Communal infant care in black-and-white ruffed lemurs (*Varecia variegata*).

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Abstract of the Dissertation

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Cooperative breeding describes a system where group members provide regular, unsolicited allomaternal care for offspring that are not genetically their own (Emlen 1991; Hrdy 2009). Most cooperative breeders live in groups with high reproductive skew (i.e., singular breeders with helpers at the nest); however, skew falls along a continuum (Sherman et al. 1995; Vehrencamp, 2000), and, while rare, some cooperative breeders live in groups which experience low skew, subordinates commonly breed, and many if not all breeding individuals communally rear offspring (i.e., plural or communal breeders) (Keller and Reeve 1994).

Though phylogenetically widespread, communal breeding is rare. Among birds, communal breeding is typical in only a few species (e.g., groove-billed ani, *Crotophaga sulcirostris*: Koford et al., 1990; pukeko, *Porphyrio porphyria*: Craig and Jamieson, 1990; Guira cuckoo, *Guira guira*: Macedo, 1992), while within mammals, this reproductive strategy is common only in the banded mongoose (Cant, 2000; Rood, 1975), some rodents (e.g., the house mouse, *Mus musculus domesticus*; Norwegian rat, *Rattus norvegicus*; various caviids: Hayes, 2000; Solomon and Getz, 1997), and social carnivores (lions, *Panthera leo*: Packer et al. 1990; spotted hyenas, *Crocuta crocuta*: Owens and Owens 1984). Within the Primate order, communal breeding is particularly rare; in fact, humans are often regarded as the only communally breeding primates.

Though understudied and rarely cited, this reproductive system has also been tentatively described in ruffed lemurs (*Varecia* sp.), a diurnal, 3-4 kg Malagasy strepsirrhine that lives in large, communally-defended territories characterized by fission-fusion dynamics (Morland 1991a; Morland 1991b; Rigamonti 1993; Vasey 1997; Vasey 2006). Although, like most primates, ruffed lemurs are characterized by relatively slow life histories, due in part to their strict patterns of seasonal breeding, they are distinctive in that they are the only known diurnal primate to bear litters of altricial offspring during seasonal reproductive events (Foerg 1982; Rasmussen 1985; Brockman et al. 1987). Mothers park litters in nests and tree tangles throughout early infant development and it is during this time that evidence of communal breeding has been reported, including use the of communal nests (i.e., crèches) and cooperative infant care (Morland 1990; Vasey 2007).

Among communal breeders, the evolution of non-offspring infant care, which can include grooming, guarding, predator protection, and energy transfer (e.g., food transfer, allonursing), has been explained by a number of adaptive hypotheses. It is argued, though rarely empirically demonstrated, that communal breeding might confer benefits to participating mothers and infants by enabling lactating females to increase food consumption, improve infant thermoregulation and/or growth, guard against predators, and improve competition later in life (see Koenig 1997 for references). Moreover, it is unclear whether mothers show preferences for communal nesting partners, why females select these particular partners, and whether these preferences vary. Moreover, while reciprocity, mutualism, and kinship have all been used to explain why communal breeders live and reproduce in groups, the benefits of communal breeding have yet to be established for many taxa.

Thus, the goal of this dissertation was to investigate communal breeding in black-and-white ruffed lemurs (*Varecia variegata*) in an undisturbed primary rainforest habitat, Ranomafana National Park, to address whether and to what extent communal breeding conferred benefits to mothers and their offspring. This dissertation had three main research objectives: 1) to assess the spatial ecology of black-and-white ruffed lemurs (*Varecia variegata*) using Global Information System (GIS) technology to determine community membership and establish what *constitutes* a ruffed lemur community; 2) to then examine the genetic population structure of this same ruffed lemur population using molecular techniques (microsatellite analysis) to determine dispersal and patterns of within- and between-community relatedness; and finally, 3) to address how patterns of space use, genetic relatedness, and affiliation influence patterns of ruffed lemur communal breeding. I also investigate the benefits of ruffed lemur communal care to both mothers and their infants.

The use of Global Information System (GIS) analyses (Chapter 2) revealed broad patterns of communal and individual home range area and overlap which confirmed the presence of a fission-fusion social organization, as in previous studies of other wild ruffed lemur populations. I found that multiple males and females used independent, yet overlapping ranges which together comprised a large, communal territory that was more-or-less spatially distinct from other neighboring communities. Within this community, females used significantly larger home ranges than did males (MCP: $U = 10$, $p = 0.04$; kernel: $U = 9$, $p = 0.03$), though home range overlap did not differ between the sexes. Range use did not vary by reproductive season, as previously suggested, but rather by climatic season, though not in the predicted ways. However, reproductive seasonality, not climate, best predicted variation in daily distance traveled. Taken together, the patterns of ruffed lemur spatial ecology described herein do not adhere to those described for other primate fission-fusion systems (Wrangham 1979, Lehmann & Boesch 2005). Instead, ruffed lemurs appear to adhere to a new, previously unrecognized system of primate fission-fusion dynamics that combines aspects of both ‘female-bonded’ and ‘bisexually bonded’ systems of range use: both males and females are more-or-less evenly distributed throughout a female-defended communal range, with group members exhibiting equal and moderate home range overlap with other community members.

Genetic analyses (Chapter 3) revealed that ruffed lemurs within this community were characterized by unbiased dispersal (i.e., both sexes likely disperse), though females likely disperse less frequently or at closer distances than do male conspecifics. On average, community members share relatedness close to zero (average R = -0.06); however, relatives lived in significantly closer proximity and shared greater home range overlap than did unrelated neighbors (proximity: females, Mantel R = 0.490, $p = 0.007$; males, Mantel R = 0.655, $p < 0.001$; overlap: males: Mantel R = 0.373, $p = 0.03$), resulting in close spatial networks of both male and female kin within the larger communal range.

Finally, in the first systematic field study of communal breeding in ruffed lemurs to combine data on rearing behavior, genetic relatedness and infant survivorship (Chapter 4), I demonstrate that communal breeding in ruffed lemurs is biased towards kin and female affiliates, and that communal nesting significantly improves infant survival (Spearman's rho = 0.872, *p* = 0.03), particularly during early stages of infant development. As communal nesting allows an improved balance between maternal responsibility and foraging effort (communal nesters spent less time at nest than non-nesters: Mann-Whitney-*U* = 61, *Z* = 2.539, *p* = 0.01*;* more time feeding/foraging *U* = 56, *Z* = -2.049, *p* = 0.04,, it is likely that communal breeding in ruffed lemurs results in improved maternal energy balance, and ultimately confers direct fitness payoffs to communally nesting females.

Taken together, the suite of traits described herein (i.e., fission-fusion dynamics, unbiased dispersal, communal breeding) are uncharacteristic of most primates. While it is true that ruffed lemurs share these 'rare' behaviors with a handful of other primate taxa, it is only in ruffed lemurs that we find this particular suite of social and reproductive traits (e.g., fission-fusion social organization and cooperative breeding are found in a few non-human primates, but never in tandem). Instead, it seems that ruffed lemurs exhibit a social system that has gone previously unrecognized in primates, and instead loosely resembles patterns found in other communally breeding mammals such as hyenas (e.g., fission-fusion dynamics, female dominance and territory defense, and crèching behavior: Boydston et al. 2003; Henschel and Skinner 1991; Holekamp et al. 2000).

Dedications

For my friends and family in Madagascar –

Ny fifankatiavana no voalohan-karena. Misaotra betsaka ry havana malalako.

The greatest wealth in life is friendship. Thank you, my dear family.

For my parents –

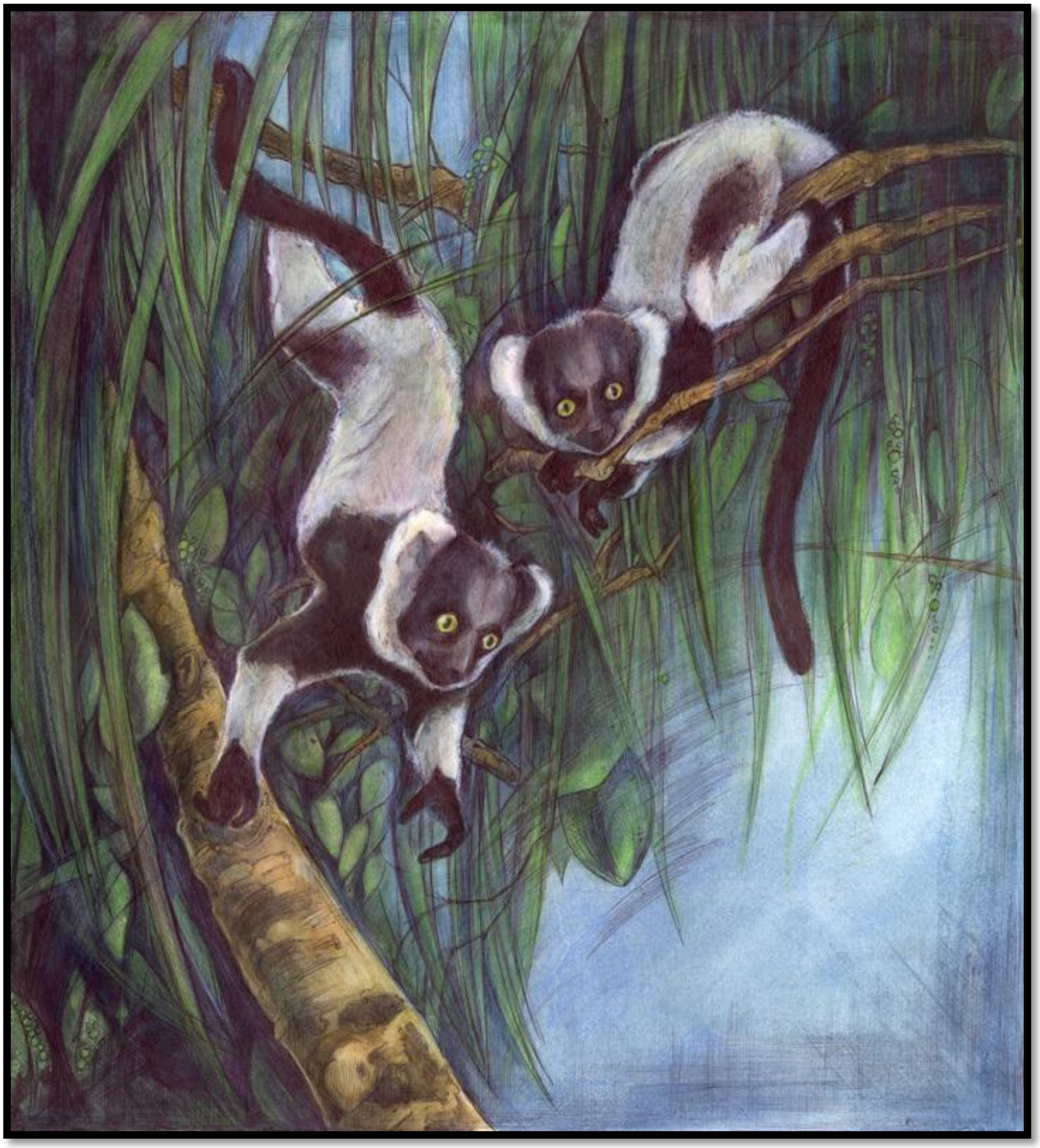
For offering me the world…

and expecting me to make good on the deal. This is for you.

For my animals –

My goal has always been to make a difference …

for your sake I hope that I can.



Radio-Blue's infants at 9 weeks of age (December 2008)

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This dissertation has been a labor of love, and would not have been possible without the support and encouragement of my friends, family, and colleagues, both here and abroad.

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Chapter 1

Communal infant care in black-and-white ruffed lemurs:

Project Introduction & Background

Cooperative breeding refers to situations where individuals regularly care for offspring that are not genetically their own (Emlen 1991; Solomon and French 1997). This breeding system is typically seen in groups with high reproductive skew, such as in systems where reproductive suppression is common and non-reproductive adults delay dispersal to assist breeders with infant-care (i.e., singular breeders with helpers at the nest). However, reproductive skew can be thought of as falling along a continuum (Sherman et al. 1995; Vehrencamp, 2000), and, while rare, some cooperative breeders live in groups which experience low reproductive skew, whereby multiple breeding females are present within a single social unit (i.e., communal or plural breeders), and many if not all breeding individuals in a group communally rear offspring (i.e., plural or communal breeders) (Keller and Reeve 1994).

Among communal breeders, group members typically defend a communal territory and group membership is generally stable through time (Brown 1978). Within these groups, however, there is considerable variation in the aggregation of crèches (i.e., dens, nests, etc.) and the degree to which group members participate in communal care (Caraco and Brown 1986). Among participants, the evolution of non-offspring care, which can include grooming, guarding, predator protection, and energy transfer (e.g., food transfer, allonursing), has been explained by a number of adaptive hypotheses, including reciprocity (Axelrod and Hamilton 1981; Trivers 1971), mutualism (Lima 1989; Maynard Smith 1983), and kin selection (Hamilton 1964), as well as maladaptive or non-adaptive explanations such as misdirected care (for review see Emlen 1991; Koenig 1997). The most common proximate explanations however, describe communal care as conferring benefits to participating mothers or to infants, by enabling lactating females to increase food consumption or enjoy other energy benefits (e.g., Rood 1978; Stanford 1992; Koenig 1997) and/or by improving infant thermoregulation (e.g., Ostfeld 1986), growth (e.g., improved infant nutrition/decreased time between meals: e.g., Caraco & Brown 1986), protection against infanticide and/or predators (e.g., Packer et al. 1990; Campagna et al. 1992), and improved competition later in life (see Koenig 1997 for references). Despite the numerous hypotheses proffered to explain why communal breeders live and reproduce in groups, the benefits of communal breeding have yet to be empirically established for a number of taxa (Koenig 1997).

Communal breeding is a widespread strategy among birds and mammals (Emlen 1991; Koenig 1997), and includes lions (*Panthera leo*) (e.g., Packer et al. 1990), spotted hyenas (*Crocuta crocuta*) (e.g., Owens and Owens 1984), and banded mongoose (*Mungos mungo*) (Gilchrist et al. 2004), among others. Among primates, however, communal breeding and cooperative infant care is comparatively rare (Hrdy 2005). Although callitrichines are well known for being cooperative breeders (Sussman and Garber 1987; Rylands 1996), humans are widely cited as the only *communally* breeding primates (Hrdy 2005, 2009; but see Fietz 1999; Eberle and Kappeler 2006). Across 'traditional' (i.e., hunter-gatherer) human societies, mothers commonly rely on the help of their spouses, grandmothers, sisters, children and other related and unrelated reproductive individuals to successfully raise their young (Bove et al. 2002; Flinn 1988; Hawkes et al. 1997; Hrdy 2009; Hrdy 1999; Hrdy 2005; Ivey 2000). In fact, this prosociality (i.e., behaviors that benefit others) is said to have led to a "shared intentionality" early in human evolution (i.e., "the ability to participate with others in collaborative activities with shared goals and intentions"; Tomasello et al. 2005: 675), a feature which has been identified as the source of many uniquely human traits (Burkart et al. 2009). However, even among the best-studied hunter-gatherer societies, communal infant care falls along a continuum (Hrdy 2009), from infrequent helping (e.g., !Kung: Konner 1976) to extensive participation in communal rearing and alloparental care (e.g., Efe: Tronick et al. 1987; Ivey 2000).

Though less well known, communal breeding has also been tentatively described in ruffed lemurs (*Varecia* sp.) (Morland 1990; Vasey 2007), a diurnal, 3-4 kg Malagasy strepsirrhine that lives in large, communally defended territories characterized by fission-fusion dynamics (Morland 1991a; Morland 1991b; Rigamonti 1993; Vasey 1997; Vasey 2006). Ruffed lemurs, as with other Malagasy primates, are characterized by strict seasonal breeding (Foerg 1982; Brockman et al. 1987), and are known for their unusual life histories (e.g., litter-bearing: Foerg 1982; Rasmussen 1985; Brockman et al. 1987) and post-natal reproductive strategies, including nest construction, nest use, and communal infant care (Morland 1993; Pereira et al. 1987; Vasey 2007).

Like many communally breeding birds (Caraco and Brown 1986) and mammals (e.g., Hoogland 1985), ruffed lemur mothers give birth in separate nests throughout the communal range and feed only their own young during the early period of infant development (Morland 1990; Vasey 2007; Baden, unpublished data). Eventually, mothers begin to transfer litters away from the natal nest, parking infants in new nests and tree tangles while feeding and foraging nearby (Morland 1990; Vasey 2007; Baden, unpublished data). It is during this time that evidence of communal breeding has been reported, including communal nest use and cooperative infant care (i.e., crèches or “kindergartens”; Morland 1990; Vasey 2007). Previous studies have proposed that crèches may confer energetic benefits to mothers (Morland 1990), though such benefits have yet to be established. Moreover, it is unclear whether mothers show preferences for communal nesting partners, why females select these particular partners, and whether these preferences vary.

Thus, the primary questions this dissertation aims to address are: ***1. To what extent do mothers participate in communal care?*** In other words, do all females participate, and if not, how do care strategies vary? ***2. Who do females select as nesting partners?*** In other words, do females preferentially direct care toward particular litters or nesting partners, and do these preferences vary? ***3. Why do females select particular litters or nesting partners?*** Here I investigate three main possibilities: i) that females nest with their neighbors, that is, females with home ranges that are in close proximity; ii) that females nest with affiliates, or females with whom they regularly associate; and iii) that females nest with relatives, or females sharing higher pairwise relatedness than expected by chance. Finally, I ask ***4. How do females benefit from communal infant care?*** Here, I test the hypotheses that i) communal nesting confers energetic benefits to mothers, and that ii) communal nesting improves infant survival.

Chapters two through four of this dissertation are organized as a collection of independent manuscripts centered on addressing the questions introduced here.

Organization of the dissertation

Research objective 1: Spatial characterization of a ruffed lemur community

Prior to understanding the cooperative and social dynamics within a ruffed lemur community, it is necessary to first determine what *constitutes* a ruffed lemur community. This task is difficult to accomplish *a priori*, first because ruffed lemurs are characterized by a high degree of behavioral flexibility in both social organization and home range use (Vasey 2003). For example, while some ruffed lemur populations (northern populations of *V. variegata*: Morland 1991a; Morland 1991b; *V. rubra*: Rigamonti 1993; Vasey 1997; Vasey 2006) have been described as exhibiting fission-fusion dynamics, others are said to live in cohesive multi-male multi-female groups (Balko 1998; Ratsimbazafy 2002) or pairs (White 1991; Britt 1997). While some of these patterns may be explained by small sample size or suboptimal sampling methods, in at least one example, the observed patterns were likely due to low population densities and a behavioral shift toward cohesive groups in response to both ecological and anthropogenic pressures (Ratsimbazafy 2002).

Moreover, in ruffed lemur populations characterized by fission-fusion dynamics, members of a social group are spatiotemporally dispersed, and individuals join and leave subgroups over the course of days, weeks and even hours (Vasey 1997; Vasey 2006), making it difficult to ascertain community membership until after substantial sampling effort has been achieved. Thus, the first aim of this dissertation is to characterize the range use patterns of black-and-white ruffed lemurs (*Varecia variegata*) in an undisturbed rainforest habitat to determine the social organization of the study population and to subsequently ascribe community membership to the focal animals observed.

Specifically, Chapter 2 utilizes Global Information System (GIS) home range analyses to i) characterize the spatial organization of the study population, and ii) subsequently examine the spatial dynamics within a ruffed lemur community, including individual annual home range size and overlap, as well as how these patterns vary according to climatic and reproductive seasons. Using results from this chapter, I will be able to characterize the social organization of this ruffed lemur population, and contextualize the observed patterns within the larger primate fission-fusion framework.

Chapter Two will test the following hypotheses:

Hypothesis 1: Ruffed lemurs are characterized by a fission-fusion social organization.

- Prediction 1.1: Individuals live in an area that is spatially distinct from neighboring areas (i.e., non-overlapping with neighboring territories).
- Prediction 1.2: Individuals live in an area that is exclusive to non-members (i.e., individuals exhibit high site fidelity).

- Prediction 1.3: Male and female ranges are independent, but overlapping within the communal range.

Hypothesis 2: Range use varies with climatic seasons.

- Prediction 2.1: Individuals use an energy maximizing (accumulating) strategy, and increase range use and daily travel in search of high quality food resources during lean seasons.
- Prediction 2.2: Individuals use an energy (time) minimizing strategy, and decrease range use and daily travel by feeding on lower quality food resources until conditions improve.

Hypothesis 3: Range use varies with reproductive seasons.

- Prediction 3.1: Female home ranges are smallest and daily travel distances shortest during lactation and early infant dependence (i.e., females are constrained in range use by the presence of dependent offspring).
- Prediction 3.2: Females share the greatest home range overlap during lactation and early infant dependence when communal infant care is highest (i.e., females expand home range overlap for the purposes of communal nesting).

- Prediction 3.3: Female ranges are largest during non-reproductive periods (i.e., females are unconstrained in the travel by dependent offspring).
- Prediction 3.4: Male ranges are largest during the non-reproductive (pre-mating) season (i.e., males expand home ranges to visit the ranges of multiple soon-to-be receptive females).
- Prediction 3.5: Male ranges show the greatest overlap with females during the non-reproductive (pre-receptive) period.

Research objective 2: Genetic characterization of a ruffed lemur community

Upon establishing the social organization of the focal ruffed lemur population, it is next necessary to characterize the population's genetic structure. In many social mammals, kin are clustered along either matrilineal or patrilineal lines, which in turn affects the distribution of genetic variation in a population (Storz 1999; Ross 2001). In general, relatedness among the philopatric sex is expected to be higher than among the dispersing sex (Clutton-Brock 1989; Vigilant et al. 2001; *but see* Lukas et al. 2005). Hence, if dispersal is sex-biased, this should result in differing degrees of genetic relatedness among males and females (Fredsted et al. 2005). As investigation of genetic population structure has been suggested to provide insight into behavioral tendencies (e.g., social structure, social organization, and dispersal) which may not be evident from observations alone (Fredsted et al. 2005), it is especially important to understand these patterns of relatedness, as they may ultimately help to explain the behavioral repertoire of the species.

Among both mammalian and avian taxa, male-biased dispersal is most common, with females being the philopatric sex (Greenwood 1980; Dobson 1982; Lambin et al. 2001; Perrin & Goudet 2001). This is also the case amongst many mammals exhibiting fission-fusion social dynamics (e.g., red deer: Albon et al. 1992; elephants: Archie et al. 2006). Among primate fission-fusion societies, however, patterns of dispersal are less clear. Among most fission-fusion primates, males are philopatric (Gerloff et al. 1999; Lawson Handley and Perrin 2007; Symington 1990); however, in some cases, both sexes disperse (e.g., Di Fiore et al. 2009). Because long-term demographic and molecular data are currently unavailable for ruffed lemurs, there is only weak behavioral evidence of female-philopatry and male-biased dispersal (Morland 1991). Thus, the second aim of this dissertation is to characterize the genetic population structure and dispersal patterns within this same ruffed lemur community.

Specifically, Chapter 3 examines the genetic structure of a ruffed lemur community, including descriptive characteristics (e.g., allele frequencies, observed and expected heterozygosities, etc.) and average measures of relatedness (*R*) both within and between sexes.

Chapter Three will test the following hypotheses:

Hypothesis 1: Individuals within a community are related.

- Prediction 1.1: Average pairwise relatedness (*R*) within a community (within-community dyads) is greater than between members from different communities (between-community dyads).

Hypothesis 2: Females within ruffed lemur communities are philopatric (i.e., males disperse), as per Morland (1991).

- Prediction 2.1: Average pairwise relatedness among adult females is greater than among adult males within a community.
- Prediction 2.2: Adult females have more adult same-sex kin than adult males within a community.

Hypothesis 3: Males within ruffed lemur communities are philopatric (i.e., females disperse), as consistent with other primate fission-fusion societies.

- Prediction 3.1: Average pairwise relatedness among adult males is greater than among adult females within a community.
- Prediction 3.2: Adult males have more adult same-sex kin than adult females within a community.

Research objective 3: Patterns of communal infant care

The third and final aim of this dissertation is to characterize patterns of ruffed lemur communal infant care within the social community using characterizations from Chapters Two and Three. In this chapter, I address how patterns of space use, genetic relatedness, and affiliation influence ruffed lemur communal infant care. In this chapter, I also investigate the benefits of ruffed lemur communal care to both mothers and their infants.

Specifically, Chapter Four addresses the following hypotheses:

Hypothesis 1: Communal infant care confers energetic benefits to participants within a ruffed lemur community.

- Prediction 1.1: Communal nesting allows mothers to spend more time away from the nest.
- Prediction 1.2: Communal nesting allows mothers to increase the time they spend feeding/foraging.

Hypothesis 2: Communal infant care confers fitness benefits to participants within a ruffed lemur community

- Prediction 2.1: Communal nesting increases infant survival.

Finally, Chapter 5 synthesizes these data and provides directions for future work.

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Chapter 2

Spatial ecology of black-and-white ruffed lemurs (*Varecia variegata*)

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ABSTRACT

Like chimpanzees and spider monkeys, ruffed lemurs (*Varecia* sp.) live in a flexible fission–fusion social system in which members of a social group are temporally and spatially dispersed throughout a communal range. Extensive work has demonstrated that the 'classic' examples of primate fission-fusion societies typically exhibit patterns of range use that are sex-segregated, with taxa exhibiting either 'male-bonded' or 'bisexually bonded' patterns of range use and association. As ruffed lemurs are also noted to exhibit a high degree of behavioral flexibility in both social organization and home range use, it is possible that at least some populations may also adhere to similar predictions. Here, we characterize the range use of one population of black-and-white ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar, an undisturbed primary rainforest habitat, and evaluate the extent to which this population conforms to previously reported patterns for this taxon, as well as to patterns observed in other classic primate fission-fusion societies. Data were collected on 28 sub-adult and adult individuals during a consecutive 12-month period resulting in over 20,000 location coordinates. Results indicate that, as with previous studies, females used significantly larger annual home ranges than did males (MCP: U = 10, $p = 0.04$; kernel: U = 9, $p = 0.03$). Despite overall differences in home range area, males and females did not differ in their patterns of home range overlap. Overall, range use did not vary across seasons; however, daily distance traveled was best predicted by reproductive state. While the patterns of range use and spatial association presented here share similarities with both 'male-bonded' and 'bisexually bonded' models of primate fission-fusion dynamics, we suggest that ruffed lemurs represent a new system of primate fission-fusion social organization relative to those that are currently recognized, and combines aspects of bisexually-bonded and female-bonded models of fission-fusion dynamics.

INTRODUCTION

Black-and-white ruffed lemurs (*Varecia variegata*) are large bodied, highly frugivorous lemurids characterized by a fission-fusion social organization (Morland 1991a,b; Rigamonti 1993; Vasey 1997, 2006). While the dispersed nature of ruffed lemur communities resembles chimpanzees and spider monkeys in that groups are characterized by low levels of temporal and spatial cohesion (Aureli et al. 2008), how their patterns of individual or sex-specific association and range use fit in to the broader context of primate fission-fusion systems (Wrangham 1979a; Lehmann & Boesch 2005) remains unclear.

Fission-fusion social dynamics, a term describing the temporary splitting and reformation of groups (Kummer 1971), is typical of some primates (Campbell et al. 2007) and other mammalian species (e.g., hyenas: Holekamp et al. 1997, 2000; toothed whales: Whitehead & Chistal 2001; dolphins: Wursig 1978; Pearson 2011; bats: Kerth & Koenig 1999; elephants: Douglas-Hamilton 1972; Archie et al. 2006), and is most commonly thought to have evolved to minimize competition over patchily distributed resources (Wrangham 1977; Klein & Klein 1977; Symington 1988b; Chapman 1990a,b; Chapman et al. 1995; Wrangham 2000). Individuals vary their patterns of association in accordance with seasonal variation in fruit abundance, as well as other ecological, social, and/or reproductive constraints (e.g., Wrangham 2000) by fissioning into temporary subunits ('subgroups' or 'parties') that range independently from other group members within the larger communal range (Aureli et al. 2008).

According to socioecological theory (Wrangham 1979b, 1980; van Schaik 1989; Sterck et al. 1997), patterns of territoriality and range use are expected to differ between the sexes. That is, male ranging patterns should depend on the costs and benefits of searching for mates, defending sexually receptive females and/or defending a preferred, resource rich territory against competitors (Emlen & Oring 1977; Clutton-Brock 1989), while female patterns should depend on food quality and quantity (Trivers 1972; Wrangham 1979a; Osterfeld 1985), as well as the presence of dependent offspring and/or reproductive state (Wrangham & Smuts 1980; Goodall 1986; Chapman 1990a; Wrangham 2000). Furthermore, if one evokes advantages arising from kin selection (Hamilton 1964), then stronger social bonds should be expected to occur primarily between members of the philopatric sex (Greenwood 1980; Waser 1988) because philopatric individuals are likely to be more closely related than those who disperse (Morin et al. 1994; Goudet et al. 2002; Di Fiore 2003a, 2009; Hammond et al. 2006) and because 'staying' individuals are more likely to gain long-term benefits from cooperation (Clutton-Brock 2002). Because fission-fusion communities are commonly characterized by male-philopatry and female-biased dispersal (e.g., Nishida & Kawanaka 1972; Pusey 1979; Goodall 1986; Symington 1990; Strier 1994), and thus males are expected to be more closely related than females (Wrangham & Smuts 1980; Morin et al. 1994; Di Fiore 2003a, 2009; Di Fiore & Campbell 2007; Symington 1990; *but see* Vigilant et al. 2001, Di Fiore et al. 2009), we might then predict males to be more social and show stronger patterns of association than their female conspecifics.

In support of these predictions, males in fission-fusion societies are typically more gregarious and spend more time in both same- and mixed-sex associations than females, who are more commonly found alone with their offspring or in association with other females rather than males (Nishida 1968;

Wrangham and Smuts 1980; Goodall 1986; Chapman 1990a; Symington 1990; Wrangham et al. 1992; Chapman et al. 1995; Wrangham 2000; Williams et al. 2002; Shimooka 2003). This variation in association is reflected in differences in individual ranging patterns and day ranges within the larger communal home range (Wrangham & Smuts 1980; Stumpf 2007). Most studies have found that males utilize significantly larger home ranges and have longer day ranges than females (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986; Wrangham et al. 1992; Nunes 1995; Shimooka 2005; Symington 1988a); exhibit extensive range use and are frequently found in peripheral zones of their range (Chapman 1990a; Chapman & Wrangham 1993; Mitani & Watts 2005; Shimooka 2005; Wallace 2008); and share large, overlapping home ranges with other males and most, if not all females within their community (Wrangham 1979a; Nunes 1995; Shimooka 2005; Symington 1988a). Females, on the other hand, occupy small, overlapping 'core areas' that shift according to the distribution of valuable food resources (Wrangham 1979a; Symington 1988b; Nunes 1995). Unlike males, females do not utilize the entire communal territory, and instead concentrate their ranging well-within the male-defended boundaries of their communal range (Nishida et al. 1985; Chapman 1990a; Boesch and Boesch-Achermann 2000; Shimooka 2005; Wallace 2008).

Patterns of sex-segregated association and range use shift, however, when food resources become more widely available, population sizes decrease, and predation and/or anthropogenic pressures are high. For example, in some populations of chimpanzees (e.g., Bossou and Taï) and spider monkeys (e.g., Yasuni), males and females tend to spend more time in mixed-sex parties, are equally affiliative, and sexes do not differ in their patterns of range use and overlap (Sugiyama 1988; Boesch 1991, 1996; Sakura 1994; Lehman & Boesch 2005, 2008; Spehar et al. 2010). Consequently, this flexibility in sociality and ranging behavior has led scholars to develop models of primate fission-fusion dynamics, including 'male-only', 'male-bonded', and 'bisexually bonded' systems (see Wrangham 1979a; Lehmann & Boesch 2005; Figure 2.1). While both chimpanzees and spider monkeys have been studied extensively in light of these models, the system of ruffed lemur fission-fusion has yet to be contextualized within this larger primate fission-fusion framework.

The ranging patterns of most ruffed lemur populations studied to-date seem to contradict both the 'male-bonded' and 'bisexually bonded' models of fission-fusion. Based on the few studies of wild populations, females appear to range widely, while males remain in smaller 'core areas' within the female-defended territory (Morland 1991a,b; Rigamonti 1993; Vasey 1997, 2006). Males are said to be less social, range primarily in same-sex parties, and are submissive to females (Vasey 1997, 2006; but see Overdorff et al. 2005). However, like chimpanzees and spider monkeys, ruffed lemurs are noted for their extreme social flexibility (Vasey 2003, Table 2.1) and could potentially exhibit variation in ranging and association patterns similar to those exhibited by other fission-fusion primate taxa. For example, northern populations of both black-and-white (*V. variegata*: Morland 1991a,b) and red ruffed lemurs (*V. rubra*: Rigamonti 1993; Vasey 1997, 2006) have been characterized by fission-fusion dynamics, while ruffed lemurs in southern populations depart from fission-fusion patterns altogether and are instead said to live in cohesive multi-male multi-female groups (Balko 1998, Ratsimbazafy 2002) or pairs (White 1991, Britt 1997). In some cases, these patterns are likely a result of limited sampling duration or suboptimal sampling methods. In at least one example, however, patterns were presumably due to a lower overall population density and a community-wide shift away from dispersed fission-fusion in response to cyclone damage, reduced plant productivity and intense hunting pressure (Ratsimbazafy 2002). This suggests that, like chimpanzees and spider monkeys, ruffed lemurs likely vary their ranging patterns in response to different ecological, demographic, and social conditions.

If ruffed lemurs in this study adhere to the 'male-bonded' model, as is characteristic of most primate fission-fusion populations, then male and female range use should differ: males should occupy large, extensively overlapping home ranges, whereas females should occupy smaller, exclusive or near exclusive ranges. Alternatively, if ruffed lemurs adhere more closely to a 'bisexually bonded' system, as is common of the Western chimpanzee populations and some spider monkeys, male and female range use should not differ: home range size and overlap amongst individuals should be similar. Finally, despite receiving little empirical support from primate studies, if ruffed lemurs adhere to the ‘male-only’ model, then male and female range use should again differ, but differently from the ‘male-bonded’ system: males should occupy large, extensively overlapping home ranges, and females should occupy smaller, exclusive or near exclusive ranges that are independent of males (i.e., males are the only sex that comprise a community; female ranges are independent of male communities, and are equally and independently dispersed across space; Wrangham 1979a). If ruffed lemurs do not adhere to any of these three models, then it is possible that they represent a new model of primate fission-fusion dynamics, with patterns resembling ‘male-bonded’ systems, only biased towards females (i.e., ‘female-bonded’ systems of fission-fusion, as has been implied by previous work (Vasey 2006)), or perhaps a pattern that has yet to be described.

Additionally, because fission-fusion is most likely in response to patterns of fruit availability and reproductive state, we anticipate that individuals will vary their home ranges in accordance with climatic changes in temperature and rainfall, seasons that often closely correlate with phenological patterns of fruit abundance and scarcity in Madagascar (Meyers & Wright 1993; Overdorff 1993a,b; Hemingway 1996, 1998; Balko 1998; Baden unpublished data), as well as across reproductive seasons, a consideration that may be particularly salient given ruffed lemurs' unique reproductive traits (e.g., litter bearing: Foerg 1982; Rasmussen 1985; nest use: Pereira et al. 1987; Morland 1993; Vasey 2007; communal infant care: Vasey 2007).

Given the uncertainty surrounding ruffed lemur fission-fusion dynamics and range use, the goal of this study was to examine the overall community size and overlap of black-and-white ruffed lemurs (*Varecia variegata*), as well as range use patterns by males and females in an undisturbed rainforest habitat community. Specifically, we will use intersexual differences in range use and overlap to evaluate 1) how ruffed lemur fission-fusion compares to the 'male only', 'male-bonded' and 'bisexually bonded' patterns observed in chimpanzees and spider monkeys, and 2) to what extent sex-biased patterns of ruffed lemur range use are influenced by climatic and reproductive seasonality. Thus, the results of this study will also add to a broader understanding of the socioecological rules governing fission-fusion dynamics in primates and whether or not adjustments to current models are needed moving forward.

METHODS

Study Site

Research was conducted at Mangevo (21°22'60"S, 47°28'0"E), a low-to-mid altitude (660-1,200m) rainforest site located within the southeastern parcel of Ranomafana National Park (RNP), Madagascar (Figure 2.2). RNP contains 435 km^2 of continuous montane rainforest located in the southeastern escarpment of Madagascar’s central high plateau (see Wright 1992 for site description).

Climatic and reproductive seasons

RNP experiences highly variable climatic conditions, such that annual rainfall, phenology and the presence and duration of wet versus dry seasons vary considerably inter-annually (Wright et al. 2005). During this study period, RNP experienced three seasons that were categorized based on natural breaks in temperature and rainfall data: a “warm-wet” (Jan-Feb’08, Nov-Dec’08), a “cool-wet” (May-Jul’08) and a “cool-dry” (Aug-Sept’08) season, with two transitional periods (transitional wet: Mar-Apr’08; transitional dry: Oct’08) (Figure 2.3). Average monthly rainfall during the warm-wet season was 618.8 ± SD 18.0 mm (range 0-89 mm/day; excluding the day prior to and of Cyclone Ivan totaling 972.6 mm rainfall) and its average minimum and maximum daily temperatures were 10 ± SD 4.1 and 38 ± SD 2.2°C, respectively. Average monthly rainfall during the cool-wet season was 258.4 ± SD 11.7 mm (range 0-48 mm/day) and its average minimum and maximum daily temperatures were 7 ± 2.0 SD and 25 ± SD 2.6°C, respectively. Average daily rainfall during the cool-dry season was 148.1 ± SD 10.3 mm (range 0-49 mm/day) and its average minimum and maximum daily temperatures were 7 ± 1.7 SD and 25 ± SD 2.5°C, respectively.

Monthly phenology was scored on the top 25 *Varecia* food resources (Balko 1998). The availability of each phytophase (i.e., flower buds, flowers, unripe and ripe fruits, leaf buds, new leaves and mature leaves) was estimated on a log scale for 1 m^3 of the crown (Janson & Chapman 1999), and overall availability extrapolated from crown volume estimates. Availability scores were significantly positively correlated with 'climatic season' described above (Baden, unpublished data). Thus, 'climatic season' is broadly used as a proxy for fluctuations in both temperature/rainfall and resource availability.

Reproductive seasons during the study were highly synchronized. Females were non-receptive January to late June ('non-reproductive season'). Mating took place over two days during the first week of July, and thus July through early-October was considered the 'gestation season'. All births were documented on the day of parturition (8 to 20 October), and thus to standardize reproductive seasons across sexes and individuals, the mid-point date of birth was used as the onset of the 'lactation season,' which spanned 14 October through December (when the study ended).

Study Subjects

We focused data collection on two neighboring communities of black-and-white ruffed lemurs (*Varecia variegata*) (n = 41 individuals). Detailed age and sex categories of study subjects are described in Chapter Three. Subjects were habituated to human observers and were individually-identified by radio-collars and colored collar-tag combinations. Collaring occurred under veterinary supervision and followed a strict protocol outlined by Glander (1993).

Data Collection

Ranging data were collected during a continuous 12-month period between January and December 2008. Data were collected during dawn-to-dusk follows on all adult and sub-adult subjects. Observational bouts ranged in duration between 8 to 11 hours depending on seasonal differences in day length and time needed to locate animals at dawn. During focal follows, location was recorded at 10-minute intervals using a handheld Garmin® HCx GPS unit. Ranging coordinates were collected only if estimated positional error was < 10m. Subgroup size (no. individuals within 25 meters), composition (identity and sex of subgroup members) and spread (i.e., greatest distance between two group members) was noted for each location coordinate collected. This allowed us to supplement our dataset for focal individuals by including location data for all non-focal members of a subgroup for any given location point.

Individuals were considered members of a subgroup if they were within sight of the focal individual (generally within 25 m) for two or more consecutive group scans and were observed associating, traveling with and maintaining proximity to the focal individual. Individuals were considered to have left the group after their absence was noted for two consecutive scans. Research was conducted with permission from and in compliance with the laws and guidelines of ANGAP (Madagascar National Parks) and Stony Brook University Animal Care and Use Committee.

Data Analysis

We calculated the communal home ranges using all location points from all focal individuals. Individual annual home ranges were calculated using location points collected while an individual was a focal, as well as location points taken when the individual was a member of the subgroup being followed. All individuals with fewer than 25 sampling days were omitted from analysis of individual annual home ranges. We also calculated individual seasonal home ranges across climatic and reproductive seasons (Table 2.2). In these cases, individuals with fewer than 10 sampling days per season were omitted from analyses. Because sub-sampling data can reduce the accuracy and precision of home range estimates (Hansteen et al. 1997; Blundell *et al.* 2001; De Solla *et al.* 1999; Fortin and Dale 2005; Fieberg 2007), all data points were used in analyses.

We estimated home range size using two methods: minimum convex polygon (MCP) and fixed kernel density estimates (KDE). MCP is the most commonly used estimate of home range size (Powell 2000). Using MCP, "home range" is defined as "the space which the animal both uses and traverses" (Burt

1943). However, the method suffers from sample size effects and is greatly affected by outliers, such that MCP estimates often contain large areas never used by an animal (Powell 2000; Laver & Kelly 2008). To help mitigate outlier effects, we calculated 95% MCPs, a method employed to control for rare, but observed excursions outside of the communal range. However, because MCP area estimates have been shown to greatly exaggerate home range size, home range areas calculated using this method were not included in statistical analyses as per Laver & Kelly (2008) and Powell (2000), and have been included here solely for the purpose of comparison with previous studies (see Table 2.1). Kernel density estimates (KDE), on the other hand, are widely regarded the most robust probabilistic estimator for making an inference on both home range size and patterns of use within the home range (utilization distribution; Worton 1989) (Powell 2000) and for this reason, will be used in statistical comparisons to assess differences in range use between sexes and across seasons.

Home range analyses were performed with home-range tools (HRT; Rodgers *et al.* 2007) for ArcGIS (ESRI, Redlands, CA). Kernel home ranges were calculated using a bivariate normal distribution, rescaling X-Y coordinates to unit variances as recommended by Silverman (1986). Raster cell size was set to 10 x 10 m to reflect the spatial resolution of our data. Kernel home range estimators are well known to be sensitive to the choice of smoothing parameter (Silverman 1986); this is especially true with large datasets and when animals exhibit strong site fidelity (Hemson et al. 2005). Given our large dataset and observations that animals regularly transverse the same areas, we used the root-n smoothing estimate, as it has been found to overcome these issues and performs well with simulated and empirical data (Steury *et al.* 2010). Home range size was evaluated using 95% MCP, where the unused area was determined by the fixed mean method (HRT manual), and 95% kernel isopleths. Incremental area analysis was used to determine whether range areas reached asymptotes and were thus reliable estimates of home range size.

MCP overlap was calculated as the proportion of shared area between two polygons. MCP overlap was calculated for communal range and individual annual home range overlap only. Kernel overlap was calculated using a utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) implemented in the R package adehabitat (Calenge 2006). The UDOI makes use of the product of two utilization distributions being compared and is recommended for quantifying space-use sharing. A UDOI of 0 indicates no home range overlap, while a UDOI of 1 indicates home ranges are uniformly distributed and overlap is 100%. UDOIs were calculated for communal range, individual annual home range, and seasonal variations in male and female home range areas.

For statistical comparison, individual annual home range areas were pooled by sex and both climatic and reproductive seasons, while UDOIs were calculated for all within- and between-sex dyads (female-female, male-male, and female-male) and then pooled by climatic and reproductive seasons. Data were analyzed using nonparametric statistics implemented in SPSS 19.0 (SPSS 2010) and α was set at $p \leq 0.05$.

Finally, to gain a finer-scale understanding of daily range use, we calculated daily path lengths (DPL) for each individual as the sum of the Euclidean distances between consecutive GPS coordinates taken every 10 minutes. We included only full-day follows of focal individuals for which locations were recorded completely between morning and evening sleep trees, or data collection started prior to 0700 h with ≥ 9 subsequent hours of observation and less than 5% missing observations.

Daily path lengths were analyzed using a generalized linear mixed-effects model in the R package lme4 (R Development Core Team 2010) to evaluate multiple fixed effects on the response variable, DPL. Fixed effects included daylight length (DayLength), mean daily rainfall (Rain), a categorical classification of climatic season (ClimateSeason: warm-wet, cool-wet, cool-dry), a categorical classification of reproductive state (ReproductiveSeason: non-breeding, gestation, lactation), sex (Sex) and the presence and number of infants (Infants). To explicitly account for individual variation in DPL, we assigned individuals (“Focal”) as a random effect. Using additive and interactive effects of our variables of interest, we *a prior* constructed biologically-driven models; I evaluated model parsimony using Akaike’s Information Criterion with a small sample size bias correction (AICc). To incorporate model selection uncertainty, we model-averaged all parameter estimates (Anderson and Burnham 2002).

RESULTS

Communal home range area and overlap

Both MCP and Kernel analyses identified two spatially distinct communities, the focal community (COM1) and a second neighboring community (COM2) (Figure 2.4). The COM1 communal home range encompassed the ranges of 22 individuals (9 males, 13 females), and was estimated to cover between 87.8 ha (KDE) and 120.4 ha (MCP). The second community, COM2, was identified from the ranges of six individuals (4 females, 2 males), though total community size remains unknown. While Community 2 was only partially sampled, communal range size was estimated at between 54.2 ha (KDE) and 90.5 ha (MCP) (Figure 2.4). Results indicate that COM1 and COM2 shared little overlap in utilization distributions (Kernel UDOI: 0.2% overlap), however MCP overlap (27.1%) supports behavioral observations that excursions in to neighboring communities did occur.

Figure 2.5 illustrates that ranging observations were sufficient to accurately describe the size of both the COM1 and COM2 ranges. However, no individual from COM2 met *a priori* standards of $\geq$ 25 sampling days during the study. Thus, further analyses of individual range use and seasonal variation were carried out for individuals from COM1 only.

Individual home range area and overlap

Females used significantly larger annual home ranges than did males, regardless of analytical method (MCP: Mann Whitney-U = 10, p = 0.04; Kernel: Mann Whitney-U = 9, p = 0.03; Table 2.3). Mean female home ranges were between 16.9 ha ± 1.74 S.E. (KDE) and 26.3 ha ± 4.50 S.E. (MCP), whereas male home ranges were estimated between 13.04 ha ± 0.98 S.E. (KDE) and 17.5 ha ± 1.22 S.E. (MCP). Females did not use their entire communal home range, as has been reported elsewhere (Vasey 1997, 2006). Instead, females concentrated their ranging to smaller proportions of the larger communal range (MCP: mean proportion of communal range used = 21.8%, n = 5, range = 11.3 – 32.2%; KDE: mean = 19.2%, n = 5, range = 13.1 – 23.5%; Figure 2.6). Conversely, males used larger proportions of their communal range than previously reported, and did not use exclusive, non-overlapping ‘‘core areas,’’ as per Vasey (2006) (MCP: mean proportion of communal range used = 11.5%, n = 7, range = 10.0 – 14.1%; KDE: mean = 15.7%, n = 7, range = 13.7 – 19.4%; Figure 2.6).

Despite differences in home range size and use, males and females did not differ significantly in their degree of home range overlap (MCP: Kruskal-Wallis H = 0.969, p = 0.62; Kernel: Kruskal-Wallis H = 0.703, p = 0.70; Table 2.3).

Rather, same-sex and mixed-sex dyads exhibited similar areas of annual home range overlap. In all groups of dyads, mean MCP overlap was moderate (35-41% overlap; Table 2.3, Figure 2.6); however, kernel home range overlap across groups was comparatively low to moderate (16-29%, Table 2.3, Figure 2.6).

Spatiotemporal variation in range use

Climatic variation

Table 2.4 and Figure 2.7 describe the variation in spatial community structure for females and males across climatic seasons. Overall, climatic variation in home rang size trended toward significance (Kruskal-Wallis H = 4.67, df = 2, $p = 0.10$). However, within sexes, female home range size did not vary by climatic season (Kruskal-Wallis H = 3.60, df = 2, $p = 0.17$). Males, on the other hand, exhibited significant variation in home range area (Kruskal-Wallis H = 6.00, df = 2, $p = 0.05$), using smaller home ranges during the cool-wet versus cool-dry season (Wilcoxon Signed Ranks test: Z = 0.00, $p = 0.04$). Male ranges during the cool-wet season were also smaller than during the warm-wet season, though this difference only approached significance (Wilcoxon Signed Ranks test: Z = 10.0, $p = 0.07$). Further, male and female home range size differed in two of three climatic seasons: males used significantly smaller home ranges than females during the cool-wet and warm-wet seasons (cool-wet: females = 14.59 ha, males = 6.42 ha, U = 3, $p = 0.02$; warm-wet: females = 16.38 ha, males = 9.64 ha, U = 4,

p = 0.02; Table 2.4). Home range areas were similar in size only during the cool-dry season, when individuals of both sexes remained within relatively small home range areas. Sexes did not differ in home range overlap according to climatic seasons (Kruskal-Wallis H = 3.27, df = 2, p = 0.20).

Reproductive variation

Table 2.5 and Figure 2.7 describe the variation in spatial community structure for females and males across reproductive seasons. Overall, sexes did not differ significantly in home range size (Kruskal-Wallis H = 0.250, df = 2, p = 0.882) or overlap (Kruskal-Wallis H = 3.128, df = 2, p = 0.209) across reproductive seasons, nor did home range size or overlap vary within sexes (males: Kruskal-Wallis H = 0.667, df = 2, p = 0.717; females: Kruskal-Wallis H = 0.400, df = 2, p = 0.819), even after controlling for the presence/absence of infants.

Mean daily path length

While home range area varied significantly across climatic seasons, it did not significantly predict daily path length (DPL). Rather, we found strong support that DPL was positively related to day light length ($\hat{\beta}$ = 0.654, SE=0.111) and varied with reproductive season (Table 2.6; Model Weight = 88.1 %); the only two models with any support included both of these variables (Table 2.6). We also found strong support for a sex difference by reproductive season and day light length; the model including the sex variable had 7 times (0.881/0.119) the support than the model without it. We found males to generally move more per day than females ($\hat{\beta}$ = 11.49, SE=3.79; males = 1, females = 0), with the strongest difference occurring in the birth/infant dependence season (Table 2.7). Standardizing to 12 hours of day light, female DPL in the birth/infant dependence season was estimated at 840.6 ± SE 106.2 m, while male DPL was 1824.6 ± SE 196.7 m. During the mating/gestation season, female DPL was estimated at 1736.1 ± 99.48 m, while male DPL was 1917.0 ± 296.8 m. Lastly, we found during the non-breeding season, female DPL was estimated at 1761 ± SE 57.6 m, while male DPL was 1948.6 ± SE 122.0 m.

DISCUSSION

Range use within a ruffed lemur community

Overall, results from this study reveal broad patterns of communal and individual home range area and overlap which confirm the presence of a fission-fusion social organization, as in previous studies of other wild ruffed lemur populations (Morland 1991a,b; Rigamonti 1993; Vasey 1997, 2006). We found that multiple males and females used ranges which together comprised a large, communal territory that was more-or-less spatially distinct from other neighboring communities. Within the community, males and females differed significantly in annual home range size, with males having home ranges that were, on average, 20 percent smaller than females. Despite overall differences in home range area, males and females did not differ in their patterns of spatial association. Contrary to previous studies, neither sex ranged widely throughout their communal territory; rather, home ranges were distributed evenly throughout the communal range, and both males and females exhibited moderate levels of annual home range overlap.

Seasonal variation in range size, overlap and daily distances traveled

Home range area & overlap

Surprisingly, neither climatic nor reproductive seasons influenced overall variation in home range size. Between sexes, we detected significant variation across climatic but not reproductive seasons. Despite variation, female ranges did not differ significantly throughout the year. Thus, sex differences in range use were driven by males, whose ranges varied significantly across climatic seasons. While unexpected, we believe that a number of variables can explain the observed patterns.

First, we ascribe the lack of significant seasonal differences in female home range area to small sample sizes and the unusually high variation observed among the females in our sample. While three females exhibited the predicted patterns of home range variation (i.e., large ranges during warm-wet periods of resource abundance, small ranges during cool-dry periods of resource scarcity, as per Vasey (1997, 2006)), two females used considerably smaller, less variable home ranges than expected. Thus, although the patterns observed were not significant, we believe that by increasing sample size and study duration, females will likely also exhibit significant variation in range size across climatic seasons, much like their male counterparts.

Additionally, while we ascribed climatic seasons according to natural ‘breaks’ in the data, our ‘climate’ assignments may not have been the appropriate scale by which to measure spatial variation. While we found a significant relationship between resource availability and climatic season, it may be more appropriate to look at the actual density and distribution of food resources throughout the community, a method that was beyond the scope of this project. In other primate fission-fusion systems, the density and distribution of food resources, among other variables (e.g., predation pressure, population density) impact whether animals associate in ‘male-bonded’ or ‘bisexually bonded’ communities (e.g., Lehmann & Boesch 2005). Thus, given that female range use patterns did not vary according to climatic seasonality in this study, it is possible that resources were evenly and/or abundantly distributed throughout the communal range, and that female ranges each encompassed high quality resources. Alternatively, it could be that females adopted an ‘energy minimizing strategy’ by traveling less, reducing or maintaining home range size, and feeding on lower quality food resources until conditions improved, as has been observed in other lemurid taxa (see Tecot 2008 for review).

Why, then, did males but not females exhibit variation according to climatic seasons? While it is true that male range size varied significantly with climatic season, changes in home range area did not meet the predicted patterns. Contrary to predictions, rather than ranging most widely during the warm-wet period of fruit abundance (as seen by Vasey 2006), male ranges peaked during the cool-dry season, a period of low-to-moderate resource availability. Considering females did not also follow this pattern suggests that males may not be modifying spatial patterns according to fruit availability. In fact, males may be varying their range use according to the distribution of females, as per socioecological theory (Wrangham 1979b, 1980; van Schaik 1989; Sterck et al. 1997). Rather than varying their range use according to climatic fluctuations in food availability, we believe that males were in fact mapping their ranges on to the ranges of females (i.e., the limiting resource to males), particularly during the cool-dry season. This season largely overlaps with the period just prior to, during, and following mating, and would explain why males diverge from the expected patterns of range use during this resource-poor time. In further support of this hypothesis, we observed higher than average association among males and females during the cool-dry period (Baden, unpublished data). Thus, we believe that the observed variation in male home range size is actually a result of males expanding their otherwise small home ranges to map their range use on to those of female associates just prior to the brief mating period in early July.

While shifts in home range area corresponded to climatic seasonality in males, home range overlap did not follow this same pattern. Instead both same- and mixed-sex dyads exhibited moderate home range overlap throughout the year. Fission-fusion dynamics is commonly cited as a means of reducing competition over highly contestable resources (Wrangham 1977; Klein & Klein 1977; Symington 1988b; Chapman 1990a,b; Chapman et al. 1995; Wrangham 2000). It has been demonstrated that when resources are scare, group members (particularly females) fission into smaller subgroups or sub-parties to feed and forage alone, resulting in smaller core areas or home ranges during lean periods (e.g., Nunes 1995; Doran 1997). Thus, it is surprising that, while home range size varied predictably with climatic season in males, home range overlap did not. Similar patterns observed in chimpanzees and spider monkeys have been attributed to occurring in habitats with higher resource availability/higher quality resources (e.g., Lehmann & Boesch 2005), and thus, like patterns of home range area, may help to explain the variation in home range overlap observed here.

Why reproductive seasonality did not influence ranging patterns, particularly among females, is likely an issue of scale. Ruffed lemurs, as with other Malagasy primates, are characterized by strict seasonal breeding, and are generally only receptive for two to three days during the year (Foerg 1982;

Brockman et al. 1987; Baden, unpublished data). Moreover, ruffed lemurs are known for their unusual life histories (e.g., litter-bearing: Foerg 1982; Rasmussen 1985) and post-natal reproductive strategies, including nest construction, nest use, and communal infant care (Pereira et al. 1987; Morland 1993; Vasey 2007). Thus, one might expect patterns of home range area and overlap to correspond with patterns of female reproductive state. In particular, females should be constrained in their movement by litters of dependent offspring, thus having relatively smaller home range sizes during lactation and high infant dependence. Given their communal care strategies, we would have also expected female-female dyads to exhibit higher home range overlap during this time. Males, on the other hand, might not vary home range size, necessarily, though male-female overlap should increase significantly just prior to and during the brief reproductive season.

During our study, females did not modify their range use during the period of lactation and communal infant care, such that home range area and overlap remained consistent across reproductive seasons. While we observed an influx of males during the "courtship" (pre-receptive, nonbreeding) period (March-June), these changes in behavior were not reflected in our results. In fact, female-male kernel overlap was lowest during the non-breeding season relative to both gestation and lactation seasons. Unfortunately, we believe that our current temporal scale, which ranged from three to five months per season, was too large to accurately represent the shifting patterns of range use throughout these reproductive stages.

While home range size and overlap remained the same across reproductive seasons, it is possible that the number of individuals with whom they overlapped increased during the lactation season relative to non-reproductive periods, though this hypothesis currently remains untested. In future studies, we recommend considering a more continuous measure of home range variation that better maps on to short term fluctuations in reproductive state (but see Daily Path Length).

Finally, ruffed lemurs are ‘boom-or-bust’ breeders, in that they are said to only reproduce during years of resource abundance (Ratsimbazafy 2002). It may be that patterns of home range area and overlap differ during non-reproductive years, and that the moderate overlap in home ranges observed during this study are actually high relative to years when females do not reproduce. This may also help explain reports of monogamy in the taxon if studies were conducted during non-reproductive years when animals are less social, group members are less cohesive and individuals use smaller, less overlapping home ranges (Baden, unpublished data). Future studies will attempt to document ruffed lemur ranging behaviors across boom and bust years to allow us to test this hypothesis.

Daily path length

Travel patterns and range use are assumed to optimize an individual's energy intake while minimizing energy expenditure (Krebs 1978; Milton 1980; Barton et al. 1992). Often, animals are thought to do this by altering daily path length and home range area according to the availability, density, and distribution of food resources. Consequently, patterns of space use often adjust seasonally in response to changes in the relative resource abundance (Milton and May 1976; Milton 1980; Barton et al. 1992; Olupot et al. 1997; Di Fiore 2003b; Buzzard 2006). Although primates generally increase their daily path lengths when food resources become scarce (Fossey and Harcourt 1977; Goodall 1977; McKey and Waterman 1982; Barton et al. 1992; Bocian 1997; Doran and McNeilage 1998), some actually decrease their daily travel during lean periods (Standford 1991; Boinski 1987; Doran 1997; Bartlett 1999), variation which probably reflects differences in foraging strategies. Primates can adopt either an energy maximizing/accumulating strategy (i.e., moving farther and covering a larger seasonal range in search of high-quality foods under resource-scarce conditions) or an energy/time minimizing strategy (i.e., decreasing daily travel, covering smaller seasonal ranges and exploiting lower-quality foods until conditions improve) (Di Fiore 2003b; Tecot 2008). In this study, we were surprised to find that daily path length did not differ between or within sexes according to climatic seasonality in ruffed lemurs, perhaps suggesting an energy minimizing strategy during periods of resource scarcity. Rather, daily path length was best predicted by reproductive season, with males traveling longer distances overall, and particularly during the lactation/early infant dependence when females are constrained by litters of dependent offspring. Interestingly, similar patterns were also found in brown lemurs (*Eulemur fulvus rufus*) and red-bellied lemurs (*E. rubriventer*) (Overdorff 1993, 1996), where neither species varied DPL according to climatic season. Instead, changes in brown lemurs' diet and ranging were related to seasonal reproductive patterns (Overdorff 1993a), with individual DPL peaking during lactation through weaning, patterns which have also been shown in other primate taxa (e.g., *Papio anubis*: Rasmussen 1979, 1983). Thus, it is possible that while DPL in this study reflects a mother's need to stay at the net with altricial offspring, a females' dietary preferences may shift, diversifying their diets and feed more frequently (but at closer distances) throughout the day because of the energetic burden of nursing (Overdorff 1993a).

These results are contrary to those from red ruffed lemurs; while males showed relatively few seasonal differences in DPL, females showed marked variation across climatic seasons, traveling longer distances during the warm-wet season (high resource abundance) than any other (Vasey 1997, 2006). Further, males and females did not exhibit overall differences according to reproductive season, though sexes did show similar patterns within reproductive stages. Most notably, animals traveled the longest distances during the period of lactation and high infant dependence, and the shortest differences during gestation.

One final consideration regarding daily path length is that ruffed lemurs may be cathemeral, particularly during nights of high moon illumination (Morland 1991a; Wright 1999; Donati & Borgogini-Tarli 2008; Baden unpublished data). This study only measured daily path length based on diurnal samples. Seasonal patterns of night time activity and ranging must be further studied to provide a complete picture of how seasonality influences daily distance traveled in ruffed lemurs.

Inter-site variation in ruffed lemur ranging

Results from this study are mixed in regard to previous reports. Broad patterns of sex differences in home range size are largely consistent with previous studies. As in all cases where fission-fusion has been documented (Morland 1991a,b; Rigamonti 1993; Vasey 1997, 2006), females consistently used significantly larger home ranges than males. Vasey (2006) found that females used ranges that were twice the size of males. In our study, while sex-differences did exist, they were less pronounced, and only differed by approximately 20 percent. Furthermore, patterns of spatial association both within and among sexes contrast starkly with results which reported that sex differences in range use were due to seasonal fluctuations among females, rather than males (Vasey 1997, 2006). In these studies, males largely resided within small, exclusive core areas within a larger female-defended communal range. While it is true that males in our study used relatively smaller ranges than females, neither sex used exclusive ranges. In fact, both males and females shared equal levels of overlap. Thus, while finding similar overall patterns of range use, we report fine-grained details that deviate from previous studies, results which reinforce the behavioral flexibility evident for this taxon.

Based on the available data and preliminary comparisons with similar sites, we propose that ruffed lemurs, like chimpanzees and spider monkeys, exhibit variation in ranging and association patterns between sites owing to a variety of ecological, demographic, and/or anthropogenic factors. However, further research documenting the correlation between these variables and ranging and association patterns is necessary before these hypotheses can be strongly supported.

Models of primate fission-fusion & future directions

Taken together, the patterns of range use and overlap in ruffed lemurs reported here and elsewhere suggest that ruffed lemurs do not adhere to patterns described in other primate fission-fusion systems (as described by Wrangham 1979, Lehmann & Boesch 2005). Instead, ruffed lemurs appear to adhere to a new, previously unrecognized system of primate fission-fusion dynamics, whereby individuals exhibit a combination of ‘female-bonded’ and ‘bisexually bonded’ systems of range use: both males and females are more-or-less evenly distributed throughout a female-defended communal range, with group members exhibiting equal and moderate home range overlap with other community members.

While we have broadly addressed sex-differences in ranging, future studies should examine finer-grained patterns of range use by developing better, more continuous measures of both climatic and reproductive seasonal variation. Even more importantly, we suggest that an important next step is to examine sex-differences in the use of boundary areas. Already a number of studies have anecdotally described aggressive encounters between females observed in the peripheries of the communal range (Morland 1991a; Vasey 1997; Baden unpublished data). While these are typically described as communal defense, there has yet to be a study that systematically documents the intricacies of these interactions. Future studies should examine who uses boundary areas, who participates in boundary defense, and how males and females differ in their use of these peripheral zones.

Future studies should also include patterns of male and female social association, rather than simply spatial association, to better understand differences in patterns of affiliation, subgroup membership, and whether same- and mixed-sex associations occur in particular areas or during particular times of year.

Understanding these details will further help to elucidate how ruffed lemurs fit in to the framework of primate fission-fusion dynamics.

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Figure 2.1 Models of primate fission-fusion social organization, including predicted sex-differences in home range size and overlap (modified from Lehmann & Boesch 2005)

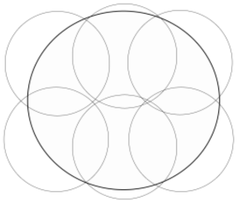
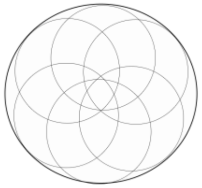
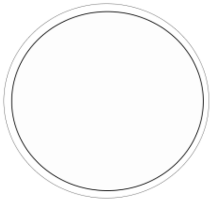
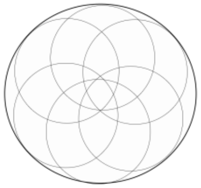
Social organization	male only	male bonded	bisexually bonded	female bonded
Description	females evenly and independently distributed throughout a male-defended communal range; some core area overlap	females occupy areas within a larger male-defended range; female core areas may or may not overlap	males and females are equally social and use the entire range together	males occupy areas within a larger female-defended range; male core areas may or may not overlap
Spatial model				
Predictions:				
Size	M > F	M > F	M = F	M < F
Overlap	MM overlap low FF overlap low FM overlap low	MM overlap high FF overlap low FM overlap moderate	MM HR overlap high FF HR overlap high FM HR overlap high	MM HR overlap low FF HR overlap high FM HR overlap moderate
References	Wrangham 1979a	Wrangham & Smuts 1980, Goodall 1986	Lehmann & Boesch 2005, 2008	Vasey 1997, 2006

Figure 2.2 Location of Mangevo research site within the larger Ranomafana National Park, Madagascar

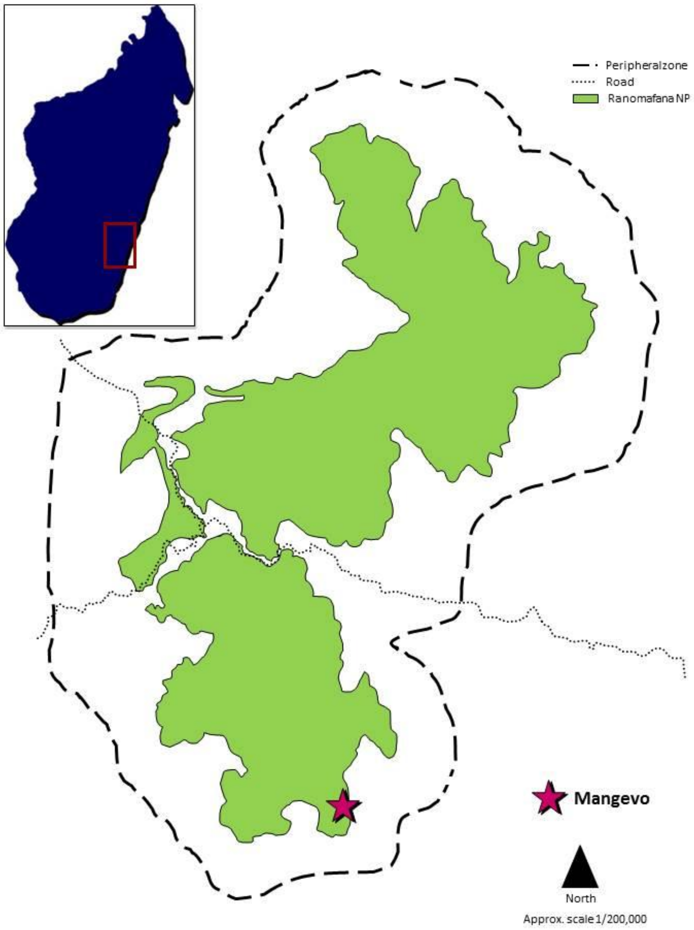


Figure 2.3 Rainfall and temperature (average minimum and maximum) patterns in Ranomafana National Park, during the study period (January – December 2008). Mean February rainfall calculated after excluding the day of and one day prior to and following Cyclone Ivan (February 17-19, 2008)

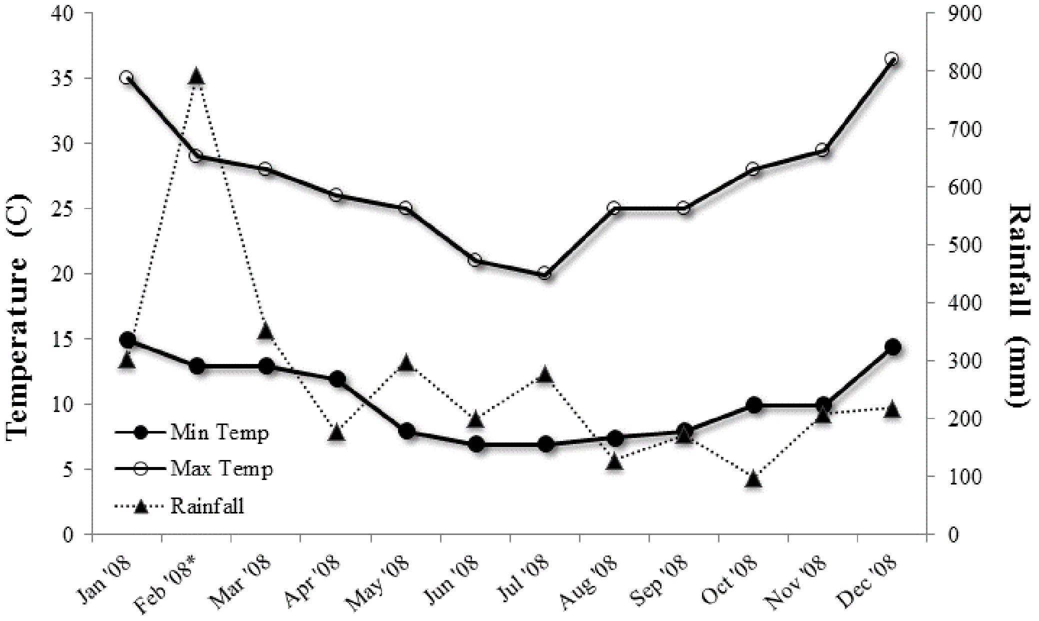


Figure 2.4 Communal home range area and overlap. a) Ranging coordinates collected between January and December 2008. Each point represents one location point taken at 10-minute intervals (n = 38,006 points). b) 95% Minimum Convex Polygons and 95% Fixed Kernel Density estimates of home range size and overlap. Purple = Community 1 (COM1), Pink = Community 2 (COM2)

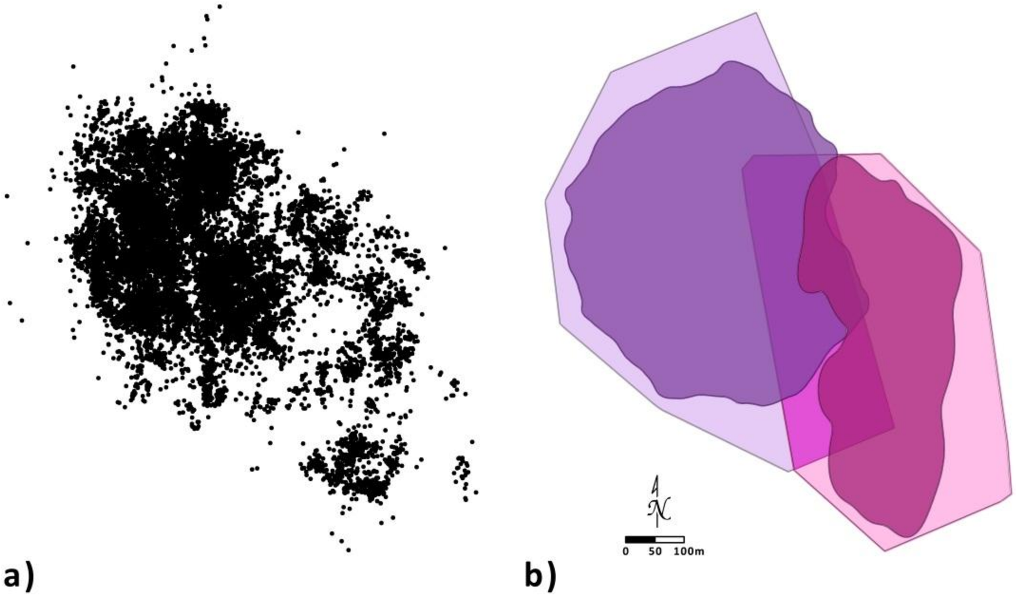


Figure 2.5 Cumulative communal home range area (ha) with increasing sampling effort. Samples from both a) Community 1 (COM1) and b) Community 2 (COM2) were sufficient to reliably estimate annual community home range size

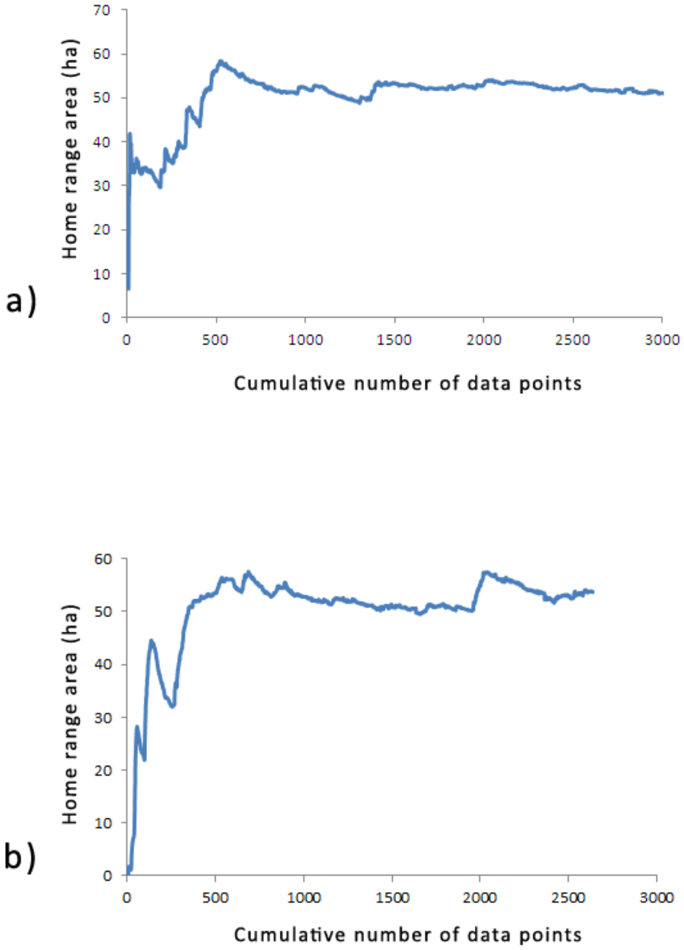


Figure 2.6 Individual annual home range area and overlap. Home range estimates using 95% minimum convex polygons a) and 95% kernel density estimates b) for females and males. Female utilize significantly larger annual home ranges than do male conspecifics (Mann-Whitney U = 9, *p* = 0.028). Both females and males within the communal range exhibit moderate annual home range overlap (MCP = 35-41%; Kernel = 16-29%). Analysis excludes individuals with fewer than 25 observation days

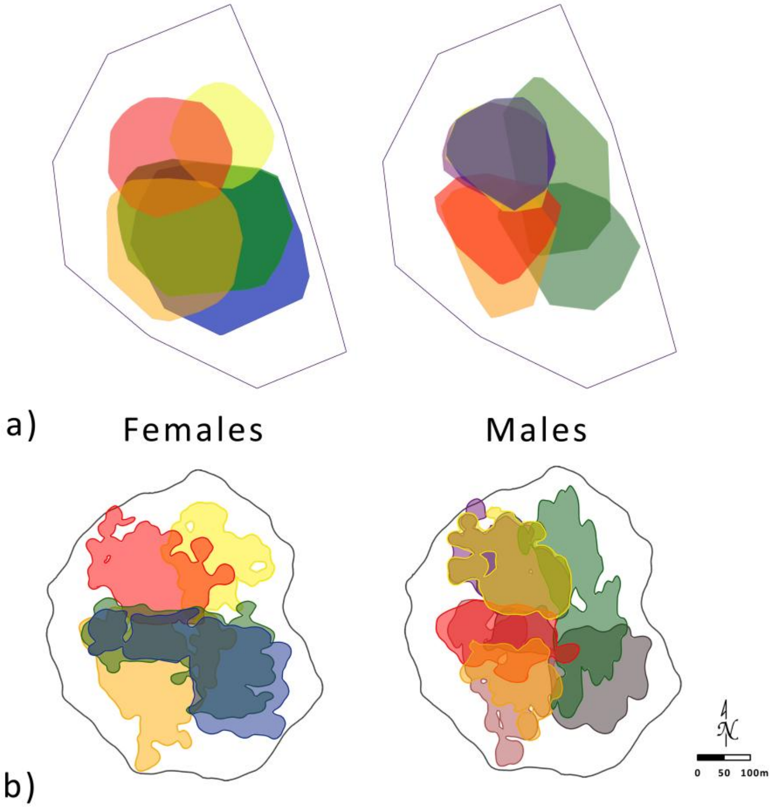
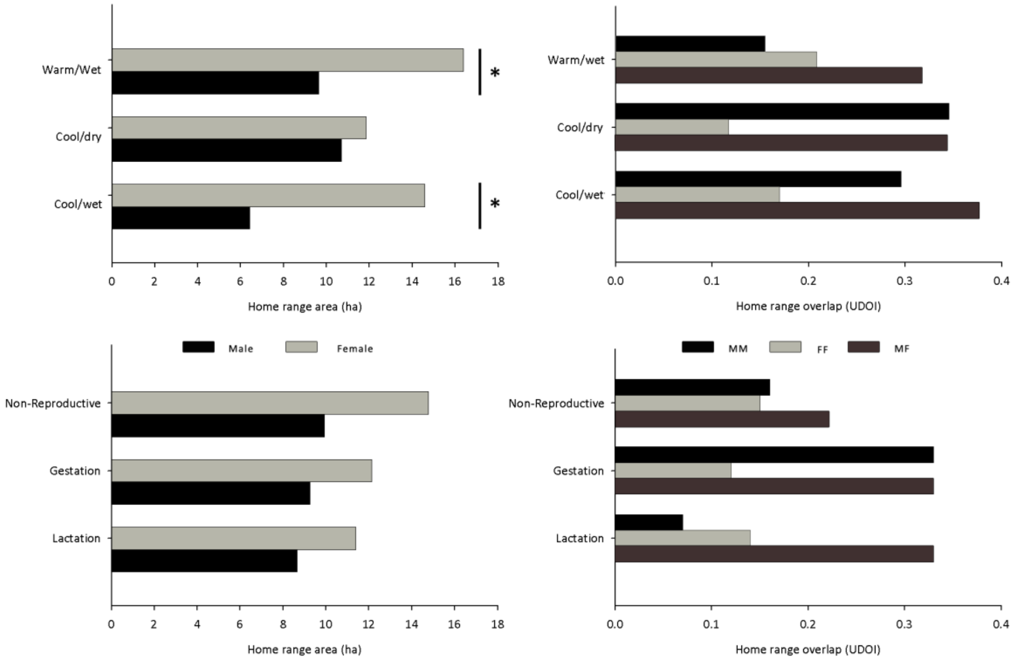


Figure 2.7 Seasonal variation in home range area and overlap. Home range area differs significantly between sexes during climatic seasons (cool-wet: U = 22.0, *p* = 0.014; warm-wet: U = 25.0, *p* = 0.038), but not reproductive seasons. Home range areas did not vary significantly by reproductive season within sexes. However, males exhibited significantly smaller home ranges during cool-wet versus cool-dry climatic seasons (see Table 2.4). Home range overlap did not vary significantly between sexes or seasons



a) Home range area (ha)

b) Home range overlap (UDOI)

Table 2.1 Summary of results from studies of *Varecia* spatial ecology

Species	**Study site**	**Data collection**	**Analysis method**	**Communal range (ha)**	**Female home range (ha)**	**Male home range (ha)**	**Ind. Range size**	**Sample size**	**Duration (months)**	**Focal hours**
Varecia rubra	Ambatonakolahy (Masoala)[1]	travel mapped during observations	Quadrats	23.3 - 25.8	unk.	unk.	-	8 (4 females, 4 males)	11	704
Varecia rubra	Andranobe (Masoala)[2]	travel mapped during observations	MCP	57.7	30.9	16.2	F > M	8 (5 females, 3 males)	12	672
Varecia variegata	Nosy Mangabe[3]	sleep and feed trees mapped during	MCP	8.5 - 30	unk.	unk.	-	14 (9 females, 5 males)	13	1,793
Varecia variegata	Manombo[4]	GPS coordinates (5-min)	MCP	30 - 70	unk.	unk.	F > M	5 (3 females, 2 males)	18	1,431
Varecia variegata	Vatoharanana (Ranomafana)[5]	unk.	unk.	197	unk.	unk.	-	2 (1 female, 1 male)	2	112
Varecia variegata	Vatoharanana (Ranomafana)[6]	travel mapped during observations	MCP	100 - 150	unk.	unk.	-	13 (3 females, 10 males)	18	1,700
Varecia variegata	Mangevo (Ranomafana)[7]	GPS coordinates (10-min)	MCP (Kernel)	120.4 (87.8)	26.3 (16.9)	17.5 (13.8)	F > M	28 (13 females, 15 males)	12	4,000+

[1]Rigamonti 1993; [2]Vasey 1997, 2006; [3]Morland 1991; [4]Ratsinbazafy 2002; [5]White 1991; [6]Balko 1998; [7]Baden *this study*

Table 2.2 Patterns of climatic, phenological and reproductive seasonality of *Varecia* in Ranomafana National Park, Madagascar

Season	Warm wet		Trans. cool		Cool wet			Cool dry		Trans. warm	Warm wet	
Fruit availability	peak[a,b,e]	peak[a,b,e]		lean[a-e]	lean[a-e]	lean[a-e]	lean[a-e]	lean[a-e]	rise[a,e]	rise[e]/peak[a,b]	rise[e]/peak[a]	peak[a,e]
Reproduction	Nonreproductive						Gestation			Lactation, nest, communal care		
Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec

[a] Phenological data from Overdorff (1993a,b); [b] Phenological data from Balko (1998); [c] Meyers and Wright (1993); [d] Hemingway (1996, 1998); [e] Baden, this study (unpublished phenological data); *Note: No infants were born in 2007, thus January-July 2008 were considered nonreproductive. In other years, this may be considered a continuation of lactation

Table 2.3 Individual annual home range area and overlap

Collar ID	Sex	Located days	# location points	95% MCP (ha)	95% Kernel (ha)
RADIO-BLUE (rB)	F	90	4277	38.7	20.6
RADIO-BLUE-GREEN (rG)	F	107	4578	32.9	19.4
RADIO-ORANGE (rO)	F	75	3386	26.6	18.7
RADIO-RED (rR)	F	92	3960	19.6	14.1
RADIO-BLUE-YELLOW (rY)	F	72	3640	13.6	11.5
Female Mean		**(N = 5)**		**26.3**	**16.9**
BLACK-GREEN (BG)	M	48	808	22.8	17.0
NO COLLAR (NC)	M	49	735	18.3	13.8
RADIO-BLACK-GREEN (rBG)	M	74	2163	20.6	16.1
RADIO-PURPLE-SILVER (rPS)	M	76	2403	14.8	12.3
BLACK-BLUE (BB)	M	58	1792	14.9	12.0
RED-GREEN (RG)	M	58	1276	15.8	12.4
YELLOW-PURPLE (YP)	M	56	1607	15.0	12.7
Male Mean		**(N = 7)**		**17.5**	**13.8**
p				*0.04*	*0.03*

		Overlap	
Sex-Sex	**N**	**95% MCP**	**95% Kernel**
Female-Female	10	0.41 ± 0.09	0.16 ± 0.05
Male-Male	21	0.35 ± 0.07	0.24 ± 0.09
Female-Male	35	0.40 ± 0.05	0.29 ± 0.07
p		0.62	0.70

Females used significantly larger home ranges than males (MCP: U = 10, $p = 0.04$; Kernel: U = 9, $p = 0.03$). However, sexes did not differ in their degree of home range overlap. Analysis includes individuals with ≥ 25 annual sampling days.

Table 2.4 Seasonal home range area and overlap: Climatic Season. Includes only individuals with > 10 sampling days.

Home Range Area (ha)

Sex	**N**	**Cool/wet**	**N**	**Cool/dry**	**N**	**Warm/wet**	***p***
Females	4	14.59 ± 2.42	5	11.84 ± 1.05	7	16.38 ± 1.81	0.17
Males	5	6.08 ± 0.41	7	10.69 ± 0.94	4	8.78 ± 1.42	***0.05***
p		***0.02***		0.47		***0.02***	

Home range overlap (UDOI)

Sex-Sex	**N**	**Cool/wet**	**N**	**Cool/dry**	**N**	**Warm/wet**	***p***
Female-Female	10	0.11 ± 0.06	10	0.12 ± 0.06	28	0.21 ± 0.07	0.46
Male-Male	21	0.30 ± 0.12	21	0.34 ± 0.16	10	0.10 ± 0.09	0.68
Female-Male	35	0.31 ± 0.10	35	0.34 ± 0.09	40	0.32 ± 0.07	0.34
p		0.49		0.22		0.16	

Table 2.5 Seasonal home range area and overlap: Reproductive Season. Includes only individuals with > 10 sampling days.

Home Range Area (ha)

Sex	N	Nonbreeding	N	Gestation	N	Lactation	*p*
Females	6	13.80 ± 2.21	5	12.04 ± 1.08	7	11.40 ± 1.05	0.8
Males	7	9.93 ± 0.94	8	9.24 ± 0.88	5	8.64 ± 0.92	0.7
p		0.32		0.09		0.12	

Home range overlap (UDOI)

Sex-Sex	N	Nonbreeding	N	Gestation	N	Lactation	*p*
Female-Female	10	0.15 ± 0.09	10	0.12 ± 0.07	15	0.14 ± 0.08	0.5
Male-Male	23	0.15 ± 0.07	26	0.35 ± 0.16	10	0.07 ± 0.06	0.1
Female-Male	35	0.22 ± 0.07	40	0.33 ± 0.09	30	0.33 ± 0.11	0.3
p		0.45		0.64		0.64	

Table 2.6 Models using a generalized linear mixed-effects model to estimate daily path length of *Varecia variegata* in a primary- unlogged rainforest site within Ranomafana National Park, Madagascar. Sampling occurred between 6am and 5pm

Model[a]	**K**[b]	**AIC_c**	**ΔAIC_c**	**Model Likelihood**	**Model Weight (w_i)**	**Deviance**
RS*daylength*sex	13	5721.529	0.000	1.000	0.881	5695.529
RS*daylength	7	5725.525	3.995	0.136	0.119	5711.525
CS*daylength*sex	17	5745.850	24.321	0.000	0.000	5711.850
CS*daylength	9	5747.597	26.068	0.000	0.000	5729.597
daylength	3	5748.465	26.936	0.000	0.000	5742.465
CS*sex	9	5749.193	27.664	0.000	0.000	5731.193
CS	5	5750.870	29.341	0.000	0.000	5740.870
rain	3	5754.580	33.051	0.000	0.000	5748.580
Null	2	5755.660	34.131	0.000	0.000	5751.660
sex	3	5757.409	35.880	0.000	0.000	5751.409
rain*sex	5	5757.788	36.260	0.000	0.000	5747.788
RS	4	5758.921	37.392	0.000	0.000	5750.921
infants*sex	4	5759.445	37.916	0.000	0.000	5751.445
RS*sex	7	5761.003	39.474	0.000	0.000	5747.003

[a] Fixed effect variables include Reproductive Season: define here (RS), daylight length (daylength), rainfall (rain), Climate Season: define here (CS), males vs. females (sex), and number of infants (infants). To account for individual variation, ‘individual’ was treated as a random effect; [b] number of model parameters

Chapter 3

Dispersal and genetic population structure in black-and-white ruffed lemurs (*Varecia variegata*).

ABSTRACT

The genetic structure of a population, or the distribution of genetic variation within and among social groups, is inextricably linked to aspects of an organism's biology, including life history variables such as patterns of natal dispersal. Among non-human primates, dispersal is rarely female-biased; however, in some taxa, particularly those living in groups characterized by fission-fusion dynamics, females disperse and males are typically the more philopatric sex. As such, males within these communities are expected to share a higher relatedness than females within the same community. Contra to these expectations, in ruffed lemurs, one such fission-fusion taxon, females are generally considered the philopatric sex. Accordingly, it can be hypothesized that communities consist of unrelated males and closely related females, though this hypothesis has never been empirically tested. Here, I characterize the genetic community structure and dispersal patterns of black-and-white ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar, an undisturbed primary rainforest habitat and evaluate the extent to which this population conforms to previously reported patterns for this taxon, as well as to patterns observed in other classic primate fission-fusion societies. Using 15 polymorphic microsatellite markers, I genotyped 38 adult individuals to test for within-community relatedness and patterns of sex-biased dispersal. Results suggest that both sexes likely disperse. Average relatedness within the community is low (R = -0.06). However, despite low overall relatedness, both males and females kin live in close spatial proximity, forming networks of kin within the larger communal range. These results are contrary to most primates with fission-fusion social organization, but are not unusual among primates, instead resembling a number of platyrrhine, colobine and strepsirrhine taxa.

INTRODUCTION

Dispersal is a fundamental aspect of an organism's life history that can influence processes of evolution, social behavior, and the long-term persistence of populations (Koenig et al. 1996). In most vertebrates, it is typical for individuals to disperse from their natal home range (Howard 1960). While most birds are characterized by male philopatry, among mammals, females are typically the philopatric sex, with males dispersing more frequently and at longer distances (Greenwood 1980; Pusey and Packer 1987). Such sexual asymmetries in dispersal can have important consequences for population demographics and can substantially affect the genetic structure of a population, or the distribution of genetic variation within and among social groups (Ross 2001; Storz 1999).

Because patterns of genetic relatedness are largely a result of and are directly influenced by dispersal patterns and mating system (Ross 2001; Storz 1999), the knowledge of genetic population structure can help to provide insight into behaviors which may not be easily detectable with observations alone (*sensu* Kappeler and van Schaik 2002). For example, characterizing dispersal patterns from field observations typically requires intensive, long-term demographic studies (Koenig et al. 1996), particularly in long-lived taxa such as primates which are characterized by relatively slow life histories (Harvey and Clutton-Brock 1985). Genetic studies can provide an alternative, and potentially less labor-intensive, means of quantifying dispersal (e.g., Bradley et al. 2004, 2007). Moreover, understanding the degree and distribution of genetic relatedness within a population can allow us to address whether and how kinship influences aspects of an organism's sociality (e.g., by determining the presence and abundance of kin), as well as providing the context for the potential evolution and maintenance of kin selected social behaviors (Hamilton 1964; Ross 2001).

Among most group-living primates, dispersal can be characterized as either unbiased (i.e., both sexes disperse; e.g., brown lemurs: Kappeler 1997; gorillas: Bradley et al. 2004; 2007; howler monkeys: Pope 1992) or male-biased, with males tending to disperse more often or at greater distances than females (e.g., baboons: Altmann et al. 1996; macaques: de Ruiter and Geffen 1998; mouse lemurs: Radespiel et al. 2003; sifakas: Lawler et al. 2003) (reviewed in Pusey & Packer 1987; Strier 1994b; Lawson Handley & Perrin 2007). However, in some primate taxa, particularly those characterized by fission-fusion social organization, females disperse and males are typically the more philopatric sex (e.g., bonobos: Gerloff et al. 1999; chimpanzees: Nishida & Kawanaka 1972; Pusey 1979; Goodall 1986; Morin et al. 1994; spider monkeys: Symington 1988; woolly monkeys: Strier 1994a; *but see* Di Fiore and Fleischer 2005; Di Fiore et al. 2009). Consequently, males living in fission-fusion societies are expected to be more closely related than dispersing females (Di Fiore and Campbell 2007; Di Fiore et al. 2009; Di Fiore 2003a; Morin et al. 1994; Symington 1990; Wrangham and Smuts 1980; but see Lukas et al. 2005; Vigilant et al. 2001). Males also show stronger patterns of association than their female conspecifics (Chapman 1990; Chapman et al. 1995; Nishida 1968; Shimooka 2003; Symington 1990; Williams et al. 2002; Wrangham 2000; Wrangham et al. 1992; Goodall 1986; Wrangham and Smuts 1980) and exhibit higher levels of cooperation (e.g., hunting parties: Watts and Mitani 2002). The strong social bonds and cooperative behaviors evident among male chimpanzees were long-thought to reflect kin associations (Morin et al. 1994 and references therein), much like patterns found in other vertebrate taxa (Baglione et al. 2003; Eberle and Kappeler 2006; Eberle and Kappeler 2008; Silk 2002; Viblanc et al. 2010), though later studies demonstrated that this might not actually be the case. In fact, studies have not found the expected patterns of within group relatedness (i.e., average relatedness among (philopatric) males did not differ significantly from that among females) (Vigilant et al. 2001; Lukas et al. 2005). While surprising, these patterns can be ascribed to a number of variables, including low reproductive skew and large group size (Lukas et al. 2005). Thus, the relationship between dispersal patterns, genetic population structure, and cooperative behaviors within other primate fission-fusion communities warrants further investigation.

Like chimpanzees and spider monkeys, ruffed lemurs live in a fission-fusion social organization characterized by spatiotemporal variation in range use and home range overlap (Morland 1991a; Morland 1991b; Rigamonti 1993; Vasey 1996; Vasey 2006; Baden Chapter 2). Studies have found some (weak) evidence of male transfer between communities (Balko 1998; Morland 1991a), and females are generally considered the philopatric sex (Kappeler 1997; but see Balko 1998, cited in Erhart and Overdorff 2008). Accordingly, it can be hypothesized that communities consist of unrelated males and closely related females, though this hypothesis has never been empirically tested. If, in fact, ruffed lemur females are philopatric, this would represent the only case of male-biased dispersal in primates characterized by fission-fusion dynamics. The taxon is also among one of the few primates that cooperatively rears its young (Morland 1990; Vasey 2007). Thus, depending on dispersal and patterns of genetic population structure, high levels of within-group genetic relatedness, particularly among females, might set the stage for kin-selected, cooperative infant care.

Unfortunately, few data exist regarding the genetic population structure and dispersal patterns in ruffed lemur communities. Thus, the goals of this study are to genetically assess aspects of black-and-white ruffed lemur (*Varecia variegata*) social structure using DNA extracted from blood and tissue samples collected during annual capture seasons (2005-2008). In this chapter, I will determine, through genetic analysis, the dispersal patterns and genetic community structure of black-and-white ruffed lemurs living in a contiguous rainforest habitat. Specifically, I test the hypotheses that ruffed lemur communities are characterized by female-philopatry and male-biased dispersal. If individuals within a community are related, average pairwise relatedness (*R*) within a community (within-community dyads) should be greater than between members from different communities (between-community dyads). Further, if females within ruffed lemur communities are philopatric (i.e., males disperse), as per Morland (1991), then average pairwise relatedness among adult females should be greater than among adult males within a community. Adult females should also have more adult same-sex kin than adult males within a community. Alternatively, if males within ruffed lemur communities are philopatric (i.e., females disperse), as consistent with other primate fission-fusion societies, then average pairwise relatedness among adult males is greater than among adult females within a community. Moreover, adult males have more adult same-sex kin than adult females within a community.

METHODS

Study site & sample collection

I focused data collection on a minimum of two neighboring black-and-white ruffed lemurs (*Varecia variegata*) communities at Mangevo, a low-to-mid altitude rainforest site located within the southeastern most parcel of Ranomafana National Park, Madagascar (see Wright 1992) for site description; Baden Chapter 2 for spatial location of communities). Genetic samples were collected from 38 black-and-white ruffed lemurs during five capture seasons spanning four consecutive years of study (2005-2008; see Table 3.1 for details). This sample comprised all individuals from the Mangevo community (n = 28; 21 adults, 7 juveniles), and 12 individuals (n = 11 adults, 1 juvenile) from neighboring communities. Sample collection occurred under veterinary supervision and followed a strict protocol outlined by Glander (1993). All capture procedures occurred during non-reproductive seasons in the absence of infants and dependent offspring.

For each individual captured, approximately 1 ml/kg of whole blood (~4 cc) was collected from the femoral vein and four 2mm tissue biopsies were collected from ear pinnae. All samples were stored in 5ml of lysis buffer solution

(0.1 M Tris-HCl pH, 8.0, 0.1 M EDTA, 0.01 M NaCl, and 0.5% w/v SDS) at ambient temperature until they could be brought back from the field (7 to 21 days) (Longmire et al. 1992). Samples were then banked in a −80°C freezer at the Madagascar Biodiversity Partnership headquarters in Antananarivo, Madagascar and subsequently at the Yale Molecular Anthropology Lab in New Haven, CT.

Genetic Analysis

DNA Extraction

Nuclear DNA was extracted from blood and tissue samples using standard nucleic acid extraction kits (QIAamp DNA Mini Kit®). Extraction procedures followed the manufacturer's protocols, with the following modification to the tissue extraction procedures: samples were allowed to lyse initially in ASL buffer for 24-48 hours rather than 10 minutes. Following extractions, DNA concentrations and sample purity were quantified via spectrophotometric analysis using a NanoDrop© (Thermo Fisher Scientific).

Microsatellite genotyping

Samples were amplified at 15 variable microsatellite loci (Table 3.2). Primer sequences and polymerase chain reaction (PCR) conditions were optimized from those described in Louis et al. (2005). PCR amplification was carried out in a total reaction volume of 25 μl using an ABI 480 thermocycler

(Perkin-Elmer) with 25 – 50 ng DNA template. Final amplification conditions consisted of 2μ DNA template, 12.5 μl Qiagen HotStarTaq Master Mix, 10 μM of each primer, and 5.5 μl doubly-distilled H_2O. Amplification conditions were as follows: initial denaturation at 95°C for 15 minutes; 35 cycles of 30 s at 94°C, 40 s at 54 to 60°C (see Table 3.2 for marker-specific annealing temperatures), 1 min at 72°C, and a final extension of 7 min at 72°C.

The 5’ end of forward primers were fluorescently labeled and amplification products were separated using capillary electrophoresis (ABI 3730xl Genetic Analyzer). Alleles were sized relative to an internal size standard (ROX-500) using Gene Mapper software (Applied Biosystems®) and allele binning was performed by eye. Allele sizes were carefully checked by comparing locus-specific patterns across individuals. To ensure genotype accuracy, scoring followed stringent criteria of numerous independent replications using the “multiple tubes” approach (Taberlet et al. 1996), in that homozygous genotypes were confirmed by an average of 3.2 independent replications (range: 2 to 7) and heterozygous genotypes were confirmed by scoring each allele at least twice in two or more independent reactions.

Statistical Analysis

Summary Statistics

Prior to statistical analysis, data were screened for scoring errors and allelic dropout (i.e., where one allele of a heterozygote randomly fails to amplify) using the software package MICROCHECKER (Van Oosterhout et al. 2004). To confirm that loci were independent (i.e., to test for linkage disequilibrium among all pairs of loci) the log likelihood ratio of genotypic linkage disequilibrium was calculated in GENEPOP 3.3 using default Markov chain parameters (as described above).

GENEPOP 3.3 (Raymond and Rousset 1995) and ML-RELATE (Kalinowski et al. 2006) were used to identify loci with high rates of null alleles (i.e., allelic dropout or alleles that were not amplified by the PCR process; Pemberton et al. 1995), as indicated by heterozygote deficiency (F_{IS}) relative to Hardy-Weinberg expectations. ML-RELATE uses Monte Carlo randomization set to 10,000 randomizations following Guo and Thompson (1992) and the *U* test statistic described by Rousset and Raymond (1995). GENEPOP 3.3 was set to implement default Markov chain parameters [dememorization number = 1,000; number of batches = 100; number of iterations per batch = 1,000] using Hardy Weinberg exact tests. Possible F_{IS} values range from -1 to 1: A positive F_{IS} indicates an excess of homozygotes/deficiency of heterozygotes, and suggests the possibility of inbreeding, assortative mating, population admixture, or small population size, whereas negative F_{IS} values indicate an excess of heterozygotes/deficiency of homozygotes, resulting from outbreeding, dissortative mating, or the mating of individuals from distant populations.

Once data screening was complete, background population allele frequencies were calculated using the software package CERVUS 3.0.3 (Marshall et al. 1998). To minimize sampling bias towards known/suspected relatives (e.g., parent-offspring dyads), allele frequencies were calculated using genotype data from adult individuals *only*.

Finally, genetic diversity and allelic richness were calculated using GENEPOP 3.3 (using default parameters) and FSTAT 2.9.3.2 (Goudet 1995; Goudet 2001).

Patterns of Within Community Relatedness

To confirm that the diversity of makers was sufficient to ascribe measures of pairwise relatedness (as described below), I used the program CERVUS to estimate the probability that two randomly drawn individuals would have the same genotype across a given set of loci based on the allele frequencies in the population, also known as the probability of individual identity (P_{ID}) (Paetkau and Strobeck 1994). In addition, I calculated the more conservative probability of individual identity among siblings, or the probability that a pair of siblings will have the same genotype across a given set of loci, $P_{ID\text{-}SIB}$, following methods described in Waits et al. (2001).

Pairwise relatedness

Dyadic (pairwise) relatedness was then estimated for all possible dyads of individuals from the population using the regression-based Queller and Goodnight (1989) relatedness estimator as implemented in GenAlEx (Peakall and Smouse 2006). To simplify notation, dyadic relatedness values are noted here as “r-values” while average relatedness values across multiple dyads within a category are noted here as “R”, “average R” or “average relatedness.” Confidence intervals and standard errors of r-values were generated by using a Jackknife procedure across loci.

The robusticity of this suite of loci for estimating relatedness was tested with a rarefaction analysis as in Altmann et al. (1996) and de Ruiter and Geffen (1998) using the program RE-RAT (http://people.musc.edu/~schwaclh/).

Average relatedness, R, among demographic categories could not be compared directly because data points (i.e., r-values) were non-independent. Therefore, statistical significance in average relatedness among categories was evaluated via permutation analyses, following Bradley et al. (2007) using code available from Dieter Lukas.

Parentage: Maternity and Paternity Exclusion

Mother-infant relatedness in this study, although not genetically verified, was certain; all infants were observed on their day of birth, and in all cases, ruffed lemur mothers exhibited exclusive infant care and natal nest use during the first two to three weeks of infant development (Chapter 4). In contrast, although mother-juvenile relationships could be inferred from behavioral observations, these relationships were uncertain, in part because party composition and cohesion were flexible, and thus juveniles were not regularly observed in proximity to a particular adult female (i.e., candidate mother). Thus, all adult females (n = 16) were considered as potential mothers to all juveniles sampled in this study (n = 8). Maternity was estimated using the maximum likelihood method as implemented in CERVUS. Using this method, CERVUS assigns all candidate mother-offspring pairs an “LOD score”, that is, the natural log of the overall likelihood ratio for each mother-offspring pair (Marshall et al. 1998). For each offspring considered, the candidate mother receiving the highest LOD score indicates the female representing the most likely mother to that particular offspring. Confidence values for maternity assignments are calculated by comparing the difference between LOD scores for the two most-likely candidate mothers against a distribution of simulated values. Following convention, alpha was set to 95% (strict) and 90% confidence (relaxed), and can be thought of as tolerance of false positive parentage assignments (i.e., parentage assignments made to candidate parents who match by chance, a Type I Error).

Attempts were made to further confirm all maternity assignments with behavioral observations (e.g., group membership, home range overlap, patterns of affiliation). All strict maternity assignments which were also confirmed via behavioral records (n = 6) were then provisionally included as ‘known’ mothers in subsequent paternity analyses.

Paternity assignments were conducted in the same manner as maternity assignments, as described above. All adult males from the population (n = 14) were included as potential sires to all juveniles (n = 8), and LOD scores were calculated with and without the ‘known’ mothers’ genotypes. In all cases, adults were excluded from parentage if they mismatched at a single locus.

In an effort to further discriminate relationships within the community, maternity and paternity assignments were then performed among all adult female and adult male dyads (e.g., including all adult females as both offspring and candidate parents) to determine whether adult dyads could be eliminated as possible mother-daughter and father-son pairs based on allelic exclusion following Gerloff et al. (1999).

Genetic community structure

Because ruffed lemurs are characterized by fission-fusion dynamics (i.e., fluid party composition and cohesion through space and time; Morland 1991, Vasey 2006), genetic relatedness within social groups could not be evaluated, *per se*. I was, however, able to examine genetic community substructure by examining whether and how the patterns of dyadic relatedness were spatially distributed across the communal territory (i.e., the relationship between genetic relatedness and geographic distribution) using two measures: percent of home range overlap and distances between home range centroids (i.e., centers of activity).

All GPS ranging coordinates were collected from beneath the focal individual at 10-minute intervals, and spanned a continuous 12-month study period (see Chapter 2 for details). Using the Spatial Analyst tool in ArcMap 9.3, I first calculated the percent of home range overlap using 95% kernel home range estimates for all individuals for which I had more than 24 days of sampling (n = 17). I then used these same ranging coordinates to calculate the center (centroid) of all subjects' home ranges within the larger communal territory. Using the Hawth's Tools extension of ArcMap, I calculated the distance between individual home range centroids for all dyads included in this study.

Relationships among spatial proximity (calculated between centroids) and overlap (calculated from kernel estimates) were compared with dyadic r-values (described above). To test for relationships between all dyadic same-sex relatedness values (e.g., male-male, female-female dyads) and geographical distances, Mantel tests (Manly 1997) were performed in MatMan. To test these same relationships among male-female dyads, row wise Mantel tests were used. To evaluate significance, resulting Mantel's Z statistics were compared with distributions of Z generated by randomizing the geographic distance matrix 10,000 times following Kappeler et al. (2003). Alpha was set at 0.05 and adjusted using the Holm-Bonferroni method, a sequentially rejective multiple test procedure which controls for family wise error for all *k* hypotheses at level alpha in the strong sense (Holm 1979). All tests were two-tailed.

Sex-Biased Dispersal

Following Lampert et al. (2003), FSTAT 2.9.3 was used to implement four tests for sex-biased dispersal: F_{IS}, F_{ST}, mean Assignment Index (*m*AIc), and variance in Assignment Indices (*v*AIc). F_{IS} represents a measure of how well genotype frequencies within a population match expectations of Hardy Weinberg Equilibrium (Hartl & Clark 1997), and can be used to detect a reduction in heterozygosity that is typically caused by population substructure (see Summary Statistics, above, for details). Because the dispersing sex in a population often includes a combination of both immigrants and residents, the admixture of these two populations should lead to a consequent heterozygote deficiency (and a positive F_{IS}) within the dispersing sex. The dispersing sex should also have a lower average relatedness (*R*) than the philopatric sex, as through time, genetic relatedness accumulates in the sex which does not disperse. Consequently, F_{ST}, or the measurable proportion of genetic variance attributable to among-population differentiation, should be lower in the dispersing sex because the less philopatric sex should be less differentiated in its allele frequencies among populations (i.e., increased gene flow yields fewer genetic differences between populations in the dispersing sex) (Hartl & Clark 1997). Finally, members of the dispersing sex should show significantly lower mean Assignment indices, but higher variance than members of the more philopatric sex (Lawson Handley and Perrin 2007). Assignment Indices are statistics that are used to summarize the likelihood that an individual's multilocus genotype originated in the population from which it was sampled, and can be used to test for differences in the mean values (*m*AIc) and the variance (*v*AIc) of assignments between the sexes. These indices can then be standardized, subtracting the population mean AI from each individual's AI (Favre et al., 1997), such that animals with positive 'corrected' assignment indices (AI_c) are those which are more likely to have been born in the population, while immigrant genotypes are less likely to occur in the sample and should therefore have negative AI_c values (Goudet et al 2002).

In sum, the dispersing sex is predicted to have 1) positive F_{IS} values, 2) lower values of F_{ST}, 3) lower mean assignment scores (*m*AIc) and 4) greater variance in assignment (*v*AIc).

To confirm results from the first set of dispersal analyses, permutation tests were conducted in Permute v1 (DiFiore 2005), an Excel VBA module that allows the user to evaluate differences in "average pairwise relatedness values" for different demographic groups within a population (e.g., average male versus average female relatedness within social groups). If sex-biased dispersal is present, then the dispersing sex should have a significantly lower r-value than the members of the philopatric sex.

RESULTS

Summary statistics

Overall, genotypes across the 15 microsatellite loci were 93% complete (Table 3.3, Appendix 1). All subjects (n = 38) were scored for at least 12 loci (Appendix 1). Allele frequencies based on adults only are shown in Table 3.3, with specific frequencies of each allele at each locus detailed in Appendix 2. Allelic richness, or the mean number of alleles per locus, was 4.33 (range = 2 to 7; Table 3.3). Expected heterozygosities (H_e) ranged from 0.332 to 0.804, whereas observed heterozygosities (H_o) for each locus ranged from 0.400 to 0.833. Analysis of allele frequencies did not indicate significant deviation from

Hardy-Weinberg expectations and null alleles (i.e., allelic dropout) were not detected (Table 3.3, Appendix 2). Using marker-pair comparison, only 4 of 105 (3.8%) possible combinations of loci (VVV598/ VVV963, VVV598/ VVV816, VVV20/ VVV941, VVV247/ VVV560) showed any evidence of being in linkage disequilibrium.

Individual identity

The probability of individual identity, P_{ID}, calculated across all 15 loci was 2.13×10^{-11}. The probability of individual identity among siblings, $P_{ID\text{-}SIBS}$ was 2.28×10^{-5}, demonstrating the very low probability that any two individuals, even siblings, would be expected to share the same multilocus genotype by chance (i.e., probability less than 0.0001%). However, since not all samples were completed at all fifteen loci, the worst case scenario P_{ID} was calculated using the fewest possible, least variable loci (i.e., the most conservative estimate of individual identity using the smallest possible subset -- of the least variable loci -- to provide estimates of individual identity having a probability of lower than 1%). Results for P_{ID} were very low (less than 1% probability) when using suites of 5 or more of the least variable loci (4.00×10^{-3}), indicating that two randomly drawn individuals would have the same genotype at these five or more loci less than 1% of the time (Appendix 3). Similarly, $P_{ID\text{-}SIB}$ scores were calculated using the fewest possible, least variable loci; the least variable set of eight loci resulted in a

< 1% chance of two individuals sharing the same genotype (9.67 x 10^{-3}). P_{ID-SIB} values for suites of seven or fewer loci exceeded 0.01). Because all individuals were scored at a minimum of 12 loci, individual identities can be viewed with confidence.

Patterns of kinship within the Mangevo community

Robustness of genotype data

The results of the generated rarefaction curve (y = 0.7991, r^2 =0.9992; Appendix 4) show average relatedness values stabilizing after 5 loci, with the difference between mean relatedness using 5 loci and 6 loci changing by only 0.95% (0.023), and the difference between using 6 loci and 7 loci changing by only 0.56% (0.016). Thus, subsequent dyadic r-value calculations included all possible dyads (n = 703 dyads), as all individuals could be compared at 5 or more loci. The relatively high standard errors shown in the rarefaction analysis reinforce, however, that these values represent only general estimates of genetic relationships. Fine scale relatedness assessments (e.g., distinguishing between full and half-sibs) are not possible in most microsatellite studies, and in fact, the ability to differentiate relatedness disjunctions on such a scale would probably require 30 to 60 microsatellite loci (Stone and Bjorklund 2001). Therefore, in this study I broadly consider "related dyads" to be those with r-values ≥ 0.25 and I made no attempt to further distinguish categories or degrees of relatedness other than exclusion of parentage based on allelic mismatches (see below).

Average relatedness within the community

Although the individuals sampled in this study comprised > 1 social community (Table 3.1), samples used in all analyses were collected from a single genetic population (i.e., no significant genetic differentiation among adults within versus outside of the community, $F_{ST} = -0.0003$, $p < 0.05$). Average relatedness, R, and standard deviations of various demographic categories are shown in Figure 3.1 and Table 3.4. Large variance was observed for all categories. However, both mother-offspring and father-offspring relatedness was generally consistent with expectations (i.e., expected R ≈ 0.5, observed R = 0.44 - 0.48).

Average relatedness among adults within the Mangevo community was -0.06 ± 0.02 (n = 19 individuals; 171 dyads). Average R for both adult male and adult female dyads was -0.13 ± 0.04 (females: n = 45 dyads; males: n = 36 dyads) (Figure 3.1, Table 3.4). These observed values were compared to the distribution of average R values that would be expected by chance. Through permutation analysis, all adults were pooled and then sorted randomly into two categories (according to observed N in each group) 10,000 times and average R was calculated each time, thus generating a distribution of average relatedness values expected by chance. Neither the observed average male relatedness nor the observed average female relatedness was significantly different from chance (p = 0.08), suggesting that dispersal is not sex-biased (but see Dispersal patterns below). In all cases, resident males were excluded as sires of resident (adult) females within the community (see below).

Parentage: Maternity and Paternity Exclusion

Total exclusionary power generated from adult allele frequencies was 0.998 for the first parent (i.e., neither parent known), and 1.00 for the second parent (one parent known) (Table 3.3). Maternity was strictly assigned to 6 of 8 juveniles within the population (Table 3.5), and was confirmed by behavioral observations.

Among older community members (i.e., adult dyads), allelic mismatches excluded the possibility of mother-daughter relationships for 38 of the possible 45 adult female-female dyads (Figure 3.2). Seven adult dyads, however, could potentially represent mother-daughter pairs, as they shared an allele at each locus and had relatively high r-values (average R = 0.24 ± 0.08). Of these seven dyads, six could potentially represent mother-daughter dyads under strict confidence ($p < 0.05$) and shared an average R of 0.40 ± 0.05. Moreover, two female-female dyads which were excluded as mother-daughter pairs based on allelic mismatches also yielded high r estimates (average R = 0.28 ± 0.02).

Potential mother-dyad pairs were also identified across communities (i.e., adult dyads including community and extra-community females) (Figure 3.2), though to a lesser degree. When examining all possible adult female across-community dyads, allelic mismatches excluded the possibility of mother-daughter relationships for 53 of the possible 60 adult female-female dyads. Seven of the 60 adult female dyads could potentially represent mother-daughter pairs, as they shared an allele at each locus, however females in this case showed a lower average R than did within-community dyads (average R = 0.10 ± 0.06). Moreover, only one of seven pairs could be assigned as a mother-daughter dyad, and only under relaxed confidence ($p < 0.10$), though this dyad shared a relatively high r-value of 0.31.

It should be noted that relatedness patterns in Figure 3.2 indicates conservative patterns of dyadic relatedness. Occasionally, biologically related dyads might share lower r-values, especially if the alleles shared by the dyad are common within the population. Of these same adult females, four could be assigned as candidate mothers to four adult males within the larger genetic population. In all cases, however, candidate mothers resided in different, albeit neighboring communities from their adult male offspring.

Paternity was strictly assigned to juveniles in 4 of 8 cases when the mothers' identity was left as 'unknown'. When the mothers' identity was provisionally assigned (using strict maternity assignments described above), 6 of

8 cases could be determined with confidence; again, paternity could be assigned with confidence in 4 of 8 cases, while in 2 cases, results confidently determined that the potential sire was not included in the sample (Table 3.6). It is important to note, that even paternity assignments which did not meet relaxed significance criteria ($p < 0.1$) in the first analysis (mother ID unknown) were consistent with strict confidence assignments ($p < 0.05$) resulting from the second analysis (mother ID known) in all cases but one (Table 3.6).

Behavioral observations were less informative for confirming paternity assignments, as juveniles were rarely found in association with adult males. It is worth noting, however, that in 3 of the 4 cases of confident paternity assignment, the most likely fathers (i.e., males receiving the highest LOD scores and exhibiting no allelic mismatches) were classified as extra-community males or males which were rarely, if ever, observed in or near the communal territory during behavioral observations.

Within the community, allelic mismatches excluded the possibility of father-son pairs for 31 of the possible 36 adult male-male dyads (Figure 3.3). Five adult dyads, however, could potentially represent father-son pairs, as they shared an allele at each locus and shared high r-values (average $R = 0.40 \pm 0.12$). Of these five dyads, two could be assigned as father-son dyads with strict confidence ($p < 0.05$). Moreover, three adult male-male dyads which were excluded as father-son pairs based on allelic mismatches also yielded high r estimates (average R = 0.28 ± 0.12).

In one case, an adult male was assigned as a candidate father to an adult female in a neighboring community, but in no cases were adult males assigned as "most likely fathers" to adult females residing in the same community.

Much like with females, dyadic adult male relatedness was also common across communities (i.e., dyads including community and extra-community males) (Figure 3.3). However, when looking at all possible adult male-male dyads, allelic mismatches excluded the possibility of father-son relationships for all of the possible 48 adult male-male dyads across communities.

Genetic community structure

Male and female centroids, or their centers of activity within the larger communal territory, are presented in Figures 3.2 – 3.4 and are indicated by colored circles, or nodes. Lines extending between nodes indicate related dyads, or pairs of individuals sharing dyadic relatedness values ≥ 0.25. Communal territories are denoted by a large oval. Nodes falling outside of 'communal territories' represent individuals of unknown community descent/membership.

Mantel tests comparing adult same-sex dyads reveal significant positive relationships between dyadic relatedness and measures of spatial proximity, including both % home range overlap (males, Mantel R = 0.373, $p = 0.03$) and proximity between centers of activity (females, Mantel R = 0.490, $p = 0.007$; males, Mantel R = 0.655, $p < 0.001$). While a significant relationship between female dyadic relatedness and % home range overlap was not detected (Mantel R = 0.284, $p = 0.08$), values approached significance.

Based on these results, it seems that related same-sex dyads live in significantly closer proximity and share significantly greater home range overlap than unrelated dyads within the same community.

Adult male-female dyads, on the other hand, showed no significant relationship between spatial location and genetic relatedness (centroid distance, $p = 0.798$; % overlap, $p = 0.112$).

Dispersal patterns

Results yielded mixed evidence of sex-biased dispersal in ruffed lemurs (i.e., 3 of 5 predictions met; Table 3.7). Females had significantly higher mean assignment indices (*m*AIc: females = 1.09 versus males = -1.25, $p < 0.05$) and less variance in their assignments (*v*AIc: females = 5.35 versus males = 11.34, $p = 0.11$) than did males (Figure 3.5), suggesting a bias toward female philopatry and male natal dispersal, a finding that was further supported by positive values of F_{IS} in males but not females (F_{IS}: females = -0.096 versus males = 0.0077, $p = 0.24$). However, neither F_{ST} values (F_{ST}: females = 0.041, males = 0.065, p = 0.47) nor permutation tests (mean R males and females, R = -0.13 ± 0.04; $p = 0.08$)

detected significant patterns of dispersal bias in either sex. It should be noted that only one test, mean AIc, revealed a significant difference between male and female genotypes, and thus should be interpreted with caution.

DISCUSSION

In many mammals, female philopatry, male natal dispersal and a polygynous mating system form the basis of the social system (Greenwood 1980; Pusey and Packer 1987; but see Strier 1994b). Behavioral evidence of dispersal in ruffed lemurs, albeit weak, has suggested that females fit this typical mammalian pattern and are likely the philopatric sex, with males transferring to nearby communities (Balko 1998; Kappeler 1997; Morland 1991a). Results from this study, however, are equivocal.

I found mixed evidence of sex-biased dispersal in ruffed lemurs. Similar to other fission-fusion primates (e.g., chimpanzees: Lukas et al. 2005; Vigilant et al. 2001; some spider monkeys: Di Fiore et al. 2009), neither male nor female ruffed lemurs shared higher average pairwise relatedness than expected by chance. Moreover, neither sex showed genetic differentiation (F_{ST}) that might be indicative of a sex-bias in dispersal. In fact, average relatedness within the Mangevo community was generally low. At first glance, these patterns might indicate unbiased dispersal; however, they might also be a result of low reproductive skew and large relative group size, patterns which have also been shown to decrease average relatedness among members of the philopatric sex (Lukas et al. 2005). Data on reproductive skew in ruffed lemurs are currently unavailable, thus future studies should aim to quantify these variables, as well as addressing larger questions of mating strategies and reproductive success, in order to address this question.

While females shared low overall relatedness, they had significantly higher mean assignment indices and less variance in their assignments than did males, suggesting a bias toward female philopatry and male natal dispersal. This finding was further supported by reduced heterozygosity (positive values of F_{IS}) and population substructure in males but not females. These results suggest that, while both sexes disperse, females may disperse at closer distances or perhaps less frequently than males. This would help to explain the prevalence of extended female kin networks within the larger communal territory (see below).

While contrary to some (weak) behavioral evidence (e.g., Morland 1991; Balko 1998), the dispersal patterns presented here are congruent with those from the only other molecular study to examine ruffed lemur dispersal patterns in the wild (*V. rubra*: Razakamaharavo et al. 2010).

Though less than ten percent (8.8%) of adults within the community were genetically related, nearly three-quarters of adult females (70%) and more than half of adult males (56%) had at least one same-sex relative within the same community. Kin lived in significantly closer proximity and shared greater home range overlap than did unrelated community members, supporting the notion of “neighborhoods” (Richard 1985) of affiliates within the larger communal range. Thus, overall patterns of dyadic relatedness suggest that ruffed lemur communities are composed of both related and unrelated females and males, with related dyads forming spatial networks of kin within the larger communal range.

There are several possible ways that such patterns of kin association could have evolved. The combination of litters and synchronous, seasonal breeding makes natal co-dispersal of related kin a possibility in this taxon. For example, in the current study, eight of nine community females gave birth to litters of two to three offspring (Chapter 4). Should offspring survive to dispersal age, then natal co-dispersal of litter mates would be possible.

Alternatively, recruitment of dispersal aged kin or secondary co-transfer are also a possibility, particularly for females, a pattern also characteristic of gorillas (Bradley et al. 2007), suggesting that females can maintain social associations with their relatives despite natal dispersal. Within this study, however, related female dyads varied notably in age, making it unlikely that related females were of the same cohort. In fact, while relatedness in this study cannot be assigned beyond broad kin categories (kin versus nonkin), age estimations and r-values make it likely that female dyads were, in many cases, mother-daughter pairs. Male relatives, on the other hand, were often like-aged, and thus may represent cohorts of brothers and may even, perhaps, represent pre-dispersal litter mates. Unfortunately, until there is further investigation in to the dispersal patterns of this taxon, these hypotheses will likely remain untested.

This being said, the fact that at least some adult females remain in their natal range cannot be ignored. While cooperation in resource defense (Wrangham 1980) is an unlikely cause for the evolution and maintenance of female-philopatry in ruffed lemurs due to the nature of their fission-fusion social organization, a strategy which is thought to have evolved to reduce competition over patchily distributed resources (e.g., Klein and Klein 1977; Wrangham 1977), patterns of reproduction and infant care might provide an alternative explanation. Ruffed lemurs are said to have among the highest reproductive burdens in primates (Young et al. 1990), and are known to participate in communal infant care (Morland 1990; Vasey 2007; Baden Chapter 4). It has been shown that communal breeding in ruffed lemurs is biased toward kin, and confers significant reproductive advantages to females who cooperate (Chapter 4). Thus, while it is difficult to discern cause from consequence in this case, that female kin are more likely to remain in the natal community than males may set the stage for the evolution of the observed kin-cooperation in infant care.

Finally, while the current study focuses on the dispersal patterns and the consequent genetic community structure of a ruffed lemur population, it is widely known that two variables primarily influence patterns of genetic relatedness within a population: dispersal and mating system (Greenwood 1980; Storz 1999).

Mating strategies and reproductive skew can influence the number of matrilines and patrilines within a group, the nature of relationships between and within these lines, and the relative frequencies of these relationships (Ross 2001). Unfortunately, few data are currently available for ruffed lemurs (Morland 1993; Vasey 2007), thus future research should focus on quantifying mating effort and reproductive skew in the species. Preliminarily results revealed little reproductive skew across males (3 of 4 males confidently assigned paternity to four juveniles; Baden unpublished data); however, additional behavioral and genetic sampling will be necessary to better understand the mating system of this taxon. For example, do females mate with different males across years? Or do they exhibit preference for a particular male through time? Do preferred mating partners coincide with preferred social partners? And what determines these preferences? Ratsimbazafy (2002) noted that males form social pair bonds with preferred females and then mate promiscuously. Future paternity analyses of infants born during this study will help to clarify these questions.

CONCLUSIONS

In summary, ruffed lemurs live in communities characterized by dispersal of both sexes, though it is likely that females disperse less frequently or at closer distances than do male conspecifics. On average, individuals share relatedness close to zero; however, communities are comprised of networks of both male and female kin. Relatives tend to live in close proximity and share higher degrees of home range overlap than unrelated neighbors, despite living within a communally defended range.

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Figure 3.1 Location of Mangevo research site within the larger Ranomafana National Park, Madagascar

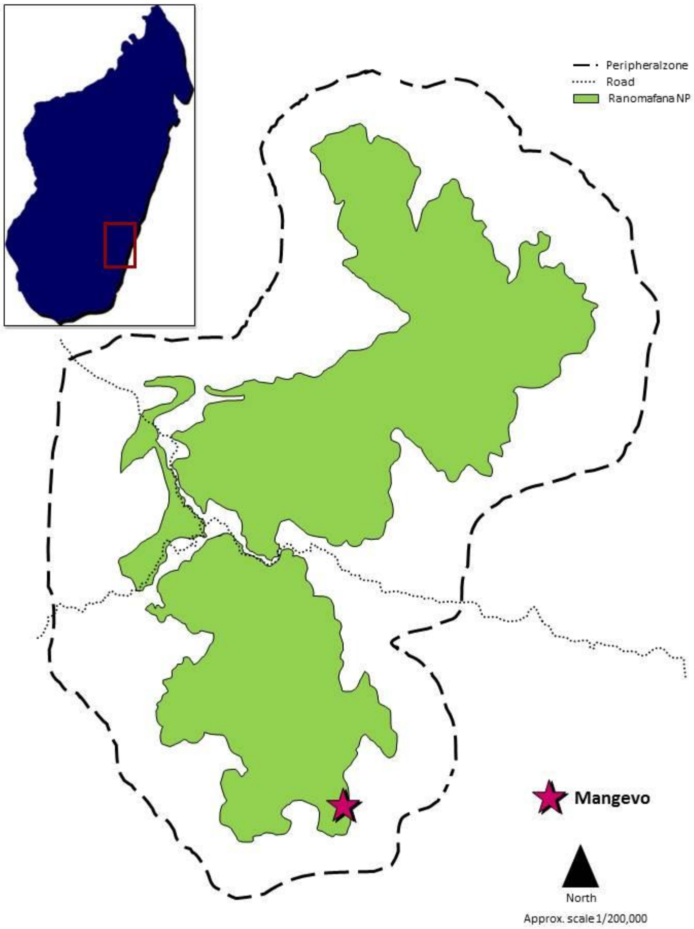

Figure 3.2 Distribution of relatedness scores among age/sex classes

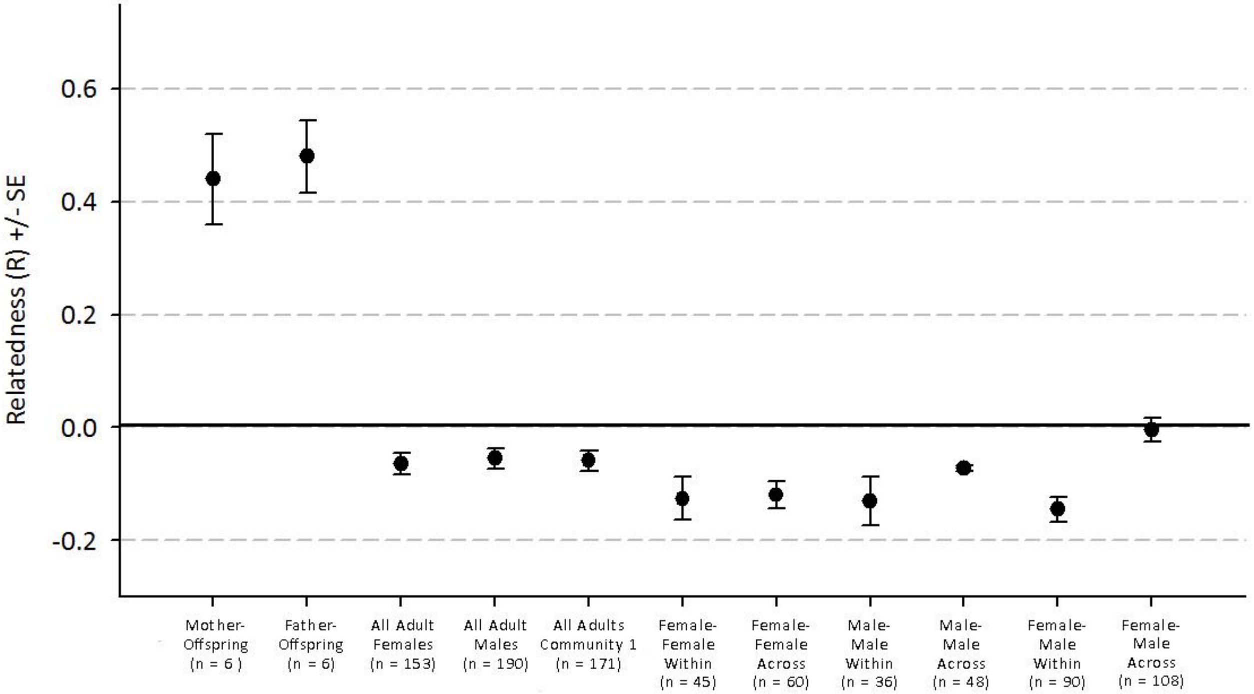

Figure 3.3 Genetic relationships among all female dyads sampled throughout the population (within and between communities, focal and non-focal). Nodes indicate individual identities and are placed relative to their calculated home range centroids within the larger communal territory. Hashed nodes indicate little to no behavioral or ranging data; centroid locations are estimates. Larger ellipses indicate communal territories. Nodes falling outside of communal territories are of unknown community descent. Lines between wedges indicate genetic relatedness of $R \geq 0.25$. Asterisks (*) indicate juvenile status at the time of sampling

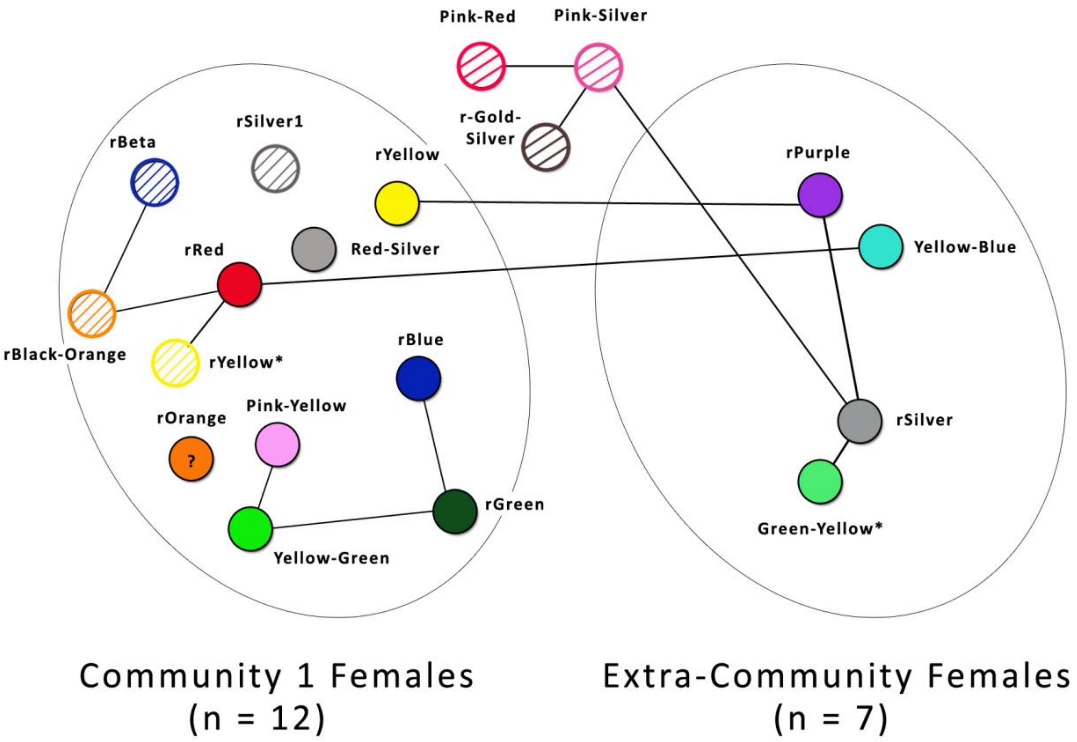
Pink-Red
Pink-Silver
r-Gold-Silver
rBeta
rSilver1
rYellow
rPurple
Yellow-Blue
rRed
Red-Silver
rBlack-Orange
rYellow*
rBlue
rOrange
?
Pink-Yellow
rSilver
rGreen
Green-Yellow*
Yellow-Green
Community 1 Females
(n = 12)
Extra-Community Females
(n = 7)

Figure 3.4 Genetic relationships among all male dyads sampled throughout the population (within and between communities, focal and non-focal). Nodes indicate individual identities and are placed relative to their calculated home range centroids within the larger communal territory. Hashed nodes indicate little to no behavioral or ranging data; centroid locations are estimates. Larger ellipses indicate communal territories. Nodes falling outside of communal territories are of unknown community descent. Lines between wedges indicate genetic relatedness of $R \geq 0.25$. Asterisks (*) indicate juvenile status at the time of sampling

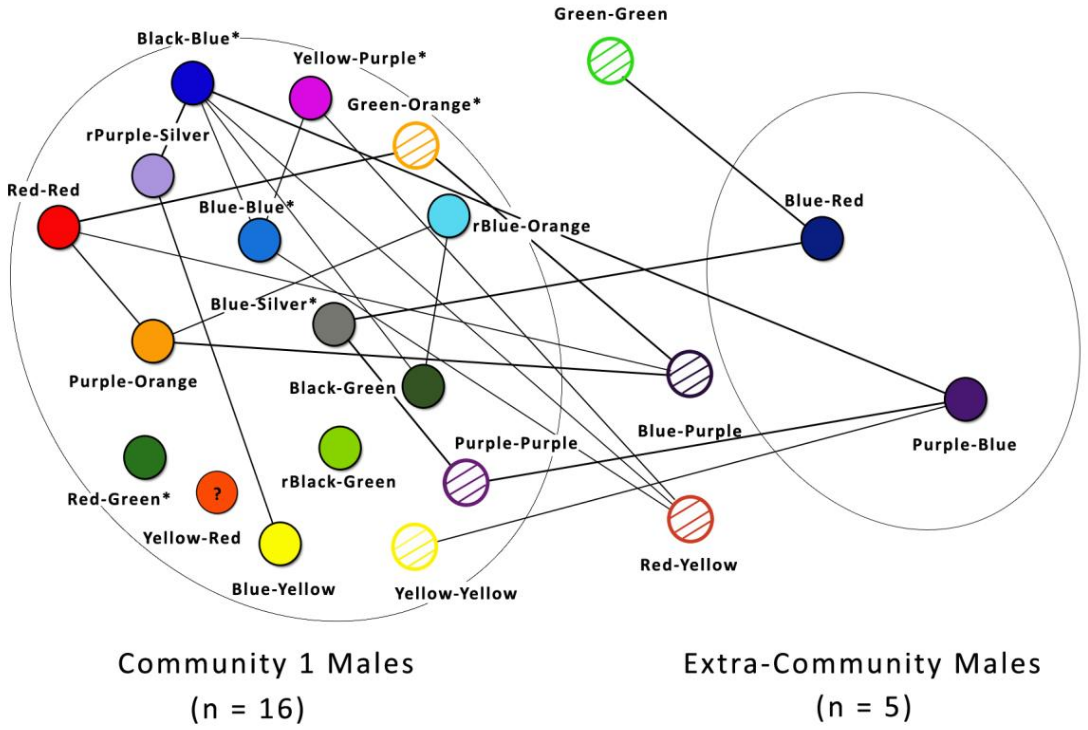
Green-Green
Black-Blue*
Yellow-Purple*
Green-Orange*
rPurple-Silver
Red-Red
Blue-Blue*
rBlue-Orange
Blue-Red
Blue-Silver*
Purple-Orange
Black-Green
Blue-Purple
Purple-Blue
Purple-Purple
Red-Green*
?
rBlack-Green
Yellow-Red
Red-Yellow
Blue-Yellow
Yellow-Yellow
Community 1 Males
(n = 16)
Extra-Community Males
(n = 5)

Figure 3.5 Genetic relationships among a) focal female (n = 8) and b) focal male (n = 10) dyads within the Mangevo community. Nodes indicate individual identities and are placed relative to their calculated home range centroids within the larger communal territory. Lines between wedges indicate genetic relatedness of R ≥ 0.25. Asterisks (*) indicate that individuals were juveniles at the time of behavioral sampling

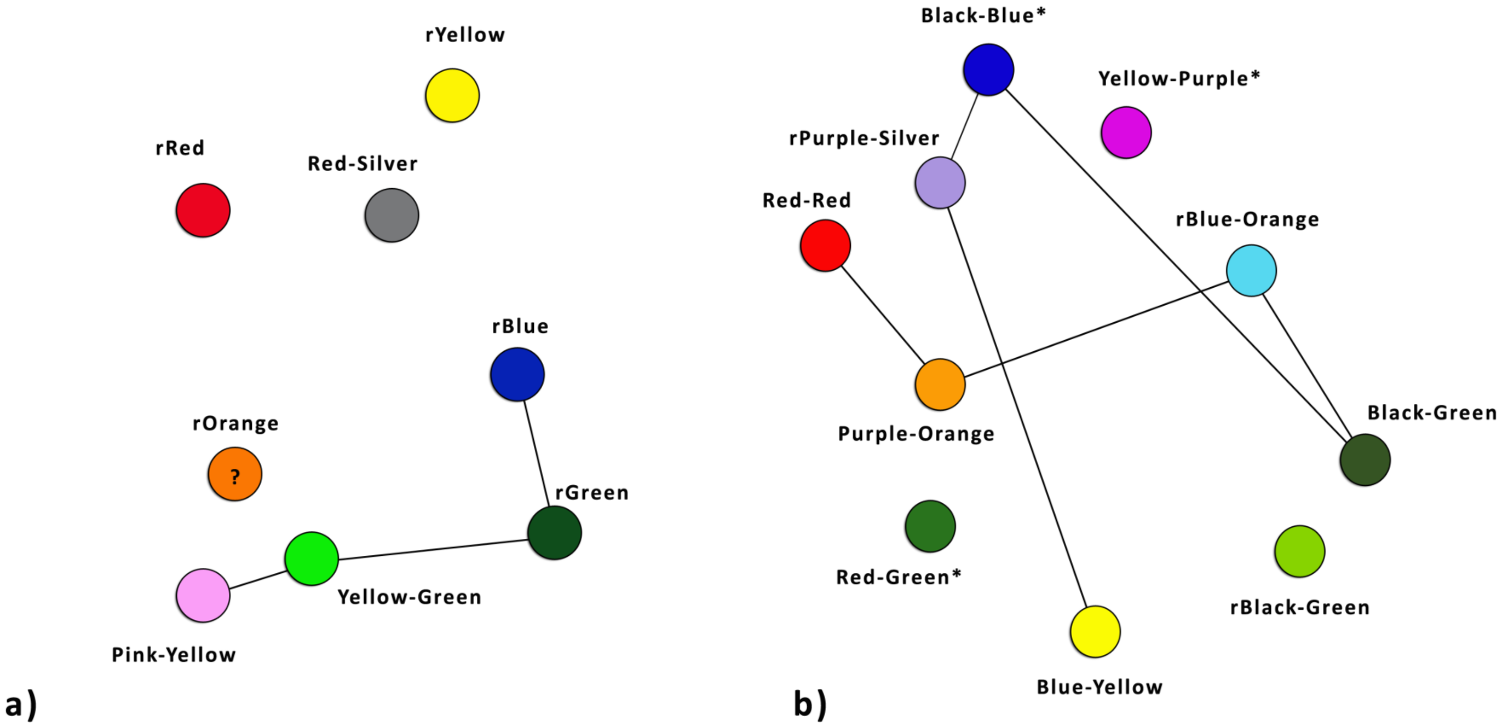
rYellow
rRed
Red-Silver
rBlue
rOrange
?
rGreen
Yellow-Green
Pink-Yellow
a)
Black-Blue*
Yellow-Purple*
rPurple-Silver
Red-Red
rBlue-Orange
Purple-Orange
Black-Green
Red-Green*
rBlack-Green
Blue-Yellow
b)

Figure 3.6 Average corrected assignment indices (*m*AIc ± S.E.) for adult male and female ruffed lemurs in the Mangevo population. Females had significantly higher *m*AIc than males ($p < 0.05$), though the sexes did not differ significantly in their variance (*v*AIc)

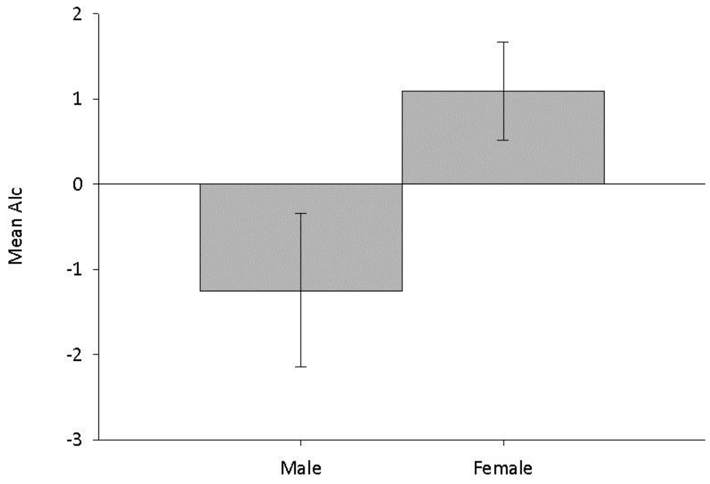

Table 3.1 Capture and sampling information for all subjects in this study, including sampling year, individual sample identification, community, sex, age, collar information and AVID microchip number

2005	2006	2007	2008	Community	Sample ID	Sex	Age	Collar ID	AVID ID
-	-	X	-	1	BADEN7.09	F	Ad	RADIO-Bk-Or1 (rBO1)*	476E64712C
-	-	-	X	1	BADEN8.3	F	Ad	RADIO-BLACK-ORANGE (rO)[¥]	4959180F3B
-	-	-	X	1	BADEN8.4	F	Ad	YELLOW-GREEN (YG)	49437A0B6B
X	X	X	-	1	RANO5.05	F	Ad	RADIO-BLUE (rB)	464D03624C
X	-	-	-	1	RANO5.07	F	Ad	RADIO-BETA*	4639530D2D
X	X	X	-	1	RANO5.08	F	Ad	RADIO-BLUE-GREEN (rG)	462B1A1171
X	X	X	X	1	RANO5.10	F	Ad	RADIO-RED (rR)	46201B2335
X	-	-	-	1	RANO5.11	F	Ad	RADIO-SILVER (rS)*	462B1A1171
-	X	X	-	1	RANO6.16	F	Ad	RADIO-BLUE-YELLOW (rY)	4721526F36
-	X	-	-	1	RANO6.17	F	Ad	RED-SILVER (RS)	4703297423
-	X	-	-	1	RANO6.26	F	Ad	PINK-YELLOW (PY)	471E0E0E29
-	-	X	-	1	BADEN7.02	F	Juv	RADIO-YELLOW, Juv.*	494A195678
-	-	X	-	1	BADEN7.03	M	Ad	RADIO-PURPLE-SILVER (rPS)	4949454E05
-	-	X	-	1	BADEN7.05	M	Ad	BLACK-GREEN (BG)	495C792510
-	-	X	-	1	BADEN7.11	M	Ad	YELLOW-YELLOW (YY)	47760D552C
-	-	-	X	1	BADEN8.1	M	Ad	RADIO-BLACK-GREEN (rBG)	49450e753a
-	-	-	X	1	BADEN8.2	M	Ad	YELLOW-RED (YR)[¥]	493006430A
X	X	-	-	1	RANO5.04	M	Ad	PURPLE-ORANGE (PO)	472049461C
X	-	-	-	1	RANO5.09	M	Ad	BLUE-YELLOW (BY)	46201C3439
X	X	-	-	1	RANO5.12	M	Ad	BLUE-PURPLE (BP)	464D220F4A
-	X	-	-	1	RANO6.15	M	Ad	RED-RED (RR)	4716203407
-	X	X	X	1	RANO6.23	M	Ad	RADIO-BLUE-ORANGE (rBO)	47147C0C1D
-	-	X	-	1	BADEN7.01	M	Juv	BLACK-BLUE (BB)	494A043B5E
X	X	-	-	1	RANO5.02	M	Juv	BLUE-SILVER (BS)	4639567277
X	-	-	X	1	RANO5.03	M	Juv	RED-GREEN (RG)	461E661F35
X	-	-	-	1	RANO5.06	M	Juv	BLUE-BLUE (BB)*	46386B7976
X	-	-	-	1	RANO5.13	M	Juv	GREEN-ORANGE (GO)	464C25222D
-	X	-	-	1	RANO6.14	M	Juv	YELLOW-PURPLE (YP)	472163525B
-	-	X	-	2	BADEN7.08	F	Ad	RADIO-SILVER-SILVER (rS)	4959551519
-	-	X	-	2	BADEN7.10	F	Ad	YELLOW-BLUE (YB)	4777101A59
-	X	X	-	2	RANO6.20	F	Ad	RADIO-PURPLE (rP)	47147F7B67
-	-	X	-	2	BADEN7.06	F	Juv	GREEN-YELLOW (GY)	49321B1C12
-	-	X	-	2	BADEN7.07	M	Ad	PURPLE-BLUE (PB)	4946361165
-	X	-	-	2	RANO6.19	M	Ad	BLUE-RED (BR)	471B756730
-	X	-	-	2	RANO6.25	M	Ad	PURPLE-PURPLE (PP)	4720447F2B
-	X	-	-	UNK.	RANO6.21	F	Ad	PINK-SILVER (PS)	472B140153
-	X	-	-	UNK.	RANO6.22	F	Ad	PINK-RED (PR)	4721781349
-	X	-	-	UNK.	RANO6.24	F	Ad	RADIO-GOLD-SILVER (rGS)*	471E184D40
-	-	X	-	UNK.	BADEN7.04	M	Ad	RED-YELLOW (RY)	49453A100E
-	X	-	-	UNK.	RANO6.18	M	Ad	GREEN-GREEN (GG)	471B554D56

*Predation event/animal lost/too few data;not included in behavioral analyses, however included in background allele

[¥] samples destroyed/lost in transport; not included in genet

Table 3.2 Microsatellite sequences/markers used, their annealing temperatures

Primers	Sequence	Annealing Temp (°C)	Size (bp)	Range	Reference
51HDZ20	F: 5'- ATG ACT TGT AGC TTA AAT CTT TTG G-3'	50	240	225-240	Louis et al. 2005
	R: 5'-TAC TTG GCT GAT TCG GGA G-3'				
51HDZ25	F: 5'-GTC AAA CGG GGA AAA TGC-3'	54	174	165-175	Louis et al. 2005
	R: 5'-TCA AAT CGG TAG CTC TCG G-3'				
51HDZ160	F: 5'-TTC TTT TTC TTT CCT TAC TTC AGC-3'	54	158	243-245	Louis et al. 2005
	R: 5'-GAT TTT GAT TAG TGT TTT TTA GAT GG-3'				
51HDZ204	F: 5'-AAT CAT GTT TTG TGG GAG GGG-3'	60	139	130-140	Louis et al. 2005
	R: 5'-GTA TAC CTC ACT GGC TCC CTG C-3'				
51HDZ247	F: 5'-AGG AAG GTA CAC TAA AAC AGA GAC T-3'	50	222	240-260	Louis et al. 2005
	R: 5'-TGT ATC CTC CAT TTA TCT CCT TG-3'				
51HDZ485	F: 5'-GCT CTC CCC CCT CAT CAA-3'	52	132	120-140	Louis et al. 2005
	R: 5'-TCA AGC GTG TCC ATT CCC-3'				
51HDZ560	F: 5'-CAC TTC TGC CTC CAA TCA CTC-3'	52	252	250-260	Louis et al. 2005
	R: 5'-AAC ATC CCG TGG TCA CTA CAG-3'				
51HDZ598	F: 5'-ATT CAG AAG TGT TAC ATT TAC GGA GG-3'	50	207	195-210	Louis et al. 2005
	R: 5'-GAG TGG GTG GCA AGG TTC G-3'				
51HDZ691	F: 5'-CCA TGA CGT TAA TTC CTC TGC-3'	50	249	230-250	Louis et al. 2005
	R: 5'-GCC ACC ATC ACC CAG TTG-3'				
51HDZ790	F: 5'-CCA CCC CAG TCC TGT CCT TA-3'	50	214	207-212	Louis et al. 2005
	R: 5'-TTG TTG CCT CTC TGC CAA GTA G-3'				
51HDZ816	F: 5'-AGA GGC CAC TAC TGA CAA CG-3'	54	288	280-300	Louis et al. 2005
	R: 5'-CCC CCA CAC ACA AAT ACT AAA C-3'				
51HDZ833	F: 5'-CTT TCA AGG ATT CTA GTC ACA CAT AT-3'	56	329	320-340	Louis et al. 2005
	R: 5'-GTA GAC AGG GCA TTA AAA GCA G-3'				
51HDZ941	F: 5'-CAT GGC TGA ATG GAT AGA GAA TGT G-3'	50	125	115-135	Louis, unpublished
	R: 5'-AGG ATT TCC TTC CCT TTT AAT ATC TG-3'				
51HDZ963	F: 5'-GGC TCC TTG GAT AGA TGT GC-3'	60	162	145-160	Louis et al. 2005
	R: 5'-TCA CCT ACA GCA GTT TCC CAG-3'				
51HDZ988	F: 5'-CTC CCC CAC ACC CAC ATA-3'	50	107	95-105	Louis et al. 2005
	R: 5'-GCC TGA AGA AGC ACC AAC A-3'				

Table 3.3 Panel of microsatellite markers, their variability and deviations from Hardy-Weinberg Equilibrium. Only adults were used to calculate background allele frequencies. Juveniles were excluded from these analyses.

Marker	k	N	Hets	Homs	H_o	H_e	PIC	NE-1P	NE-2P	NE-PP	P_{ID}	$P_{ID\text{-}SIB}$	*p*	F(Null)
20	5	28	17	11	0.607	0.575	0.503	0.830	0.686	0.525	0.251	0.530	1.00	-0.0405
25	3	27	15	12	0.556	0.595	0.506	0.830	0.698	0.553	0.251	0.521	0.71	0.0206
160	4	20	9	4	0.550	0.590	0.526	0.824	0.665	0.494	0.230	0.520	0.61	0.041
204	2	29	16	13	0.552	0.407	0.320	0.920	0.840	0.752	0.440	0.660	0.07	-0.1596
247	5	17	13	4	0.765	0.804	0.744	0.615	0.436	0.257	0.084	0.381	0.61	0.0093
485	3	30	12	18	0.400	0.332	0.283	0.947	0.853	0.758	0.498	0.711	0.63	-0.1075
560	3	29	15	14	0.517	0.649	0.562	0.797	0.654	0.505	0.207	0.483	0.43	0.1037
598	5	30	18	12	0.600	0.592	0.538	0.815	0.650	0.472	0.219	0.514	0.28	0.0123
691	4	30	23	7	0.767	0.711	0.646	0.725	0.556	0.382	0.144	0.436	0.26	-0.0543
790	3	30	19	11	0.633	0.612	0.519	0.819	0.688	0.544	0.241	0.509	1.00	-0.0211
816	5	30	25	5	0.833	0.764	0.711	0.654	0.475	0.293	0.102	0.400	0.58	-0.0563
833	5	29	22	7	0.759	0.644	0.578	0.777	0.617	0.439	0.190	0.481	0.69	-0.0971
941	5	29	20	9	0.690	0.756	0.701	0.664	0.487	0.303	0.108	0.405	0.56	0.0405
963	6	30	19	11	0.633	0.635	0.569	0.789	0.629	0.457	0.196	0.487	0.35	-0.0162
988	5	30	18	12	0.600	0.727	0.673	0.693	0.515	0.327	0.123	0.423	0.30	0.0904

Mean number of alleles per locus:	4.20
Mean proportion of individuals typed:	0.93
Mean expected heterozygosity:	0.63
Mean polymorphic information content (PIC):	0.56
Combined non-exclusion probability (first parent):	2.16×10^{-2}
Combined non-exclusion probability (second parent):	7.48×10^{-4}
Combined non-exclusion probability (parent pair):	6.05×10^{-6}
Combined non-exclusion probability (identity):	2.13×10^{-11}
Combined non-exclusion probability (sib identity):	2.28×10^{-5}

k = number of alleles; N = number of individuals genotyped
Hets = number of heterozygotes; Homs = number of homozygotes
Ho = observed heterozygosity; He = expected heterozygosity under HWE
PIC = polymorphic information content
Excl (1) = single locus exclusionary power (mother's genotype unknown)
Excl (2) = single locus exclusionary power (mother's genotype known)
ns = non-significant deviation between Ho and He ($p < 0.05$)

Table 3.4 Summary of observed values for average relatedness in various demographic categories

	Observed R		
Demographic	**N**	**Average**	**SE**
All individuals	703	-0.03	0.01
Mother-Offspring	6	0.44	0.08
Father-Offspring	6	0.48	0.06
All Adult Females	153	-0.06	0.02
All Adult Males	190	-0.05	0.02
Community 1 Adults	171	-0.06	0.02
Female-Female Within	45	-0.13	0.04
Female-Female Across	60	-0.12	0.02
Male-Male Within	36	-0.13	0.04
Male-Male Across	48	-0.07	0.00
Female-Male Within	90	-0.15	0.02
Female-Male Across	108	0.00	0.02

Table 3.5 Maternity results for the 8 juvenile offspring analyzed in this study

Offspring	Mother	r-value	No. loci compared	No. loci mismatch	NE-1P	Probability of exclusion	Critical LOD	Pair LOD score	Pair confidence	Non-excluded females
RANO5.2	RANO5.8	0.47	15	0	0.03	0.974	2.50	3.66	*	RANO5.11
RANO5.3	RANO5.11	0.28	12	0	0.02	0.983	2.50	1.66		
RANO5.6	RANO6.17	0.49	13	0	0.01	0.989	2.50	5.15	*	RANO5.7
RANO6.14	BADEN7.8	0.47	12	0	0.01	0.988	2.50	3.41	*	RANO6.26
BADEN7.1	RANO5.7	0.25	13	0	0.06	0.941	2.50	2.56	*	RANO5.10 RANO5.11 RANO6.26
RANO5.13	RANO5.7	0.37	14	0	0.02	0.980	2.50	4.25	*	RANO6.26
BADEN7.6	BADEN7.8	0.62	13	0	0.01	0.991	2.50	4.31	*	
BADEN7.2	RANO5.10	0.25	14	1	0.02	0.982	2.50	-2.28		

NE-1P = non-exclusion probability where second parent is unknown

Pair LOD score = loglikelihood ratio for a parent-offspring relationship between the known parent and the offspring

Pair LOD confidence: * = $p < 0.05$

Table 3.6a Paternity results for the 8 juvenile offspring analyzed in this study. This page: Mother's identity unknown. Next page: Mother's identity known.

Offspring	Mother	Candidate father	No. loci compared	No. loci mismatch	NE-1P	Probability of exclusion	Critical LOD	Pair LOD score	Pair confidence
RANO5.3	-	RANO6.23	13	0	0.02	0.983	6.00	3.11	
RANO5.6	-	BADEN7.4	14	0	0.01	0.989	6.00	7.50	*
RANO6.14	-	BADEN7.4	12	0	0.01	0.988	6.00	6.70	*
BADEN7.1	-	BADEN7.4	13	0	0.06	0.941	6.00	4.64	
BADEN7.2	-	BADEN7.5	14	0	0.02	0.980	6.00	7.02	*
RANO5.13	-	RANO5.12	14	0	0.01	0.991	6.00	6.88	*
RANO5.2	-	RANO6.19	14	1	0.03	0.974	6.00	0.22	
BADEN7.6	-	BADEN7.7	12	1	0.02	0.982	6.00	-1.08	

Table 3.6b Paternity results for the 8 juvenile offspring analyzed in this study. Previous page: Mother's identity unknown. This page: Mother's identity known.

Offspring ID	Mother ID	Candidate father ID	Trio loci compared	Trio loci mismatching	NE-2P	Probability of exclusion	Critical LOD	Trio LOD score	Trio confidence
RANO5.3	-	RANO6.23	0	0	0.02	0.983	-6.50	0.00	
RANO5.6	RANO6.17	BADEN7.4	14	0	0.00	0.998	-6.50	7.60	*
RANO6.14	BADEN7.8	BADEN7.4	12	0	0.00	0.998	-6.50	7.99	*
BADEN7.1	RANO5.7	BADEN7.7	12	0	0.00	0.996	-6.50	5.99	*
BADEN7.2	-	BADEN7.5	0	0	0.02	0.980	-6.50	0.00	
RANO5.13	RANO5.7	RANO5.12	14	0	0.00	1.000	-6.50	10.70	*
RANO5.2	RANO5.8	RANO6.19	14	2	0.00	1.000	-6.50	-2.63	*
BADEN7.6	BADEN7.8	BADEN7.7	12	2	0.00	0.999	-6.50	-3.54	*

NE-1P = non-exclusion probability where second parent is unknown

NE-2P = non-exclusion probability when second parent is known (in this case, where most-likely mother is assigned)

Pair LOD score = loglikelihood ratio for a parent-offspring relationship between the known parent and the offspring

Trio LOD score = for a parent-offspring relationship between the candidate parent and the offspring given the known parent. This value is zero if either the

Pair & Trio LOD confidence: * = $p < 0.05$

Table 3.7 Test results for sex-biased dispersal

					Association Index	
Sex	**n**	**F_{IS}**	**F_{ST}**	***R***	**Mean**	**Variance**
Females	16	-0.10	0.04	-0.13	1.09	5.35
Males	14	0.01	0.07	-0.13	-1.25	11.34
	p	0.24	0.47	0.08	**0.05**	0.11

**All results are based on 1,000 permutations in FSTAT*

Significant values are **bold**

Chapter 4

Maternal cooperation and communal nesting

[Formatted for submission to Proceedings of the Royal Society B – Biological Sciences in collaboration with Edward E. Louis Jr., Center for Conservation and Research, Henry Doorly Zoo, 3701 S 10th Street, Omaha, NE 68107; Brenda J. Bradley, Department of Anthropology, Yale University, New Haven, CT 06511]

ABSTRACT

Cooperative breeding is common among some avian and mammalian taxa. However, this system of shared infant care is rare among primates. While some primates participate in extensive alloparental care, and others are characterized by cooperative breeding with helpers at the nest, it is arguably only humans that participate in communal breeding, a system in which all females within a single social unit reproduce and then collectively share in maternal responsibilities. Though little known, this reproductive system has also been suspected for ruffed lemurs (*Varecia* sp.), a diurnal Malagasy strepsirrhine, suggesting that ruffed lemurs may represent the only diurnal primate to converge with humans on this unusual reproductive strategy. Here, we present results from the first systematic field study of communal breeding in ruffed lemurs to combine data on rearing behavior, genetic relatedness and infant survivorship. We demonstrate that communal care is biased towards kin and female affiliates, and it improves infant

survival, particularly during early stages of infant development. As communal nesting allows an improved balance between maternal responsibility and foraging effort, our results indicate that communal breeding in ruffed lemurs results in improved maternal energy balance, and ultimately confers direct fitness payoffs to communally nesting females.

INTRODUCTION

Cooperative breeding is a relatively rare though phylogenetically widespread reproductive strategy among avian and mammalian taxa and refers to situations where individuals regularly care for infants that are not genetically their own (Emlen 1991; Solomon & French 1997; Koenig 1997). Although the majority of cooperatively breeding species live in family units comprising both breeding individuals and their offspring helpers (Emlen 1991), group composition in these systems can range in reproductive skew from a single reproductive pair (cooperative or singular breeders) to multiple breeding females within a single social unit (communal or plural breeders) (Keller & Reeve 1994). As with classic cooperative breeders, communal breeding is a broadly distributed phenomenon within the Animal kingdom (Koenig 1997; Gittleman 1985) but is a strategy which is exceedingly rare in the Primate Order (Hrdy 2005). In fact, humans are widely cited as the only communally breeding primate species, with multiple reproducing females collectively sharing in child-rearing responsibilities ranging from babysitting to allonursing (Hrdy 2005; Burkart et al. 2009; but see Fietz 1999; Eberle & Kappeler 2006).

Communal breeding, however, has also been suspected for ruffed lemurs (*Varecia* sp.) (Morland 1990; Vasey 2007), a distantly related Malagasy strepsirrhine. Ruffed lemurs are highly social, 3 to 4 kilogram primates that live in large, communally-defended territories characterized by fission-fusion dynamics (Morland 1991). Like most primates, they exhibit relatively slow life histories, due in part to their strict patterns of seasonal breeding (Foerg 1982; Rasmussen 1985; Morland 1993); however, they are distinctive in that they are the only known diurnal primate to bear litters of two to five altricial offspring during annual reproductive events (Foerg 1982; Rasmussen 1985). Because they cannot cling, litters are parked in nests and tree tangles until capable of independent travel (Morland 1990), and it is during this time that evidence of communal breeding has been reported, including use of communal nests (i.e., "kindergartens") and cooperative infant care (Morland 1990; Vasey 2007). Previous studies have proposed that *Varecia* kindergartens may confer energetic advantages to mothers (Morland 1990), though such benefits have yet to be established. Moreover, it is unclear whether mothers show preferences for communal nesting partners, why females select these particular partners, and whether these preferences vary.

Among other communal breeders, the evolution of non-offspring care, which can include grooming, guarding, predator protection, and energy transfer (e.g., provisioning, allonursing), has been explained by a number of adaptive hypotheses (Emlen 1991; Koenig 1997). For instance, it is argued, though rarely empirically demonstrated, that communal care might confer benefits to participating mothers and infants by enabling lactating females to increase food intake, improve infant thermoregulation and/or growth, guard against predators, and improve competitive abilities later in life (Koenig 1997; Sparkman et al. 2011). Moreover, while reciprocity, mutualism, and kinship have all been used to explain why communal breeders live and reproduce in groups, the benefits of communal breeding have yet to be established for several taxa (Koenig 1997).

In this study, we examine the effects of communal breeding in black-and-white ruffed lemurs (*Varecia variegata*). Specifically, we test whether communal nesting influences maternal energetics and infant survival. Moreover, we address the potential variables influencing the incidence and intensity of alloparental care behaviors exhibited amongst communally nesting females.

MATERIAL & METHODS

Study site and subjects

Study subjects were members of one black-and-white ruffed lemur population (N = 41 individuals) from Mangevo, a mid-altitude primary rainforest site within Madagascar’s Ranomafana National Park (Wright1992). Prior to the onset of behavioral sampling, all members of the focal community were captured and fitted with unique collar-tag combinations and blood and tissue samples were collected for genetic analyses following established protocols (Glander 1993; Louis et al. 2005). During subsequent behavioral observations, we collected data on maternal activity budget and diet, range use, and patterns of female affiliation and aggression, as well as details of communal nesting and infant care during the only reproductive season that occurred during six consecutive years of study between 2005 and 2010.

Behavioral observations

All-day follows of focal individuals (Altmann 1974) were focused on eight females and their litters (n = 7 litters, 18 infants; Table 4.1) studied during one birth season from late gestation through the onset of independent infant travel (September–December 2008; 1,202 hours). Thereafter, communal nesting ceased. Instantaneous sampling was conducted on a focal female at five-minute intervals and was used to document individual activity budget and diet, as well as group size, composition and cohesion, while a continuous record was kept of all affiliative and aggressive interactions and infant-care related behaviors, such as nest construction and both maternal and non-maternal infant care. Following parturition, instantaneous nest scans were also employed at five-minute intervals to document infant care behaviors exhibited at the nest in the mothers' absence, including the number and identity of helpers at the nest. Continuous data were collected during all occurrences of infant-care behaviors to document frequency, duration and types of care provided, as well as the identities of care providers. Finally, to document infant mortality, the number and identities of surviving infants was noted at the beginning of each observation bout.

During behavioral observations, GPS coordinates were collected from below the focal individual at 10-minute intervals to document range use and determine spatial proximity among females' ranges.

Data analysis

Mothers were designated as communal or singular nesters prior to statistical comparisons ("singular": communal nesting comprised < 1% of total observed nesting time; "communal": communal nesting comprised > 1% of total observed nesting time). Nonparametric statistics were used in all cases and all tests were one-tailed, unless otherwise noted.

Behavioral data were used to calculate two association indices: a standard Association Index (AI) and a Communal Nesting Association Index (CNI). AIs were calculated following Symington (1990) and CNIs were calculated as the proportion of scans that dyads were observed nesting together divided by the sum of their total observed nesting time. In all cases, possible indices ranged from 0 to

1. Subsequent social and nesting networks were created in UCINET using the NetDraw extension and modified in Photoshop CS2 to visually illustrate the strength of relationships amongst subjects.

ArcMap 9.3 (Hawth's Tools) was used to calculate home ranges (95% MCP, Fixed Kernel Density) for each female using GPS coordinates collected between October and December 2008. Spatial proximity between female home ranges was calculated as the straight line distances between the centroids of any two females' ranges.

Variance in litter size was small (0.085; range: 2 – 3 infants/litter) and was not included in the analysis. Spatial proximity, AIs and pairwise relatedness (*R*; see Molecular methods) were significantly correlated at $p < 0.05$. Therefore, we used partial Mantel tests to examine the potential relationships between each of these three variables and communal nesting associations (CNIs). The partial Mantel method uses a randomization approach to conduct pairwise comparisons between the elements of two distance matrices while holding a third distance matrix constant. For each dataset, all variables were transformed into z-scores (Sokal & Rohlf 1995). Ten thousand randomizations were performed for each test to determine statistical significance. Using this method, the relationship between each independent variable and the predictor variable was evaluated twice, controlling for each of the two remaining variables in sequence. Alpha was set at 0.05 and adjusted using the Holm-Bonferroni method, a sequentially rejective multiple test procedure which controls for family wise error for all *k* hypotheses at level alpha in the strong sense (Holm 1979). All tests were one-tailed.

Molecular methods

Nuclear DNA was extracted from blood and tissue samples using standard nucleic acid extraction kits (QIAamp DNA Mini Kit). Extraction procedures followed the manufacturer's protocols, with the following modification to the tissue extraction procedures: samples were allowed to lyse initially in ASL buffer for 24-48 hours rather than 10 minutes. Samples were then genotyped with a suite of 15 polymorphic microsatellite loci (Louis et al. 2005). PCR amplification was carried out in a total volume of 25 μl consisting of 2 μl template, 12.5 μl Qiagen HotStarTaq Master Mix, 10 μM of each primer, and 5.5 μl doubly-distilled H_2O. Amplification conditions were as follows: initial denaturation at 95°C for 15 minutes; 35 cycles of 30 s at 94°C, 40 s at 54 to 60°C (see Louis et al. 2005), 1 min at 72°C, and a final extension of 7 min at 72°C. The 5' end of the forward primer was fluorescently labeled, and amplification products were separated using capillary electrophoresis (ABI 3730xl Genetic Analyzer). Alleles were sized relative to an internal size standard (ROX-500) using Gene Mapper software (Applied Biosystems) and allele binning was performed by eye. The number of replicates necessary to ensure the detection of allelic dropout was calculated based on the amount of DNA per reaction and the observed rates of allelic dropout (Morin et al. 2001). Panels yielded PI_{sib} values of 2.7×10^{-5}, demonstrating the very low probability that any two individuals would be expected to share the same multilocus genotype by chance. Using these multilocus genotypes, an estimate of genetic relatedness (*R*) was calculated for every pair of individuals in the population using ML-RELATE (Kalinowski et al. 2006). Pairwise relatedness scores were calculated using allele frequencies derived from a larger population of 38 multilocus genotypes. Mothers were considered related if *R* scores were greater than or equal to 0.25. Permutation tests were executed in Excel 2007 to evaluate the significance of the differences in mean pairwise relatedness among cooperating and single mothers (Bradley et al. 2004).

RESULTS

Litter size and nesting strategy

With one exception, all seven females within the community reproduced within a two-week period, each bearing litters of two or three altricial offspring ($\bar{x}$ = 2.7 ± 0.45 s.d., n = 7 litters). Of these females, six of seven nested their litters communally. The extent of communal nesting differed markedly among mothers (Table 4.1), as did their patterns of communal nesting associations (Figure 4.1). Of the five females for which focal data were available, three nested their litters communally for greater than 1% of their total nesting time ($\bar{x}$ =18.9% ± 3.32 s.d., range = 15-23%; n = 3 mothers), and were thus considered “communal nesters”. One female nested her infants communally for only 0.4% of her total nesting effort and was thus considered a “singular nester” along with one female whose litter was never observed in a communal nesting situation. Focal data were unavailable for the remaining two females, but they were regularly observed in co-nesting associations with focal mothers, and were thus also considered communal nesters.

Factors influencing nesting strategy

While spatial proximity and litter size did not influence patterns of co-nesting associations, genetic relatedness and affiliative social relationships played an important role; communal nesters shared significantly higher average pairwise relatedness (*R*) than the mean relatedness found among female-female dyads overall (mean $R_{\text{communal nesters}} = 0.28 \pm 0.09$ s.e.m. versus mean $R_{\text{overall}} = -\ 0.13 \pm 0.02$ s.e.m., $p < 0.001$), and both pairwise relatedness (partial Mantel $r_{\mathrm{CNIx}R\mathrm{.PROX}} = 0.692$, $p < 0.001$; partial Mantel $r_{\mathrm{CNIx}R\mathrm{.AI}} = 0.409$, $p = 0.010$) and association indices (partial Mantel $r_{\mathrm{CNIxAI.PROX}} = 0.704$, $p < 0.001$; partial Mantel $r_{\mathrm{CNIxAI.}R} = 0.432$, $p = 0.004$) were positively correlated with the occurrence and intensity of communal nest use (Figure 4.1). That relatedness, proximity, and association were also positively correlated suggests that female philopatry may result in networks of closely related, potentially cooperating females, a pattern that is not unlike those seen in bell miners (Painter et al. 2000) and other cooperatively breeding birds and mammals, including humans (Scelza et al. 2008). It is worth noting, however, that not all cooperative dyads were related and not all related dyads cooperated (Figure 4.1). Moreover, at least one singular nester had a relative in close proximity.

Energetic benefits of communal nesting

We detected significant changes in female activity budget before and after birth, such that females' feeding time, and with it their potential for energy intake, significantly declined post-parturition (Wilcoxon Signed Ranks test, *Z*: -2.023, *p* = 0.043, Figure 4.2). While we cannot account for changes in feeding rate pre- and post-birth, the observed change in feeding time did not correlate with changes in dietary composition (Spearman's rho, two-tailed: 0.1, *p* = 0.873), suggesting that the reduction in feeding time was not a consequence of food quality. Among females, however, feeding time did not differ (Mann Whitney-*U* = 51.10, *Z* = -0.04, *p* = 0.971, Figure 4.3), despite variation in litter size, suggesting that the burden of infant care was similar across females during the earliest stages of infant development. After the onset of communal nesting, however, maternal activity budgets diverged; communally nesting females spent significantly less time at their nests and significantly more time feeding than did singular nesters (Mann-Whitney-*U* = 61, *Z* = 2.539, *p* = 0.01*;* *U* = 56, *Z* = -2.049, *p* = 0.04, respectively; Figure 4.3). Moreover, as kindergarten use increased among communal nesters, mothers spent increasingly less time at their nests (Spearman's rho, one-tailed: -0.572, $p = 0.04$) and more time feeding and foraging (Spearman's rho, one-tailed: 0.792, $p = 0.003$).

Fitness benefits of communal nesting

As with many other lemur species, infant mortality during this study was relatively high ($\bar{x} = 21\%$; Table 1); however, infants belonging to singular nesters suffered significantly greater mortality ($\bar{x} = 60\%$, 3 of 5 infants, n = 2 mothers) than did infants belonging to communal nesters ($\bar{x} = 7\%$; 1 of 14 infants, n = 5 mothers)(Mann Whitney-U = 0.000, $Z = -2.137$, $p = 0.033$, Figure 4.4). We also detected a significant positive relationship between the overall proportion of communal nest use and infant survival (Spearman's rho = 0.872, $p = 0.026$, Figure 4.4), suggesting that it is not simply the presence or absence of communal care, but rather its intensity which predicts infant survival.

DISCUSSION

Many lemur traits are thought to have evolved as a means of coping with Madagascar's often erratic climate (Wright 1999). As evidenced by this study and others (Ratsimbazafy 2002), ruffed lemurs, the most frugivorous of the Malagasy strepsirrhines, have adapted to this unpredictability by means of a "boom or bust" reproductive strategy, bearing litters of young only during years of resource abundance. During these rare reproductive events, mothers bear large litters of rapidly growing, altricial infants (Morland 1990); this, along with the most energetically rich milk known for primates (Tilden & Oftedal 1997) makes the lactation period particularly energetically costly for these females. Communal nesting may therefore be a necessary strategy to help offset these costs. Here, we demonstrate that communal nesting allows females increased time away from the nest to feed and forage, a trade-off which appears to be particularly important to ensuring infant survival during these rare reproductive events. Our results are consistent with previous research on primate alloparental care, which demonstrates that helpers relieve mothers from the burdens of infant care (Mitani & Watts 1997), allowing mothers to feed longer or at faster rates than when they themselves are the sole care providers (Stanford 1992), and confers benefits which may directly affect infant survival (Lemon & Barth 1992; Fairbanks & McGuire 1995; Ross & MacLarnon 2000; Mann & Watson-Capps 2005; Lewis & Kappeler 2005).

In light of these great energetic demands and the benefits gained by cooperative infant care, one might expect all ruffed lemur females to participate in communal nest use. In this study, however, we demonstrate that communal nesting and cooperative infant care is biased towards, though not limited to, kin and close affiliates. That the two singularly nesting females were either primiparous (i.e., inexperienced) or lacked neighboring reproductive kin suggests that singular nesting may be the exception rather than the rule. Thus, while communal breeding can be difficult to explain in light of individual selection, kin selection may help to explain maternal cooperation during these so-called gambles in reproduction.

Given that females in this taxon can either 'make it' or 'break it' during any given reproductive season, inclusive fitness benefits gained by communally nesting relatives may provide a necessary incentive. The obvious question remaining is whether extra-parental care providers such as juveniles and non-reproducing adults also share some level of genetic relatedness, as is seen in some nocturnal strepsirrhines (Eberle & Kappeler 2006) and callitrichines (Garber 1997). Previous studies offer equivocal support for the role of kin selection in primate alloparental care behaviors (McKenna 1979; Garber 1997), though it has been demonstrated to play a prominent role in the infant care strategies of other mammalian taxa (Tilden & Oftedal 1997; but see Clutton-Brock 2002). Future research will address whether non-maternal care providers are also kin, allowing us to further elucidate the evolutionary impetus for cooperative care in this unusual primate.

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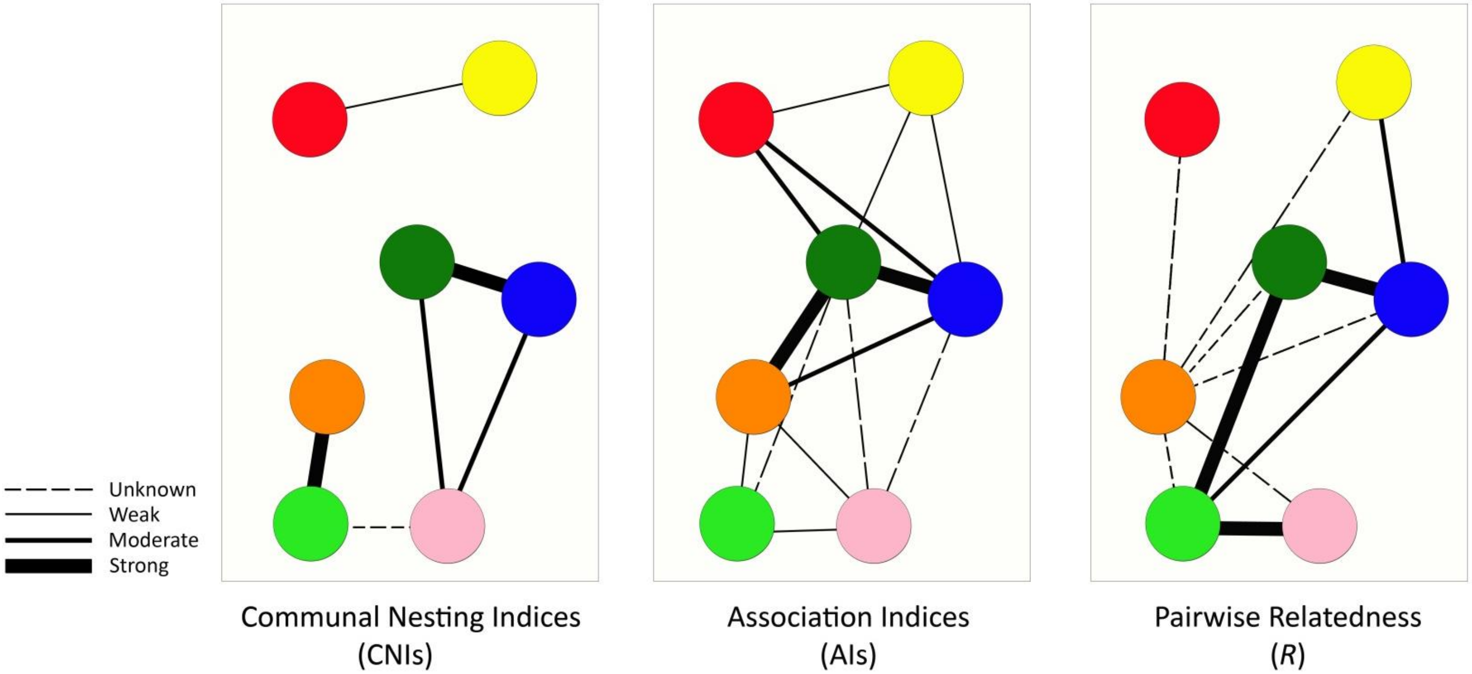
Figure 4.1 Network analyses demonstrating the strength of female co-nesting associations (as calculated by Communal Nesting Indices), strength of female affiliation patterns (as calculated by Association Indices), and pairwise relatedness (as calculated by the relatedness coefficient, R). Colored nodes indicate mothers. (Nodes are arranged according to spatial location, i.e., female home range centroids, within the larger communal territory.) Solid lines indicate dyadic relationships. Dashed lines indicate unresolved relationships or missing data. Line weight indicates the strength of relationships. For Communal Nesting and Association Indices, heavy line weight indicates an index of of ≥ 0.1; medium weight indicates an index of 0.099 to 0.001; light weight indicates an index of < 0.001. For pairwise relatedness, heavy line weight indicates that individuals are related at $R \geq 0.5$; medium weight indicates R of 0.25 to 0.49; dyads exhibiting $R < 0.25$ are considered unrelated



Communal Nesting Indices (CNIs)

Association Indices (AIs)

Pairwise Relatedness (*R*)

Figure 4.2 Maternal activity budgets significantly changed post-parturition (Friedman's Two-Way ANOVA by rank, $\chi^2 = 24.646$, $p < 0.001$). Female feeding and resting time significantly declined (Wilcoxon signed ranks, $Z = -2.023$, $p = 0.043$), while infant care significantly increased (Wilcoxon signed ranks, $Z = 2.023$, $p = 0.043$. Travel and Other/Social did not differ. $*p < 0.05$. Error bars calculated as standard error

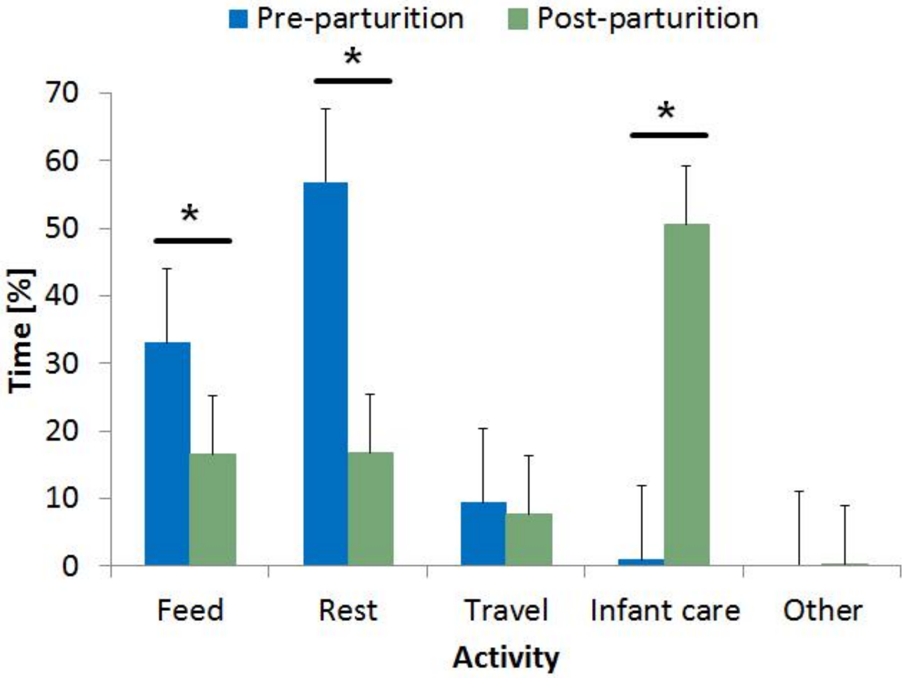


Figure 4.3 Average female feeding time before and after the onset of communal nesting. Prior to the onset of communal nest use, females did not differ significantly in their percentage of time spent feeding (Mann Whitney-*U* = 51.10, *Z* = - 0.04, *p* = 0.971). After the onset of communal nesting, however, cooperating females (i.e., communal nesters) spent a significantly greater percentage of their time feeding than did single nesters (*U* = 56, *Z* = -2.049, *p* = 0.04). * $p < 0.05$. Error bars calculated as 95% CIs

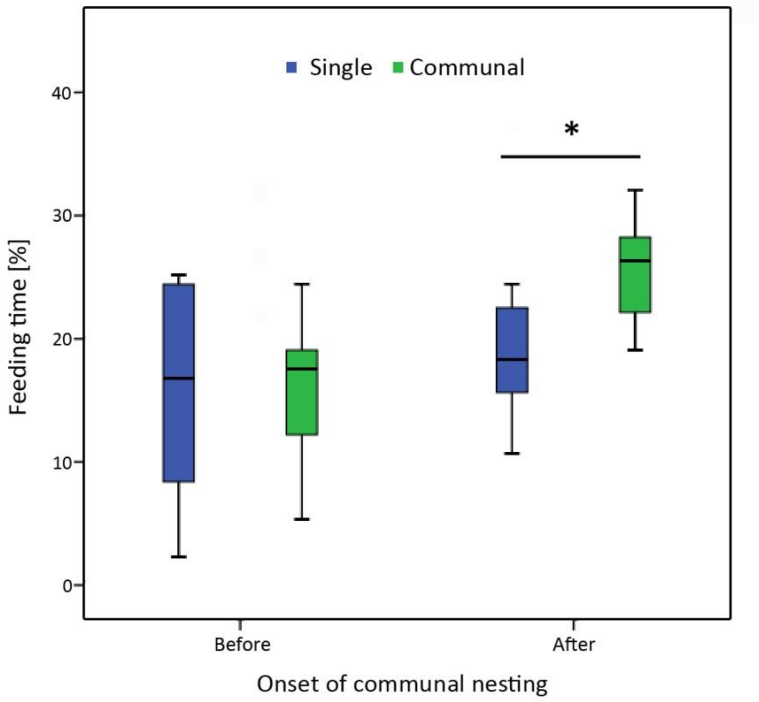
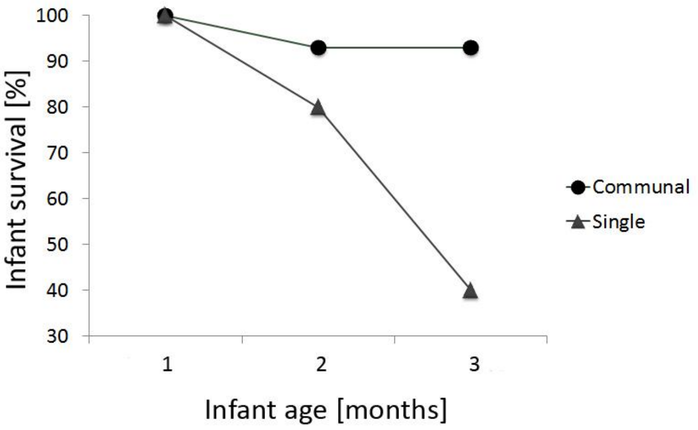


Figure 4.4 Effects of nesting strategy on infant survival. Infants belonging to communal nesters experienced significantly higher survival than did those belonging to single nesters (Mann Whitney-U = $Z = -2.213$, $p = 0.03$) (top). Moreover, infant survival is positively correlated with the intensity of communal nesting (Spearman's rho = 0.872, $p = 0.03$) (bottom)



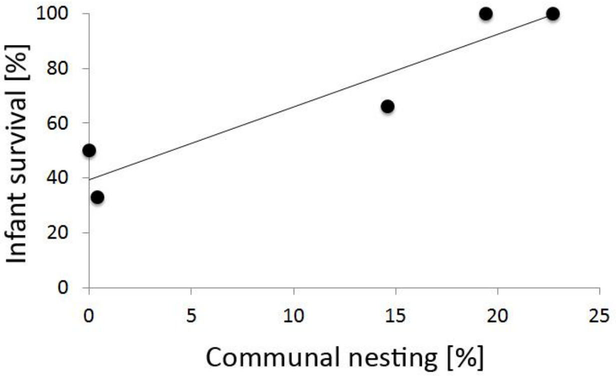


Table 4.1 Observed matings and births between 2005-2010

Year	Red	Orange	Yellow	Green	Blue	Yel-Grn	Pnk-Slv	Red-Slv
2005m	*no*	n.d.	n.d.	*no*	*no*	n.d.	n.d.	n.d.
2005b	*no*	n.d.	n.d.	*no*	*no*	n.d.	n.d.	n.d.
2006m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
2006b	***yes?*** †	n.d.	n.d.	*no*	*no*	n.d.	n.d.	n.d.
2007m	*no*	n.d.	*no*	*no*	*no*	n.d.	n.d.	n.d.
2007b	*no*	*no*	*no*	*no*	*no*	*no*	*no*	*no*
2008m	***yes***	***yes***	***yes***	***yes***	***yes***	n.d.	n.d.	n.d.
2008b	***yes***	***yes***	***yes***	***yes***	***yes***	***yes***	***yes***	*no*
2009m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
2009b	*no*	*no*	*no*	*no*	*no*	*no*	*no*	*no*
2010m	n.d.	n.d.	n.d.	n.d.	n.d.	*	n.d.	n.d.
2010b	*no*	*no*	*no*	*no*	*no*	*	*no*	n.d.

†: Juvenile (<1 year) present in group during September 2007; maternity uncertain (genetics pen

*: death related to predation event; m: mating; b: birth

Table 4.2 Study subjects, litter size at birth, care strategy and infant survival during the first three months post-parturition

FemaleID	Focal	Genotype	Care Strategy	Communal nesting [%]	Litter size at birth	No. surviving offspring			Mortality [%]
						Month 1	Month 2	Month 3	
rRed	Y	Y	Single	0.4	3	3	3	1	66.6
rYellow	Y	Y	Single	0	2	2	1	1	50
rOrange	Y	N	Communal	14.7	3	3	2	2	33.3
rGreen	Y	Y	Communal	22.8	3	3	3	3	0
rBlue	Y	Y	Communal	19.4	2	2	2	2	0
Pink-Yellow	N	Y	Communal	-	3	3	3	3	0
Yellow-Green	N	Y	Communal	-	3	3	3	3	0
Red-Silver	N	Y	-	-	-	-	-	-	-
Total (N)	8	7			19	19	17	15	21.4

Chapter 5

Communal infant care in black-and-white ruffed lemurs: Synthesis of findings and proposal for future directions

The overarching goal of this dissertation was to describe ruffed lemur communal infant care and to address four main questions: 1. To what extent do mothers participate in communal care (i.e., is there variation in care strategies)? 2. Who do females select as nesting partners (i.e., do females show preferences for communal care partners)? 3. Why do females select these particular nesting partners? 4. How do females benefit from communal infant care?

To address these questions, my dissertation had three aims: 1) to characterize the spatial ecology of a black-and-white ruffed lemur community using Global Information System (GIS) techniques; 2) to then characterize the genetic population structure of this same community using molecular techniques; and finally 3) to describe the patterns of communal nest use in ruffed lemurs and to examine how spatial, genetic and social variables influenced patterns of ruffed lemur communal breeding.

Together, results from this study revealed that the ruffed lemurs in Ranomafana National Park lived in a dispersed fission-fusion society unlike any other primate fission-fusion social system (Table 5.1). Ruffed lemur communities are not characterized by male-philopatry and female-biased dispersal, as are most primate fission-fusion societies (e.g., Goodall 1986; Nishida & Kawanaka 1972; Pusey 1979; Strier 1994; Symington 1990; but see Di Fiore et al. 2009). Rather, in ruffed lemurs, both sexes disperse from their natal territory. Moreover, while ruffed lemur communities are characterized by sex-segregated range use, as are most fission-fusion systems (e.g., Chapman 1990; Chapman et al. 1995; Goodall 1986; Nishida 1968; Shimooka 2003; Symington 1990; Williams et al. 2002; Wrangham 2000; Wrangham et al. 1992; Wrangham and Smuts 1980; but see Lehmann and Boesch 2005; Lehmann and Boesch 2008; Spehar et al. 2010), in this case, females – not males – use larger annual home ranges. What's more, despite overall differences in range size, home range overlap does not follow these same sex-segregated patterns typical of most primate fission-fusion systems (Nunes 1995; Symington 1988; Wrangham et al. 1992; Wrangham and Smuts 1980); both males and females within the focal ruffed lemur community exhibited moderate home range overlap with both same- and opposite-sex conspecifics. Female ruffed lemurs were also anecdotally responsible for territory defense, though this pattern has yet to be quantitatively verified. Thus, rather than adhering to either the 'male-bonded' or 'bisexually-bonded' systems characteristic of most primate fission-fusion societies (Wrangham 1979; Lehmann and Boesch 2005; Lehmann and Boesch 2008) ruffed lemurs appear to combine aspects of both ‘bisexually-bonded’ and female-biased (‘female-bonded’) systems of fission-fusion dynamics.

Unsurprisingly, given the dispersal patterns identified in this study, average relatedness between community members was low. Within the community, however, group members lived in close spatial proximity to and frequently affiliated with other related individuals, thus forming kin networks within the larger social community.

During the reproductive season, females used two infant care strategies: exclusive maternal care and communal infant care (i.e., crèching). Mothers without neighboring kin or whose kin were non-reproductive were their infants’ sole care providers, whereas related females participated in crèching behavior, which consisted of communal nesting and babysitting. Relative to females who provided exclusive infant care, mothers who crèched their young were afforded the opportunity to trade-off between infant care responsibilities and other important maintenance activities, including feeding/foraging and social interactions. Ultimately, these same females had higher infant survival, a benefit that may ultimately translate into higher lifetime fitness benefits.

The suite of traits described herein (i.e., fission-fusion, unbiased dispersal, communal breeding) are uncharacteristic of most primate taxa (Table 5.2). While it is true that ruffed lemurs share these ‘rare’ behaviors with a handful of other primates, even those taxa differ from ruffed lemurs in their suite of social and reproductive traits (e.g., fission-fusion social organization and cooperative breeding are found in a few non-human primates, but never in tandem). Instead, it seems that ruffed lemurs exhibit a social system that has gone previously unrecognized in primates, and instead loosely resembles patterns found in other communally breeding mammals such as hyenas (e.g., fission-fusion dynamics, female dominance and territory defense, and crèching behavior: Boydston et al. 2003; Henschel and Skinner 1991; Holekamp et al. 2000).

Among primates, then, what makes ruffed lemurs special? While this study has succeeded in further establishing a baseline understanding of ruffed lemur social and reproductive strategies, the answers herein have only led to more questions. The following sections will attempt to synthesize what we now know of ruffed lemur social and infant care strategies, what remains to be learned, and suggestions for how to approach these questions in future research.

Ruffed lemur social organization: How variable is it?

Chapter Two focused on the spatial ecology of black-and-white ruffed lemurs. Specifically, I addressed inter-sexual and seasonal variation in home range area, overlap and daily distance traveled. While results from this study resembled previous studies in certain regards (e.g., fission-fusion social organization, larger female versus male home ranges; Morland 1991a; Morland 1991b; Rigamonti 1993; Vasey 1997; Vasey 2006), they differed in others (e.g., no seasonal variation in female home range size contra Vasey (2006). Furthermore, other studies have reported pair-living (White 1991) and cohesive multi-male/multi-female groups of ruffed lemurs (Britt 1997; Balko 1998; Ratsimbazafy 2002), though these studies varied in duration and sampling regime. Thus, the question remains: how variable *is* ruffed lemur social organization? Is the variation observed across studies representative of inter-population and inter-annual variation in social organization (i.e., due to ecological/demographic variation across sites)? Or are these differences a result of sampling methods and study duration?

Spehar and colleagues (2010) found variation in spider monkey range use and association, differences which were attributed to anthropogenic pressures characteristic of the study site (e.g., hunting pressure and forest exploitation). Furthermore, variation in predation pressure, the distribution and availability of food resources and population density were used to explain between-site differences in chimpanzee range use and association (Lehmann & Boesch 2005, 2008). Thus, it is quite possible that such behavioral flexibility also exists across ruffed lemur populations. Unfortunately, studies on ruffed lemurs are comparatively few and shorter in duration. Moreover, few data are available on population density, anthropogenic influences and habitat characteristics at these sites. Thus, before we can begin to understand the behavioral diversity across ruffed lemur populations, we must first understand the ecological context in which these behaviors occur. In the future, efforts should be made not only to quantify variation in grouping patterns and social organization, but also to characterize habitats, resource availability, and human impacts, if any exist. Further, long-term monitoring is a priority if our aim is to address inter-annual variation in ruffed lemur ranging patterns.

Using the data in hand, however, the obvious next step toward contextualizing ruffed lemur social organization within the larger primate fission-fusion framework is to quantify patterns of sex-specific association and the use of boundary areas. As indicated by Table 5.1 (and references therein), most primate fission-fusion systems exhibit sex-segregated patterns of association and range use, with males showing greater affiliation and more extensive range use, including a higher incidence of territorial boundary patrols and the use of peripheral zones. Currently, the only data available for ruffed lemurs are anecdotal reports of communal territory defense by females (Morland 1991b; Vasey 1997; Baden unpublished data); while this reinforces the differences between ruffed lemurs and other primate fission-fusion taxa, more data are needed to fully understand the extent to which ruffed lemur fission-fusion diverges.

Finally, in order to facilitate future comparisons across taxa, researchers must devise a better method of quantifying fission-fusion dynamics across primates. Aureli and colleagues (2008) have taken an important first step toward developing such a framework, proposing that we quantify variation in fission-fusion dynamics, or *"the extent of variation in spatial cohesion and individual membership in a group over time,*" in three temporal dimensions: size, composition and cohesion of groups. Doing so will allow future studies to characterize *any* animal society based on its degree of fission-fusion dynamics (e.g., as stable, cohesive groups or as fluid groups with either stable or flexible subgroup membership). By eliminating modal categories of social organization, this method will allow researchers to more accurately depict the spatiotemporal flexibility in primate grouping patterns, a phenomenon that is more common, and more complex, than generally acknowledged (Aureli et al. 2008 for references).

Molecular methods for addressing behavioral questions

Using results from Chapter Two, Chapter Three examined the genetic population structure of the focal ruffed lemur community, including descriptive characteristics (e.g., allele frequencies, observed and expected heterozygosities, etc.) and average measures of relatedness (*R*) both within and between sexes. Results revealed that both sexes disperse, resulting in low average relatedness within the community, but that community members organized themselves into social and spatial networks of related kin. These results are consistent with northern ruffed lemur populations (Razakamaharavo et al. 2010); however, extensive sampling will be required to understand whether these patterns of dispersal widely apply. Furthermore, this dissertation focuses solely on intracommunity genetic parameters. The next step will be to look between communities to examine patterns of gene flow between populations, both within protected areas and across fragmented landscapes (e.g., Holmes et al. 2011). This will be important for conservation management strategies, given that ruffed lemurs are among the most critically endangered primates in the world (IUCN 2011).

Finally, as noted in Chapter Three, two main variables influence the genetic population structure of animal social groups: dispersal patterns and mating system (Ross 2001; Storz 1999). While this dissertation focused primarily on dispersal, the mating system of ruffed lemurs has yet to be examined in any detail. Our knowledge of ruffed lemur mating behavior consists of anecdotal observations of females copulating with both resident and extra-community males (Morland 1993; Vasey 2007; Baden unpublished data) and suggests that, while ruffed lemur communities are closed social units, they are unlikely to also comprise closed reproductive units. Evidence of extra-community paternity in several other primate species characterized by fission-fusion dynamics (e.g., chimpanzees: Vigilant et al. 2001; bonobos: Gerloff et al. 1999) demonstrates that while extra-group paternities are not uncommon, their incidence is lower than previous studies may have led us to believe (e.g., Gagneux et al. 1997; Gagneux et al. 1999). In the current study, preliminary genetic analyses suggest that in ruffed lemurs, extra-community paternities are pervasive; however, sample sizes are currently low. Moreover, although paternities were assigned to sub-adults, and thus presumed pre-dispersal individuals, it is possible that, in fact, these individuals originated from the neighboring community (where their most-likely sires reside). With the inclusion of infants born during the 2008 reproductive season, patterns of within- and between-community paternity assignments can hopefully be resolved. Moreover, detailed information on the distribution of reproduction across males will allow further examination of reproductive skew within the community to see whether and how reproductive success reflects mating efforts, and will help us to better understand the mating strategies of ruffed lemurs, something for which very few data currently exist.

Communal infant care: It takes a village?

Chapter Four addressed how patterns of space use (from Chapter Two), genetic relatedness (from Chapter Three), and affiliation influenced ruffed lemur communal nesting (i.e., crèching) and infant care. In this chapter, I also addressed whether and how communal care benefitted mothers and infants. Results from this chapter revealed that ruffed lemur mothers preferentially crèched infants with females who were regular associates, and who were also close genetic relatives. Spatial proximity did not correlate with whether females communally nested, and thus crèching was not simply a matter of convenience. Among communal nesters, mothers spent less time at their nests and more time feeding, and ultimately had higher infant survival relative to singly-nesting females.

While crèching behavior correlated with higher infant survival, how communal nesting contributed to ruffed lemur reproductive success remains unclear. Previous studies have shown that ruffed lemur mothers have among the heaviest litters (Young et al. 1990) and the highest quality milk, similar to anthropoids (Tilden and Oftedal 1997), suggesting that ruffed lemur mothers have among the highest maternal investment of any primate (Young et al. 1990). It is likely that high inter-annual variation in birth (i.e., ‘boom or bust’ reproduction; Ratsimbazafy 2002) and infant mortality rates (Morland 1990, Balko 1998), as well as increased time spent foraging during lactation are a reflection of this reproductive stress (Morland 1990). Infant-nesting is thus thought to free mothers from the burden of continual infant transport, the consequence being that infant vulnerability increases while mothers are away from the nest. Morland (1990) found that accidental falls were among the leading causes of infant mortality in ruffed lemur infants in Nosy Mangabe, a finding that was consistent with other studies of arboreal rainforest primates (e.g., Struhsaker 1975; Rijksen 1978), and proposed that alloparental assistance and communal infant care may aide mothers by protecting and guarding their parked infants. Further, it has been suggested that alternating adult vigilance over infants may simultaneously improve female foraging efficiency while also increasing the likelihood of infant survival

(Morland 1990; Pereira et al. 1987), although until now these hypotheses remained to be tested.

Results from this study provide the first evidence of direct benefits gained by communal infant care (e.g., increased female foraging potential and improved infant survival). However, these results only broadly characterize the benefits gained from communal nesting. In the future, studies should examine the energetics of care, looking at both energy intake (e.g., feeding rates, nutritional quality of food resources, dietary diversity) as well as energy expenditure. The use of doubly-labeled water is one technique that has been used with increasing frequency in wild primate studies (e.g., Rasimimanana et al. 2006); however the invasive nature of this method (i.e., anaesthetization and capture techniques) makes the option less than ideal for mothers with litters of altricial (non-clinging) offspring. If, perhaps, these same methods could be applied under controlled conditions in captivity or in a free-ranging environment, as is becoming more common with other primate taxa (e.g., Ainslie et al. 2003; Pontzer et al. 2011; Rosetta et al. 2011), it might prove a fruitful method to begin exploring the effects of communal nesting on energy balance in ruffed lemurs during this energetically stressful time.

In addition to using finer-scaled measures of energy intake and expenditure in mothers, it is also important for future studies to document alloparental care among non-reproductive females, males, and sub-adult individuals within the community. Though not discussed in this dissertation, non-mothers also contributed to communal infant care during the study, suggesting that it may, in fact, take a village to rear ruffed lemur infants. How and why non-reproductive individuals helped will be of particular note. The obvious question is whether extra-parental care providers such as juveniles and non-reproducing adults also share some level of genetic relatedness, as is seen in some nocturnal strepsirrhines (Eberle and Kappeler 2006) and callitrichines (Garber 1997), and thus inclusive or indirect fitness benefits can be used to explain these seemingly altruistic behaviors.

In ultimate terms, the infant care behaviors exhibited by ruffed lemurs and the benefits gained by communal breeding are consistent with theories of both kin selection and mutualism. Mothers in this study communally nested their offspring with close kin more often than with non-kin, behaviors which resulted in the improved survival of young. That non-kin also communally nested suggests that mutualism and/or reciprocity may also be involved. Reciprocity and mutualism differ only in that reciprocity requires individuals to base their decision to cooperate on the recent behaviors of their companions (i.e., reciprocating with cooperators and excluding non-cooperators from further cooperative acts) (Trivers 1971; Axelrod and Hamilton 1981). Thus, future studies should compare babysitting behaviors among communally nesting mothers to determine whether mothers contribute equally to infant care-related behaviors (i.e., are there cheaters?). If cheaters are present and are excluded from future crèching behaviors, then this would indicate strong evidence for the presence of reciprocity. If, however, mothers communally nest without regard for unequal participation in babysitting, this would provide further evidence for the presence of mutualistic interactions (i.e., cooperation always yields the highest payoff regardless of the opponent's behavior) (Maynard Smith 1983; Packer & Ruttan 1988; Dugatkin et al. 1992). In the future, studies may be able to tease apart which ultimate mechanism is most responsible for the evolution of ruffed lemur communal infant care, or they may confirm that multiple selective pressures are working together to produce the patterns observed here.

Finally, as lemur adaptations are thought to have evolved in response to Madagascar's seasonal, yet unpredictable climate (Wright 1999), it has been suggested that ruffed lemurs, the most frugivorous of the Malagasy strepsirrhines, have adopted a "boom or bust" reproductive strategy, bearing litters of young only during years of resource abundance (Ratsimbazafy 2002). Despite this claim, few data are available to test this hypothesis. While it is true that extrinsic factors such as rainfall (Goldizen et al. 1988; Srivastava and Dunbar 1995; Lycett et al. 1999), ambient temperature (Dunbar 1980; Oshawa and Dunbar 1984; Dunbar 1990; Hill et al. 2000) and food availability (Taylor and Green 1976; Mori 1979; Ford and Pitelka 1984; van Schaik and van Noordwijk 1985) can influence birth rates and interbirth intervals in other vertebrates, how these factors influence ruffed lemur reproductive patterns remains unexplored. Future studies should examine the long-term relationships between inter-annual variation in both trophic (e.g., resource availability) and non-trophic factors (e.g., day length, temperature, humidity, rainfall) and patterns of ruffed lemur reproduction to determine whether and to what extent this pattern exists.

CONCLUSIONS

In conclusion, results from this study reveal an unusual and previously unrecognized form of primate sociality. I demonstrate that ruffed lemurs in Ranomafana National Park 1) live in a social organization that is characterized by fission-fusion dynamics or spatiotemporal variation in range use that differs between sexes and across seasons; 2) that ruffed lemurs are characterized by dispersal that is not sex-biased, but live in communities which contain networks of related kin; and 3) that kin and close affiliates participate in communal nest use and infant care within a ruffed lemur community and that crèching mutually benefits participating mothers by allowing them to spend more time away from their nests to feed and forage, while also increasing infant survival.

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Table 5.1 Patterns of dispersal, range use and overlap, territory defense and association across primate fission-fusion social systems

	Dispersal			**Range size**			**Range overlap**			**Territory defense**			**Boundary use**			**Association**		
Taxon	**Males**	**Females**	**Both**	**M > F**	**M = F**	**M < F**	**M > F**	**M = F**	**M < F**	**Males**	**Females**	**Both**	**M > F**	**M = F**	**M < F**	**M > F**	**M = F**	**M < F**
Chimpanzees	-	+	-	+	+	-	+	+	-	+	-	+	+	+	-	+	+	-
Bonobos	-	+	-	-	+	-	-	+	-	-	-	+	-	+	-	-	-	+
Spider monkeys	-	+	+	+	+	-	+	+	-	+	-	+	+	+	-	+	+	-
Muriquis	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Ruffed lemurs	-	-	+	-	-	+	-	+	-	-	+	-	-	-	*?*	-	-	*?*

References: Dias & Strier 2003; Furuichi 2010; Gerloff et al. 1999; Hohmann & Fruth 2002; Lawson Handley & Perrin 2007; Lehmann & Boesch 2005, 2008; Morland 1991a,b; Razakamaharavo et al. 2010; Spehar et al. 2010; Strier 1990; Vasey 1997, 2006

Table 5.2 Summary of primate social organization, dispersal and infant care

	Social organization				Dispersal			Infant Care		
Taxon	**Solitary**	**Pair**	**Group**	**FissFus**	**Male**	**Female**	**Both**	**Mat**	**Allo**	**Coop**
Strepsirrhines										
Lorises	+‡	-	-	-	-	-	+	+	-	-
Galagos	+‡	-	-	-	+	-	-	+	-	-
Tarsiers	+‡	+	+	-	-	-	-	+	-	-
Mouse lemurs	+	-	-	-	+	-	+*	-	-	+
Dwarf lemurs	-	+	-	-	-	-	+	-	-	+
Sifakas	-	-	+	-	+	-	-	+	+	-
Bamboo lemurs	-	+	+	-	-	+	-	-	-	-
Ringtailed lemurs	-	-	+	-	+	-	-	-	+	-
Brown lemurs	-	-	+	-	+	-	-	+	+	-
Redbellied lemurs	-	+	-	-	-	-	+	-	+	-
Ruffed lemurs	-	+	+	+	-	-	+	-	-	+
Platyrrhines										
Owl monkeys	-	+	-	-	-	-	+	+◊	+	-
Marmosets, tamarins	-	-	+	-	-	-	+	-	+	+
Howler monkeys	-	-	+	-	-	+	+*	+	+	-
Spider monkeys	-	-	-	+	-	+	+	+◊	-	-
Muriquis	-	-	+	+	-	+	-	-	+	-
Woolly monkeys	-	-	+	-	-	+	+	+◊	-	-
Capuchins	-	-	+	-	+	+	-	-	+	-
Squirrel monkeys	-	-	+	-	+	+	-	-	+	-
Colobines										
Hanuman langurs	-	-	+	-	+	-	-	-	+	-
Leaf monkeys	-	-	+	-	-	+	-	-	+	-
Surili monkeys	-	-	+	-	-	+	-	-	+	-
Snub-nosed monkeys	-	-	+	-	-	-	+	-	+	-
Colobus monkeys	-	-	+	-	+	+	+	-	+	-
Cercopithecines										
Gelada baboons	-	-	+	+	+	-	-	+	-	-
Hamadryas baboons	-	-	+	+	-	+	-	+	-	-
Yellow, olive baboons	-	-	+	-	+	-	-	+	+	-
Macaques	-	-	+	-	+	-	-	+	+	-
Guenons	-	-	+	-	+	-	-	-	+	-
Mangabeys	-	-	+	-	+	-	-	+	+	-
Hominoids										
Gibbons	-	+	-	-	-	-	+	+◊	-	-
Gorillas	-	-	+	-	-	+	+*	+	-	-
Bonobos	-	-	-	+	-	+	-	+	-	-
Chimpanzees	-	-	-	+	-	+	-	+	-	-
Humans	-	+	+	+	-	+	-	-	+	+

*: Indicates cases where both sexes disperse, but one sex disperses at closer distances resulting in dispersed kin ne

◊: biparental care ‡: solitary but social sleepers; more data needed

References: Bartlett 2007; Borries et al. 2004; Bradley et al. 2004; Chism 2000; Di Fiore and Campbell 2007; Di Fiore and Fleischer 2005; Di Fiore et al. 2009; Digby et al. 2007; Eberle and Kappeler 2006; Enstam and Isbell 2007; Fashing 2007; Fernandez-Duque 2007; Fietz 1999; Fredsted et al. 2007; Gatti et al. 2004; Gerloff et al. 1999; Gursky 2007; Handley and Perrin 2007; Hrdy 2009; Jack 2007; Jolly 2007; Kappeler 1997; Kirkpatrick 2007; Larney, unpublished data; Layton et al. 2004; Martins et al. 2007; Mitani and Watts 1997; Nekaris and Bearder 2007; Radespiel et al. 2003; Range et al. 2007 (in Tai Primates book); Razakamaharavo et al. 2010; Robbins 2007; Ross and MacLarnon 2000; Parnell 2002; Spehar et al. 2010; Stokes et al. 2003; Strier 1990; Stumpf 2007; Theirry 2004; Thierry 2007; Zhao et al. 2008

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APPENDICES

Appendix 1. Allele frequencies at each locus

VVV20

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
227	3	3	0	0.0536	0.055
229	3	3	0	0.0536	0.055
233	16	12	2	0.2857	0.2923
235	33	15	9	0.5893	0.6202
237	1	1	0	0.0179	0.018

Number of individuals typed:	28
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	-0.0405

VVV25

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
169	18	12	3	0.3333	0.3332
171	29	13	8	0.537	0.5282
173	7	5	1	0.1296	0.118

Number of individuals typed:	27
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.0103
Degrees of freedom:	1
P-value:	0.9193
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	0.0206

VVV160

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
233	6	6	0	0.15	0.163
239	24	8	8	0.6	0.5513
241	8	6	1	0.2	0.1934
243	2	2	0	0.05	0.0512

Number of individuals typed:	20
Hardy-Weinberg Equilibrium test:	done
Null allele frequency estimate:	0.041

VVV204

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
133	16	16	0	0.2759	0.3199
135	42	16	13	0.7241	0.8393

Number of individuals typed:	29
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	-0.1596

VVV247

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
245	9	7	1	0.2647	0.2724
247	3	3	0	0.0882	0.0925
249	8	6	1	0.2353	0.233
251	6	4	1	0.1765	0.1598
253	8	6	1	0.2353	0.233

Number of individuals typed:	17
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	0.0093

VVV485

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
124	11	11	0	0.1833	0.2013
126	48	12	18	0.8	0.8887
128	1	1	0	0.0167	0.0166

Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	-0.1075

VVV560

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
259	12	8	2	0.2069	0.1883
261	26	12	7	0.4483	0.4068
263	20	10	5	0.3448	0.3012

Number of individuals typed:	29
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.4861
Degrees of freedom:	1
P-value:	0.4857
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	0.1037

VVV598

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
199	3	3	0	0.05	0.0513
203	10	10	0	0.1667	0.1835
205	1	1	0	0.0167	0.0168
207	36	12	12	0.6	0.5527
211	10	10	0	0.1667	0.1835

Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	0.0123

VVV691

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
231	9	7	1	0.15	0.1432
243	24	16	4	0.4	0.4209
247	8	6	1	0.1333	0.124
249	19	17	1	0.3167	0.3661

Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	-0.0543

VVV790

Allele	**Count**	**Heterozygotes**	**Homozygotes**	**Frequency**	**Frequency with null**
207	29	15	7	0.4833	0.4833
209	8	8	0	0.1333	0.1436
211	23	15	4	0.3833	0.3942

Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.0441
Degrees of freedom:	1
P-value:	0.8336
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	-0.0211

VVV816

Allele	**Count**	**Heterozygotes**	**Homozygotes**	**Frequency**	**Frequency with null**
278	4	4	0	0.0667	0.0688
280	21	17	2	0.35	0.3928
282	9	7	1	0.15	0.1432
286	16	12	2	0.2667	0.2687
288	10	10	0	0.1667	0.1829

Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	-0.0563

VVV833

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
334	30	18	6	0.5172	0.5755
336	5	5	0	0.0862	0.0894
338	2	2	0	0.0345	0.0348
340	4	4	0	0.069	0.0708
342	17	15	1	0.2931	0.3266

Number of individuals typed:	29
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.879
Degrees of freedom:	1
P-value:	0.3485
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	-0.0971

VVV941

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
115	9	9	0	0.1552	0.1692
123	19	9	5	0.3276	0.2803
125	19	13	3	0.3276	0.3298
129	6	4	1	0.1034	0.0901
135	5	5	0	0.0862	0.0901

Number of individuals typed:	29
Hardy-Weinberg Equilibrium test:	not done
Null allele frequency estimate:	0.0405

VVV963

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
145	1	1	0	0.0167	0.0168
157	15	13	1	0.25	0.2696
159	32	16	8	0.5333	0.5526
161	10	6	2	0.1667	0.1436
163	1	1	0	0.0167	0.0168
165	1	1	0	0.0167	0.0168

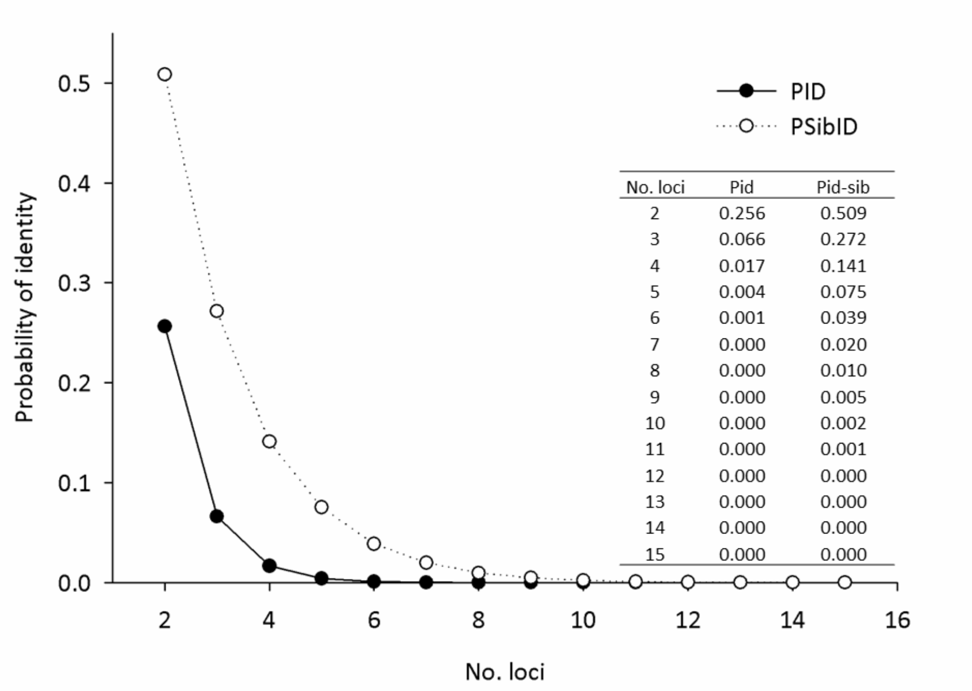
Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.0089
Degrees of freedom:	1
P-value:	0.925
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	-0.0162

VVV988

Allele	Count	Heterozygotes	Homozygotes	Frequency	Frequency with null
98	8	6	1	0.1333	0.1233
102	26	12	7	0.4333	0.3902
104	6	4	1	0.1	0.0864
106	15	9	3	0.25	0.2233
112	5	5	0	0.0833	0.0864

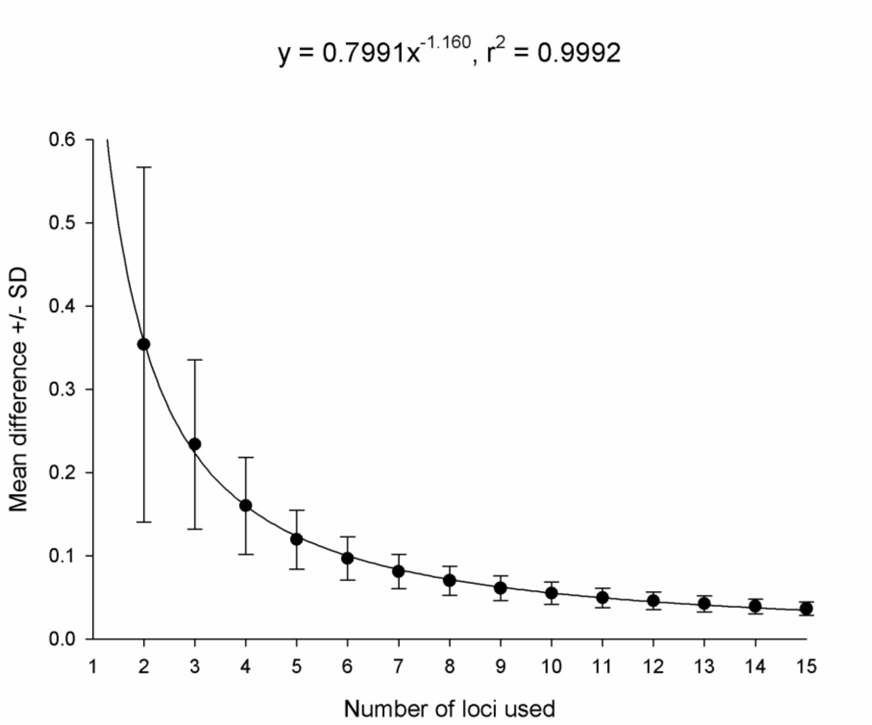
Number of individuals typed:	30
Hardy-Weinberg Equilibrium test:	
Minimum expected frequency	5
Chi-square value (using Yates ' correction):	0.6934
Degrees of freedom:	1
P-value:	0.405
Significance (with Bonferroni correction):	NS
Null allele frequency estimate:	0.0904

Appendix 2. Relationship between the number of loci examined and the probability of both individual identity (P_{ID}) and sibling identity ($P_{ID\text{-}SIB}$), or the probability that full siblings would yield the same multilocus genotype by chance. In this study, P_{ID} yields less than a 1% chance that two individuals will share the same genotype when using five or more loci, whereas $P_{ID\text{-}SIB}$ yields less than a 1% chance that two siblings will share the same genotype when using eight or more loci

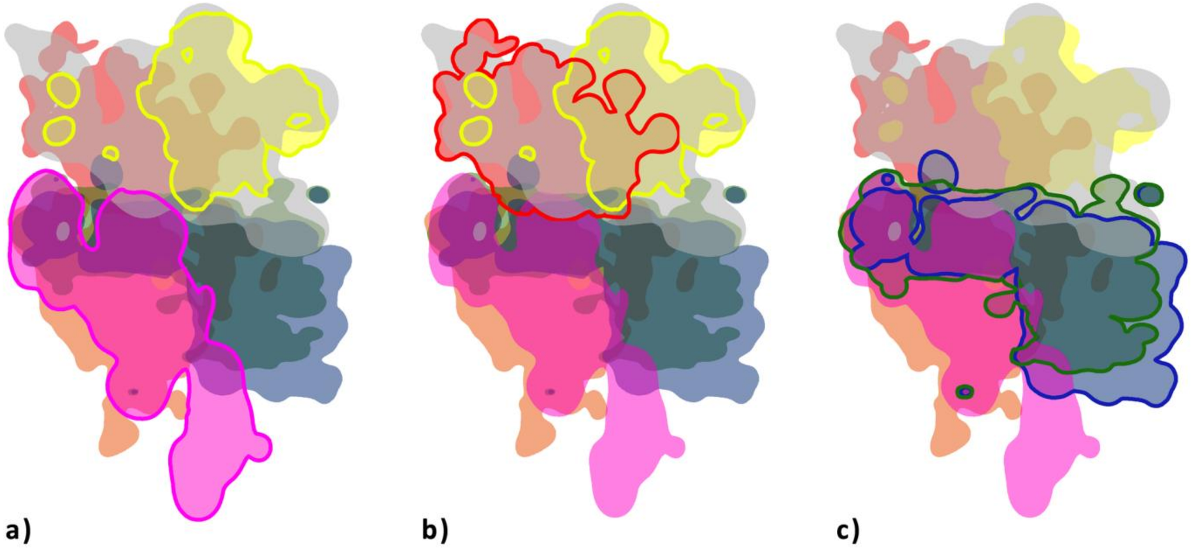


No. loci	Pid	Pid-sib
2	0.256	0.509
3	0.066	0.272
4	0.017	0.141
5	0.004	0.075
6	0.001	0.039
7	0.000	0.020
8	0.000	0.010
9	0.000	0.005
10	0.000	0.002
11	0.000	0.001
12	0.000	0.000
13	0.000	0.000
14	0.000	0.000
15	0.000	0.000

Appendix 3. Results of the rarefaction analysis, as generated in RE-RAT



Appendix 4. Variation in home range overlap amongst community members, and ranging from a) no home range overlap, as illustrated by females Pink-Yellow and Radio-Yellow, b) some home range overlap, as illustrated by females Radio-Red and Radio-Yellow, and c) substantial home range overlap, as illustrated by females Radio-Green and Radio-Blue



Appendix 5. a) Distribution of home range centroids within the context of female 95% kernel home range estimates. Distances between centroids were calculated via straight line distance measurements as calculated in Hawth's Tools of ArcMap9.3. Here, b) illustrates dyadic centroid distances between Radio-Red female and all other females within the community