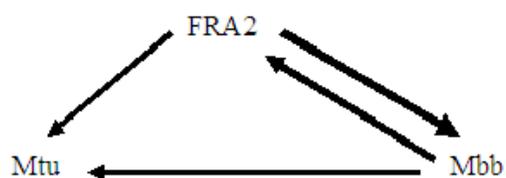
Seasonal relationships of reproductive season with association were found for FVM and FRA2. FVM spent a greater total percentage of time in association with Mlm during Early Gestation (Mlm: 52.3% > Mpl: 22.2%), and Lactation (Mlm: 30.4% > Mpl: 6.1%), but not during Late Gestation (Mpl: 22.0% \approx Mlm: 18.8%). A similar pattern emerged for FRA2; although FRA2 showed a preference for one male over the other during Early Gestation (Mbb: 43.8% > Mtu: 24.5%) and Lactation (Mtu: 32.8% > Mbb: 0.0%), she spent an equal total percentage of time in association with each male during Late Gestation (Mtu: 17.1% \approx Mbb: 17.2%) (Fig 3-6).

Figure 3-5 Total association sociograms for Group 1 and Group 2 by season of food availability.

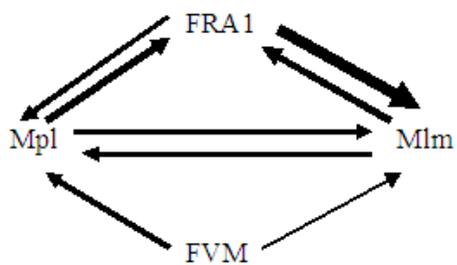
Group 1 – Low 1



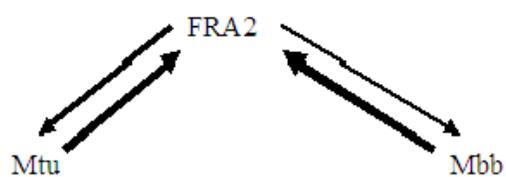
Group 2 – Low 1



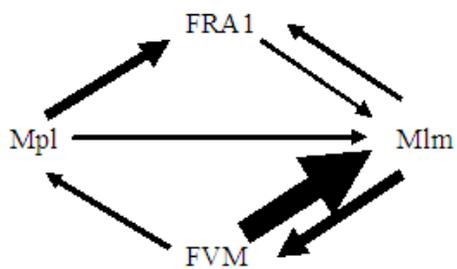
Group 1 – High



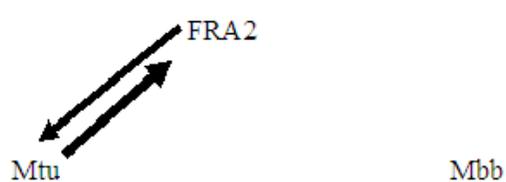
Group 2 – High



Group 1 – Low 2



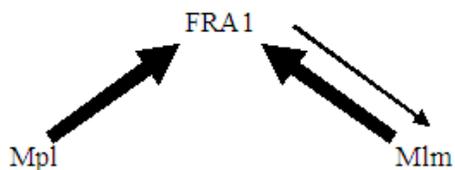
Group 2 – Low 2



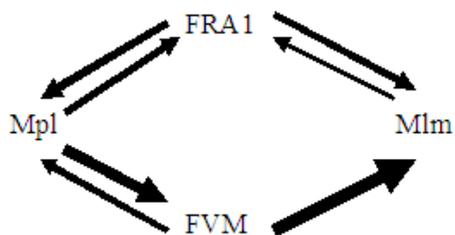
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Figure 3-6 Total association sociograms for Group 1 and Group 2 by reproductive seasons.

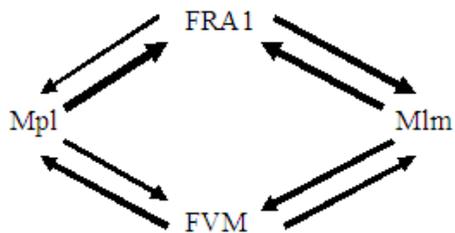
Group 1 – M (FRA1)



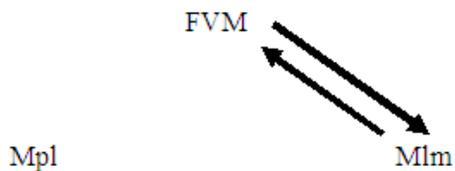
Group 1 – G1 (FRA1 + FVM)



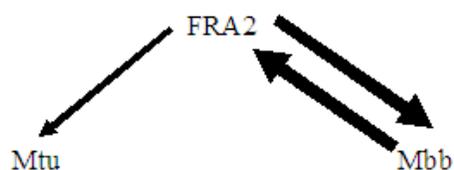
Group 1 – G2 (FRA1 + FVM)



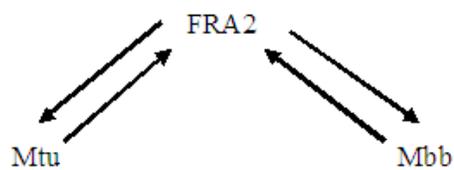
Group 1 – L (FVM)



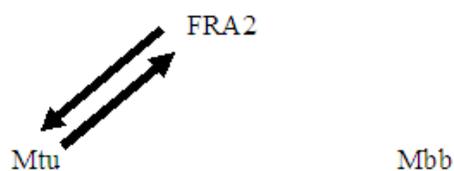
Group 2 – G1



Group 2 – G2



Group 2 – L



Legend as in previous figure.

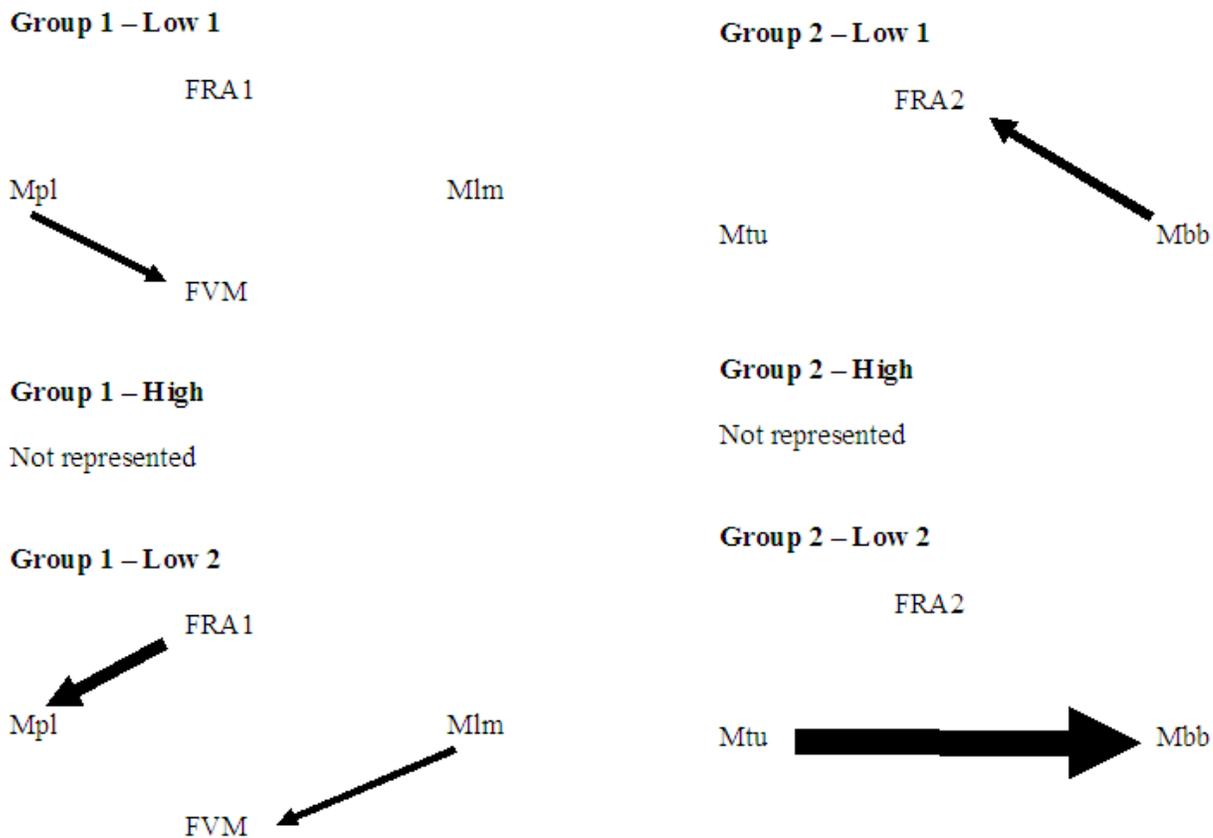
3.2.2.2 Maintenance of proximity

Hinde's Index (H.I.) was calculated to determine which individual within a dyad was responsible for maintaining proximity, and thus which individual had a greater interest in maintaining the relationship. Index values above +0.29 indicated that individual A bore responsibility, values below -0.29 indicated that responsibility was borne by individual B.

Overall, all potential pairings in Group 1 and Group 2 bore equal responsibility for maintenance of proximity. When analysed by season, the responsibility indices had a more uneven distribution. A seasonal relationship of food availability with H.I. did not exist between individual dyads, but it should be noted that responsibility was unevenly distributed during the seasons of low food availability, with males bearing responsibility, but equal during the season of food abundance (Fig 3-7) (Appendix B: Table B.1).

During reproductive seasons, when individuals were not equally responsible for maintaining proximity, males bore the responsibility. This trend was observed in Early Gestation (Mpl-FVM: 0.33; Mbb-FRA2: 0.56), and Late Gestation (Mlm-FVM: 0.36) (Appendix B: Table B.2).

Figure 3-7 Hinde's Index (H.I.) of association for Group 1 and Group 2 by season of food availability.



Tail end of arrow indicates individual responsible for maintaining proximity with the individual indicated by the head of the arrow. The thickness of the arrows represents the value of H.I. where thickness is directly proportional to H.I. value.

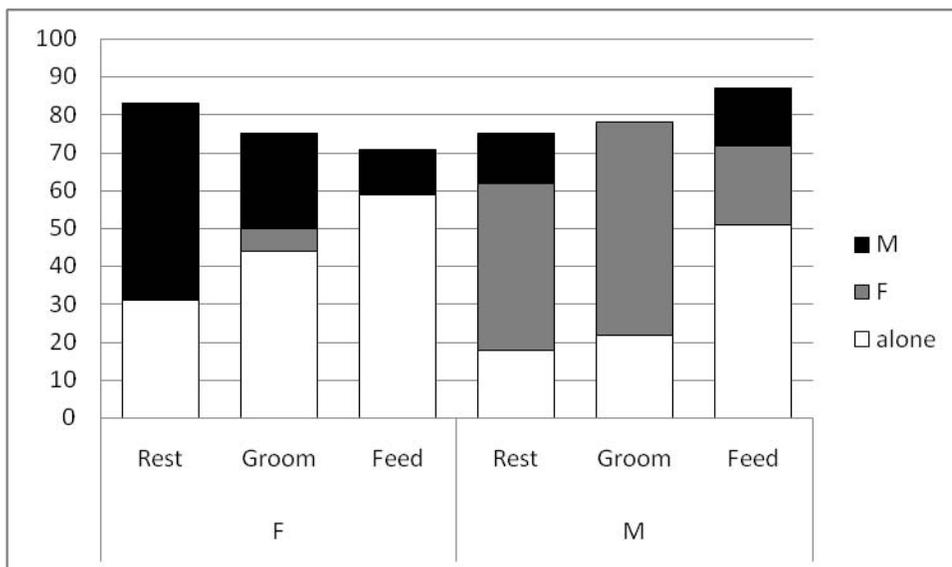
3.2.3 Overall male-female association and affiliation

Individuals in both groups spent a greater percentage of time resting and grooming with an individual of the opposite sex than with an individual of the same sex. Females spent more time feeding with an opposite sex partner (the female in Group 2 – FRA2 – did not have the choice of associating with a female), but males in both groups spent an equal percentage of time feeding with females and males (Group 1: 21% vs. 15%; Group 2: 14% vs. 11%) (Fig 3-8).

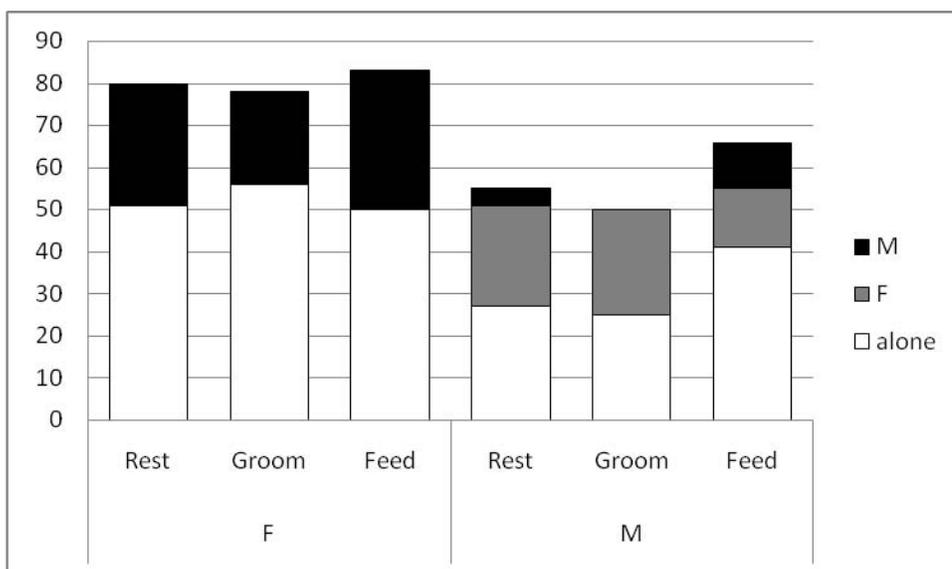
Although females in both groups spent a greater percentage of time engaged in behaviours alone than with a nearest neighbour, females in Group 1 spent more time resting with males than alone (52% vs. 31%) (Fig 3-8a). Males in Group 1 spent more time resting and grooming with females as their nearest neighbour than alone (rest: 44% vs. 18%; groom: 56% vs. 22%) (Fig 3-8a), while males in Group 2 spent an equal percentage of time resting and grooming with females or alone (rest: 24% vs. 27%; groom: 25% vs. 25%) (Fig 3-8b). Males and females in both groups spent more time feeding alone than with a nearest neighbour (Fig 3-8).

Figure 3-8 Percentage of time spent by females and males resting, grooming, or feeding alone or with a male or female as nearest neighbour.

a. Group 1^a



b. Group 2^{a,b}



^aInstances in which the nearest neighbour was a juvenile are not included. Amounts thus do not add up to 100%.

^bFRA2 in Group 2 did not have a potential female partner. Her F values are thus not zero, but not possible.

3.2.4 Cohesion

To measure cohesion, group composition (adult individuals only) and group spread were noted every 10 minutes during point samples. These data provide information regarding the potential variation in sub-group composition, the relationship of fissioning with sub-group spread, and the duration of fission events. Cohesion measures are not available for every point sample due to poor visibility conditions or whether the group was travelling at the time of the point sample. Of 1863 point samples, group composition and group spread were not known for 510 (or 27.4%) point samples. Cohesion data are thus a subset of the overall data. The composition of Group 1 was known for 687 point samples, 9.6% of which represented group fissions. The composition of Group 2 was known for 666 point samples, 11.3% of which represented group fissions. Group fissioning did not track resource availability closely. Fissioning in both groups was highest in the first period of low food availability and lowest in the second (Table 3-1).

Table 3-1 Percentage of point samples for which group composition was known in which sub-grouping occurred.

Season	% of sub-grouping	
	Group 1	Group 2
Overall	9.6	11.3
Low 1	15.1	22.4
High	6.5	10.3
Low 2	0.0	2.1

For both groups, group spread was smaller when fissioned than when the groups were whole. In Group 1, group spread was largest during the season of food abundance regardless of whether the group was whole or fissioned (Table 3-2a). In Group 2, the spread of the group when whole did not track resource availability. Sub-group spread was relatively small, averaging 1.5m during the first season of low food availability and 0.0m (contact) during the second season of low food availability. The sub-group observed during the season of food abundance consisted of only one adult individual, FRA2, and sub-group spread was not applicable (Table 3-2b).

In Group 1, the most common sub-group consisted of FRA1, Mlm, and Mpl. The second most common sub-group consisted of FVM (Table 3-3a). Though it is not known whether individuals not found in a sub-group formed a single sub-group of their own or split into multiple sub-groups, the sub-groupings mentioned above hint towards a distinct sub-grouping pattern during fission events. The most common sub-group in Group 2 consisted of the two adult males, Mtu and Mbb. The second most common sub-group consisted of FRA2 and Mbb. (Table 3-3b). A seasonal effect of food availability on sub-grouping pattern was not observed for either group.

The duration of fission events was estimated from the number of consecutive point samples (taken at 10 minute intervals) for which a specific sub-group was observed. This estimate does not reflect the actual duration of fission events (they may have been from 0.02 to 9.98 minutes longer than the estimate), however the same estimation method was applied to calculate the duration of every fission event. Fission events lasted from 10 to 180 minutes in Group 1, with an average duration of 62 minutes overall, and lasted 10 to 330 minutes in Group 2, with an average duration of 93.8 minutes overall. A seasonal

fluctuation of duration of fission events with food availability was not observed for either group (Table 3-3).

Table 3-2 Group spread (m) when group is whole vs. when group is fissioned into sub-groups.

a. Group 1

Season	Whole group			Sub-groups		
	N	Mean \pm SD	Range	N	Mean \pm SD	Range
Overall	521	12.3 \pm 0.3	1 - 29	62	4.1 \pm 0.9	0 - 25
Low 1	251	8.3 \pm 0.4	1 - 25	45	2.5 \pm 0.6	0 - 15
High	207	16.1 \pm 0.5	3 - 29	17	8.5 \pm 2.5	0 - 25
Low 2	63	14.8 \pm 0.7	8 - 27	0	-	-

b. Group 2

Season	Group whole			Sub-groups		
	N	Mean \pm SD	Range	N	Mean \pm SD	Range
Overall	500	13.2 \pm 0.3	0 - 28	51	1.4 \pm 0.3	0 - 10
Low 1	139	12.0 \pm 0.6	0 - 28	48	1.5 \pm 0.4	0 - 10
High	172	12.1 \pm 0.5	2 - 27	22	-	-
Low 2	189	15.1 \pm 0.4	5 - 28	3	0.0 \pm 0.0	0 - 0

Table 3-3 Composition of sub-groups and duration of sub-grouping events**a. Group 1**

Date	Sub-group members	Individuals absent from sub-group	Duration (min)
19 - Jun	FRA1	FVM, Mpl, Mlm	80 ^a
19 - Jun	FRA1, FVM, Mlm	Mpl	40
19 - Jun	FRA1, Mlm, Mpl	FVM	10
20 - Jun	FVM, Mlm	FRA1, Mpl	100
3 - Jul	FVM	FRA1, Mlm, Mpl	180
4 - Jul	FRA1, Mlm + Mpl	FVM	70
12 - Sep	FRA1, Mlm	FVM, Mpl	10
12 - Sep	FRA1, Mlm, Mpl	FVM	10
25 - Sep	FVM	FRA1, Mlm, Mpl	60
26 - Sep	FRA1, Mlm, Mpl	FVM	60

^a equivalent to 8 point samples.

b. Group 2

Date	Sub-group members	Individuals absent from sub-group	Duration (min)
10 - jul	FRA2, Mtu	Mbb	100
11 - Jul	FRA2, Mbb	Mtu	330
12 - Jul	FRA2, Mbb	Mtu	10
20 - Aug	Mbb, Mtu	FRA2	10
20 - Aug	Mbb, Mtu	FRA2	10
20 - Aug	FRA2, Mbb	Mtu	20
17 - Sep	FRA2	Mbb, Mtu	220
2 - Oct	FRA2	Mbb, Mtu	50

3.2.5 Relationship strength

High affiliation, association, and the propensity towards sub-grouping together indicate a strong relationship between two adult individuals. These measures were ranked and summed for each dyad to illustrate the configuration of relationships within each group.

Analysed overall, the strongest relationships are mainly found in male-female dyads vs. male-male or female-female dyads (Table 3-4) The strongest relationships in Group 1 are FRA1 - Mlm (strength = 16) and FVM - Mlm (strength = 14) (Table 3-4a). The strongest relationships in Group 2 are FRA2 – Mbb (strength = 7.5) and FRA2 – Mtu (strength = 7.5) (Table 3-4b).

When analysed seasonally, in Group 1 the relationship between FRA1 and Mlm remained strong throughout all three seasons of food availability (Low 1: 12, High: 17, Low 2: 5). FVM and Mlm's relationship became weak only during the season of high food availability (Low 1: 13, High: 6, Low 2: 6). Seasonal relationships appear to involve a centralized configuration. During the first and second seasons of food scarcity, both females organized themselves around Mlm. During the season of high food availability, both males organized themselves around FRA1 (Table 3-5a). A seasonal effect of food availability on relationship strength was not observed for Group 2 (Table 3-5b).

Table 3-4 Strength of relationship between dyads relative to other dyads: defined as the total reversed rank scores for percentage of time spent grooming (affiliation), in association, and in sub-groups (cohesion).

a. Group 1

Dyad	Affiliation %	Rank	Association %	Rank	Cohesion %	Rank	Strength
FRA1 - Mlm	0.25	4	0.32	6	0.47	6	16
FVM - Mlm	0.63	6	0.25	5	0.21	3	14
FRA1 - Mpl	0.26	4	0.20	3	0.39	5	12
Mpl - Mlm	0.27	4	0.21	3	0.30	4	11
FVM - Mpl	0.26	4	0.20	3	0.00	0	7
FRA1 - FVM	0.06	1	0.01	1	0.06	2	4

b. Group 2

Dyad	Affiliation %	Rank	Association %	Rank	Cohesion %	Rank	Strength
FRA2 - Mtu	0.21	2.5	0.21	3	0.12	2	7.5
FRA2 - Mbb	0.23	2.5	0.18	2	0.32	3	7.5
Mtu - Mbb	0.02	1	0.05	1	0.03	1	3

Table 3-5 Strength of relationship per season of food availability between dyads relative to other dyads: defined as the total reversed rank scores for of time spent grooming (affiliation), in association, and in sub-groups (cohesion).

a. Group 1

Low 1		High		Low 2	
Dyad	Strength	Dyad	Strength	Dyad	Strength
FVM - Mlm	13	FRA1 - Mlm	17	FVM - Mlm	6
FRA1 - Mlm	12	FRA1 - Mpl	14	FRA1 - Mlm	5
Mpl - Mlm	8.5	Mpl - Mlm	7	FRA1 - Mpl	3
FRA1 - FVM	8	FVM - Mlm	6	FVM - Mpl	3
FRA1 - Mpl	6.5	FVM - Mpl	3	Mpl - Mlm	2
FVM - Mpl	4	FRA1 - FVM	1	FRA1 - FVM	0

b. Group 2

Low 1		High		Low 2	
Dyad	Strength	Dyad	Strength	Dyad	Strength
FRA2 – Mbb	6	FRA2 – Mbb	5.5	FRA2 – Mtu	6
FRA2 – Mtu	3.5	FRA2 – Mtu	2.5	Mtu – Mbb	1
Mtu - Mbb	2.5	Mtu - Mbb	1	FRA2 - Mbb	0

3.3 Female foraging strategies

In response to changes in food availability or energetic requirements, females may adopt flexible foraging strategies. These strategies could include a change in diet composition, association with a ‘helper’ individual to increase foraging success, or social isolation to decrease intragroup competition over resources.

3.3.1 Seasonal variation in diet composition

Variations in diet according to food availability indicate dietary flexibility. Sex differences in the variation of diet composition according to food availability and energetic requirements may suggest sex-specific foraging strategies. Fruit was the primary food choice for both males and females regardless of season. Females' use of fruit showed no relationship with availability, though males showed a slight decrease in their use of fruit during the season of abundance. Males' use of fruit was equal to or higher than females' during all seasons (respectively Low 1: 88.2% vs. 76.2%; High: 86.0% vs. 86.8%; Low 2: 90.9% vs. 90.2%) (Appendix C: Table C.1).

Depending on season, insects were 0.0 - 10.5% of females' diet but only 0.0 - 0.7% of males' diet. Young leaves were 3.9 – 8.6% of females' diet and 1.3 – 11.8% of males' diet, while flowers were 1.9 – 5.9% of females' diet and 0.0 – 11.3% of males' diet. The proportion of females' diets accounted for by food other than fruit did not vary according to food availability seasons. Males relied more heavily on, and consumed a greater variety of, alternative food sources during the season of relative abundance (Appendix C: Table C.1).

In contrast with resource availability, females' diet composition did vary according to reproductive state. Females' fruit consumption was lowest during Mating (75.0%) and highest during Lactation (92.1%). Females' diets were equally varied during Early and Late Gestation, but the most restricted during Lactation, when young leaves were the only alternative selected (Appendix C: Table C.2).

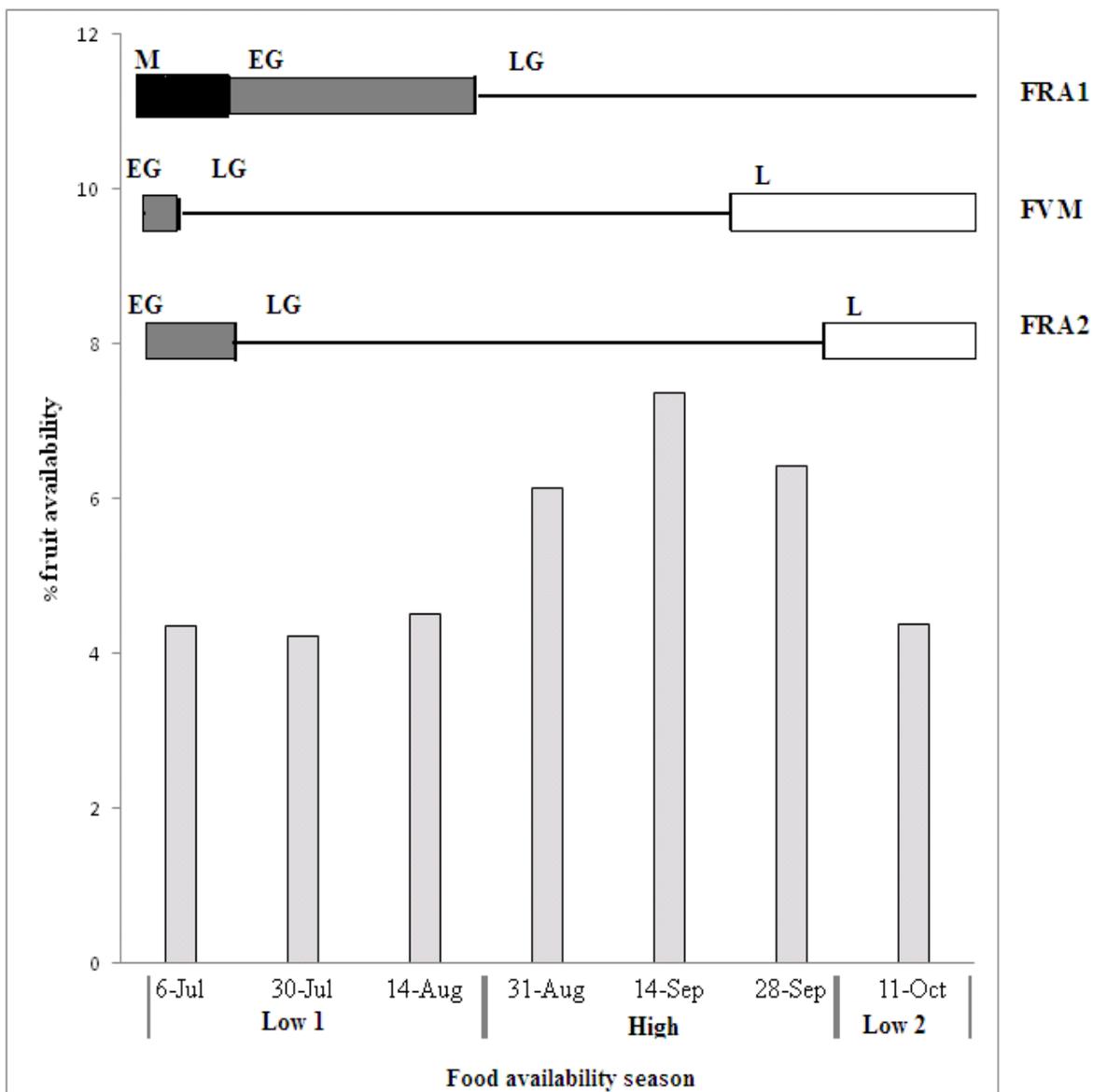
In comparing food availability to reproductive state it should be noted that two of the three females were synchronous while the remaining female's reproductive phases

aligned with different food availability seasons. This particular female, FRA1, was the only female for whom data were collected during the Mating season. The index of food availability was low during this season (4.4%) (Fig 3-9). The consumption of fruit was lowest while insect consumption was highest during this reproductive phase (Appendix C: Table C.2). Early Gestation, during which females consumed 78.3% fruit and had high dietary variation, corresponded to low fruit availability (Fig 3-9). Fruit availability increased gradually during Late Gestation, tapering off only at the very end of gestation for two of the three females (Fig 3-9), though fruit consumption did not vary accordingly. During Lactation, when food availability was low (4.4%) (Fig 3-9), females consumed the most fruit and had the least dietary variation (Appendix C: Table C.2).

3.3.2 Nearest neighbour when feeding

To examine potential patterns in partner preference in the context of feeding, I compared focal individuals' feeding time with same sex adult individuals, opposite sex adult individuals, and alone. Females and males in both groups spent an equal or greater percentage of time feeding alone than with an adult nearest neighbour (Group 1: F: 59.7% > 20.0%; M: 40.3% \approx 41.3%; Group 2: F: 65.3% > 23.0%; M: 40.7% > 25.0%). When feeding with a nearest neighbour, females only fed with males (although in Group 2 the female did not have a choice), while males did not show a clear preference for either females or males (Group 1: F: 21.3% \approx M: 20.0%; Group 2: F: 14.0% \approx M: 11.0%).

Figure 3-9 Females' reproductive seasons compared to fruit availability.



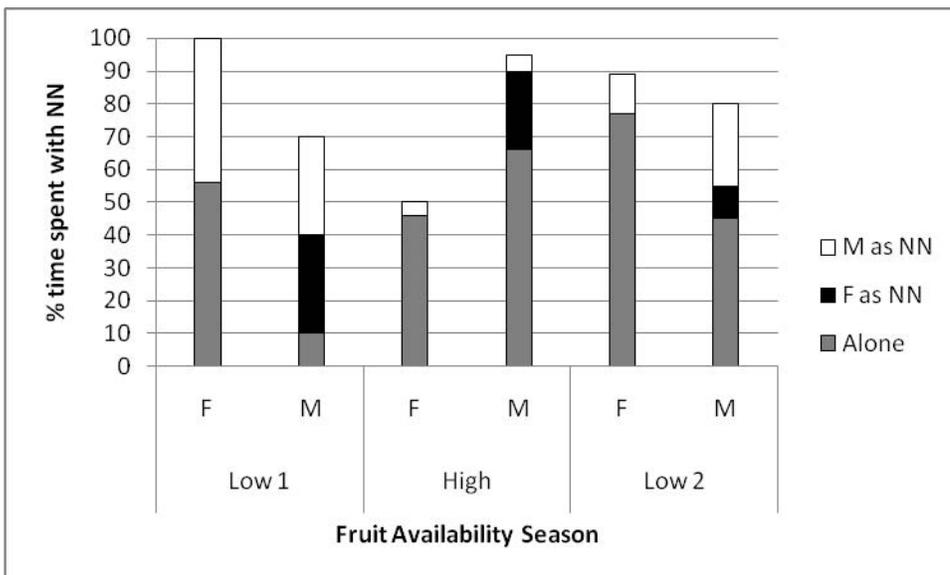
Fruit availability is measured on the y-axis, while reproductive seasons are grouped by female above (M=Mating season: black; EG= Early Gestation: grey; LG= Late Gestation: thin black; L=Lactation: white).

A seasonal relationship of food availability with nearest neighbour when feeding was observed for Group 1. Females spent a lower percentage of time feeding alone during the season of food abundance than during seasons of low food availability (High: 46.0% vs. Low 1: 56.0% and Low 2: 77.0%), though they also spent a lower percentage of time feeding with a male during the season of food abundance (High: 4.0% vs. Low 1: 44.0% and Low 2: 12.0%) (Fig 3-10a). Males spent a greater percentage of time feeding alone during the season of food abundance than during seasons of low food availability (High: 66.0% vs. Low 1:10.0% and Low 2: 45.0%) , but it was also the only season during which males showed a preference for females over males as nearest neighbour when feeding (F: 24.0% vs. M: 5.0%) (Fig.3-10a). A seasonal relationship was not observed for Group 2 (Fig 3-10b).

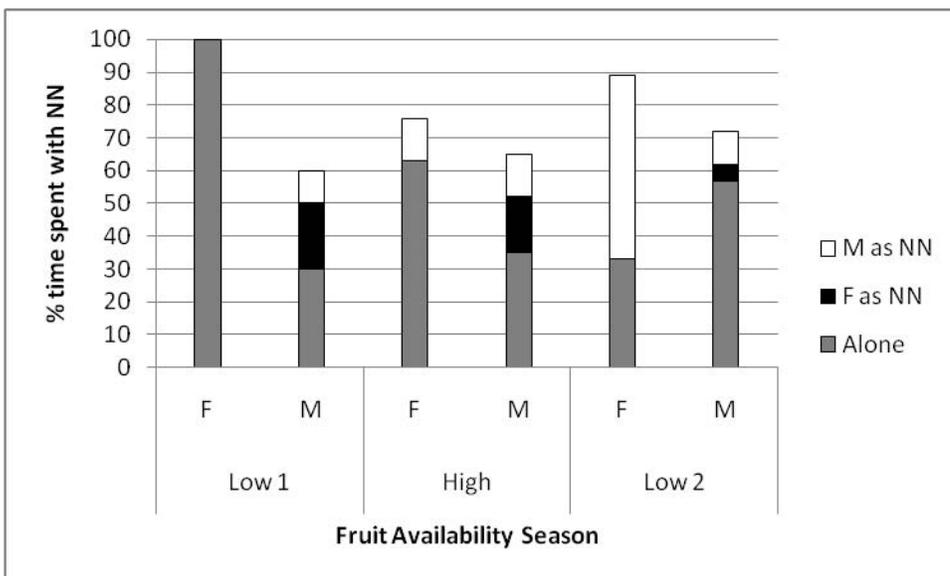
When analysed per reproductive season, during the Mating and Late Gestation seasons females spent the majority of their feeding time alone (Fig 3-11). Although it may appear according to Figure 3-11 that during Early Gestation females preferred feeding with males to feeding alone, the sample size is small and indicates that there was no clear preference (alone: N=2 vs. M: N=3) (Table 3-6). Results were biased during Lactation (Fig 3-11) by the large sample size for FVM (who only fed alone: N=17) over FRA2's lack of preference (alone: N=4 vs. M: N=5) (Table 3-6).

Figure 3-10 Percentage of observed feeding time spent alone, with a female (F) or with a male (M) as nearest neighbour (NN), per season of food availability.

a. Group 1



b. Group 2



There is only one female in Group 2, and this female could not have had a female as nearest neighbour. Her 'F as NN' values are thus not zero, they are not applicable.

Figure 3-11 Percentage of females' observed feeding time spent alone or with a male (M) as nearest neighbour (NN) per reproductive season.

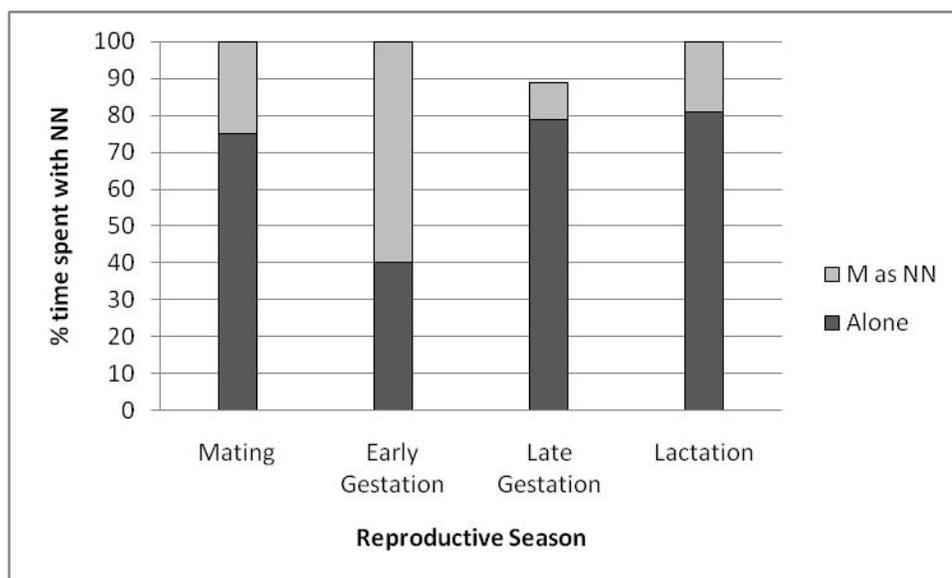


Table 3-6 Focal females' nearest neighbour within 5m when feeding, per reproductive season.

Female	Mating			Early Gestation			Late Gestation			Lactation		
	N ^a	alone	male	N	alone	Male	N	alone	male	N	alone	male
FRA1	4	3	1	0	0	0	19	13	2	-	-	-
FVM	-	-	-	5	2	3	14	12	1	17	17	0
FRA2	-	-	-	0	0	0	9	8	1	9	4	5

^a N= # of point samples for which the focal individual was observed feeding

3.3.3 Feeding rate

Focal individuals' feeding rates were compared when alone, with a male, or with a female as nearest neighbour. Feeding rate data are a subset of the general feeding data and were recorded only when visibility permitted. Sample sizes are thus small and

seasonal comparisons are limited. Overall, the feeding rates of individuals in Group 1 observed feeding on medium-sized fruit did not demonstrate any pattern of relation with identity of nearest neighbour. The feeding rates of individuals in Group 2, however, were consistently higher when they fed alone than with a nearest neighbour.

The highest feeding rates for both groups were observed during the season of food abundance. Females' feeding rates were highest during Late Gestation, regardless of whether they fed with a male or alone. Feeding rate data were minimal during Early Gestation and Lactation.

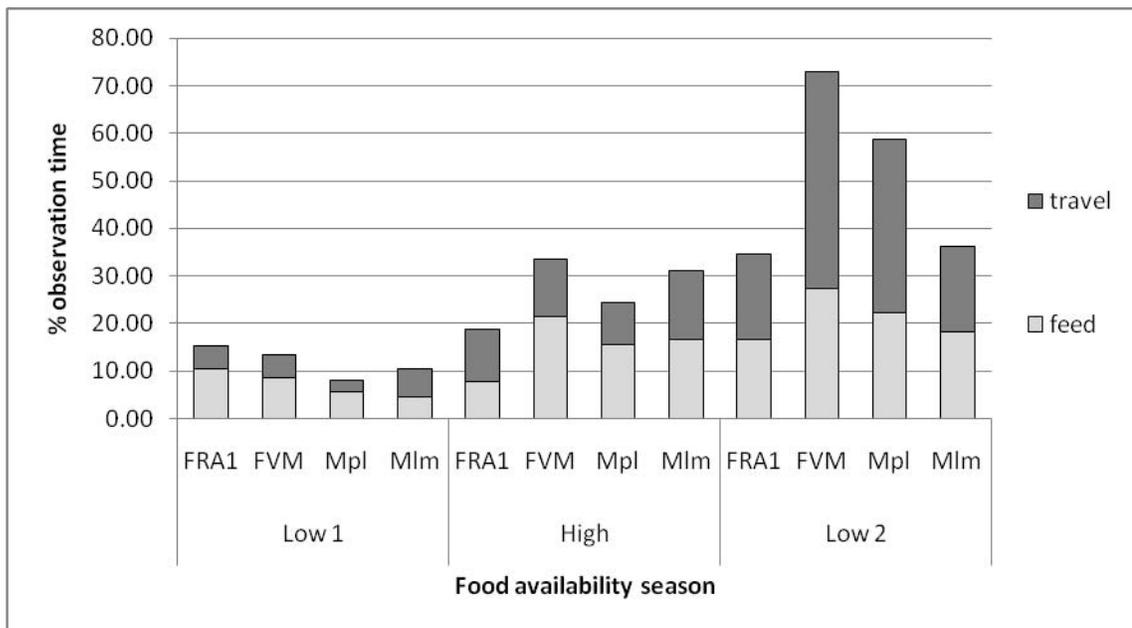
3.3.4 Foraging success

Overall, individuals in both groups spent a nearly equal percentage of time feeding and travelling (FRA1: 11.4% vs. 9.9%, FVM: 15.6% vs. 11.2%, Mpl: 10.6% vs. 6.7%, Mlm: 11.5% vs. 11.3%, Mtu: 12.3% vs. 11.7%, Mbb: 12.1% vs. 10.6%), with the exception of FRA2 (5.4% vs. 8.5%). Mean foraging success (percent of time spent travelling divided by percent time spent feeding) was higher for Group 1 (1.3 ± 0.3) than for Group 2 (0.9 ± 0.3). There were no consistent sex differences in foraging success. FRA2 had the lowest foraging success (0.6), while Mpl and FVM had the highest (1.6 and 1.4 respectively).

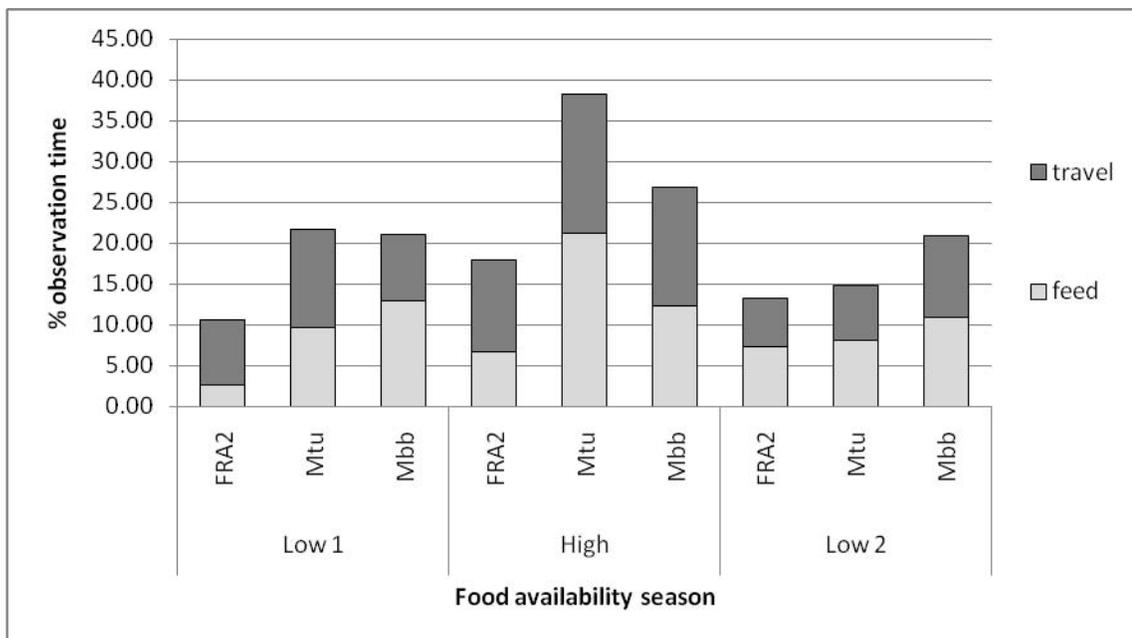
Individuals' foraging success showed no relationship with food availability (Fig 3-12), but did show a relationship with reproductive phase. Both FVM and FRA2 increased their percentage of time spent feeding as they progressed from Early Gestation to Late Gestation and then to Lactation (FVM: 6.4% to 16.7% to 23.2%; FRA2: 3.7% to 4.4% to 14.4%). FVM's travel time increased concurrently (0.6% to 12.1% to 20.5%), but FRA2's travel time decreased as she progressed through gestation to lactation (13.6%

Figure 3-12 Focal individuals' travel and feeding time per season of food availability.

a. Group 1

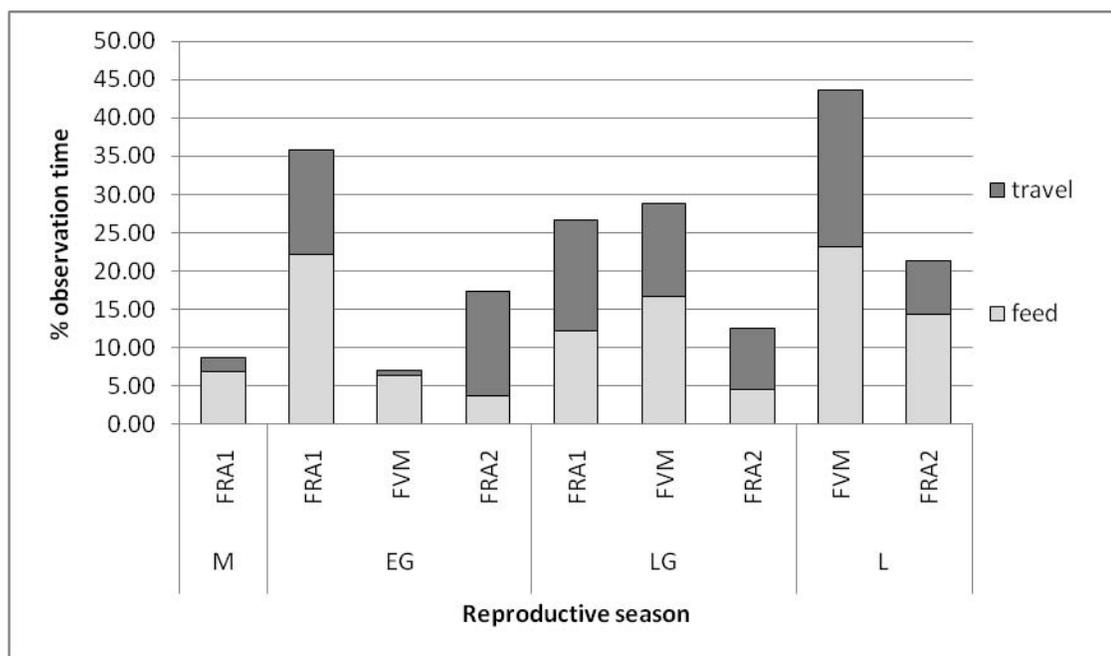


b. Group 2



to 8.0% to 7.0%). These trends resulted in FRA2 being the only female to increase her foraging success over the reproductive seasons (Fig 3-13). FRA1, whose oestrous was not synchronized with the other two females, had her lowest feeding and travel percentages during her Mating season (feed: 6.8%; travel: 1.8%). Her highest feeding time was during Early Gestation (Fig 3-13), which for her corresponded with the season of food abundance (Fig 3-9). Her travel time, however, was also high during Early Gestation and Late Gestation, resulting in a steadily decreasing foraging success over this time period (Fig 3-13).

Figure 3-13 Females' travel and feeding time per reproductive season



M = Mating season, EG = Early Gestation, LG = Late Gestation, L = Lactation

3.4 Description of rare observations

3.4.1 Intergroup agonistic interactions

Two intergroup agonistic interactions were observed, both during the first season of low food availability. The first encounter occurred on July 10, between Group 2 and an unknown group. The second encounter occurred on August 9, between Group 2 and FVM of Group 1. The composition of Group 2 was whole at the onset and end of both encounters. Interactions were brief, approximately two to three minutes in duration, and elicited loud rapid vocalizations (grunts) from all individuals involved. There was little to no physical contact between groups during the encounters, though rapid lunges and evasions were observed. In both instances Group 2 remained at the site of the interactions while the other groups departed. Individuals remained vigilant for a short time after the encounter.

3.4.2 Copulatory behaviour

Prior to animal collaring, I observed copulatory behaviour while conducting preliminary observations of Group 1. On May 23 an uncollared male (now assumed to be Mpl based on body size) was observed copulating with FVM at 9:18 am. FVM jumped rapidly from tree to tree three times with Mpl following close behind, after which copulation took place. At 9:25 am and again at 12:03 pm Mpl was observed copulating with FRA1. Copulation consisted of 10-20 quick thrusts over a period of 15-30 seconds. The male produced vocalizations consisting of rapid soft grunts like a staccato humming. The females did not vocalize during copulations. All copulations were ventro-dorsal. It was not known if ejaculation occurred. Based on parturition dates for both females, these copulations were within FVM's mating season, but well before FRA1's conceived.

Extra-seasonal copulations were observed in the month of September. On September 11, two weeks prior to FVM's parturition date, I observed two copulation attempts by Mlm towards FVM. The attempts were ventro-dorsal, with Mlm grasping FVM's haunches. Mlm emitted low grunts, FVM emitted high pitched squeals. It was not known if intromission occurred. FVM's most visible action to resist Mlm's attempt was when she turned her upper body and attempted to hit Mlm. Once disengaged, Mlm inspected and licked FVM's anogenital region.

Another extra-seasonal copulation attempt was observed on September 25 of Mlm towards FRA1. FRA1 was sitting on a branch with her posterior angled lightly off the branch and her tail straight out in mid-air, to the left of her body. Mlm, who had been sitting behind her, hung down from the branch and attempted to mount FRA1. His thrusts were quick and only lasted 5 seconds. Afterwards, he moved back onto the branch behind. FRA1 showed no reaction.

To summarize, copulations were observed during the normal mating season. It is also possible, based on these observations and FRA1's late lactation season that female WCL can cycle anew immediately after a miscarriage. In addition, extra-seasonal copulations were observed during females' gestation periods.

3.4.3 Parturition

On October 2 at 12:37 pm I witnessed the birth of FRA2's infant. At 12:14 pm, FRA2 fissioned from her group and positioned herself within the crown of a tree (animal height: 10m, tree height: 12m). She moved erratically back and forth within the crown until finally, after 12 minutes, she appeared to squat, shifted her weight, and pulled a viscous black-grey substance to her mouth and ate it. She then proceeded to lick the fluid

off her newborn infant and was still doing so when we ended observations 37 minutes later. When observations were resumed on the following morning, the group had fused, but FRA2, who maintained ventral contact with her newborn, did not associate closely with other group members.

Chapter Four: Discussion

4.1 Summary of Findings

In this study, the social organization of *E. cinereiceps* was similar to that described in previous studies. However, groups were smaller than in other locations, and though one group was multi-male multi-female, the other consisted of two males and one female (a male bias in composition). Evidence of pair-bonding or seasonal special relationships was not found in either group. These findings are contrary to the findings for other brown lemur species (Kappeler 1993; Pereira and McGlynn 1997; Overdorff 1998). Some evidence was found supporting seasonal centralized structures, both central-male and central-female, but only for Group 1. In a different environment from previous research, I confirm fission-fusion dynamics, even in small groups, but with no clear seasonal association. The highly frugivorous diet of WCL at Mahabo also was similar to that of brown lemurs in different types of forest (Tattersall 1977; Overdorff 1991, 1993; Freed 1996; Vasey 1997, 2000; Rasmussen 1999; Johnson 2002, 2006; Ralainasolo *et al.* 2008). However, females did not appear to enlist the help of males to increase their food intake. Aggressive interactions between individuals and displacement from feeding sites were rarely observed. The data thus suggest that the resource defense hypothesis may not be supported. It is interesting to note, however, that males appear to have a greater interest than females in maintaining proximity. Extra-seasonal copulations, initiated by the male, were also observed shortly prior to parturition.

4.2 Social system

The small group sizes observed in the study groups may be explained by the relatively low predation pressure (van Schaik and van Hooff 1983). Smaller group sizes

may confer a feeding advantage as each individual obtains more food and expends less energy foraging (Janson 1998). van Schaik (1983) predicts that if the costs of intra-group competition outweigh the benefits for inter-group competition, larger groups will fission. Fission-fusion was observed, even in these small groups, but it did not track food availability. This could be due to the relatively small difference in food availability between seasons qualified as low food availability and seasons qualified as abundant. In her comparison of rainforest lemur species, Wright (1999) noted that sympatric species synchronized weaning with the period of high food availability. Since the current study covered only one third of the year, and the weaning phase was not within this time period, it is likely that the true season of abundance was not observed. Whether food availability influences fission-fusion dynamics in WCL, and whether it places limitations on group size thus requires further study.

Group size, which arguably may be determined by proximate factors such as food availability and predation pressure, may also be influenced by ultimate factors. The evolutionary disequilibrium hypothesis posits that behaviour is determined by previous evolutionary forces and may be mismatched with the current environment (i.e., strong phylogenetic inertia). van Schaik and Kappeler (1996) propose that formerly nocturnal pair-living lemur species experienced an incompatibility with their new diurnal activity pattern which shaped several facets of their social system, including living in a group social structure and oestrus synchronization. Based on associative and spatial cohesion data, WCL social organization appears to resemble that of closely related *E. fulvus rufus* in male-biased sex ratio and the occurrence of group fissioning (Kappeler 1993; Pereira and McGlynn 1997; Overdorff 1998), even though the study populations live in different

habitats: lowland to montane rainforest for *E. fulvus rufus* (Overdorff 1998) and coastal littoral forest for WCL at Mahabo. In their study of the correlates of diversity in the genus *Eulemur*, Ossi and Kamilar (2006) noted that environmental characteristics were not correlated with social organization characteristics in *Eulemur* species from different habitats, but that social organization was correlated with phylogeny.

The small sizes of the groups in this study suggest that the evolutionary disequilibrium hypothesis may be partially supported. These groups are smaller than those studied in different environments (Overdorff *et al.* 1999; Johnson 2002). Brown lemur groups in Ranomafana, for example, are larger due perhaps to environmental conditions such as increased predation pressure.

It is possible that the social organization and structure observed in WCL and other brown lemurs may be a snapshot of a continuous and gradual evolution from pair-living nocturnal species to group-living diurnal species. Considering van Schaik and Kappeler's (1996) evolutionary disequilibrium hypothesis, Ossi and Kamilar's (2006) conclusions, and the current findings for WCL, it is conceivable that the social structure of brown lemurs is influenced by evolutionary forces (imposing group size parameters) as well as environmental conditions (demonstrated by the flexibility of group size within the set parameters).

Eulemur spp.'s multi-male multi-female groups have been proposed to be aggregations of several adult male and female dyads or 'pair bonds' (van Schaik and Kappeler 1993, 1996). Strong evidence of pair bonds has not been found among brown lemurs but some evidence of the less strictly defined special relationships has been found (Kappeler 1993; Pereira and McGlynn 1997; Overdorff 1998), though none of these

studies found this social structure to be ubiquitous. The current study found similar results; evidence of permanent ‘pair bonds’ was not found. This, and the previously mentioned findings, do not support van Schaik and Kappeler’s (1993, 1996) theory that multi-male multi-female groups consist of aggregations of pair-bonded dyads, a vestige of the transition from a nocturnal to cathemeral activity pattern.

Females did spend more time in association, affiliation, feeding, and in subgroups with males than females (Group 2 is not considered here due to limitations posed by group composition). According to the definition of special relationships (a more flexible pair bond), measures of association and affiliation had to be greater and reciprocal for one pair over all others and the pair needed to maintain social cohesion with each other. Such was not the case for any pair over all others. There is stronger support in Group 1 for a central-male social structure during seasons of low food availability, and a central-female structure during the season of high food availability. Throughout the study, one pair (FRA1 – Mlm) maintained a strong relationship (though not consistently stronger than their other pairings), and it could be that they formed the basis of the seasonally changing centralized configuration (FVM joined them in the low seasons, Mpl joined them during the high season). Due to the small size of both groups, any behavioural change in one individual potentially changes the social structure of the group (see Pochron and Wright (2003) for an example of how small group size can affect social system classification).

The central female social structure finds additional support in Group 2. Both males significantly preferred the female in terms of association and affiliation. It should be noted that while the adult composition of group 1 has changed over the last two years

(December 2005 – October 2007) with males leaving the group and being replaced by new males, the adult composition of Group 2 has remained stable (H.E. Andriamaharoa, pers. comm.). Given that genetic data on the members of groups 1 and 2 are not available at the time of this study, we do not know if FRA2 is related to either Mtu or Mbb (adults in Group 2). If she is, then group 2 may be the structure of a monogamous family group composed of a pair-bonded couple and an adult male offspring. If she is not related to either Mtu or Mbb then it is possible that the social structure of group 2 may be female centred, though year-round data would be required to verify this.

The female-centred social structure is further supported by the fact that according to Hinde's Index the males bore the responsibility of maintaining proximity with the central female. The question raised by these findings is whether this female-centred social structure is a polyandrous mating system. A polyandrous mating system consists of one female mating with two or more males, while males of the group mate only with that female (Goldizen, 1987; Tardif and Garber 1994; Garber 1997; Kappeler 1997). Social organization of polyandrous groups is variable: pairs as well as multi-male multi-female groups can be observed, although usually only one female reproduces (Kappeler 1997). Polyandry is rare in primates and has only been documented for New World callitrichids (Goldizen 1987). Promiscuous female mating and a limit of one to two reproductive females per group (or 50%) have been observed for lemurs within the brown lemur species complex (Overdorff *et al.* 1999). Infant grooming and handling by males was observed in this study shortly after parturition. Nonmaternal infant care has been suggested as an evolved behaviour in response to the high energetic costs of reproduction to smaller primates (Kleiman 1977; Leutenegger 1980; Wright 1990; Ross 1991). Though

the potential for this behaviour, a component of polyandry (Kappeler 1997), was observed for WCL, the female-centred group structure observed for both groups was prior to parturition, not after, and all the females in the study groups reproduced; thus typical primate patterns of polyandry were not present in WCL.

Assessment of special relationships was limited by the low frequency of affiliative behaviour and the poor visibility conditions for recording cohesion. It is worth noting that the infrequency of affiliative behaviour recorded here may indicate that other forms of interaction are important in WCL social structure (Hinde 1976; Whitehead and Dufault 1999); other behavioural criteria may be needed to measure and qualify social relationships in WCL, such as frequency of chemical communication via scent-marking and inspection or frequency and direction of vocal communication. Also, data on vocal and olfactory communication could have been collected to assess whether sub-groups maintained contact with one another by these means.

Despite the importance of phylogeny in shaping behaviour in *Eulemur* (Ossi and Kamilar 2006), there is variation in the social structure of *E. cinereiceps* and closely related species. Research on *E. fulvus* has found male-female dyads (Kappeler 1993; Overdorff 1998) and one study found both male-female dyads and central-male social structure in two different groups (Pereira and McGlynn 1997). Female-centred social structures have not previously been recorded for *Eulemur* spp. It is conceivable that WCL and other species within the brown lemur species complex have a very high degree of social plasticity which allows them to adapt to the stochastic environment of Madagascar. This social plasticity appears to be the unifying theme for brown lemur social structure and organization. Yet another example of this can be seen in the fission-fusion social

organization of WCL (Johnson 2002) which was also documented in this study. Fission-fusion has also recently been observed in one *E. fulvus rufus* population (D. Overdorff, pers. comm., cited in Johnson 2006). This type of social organization is exceptional since brown lemur groups typically maintain very cohesive social groups (Vasey 1997; Overdorff and Johnson 2003; Johnson 2006).

According to data on group history, some male dispersal exists among the WCL groups at Mahabo. There is no record of female dispersal, but there is evidence that males left Group 1 in the spring of 2007 and two males (Mpl and Mlm) entered this group in May 2007. Whether this was a forceful group takeover, or even whether Mpl and Mlm are related, is not known. Overdorff *et al.* (1999) found evidence of male-biased dispersal in *E. fulvus rufus*. Several isolated male pairs were also observed during the study. Just as in this study, Overdorff *et al.* did not find any indication of the social structure usually observed in primate groups with male-biased dispersal, such as female dominance in *L. catta* (Kappeler 1990) or female-bonding in *Cebus capucinus* (Jack and Fedigan 2003).

4.3 Female foraging strategies

While the evolutionary disequilibrium hypothesis attributes unusual lemur traits to a partial mismatch of evolved traits with a new activity period (van Schaik and Kappeler 1996), the energy conservation hypothesis accredits lemur social structure to female energetic requirements (Jolly 1966, 1984). This hypothesis postulates that the stochastic nature of Madagascar's environment imposes significant energetic stress on reproductive female lemurs (Jolly 1966, 1984; Richard and Nicoll 1987; Young *et al.* 1990; Wright 1993, 1999). Lemurs consequently evolved female dominance to ensure female feeding priority, thereby increasing reproductive success (Jolly 1984; Young *et al.*

1990). Another evolved trait in response to Madagascar's variable resource seasonality is the extreme synchronization of oestrous periods regulated by photoperiodicity (van Horn 1975; Jolly 1984; Rasmussen 1985). Wright (1999) proposes the energy frugality hypothesis as a further development of the energy conservation hypothesis, incorporating strategies evolved to conserve energy and others evolved to capitalize on scarce resources. Sperm competition, oestrous synchrony, low basal metabolic rate, and small group sizes are all tactics that have evolved to conserve energy, while female dominance, weaning synchrony across sympatric species, and cathemerality are tactics employed to take full advantage of resources that are patchily distributed both in time and space (Wright 1999). In contrast, the evolutionary disequilibrium hypothesis presumes that cathemerality is a consequence of a reduction in diurnal predation pressure, and group size is moderated by predation-risk and strategies to reduce infanticide risk (van Schaik and Kappeler 1993, 1996; Kappeler and van Schaik 2002).

- *Energy conservation strategies*

In accordance with the energy frugality hypothesis, the groups in this study were small, in fact smaller than WCL groups studied elsewhere in possibly more resource-rich environments (Johnson 2002). Two of the three females exhibited oestrous synchrony while the third may have failed to conceive during the originally synchronized oestrous period and cycled anew. It was not possible to verify sperm competition as copulations observed during the mating season consisted of one male with two females in Group 1. No other conceptive copulations were observed, though this is not surprising as observations began at the end of the mating season. Earlier studies have indicated that WCL show evidence of sperm competition and exhibit canine sexual dimorphism but not

body mass sexual dimorphism (Johnson *et al.* 2005). The absence of body mass dimorphism supports the predictions of the energy frugality hypothesis; males are as large as permitted by the availability of resources (Wright 1999). The presence of canine sexual dimorphism may contradict this hypothesis and suggests male-male direct competition. The energy frugality hypothesis supposes that females, not males, have larger canines due to female-female competition (Plavcan and van Schaik 1997), and that female choice results in smaller males (Small 1989); both are mechanisms that maintain female dominance (Wright 1999). WCL females are thus not exclusively employing energy conservation measures in accordance with the energy frugality hypothesis.

- *Strategies used to capitalize on scarce resources*

According to the energy frugality hypothesis, strategies employed to capitalize on scarce resources include cathemerality, weaning synchrony, and female dominance (Wright 1999). One nocturnal observation was conducted to verify WCL nocturnal activity. WCL were observed to be active at night as well as during the day, thereby exhibiting a cathemeral activity pattern. Due to the short duration of this study it was not possible to note when infants were weaned, nor have data been collected on sympatric species to verify weaning synchrony as per Wright (1999). Female dominance over males is considered absent in the brown lemur species complex and they are the exception among gregarious lemur species (Pereira *et al.* 1990; Pereira and Kappeler 1997; Pereira and McGlynn 1997; Overdorff and Erhart 2001). Female dominance is characterized by the occurrence of male submissive signals directed towards females and the absence of submissive signals from females to males (Pereira *et al.* 1990; Kappeler 1993; Overdorff

et al. 2005). This pattern was not observed in this study, in fact a minimum amount of aggression was observed within the study groups.

Contrary to expectations regarding female energy requirements during reproduction, females consumed a lower percentage of fruit than males. In accordance with the predictions for energy requirements imposed by gestation and lactation, however, females ate the most fruit during Lactation, even though it was less available. Given the lack of female dominance in WCL, how do females maximize their access to resources in times of resource scarcity or during energetically expensive reproductive periods? During this study I tested the resource defence hypothesis as an alternate strategy. It is hypothesized that, for lemur species in which female dominance does not exist, females form special relationships with males in order to improve their foraging success (Pereira and Kappeler 1997; Pereira and McGlynn 1997). The findings of this study indicate that females' feeding rates were not influenced by the identity of their nearest neighbour and that in Group 2 feeding rates were higher when the female fed alone. In both groups females were observed feeding alone more often than with a male. Although feeding rates were highest during the season of food abundance and during Late Gestation, it cannot be concluded that there is a seasonal effect as feeding rate data were limited for other seasons, thereby biasing results. Different trends were observed by Overdorff (1998) in her study of *E. fulvus rufus* in Ranomafana National Park: in one of two study groups male-female dyads formed during period of resource scarcity and both individuals had higher feeding rates as a result. During early lactation, however, females isolated themselves from other group members, a behaviour not observed in the groups at

Mahabo perhaps due to the small group sizes and the corresponding reduction in competition.

In this study, a seasonal effect of reproductive phase was observed for foraging success. The solitary female in Group 2 was the only female for whom a steady increase in foraging success was observed from Early to Late Gestation and then through Lactation. Both females in Group 1 increased their travel time as they progressed through their respective reproductive phases, and foraging success actually decreased for the asynchronous female (FRA1). These results, taken together with the failure to observe females feeding with females as nearest neighbour, and the propensity towards fissioning of females into separate sub-groups, could point towards strategies to reduce competition between females for food. Females did not appear to be seeking alliance with males as per the resource defence hypothesis, however. In fact, Hinde's Index values, when not indicating equal responsibility designate males as responsible for maintaining proximity with females. In addition, males spent more time in association and affiliation with females than vice versa.

In light of these findings, rather than males providing a service to females, are females providing a service to males? It is possible that females rather than males are more vigilant for predators and alert the group to potential dangers. Overdorff (1998) found that in *E. f. rufus*, females, not males, were primarily responsible for scanning the environment and alarm calling. Alternatively, females may be more proficient at mapping food sources than males. A male would thus benefit from maintaining close proximity to a female as she led the group to feeding sites. A study of *V. variegata* did find that certain individuals led group movements to feeding sites and were the first to arrive at feeding

sites significantly more often, but these differences were not related to sex (Overdorff *et al.* 2005).

Another potential motivation for males to associate preferentially with females could be related to breeding access (mate guarding) and ensuring future group membership. It is not known whether female WCL actively control group membership, although male transfers have been observed for Group 1. Smuts (1985) proposes that if a male provides grooming and other services such as infant care to a female, this may increase his breeding priority with the female. Male infant care has been observed in *E. f. rufus* (Overdorff 1996) and within this study. Non-conceptive copulations were also observed shortly prior to the parturition dates of the synchronous females. The two females' reactions were opposite: FVM, who would give birth only two weeks later, reacted aggressively, while FRA1, the asynchronous female who would only give birth almost two months later, did not react. These non-conceptive copulation attempts may in fact be a male strategy employed to gauge whether a female is pregnant. A male's attentions may then change based on his findings. According to Huck *et al.* (2004), mate guarding behaviour is focused on a receptive female. It is possible however, that in a highly seasonal breeder such as *E. cinereiceps*, mate guarding behaviour (intensified maintenance of close proximity) particular to the mating season may lessen during the rest of the year but still remain active for the reasons postulated by Smuts (1985), namely to increase future breeding opportunities. More data (including paternity testing) would need to be collected to determine whether these behaviours do in fact increase a male's breeding opportunities.

4.4 Significance

WCL surveys were conducted in 1995, 1997, 2000, 2007, and indicated consistently low population densities and habitat quality (Johnson and Overdorff 1999; Johnson 2002; C. Ingraldi, unpublished data). In 2006 *E. cinereiceps* was listed as one of the 25 most endangered primate species due to the steady threats of logging, hunting, and habitat loss (Mittermeier *et al.* 2006). In addition, the study groups at Mahabo live in a degraded fragment of littoral forest. Mahabo forest includes some of the few remaining forests of this type which are among the most disturbed animal habitats in Madagascar (Johnson, pers. comm.). The preservation of littoral forests is important for several species (Watson *et al.* 2005). WCL, like other lemur species, are likely a crucial element in its endangered ecosystem as it contributes to the reproduction of fruit trees via seed dispersal (Bollen *et al.* 2004)

This study provides information as to how food resources affect the reproductive behaviour and social structure of WCL. Understanding *E. cinereiceps*' behavioural responses to foraging pressures due to seasonality provides conservation organizations with an understanding of the basic requirements of the species. Knowledge about the limits of social plasticity gives managers a set of ecological boundaries within which to work. In particular, because the survival of a population depends in large part on the production and survival of viable offspring, it is essential to gain an understanding of the key dynamics involved in WCL reproduction, such as female reproductive and foraging strategies.

The knowledge gained from this research contributes to the ongoing debate regarding the hypothesized function of male-female dyads in multi-male multi-female

societies. The ‘resource defence’ hypothesis may not be supported for WCL. In addition, data on the social organization (quantification of fission-fusion) and the social structure (bonding patterns) add a piece to the puzzle of lemur social systems.

4.5 Directions for future research

Information on the social structure of WCL was gained from this study, but study groups were small and the study period short. A longer period of study covering the entire year (ideally over several consecutive years), following the current study groups and additional larger groups from Mahabo and nearby Manombo is recommended to control for different environmental conditions. The study of larger groups will permit the re-evaluation of social structure in a context with increased partner selection options, providing stronger conclusions. The collection of social structure data year-round and over succeeding years will allow researchers to discern whether group structure fluctuates predictably in accordance with food availability. Following groups over successive reproductive seasons will also permit for the construction of life histories for WCL. It should be determined whether infant survival is related to female foraging success during gestation and lactation. The degree of oestrous synchrony in WCL requires investigation, as does the incidence of non-conceptive copulations.

I further recommend that predation risk be measured for WCL to determine what time of day (or night) and in which season predation risk is highest, and which individuals in a group are responsible for predator detection. In addition, data should be collected on leadership of group movements towards feeding sites, and feeding priority at feeding sites. Fission-fusion behaviour also needs to be quantified year-round to establish whether it is related to seasonal fluctuations in food availability. Although intragroup

aggression is low in WCL it would be interesting to explore reconciliation and consolation behaviours, as well as potentially subtle female relationships which may be obscured by more obvious male-female relationships.

Reproductive strategies, foraging strategies, and dominance strategies employed by WCL and other brown lemurs may have much to tell us about the evolution of similar traits across primates. WCL do not conform to many proposed models of lemur social systems and may serve to generate new hypotheses regarding the behavioural ecology and evolution of strepsirhines in Madagascar.

References

Alexander, S.A.

1974 The Evolution of Social Behavior. *Annual Review of Ecology and Systematics* 5:325-383.

Altmann, J.

1974 Observational Study of Behavior: Sampling Methods. *Behaviour* 49:227-267.

Aschoff, J.

1960 Exogenous and Endogenous Components in Circadian Rhythms. *Cold Spring Harbor Symposia on Quantitative Biology* 25:11-28.

Asensio, N., A.H. Korstjens, C.M. Schaffner, and F. Aureli

2008 Intragroup Aggression, Fission-Fusion Dynamics and Feeding Competition in Spider Monkeys. *Behaviour* 145:983-1001.

Aureli, F., C.M. Schaffner, C. Boesch, S.K. Bearder, J. Call, C.A. Chapman, R. Connor, A. Di Fiore, R.I.M. Dunbar, S.P. Henzi, K. Holekamp, A.H. Korstjens, R. Layton, P. Lee, J. Lehmann, J.H. Manson, G. Ramos-Fernandez, K.B. Strier, and C.P. van Schaik

2008 Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology* 49:627-654.

Balko, E.A.

1996 Intraspecific Variation in the Foraging Ecology of *Varecia variegata variegata* at Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 22:64.

Bateman, A.J.

1948 Intra-Sexual Selection in *Drosophila*. *Heredity* 2:349-368.

Bearder, S.K.

1987 Lorises, Bushbabies, and Tarsiers: Diverse Societies in Solitary Foragers. *In* Primate Societies. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, eds. Pp. 11-24. Chicago: University of Chicago Press.

Beecher, M.D., and I.M. Beecher

1979 Sociobiology of Bank Swallows: Reproductive Strategy of the Male. *Science* 205:1282-1285.

Berger, A., K.M. Scheibe, K. Eichhorn, A. Scheibe, and J. Streich

1999 Diurnal and Ultradian Rhythms of Behavior in a Mare Group of Przewalski Horse (*Equis ferus przewalskii*), Measured Through One Year Under Semireserve Conditions. *Applied Animal Behaviour Science* 64:1-17.

Birkhead, T.R.

1979 Mate Guarding in the Magpie *Pica pica*. *Animal Behavior* 27:866-874.

Bollen, A., L. van Elsacker, and J.U. Ganzhorn

2004 Relations between Fruits and Disperser Assemblages in a Malagasy Littoral Forest: A Community-Level Approach. *Journal of Tropical Ecology* 20:599-612.

Buettner-Janusch, J., and R.J. Andrew

1962 The Use of the Incisors by Primates in Grooming. *American Journal of Physical Anthropology* 20:127-130.

Buettner-Janusch, J., and A.E. Hamilton

1979 Chromosomes of Lemuriformes. Part IV: Karyotype Evolution in *Lemur fulvus collaris*. *American Journal of Physical Anthropology* 50:363-365.

Buss, D.H., R.W. Cooper, and K. Wallen

1976 Composition of Lemur Milk. *Folia Primatologica* 26:301-305.

Butte, N.F., and J.C. King

2005 Energy Requirements during Pregnancy and Lactation. *Public Health Nutrition* 8(7A):1010-1027.

Caughley, G.

1977 *Analysis of Vertebrate Populations*. New York: John Wiley and Sons.

Chapman, C.A.

1989 Ecological Constraints on Group Size in Three Species of Neotropical Primates. *Folia Primatologica* 73:1-9.

Clarke, J.L., M.E. Jones, and P.J. Jarman

1995 Diurnal and Nocturnal Grouping and Foraging Behaviors of Free-Ranging Eastern Grey Kangaroos. *Australian Journal of Zoology* 43:519-529.

Clutton-Brock, T.H., P.H. Harvey, and B. Rudder

1977 Sexual Dimorphism, Socioeconomic Sex Ratio, and Body Weight in Primates. *Nature* 269:797-800.

Clutton-Brock, T.H., and G.R. Iason

1986 Sex Ratio Variation in Mammals. *Quarterly Review of Biology* 61:339-374.

Colquhoun, I.C.

1987 Dominance and “Fall Fever”: The Reproductive Behaviour of Male Brown Lemurs (*lemur fulvus*). *Canadian Review of Physical Anthropology* 6:10-19.

1997 Intrapopulation Variation in the Mating Strategies of Male *Eulemur macaco macaco* at Ambato Massif, Madagascar. *American Journal of Physical Anthropology Supplement* 24:95-95.

2006 Predation and Cathemerality. *Folia Primatologica* 77(1-2):143-165.

Connor, R.C., R. Wells, J. Mann, and A. Read

2000 The Bottlenose Dolphin, *Tursiops spp.*: Social Relationships in a Fission-Fusion Society. *In Cetacean Societies: Field Studies of Whales and Dolphins*. J. Mann, R.C. Connor, P. Tyack, and H. Whitehead, eds. Pp. 91-126. Chicago: University of Chicago Press.

Conradt, L.

1998 Social Segregation is not a Consequence of Habitat Segregation in Red Deer and Soay Sheep. *Animal Behaviour* 57:1151-1157.

Cracraft, J.

1989 Speciation and its Ontology: The Empirical Consequences of Alternative Species Concepts for Understanding Patterns and Processes of Differentiation. *In Speciation and its Consequences*. D. Otte and J. Endler, eds. Pp. 28-59. Sunderland, MA: Sinauer Assoc.

Crook, J.H.

1970 The Socio-Ecology of Primates. *In Social Behavior in Birds and Mammals*. J.H. Crook, ed. Pp. 103-166. London: Academic Press.

Curtis, D.J., G. Donati, and M. Rasmussen

2006 Cathemerality. *Folia Primatologica* 77:1-2.

Curtis, D.J., and M.A. Rasmussen

2006 The Evolution of Cathemerality in Primates and Other Mammals: A Comparative and Chronoecological Approach. *Folia Primatologica* 77:178-193.

Dagosto, M.

1995 Seasonal Variation in Positional Behavior of Malagasy Lemurs. *International Journal of Primatology* 16:807-833.

Dahl, J.F., and C.A. Hemingway

1988 An Unusual Activity Pattern for the Mantled Howler Monkey of Belize. *American Journal of Physical Anthropology* 75:200.

Daniels, H.L.

1984 Oxygen Consumption in *Lemur fulvus*: Deviation From the Ideal Model. *Journal of Mammalogy* 65:584-592.

Delgado, R.A., Jr., and C.P. van Schaik

2000 The Behavioral Ecology and Conservation of the Orangutan (*Pongo pygmaeus*): A Tale of Two Islands. *Evolutionary Anthropology* 9:201-218.

Djelati, R., B. Brun, and Y. Rumpler

1997 Meiotic Study of Hybrids in the Genus *Eulemur* and Taxonomic Considerations. *American Journal of Primatology* 42:235-245.

Dunbar, R.I.M.

1987 Demography and Reproduction. *In Primate Societies*. B.B. Smuts, D.L. Cheney, R. Seyfarth, R Wrangham, and T.T. Struhsaker, eds. Pp. 240-249. Chicago: Chicago University Press.

1988 Primate Social Systems. New York: Cornell University Press.

Eberle, M., and P.M. Kappeler

2004 Sex in the Dark: Determinants and Consequences of Mixed Male Mating Tactics in *Microcebus murinus*, a Small Solitary Nocturnal Primate. *Behavioral Ecology and Sociobiology* 57:77-90.

Emlen, S.T., and L.W. Oring

1977 Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science* 197:215-223.

Engelhardt, A., M. Heistermann, J.K. Hodges, P. Nurnberg, and C. Niemitz

2006 Determinants of Male Reproductive Success in Wild Long-Tailed Macaques (*Macaca fascicularis*) – Male Monopolisation, Female Mate Choice or Post-Copulatory Mechanism? *Behavioral Ecology and Sociobiology* 59:740-752.

Engelhardt, N., N.E. Langmore, J. Komdeur, S.C. Griffith, and M.J.L. Magrath

2009 Mate-Guarding Intensity Increases with Breeding Synchrony in the Colonial Fairy Martin (*Petrochelidon ariel*). *Animal Behaviour* 78:661-669.

Fietz, J., and K.H. Dausmann

2003 Costs and Potential Benefits of Parental Care in the Nocturnal Fat-Tailed Dwarf Lemur (*Cheirogaleus medius*). *Folia Primatologica* 74:246-258.

Flowerdew, J.R.

2000 Wood Mice – Small Granivores/Insectivores with Seasonally Variable Patterns. *In* Activity Patterns in Small Mammals. An Ecological Approach. S. Halle and N.C. Stenseth, eds. Pp. 177-189. New York: Springer.

Freed, B.Z.

1996 Co-Occurrence Among Crowned Lemurs (*Lemur coronatus*) and Sandford's Lemurs (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. dissertation, Washington University.

Fuentes, A.

1999 Re-Evaluating Primate Monogamy. *American Anthropologist* 100:890-907.

2002 Patterns and Trends in Primate Pair Bonds. *International Journal of Primatology* 23:953-978.

Garber, P.A.

1997 One for All and Breeding for One: Cooperation and Competition as a Tamarin Reproductive Strategy. *Evolutionary Anthropology* 5:187-199.

Gerson, J.S.

1999 Size in *Eulemur fulvus rufus* from Western Madagascar: Sexual Dimorphism and Ecogeographic Variation. *American Journal of Physical Anthropology Supplement* 28:134.

2000 Social Relationships in Wild Red-Fronted Brown Lemurs (*Eulemur fulvus rufus*). Ph.D. dissertation, Duke University.

Goldizen, A.W.

1987 Tamarins and Marmosets: Communal Care of Offspring. *In* Primate Societies. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, eds. Pp. 34-43. Chicago: University of Chicago Press.

Goodman, S.M.

1994a The Enigma of Anti-Predator Behavior in Lemurs: Evidence of a Large Extinct Eagle on Madagascar. *International Journal of Primatology* 15:129-134.

1994b Description of a New Species of Subfossil Eagle From Madagascar: *Stephanoatus* (Aves: Falconiformes) From the Deposits of Ampasambazimba. *Proceedings of the Biological Society of Washington* 107:421-426.

Goodman, S.M., J.U. Ganzhorn, and D. Rakotondravony

2003 Introduction to the Mammals. *In* The Natural History of Madagascar. S.M. Goodman and J.P. Benstead, eds. Pp. 1159. Chicago: The University of Chicago Press.

Gould, L.

1996a Male-Female Affiliative Relationships in Naturally Occurring Ring-Tailed Lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *American Journal of Primatology* 39:63-78.

1996b Vigilance Behaviour During the Birth and Lactation Season in Naturally Occurring Ring-Tailed Lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *International Journal of Primatology* 17:331-347.

Gray , J.P.

1985 Primate Sociobiology. New Haven (Conn.): HRAF Press.

Groves, C.P.

2001 Primate Taxonomy. Washington: DC: Smithsonian Institution Press.

2005 Order Primates. *In* Mammal Species of the World 3rd ed. D.E. Wilson and D.M. Reeder, eds. Pp. 111-184. Baltimore: The Johns Hopkins University Press.

Grüter, C.C., and D. Zinner

2004 Nested Societies – Convergent Adaptations of Snub-Nosed Monkeys and Baboons? Primate Report 70:1-98.

Gubernick, D.J.

1994 Biparental Care and Male-Female Relations in Mammals. *In* Infanticide and Parental Care. S. Parmigiani and F. vom Saal, eds. Pp. 427-463. Chur, Switzerland: Harwood Academic Publishing.

Halle, S.

2000 Voles – Small Granivores with Polyphasic Patterns. *In* Activity Patterns in Small Mammals. An Ecological Approach. S. Halle and N.C. Stenseth, eds. Pp. 191-215. New York: Springer.

Hamilton, A.E., I. Tattersall, R. Sussman, and J. Buettner-Janusch

1980 Chromosomes of Lemuriformes VI. Comparative Karyology of *Lemur fulvus*: A G-Banded Karyotype of *Lemur fulvus mayottensis* (Schlegel 1866). International Journal of Primatology. 1:81-93.

Harcourt, A.H.

1979 Social Relationships between Adult Male and Female Mountain Gorillas.

Animal Behaviour 27:325-342.

1991 Sperm Competition and the Evolution of Nonfertilizing Sperm in Mammals.

Evolution 45:314-328.

1995 Sexual Selection and Sperm Competition in Primates: What are Male

Genitalia Good For? *Evolutionary Anthropology* 4:121-129.

Harcourt, A.H., P.H. Harvey, S.G. Larson, and R.V. Short

1981 Testis Weight, Body Weight, and Breeding System in Primates. *Nature*

293:55-57.

Harrington, J.

1975 Field Observations of Social Behaviour of *Lemur fulvus rufus*. In *Lemur*

Biology. I. Tattersall and R.W. Sussman, eds. Pp. 259-279. New York, Plenum Press.

Hawkins, C.E., and P.A. Racey

2005 Low Population Density of a Tropical Forest Carnivore *Cryptoprocta ferox*:

Implications for Protected Area Management. *Oryx* 39:35-43.

Hill, D.A.

1990 Social Relationships between Adult Male and Female Rhesus Macaques: II.

Nonsexual Affiliative Behaviour. *Primates* 31:33-50.

Hinde, R.A.

1976 Interactions, Relationships, and Social Structure. *Man* 11:1-17.

Hinde, R.A., and S. Atkinson

1970 Assessing the Roles of Social Partners in Maintaining Mutual Proximity, As Exemplified by Mother-Infant Relations in Rhesus Monkeys. *Animal Behaviour* 18:169-176.

van Hooff, J., and C.P. van Schaik

1992 Cooperation in Competition: The Ecology of Primate Bonds. *In Coalitions and Alliances in Humans and Other Animals*. A.H. Harcourt and FBM de Waal, eds. Pp. 357-389. Oxford: Oxford University Press.

van Horn, R.N., and J.A. Resko

1977 Reproductive Cycle of the Ring-Tailed Lemur *Lemur catta*: Sex Steroid Levels and Sexual Receptivity under Controlled Photoperiods. *Endocrinology* 101:1579-1590.

Hrdy, S.B.

1974 Male-Male Competition and Infanticide among the Langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica* 22:19-58.

Huck, M.A., P. Lottker, and E.W. Heymann

2004 Proximate Mechanisms of Reproductive Monopolization in Male Moustached Tamarins (*Saguinus mystax*). *American Journal of Primatology* 64:39-56.

Hyttén, F.E., and G. Chamberlain

1980 *Clinical Physiology in Obstetrics*. Oxford, United Kingdom: Blackwell Scientific Publications.

Irwin, M.T., S.E. Johnson, and P.C. Wright

2005 The State of Lemur Conservation in South-Eastern Madagascar: Population and Habitat Assessments for Diurnal and Cathemeral Lemurs Using Surveys, Satellite Imagery and GIS. *Oryx* 39:204-218.

Isbell, L.A., and T.P. Young

2002 Ecological Models of Female Social Relationships in Primates: Similarities, Disparities, and Some Directions for Future Clarity. *Behaviour* 139:177-202.

Izard, K., B. Coffman, A. Katz, and E. Simons

1993 Reproduction in the Collared Lemur (*Eulemur fulvus collaris*). *American Journal of Primatology* 30:320.

Izard, K., B. Epps, and E. Simons

1995 Reproduction in the Brown Lemur (*Eulemur fulvus fulvus*). *American Journal of Primatology* 36:129.

Jack, K.M., and L. Fedigan

2003 Male Dispersal Patterns in White Faced Capuchins, *Cebus capucinus*: Part 2: Patterns and Causes of Secondary Dispersal. *Animal Behaviour* 67:771-782.

Janson, C.H.

1998 Testing the Predation Hypothesis for Vertebrate Sociality: Prospects and Pitfalls. *Behaviour* 135:389-410.

Johnson, S.E.

2002 Ecology and Speciation in Brown Lemurs: White-Collared Lemurs (*Eulemur albocollaris*) and Hybrids (*Eulemur albocollaris* X *Eulemur fulvus*)

rufus) in Southeastern Madagascar. Ph.D. dissertation, The University of Texas at Austin.

2006 Evolutionary Divergence in the Brown Lemur Species Complex. *In* Lemurs: Ecology and Adaptation. L. Gould and M.L. Sauther, eds. Pp. 187-210. New York: Springer Science and Business Media.

Johnson, S.E., A.D. Gordon, R.M. Stumpf, D.J. Overdorff, and P.C. Wright

2005 Morphological Variation in Populations of *Eulemur albocollaris* and *E. fulvus rufus*. *International Journal of Primatology* 26(6):1399-1416.

Johnson, S.E., R. Lei, S.K. Martin, M.T. Irwin, and E.E. Louis

2008 Does *Eulemur cinereiceps* Exist? Preliminary Evidence From Genetics and Ground Surveys in Southeastern Madagascar. *American Journal of Primatology* 70:372-385.

Johnson, S.E., and D.J. Overdorff

1999 Census of Brown Lemurs (*Eulemur fulvus* spp.) in Southeastern Madagascar: Methods Testing and Conservation Implications. *American Journal of Primatology* 47:51-60.

Johnson, S.E., and Y. Wyner

2000 Notes on the Biogeography of *Eulemur fulvus albocollaris*. *Lemur News* 5:25-28.

Jolly, A.

1966 *Lemur Behavior*. Chicago: University of Chicago Press.

1984 The Puzzle of Female Feeding Priority. *In* *Female Primates: Studies by Women Primatologists*. M. Small, ed. Pp. 197-215. New York: Alan R. Liss.

1998 Pair-Bonding, Female Aggression and the Evolution of Lemur Societies.

Folia Primatologica 69:1-13.

Jolly, C.J., and J.E. Phillips-Conroy

2003 Testicular Size, Mating System, and Maturation Schedules in Wild Anubis and Hamadryas Baboons. *International Journal of Primatology* 24:125-142.

Kappeler, P.M.

1990 Female Dominance in *Lemur catta*, More Than Just Feeding Priority? *Folia Primatologica* 55:92-95.

1993 Variation in Social Structure: The Effects of Sex and Kinship on Social Interactions in Three Lemur Species. *Ethology* 93:125-145.

1996 Causes and Consequences of Life-History Variation among Strepsirhines Primates. *American Naturalist* 148:868-891.

1997 Determinants of Primate Social Organization: Comparative Evidence and New Insights from Malagasy Lemurs. *Biological Review* 72:111-151.

1999 Primate Socioecology: New Insights from Males. *Naturwissenschaften* 86:18-29.

Kappeler, P.M., and H.G. Erkert

2003 On the Move Around the Clock: Correlates and Determinants of Cathemeral Activity in Wild Redfronted Lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology* 54:359-369.

Kappeler, P.M., and E.W Heymann

1996 Nonconvergence in the Evolution of Primate Life History and Socio-Ecology. *Biological Journal of the Linnean Society* 59:297-326.

Kappeler, P.M., and C.P. van Scahik

2002 Evolution of Primate Social Systems. *International Journal of Primatology*
23(4):707-740.

Kerth, G., and B. König

1999 Fission, Fusion and Nonrandom Association in Female Bechstein's Bats
(*Myotis bechsteinii*). *Behaviour* 136:1187-1202.

Kleiman, D.G.

1977 Monogamy in Mammals. *Quarterly Review of Biology* 52:39-69.

Kummer, H.

1968 *Social Organization of Hamadryas Baboons*. Chicago: University of
Chicago Press.

1971 *Primate Societies: Group Techniques of Ecological Adaptation*. Chicago:
Aldine.

Leutenegger, W.

1980 Monogamy in Callitrichids: A Consequence of Phyletic Dwarfism.
International Journal of Primatology 1:95-98.

Linnaeus, C.

1758 *Systema naturae per regna tria naturae, secundum classes, ordines, genera,*
species, cum characteribus, differentiis, synonymis, locis. Tomus I. 10th ed.
Holmiae: Impensis Direct Laurentii Salvii.

Mayr, E.

1963 *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.

Martin, R.D.

1990 Primate Origins and Evolution: A Phylogenetic Reconstruction. New Jersey: Princeton University Press.

Mass, V., M. Heistermann, and P.M. Kappeler

2009 Mate-Guarding as a Male Reproductive Tactic in *Propithecus verreauxi*.
International Journal of Primatology 30:389-409.

McCowan, B., K. Anderson, A. Heagerty, and A. Cameron

2008 The Utility of Social Network Analysis in Primate Behavioral Management.
Applied Behaviour Science 109:396-405.

Merritt, J.F., and S.H. Vessey

2000 Shrews – Small Insectivores with Polyphasic Patterns. Ecological Studies
141:1-320.

Mesnick, S.L.

1997 Sexual Alliances: Evidence and Evolutionary Implications. *In* Feminism and
Evolutionary Biology: Boundaries, Intersections and Frontiers. P.A. Gowaty,
ed. Pp. 207-260. University of Georgia Press, Georgia.

Milne-Edwards, A., and A. Grandidier

1890 Histoire Physique, Naturelle et Politique de Madagascar. 10. Histoire
Naturelle des Mammifères 5 (Atlas). Paris.

Mittermeier, R. J. Ganzhorn, W. Konstant, K. Glander, I. Tattersall, C. Groves, A.

Rylands, A. Ratsimbazafy, M. Mayor, E. Louis, Y. Rumpler, C. Schwitzer, and R.

Rasoloarison

2008 Lemur Diversity in Madagascar. *International Journal of Primatology*
29:1607-1656.

Mittermeier, R.A., J. Ratsimbazafy, A.B. Rylands, L. Williamson, J.F. Oates, D. Mborá,
J.U. Ganzhorn, E. Rodríguez-Luna, E. Palacios, E.W. Heymann, M.Cecilia, M. Kierulff,
L. Yongcheng, J. Supriatna, C. Roos, S. Walker, and J.M. Aguiar

2007 Primates in Peril: The World's 25 Most Endangered Primates, 2006-2008.
Primate Conservation 22:1-40.

Mittermeier, R.A., I. Tattersall, W.R. Konstant, D.M. Meyers, and R.B. Mast

1994 Lemurs of Madagascar. Washington, D.C.: Conservation International.

Mittermeier, R.A., C. Valladares-Pádua, A.B. Rylands, A.A. Eudey, T.M. Butynski, J.U.
Ganzhorn, R. Kormos, J.M. Aguiar, and S. Walker

2006 Primates in Peril: The World's 25 Most Endangered Primates, 2004-2006.
Primate Conservation 20:1-28.

Møller, A.P.

1988 Testes Size, Ejaculate Quality, and Sperm Competition in Birds. *Biological*
Journal of the Linnean Society 33:273-283.

Møller, A.P., and T.R. Birkhead

1991 Frequent Copulations and Mate Guarding as Alternative Paternity Guards in
Birds: A Comparative Study. *Behaviour* 118:170-186.

Morland, H.S.

1991a Preliminary Report on the Social Organization of Ruffed Lemurs (*Varecia*
variegata variegata) in a Northeast Madagascar Rainforest. *Folia*
Primatologica 56:157-161.

1991b Social Organization and Ecology of Black and White Ruffed Lemurs (*Varecia variegata variegata*) in a Lowland Rainforest, Nosy Mangabe, Madagascar. Ph.D. dissertation, Yale University.

1993 Seasonal Behavioral Variation and its Relationships to Thermoregulation in Ruffed Lemurs. *In* Lemur Social Systems and Their Ecological Basis. P.M. Kappeler and J.U. Ganzhorn, eds. Pp. 193-205. New York: Plenum.

Müller, A.E., and U. Thalmann

2000 Origin and Evolution of Primate Social Organisation: A Reconstruction. *Biological Review of the Cambridge Philosophical Society* 75:405-435.

Nishida, T., and M. Hiraiwa-Hasegawa

1987 Chimpanzees and Bonobos: Cooperative Relationships Among Males. *In* Primate Societies. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, eds. Pp. 165-177. Chicago: University of Chicago Press.

O'Brien, T.

1991 Female-Male Social Interactions in Wedge-Capped Capuchin Monkeys: Benefits and Costs of Group Living. *Animal Behaviour* 41:555-568.

Olupot, W., C.A. Chapman, P.M. Waser, and G. Isabirye-Basuta

1997 Mangabey (*Cercocebus albigena*) Ranging Patterns in Relation to Fruit Availability and the Risk of Parasite Infection in Kibale National Park, Uganda. *American Journal of Primatology* 43:65-78.

Ossi, K., and M. Kamilar

2006 Environmental and Phylogenetic Correlates of *Eulemur* Behavior and Ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology* 61:53-64.

Ostner, J.

2002 Social Thermoregulation in Redfronted Lemurs (*Eulemur fulvus rufus*) *Folia Primatologica* 73:175-180.

Ostner, J., and M. Heistermann

2003 Endocrine Characterization of Female Reproductive Status in Wild Redfronted Lemurs (*Eulemur fulvus rufus*). *General and Comparative Endocrinology* 131:274-283.

Ostner, J., and P.M. Kappeler

1999 Central Males Instead of Multiple Pairs in Redfronted Lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? *Animal Behaviour* 58:1069-1078.

Overdorff, D.J.

1991 Ecological Correlates to Social Structure in Two Prosimian Primates: *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. Ph.D. dissertation, Duke University.

1993 Similarities, Differences, and Seasonal Patterns in the Diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology* 14:721-753.

1996 Ecological Correlates to Social Structure in Two Lemur Species in Madagascar. *American Journal of Physical Anthropology* 100:487-506.

1998 Are *Eulemur* Species Pair-Bonded? Social Organization and Mating Strategies in *Eulemur fulvus rufus* from 1988-1995 in Southeast Madagascar. *American Journal of Physical Anthropology* 105:153-166.

Overdorff, D.J., and E.M. Erhart

2001 Ecological Correlates to Female Dominance in Day-Active Prosimian Primates. *American Journal of Physical Anthropology*. Suppl 32:116.

Overdorff, D.J., and S.E. Johnson

2003 *Eulemur*, True Lemurs. In *The Natural History of Madagascar*. S.M. Goodman and J.P. Benstead, eds. Pp. 1320-1324. Chicago: University of Chicago Press.

Overdorff, D.J., A.M. Merenlender, P. Talata, A. Telo, and Z.A. Forward

1999 Life History of *Eulemur fulvus rufus* from 1988-1998 in Southeastern Madagascar. *American Journal of Physical Anthropology* 108:295-310.

Overdorff, D.J., and S.R. Tecot

2006 Social Pair-Bonding and Resource Defense in Wild Red-Bellied Lemurs (*Eulemur rubriventer*). In *Lemurs, Ecology, and Adaptations*. L. Gould and M.L. Sauter, eds. Pp. 235-254. New York: Springer.

Palombit, R.A.

1995 Longitudinal Patterns of Reproduction in Wild Female Siamang (*Hylobates syndactylus*) and White-handed Gibbons (*Hylobates lar*). *International Journal of Primatology* 16:739-760.

1999 Infanticide and the Evolution of Pair Bonds in Nonhuman Primates.

Evolutionary Anthropology 7:117-129.

2000 Infanticide and the Evolution of Male-Female Bonds in Animals. *In* Infanticide by Males and its Implications. C.P. van Schaik, and C.H. Janson, eds. Pp. 239-268. Cambridge, UK: Cambridge University Press.

Parga, J.A.

2003 Copulatory Plug Displacement Evidences Sperm Competition in *Lemur catta*. *International Journal of Primatology* 24:889-899.

Pereira, M.E.

1991 Asynchrony within Estrous Synchrony among Ringtailed Lemurs (Primates: Lemuridae). *Physiology and Behavior* 49:47-52.

1993 Agonistic Interaction, Dominance Relation, and Ontogenetic Trajectories in Ringtailed Lemurs. *In* Juvenile Primates: Life History, Development, and Behavior. M.E. Pereira and L.A. Fairbanks, eds. Pp. 285-305. New York: Oxford University Press.

Pereira, M.E., and P.M. Kappeler

1997 Divergent Systems of Agonistic Behaviour in Lemurid Primates. *Behaviour* 134:225-274.

Pereira, M.E., R. Kaufman, P.M. Kappeler, and D. Overdorff

1990 Female Dominance Does Not Characterize All of the Lemuridae. *Folia Primatologica* 55:96-103.

Pereira, M.E., and C.A. McGlynn

1997 Special Relationships Instead of Female Dominance for Redfronted Lemurs, *Eulemur fulvus rufus*. *American Journal of Primatology* 43:239-258.

Pereira, M.E., and M.L. Weiss

1991 Female Mate Choice, Male Migration, and the Threat of Infanticide in Ringtailed Lemurs. *Behavioral Ecology and Sociobiology*. 28:141-152.

Petter-Rousseaux, A.

1980 Seasonal Activity Rhythms, Reproduction, and Body Weight Variations in Five Sympatric Nocturnal Prosimians in Simulated Light and Climatic Conditions. *In* Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior. P. Charles-Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, J.J. Petter, and A. Schilling, eds. Pp. 137-152. *Nocturnal Malagasy primates: Ecology, physiology and behavior*. New York: Academic Press.

Plavcan, J.M., and C.P. van Schaik

1997 Intrasexual Competition and Body Weight Dimorphism in Anthropoid Primates. *American Journal of Physical Anthropology* 103:37-68.

Pochron, S.T., and P.C. Wright

2003 Variability in adult group compositions of a prosimian primate. *Behavioural Ecology and Sociobiology* 54:285-293.

Ralainasolo, F.B., J.H. Ratsimbazafy, and N.J. Stevens

2008 Behavior and Diet of the Critically Endangered *Eulemur cinereiceps* in Manombo Forest, Southeast Madagascar. *Madagascar Conservation and Development* 3:38-43.

Ramos-Fernandez, G., D. Boyer, and V.P. Gomez

2006 A Complex Social Structure with Fission-Fusion Properties Can Emerge From a Simple Foraging Model. *Behavioral Ecology and Sociobiology* 60:536-549.

Rasmussen, M.A.

1985 A Comparative Study of Breeding Similarity and Litter Size in Eleven Taxa of Captive Lemurs (*Lemur* and *Varecia*). *International Journal of Primatology* 6:501-517.

1999 Ecological Influences on Activity Cycle in Two Cathemeral Primates, the Mongoose Lemur (*Eulemur mongoz*) and the Common Brown Lemur (*Eulemur fulvus fulvus*). Ph.D. dissertation, Duke University.

Ratsimbazafy, J.

2002 On the Brink of Extinction and the Process of Recovery: Responses of Black-and-White Ruffed Lemurs (*Varecia variegata variegata*) to Disturbance in Manombo Forest, Madagascar. Ph.D. dissertation, State University of New York at Stony Brook.

Reppert, S.M., and D.R. Weaver

2002 Coordination of Circadian Timing in Mammals. *Nature* 418:935-941.

Richard, A.F., and M.E. Nicoll

1987 Female Social Dominance and Basal Metabolism in a Malagasy Primate. *Propithecus verreauxi*. *American Journal of Primatology* 12:309-314.

Richard, A.F., P. Rakotomanga, and M. Swartz

1991 Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex Ratio, Survival, and Fertility, 1984-1988. *American Journal of Physical Anthropology* 84:307-322.

Rigamonti, M.M.

1993 Home Range and Diet in Red Ruffed Lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. *In* *Lemur Social Systems and Their Ecological Basis*. P.M. Kappeler and J.U. Ganzhorn, eds. Pp. 25-40. New York: Plenum Press.

Rodseth, L., R.W. Wrangham, A.M. Harrigan, and B.B. Smuts

1991 The Human Community as a Primate Society. *Current Anthropology* 32:221-254.

Ross, C.

1991 Life History of New World Monkeys. *International Journal of Primatology* 12:481-502.

Rowell, T.E.

1979 How Would we Know if Social Organization Were Not Adaptive? *In* *Primate Ecology and Social Organization*. I.S. Berstein and E.O. Smith, eds. Pp. 1-22. New York: Garland.

1993 Reification of Social Systems. *Evolutionary Anthropology* 84:463-477.

Ruckstuhl, K.E.

1998 Foraging Behaviour and Sexual Segregation in Bighorn Sheep. *Animal Behaviour* 56:99-106.

Rumpler, Y.

1989 Chromosomal Evolution in Malagasy Prosimians. *In Perspectives in Primate Biology*. P.K. Seth and S. Seth, eds. Pp. 167-190. New Delhi, Today & Tomorrow's Printers and Publishers.

Sauther, M.L.

1991 Reproductive Behavior of Free-Ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84:463-477.

van Schaik, C.P.

1983 Why Are Diurnal Primates Living in Groups? *Behaviour* 87:120-144.

1999 The Socioecology of Fission-Fusion Sociality in Orangutans. *Primates* 40:69-86.

van Schaik, C.P., and R.I.M. Dunbar

1990 The Evolution of Monogamy in Large Primates: A New Hypothesis and Some Crucial Tests. *Behaviour* 115:30-62.

van Schaik, C.P., and J.A.R.A.M. van Hooff

1983 On the Ultimate Causes of Primate Social Systems. *Behaviour* 85:91-117.

van Schaik, C.P., and P.M. Kappeler

1993 Life History, Activity Period and Lemur Social Systems. *In Lemur Social Systems and their Ecological Basis*. P.M. Kappeler and J.U. Ganzhorn, eds. Pp. 241-260. New York: Plenum.

1996 The Social Systems of Gregarious Lemurs: Lack of Convergence with Anthropoids Due to Evolutionary Disequilibrium? *Ethology* 102:915-941.

1997 Infanticide Risk and the Evolution of Male-Female Association in Primates.

Proceedings of the Royal Society B: Biological Sciences 264:1687-1694.

van Schaik, C.P., and M.A. van Noordwijk

1988 Scramble and Contest Feeding Competition Among Female Long-tailed

Macaques (*Macaca fascicularis*). Behaviour 105:77-98.

1989 The Special Role of Male *Cebus* Monkeys in Predation Avoidance and its

Effect on Group Composition. Behavioral Ecology and Sociobiology 24:265-276.

van Schaik, C.P., M.A. van Noordwijk, B. Warsono, and E. Sutriyono

1983 Party Size and Early Detection of Predators in Sumatran Forest Primate.

Primate 24:211.

Schülke, O., and J. Ostner

2005 Big Times for Dwarfs: Social Organization, Sexual Selection, and

Cooperation in the Cheirogalidae. Evolutionary Anthropology 14:170-185.

Simons, E.I., and Y. Rumpler

1988 *Eulemur*: New Generic Name for Species of *Lemur* other than *Lemur catta*.

Comptes Rendus de l'Academie des Sciences Serie III. Sciences de la Vie – Life Sciences 307:547-551.

Small, M.F.

1989 Female Choice in Nonhuman Primates. Yearbook of Physical Anthropology

32:103-127.

Small, M.F., and D.G. Smith

1986 The Influence of Birth Timing upon Infant Growth and Survival in Captive Rhesus Macaques (*Macaca mulatta*). *International Journal of Primatology* 7:289-304.

Smith, J.E., J.M. Kolowski, K.E. Graham, S.E. Dawes, and K.E. Holekamp

2008 Social and Ecological Determinants of Fission-Fusion Dynamics in the Spotted Hyaena. *Animal Behaviour* 76:619-636.

Smuts, B.B.

1985 *Sex and Friendship in Baboons*. Aldine: Hawthorne.

Stammbach, E.

1987 Desert, Forest, and Montane Baboons: Multilevel Societies. *In Primate Societies*. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, eds. Pp. 112-120. Chicago: University of Chicago Press.

Sterck, E.H.M, D.P. Watts, and C.O. van Schaik

1997 The Evolution of Female Social Relationships in Nonhuman Primates. *Behavioral Ecology and Sociobiology* 41(5):291-309.

Struhsaker, T.T.

1969 Correlates of Ecology and Social Organization among African Cercopithecines. *Folia Primatologica* 11:80-118.

Sussman, R.W.

1974 Ecological Distinctions of Sympatric Species of Lemur. *In Prosimian Biology*. R.D. Martin, G.A. Doyle, and A.C. Walker, eds. Pp. 75-108. Pittsburgh: University of Pittsburgh Press.

1975 A Preliminary Study of the Behaviour and Ecology of *Lemur fulvus rufus*, Audebert 1800. In *Lemur Biology*. I. Tattersall and R.W. Sussman, eds. Pp. 237-258. New York: Plenum Press.

1977 Feeding Behavior of *Lemur catta* and *Lemur fulvus*. In *Primate Ecology*. T.H. Clutton-Brock, ed. Pp. 1-36. London: Academic Press.

1991 Demography and Social Organization of Free-Ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84:43-58.

1992 Male Life History and Intergroup Mobility among Ring-tailed Lemurs (*Lemur catta*). *International Journal of Primatology* 13:395-413.

Symington, M.M.

1990 Fission-Fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology* 11:47-61.

Takahata, Y.

1982 Social Relations Between Adult Males and Females of Japanese Monkeys in the Arashiyama B Troop. *Primates* 23:1-23.

Tardif, S., and P. Garber

1994 Social and Reproductive Patterns in Neotropical Primates: Relation to Ecology, Body Size, and Infant Care. *American Journal of Primatology* 34:111-114.

Tattersall, I.

1977 Ecology and Behavior of *Lemur fulvus mayottensis* (Primates, Lemuriformes). *Anthropological Papers of the American Museum of Natural History* 54:421-482.

1982 *The Primates of Madagascar*. New York: Columbia University Press.

1987 Cathemeral Activity in Primates: A Definition. *Folia Primatologica* 49:200-202.

1992 Systematic Versus Ecological Diversity: The Example of Malagasy Primates. *In Systematics, Ecology, and the Biodiversity Crisis*. N. Eldredge, ed. Pp. 25-39. New York: Columbia University Press.

Tattersall, I., and R. Sussman

1998 'Little Brown Lemurs' of Northern Madagascar. *Folia Primatologica* 69(Suppl. 1):379-388.

Terborgh, J., and C.H. Janson

1986 The Socioecology of Primate Groups. *Annual Review of Ecology and Systematics* 17:111-136.

Tilden, C.D.

1997 Low Rates of Maternal Reproductive Investment Characterize Lemuriform Primates. *American Journal of Physical Anthropology* 24(Suppl):228.

Tilden, C.D., and O.T. Oftedal

1995 The Bioenergetics of Reproduction in Prosimian Primates: Is it Related to Female Dominance? *In Creatures of the Dark: The Nocturnal Prosimians*. M.K.

Izard, L. Alterman and G.A. Doyle, eds. Pp. 119-131. New York: Plenum Press.

Trivers, R.L.

1972 Parental Investment and Sexual Selection. *In* Sexual Selection and the Descent Of Man. B. Campbell, ed. Pp. 136-179. Chicago: Aldine.

Tutin, C.E.G.

1979 Mating Patterns and Reproductive Strategies in a Community of Wild Chimpanzees (*Pan troglodytes schweinfurthii*). Behavioral Ecology and Sociobiology 6:29-38.

Vasey, N.

1997 Community Ecology and Behavior of *Varecia variegata rubra* and *Lemur fulvus albifrons*, on the Masoala Peninsula, Madagascar. Ph.D. dissertation, Washington University.

2000 Niche Separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Intersepcific Patterns. American Journal of Physical Anthropology 112:411-432.

Vick, L.G.

1977 The Role of Interindividual Relationships in Two Troops of Captive Lemur fulvus. Ph.D. dissertation, University of North Carolina at Chapel Hill.

Vick, L.G., and J.M. Conley

1976 An Ethogram for *Lemur fulvus*. Primates 17:125-144.

Vick, L.G., and M.E. Pereira

1989 Episodic Targeting Aggression and the Histories of Lemur Social Groups.
Behavioural Ecology and Sociobiology 25:3-12.

Wanker, R.

2002 Social System and Acoustic Communication of Spectacled Parrotlets
(*Forpus conspicillatus*): Research in Captivity and the Wild. In Bird Research
and Breeding. C. Mettke-Hofmann and U. Ganzloss, eds. Pp. 83-108. Fürth:
Filander Verlag.

Waser, P.M.

1974 Spatial Associations and Social Interactions in a "Solitary" Ungulate: The
Bushback *Tragelaphus scriptus* (Pallas). Zeitschrift für Tierpsychologie 37:24-
36.

Wasserman, M.D., and C.A. Chapman

2003 Determinants of Colobine Monkey Abundance: The Importance of Food
Energy, Protein and Fiber Content. Journal of Animal Ecology 72:650-659.

Watson, J.E.M., R.J. Whittaker, and T.P. Dawson

2005 The Importance of Littoral Forest Remnants for Indigenous Bird Species
Conservation in South Eastern Madagascar. Biodiversity and Conservation
14(3):523-545.

Watts, D.P.

1990 Ecology of Gorillas and its Relation to Female Transfer in Mountain
Gorillas. International Journal of Primatology 11:21-45.

White, F.J.

1991 Social Organization, Feeding Ecology, and Reproductive Strategy of Ruffed Lemurs, *Varecia variegata*. In *Primate Today: Proceedings of the XIII Congress of the International Primatological Society*. A. Ehara, T. Kimura, O. Takenaka, and M. Iwamoto, eds. Amsterdam: Elsevier Science Publishers.

White, F.J., and M.A. Burgman

1990 Social Organization of the Pygmy Chimpanzee (*Pan paniscus*): Multivariate Analysis of Intracommunity Associations. *American Journal of Physical Anthropology* 83:193-201.

Whitehead, H., and S. Dufault

1999 Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. *Advances in the Study of Behavior* 28:33-74.

Willis, C.K.R., and R.M. Brigham

2004 Roost Switching, Roost Sharing and Social Cohesion: Forest-Dwelling Big Brown Bats, *Eptesicus fuscus*, Conform to the Fission-Fusion Model. *Animal Behaviour* 68:495-505.

Wrangham, R.W.

1979 On the Evolution of Ape Social Systems. *Social Sciences Information* 18:335-368.

1980 An Ecological Model of Female-Bonded Primate Groups. *Behaviour* 75:262-300.

Wright, P.C.

1989 The Nocturnal Primate Niche in the New World. *Journal of Human Evolution* 18:635-658.

1993 The Evolution of Female Dominance and Biparental Care among Non-Human Primates. *In Sex and Gender Hierarchies*. B. Miller, ed. Pp. 127-147. Cambridge: Cambridge University Press.

1999 Lemur Traits and Madagascar Ecology: Coping With an Island Environment. *Yearbook of Physical Anthropology* 42:31-72.

Wyner, Y., R. Absher, G. Amato, E. Sterling, R. Stumpf, Y. Rumpler, and R. DeSalle

1999 Species Concepts and the Determination of Historic Gene Flow Patterns in the *Eulemur fulvus* (Brown Lemur) Complex. *Biological Journal of the Linnean Society* 65:39-56.

Wyner, Y.M., S.E. Johnson, R. Stumpf, and R. De Salle

2002 Genetic Assessment of a White-Collared X Red-Fronted Lemur Hybrid Zone at Andringitra, Madagascar. *American Journal of Primatology* 57: 51-66.

Young, A.L., A.F. Richard, and L.C. Aiello

1990 Female Dominance and Maternal Investment in Strepsirhines Primates. *American Naturalist* 135:473-488.

Zielinski, W.J.

2000 Weasels and Martens – Carnivores in Northern Latitudes. *In Activity Patterns in Small Mammals. An Ecological Approach*. S. Halle and N.C. Stenseth, eds. Pp. 95-118. New York: Springer.

APPENDIX A:

A.1. Mean proximity, contact, and total association scores overall, per season of fruit availability, and reproductive season.

a. Group 1

Season	N ^a	Proximity		Contact		Total association	
		Mean % ^b	St. Dev.	Mean %	St. Dev.	Mean %	St. Dev.
Overall	12	3.1	2.1	17.0	9.3	20.1	10.6
Low 1	12	2.4	2.4	21.9	12.0	24.3	13.1
High	12	3.6	3.1	12.4	11.7	16.0	11.5
Low 2	12	4.1	4.3	17.3	24.5	21.3	27.0
Mating	4	5.8	5.4	34.0	18.5	39.9	22.8
Early Gestation	8	1.0	1.2	25.9	13.9	26.9	14.5
Late Gestation	8	5.3	2.4	16.9	6.6	22.2	6.0
Late Gestation	4	2.2	1.5	14.0	13.1	16.2	14.5

^a N= # of samples (dyads)

^b Mean %= the mean percentage of individuals' total observation time spent either in proximity, contact, or proximity + contact with an adult nearest neighbour.

b. Group 2

Season	N ^a	Proximity		Contact		Total association	
		Mean % ^b	St. Dev.	Mean %	St. Dev.	Mean %	St. Dev.
Overall	6	1.9	1.4	12.9	6.7	14.8	7.6
Low 1	6	1.3	1.2	16.1	10.3	17.4	10.2
High	6	2.1	1.9	13.8	11.8	15.9	12.9
Low 2	6	2.6	4.0	8.3	12.9	10.9	16.7
Early Gestation	4	1.7	3.0	28.0	20.8	29.7	22.6
Late Gestation	4	1.7	1.0	16.4	1.3	18.1	1.3
Lactation	4	4.4	5.5	12.8	14.8	17.2	19.9

^a N= # of samples (dyads)

^b Mean %= the mean percentage of individuals' total observation time spent either in proximity, contact, or proximity + contact with an adult nearest neighbour.

APPENDIX B:**B.1. Hinde's Index (H.I.) of maintenance of proximity per season of fruit availability****a. Group 1**

Dyad	Low 1		High		Low 2	
	N^a	H.I.	N	H.I.	N	H.I.
FRA1 - FVM	9	-0.15	4	0.50	0	0.00
FRA1 - Mpl	37	0.11	71	-0.02	43	0.49
FRA1 - Mlm	56	-0.09	91	-0.14	80	-0.19
FVM - Mpl	38	-0.30	40	0.19	43	-0.07
FVM - Mlm	63	-0.14	94	-0.26	84	-0.31
Mpl - Mlm	61	-0.06	69	-0.16	22	-0.27

^aN=total # of approaches and leaves**b. Group 2**

Dyad	Low 1		High		Low 2	
	N^a	H.I.	N	H.I.	N	H.I.
FRA2 - Mtu	29	0.06	54	-0.10	33	-0.22
FRA2 - Mbb	48	-0.38	37	-0.19	0	0.00
Mtu - Mbb	25	0.07	18	-0.22	3	1.00

^aN= total # of approaches and leaves

B.2. Hinde's Index (H.I.) of association for female-male dyads per reproductive season.

a. Group 1

Dyad	Mating		Early Gestation		Late Gestation		Lactation	
	N ^a	H.I.	N	H.I.	N	H.I.	N	H.I.
FRA1 – Mpl	26	0.11	15	0.07	108	0.15	–	–
FRA1 – Mlm	44	-0.13	20	0.10	159	-0.24	–	–
FVM – Mpl	–	–	27	-0.33	46	0.04	48	0.0
FVM - Mlm	–	–	48	-0.21	97	-0.36	86	-0.28

^aN= total # of approaches and leaves

b. Group 2

Dyad	Mating		Early Gestation		Late Gestation		Lactation	
	N ^a	H.I.	N	H.I.	N	H.I.	N	H.I.
FRA2 – Mtu	–	–	4	-0.50	82	-0.02	30	-0.22
FRA2 - Mbb	–	–	32	-0.56	53	-0.13	0	0.00

^aN= total # of approaches and leaves

APPENDIX C:

C.1. Diet composition (% of feeding bouts) for each food type per season of food availability

Food type	Low 1		High		Low 2	
	Males (N ^a =76)	Females (N=105)	Males (N=150)	Females (N=83)	Males (N=55)	Females (N=51)
Fruit	88.2%	76.2%	86.0%	86.8%	90.9%	90.2%
Young Leaves	11.8%	8.6%	1.3%	7.2%	1.8%	3.9%
Flowers	0.0%	1.9%	11.3%	4.8%	5.5%	5.9%
Insects	0.0%	10.5%	0.7%	1.2%	0.0%	0.0%
Mature Leaves	0.0%	1.9%	0.7%	0.0%	0.0%	0.0%
Fungus	0.0%	1.0%	0.0%	0.0%	1.8%	0.0%

^aN= # of feeding bouts

C.2. Diet composition (% of feeding bouts) for each food type per reproductive season.

Food type	Mating (N ^a =20)	Early Gestation (N=46)	Late Gestation (N=135)	Lactation (N=38)
Fruit	75.0%	78.3%	83.0%	92.1%
Young Leaves	5.0%	10.9%	5.9%	7.9%
Insects	15.0%	6.5%	4.4%	0.0%
Flowers	5.0%	2.2%	5.2%	0.0%
Mature Leaves	0.0%	2.2%	0.7%	0.0%
Fungus	0.0%	0.0%	0.7%	0.0%

^aN= # of feeding bouts