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**Dispersal, Kinship, and Genetic Structure of an Endangered Madagascar Primate,**
***Propithecus edwardsi***

A Dissertation Presented

by

**Toni Lyn Morelli**

to

The Graduate School

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Abstract of the Dissertation

**Dispersal, Kinship, and Genetic Structure of an Endangered Madagascar Primate,**
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In this dissertation, I explored the mating system, social interactions, dispersal behavior, and genetic structure of a population of rainforest lemurs.

I first studied the factors that determine grouping in sifakas. *Propithecus edwardsi* live in groups of 2-9 individuals including one breeding male and one to two related breeding females. Using the theories of kin selection, ecological constraints, and reproductive skew, I examined the effects of relatedness, environment, and mate availability on cooperation, group composition, and reproduction. To do this, I used standard field behavior methods, conducting focal follows of a population of Milne-Edwards' sifakas in the submontane rainforest of Ranomafana National Park (RNP) in southeastern Madagascar. Supplementing this information with data from long-term study of this population, I analyzed affiliative and aggressive interactions and biometric data. I also conducted microsatellite analyses to determine paternity and relatedness between individuals. I found that infants were sired by group males. Moreover, social interactions met the predictions of the theories of kin selection and reciprocal altruism.

*Propithecus edwardsi* show a remarkable system of unbiased sex dispersal. Since most classic theories predict male-biased dispersal in mammals, I developed the Local Mate Availability Model to predict when dispersal should occur in both sexes. Data from 21 years of study of sifakas were used to test the model. Results showed that one factor predicted the majority of dispersal events in this population: presence of an available unrelated opposite sex adult (a "mate"). Most unpredicted dispersal events were the result of aggressive takeovers by immigrant same-sex adults. These takeovers were usually associated with infanticide; both female and male immigrants killed the infants of the group into which they dispersed. As a result of infanticide by male immigrants, females came into estrus sooner. As a result of infanticide by female immigrants, females dispersed out of the group.

Finally, I used population genetics tools to examine the movement of individuals around RNP, focusing on groups found on either side of natural and man-made barriers that divide the protected area. Sifakas there are genetically diverse and RNP has successfully conserved their habitat. However, gene flow may be disrupted by the barrier in the future, with potential management and conservation implications.

**Dedication**

This dissertation is dedicated to Felix Ratelolahy, my best friend in Madagascar.

Thanks for helping me find my way home.

Now it's your turn.

*Tsy misy ala,*

*Tsy misy rano,*

*Tsy misy vary.*



*(There is no forest,*

*There is no water,*

*There is no rice.)*



-Malagasy Proverb

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# Chapter 1
## Introduction


Through this dissertation, I sought to examine the population dynamics of the Milne-Edwards' sifaka, *Propithecus edwardsi*, using behavioral observations and genetic analysis. Specifically, I wanted to understand the effect of relatedness on social interactions, dispersal, and genetic viability in this endangered lemur.  I explored three major questions:

1) What determines social dynamics in *P. edwardsi*?
2) What determines dispersal in *P. edwardsi*?
3) How is the population of sifakas in Ranomafana National Park structured?

The superfamily Lemuroidea contains a diverse array of primates, with great variation in behavior, ecology, and morphology, all inhabiting the island of Madagascar and a few nearby islands.  This great diversity allows for interesting questions to be asked of animals with shared ancestry living in similar or different environments and pursuing similar or different behavioral and ecological strategies.

Lemurs are different from other primates because they live in small groups with on average even sex ratios (Kappeler 2000). They communicate extensively through olfaction, like many mammals but unlike most primates.  Lemurs are almost all female dominant, a trait that is extremely rare among primates and among mammals in general.  They also show a very short period of female receptivity, only a few days per year.  These characteristics influence the behavior of this taxon in a way that can be contrasted to other group-living vertebrates.

This dissertation research focused specifically on the Milne Edwards' sifaka *Propithecus edwardsi.  P. edwardsi* is a frugivorous/folivorous, large-bodied lemur that lives in multi-male, multi-female territorial groups of 2-10 individuals.  The sifakas inhabiting Ranomafana National Park (RNP) in southeastern Madagascar are among the most intensively sampled animal populations (Wright 1995, 1999, Pochron et al. 2004, Irwin et al. 2005, King et al. 2005, Pochron et al. 2005, Arrigo-Nelson 2006, Karpanty and Wright 2006, Dunham et al. 2008, Wright et al. 2008, In Press).  Moreover, RNP has been one of the most successfully managed protected areas in Madagascar (Wright and Andriamihaja 2002). Capitalizing on the availability of genetic techniques and a database of morphometric, behavioral, and population information, I analyzed the population dynamics of this species.

*Social Dynamics in Sifakas*

In Chapter 2, I explore the effects of relatedness, reproductive opportunities, and ecological factors on group composition and dynamics of sifakas.

Most current discussions of social systems begin with Emlen and Oring's classic 1977 paper, which proposed that species and populations differ in intensity of sexual selection because of the ability of a portion of the population to control access to potential mates.  They believed that environmental risks and the availability of resources determine the

degree to which females can be monopolized; thus, ecology determines mating and social systems. They introduced the idea of an environmental potential for polygyny (EPP): in species with little or no obligate paternal care, the degree to which resources are defensible determines the ability of males to monopolize more than one female.

In the 1980s and 1990s, several major models of primate social system evolution and variations on these models were published. Based in the Emlen and Oring tradition, these models focused on the reasons for females to be grouped or solitary, assuming that males will then base their behaviors around the females. This is a particularly intriguing question in primates because this order is much more social than other mammals: 73% compared to 32% in marsupials, the highest rate among mammalian orders (van Schaik and Kappeler 1997).

The issue of sociality in primates has been a controversial one. The only non-gregarious primates besides orangutans (and even these are arguably not solitary) are strepsirrhines. Reasons developed for a solitary lifestyle include nocturnality, small body size, and predation pressure. In a recent review, Kappeler and van Schaik (2002) examined the applicability of these explanations in lemurs, galagos, and lorises and showed that there is no consistent adaptive explanation as to why primates do not live in groups. Not all nocturnal strepsirrhines are solitary and not all solitary primates are nocturnal. Similarly, although small body size has been suggested to correlate with a solitary lifestyle, this is not a rule (e.g., Callitrichids, *Pongo pygmaeus*). Neither is dietary specialization a convincing explanation; although some solitary primates are insectivorous, many others are not. Finally, predation pressure, either release from or increase in, has been proposed as a reason, but the evidence is mixed. However, the actual impact of predation on behavior is difficult to quantify (Janson 1998).

On the other hand, researchers have proposed many explanations for the advantages of living in pairs or groups, with their relative importance still highly debated. Pair-living may result from selection for infanticide protection, but other explanations include obligate paternal care (although rare among primates) or simply low EPP due to low population density or other factors mentioned above. Some evidence indicates that infanticide protection is not a widely applicable explanation, but that predator defense, as well as mate-guarding and biparental care, is a viable explanation (Fuentes 2000). Jolly (1998) proposed that pair-living is widespread among lemurs because it is the ancestral state. Explanations for pair-living are still debated.

van Schaik and Kappeler (1997) proposed infanticide avoidance as the answer for why females live in groups. Other major reasons include predator deterrence and intergroup competition (see Janson 2000 for review). Limits on group size include many of the same causes: infanticide, intragroup feeding competition, as well as neocortex size. On the other hand, researchers have also presented ideas that explain the low cost of group living, therefore making benefits, at least large ones, unnecessary. For example, the resource dispersion hypothesis predicts that grouping may be expected to occur, since it incurs no resource costs, whenever resources are heterogeneous (Johnson et al. 2002). Furthermore, grouping can have benefits for resource acquisition.

Nunn (1999) tested whether temporal effects actually determine social systems, as previous studies had obtained mixed results. Potential problems with previous findings were that female estrus synchrony is difficult to estimate so researchers use proxies (e.g., breeding seasonality). He found that male number is tightly correlated to female number and breeding season duration and that male number increases with female overlap. Thus, three independent estimates showed that temporal overlap is correlated with male number.

In sum, ecology seems to determine the distribution of primate females, which in turn determines the distribution of primate males and thus the mating system (Terborgh and Janson 1986, Paul 2002). In the case of scramble competition polygyny, traits that aid a male in inseminating the most females, specifically in finding females and producing many and large ejaculates, are expected to be favored; traits that help in direct competition, such as fighting and larger male size, will not be selected for (Kappeler 1997). The reverse is expected for contest competition.

Beyond general theories of sociality, there are a variety of models proposed to explain the delayed dispersal of individuals from their natal groups, including the apparent paradox of helpers that remain in the natal territories and forego personal reproduction. These explanations were compiled by Emlen (1995) into his Evolutionary Theory of the Family. In Chapter 2, using this model as a platform, I test whether ecological constraints, kinship, and reproductive skew affect grouping and social interactions within groups. I focus on grooming, proximity, and aggression data that have been gathered over 18 years on four groups of sifakas in the Talatakely area of RNP.

*Dispersal in Sifakas*

The movement of individuals around the landscape has a profound effect on everything from individual fitness to species viability. Whereas Chapter 2 explores how and why animals stay in their natal group beyond reproductive maturity, Chapter 3 examines when and why animals choose to disperse instead of remaining in a group to reproduce. These results can help visualize these groups as a metapopulation, moving and reproducing at different times and under different circumstances. I test the effects of relatedness between groupmates as well as the impact of new immigrants and their infanticidal tendencies. I also develop a model to predict the dispersal behavior of species in which both sexes disperse.

*Genetic structure of Sifakas*

Dispersal locally directs the flow of genes in a population. To understand the movement of individuals from a broader perspective, Chapter 4 examines the genetic structure of Milne-Edwards' sifakas found in RNP, with a comparison site located 110 km south in Andringitra National Park. Samples were collected from either side of the river/road complex that divides RNP; I analyzed microsatellite variation across the sites to examine whether these geographic barriers are creating impediments to gene flow within RNP. In addition, I inspected the relationships within one site, the Talatakely groups, to see whether reproduction is distributed evenly within the groups. These results, both intra-group and inter-site, reveal information important to the conservation and management of species with limited ranges or population sizes.

In this dissertation, I explored the population dynamics of an endangered lemur to understand its population biology and evolutionary pressures, as well as to gather information that can be used to help to conserve this species and the rainforest it inhabits.

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**Chapter 2**
**A Test of the Evolutionary Theory of the Family in Lemurs**

**INTRODUCTION**

In 1995, Stephen Emlen proposed a model to illuminate the composition of and reproductive skew in vertebrate groups and to examine the adaptive significance of non-reproductive helpers.  His Evolutionary Theory of the Family (Emlen 1995) synthesized the major evolutionary models of social grouping, including 15 predictions to test this theory.  This chapter presents one of the first tests of the Evolutionary Theory of the Family, focusing particularly on lemurs.

With his Evolutionary Theory of the Family (ETF), Emlen synthesized the established theories of ecological constraints (Emlen 1982, Koenig et al. 1992, Emlen 1994, Sterck et al. 1997), kin selection (Hamilton 1964a, b, West et al. 2002), and reproductive skew (Vehrencamp 1983a, b, Reeve et al. 1998, Johnstone 2000, Kokko et al. 2001) into a model of social grouping in vertebrates, focusing on birds and mammals.  A family was defined as a kin group consisting, at a minimum, of parent(s) and offspring, where offspring continue to interact regularly with their parent(s) past the age of sexual maturity by delaying dispersal.  Although Emlen's model was specifically catalyzed by the desire to incorporate human social behavior into an evolutionary context, he developed a set of predictions that were broad enough to be tested in other social animals.

I chose to test the ETF in one of the most well-studied wild animal populations (Wright 1995, 1998, Pochron and Wright 2003, Pochron et al. 2004), the Milne-Edwards' sifaka *Propithecus edwardsi*.  The depth and breadth of the research on the population of *P. edwardsi* inhabiting RNP particularly enables a test of Emlen's ETF.  Moreover, the diversity of lemur social systems, their seasonal breeding patterns, their lack of sexual size dimorphism, and their female dominance make them interesting for such a study (Kappeler 1997, Wright 1999).

*An Evolutionary Theory of the Family*

According to Emlen (1995), one could consider just four basic parameters, genetic relatedness, social dominance, the benefits of group living, and the probable success of independent reproduction, to understand why individuals act cooperatively and even forego personal reproduction in groups.  These four parameters were the basis of three major ecological theories which he synthesized to produce the ETF.  Ecological constraints theory purports that the availability of reproductive opportunities elsewhere may drive the delayed dispersal of sexually mature offspring (Emlen 1982).  Kin selection theory, based upon Hamilton's formulation of costs and benefits of an altruistic action on shared genes, predicts that costly behaviors will be directed towards relatives (Hamilton 1963, 1964a, b, Alexander and Borgia 1978).  Finally, reproductive skew theory dictates the conditions in which dominant individuals are expected to share reproduction with subordinates to avoid conflict and discourage dispersal (Clutton-Brock 1998, Johnstone 2000).  Using these theories as

grounding, Emlen enumerated 15 predictions for his ETF (summarized in italics below), delineated into three categories: Family Formation and Stability, Family Dynamics, and Family Structure.

*a) Family Formation and Stability*

The ETF provides a framework to consider the variation in group assembly and maintenance. The null expectation for family groups is that offspring disperse as soon as they are sexually mature. However, family groups consisting of adult offspring are fairly common. In order to explain these patterns, the ETF forms two predictions for when this delayed dispersal would occur, as well as when these family groups would be expected to break up.

<u>*Predictions 1 & 2*</u>: *Family groupings will form and expand when there is a shortage of acceptable reproductive opportunities for mature offspring and diminish in size or break up as acceptable opportunities become available. Families that control high quality resources will be more stable, with some resource-rich areas supporting genetic dynasties.*

Reproductive opportunities in most social species are limited by the availability of unrelated individuals in their group. The complications that arise from inbreeding are the result of inbreeding depression, when reduced genetic variation causes lowered resistance to disease through reduced diversity in the immune system and higher vulnerability to chance environmental mishaps. Inbreeding can also result in the "unmasking" of deleterious recessive alleles, wherein rare recessives come together with a greater probability when relatives mate (Hoogland 1982, Charlesworth and Charlesworth 1987, Pusey & Wolf 1996). Data from many species show an avoidance of inbreeding within groups (Pusey and Wolf 1996, Muniz et al. 2006), either through sex-biased dispersal, active avoidance, or selective abortion. However, there are few empirical data showing the effects of inbreeding on primates (although see Smith 1995, Charpentier et al. 2007).

Therefore, if there are no unrelated adults available in the group, it is expected that an individual will not breed. This situation leaves individuals with three options: remain in their natal (birth) group and delay breeding, remain and mate outside of the group, or disperse (Charpentier et al. 2007). The decision, according to selection pressures, should depend on the number of mating opportunities in the surrounding population, the chances of reproducing eventually in the natal group, the availability of resources in the natal group, and the costs associated with dispersal.

Although this question is notoriously difficult to answer in long-lived species, the information gathered by following the *P. edwardsi* population for two decades allows for an analysis of the composition of groups over time. Sifakas live in a diverse array of group configurations (Chapter 3: Table 1; Pochron and Wright 2003). These changes, and the stasis in-between, can be examined to test the predictions about family formation and stability presented by Emlen's ETF.

*b) Family Dynamics: Kinship and Cooperation*

The predictions about family dynamics are based in the theory of kin selection and thus predict that relatives will assist offspring according to their degree of relatedness. Although the ETF focuses primarily on classical cooperative breeding systems, the sifaka

social system is relevant. Sifakas in RNP show delayed dispersal, variation in relatedness, and potential for helping behavior and thus can be used as a system to test the ETF.

*Predictions 3 & 4: Assistance in rearing offspring will be more prevalent in family groups and will be expressed to the greatest extent between those family members that are the closest genetic relatives.* Following from the principles of kin selection, behaviors that are costly to the actor but beneficial to the receiver should be directed toward relatives. Behaviors that can be considered as assistance in sifakas can be divided into affiliative, (lack of) aggressive, and anti-predator behaviors. In this analysis, I focus specifically on allogrooming, mutual grooming, and aggression. Aggression data are appropriate for addressing the predictions of helping behavior because they have been shown to occur mostly in a feeding context in this population (Pochron et al. 2003) and thus indicate a lack of tolerance for sharing food as well as other resources. Grooming was considered because, as well as being costly in terms of energy and time, it has been shown to have hygienic, stress-relieving, and social benefits (Spruijt et al. 1992). When relatives groom, the benefits to their shared genes might offset any costs in terms of time and energy.

I also tested an alternative hypothesis, not addressed in the ETF, that nonkin engage in grooming in exchange for services. Researchers have argued, through the theories of reciprocal altruism (Trivers 1971) and biological markets (Noë and Hammerstein 1995), that grooming is a commodity to be traded. This could occur directly and immediately through simultaneous (mutual) grooming or eventually for another beneficial behavior, such as tolerance or mating opportunities (Barrett et al. 1999, Henzi and Barrett 1999). According to these theories, subordinates will be more likely to groom groupmates in exchange for grooming and tolerance. In addition, males should groom females, the choosy sex (Trivers 1972, Emlen and Oring 1977), in exchange for future mating opportunities.

*Prediction 5: Sexually related aggression will be less prevalent in family groups than in otherwise comparable groups composed of non-relatives. This is because opposite-sex close genetic relatives will avoid incestuously mating with one another.*
Because mates are the limiting factor in reproduction for males but not females (Emlen and Oring 1977), males are expected to fight for females during the breeding season; female aggression should be focused around resources. Aggression rates between sifakas are extremely low and sexually related aggression is potentially limited by the extremely short breeding season for sifakas: 12-24 hours/year (Pochron et al. 2003). Nevertheless, given the depth of the dataset, there are opportunities to test this prediction.

*Prediction 6: Breeding males will invest less in offspring as their certainty of paternity decreases.*
There have been a variety of studies showing both that paternity certainty affects paternal investment (Moller and Birkhead 1993, Cowlishaw and O'Connell 1996, Sheldon and Ellegren 1998, Fishman and Stone 2002, Anderson et al. 2007, Gray et al. 2007) and that it has no effect (Kempenaers and Sheldon 1996, Dickinson 2003). Studies that have shown no correlation hypothesize different causes, from inability to discriminate to delayed reproductive benefits to males.

*c) Family Dynamics: Disruption After Breeder Loss or Replacement*

*Prediction 7 & 8: The loss of a breeder will result in family conflict over the filling of the resulting reproductive vacancy. The conflict will be especially severe when offspring are of the dominant sex and when*

*resources controlled by the family are of high quality. Sexually related aggression will increase after the re-pairing of a parent…The surviving parent and its mature same-sex offspring will now compete for sexual access to the replacement mate (step-parent).*

Breeder turnovers happen regularly in *P. edwardsi.* Moreover, these predictions are particularly interesting to test in this species, as they are known to be female dominant (Pochron et al. 2003).

*Prediction 9 & 10: Replacement breeders (step-parents) will invest less in existing offspring than will biological parents. They may infanticidally kill current young when such action speeds the occurrence, or otherwise increases the success, of their own reproduction. This will be more likely when the replacement mate is of the dominant sex. Non-reproductive family members will reduce their investment in future offspring after the replacement of a closely related breeder by a more distantly related or unrelated individual.*

Kin selection theory predicts that group young may receive less investment, e.g., less affiliation, more aggression, and less anti-predator behaviors, from unrelated breeders. Furthermore, infanticide occurs in many primate species (Sterck et al. 1997, van Schaik and Kappeler 1997, Erhart and Overdorff 1998, Brockman and Whitten 1999, Jolly et al. 2000, Soltis et al. 2000, Watts and Mitani 2000, Weingrill 2000) and plays a critical role in sifaka population dynamics (Wright 1995, Erhart and Overdorff 1998). Moreover, female infanticide has been reported in some species (Corbett 1988, Veiga 2004, Mahalingam 2007, Saltzman et al. 2008), although rarely in non-human primates. Finally, kin selection theory predicts that helping by non-reproductive groupmates may be less apparent toward less related offspring of replacement breeders.

*Prediction 11: Replacement (step-) families will be inherently less stable than biologically intact families. This will be especially true when offspring from the originally intact family are of the same sex as the step-parent.*

The ETF predicts that kinship is a strong determinant of the stability of groups and thus tenure will be affected by the immigration of unrelated individuals. Any offspring produced by a parent and a replacement breeder will be half as related to current group young, thus decreasing the advantage of remaining in the group to help raise future offspring. However, if the replacement breeder is of the opposite sex, offspring may have an opportunity to breed with that immigrant or even eventually replace their parent as the group breeder. A same sex replacement breeder does not offer these opportunities.

*d) Family Structure: Reproductive Sharing Leads to Extended Families*

*Predictions 12-15: Reproduction within a family will be shared more equitably: as the severity of ecological constraints decreases, as the asymmetry in social dominance between potential cobreeders decreases, when the potential cobreeders consist of siblings than when they consist of parent(s) and grown offspring, and with family members to whom the dominant breeders are least closely related.*

The predictions set out in the last section of Emlen's ETF relate to reproductive skew. They predict that reproduction will be more shared when there are fewer ecological constraints on dispersal; if environmental conditions are benign, more incentives must be offered to discourage group members from dispersing. Subordinates will be most likely to initiate a potentially dangerous challenge to the dominant when the asymmetry in social dominance is lowest; thus, reproduction will be most equitably shared in these circumstances. Likewise, because parents are less related to their offspring's offspring than vice versa, but siblings are equally related to each other's offspring, parent/offspring

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associations will lead to more reproductive skew.  However, as Emlen pointed out, this is only true if there is no parental mate change or extra-pair parentage.  Finally, reproductive skew theory meets kin selection theory to predict that group members that are less closely related will be offered more reproductive opportunities to compensate the lack of indirect fitness incentives.

Instances of cobreeding between siblings or parent/offspring were rare in the Talatakely population but I considered each case where these relationships were known in order to determine whether the occurrence of cobreeding correlated with the breeders' relationship and whether groups that had sisters or brothers breeding had a longer tenure than groups that consisted of mother/daughter or father/son breeders.

## METHODS

*Field Collection*

This study focused on four social groups of *Propithecus edwardsi* in the Talatakely trail system of Ranomafana National Park (RNP), located at 12°16' S latitude and 47°20' E longitude in southeastern Madagascar. This 43,500 ha submontane rainforest was declared a national park in 1991 (Wright 1992) and a UNESCO World Heritage site in 2007. The area of the study groups was selectively logged by hand from 1986-1989 (Wright and Andriamihaja 2002). Rainfall varies from 1.8-4.0 m/year with a mean of 3.0 m (Wright 2006). Temperature varies with a cold season in June-August and with an average annual temperature of 21° C.

Sifakas in the Talatakely region of RNP have non-overlapping territories (Chapter 3: Figure 1). Patricia Wright and colleagues have followed Groups 1 and 2 since 1986, Group 3 since 1991, and Group 4 since 1996 (Wright 1995; Chapter 3: Figure 2), with consistent data on marked individuals taken from 4-25 days/month for 4-12 months since 1987 (Total = 1,402 days). By 2007, two of these four groups had dissolved, with the final group members dispersing to the nearby area of Sakaroa (see Chapter 4: Figure 1 for map).

Animals were named and identified by a collar/tag combination (e.g., Blue Purple/BP had a blue collar and purple tag) that they received after two years old or as soon as possible in the case of immigrants (Glander et al. 1992). In rare cases where there were more than two non-collared animals in a group, these animals were identified according to sex, morphologically distinct characteristics, or, in the case of very young animals, proximity to their mother.

The length and continuity of this study allowed us to assign categories to missing or new animals with confidence (Pochron et al. 2004). Sifakas that had never before been sighted in the group were considered "immigrants." Animals that disappeared before the age of 3 years without their mothers were assumed dead. Occasionally, young animals may disperse with their mothers, particularly in instances of matriline splitting. Thus, I did not automatically assign these cases as deaths. However, many deaths were directly observed, either through infanticide events or the physical remains of predation. The fossa (*Cryptoprocta ferox*) is the only observed predator of sifakas in RNP. Fossa predation events are obvious. Direct evidence includes disemboweled corpses with deep tooth marks on long bones and/or the cranium; indirect evidence includes injured group mates, footprints, scat, and sightings (Wright et al. 1997, Wright 1998).

Fifty-eight individuals were followed from birth until dispersal or death in Groups 1, 2, 3, and 4. Animals seen born (or shortly after their birth) into the group in which they resided during the study were "natal." Another 21 individuals, either present at the start of study of that group ("residents") or animals who immigrated into a group from outside the study area ("immigrants"), were followed for an average of 12.2 years each (range = 2.8-21.6 years). All births, deaths, and dispersals were recorded within two months, most within one week. Unless otherwise indicated, all analyses incorporating group residence ("tenure") excluded resident animals, i.e., those whose entry date into the group was unknown.

Due to masculinized female genitalia and lack of sexual dimorphic size or coloration, the sexing of infants could be difficult within the first three months of life. However, the majority of the infants were able to be sexed from visual inspection of genital morphology, either in the wild or once captured, and only 6/56 infants died without being sexed. Infants were defined as age 0-12 months; juveniles as age 12-42 months; and subadults as animals

aged 3.5-9 years who have not yet reproduced. All natals who have reproduced and immigrants were considered adults. Three and a half years was considered sexually mature, as this was the earliest age that an animal was known to have reproduced in this population in each sex (see Chapter 3: p. 53). Sifakas are long-lived; adults frequently survive to their late twenties (King et al. 2005).

In addition to behavioral follows, Wright, Morelli, and colleagues captured 254 sifakas in Talatakely and three nearby sites within RNP (Sakaroa, Vatoharanana, and Valohoaka; unique animal captures = 84) over 24 months of capture between 1987 and 2007 (see Chapter 3: Figure 3). The darting team used a $CO_2$ rifle, which launched light-weight 9-mm darts, to tranquilize adult and juvenile sifakas. Infants were carried down with their mothers. Darts injected Telazol® (a combination of the dissociative anesthetic drug tiletamine and the benzodiazepine anxiolytic drug zolazepam) at 10 mg/kg of body weight intramuscularly. The team caught the animals with large nets as they fell. Each animal was weighed and measured and, when conditions allowed, 1-6 cc of blood was extracted from its femoral vein (about 1 cc/500 g; this amount was deemed safe by two different veterinarians). We collected blood samples from 34 of the 79 main study animals in Talatakely, with an additional 35 genetic samples captured from sifakas at the other three sites (see Chapter 4: Figure 1 for map). The blood samples were kept at room temperature in a blood storage solution until returned to the United States for analysis (Longmire et al. 1992) and then frozen at -80°C until extraction.

Scent, fecal, and parasite samples were also collected. Up to 21 separate morphometric variables were recorded on each individual. Body Mass Index was calculated as $BMI = weight/height^2$, where weight was measured in kg and height was measured in m. Testicles were measured using calipers and testicle volume was calculated using the formula $V = 4/3\pi(l/2)(w/2)^2$, where length (l) and width (w) were averages of the left and right testicle (as per Glander et al. 1992). I, along with J. Jernvall, took dental casts ($N = 65$, unique animal casts = 37) that were used to age animals born outside of the study site or period (King et al. 2005). Each new animal received a tracking microchip (AVID Friendchip) after being checked to prevent duplicates. The animals were allowed to recuperate in light-weight sacks (recovery time ≈ 4 hours) before release back to the darting site and followed to ensure successful recovery.

## *ETF*

### *Group Stability/Tenure*

Group tenure was measured as genetic dynasties by looking at the length of continuous lineages (defined as direct inheritance from the previous reproducing male and/or female).

### *Helping Behavior/Competition*

Wright and colleagues used focal time sampling methods (Altmann 1974, Baulu and Redmond Jr. 1978), recording that day's randomly chosen focal individual's location and activity (resting, feeding, grooming, mutual grooming) every five minutes for approximately 7 hours/day (Wright 1995, 1998, Pochron and Wright 2003). In addition, from 2003-2004, T. L. Morelli and field assistants recorded all instances of mating and aggression, all grooming interactions, all approaches to within 1m, including duration to the second, and initiator and terminator of the activity using continuous sampling methods (Altmann 1974),

for a total of 3,600 focal-hours and 4,350 dyad-days[*] for this analysis. I examined the following behaviors in the context of assistance in rearing offspring: allogrooming (unidirectional grooming, hereafter "grooming"), mutual grooming (simultaneous exchange of grooming between two individuals), proximity, and aggression. I used aggression events in this analysis only if they were decided, i.e., the aggressor performed physical aggression, threats, or vocal aggression and the victim responded submissively either by leaving or by grooming the aggressor (as per Pochron et al. 2003). I adjusted bout rates from focal follows, count data from continuous follows, and aggression counts by time watched and square-root transformed to normality. I adjusted duration data by time watched and log square-root transformed to normality.

*Reproduction*

To estimate reproductive opportunities, I calculated the number of potential mates that were available to each female and male. Potential mates were males and females at least 3.5 years old, of $r < 0.25$, and seen in the group near the breeding season.

The breeding season occurred in this population in November, December, or January each year (see Chapter 3: Figure 9, 10), with births occurring in the following May-July (see Chapter 3: Figure 6). As sifaka estrus is extremely short (12-48 hours), mating was rarely seen. Therefore, paternity certainty was extrapolated from presence of the male in the group during the previous breeding season. Breeder loss was indicated by the disappearance of the reproducing male or female in the group in a single breeder group. I analyzed the loss of the extra adult male or female in groups with more than one breeding male or female in a separate analysis. Reproductive skew was measured as the ratio of same sex adults and subadults in the group that reproduce to those that did not reproduce.

*Group relatedness*

To determine group relatedness, I averaged $r$ values of all dyads (calculated as described below) present in the group on each day of study to produce a group $r$ value for each day in each group.

**Determining Genetic Relationships**

I isolated genomic DNA from blood samples according to standard procedures (Sambrook et al. 1989). I conducted PCR (polymerase chain reaction) in a 25 μL reaction volume using an ABI 480 thermocycler (Perkin-Elmer) with approximately 25 ng of genomic DNA as template. I used 16 genus-specific microsatellite primers for this analysis (from Lawler et al. 2001, Mayor et al. 2002, Rakotoarisoa et al. 2006, and unpublished markers developed by E.E. Louis and colleagues; see Chapter 4: Table 2). Final amplification conditions consisted of 12.5 pmol unlabelled reverse primer, 12.5 pmol fluorescently-labeled forward primer, 1.5 mM $MgCl_2$, 200 μM each dNTP, and 0.5 U of *Taq* DNA polymerase

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*A dyad is two individuals within the same group. A dyad-day counted the 2-10 hour continuous time period that two individuals were observed within a group; thus, if a group with three individuals was observed for 7.5 hours, that was counted as 3 dyad-days: Sifaka 1/Sifaka 2, Sifaka 2/Sifaka 3, and Sifaka 1/Sifaka 3.

for 5 min, followed by 35 cycles of 95°C for 30 s, a primer-specific annealing temperature for 30 s, 72°C for 30 s, and ending with a single extension of 72°C for 10 min.

       I determined allele sizes by separation of the PCR products on a 7% polyacrylamide gel run on an ABI 377 DNA Analyser (Applied Biosystems) and assigned fragment length using Genescan software (Applied Biosystems) with a Genescan-500 [Tamra] size standard. I analyzed the dataset for errors using MICRO-CHECKER (van Oosterhout et al. 2004) and MSA (Dieringer and Schlotterer 2003). Marker independence was assured in FSTAT 2.9.3.2 (Goudet 1995, 2001) before population genetic parameters were estimated in GENEPOP 3.3 (Raymond and Rousset 1995). To analyze relatedness, I used ML-RELATE (Kalinowski et al. 2006) and CERVUS (Marshall et al. 1998, Slate et al. 2000). Kin were defined as related at $r \geq 0.25$, nonkin as $r < 0.25$. Further details of the genetic analysis, as well as population parameter estimates for samples collected in Ranomafana, are presented in Chapter 4.

       I analyzed data according to statistical procedures described in Sokal and Rohlf (1995) using Statistica 6.0. I used non-parametric statistics for data that were not normally distributed. I conducted one-way and factorial ANOVAs for most analyses. For smaller, non-normally distributed sets of data, I used Mann-Whitney U and Kruskal-Wallis tests. Differences between groups were considered significant at $P < 0.05$.

# RESULTS

Results of testing the following predictions of the ETF are summarized in Table 1.

*Predictions 1 & 2*

To test whether dispersal was related to ecological constraints and reproductive opportunities, I first examined whether individuals bred with their relatives. I found that no natal animal whose opposite sex parent (OSP) was still present in the group reproduced, although two females and one male reproduced once their OSP had died or dispersed from the natal group. The genetic data support the lack of inbreeding in this population (Chapter 4: Table 7).

To test for the stability of family groupings, I looked at the size and composition of the groups over time. Across the study, the four focal groups ranged in size from ten individuals down to zero (Groups 2 and 3 dissolved in 2007). However, there were never more than two breeding males or breeding females in a group across this time; the remainder of the variation comes from non-breeding offspring from newborn to nine years old (Chapter 3: Table 1). There was never a third female present that was known to be unrelated to the group breeding male; genetic data, when available, indicated that subadult females present in the group were daughters of the breeding male.

There were 12 losses (through death or dispersal) of the group breeding female and 8 losses of the group breeding male throughout the study. Most (9/20) of the losses followed takeovers, with resident breeders dispersing after a same sex immigrant entered the group. In most other cases, there was another breeder already present in the group ($N = 4$) or a natal subadult that began breeding ($N = 2$). Therefore, from 1987 until 2007, only five times were one of the four territories left without a breeding male or breeding female, a total of $14 \pm 3$ months (variation due to observation error) out of 858 group months. A single occurrence made up 9-11 months of this duration, in which neither a breeding male nor female was present in Group 3. An additional 18 months at the end of 2007 occurred with Groups 2 and 3 territories left vacant after a death in the group followed by the remaining members in those groups dispersing out of Talatakely.

Residency in the natal group before dispersing was shorter on average for non-reproductive females (mean = 52 months, $N = 4$) than non-reproductive males (mean = 80 months, $N = 7$; $Z = 2.65$, $P = 0.0082$). However, four males immigrated into and dispersed out of groups without reproducing (mean tenure = 19 months), whereas no immigrant females dispersed without reproducing. Thus, overall there was no difference between tenure of non-reproductive females (mean = 52 months) and males (mean = 58 months; $Z = -0.78$, $P = 0.43$; Figure 1). For immigrants and natals that did reproduce in the group, there was no difference between female (mean = 59.5, $N = 10$) and male (mean = 74.6, $N = 9$) residence time ($Z = -0.33$, $P = 0.74$; Figure 1).

Average residency differed significantly between groups (F(3, 32) = 4.3, $P = 0.011$), with individuals in Group 1 and Group 4 averaging longer residencies than individuals in Group 2 and Group 3; this effect reduced slightly when including residencies that ended in death (F(3, 40) = 3.5, $P = 0.024$; Figure 2). There was no interaction effect with sex (F(3, 32) = 1.2, $P = 0.32$). Focusing specifically on subadults, there was no significant difference in residency time until first dispersal between groups (Group 1 mean = 85 months, Group 2 mean = 56 months, Group 3 mean = 53 months, Group 4 mean = 68 months; $H(3, 11) = 2.48$, $P = 0.48$).
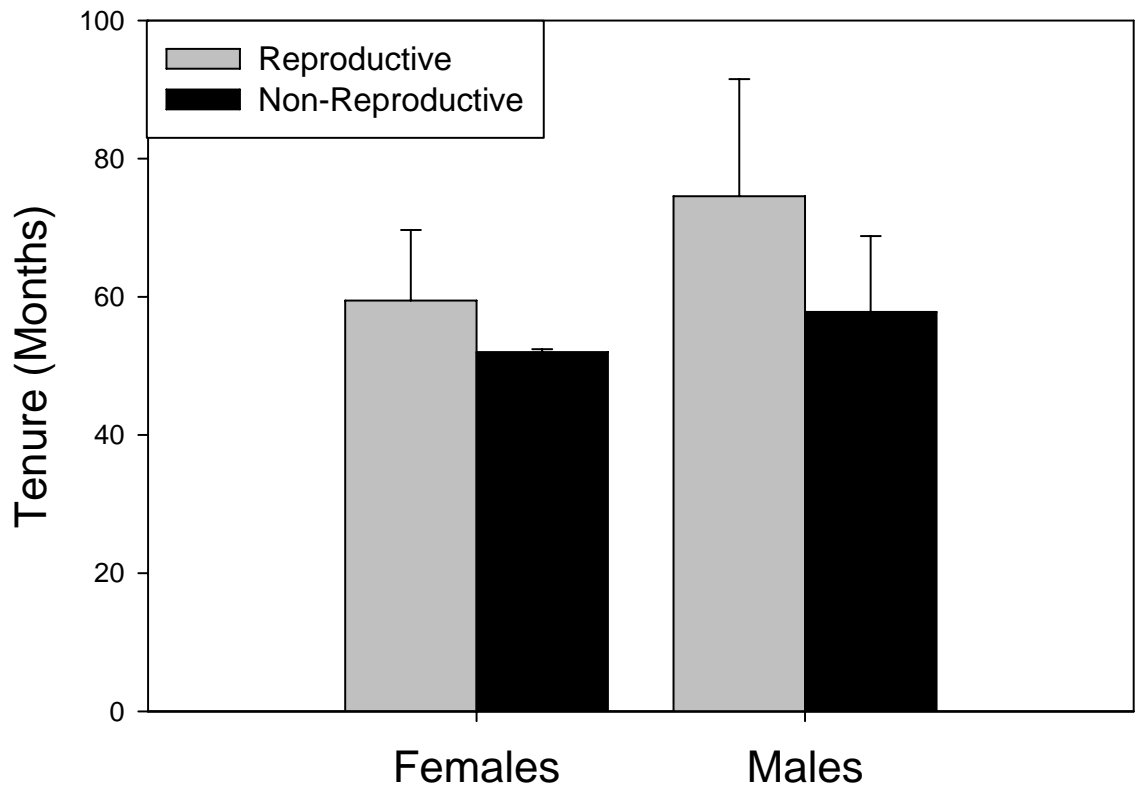
**Figure 1.** Mean (± SE) group tenure in months of females and males considering whether they produced offspring in the group (reproductive) or not (non-reproductive). There was no difference between tenure of non-reproductive females (mean = 52 months, $N$ = 4) and males (mean = 58 months, $N$ = 11; $P$ = 0.43) or reproductive females (mean = 59.5, $N$ = 10) and males (mean = 74.6, $N$ = 9; $P$ = 0.74).
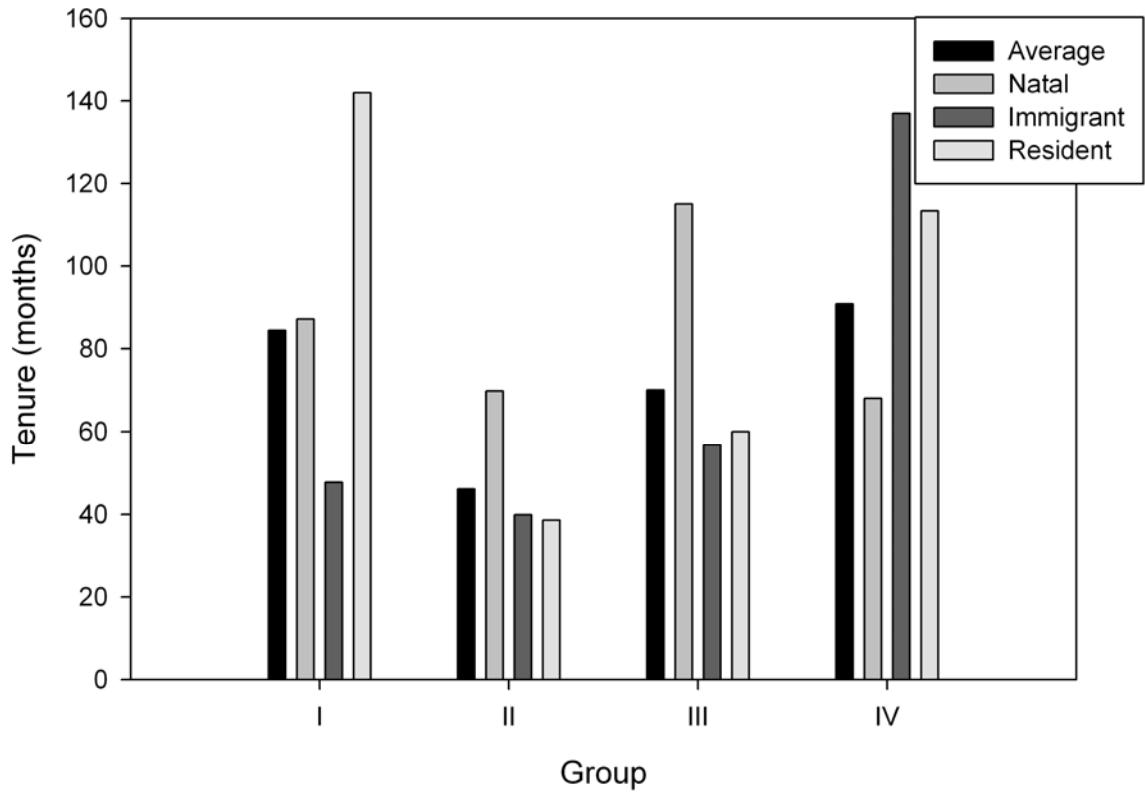
**Figure 2.** Average tenure in months by natals, immigrants, and residents (animals present before the start of the study) in Groups 1-4. Tenure averaged across all categories differed significantly between groups ($P = 0.011$).

To assess territory quality, size of individuals within age-classes was compared across groups. In general, female infants and juveniles did not differ from male infants and juveniles in weight ($F(1, 73) = 0.80$, $P = 0.37$) or body mass index (BMI: $F(1, 56) = 0.96$, $P = 0.33$). However, adult (greater than 3.5 years) females were on average 5% heavier than adult males (females = 5.67 kg, males = 5.41 kg; $F(1, 170) = 28.1$, $P < 0.0001$), although adults did not differ significantly in average BMI ($F(1, 111) = 2.2$, $P = 0.14$). Thus, adult females weighed more than but did not differ in body length from adult males ($F(1, 111) = 0.21$, $P = 0.65$). This effect held from July through December, months outside of the gestation season (weight: $F(1,87) = 13,862$, $P = 0.0004$; BMI: $P = 0.27$).

Across age classes, Group 3 individuals had lower average BMI (21.31, $N = 23$) and Group 4 showed slightly higher average BMI (24.71, $N = 29$) than Group 1 (23.74, $N = 39$) and Group 2 (23.10, $N = 34$; $H(3, 136) = 6.34$, $P = 0.096$). When using group size as a covariate (mean = 5.51), juveniles (< 3.5 years) and subadults (3.5-9 years) did not differ among groups in average log weight ($F(3, 98) = 3.4$, $P = 0.79$; Figure 3). When using group size as a covariate for animals older than seven years (mean = 4.98), there was a difference among groups in average log weight $F(3, 99) = 4.1$, $P = 0.0080$), with Group 4 significantly lower than Groups 1, 2, and 3 (Figure 4). Finally, I found no effect of rainfall on group size across study years ($F(1,1490) = 1.9$, $P = 0.17$; Figure 5).

In sum, there was no inbreeding and no more than two adult males or females bred in the same group. Group vacancies were very rare and turnovers were common. The residency for natal females was shorter but overall average male and female tenures were equivalent. Residency time did not differ significantly between groups. There was no effect of rainfall on group size. Thus, Predictions 1 and 2 were not supported by this analysis.

*Predictions 3 & 4*

To determine whether offspring care is correlated with relatedness within and between groups, I analyzed affiliation and aggression. For affiliative interactions, I examined grooming and mutual grooming. This amounted to 11631 grooming bouts, although the bout rate, which was calculated by considering how many times dyads were observed grooming during the 5 minute scans of the focal animal, were very low when averaged across all dyads. Aggression was also a rare event, with only 723 acts of aggression over 460 days.

I found that, overall, more affiliative interactions occurred between kin than between nonkin (kin = 0.16 bouts/hour, nonkin events = 0.13 bouts/hour; $F(1, 1717) = 49.9$, $P < 0.0001$; Figure 6). When considering individual activities, I found that relatives with an average r = 0.5 groomed more frequently than relatives of lower r ($F(3, 2331) = 8.5$, $P < 0.0001$) but that there was an interaction between kinship and sex ($P < 0.01$). Females directed ten times more grooming bouts toward related juveniles and infants than unrelated juveniles and infants (kin = 0.0035 bouts/hour, nonkin = 0.00033 events/hour; $F(1, 653) = 19.0$, $P < 0.0001$). However, male adults did not groom related group infants and juveniles more than they groomed unrelated group infants and juveniles (kin = 0.0012 bouts/hour, nonkin = 0.002 events/hour; $F(1, 357) = 2.6$, $P = 0.11$; Figure 7). Non-cohort siblings groomed longer (siblings = 14.1 s/hour, halfsiblings = 11.3 s/hour; $F(1, 1389) = 8.9$, $P = 0.0028$) and more often (siblings = 0.24 bouts/hour, halfsiblings = 0.20 bouts/hour; $F(1, 2279) = 14.3$, $P = 0.00016$) than non-cohort halfsiblings, and both groomed longer ($F(2, 2267) = 15.8$, $P < 0.0001$) and more often ($F(2, 3735) = 46.2$, $P < 0.0001$) than grandparents/grandoffspring; the pattern was slightly weaker when including cohort-mates (siblings = 14.1 s/hour, halfsiblings = 12.7 s/hour; $F(1, 1906) = 4.5$, $P = 0.034$).
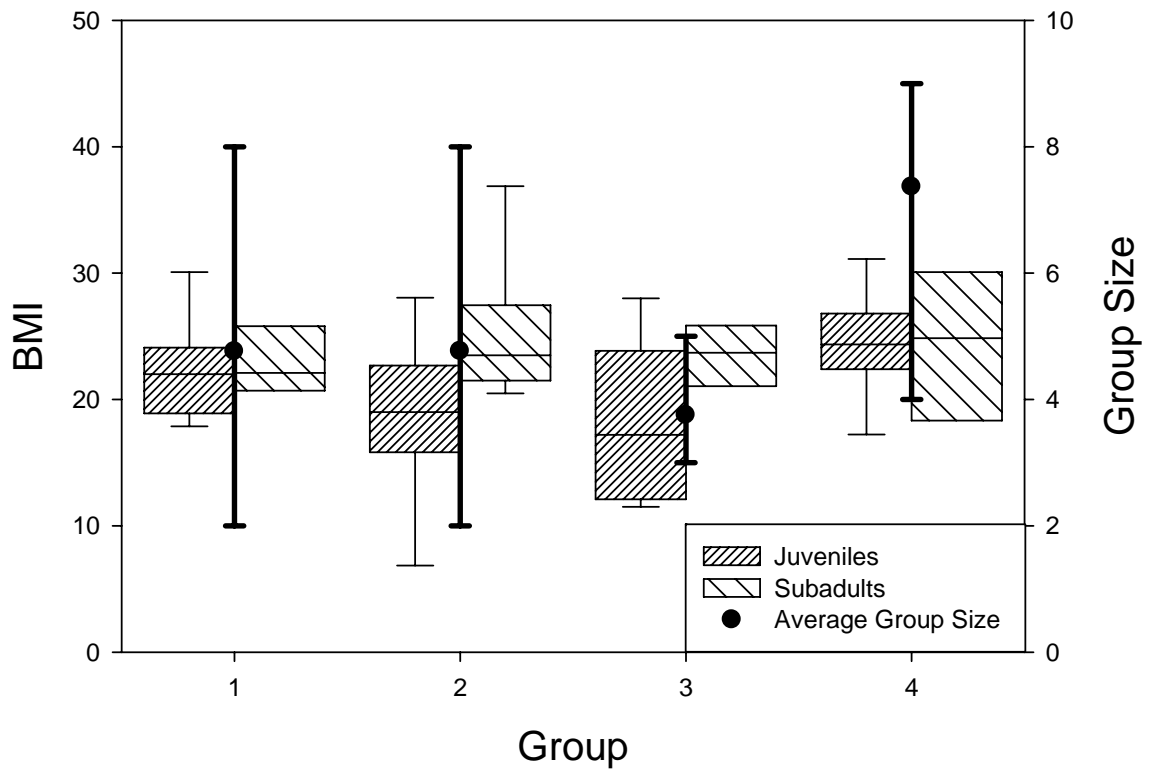
**Figure 3.** Mean (± SE) Body Mass Index (BMI) of juveniles (1-3.5 years) and subadults (3.5-7 years) and average group size (with max. and min. limits) in Groups 1-4, 1988-2004. Group 3 had lower average BMI (21.31, $N = 23$) and Group 4 showed slightly higher average BMI (24.71, $N = 29$) than Group 1 (23.74, $N = 39$) and Group 2 (23.10, $N = 34$; $P = 0.096$).
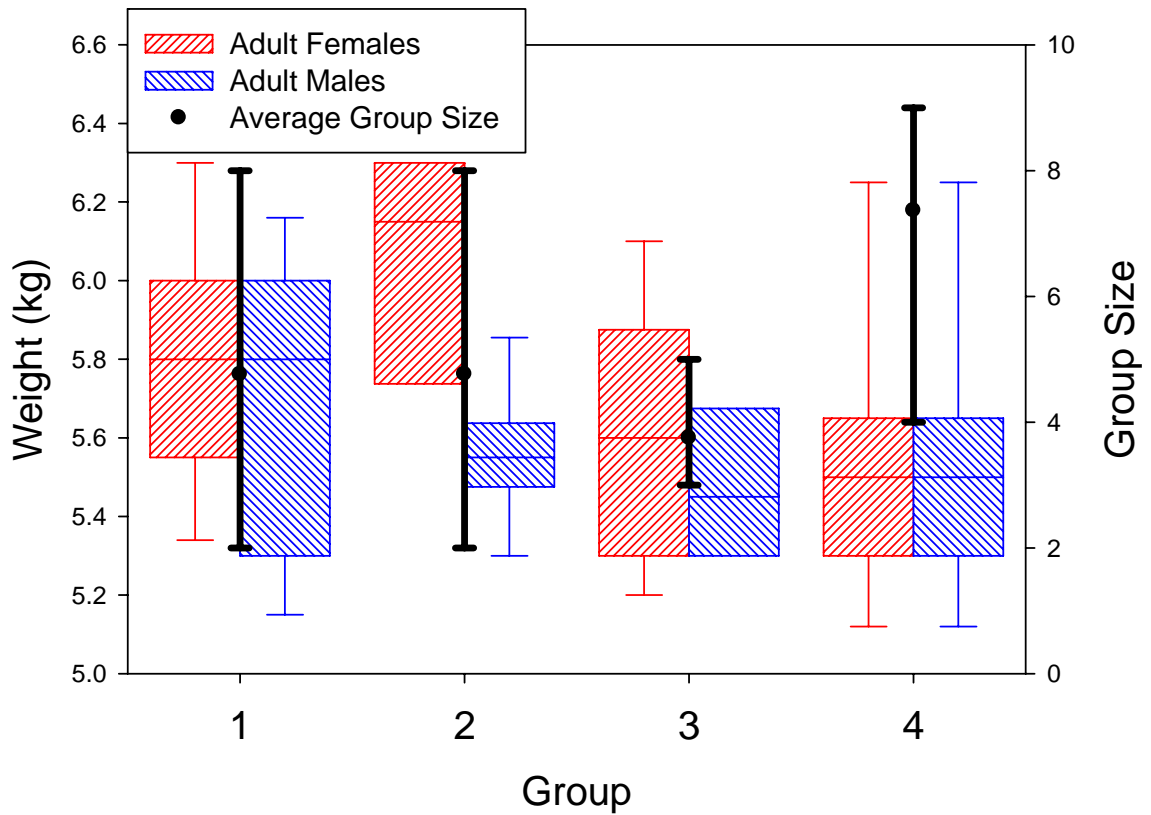
**Figure 4.** Mean (± SE) weight in kg of adult (> 7 years) females and males and average group size (with max. and min. limits) in Groups 1-4, 1988-2004. When using group size as a covariate (mean = 4.98), there was a difference between groups in average log weight, with Group 4 significantly lower than Groups 1, 2, and 3 ($N = 99$, $P = 0.0083$).
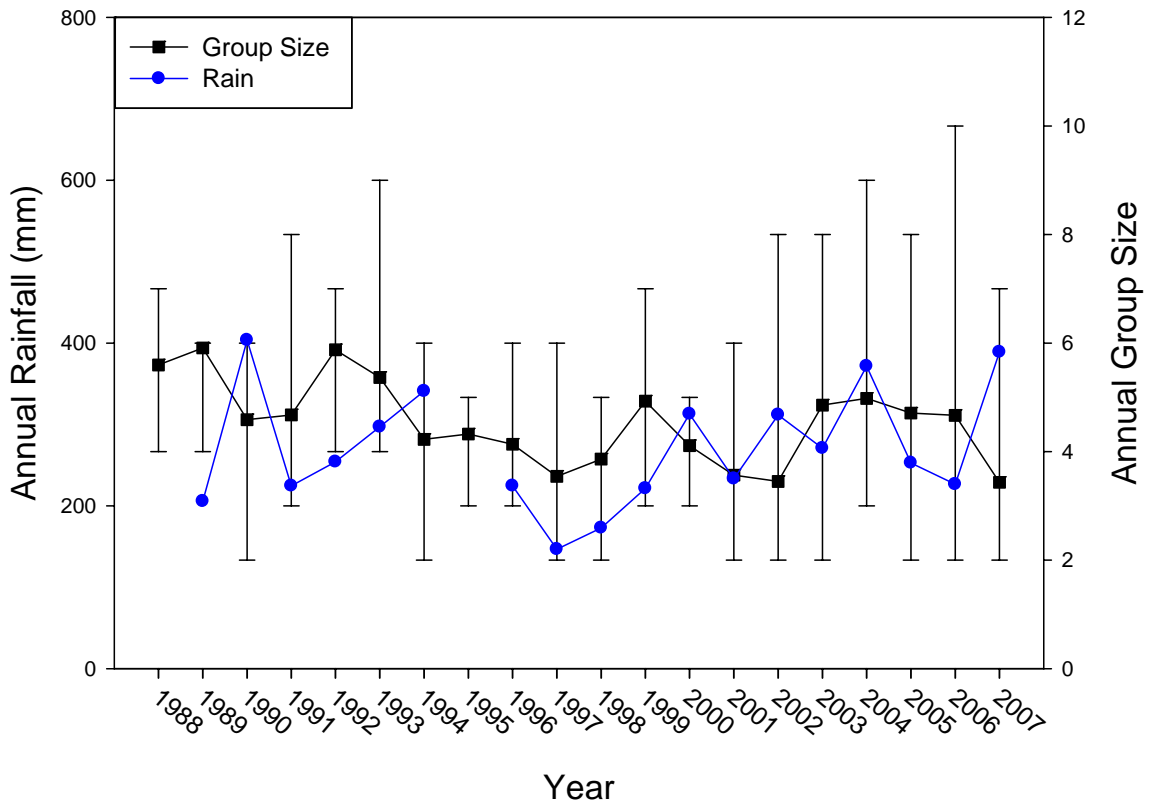
**Figure 5.** Mean (± SE) annual group size (*N* = 1576) compared with average annual rainfall (*N* = 210). There was no effect of rainfall on group size across study years (*P* = 0.17).
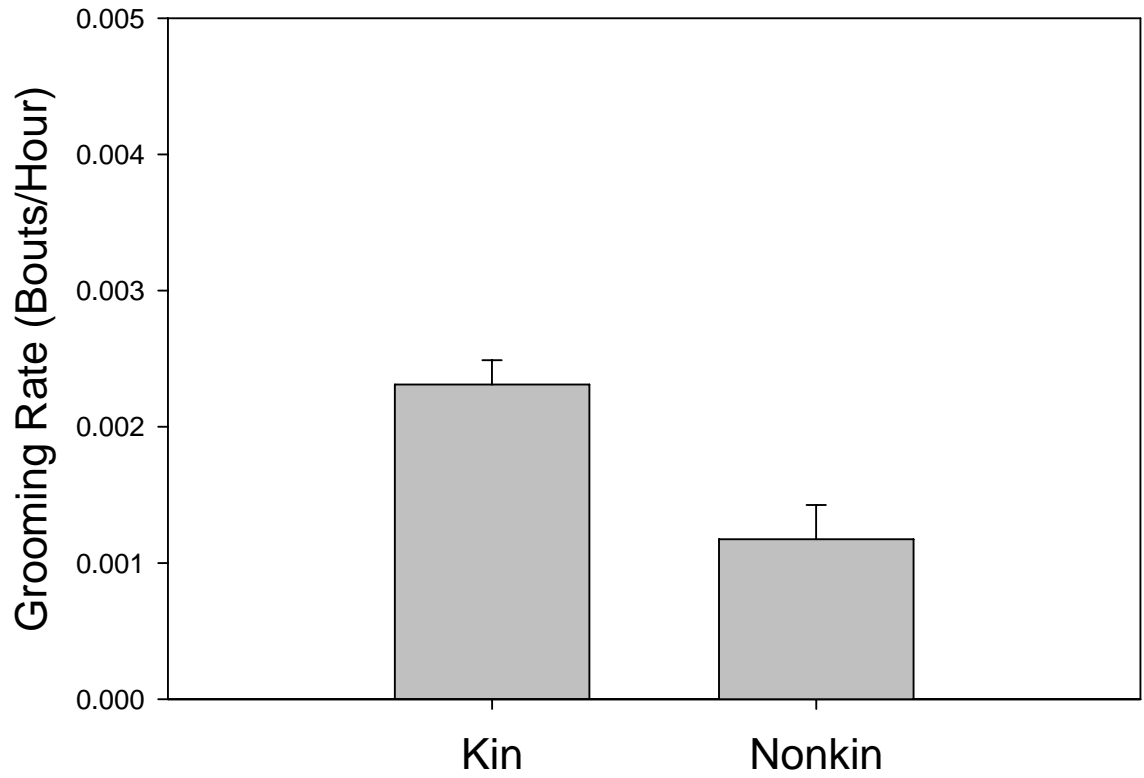
**Figure 6.** Mean (± SE) allogrooming rate by kin (r ≥ 0.25, $N$ = 1717) and nonkin (r < 0.25, $N$ = 212) across all age classes. Kin groomed more frequently than nonkin ($P$ < 0.0001).
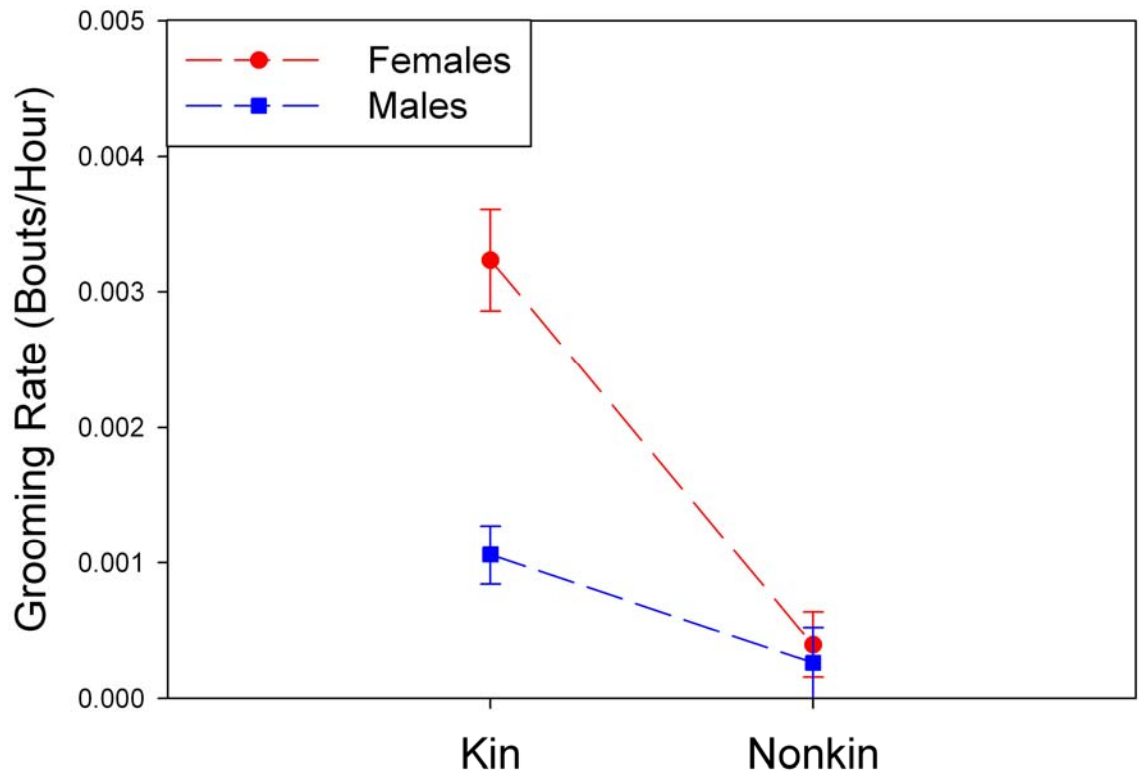
**Figure 7.** Mean (± SE) allogrooming rate of group young by adults. Grooming by adult females toward kin (r ≥ 0.25; $N = 568$) was more frequent than toward nonkin (r < 0.13; $N = 60$) juveniles and infants ($P < 0.0001$). Adult males did not groom kin (r ≥ 0.25; $N = 458$) significantly more than nonkin (r < 0.13; $N = 31$) juveniles and infants ($P = 0.16$). There was a significant interaction between sex and kinship ($P < 0.01$).

Mutual grooming showed a distinctively different pattern: whereas grooming was directed between parents and offspring much more frequently than toward unrelated dyads, mutual grooming occurred more frequently between unrelated dyads than between parents and offspring ($F(1, 1823) = 20.5$, $P < 0.0001$), even when excluding adult male/female pairs ($F(1, 1006) = 39.3$, $P < 0.0001$). Even when excluding parent/offspring dyads, unrelated adults and juveniles engaged in mutual grooming much more often than adult and juvenile kin ($F(1, 449) = 33.2$, $P < 0.0001$). There was an interaction between sex and kinship with the increased mutual grooming between nonkin mostly initiated by adult females ($P < 0.05$).

Conversely, rates of aggression were much higher between nonkin than between kin ($F(1, 4672) = 71.9$, $P < 0.0001$; Figure 8), even when excluding adults ($F(1, 3493) = 21.5$, $P < 0.0001$). When focusing on adult and juvenile behavior toward younger juveniles and infants, I found the same pattern, with rates of aggression much higher between nonkin than between kin ($F(1, 2065) = 36.9$, $P < 0.0001$). When only examining interactions between adults and group young, kin were less aggressive ($F(1, 1131) = 18.6$, $P < 0.0001$), although the pattern of adult males directing less aggression toward offspring than nonkin group young was not statistically significant ($F(1, 457) = 2.0$, $P = 0.16$) unless considering approaches and displacements ($F(1, 457) = 10.7$, $P = 0.0012$). There was no interaction between sex and kinship ($P = 0.29$; Figure 9).

I also examined rates of aggression and affiliation between groups considering group relatedness. The amount of variation explained by group r when examining grooming, mutual grooming, overall affiliation, and aggression, either between all individuals or just adults and juveniles toward juveniles and infants, was less than 2%.

Overall, tests of predictions 3 and 4 produced mixed results: assistance was directed more toward group young according to relatedness, although this was not true for adult males. Furthermore, there was no effect of group r on assistance of young within groups.

*Prediction 5*

The ETF predicts that sexually related aggression will be most frequent when group members are least related. Aggression between unrelated adult males was not significantly higher in the breeding season ($N = 72$, $P = 0.21$). Generally, aggression was much more frequent by adult females toward adult males, with only eight incidents of aggression (out of 2833 hours) by adult males toward adult females ($F(1, 1367) = 109.2$, $P < 0.0001$). Moreover, adult females aggressed more toward adult males in the breeding season ($F(1, 683) = 4.6$, $P = 0.033$). There was no change in aggression during the breeding season when excluding adults ($F(1, 4244) = 0.006$, $P = 0.94$). There was also no change in aggression rates between unrelated adults and subadults considering season ($F(1, 225) = 0.10$, $P = 0.75$).

Affiliation within breeding pairs followed similar patterns: males initiated affiliative activities more often than females ($F(1, 3619) = 89.3$, $P < 0.0001$). Adult males groomed unrelated adult females more frequently ($F(1, 1345) = 223.5$, $P < 0.0001$) and with bouts of longer duration ($F(1, 476) = 20.2$, $P < 0.0001$) than vice versa. However, males did not initiate more mutual grooming bouts than females within breeding pairs ($F(1, 1068) = 3.1$, $P = 0.079$), with an interaction between sex initiating and the activity that was initiated ($P < 0.01$; Figure 10). Male grooming behavior did not depend on season ($F(1, 1070) = 0.00070$, $P = 0.98$). Adult females did not change frequency of grooming adult males in the breeding season either but initiated less mutual grooming toward unrelated adult males in the breeding season (interaction effect: $F(1, 1068) = 6.3$, $P = 0.012$; Figure 11).
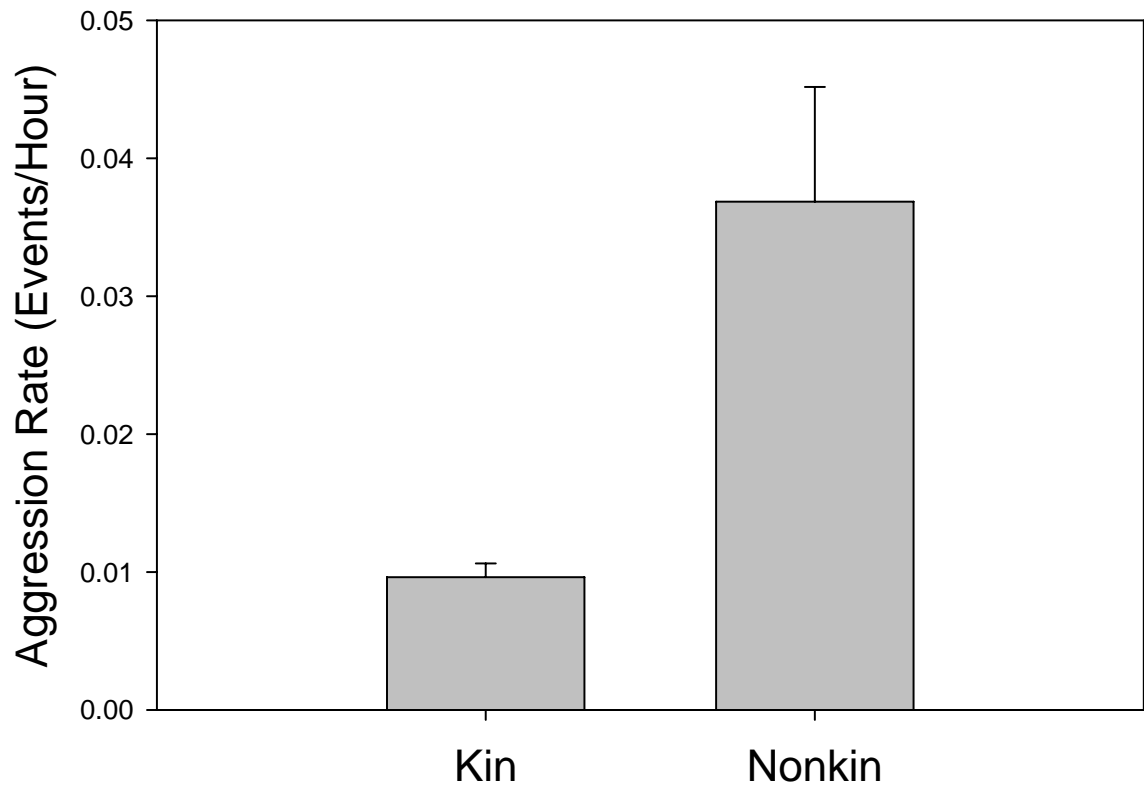
**Figure 8.** Mean (± SE) aggression rate between kin and nonkin. Aggression rates were lower between kin (r ≥ 0.25; $N$ = 1781) than nonkin (r < 0.25; $N$ = 277) across the population.
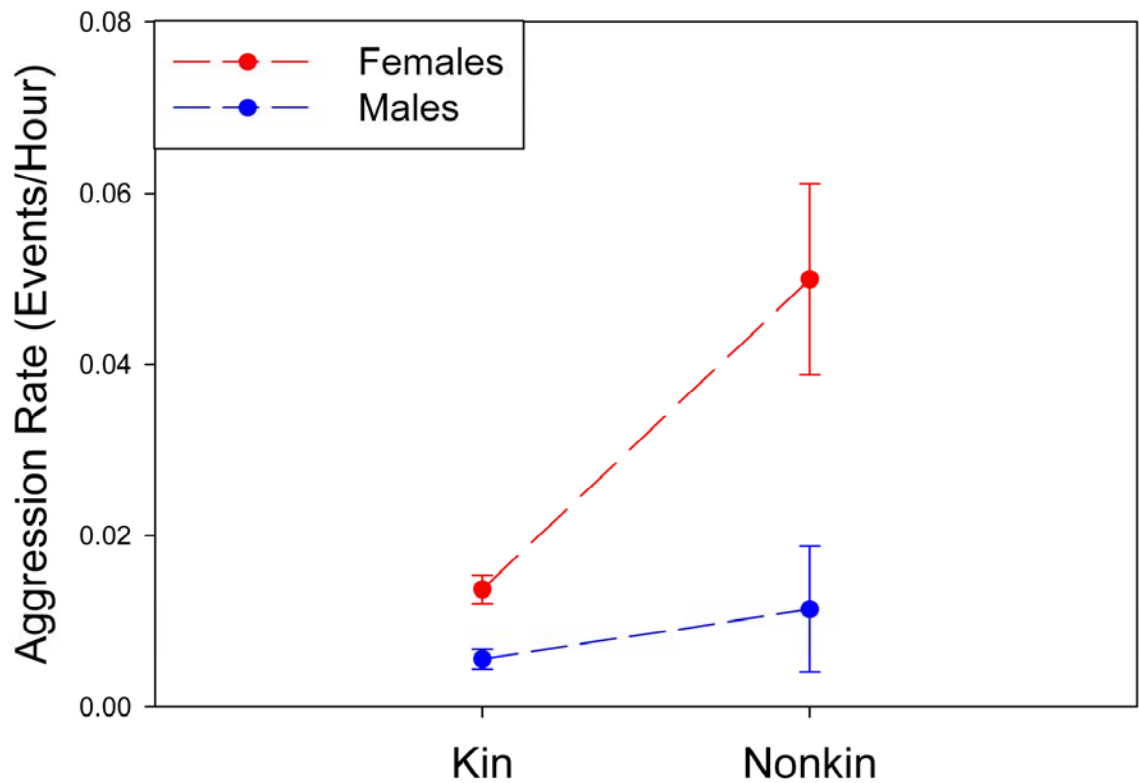
**Figure 9.** Mean (± SE) aggression rate by adults toward group young. Aggression by adult females toward kin (r ≥ 0.25; $N$ = 837) was more frequent than toward nonkin (r < 0.13; $N$ = 78) juveniles and infants ($P$ = 0.03). Adult males did not groom kin (r ≥ 0.25; $N$ = 739) significantly more than nonkin (r < 0.13; $N$ = 40) juveniles and infants ($P$ = 0.16). There was no significant interaction effect between sex and kinship ($P$ = 0.29).
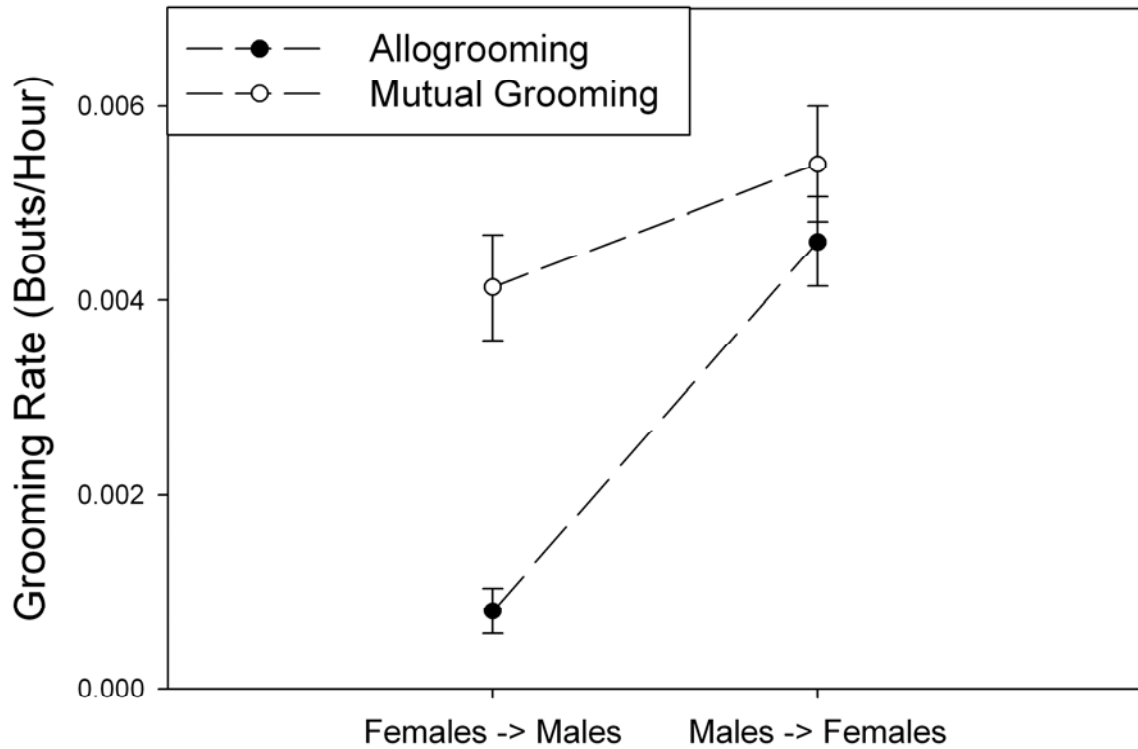
**Figure 10.** Mean (± SE) grooming rate and mutual grooming rate initiated by females toward males and males toward females. Males groomed females more frequently than females groomed males ($N = 3619$, $P < 0.0001$). Males and females initiated the same number of mutual grooming bouts ($N = 1068$, $P = 0.079$). There was an interaction between sex initiating and the activity that was initiated ($P < 0.01$).
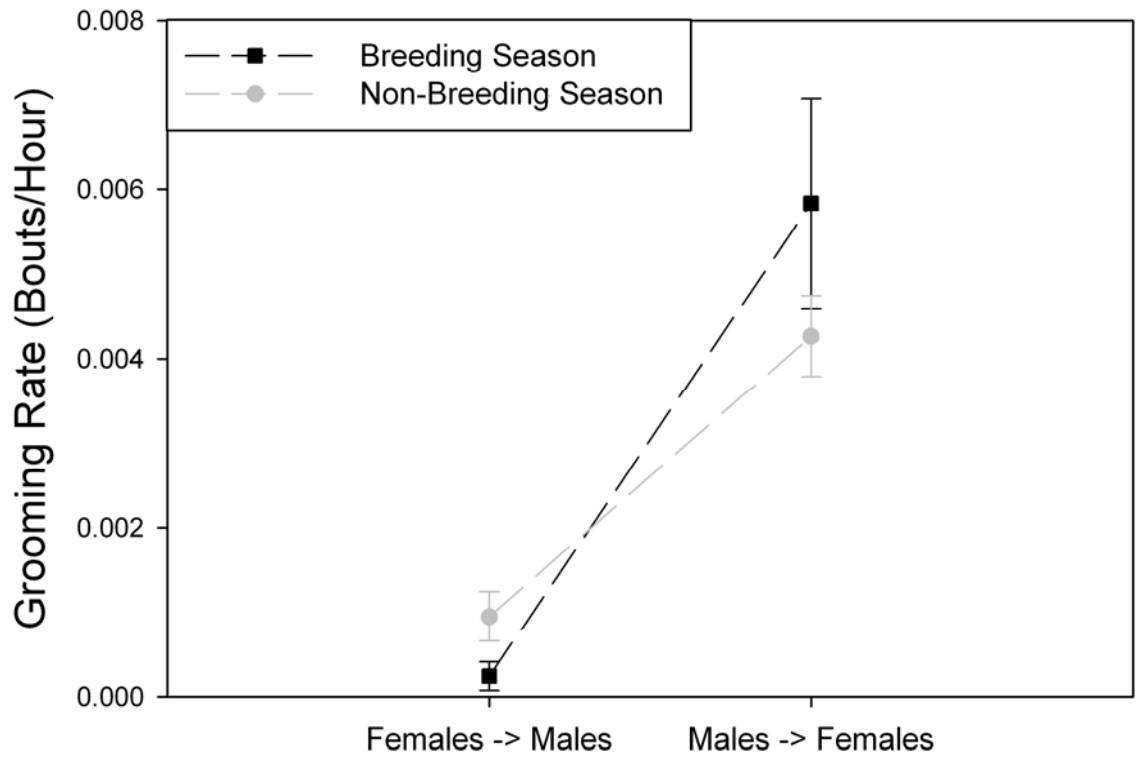
**Figure 11.** Mean (± SE) grooming rate initiated by females toward males and males toward females in the breeding season and the non-breeding season. There was no effect of season on grooming rate ($N = 1070$, $P = 0.98$).

Prediction 5 was partially supported.  Rates of aggression were highest within breeding pairs, specifically directed from females to males.  However, there was no effect of season and aggression was unidirectional.  Affiliation results were similar.

*Prediction 6*

Because sifaka estrus is extremely short, observations of mating have been rare.  Because multiple mating may not be observed, either by a human or a lemur, a reasonable proxy for paternity uncertainty is presence of another adult male.  Therefore, to determine whether resident males were investing less in offspring as their paternity certainty decreased, I examined 20 dyads in which the infant was conceived while there was more than one adult male present in the group.  Aggression rates by adult males toward infants and juveniles were much higher when they were conceived with more than one adult male in the group (1 male present = 0.0059, >1 male present = 0.017; $F(1, 498) = 7.8$, $P = 0.0054$), although there was no interaction effect with kinship (Figure 12).  Grooming was more frequent by fathers toward offspring who were conceived with more than one male in the group (1 male present = 0.0011, >1 male present = 0.0017; $F(1, 475) = 7.3$, $P = 0.0073$), with more grooming towards non-relatives when paternity was uncertain (kin = 0.0013, nonkin = 0.0031; $F(1, 137) = 4.2$, $P = 0.042$).  Thus, Prediction 6 was supported by the aggression data, with males more aggressive toward group young when paternity was uncertain.  Grooming data produced mixed results, with males grooming nonkin group young more often when paternity was uncertain.

*Predictions 7 & 8*

To determine whether resident adult turnover results in family conflict, I considered situations in which the breeder died or dispersed and there was a subadult (at least 3.5 years old) present in the group.  Most ($N = 10$) dispersals occurred after takeovers by same sex (SS) immigrants (see Chapter 3).  Excluding these takeovers, there was an average of one breeding vacancy/group every six years ($N =12$).  This included four cases of known predation of the group breeder by fossa and eight cases of suspected voluntary dispersal with no concurrent immigration (e.g., BP male dispersed from Group 3 after the breeding female BB was killed by a fossa).  In four of these twelve cases, there was a female already breeding in the group when the other breeding female disappeared and no new adult immigrated to the group.  In only one of these cases was there a SS subadult present; she bred along with her mother, the remaining female breeder, once she reached 3.5 years.  Likewise, in the one case where there was a female subadult present when the single female breeder was killed, she bred the following season at 3.5 years.  In a similar case, when the male breeder dispersed from Group 3 in 1999, the single group subadult BP became the group breeding male.  On the other hand, in two other situations, the groups' single subadults dispersed after their SS breeder died; these subadults were known to be, in one case, and suspected to be, in the other case, the close kin (offspring or sibling) of the remaining breeders.  In the four remaining cases, there was no SS individual present in the group when the group breeder disappeared.  These disappearances (either death or dispersal) resulted in vacancies that were not filled for months in one case and never filled when the breeders dispersed from Group 2 and 3 territories in 2007.  Therefore, there was never a situation with two offspring present in a group with an unrelated potential mate and the SS breeder died.
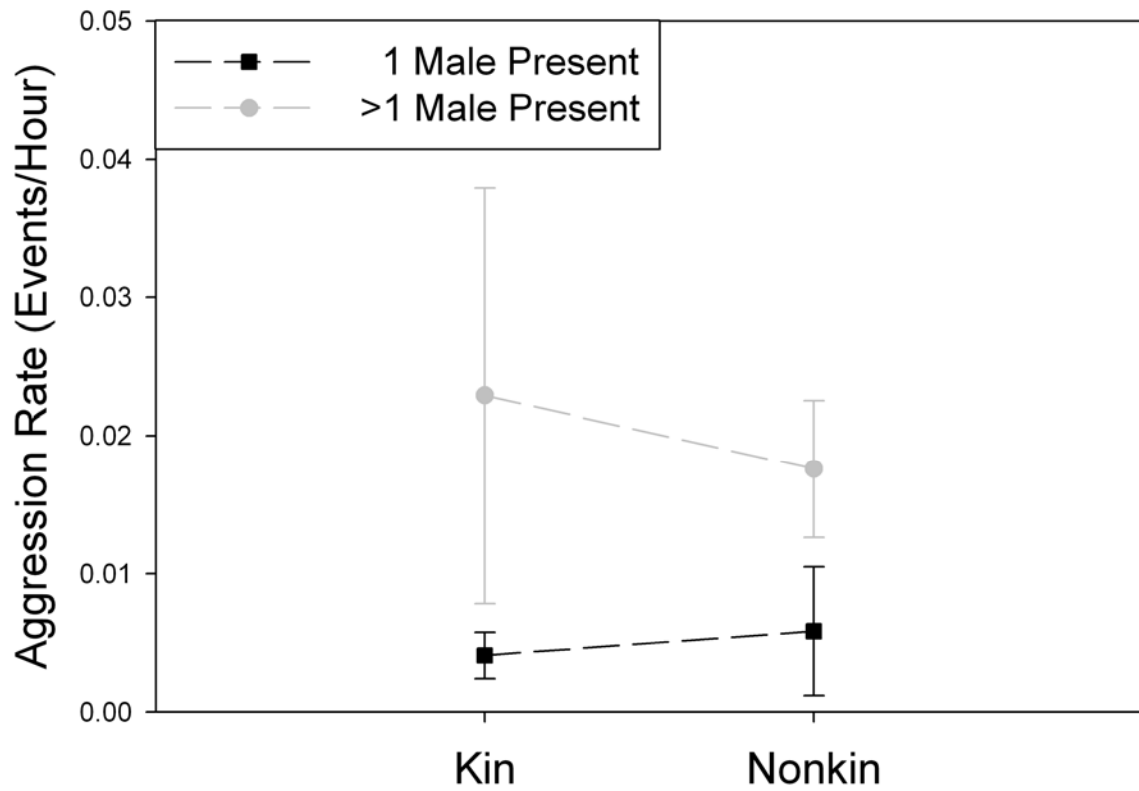
**Figure 12.** Mean (± SE) aggression rate of kin (offspring) and nonkin when paternity was certain (1 male present) and paternity was uncertain (>1 male present). Adult males were more aggressive toward group young conceived with more than one adult male present than toward group young conceived with one adult male present ($N = 498$, $P = 0.0054$). There was no effect of kinship.

Once a new breeder entered the group, I tested whether the group's subadult(s) competed for the new mate with their SS parent. In the two cases where there were two related females present in a group when a new male immigrated, they both began to breed. For males, there were four cases where a new female entered the group and bred and there were natal subadults present. In only one of these cases was the subadults' father present. In this case, the subadults (age 4.5 and 6.5 years) remained in the natal group for an additional three years. The new resident female had two infants at this time but paternity is unclear.

Examining the only five unrelated SS adult dyads found in the same group, I found that the aggression rate was higher between the females ($F(1, 148) = 70.1$, $P < 0.0001$) but not significantly higher between the males ($F(1, 362) = 0.14$, $P = 0.71$) than between related SS adults. There was no difference in grooming rates between unrelated SS adults and between related SS adults ($F(1, 450) = 0.15$, $P = 0.70$), or mutual grooming between the two females ($F(1, 141) = 0.86$, $P = 0.35$); however, there was a higher frequency of mutual grooming between the unrelated males than between other males ($F(1, 307) = 13.6$, $P = 0.00027$).

Predictions 7 and 8 were difficult to test in this population, as the opportunity for family conflict over a breeding spot was so rare. As predicted, the conflict, in the form of aggression rate, was more severe between unrelated females, the dominant sex, than between unrelated males. The prediction of conflict following the re-pairing of a SS parent failed for females; in each case the second female (there was never a third) began to breed as well. For males, there were not enough data to test the prediction.

## Predictions 9 & 10

To determine whether replacement breeders invested less in existing offspring than biological parents do, I examined rates of aggression, affiliation, and infanticide. Replacement breeders of both sexes were more aggressive toward group young than were the parents of those young ($F(1, 429) = 34.4$, $P < 0.0001$). Female replacement breeders groomed group young less often than parents did (offspring = 0.0048, nonkin = 0.00021; $F(1, 482) = 21.4$, $P < 0.00001$); there was no difference in grooming rate by males ($F(1, 325) = 2.1$, $P = 0.14$; Figure 13). There was an interaction between sex and kinship ($P < 0.001$).

I also examined whether replacement breeders committed infanticide when entering new groups. All immigration events ($N = 9$) were associated with the disappearance or observed death of group infants ($N = 10$; Chapter 3: Table 2), regardless of the immigrant's sex. Thus, there were no effects of dominant sex. All females whose offspring disappeared when a female immigrated immediately (within one week) dispersed from the group. All females whose offspring disappeared when males immigrated gave birth the following season, resulting in 60% decrease in the interbirth interval.

Predictions 9 and 10 were supported by this study, as replacement breeders (both sexes) were more aggressive toward group young and female replacement breeders (though not males) were less affiliative toward group young. Moreover, most replacement breeders appeared to commit infanticide. However, the sex of the replacement breeder had no effect.

## Prediction 11

To determine whether biologically intact families were more stable than families with one or two replacement breeders, I looked at the age of dispersal of subadults. There
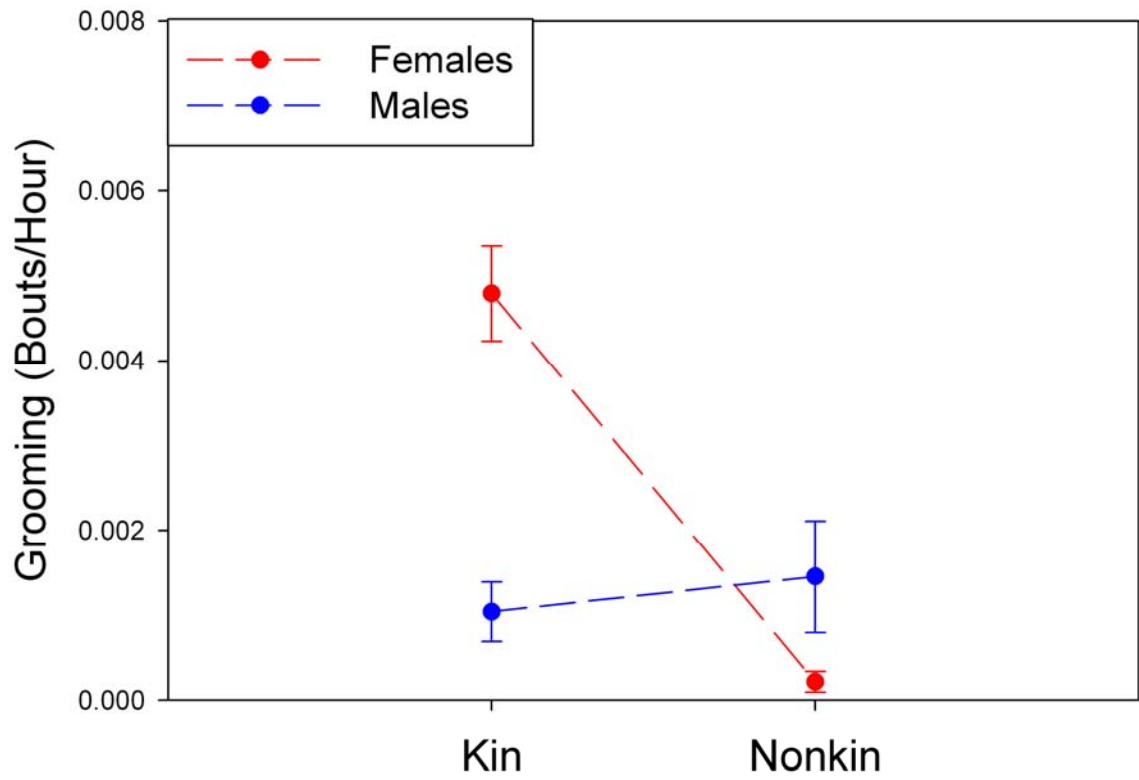
**Figure 13.** Mean (± SE) grooming rate by breeding males and breeding females of offspring (kin) or unrelated group young (nonkin). Female replacement breeders groomed group young less often than parents did ($N = 482$, $P < 0.00001$). Kinship did not have an effect on grooming rate by males ($N = 325$, $P = 0.14$). There was an interaction between sex and kinship ($P < 0.001$).

were 15 juveniles that survived until sexual maturity. Three of these (two females and one male) remained in the group to reproduce with the replacement breeder; in these cases, there were no other infants or subadults present at the time that the new breeder immigrated. Of the remaining four females and eight males, one female and three males were part of replacement families (remained in their natal group after their parent was replaced by an immigrant). These male subadults stayed in the group until 6.4 years old, on average (range 5-9.3 years). This is not different from the average age that males disperse from intact families ($N$ = 5.6 years; $U$ = 0.51, $N$ = 3, 8, $P$ = 0.61). The only female that was part of a replacement family remained until age 4.3 years, similar to the average age that natal females dispersed from intact families (mean = 4.4 years, range = 4.3-4.6 years). When considering the two dispersers in SS replacement breeder families, the average age at dispersal of subadults was 4.65 years, compared to an average of 5.6 years in intact families. Overall, Prediction 11 was not supported. Replacement families were not less stable than biologically intact families, with no apparent effect of the sex of the step-parent.

*Predictions 12-15*

Because of small family size, rare joint breeding, and incomplete genetic sampling, it was difficult to measure the effect of ecological constraints, asymmetry in social dominance, relationship, and relatedness on reproductive skew in this population. I first identified all cases of more than one same sex breeder in the population. I found 20 out of 71 breeding seasons in which two to three males older than 3.5 years were in the same group and an unrelated sexually mature female was present (as I show in Chapter 4, neither parents and offspring nor siblings breed together in this population). In total, 13 offspring were born while these eight dyads and one triplet were sharing a group. I was able to obtain DNA samples to determine paternity for only four of these and only one of the four cases suggested reproductive sharing, i.e., more than one male fathering offspring in a group. This male was the son of the breeding male.

Two unrelated females were found in the same group as an unrelated adult male four times. In all four cases, both females bred, producing a total of 28 offspring while cobreeding. Two of the pairs produced the same number of offspring while cobreeding, with one female in the other two pairs only producing one more offspring than her groupmates. The age difference within two of the pairs indicated that they were mother/daughter pairs. A third pair was suspected to be a grandmother/granddaughter pair. The fourth pair was either mother/daughter or siblings. An immigrant adult female was never known to share a group with another immigrant or natal female during the breeding season.

I investigated these cobreeding cases for effects of ecological constraints, dominance, and relatedness. To test for ecological constraints effects, I examined whether cobreeding occurred in certain groups, signifying an effect of territory quality, or in certain years, signifying an effect of climate. Group 1 had related female cobreeders for seven breeding seasons, whereas Group 2 had female cobreeders for six seasons, and Group 4 for 10 breeding seasons, while Group 3 had no instances of female cobreeding (mean = 5.75; $\chi^2$ = 9.17, $P$ = 0.027). There were 12 breeding seasons of more than one potentially breeding male in Group 1, two breeding seasons in Group 2, seven in Group 3, and none in Group 4 (mean = 5.25; $\chi^2$ = 16.5, $P$ = 0.00091). There was no effect of year on number of breeding males or females (mean = 2.4; $\chi^2$ = 12.8, $P$ = 0.85). I also did not find an effect of cobreeding on weight for either adult males or adult females (F(1, 130) = 0.0001, $P$ = 0.99).

Thus, the circumstances determining reproductive skew did not appear to be dictated by ecological constraints or dominance but by relatedness.  Reproduction was shared equitably between related females and not at all between unrelated males or females.

**Table 1.** Summary of ETF predictions and the results of their testing.

| | Prediction | Results |
|---|---|---|
| Prediction 1-2 | Family size and tenure will depend on reproductive opportunities and resources. | Rejected |
| Prediction 3-4 | Assistance in rearing offspring will be directed toward relatives. | Partially Supported |
| Prediction 5 | Mating and aggression will happen between unrelated adults. | Partially Supported |
| Prediction 6 | Paternity uncertainty will lead to a decrease in investment in offspring. | Partially Supported |
| Prediction 7-8 | Breeder loss will cause family conflict. | Partially Rejected |
| Prediction 9-10 | Breeder replacement will lead to a decrease in investment in offspring and infanticide. | Supported |
| Prediction 11 | Replacement families will be less stable. | Rejected |
| Prediction 12-15 | Reproduction will be shared less with relatives when ecological conditions are bad and when cobreeders are parents and offspring rather than siblings. | Rejected |

**DISCUSSION**

*Family Formation and Stability*

Data from the Talatakely population indicated that inbreeding does not occur in Milne-Edwards' sifakas. Genetic data support these conclusions (Chapter 4), as do scent-marking data, with natal individuals scent-marking significantly less than non-natal animals (Pochron et al. 2005). Natal sifakas whose opposite sex parents were still living in the group did not reproduce; in some cases, they became reproductive shortly after their opposite sex parent dispersed or died. This suggests that sifakas have an effective mechanism in place for kin recognition, perhaps using olfactory cues (Sun & Muller-Schwarze 1997, Todrank et al. 1998, Penn 2002, Knapp et al. 2006, Charpentier et al. 2008).

Although I was unable to measure reproductive opportunities in the surrounding community, the lack of unrelated same sex breeding adults sharing the same group, the rarity of breeding vacancies in the focal groups, the lengthy average tenure of breeding males and females, and the absence of extra-group copulations and extra-pair young (see Chapter 4: Table 6) indicate that reproductive opportunities were indeed scarce. Generally, males and females had similar tenure length; however, males occasionally dispersed in and out of groups without reproducing and two (related) breeding females often reproduced in the same group, indicating that reproductive opportunities were more constrained and reproductive skew was higher among males than among females.

Tenure differed between groups, with longer average tenure in Group 1 and Group 4. Yet, there was no evidence that territories with the best resources supported the largest groups or the longest dynasties; Group 4, one of the most stable and largest groups throughout the study, had the lowest average body weights for adults and inhabited the most marginal territory. However, this group contained subadults well past sexual maturity that remained in the group despite the lack of reproductive opportunities. There was no effect found of rainfall on group size.

Thus, Predictions 1 and 2 from Emlen's Evolutionary Theory of the Family were not supported in sifakas; family size and tenure did not appear to depend on reproductive opportunities and resources. However, a more detailed analysis of microclimate and phenology could reveal correlations between delayed dispersal and ecological constraints.

*Family Dynamics: Kinship and Cooperation*

There was no effect of overall group relatedness on cooperation; however, the low variance in this value and the rarity of very low r groups may be an explanation. Within groups, affiliative activities increased and aggression decreased between relatives, although this pattern was driven by females. Male adults actually groomed nonkin more frequently and longer, possibly a result of females preventing males from having access to group infants. However, the lack of difference in aggression rates indicates that males may simply not distinguish between their own offspring and other infants and juveniles. Karpanty (2005) examined predator response behaviors in these groups for one season (2003) and found that adult males reacted more strongly to predator presentations (decoys and vocalizations of fossa and predatory birds) than other group members, primarily by mobbing the stimulus. This behavior could be a good test for kin selection; one could examine whether males respond more strongly to predator presentations when group young are their offspring than when they are unrelated. Notably, Karpanty's short study showed no

difference between groups, despite variation in offspring presence between groups: one of the four groups had no young and another had juveniles and infants.

Interestingly, mutual grooming showed a different pattern from allogrooming, with nonkin engaging in more mutual grooming. This result was predicted by reciprocal altruism theory, which Emlen did not consider in his ETF model. Reciprocal altruism theory states that behaviors will be given at a cost to the actor in exchange for receiving the same or another beneficial act in the future (Trivers 1971, Seyfarth 1977, Axelrod and Hamilton 1981, Seyfarth and Cheney 1984).

In addition, biological markets theory (Barrett et al. 1999, Henzi and Barrett 1999) predicts that costly helpful behaviors are commodities that can be exchanged for later benefits, such as reduced aggression, tolerance at feeding sites, or mating opportunities. Given that females are both dominant and also the choosy sex in this species (Trivers 1972, Emlen and Oring 1977), males should be more affiliative and less aggressive toward females than females should be toward males. The results supported these predictions: males groomed females much more than females groomed males and females reduced grooming of males even further during the breeding season. Moreover, females directed most aggression towards males, with slightly more in the breeding season. Adult males were effectively never aggressive toward females. Contrary to predictions of the ETF, however, I did not find a significant increase in male-male aggression in the breeding season, perhaps due to lack of power from small sample size. Future studies could examine whether tolerance at feeding sites, mating, or male tenure correlates with grooming rate.

Finally, I used the presence of more than one unrelated adult male at conception as a proxy for paternity uncertainty and asked whether males interacted with group young differently according to this factor. I found that males were more aggressive when paternity was uncertain. However, they seemed to groom offspring of lower paternity certainty more often as well, potentially for the purposes of coalition building (Schino 2006).

Overall, there was a distinct effect of relatedness that was not consistent across all dyads. This inconsistency may have resulted from the behaviors that were examined to test these predictions. Although grooming is costly in terms of time and energy, it is not a high-risk activity and may not, in fact, be driven by r. It is possible that grooming and aggression are behaviors directed toward group members based on distance and frequency of interaction. *P. edwardsi* belong to very small groups of high relatedness. Future analyses should test kin hypotheses against a null of nearest neighbor interactions.

*Family Dynamics: Disruption After Breeder Loss or Replacement*

Predictions 7-11 were difficult to test in this species. The rarity of breeding vacancies, combined with small group size, left little opportunity for family conflict over a breeding spot. There was some evidence of increased aggression between unrelated females, and, as the dominant sex, their aggression rate was higher than between unrelated males, as predicted. However, *P. edwardsi* appear either to share reproduction equitably (related females) or not at all (males and nonkin). The takeover events that led to this situation were indeed highly aggressive and often led to severe injuries among residents, who always subsequently dispersed. Female replacement breeders were more aggressive and less affiliative toward group young that were not their offspring and every takeover was associated with the disappearance or death of the natal infant(s). However, the remaining breeder remained to reproduce and thus replacement families were not less stable than

biologically intact families.  Therefore, the disruption after breeder loss or replacement that was predicted by the ETF was only partially supported.

*Family Structure: Reproductive Sharing Leads to Extended Families*

There was no indication that reproductive sharing was promoting delayed dispersal in this population.  Cobreeding, although it always happened between relatives, was extremely rare and mostly occurred between adult females of $r = 0.5$.  Incentives such as reproductive opportunities should be offered to encourage juveniles and subadults to stay in the group only if there are clear benefits of having them remain in the group.  However, juveniles did not carry infants, help feed young, or participate in sentry duty, as occurs in some cooperative breeders (Creel and Creel 1995, Clutton-Brock et al. 2001, Huck et al. 2004).  Although overall weights were not different according to group size, adults in the group with the most subadults and juveniles (Group 4) showed the lowest weights.  Alternatively, subadults may be remaining to take advantage of a future breeding vacancy in the group once their parents die or disperse (Woolfenden and Fitzpatrick 1984), which happened three times over the course of this study, or to wait for an opening in a nearby territory.  Group members may tolerate the delay of dispersal by a relative for purposes of increasing inclusive fitness (Hamilton 1964a, b, Alexander and Borgia 1978).  Reproductive skew, on the other hand, seemed to follow clear delineations: breeding females shared reproduction when there was a sexually mature female relative present and the breeding male was not her father.  Males did not appear to share reproduction with relatives, with one possible exception, although the number of males sampled genetically prevents this to be concluded definitely.

The ETF prediction that there should be effects of environmental conditions on dispersal behavior is robust but was not clearly tested in this study.  There appeared to be no effect of year or group on cobreeding, but some groups had juveniles that dispersed much later than others.  It remains unclear what drives the variance (3.5-9 years) in dispersal age in this population.  Future research should consider further ecological constraints, such as detailed phenology and microclimate data, as well as breeding vacancies in other territories.

Finally, one must consider the particular habitat in which this study was conducted.  Talatakely lies on the edge of a protected area and encompasses previously disturbed habitat.  It is possible that the delay in dispersal is a result of behavioral responses to habitat quality.  If so, this would be important information for managing this endangered species.

Overall, the Evolutionary Theory of the Family does not accurately model sifaka social interactions.  The theories of ecological constraints and kin selection did provide a useful framework for which to understand social dynamics in this population.  Reproductive skew theory did not seem applicable, although perhaps with more data the theory would be supported.  Moreover, reciprocal altruism may be a useful model to apply to understand the interactions between nonkin and breeding pairs in this population.

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# Chapter 3
## The Rules of Disengagement:
### The Local Mate Availability Model of Dispersal in Rainforest Sifakas

## INTRODUCTION

Dispersal is an issue that unites biologists across disciplines. Population geneticists and theoreticians model the movement of genes and individuals through simplified environments; evolutionary biologists consider these movements as a critical component of natural selection; behaviorists and ecologists study the individual decisions that determine group dynamics; and conservation biologists use this information to manage populations in the face of habitat degradation, invasive species threats, and anthropogenic climate change.

Through observations on a variety of study species, biologists have discovered general patterns of dispersal (here defined as an animal's movement from its group to the place where it reproduces or attempts to reproduce-Howard 1960). These patterns have been the focus of abundant theoretical discussion, culminating in four major models for the adaptive function of dispersal (Dobson and Jones 1985, Waser 1985, Handley and Perrin 2007): Local Mate Competition (LMC), Local Resource Competition (LRC), Local Resource Enhancement (LRE), and Inbreeding Avoidance (IA).

Three models that focus on the effects of competition and cooperation between relatives were originally developed to explain sex ratio bias. In Hamilton's LMC model (Hamilton 1967), groupmates disperse to prevent reducing their inclusive fitness by competing for mates with relatives (Dobson 1982). LRC (Clark 1978) is a similar model which predicts dispersal to avoid competing with kin for resources. Conversely, the LRE model (Clark 1978, Gowaty and Lennartz 1985, Schwarz 1988, Pusenius et al. 1998, Perrin and Mazalov 2000) predicts that, in certain circumstances, the advantage of same sex kin in increased survival or reproduction will lead to delayed dispersal of same sex offspring from the group. Finally, perhaps the most widely recognized driver of dispersal patterns is the avoidance of inbreeding (Bengtsson 1978, Pusey and Packer 1987, Wolff 1994, Pusey and Wolf 1996, Perrin and Mazalov 1999, Guillaume and Perrin 2006). Inbreeding can lead to reduced fitness through inbreeding depression and loss of heterozygosity (Keller 1998, Duarte et al. 2003, Haikola et al. 2004, Facon et al. 2006, Charpentier et al. 2007).

All four models make sex-specific predictions for dispersal. Following from Emlen and Oring 1977, the costs of philopatry (e.g., inbreeding depression) should be less tolerable for the sex that invests more in reproduction, i.e., female mammals (Waser et al. 1986). Thus, if IA is driving dispersal, one sex should disperse, although delayed dispersers would be expected to mate in the natal group if opportunities were available. In a species where females invest more in offspring, it has been hypothesized that the avoidance of inbreeding should be the concern of females, and thus lead to female-biased dispersal. Others have argued that female choice, i.e., female rejection, will drive males to disperse from their natal group to increase mating opportunities (Waser and Jones 1983, Pusey 1987, Boinski et al. 2005). Perrin and Mazalov (1999, 2000) showed theoretically that inbreeding avoidance

always leads to unisexual natal dispersal. Their model showed that inbreeding avoidance alone cannot lead to the dispersal of both sexes, even if their rates are different.

The LMC model predicts that if there are no opportunities to breed in neighboring groups, individuals will delay reproduction until a breeding opportunity arises in a neighboring group (McNutt 1996). Overall, if competition avoidance is driving dispersal, males in polygynous species should disperse because males have higher reproductive potential (Olupot and Waser 2001b). Similarly the LRC model predicts sex-biased dispersal. Clark (1978) hypothesized that females should disperse because, as the primary parent, they have higher resource requirements, whereas others argued that monogamous species should show male-biased dispersal (Favre et al. 1997).

In most group-living birds and mammals, researchers have reported sexually-dimorphic dispersal trends that generally follow these predictions: in most birds, males remain in the natal territory (male philopatry) and females disperse (Greenwood and Harvey 1982); in mammals, females usually remain in the natal group or disperse short distances while males disperse more often and further than females (Greenwood 1980). The few published reversals of this pattern (Pusey 1980, Williams et al. 2002, Hammond et al. 2006, Murray et al. 2008) have been considered exceptions that prove the rule (e.g., geese and ducks-Greenwood 1980). However, despite these widely accepted generalities, a few researchers have noted that some species, including primates, may not follow these "rules" (Moore 1992, 1993, Strier 1994, Pochron and Wright 2003).

The availability of detailed data on individuals, as well as their social complexity, has made long-term studies of Platyrrhine and Catarrhine primates particularly informative and influential in developing theory about social grouping and dispersal (Alberts and Altmann 1995, Strier and Ziegler 2000, Cords 2002, Fedigan and Jack 2004, Pusey et al. 2005). Additionally, some researchers have focused on lemurs to test the hypotheses for dispersal and social grouping. A study of the solitary dwarf lemur using genetic and some behavioral data showed that *Mirza coquereli* are primarily female philopatric, with males dispersing further and more often (Kappeler et al. 2002). Other studies found similar patterns in *Eulemur fulvus rufus*; females were philopatric and males dispersed around the population (Overdorff 1996, Wimmer and Kappeler 2002, Overdorff and Parga 2007). Several studies of mouse lemurs have shown male bias in both dispersal events and distance (Radespiel et al. 2001, Radespiel et al. 2003, Dammhahn and Kappeler 2005) and one considered whether female philopatry was a result of long lifespan and low turnover (Lutermann et al. 2006). Sifakas have also been examined: *P. verreauxi*, which inhabit the south and west of Madagascar, follow the pattern of female philopatry and male dispersal (Richard and Rakotomanga 1989, Richard et al. 1993, Brockman et al. 1998, Brockman and Whitten 1999, Richard et al. 2002).

I explored the dispersal behavior and social system of a sifaka, *Propithecus edwardsi*, which does not appear to follow the predicted patterns. Both males and female sifakas have been known to disperse from natal groups over twenty-one years of study (Pochron and Wright 2003). This long-term research allows for an exploration of the factors determining dispersal in a long-lived social mammal. To explain dispersal in this species, I developed the Local Mate Availability Model, focusing on a single predictor, the presence of a mate. According to the established models regarding polygynous mammals with little paternal care, dispersal should be sex-biased, most likely towards males. On the other hand, the Local Mate Availability Model, or LMA, hypothesizes that the purpose of leaving a group is to find an unrelated breeding partner (in species where extra-group reproduction is minimal). The LMA predicts that both males and females will disperse unless an unrelated adult of the

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opposite sex is available in the current group.  Moreover, immigrants should reproduce once they enter a new group or disperse back out of the group.  This model further predicts that, in seasonally breeding species, dispersal will occur before the breeding season in time to establish in a group (Jones 1986).  Immigrant males should commit infanticide in species with long interbirth intervals (as in lions-Packer and Pusey 1983).  In species with a limited number of breeders in a group, immigrants should evict same-sex residents.

I developed the Local Mate Availability Model to explain the population dynamics of a rainforest lemur.  However, this model can be extended to other species to explain supposed exceptions as well as to catalyze a reconsideration of previously collected data.

# METHODS

This study focused on four groups of *Propithecus edwardsi* with non-overlapping territories in the Talatakely trail system of Ranomafana National Park (RNP; Figure 1). A description of the study site and behavioral data collection methods can be found in Chapter 2: Methods. Patricia Wright and colleagues have followed Groups 1 and 2 since 1986, Group 3 since 1991, and Group 4 since 1996 (Wright 1995), with consistent data on marked individuals taken from 4-25 days/month for 4-12 months since 1987 (Total = 1,402 days; Figure 2). By 2007, two of these four groups had dissolved, with the final group members dispersing to the nearby area of Sakaroa (see Chapter 4: Figure 1 for map).

Animals were named and identified by a collar/tag combination (e.g., Blue Purple had a blue collar and purple tag) that they received after two years old or as soon as possible in the case of immigrants (Glander et al. 1992). In rare cases where there were more than two non-collared animals in a group, these animals were identified according to sex, morphologically distinct characteristics, or, in the case of very young animals, proximity to their mother.

The length and continuity of this study allowed us to assign categories to missing or new animals with confidence (Pochron et al. 2004). Sifakas that had never before been sighted in the group were considered "immigrants." Animals that disappeared before the age of 3 years without their mothers were assumed dead. Many deaths were known through evidence of either infanticide or fossa predation (Wright et al. 1997, Wright 1998).

Fifty-eight individuals were followed from birth until dispersal or death in Groups 1, 2, 3, and 4. Animals seen born (or shortly after their birth) into the group in which they resided during the study were "natal." Another 21 individuals, either present at the start of study of that group ("residents") or animals who immigrated into a group from outside the study area ("immigrants"), were followed for an average of 12.2 years each (range = 2.8-21.6 years). All births, deaths, and dispersals were recorded within two months, most within one week. Unless otherwise indicated, all analyses incorporating group residence ("tenure") excluded resident animals, i.e., those whose entry date into the group was unknown.

For the purposes of this paper, dispersal out of a group ("dispersal") is distinguished from dispersal into a group ("immigration" by "immigrants"). I distinguished two types of dispersal: natal dispersal, where an animal left its birth group; and breeding dispersal, which included all subsequent dispersals from a non-natal group (Greenwood and Harvey 1982). In addition to considering dispersal events, I looked at distance of dispersal. I measured dispersal distance in two ways. First, I considered the sex of observed transfers between known groups versus dispersers that were never seen again. I also used genetic data to identify the area of origin of individuals (Nathan et al. 2003); see Chapter 4 for expanded methods.

In addition to behavioral follows, Wright, Morelli, and colleagues captured 254 sifakas in Talatakely and three nearby sites within RNP (Sakaroa, Vatoharanana, and Valohoaka; unique animal captures = 84) over 24 months of capture between 1987 and 2007 (Figure 3; see Chapter 2: Methods for full description of capture methods). Up to 21 separate morphometric variables were recorded on each individual. Body Mass Index was calculated as BMI = weight/height$^2$, where weight was measured in kg and height was measured in m. Testicles were measured using calipers and testicle volume was calculated using the formula $V = 4/3\pi(l/2)(w/2)^2$, where length (l) and width (w) were averages of the left and right testicle (as per Glander et al. 1992). I, along with J. Jernvall, took dental casts ($N = 65$, unique animal casts = 37) that were used to age animals born outside of the study
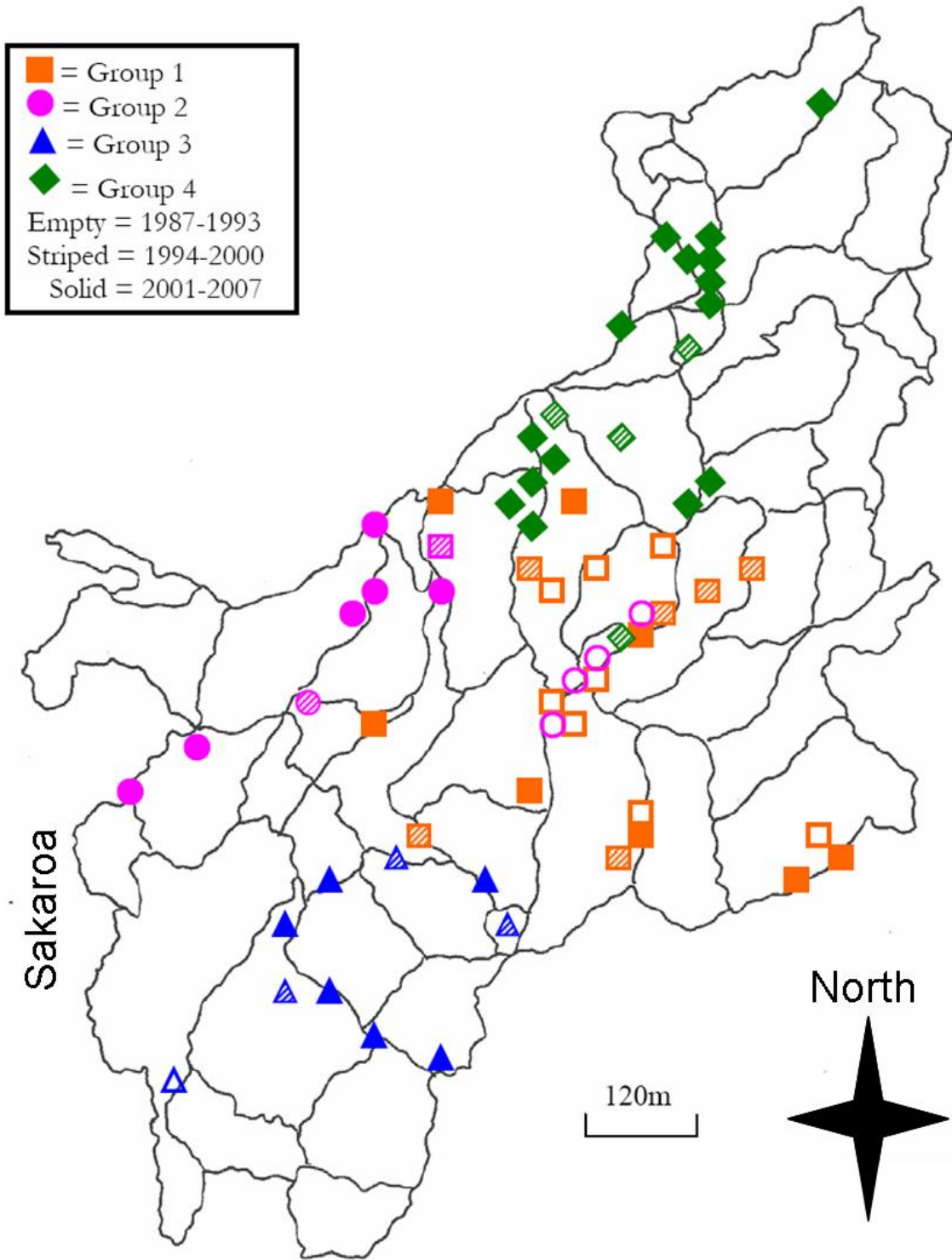
**Figure 1.** Map of Talatakely with locations of captured individuals from the four focal groups. Point color indicates group, point shape indicates time period of capture. Groups have remained stable across 21 years of study.
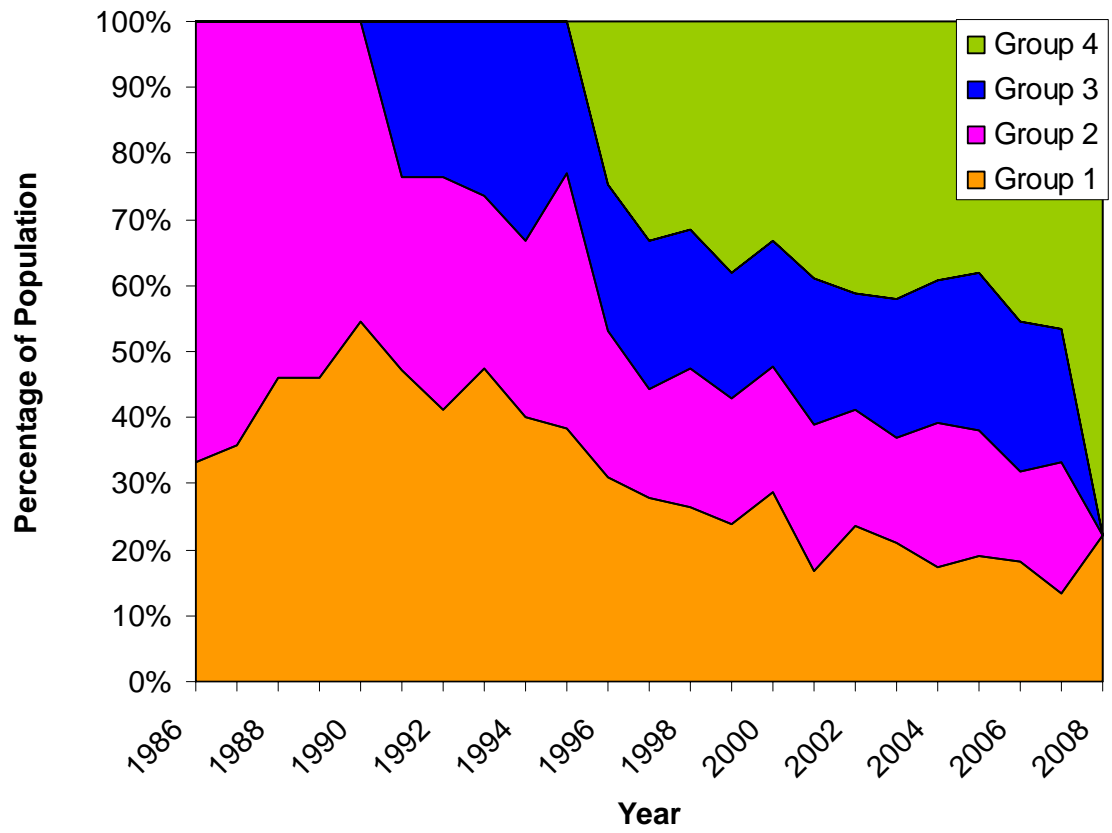
**Figure 2.** Change in group size over time. Group 3 not observed until 1991, Group 4 not observed until 1996.
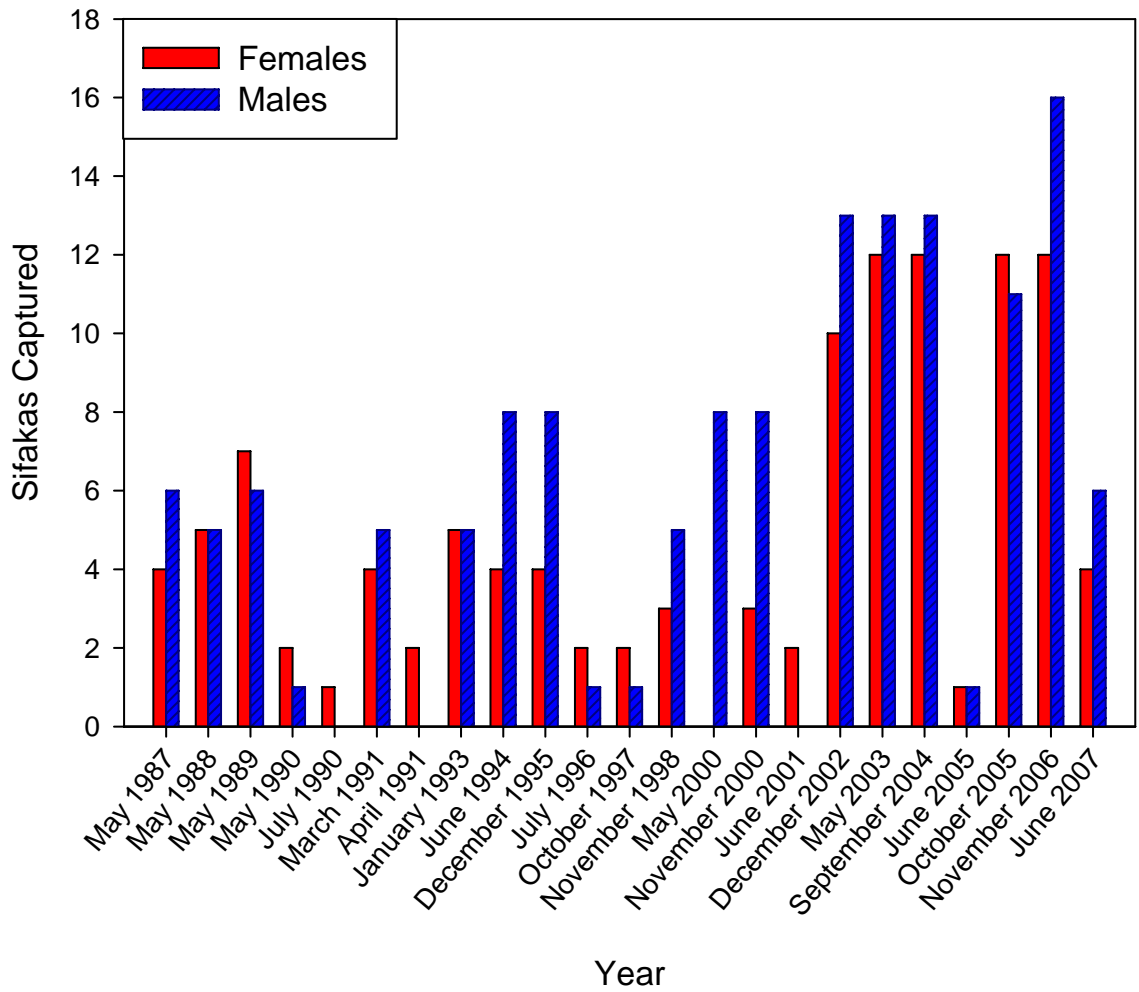
**Figure 3.** Captures of female and male sifakas included in this study from 1987-2007 ($N = 254$). More than one capture expedition occurred in 1990, 1991, 2000, and 2005, with no captures in 1992 and 1999.

period (King et al. 2005).

We also collected blood samples from 34 of the 79 main study animals in Talatakely, with an additional 35 genetic samples captured from sifakas at the other three sites (see Chapter 4: Figure 1 for map).  I used 16 genus-specific microsatellite markers to estimate relatedness between individuals.  Details of this analysis, as well as population parameter estimates for samples collected in Ranomafana, are presented in Chapter 4.

To examine the function of dispersal in sifakas, I enumerated all adult breeding, immigration, and dispersal events, the year they were first observed (through entry to the group or start of observations in that group), whether a mate was present in the group, and the mate to same sex adult ratio.  Here I define mate as an opposite sex, unrelated (r < 0.25) sifaka older than 3.5 years.

Data were analyzed according to statistical procedures described in Sokal and Rohlf (1995) using Statistica 6.0.  Non-parametric statistics were used for data that were not normally distributed.  Differences between groups were considered significant at $P < 0.05$.

# RESULTS

## *Population Characteristics*

Of the 59 individuals born during the study, 52% died their first year and 74% died before reaching sexual maturity (age 3.5 years; Figure 4). The sex ratio of the population across the study was found to be slightly female-biased (43%) at birth but the difference was not statistically significant ($\chi^2 = 0.03$, $P > 0.5$) and switched to slightly male-biased (60%) by sexual maturity due to infant deaths (Figure 5). The sex ratio among adults within the groups was slightly female-biased, with a mean of 0.46 (Table 1). However, two unrelated females were only found in the same group three times and never for longer than one year. Multi-male groups were also rare, with an average of 1.14 adult males across the study (Table 1). Extra-group mating was never observed. Using genetic sampling, the group breeding male was never excluded as the father for the 19 infants that were genetically sampled and was indicated probabilistically as the father in 15/19 cases (Chapter 4: Table 6), thus supporting behavioral observations.

The three earliest known-aged parturitions were 3.5-year-old females: Group 2 in 1991, Group 2 again in 2006, and Group 4 in 2008. Of the other females observed from birth that survived until 4 years old, all four dispersed from their natal group at age 4-4.5 years. The first recorded instance of reproduction in males was estimated to be 3.5 years as well; this animal was an immigrant and thus his age was determined from tooth casts. Similarly, the earliest birthing age found in *Propithecus verreauxi verreauxi* was 3 years, for females (Richard et al. 2002). Overall, given this congruence, sifakas were considered sexually mature at their third breeding season; these individuals were labeled as adults unless they were pre-reproductive natals, in which case they were considered subadults. Sifakas do not show reproductive senescence (King et al. 2005, Wright et al. 2008).

## *Reproduction*

Lemurs are highly seasonal breeders (Wright 1995), with only 12-48 hours of estrus/year seen in most lemur females, including sifakas (Wright 1999, Pochron et al. 2004). Although it varied annually, all observed *P. edwardsi* mating took place between November and January ("breeding season"). Nearly all births with birthdates known within a week (52/53) occurred approximately six months after the breeding season, from May through July, with June as the modal month; one birth occurred on September 24, 1999 (Figure 6).

The interbirth interval in this population was 1.85 years for individuals whose infants survived until the next birthing season and 1.5 years for those whose infants did not. Of females whose infants survived until the next birthing season, only 7/25 (28%) reproduced that year. Moreover, the interbirth interval was much different if infants died before the next breeding season (1.22 years) versus after the next breeding season but before the birthing season (1.85 years; $Z = -2.48$, $P < 0.01$): six out of eight mothers (88%) whose infants died before the breeding season gave birth the following year. One of the two females with a two year interbirth interval switched groups in the interim. Thus, most females gave birth to one offspring every two years unless that offspring died before the breeding season.
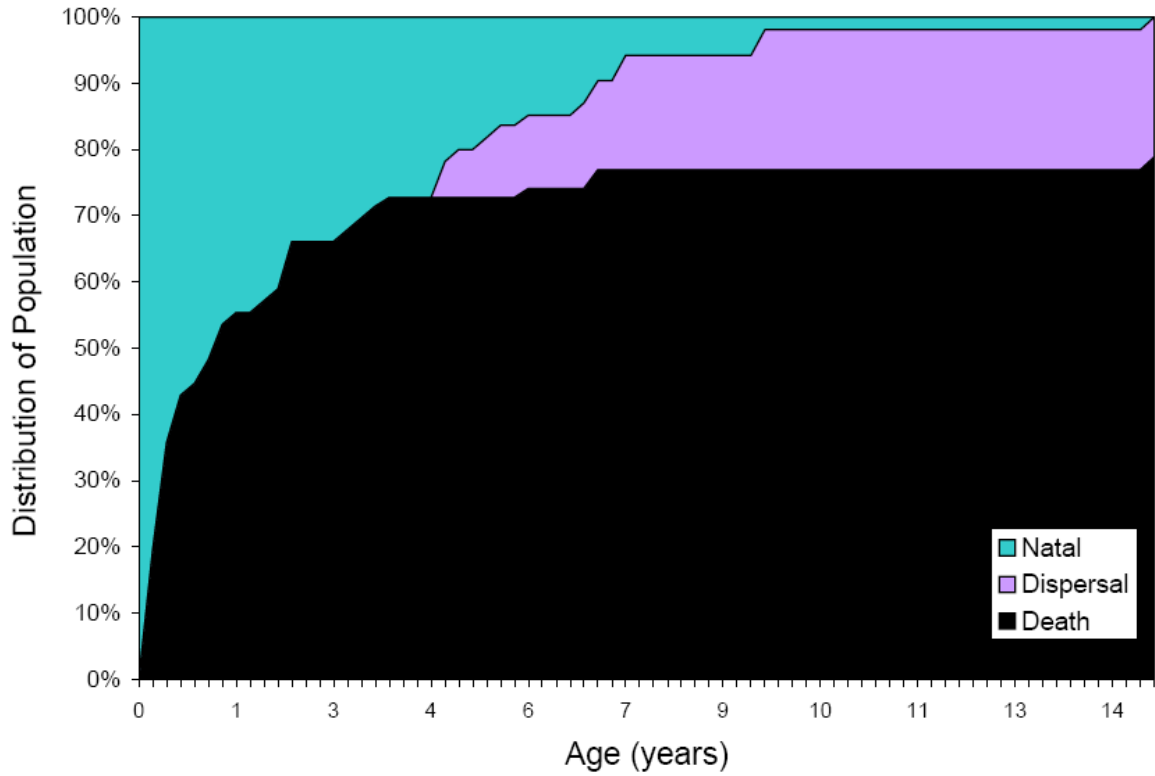
**Figure 4.** Death and dispersal by age in sifakas followed since birth (*N* = 59). Population starts 100% natal. 52% of infants died in their first year and 74% of sifakas died before reaching sexual maturity.
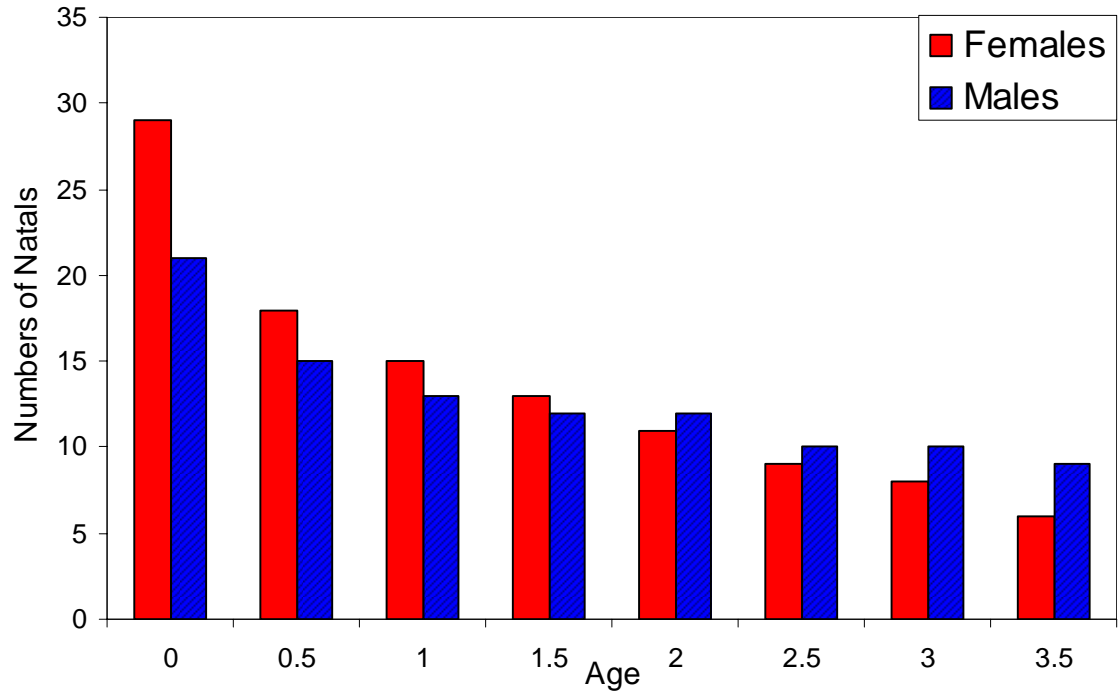
**Figure 5.** Change in sex ratio from birth through sexual maturity for all known-sex offspring in Groups 1-4 ($N = 50$). All change is due to death.

**Table 1.** Group composition and sex ratio over the study period. Values represent the greatest number of individuals sharing the group in that year.

| Year | Group 1 | | | | | | Group 2 | | | | | | Group 3 | | | | | | Group 4 | | | | | | Sex Ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | M | SA | J | I | Σ | F | M | SA | J | I | Σ | F | M | SA | J | I | Σ | F | M | SA | J | I | Σ | |
| 1986 | 2 | 1 | 1 | 0 | 0 | 4 | 2 | 1 | 3 | 1 | 1 | 8 | | | | | | | | | | | | | 0.33 |
| 1987 | 2 | 2 | 0 | 0 | 1 | 5 | 2 | 1 | 3 | 2 | 1 | 9 | | | | | | | | | | | | | 0.43 |
| 1988 | 2 | 2 | 0 | 0 | 2 | 6 | 2 | 1 | 2 | 2 | 2 | 9 | | | | | | | | | | | | | 0.43 |
| 1989 | 2 | 2 | 0 | 0 | 2 | 6 | 1 | 1 | 2 | 1 | 1 | 6 | | | | | | | | | | | | | 0.50 |
| 1990 | 2 | 2 | 0 | 2 | 0 | 6 | 1 | 1 | 1 | 1 | 0 | 4 | | | | | | | | | | | | | 0.50 |
| 1991 | 2 | 1 | 0 | 2 | 2 | 7 | 2 | 1 | 0 | 0 | 2 | 5 | 1 | 2 | 0 | 0 | 1 | 4 | | | | | | | 0.44 |
| 1992 | 2 | 1 | 0 | 4 | 0 | 7 | 2 | 1 | 0 | 2 | 1 | 6 | 1 | 2 | 0 | 0 | 1 | 4 | | | | | | | 0.44 |
| 1993 | 2 | 1 | 2 | 2 | 2 | 9 | 2 | 1 | 0 | 1 | 1 | 5 | 1 | 2 | 0 | 1 | 1 | 5 | | | | | | | 0.44 |
| 1994 | 1 | 1 | 1 | 3 | 0 | 6 | 1 | 1 | 0 | 2 | 0 | 4 | 1 | 2 | 0 | 1 | 1 | 5 | | | | | | | 0.57 |
| 1995 | 1 | 1 | 2 | 1 | 0 | 5 | 1 | 1 | 1 | 0 | 1 | 4 | 1 | 1 | 0 | 1 | 0 | 3 | | | | | | | 0.50 |
| 1996 | 2 | 1 | 1 | 1 | 1 | 6 | 1 | 1 | 1 | 1 | 1 | 5 | 2 | 1 | 1 | 0 | 1 | 5 | | | | | | | 0.38 |
| 1997 | 1 | 1 | 2 | 0 | 1 | 5 | 1 | 1 | 0 | 1 | 0 | 3 | 2 | 1 | 1 | 0 | 1 | 5 | 2 | 1 | 1 | 0 | 2 | 6 | 0.40 |
| 1998 | 1 | 1 | 2 | 0 | 1 | 5 | 1 | 1 | 0 | 1 | 1 | 4 | 1 | 2 | 0 | 0 | 1 | 4 | 2 | 1 | 1 | 2 | 0 | 6 | 0.50 |
| 1999 | 1 | 1 | 2 | 1 | 0 | 5 | 1 | 1 | 1 | 1 | 0 | 4 | 1 | 1 | 0 | 0 | 1 | 3 | 2 | 1 | 1 | 2 | 2 | 8 | 0.44 |
| 2000 | 1 | 1 | 2 | 1 | 1 | 6 | 1 | 1 | 0 | 1 | 1 | 4 | 1 | 1 | 0 | 2 | 0 | 4 | 2 | 1 | 1 | 2 | 0 | 6 | 0.44 |
| 2001 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 1 | 0 | 2 | 0 | 4 | 1 | 1 | 0 | 0 | 1 | 3 | 2 | 1 | 1 | 0 | 2 | 6 | 0.44 |
| 2002 | 1 | 1 | 0 | 1 | 1 | 4 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 3 | 2 | 1 | 1 | 2 | 2 | 8 | 0.44 |
| 2003 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 1 | 0 | 1 | 1 | 4 | 2 | 1 | 1 | 4 | 0 | 8 | 0.44 |
| 2004 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 2 | 0 | 1 | 1 | 5 | 1 | 1 | 0 | 2 | 1 | 5 | 2 | 1 | 0 | 4 | 2 | 9 | 0.50 |
| 2005 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 2 | 0 | 1 | 0 | 4 | 1 | 1 | 0 | 3 | 0 | 5 | 2 | 1 | 2 | 3 | 0 | 8 | 0.50 |
| 2006 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 5 | 2 | 1 | 4 | 1 | 2 | 10 | 0.44 |
| 2007 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 1 | 1 | 0 | 1 | 4 | 1 | 1 | 3 | 2 | 0 | 7 | 0.50 |
| Average | 1 | 1 | 1 | 1 | 1 | 5 | 1 | 1 | 1 | 1 | 1 | 5 | 1 | 1 | 0 | 1 | 1 | 4 | 2 | 1 | 1 | 2 | 1 | 7 | 0.46 |

F: Breeding natal or immigrant female; M: Breeding natal or immigrant male; SA: > 3.5-years-old non-breeding natal subadult; J: 1 - 3.5-years-old juvenile; I: < 1 year infant.
Italics indicate an estimate of age-class.
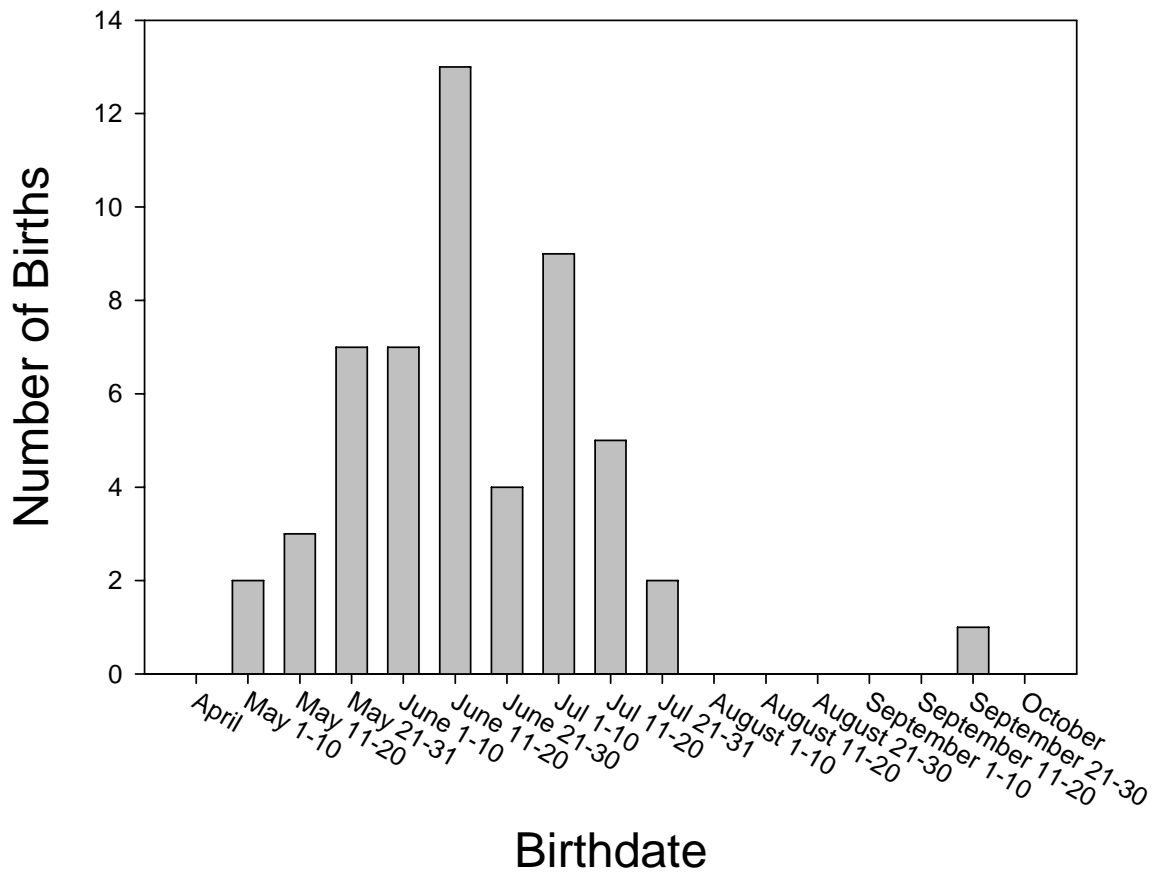
**Figure 6.** Histogram of all known birthdates across the study, 1987-2006 (*N* = 53).

*Dispersal*

Dispersal is also a seasonal event in *P. edwardsi*; more immigration and dispersal events occurred in the six months preceding the breeding season than the other half of the year, with a peak in the months of July, August, and September ($\chi^2$ = 18.0, $P$ < 0.0001; Figure 7). This pattern held true for males as well as females (88% of events by females, $\chi^2$ = 9.96, $P$ = 0.002, and 89% by males, $\chi^2$ = 21.8, $P$ < 0.0001, occurred in the six months preceding the breeding season; Figure 8), with peaks in dispersal slightly preceding peaks in testicle volume. Adult testicle volume changed seasonally (Figure 9), beginning in the fall and climaxing in December. Testicle volume more than doubled between the breeding season, November through January, and the non-breeding season, February through October (non-breeding season mean = 1.59 cm$^3$, breeding season mean = 3.31 cm$^3$; Figure 10) after controlling for weight ($F_{1,78}$ = 87.5, $P$ < 0.0001) and age ($F_{1,80}$ = 85.7, $P$ < 0.0001).

Among animals with known trajectories, one male (BP) stayed and reproduced in his natal group whereas five dispersed without reproducing in their natal group; two females (PY and BS) stayed and reproduced in their group before eventually dispersing, whereas four females dispersed without reproducing in their natal group. Thus, there was no difference between male and female dispersal behavior from the natal group ($\chi^2$ = 0.1, $P$ > 0.1; Figure 11).

I also examined breeding dispersal events, i.e., when immigrant sifakas subsequently dispersed from their non-natal group. There were known secondary dispersal events by seven males and one female, tertiary dispersal by two of these males and the female, and one of these males dispersed a fourth time. Between the sexes, the number of unique immigrants that reproduced in either their breeding or natal group versus dispersed without breeding was statistically equivalent ($\chi^2$ = 0.1, $P$ > 0.1). However, no females secondarily dispersed into and then out of a group without reproducing, whereas this behavior was conducted up to four to six times by two males (range due to paternity uncertainty; Figure 11).

Dispersal distance, measured by frequency of dispersal between study groups, was similar between the sexes: 5/12 males vs. 3/11 females dispersed from one of the Talatakely groups to another ($\chi^2$ = 1.0, $P$ > 0.1). Likewise, when considering all dispersal events, including multiple events by the same individual, males did not transfer between study groups more often than females (12/23 male transfers within Talatakely vs. 4/12 female transfers; $\chi^2$ = 0.4, $P$ > 0.1). Genetic differentiation (Chapter 4: p. 91) supports these results.

*Infanticide*

Nearly every immigration event was associated with the immediate disappearance of the group infant (younger than three months; no sifakas 3-11 months old were present when there was an immigration event). Infanticide was indicated by these sudden disappearances, combined with aggressive interactions between the immigrant and the breeding female and her infant, as well as, in some cases, recovered carcasses with stereotypical injuries. Juveniles (sifakas 1-3.5 years old) were never killed by immigrants/never disappeared during these immigration events; however, the oldest infant present during a takeover, an 11-month-old male, was believed to have been killed by the immigrant female.

Most (five of six) immigrant males appeared to commit infanticide when infants were present in the new group (Table 2); one of these males killed two newborn infants (one month apart). The single exception involved the suspected sibling of an immigrant (BR)
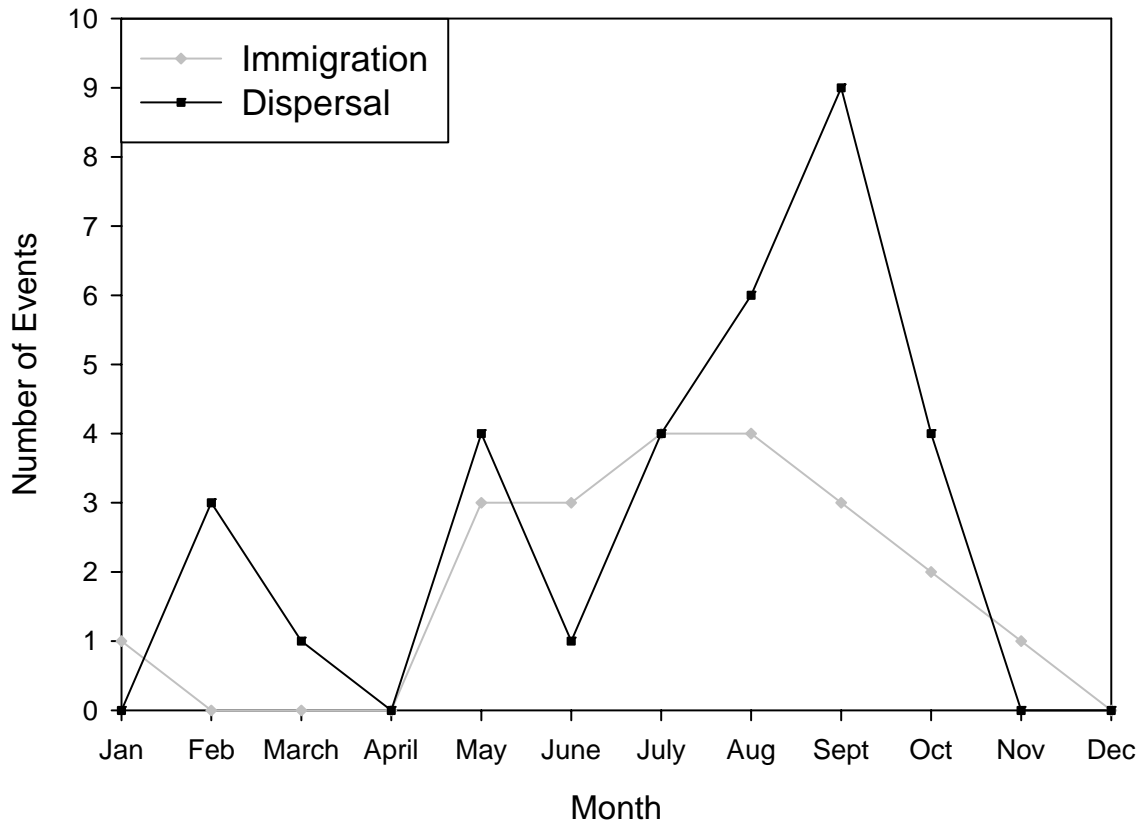
**Figure 7.** Immigration ($N = 23$) and dispersal ($N = 32$) events by month. More immigration and dispersal occurred in the six months preceding the breeding season than the other half of the year, with a peak in the months of July, August, and September ($P < 0.0001$). Months are abbreviated.
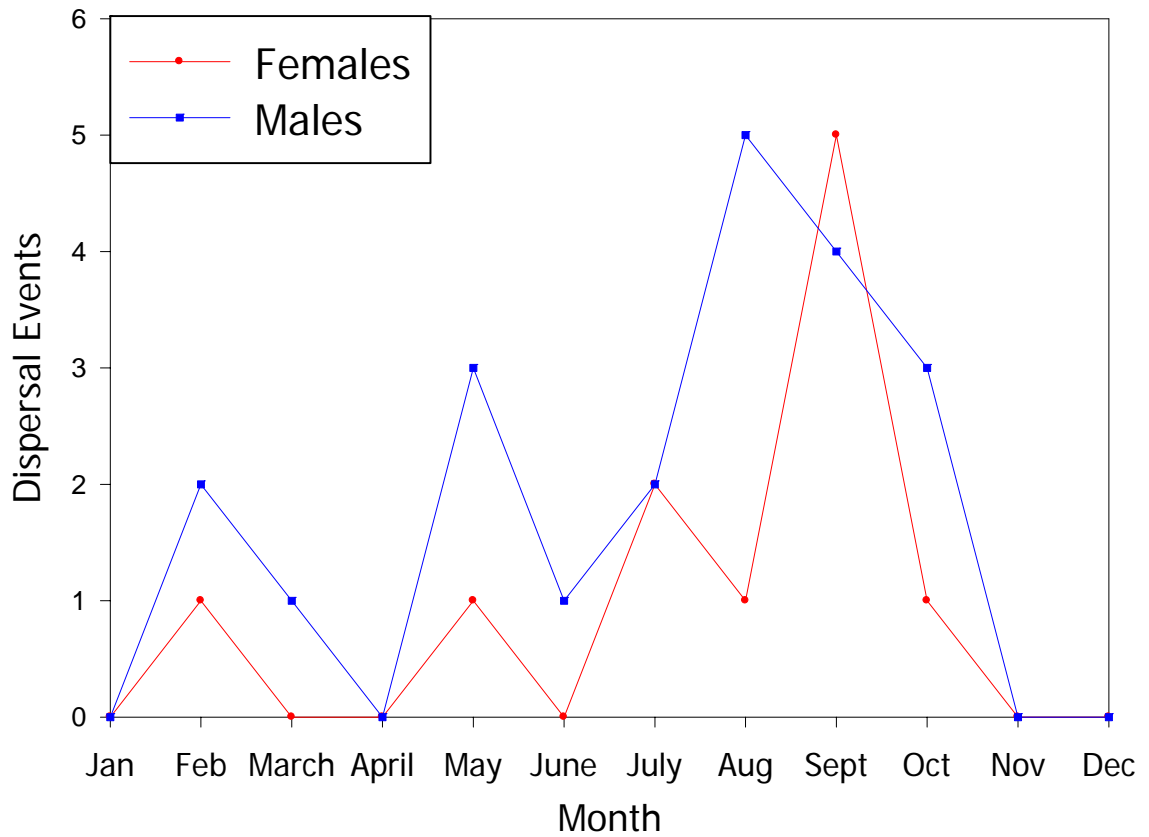
**Figure 8.** Male ($N = 20$) and female ($N = 11$) dispersal by month. Most events occurred in the six months preceding the breeding season (females: 88%, $P = 0.002$; males: 89%, $P < 0.0001$). Months are abbreviated.
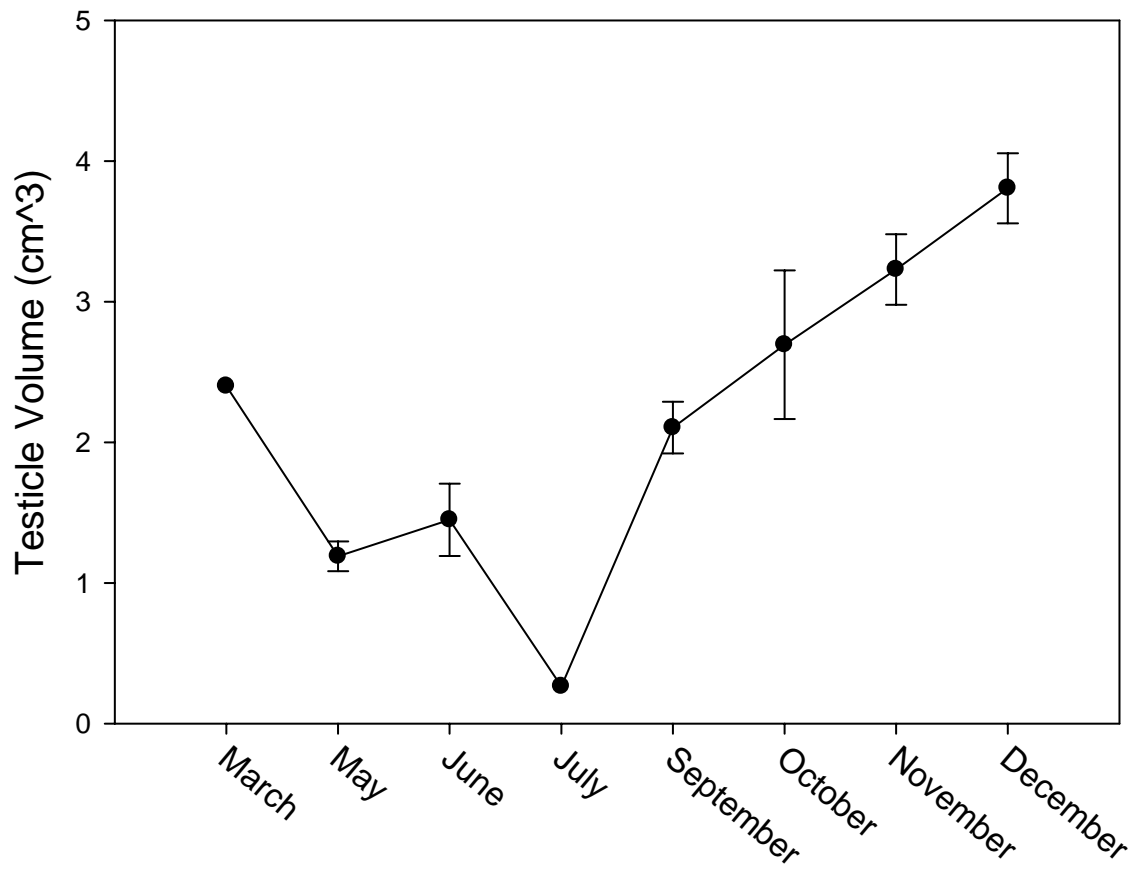
**Figure 9.** Mean (± SE) testicle volume across capture months from 1987-2007 (*N* = 53 measurements, 14 unique male sifakas). No data were collected in February, April, or August.
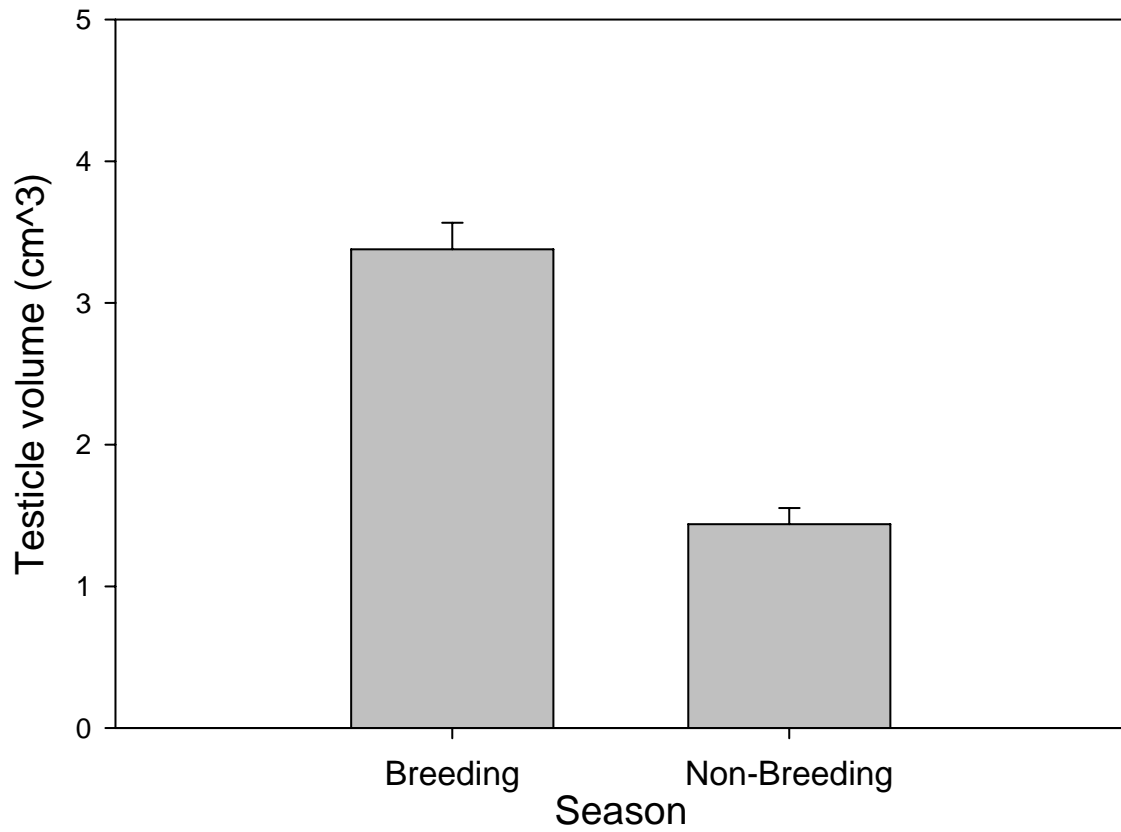
**Figure 10.** Mean (± SE) adult testicle volume by season. Testicle volume was much greater in the breeding season (November-January; $N = 24$) than the non-breeding season (February-October; $N = 29$) after controlling for weight and age ($P < 0.0001$).
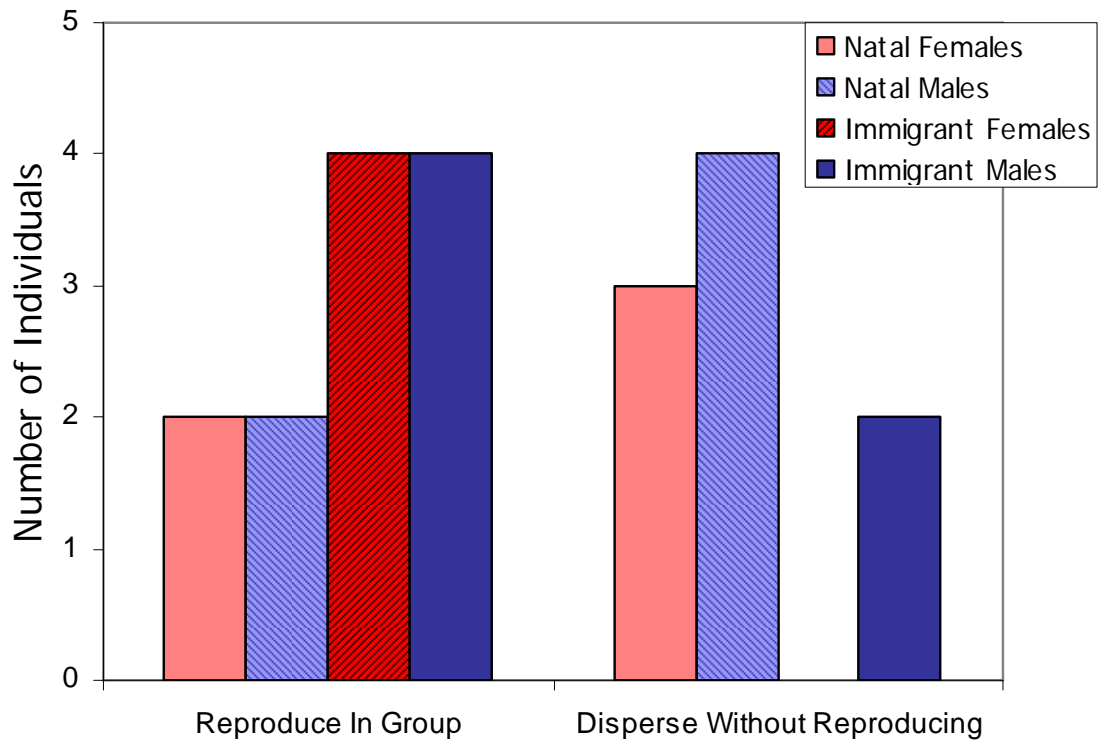
**Figure 11.** Breeding and dispersal activity of natal females ($N = 5$) and natal males ($N = 6$) and immigrant females ($N = 4$) and immigrant males ($N = 6$). There was no difference between male and female behavior ($P > 0.1$) except that no females dispersed into and then out of a group without reproducing.

**Table 2.** All observed takeovers and suspected infanticide events.

| Year | Immigrant | Sex | Group | How many infants present? | Infant disappeared? | Mother bred next season? |
|------|-----------|-----|-------|---------------------------|---------------------|--------------------------|
| 1987 | BR | M | 1 | 1 | Yes | Yes |
| 1987 | BR | M | 2 | 1 | No (sibling) | Yes |
| 1988 | O | M | 1 | 2 | Yes (both) | Yes |
| 1990 | YG | M | 3 | 0 | | Yes |
| 1990 | Y | M | 2 | 0 | | Yes |
| 1991 | P | M | 3 | 1 | Yes | Yes |
| 1994 | P | M | 2 | 0 | | Yes |
| 1995 | YG | M | 3 | 0 | | Yes |
| 2002 | OB | M | 1 | 1 | Yes | Yes |
| 2004 | OR | M | 2 | 1 | Yes | Unknown* |
| 2004 | PuO | M | 2 | 0 | | Unknown* |
| | | | | | | **Mother Dispersed?** |
| 1995 | GO | F | 3 | 0 | | No Breeding Female |
| 1996 | ZA | F | 3 | 1 | Yes | Immediately |
| 1996 | TS | F | 1 | 0 | | After 10 months |
| 1996 | GO | F | 2 | 1 | Yes | Immediately |
| 1997 | BB | F | 3 | 1 | Yes | Immediately |
| 2001 | GO | F | 1 | 0 | | Within 1 month |
| 2001 | RS | F | 2 | 1 | Yes | Immediately |

* = Female RS was killed by a fossa before she would have given birth. Her infant BS then took over as the breeding female of the group.

who received intense aggression from the group's females and returned to his natal group three months after his unsuccessful dispersal. In one case, two brothers (OR and PuO) immigrated two days apart into Group 2. The first male, OR, aggressively evicted the resident male and killed the group's infant.

Five of the six mothers whose infants disappeared reproduced the following breeding season; the sixth was a female (RS) who may have been pregnant when she was killed by a fossa the following May. One of these following-year offspring was genetically identified as the daughter of the infanticidal male; the other infants were not genetically sampled.

All (four of four) female immigration events were associated with deaths of the group infants (Table 3). All females whose offspring were killed by immigrant females immediately (within one week) dispersed from the group.

*LMA*

To ascertain the applicability of the LMA hypothesis, I followed the trajectory of 60 dispersal and/or breeding events by 38 sexually mature sifakas (older than 3.5 years). All dispersal events were examined to determine whether the availability of a potential breeding partner predicted natal and breeding dispersal (Table 3).

No sifakas dispersed or bred younger than 3.5 years. No sifakas reproduced with relatives ($r \geq 0.25$). In 12 of 15 cases where there was no unrelated opposite sex sexually mature sifaka ("mate") present in the group, the individual dispersed. The other three subadults (RP, YR, and PuPu) had not yet dispersed from their natal group in 2008 but had not bred either. In addition, there were 31 instances of individuals with a mate present in their group. In 25 of these cases, the animals remained and reproduced. In five of the remaining six instances, the dispersing male had been sharing a group with only one female and between one and three other males (the male's ratio of mates to same sex adults was $\leq$ 1), making the mate potentially not accessible. The final case was BR, who committed infanticide upon entering Group 1 but received intense aggression from the group's breeding females and dispersed back to his natal group after only a few months and before the breeding season (see Table 2).

I also examined 14 breeding dispersal events in which the group breeding male or female dispersed while his or her breeding partner was still present (last two columns of Table 3). Nine of these dispersals were associated with group takeovers and sometimes infanticide by a same sex immigrant. Four of the remaining five events were coupled with matriline splitting, when the breeding female and her daughter(s) dispersed together and left the group to her breeding relative and that female's daughter(s), or represented the last of the group members from Group 2 and Group 3 abandoning their territories in 2007 (Figure 1). These territories were still empty in 2008.

Thus, the single factor of mate availability predicted sifaka dispersal behavior in 37/60 cases. An inaccessible mate, where the sex ratio of females to males was less than 1, explained five more cases. Takeovers, and associated infanticide, led to nine more dispersal events. The Local Mate Availability Model, modified for this population, is presented in Figure 12.

**Table 3.** A test of the Local Mate Availability Model with known breeding and dispersal events for all sexually mature sifakas.

| ID | Sex | Group | Entry Year | Tenure (years) | Mate Present? | Mate:SS Ratio | LMA Prediction | Match LMA? | End Event | Infanticide/ Takeover? |
|---|---|---|---|---|---|---|---|---|---|---|
| B | M | 2 | 1996 | 5 | No | 0:1 | Disperse | Yes | Dispersal | No |
| Pu | M | 4 | 1997 | 6 | No | 0:3 | Disperse | Yes | Dispersal | No |
| PuR | F | 1 | 1989 | 4 | No | 0:2 | Disperse | Yes | Dispersal | No |
| PO | F | 4 | 2002 | 4 | No | 0:2 | Disperse | Yes | Dispersal | No |
| RG2 | F | 3 | 2002 | 5 | No | 0:0 | Disperse | Yes | Dispersal | No |
| BR | M | 2 | 1986 | 1 | *No* | *0:3* | *Disperse* | Yes | Dispersal | No |
| O | M | 2 | 1986 | 2 | *No* | *0:1* | *Disperse* | Yes | Dispersal | No |
| YG | F | 2 | 1986 | 1 | *No* | *0:2* | *Disperse* | Yes | Dispersal | No |
| YG | M | 2 | 1986 | 4 | *No* | *0:1* | *Disperse* | Yes | Dispersal | No |
| BR | M | 2 | 1987 | 2 | *No* | *0:1* | *Disperse* | Yes | Dispersal | No |
| PG | F | 2 | 1995 | 4 | *No* | *0:1* | *Disperse* | Yes | Dispersal | No |
| P2 | M | 4 | 1996 | 5 | *No* | *2:0* | *Disperse* | Yes | Dispersal | No |
| RP | M | 4 | 2001 | 7 | No | 0:3 | Disperse | No | NA | No |
| YR | M | 4 | 2001 | 7 | No | 0:3 | Disperse | No | NA | No |
| PuPu | M | 4 | 2003 | 5 | No | 0:3 | Disperse | No | NA | No |
| PB | M | 1 | 1989 | 7 | Yes | 1:3 | Disperse | Yes | Dispersal | No |
| YS | M | 1 | 1990 | 10 | Yes | 1:2 | Disperse | Yes | Dispersal | No |
| Br | M | 1 | 1993 | 7 | Yes | 1:2 | Disperse | Yes | Dispersal | No |
| PuO | M | 2 | 2002 | 1 | Yes | 1:2 | Disperse | Yes | Dispersal | No |
| YG | M | 3 | 1990 | 3 | Yes | 1:1 | Disperse | Yes | Dispersal | Takeover |
| R | M | 1 | 1986 | 16 | Yes | 1:0 | Breed | Yes | Dispersal | Takeover |
| Y | M | 2 | 1990 | 6 | Yes | 1:0 | Breed | Yes | Dispersal | Takeover |
| P | M | 3 | 1994 | 10 | Yes | 1:0 | Breed | Yes | Dispersal | Takeover |
| TS | F | 1 | 1997 | 4 | Yes | 3:0 | Breed | Yes | Dispersal | Takeover |
| ZA | F | 3 | 1995 | 2 | Yes | 2:1 | Breed | Yes | Dispersal | Both |
| GO | F | 2 | 1996 | 5 | Yes | 1:1 | Breed | Yes | Dispersal | Both |
| GO | F | 3 | 2001 | 1 | Yes | 1:1 | Breed | Yes | Dispersal | Both |
| PY | F | 2 | 1987 | 9 | Yes | 1:1 | Breed | Yes | Dispersal | Both |
| BS | F | 2 | 2002 | 5 | Yes | 1:0 | Breed | Yes | Dispersal | No[a] |
| OR | M | 2 | 2004 | 3 | Yes | 2:0 | Breed | Yes | Dispersal | No[a] |
| GS | F | 4 | 1995 | 11 | Yes | 1:1 | Breed | Yes | Dispersal | No[b] |
| Y1 | F | 1 | 1986 | 7 | Yes | 1:1 | Breed | Yes | Dispersal | No[b] |
| BR | M | 1 | 1987 | 0.2 | Yes | 2:1 | Breed | No | Dispersal | Aggression |
| BB | F | 1 | 1986 | 11 | Yes | 1:1 | Breed | Yes | Death | No |
| GG | F | 2 | 1986 | 7 | Yes | 1:1 | Breed | Yes | Death | No |
| RG | F | 2 | 1986 | 3 | Yes | 1:1 | Breed | Yes | Death | No |
| RR | M | 2 | 1986 | 4 | *Yes* | 2:0 | Breed | *Yes* | Death | No |
| BB | F | 3 | 1998 | 9 | Yes | 1:0 | Breed | Yes | Death | No |
| BP | M | 3 | 1992 | 15 | Yes | 1:0 | Breed | Yes | Death | No |
| BY | F | 3 | 1989 | 5 | Yes | 2:0 | Breed | Yes | Death | No |
| RS | F | 2 | 2001 | 4 | Yes | 1:1 | Breed | Yes | Death | No |
| B | M | 4 | 1991 | 12 | Yes | 1:0 | Breed | Yes | NA | No |
| BG | F | 4 | 1996 | 12 | Yes | 1:1 | Breed | Yes | NA | No |
| GO | F | 1 | 1995 | 7 | Yes | 1:0 | Breed | Yes | NA | No |
| OB | M | 1 | 2002 | 6 | Yes | 1:0 | Breed | Yes | NA | No |
| PY | F | Sak | 2002 | 4 | Yes | 1:0 | Breed | Yes | NA | No |

Mate = An unrelated (r<.25) opposite sex adult (>3.5 years); SS = Same sex adult.
[a] = Group (male and female) dispersed to a new territory; [b] = Matriline split.
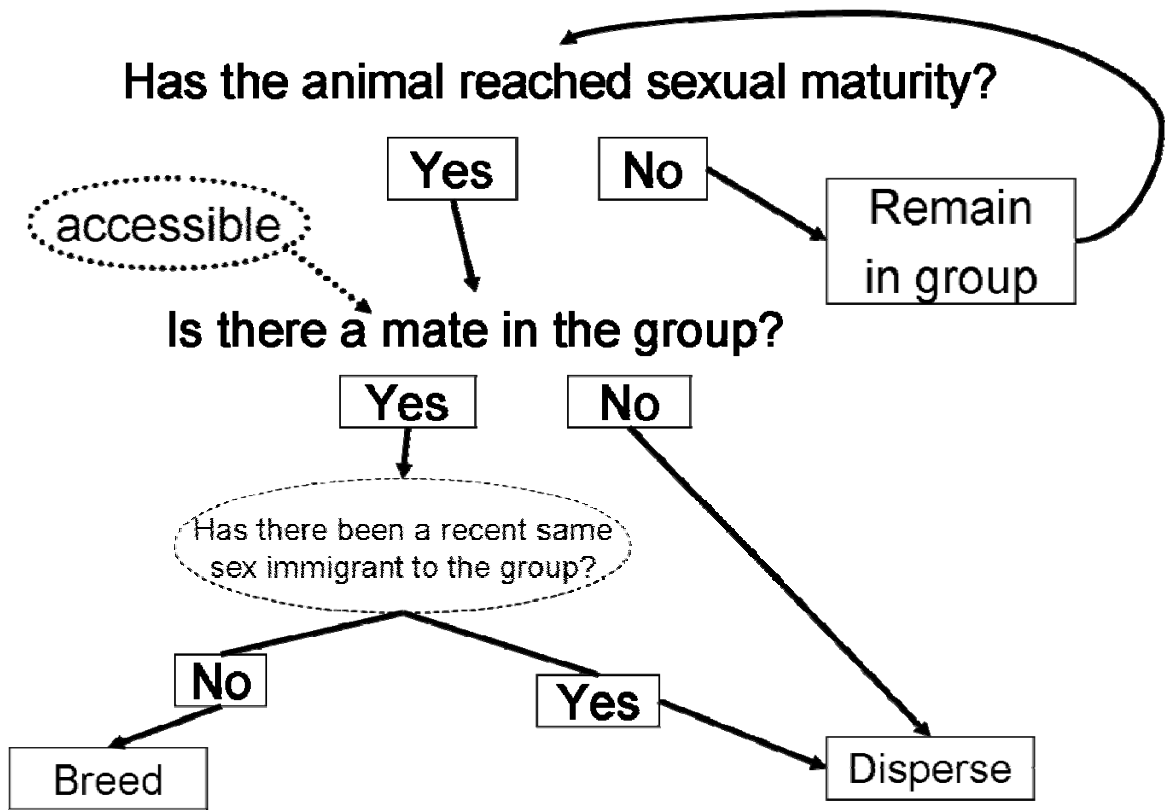Italics refer to relationships determined behaviorally but not genetically.

**Figure 12.** Local Mate Availability Model, modified for sifakas.

## DISCUSSION

This study examined the life history characteristics of *P. edwardsi* to determine their dispersal patterns and to develop a new hypothesis of dispersal for males and females, the Local Mate Availability Model.

When an individual reaches 3.5 years, it can make a decision to stay in its natal group without breeding, breed, or disperse in search of breeding opportunities. When there is an unrelated, opposite sex adult in the group, the natal male or female remains to reproduce. When only related adults are present, the natal male or female disperses without reproducing. This dispersal is seasonal, peaking 2-3 months before the breeding season, which begins in November. At the same time, testicle volume begins to increase; this result was supported by previous researchers (Pochron and Wright 2002, Pochron et al. 2002, Pochron and Wright 2005; similar to *P. verreauxi*-Brockman et al. 2001). This increase indicates a reproductive function for dispersal; sifakas may disperse early to find and establish in a group in time for the breeding season.

Dispersal is sometimes delayed until the animal is seven or eight years old. The function and circumstances of this delay are not yet understood. However, delayed dispersal may depend on opportunities outside of the group, availability of resources to maintain the individual in its natal group, and benefits in terms of inclusive fitness to remaining in the group (Woolfenden and Fitzpatrick, 1984, Goldizen and Terborgh 1989, Koenig et al. 1992, Ekman et al. 2001, Olupot and Waser 2001b, Kokko and Ekman 2002, Solomon 2003; also see Chapter 2: Discussion). Madagascar environments are known to be particularly unpredictable and resources can be dangerously scarce in the austral winter (Wright 1998). Moreover, sifakas are long-lived, with predation the largest cause of death after infancy. Sifakas may be using delayed dispersal as a bet-hedging strategy (Wright 1995, Richard et al. 2002), staying in the group until a breeding vacancy opens in the natal group or an adjacent group in order to reduce the threats involved with dispersal to an unfamiliar territory.

Males and females that enter a new group seem invariably to kill group infants. Males may commit infanticide to bring a female into estrus the following breeding season (Wright 1995, van Schaik and Kappeler 1997); a female whose infant died before the following breeding season reproduced the following year if she remained in the group. Moreover, the interbirth interval with surviving offspring is long in *P. edwardsi*, often 2 years. In the absence of this infanticide, i.e., if the infant survives, the female had a 60% lower chance of giving birth the following year.

In contrast, females seem to commit infanticide to reduce competition; all mothers dispersed from the group immediately after their infants disappeared. The infanticidal immigrant then became the group's resident breeding female. The lack of infanticide of yearlings was likely prevented by their size, weighing approximately 2/3 as much as an adult sifaka. Female infanticide seems particularly effective considering that two unrelated females breeding in the same group is extremely rare. Two unrelated breeding males sharing a group is also rare.

There was no statistical sex bias in dispersal found in this population. Moreover, from the known individuals that moved between adjacent territories and the genetic data (presented in Chapter 4), there did not appear to be a sex bias in dispersal distance. This is an uncommon pattern among primates (Moore 1993). In the mammals that do not show sex bias in the tendency to disperse, males usually disperse further than females (Lehmann and Perrin 2003, Handley and Perrin 2007; e.g., wild dogs-McNutt 1996, guanacos-Sarno et al. 2003, banner-tailed kangaroo rats-Winters and Waser 2003).

Most of the literature has focused on explaining sex-biased patterns in dispersal. Theory on neutral sex dispersal is less well-developed (although see Russell 2001 for a discussion on the function of unbiased philopatry). First, it is important to consider that there are costs of dispersing. Dispersal causes increased predation risk and loss of knowledge of food and water sources and terrain (Roff 1977, Alberts and Altmann 1995, Perrin and Mazalov 2000, Perrin and Lehmann 2001, Roze and Rousset 2005). Moreover, for social animals there is a loss of the group itself and conspecifics, including mates, must be discovered. On an evolutionary time-scale, coadapted gene complexes can be broken up by dispersal; locally-selected genotypes may be at a disadvantage in a new environment.

However, the costs of dispersal relate directly to some of the advantages of dispersal. For example, although genetic problems can arise from breaking coadapted gene complexes, the increase of genetic diversity is exactly the reason cited by most theorists (and empiricists) for dispersal (Bollinger et al. 1993, Perrin and Mazalov 1999, Olupot and Waser 2001a, Lehmann and Perrin 2003, Guillaume and Perrin 2006). Specifically, dispersal allows for the avoidance of inbreeding depression by separating individuals from their relatives. However, physical distance is not the only method for inbreeding avoidance (Moore 1992); direct kin recognition could accomplish the same goal (Koenig et al. 1992). Other purported dispersal costs that may be actual motivations to disperse relate to changing territory quality (Hansson et al. 2007), predation pressure, and finding groupmates, in the case of dwindling home group size (Hedrick and Kalinowski 2000).

Considering these ideas and the aforementioned life history traits, I have developed the Local Mate Availability Model to explain the basis for dispersal decisions in *Propithecus edwardsi*. I found that nearly all dispersal events were entirely predictable and could be attributed to just three factors: 1) lack of a sexually mature, unrelated, opposite sex breeding partner ("mate") in the group; 2) lack of access to that mate due to an unfavorable sex ratio, and 3) aggressive ousting of the individual, sometimes accompanied by infanticide, by a recent immigrant ("takeover"). The first predictor explained 37/60 events, the second predictor explained an additional five events, and the third explained 9/14 of the subsequent dispersals, for a total of 51/60. Thus, the simple rules of LMA predict nearly all of the apparently complicated dispersal behavior of sifakas.

Although in some species dispersal alone may accomplish inbreeding avoidance (Trakhtenbrot et al. 2005), that seems unlikely in this population. In nearly every instance in which an individual's parent dispersed or died, its opposite sex offspring remained to breed. If the availability of unrelated breeding partners is driving dispersal in sifakas, the next step is to understand what mechanism is being used for kin recognition. Research is ongoing to determine whether olfaction, e.g., though scent marks, is involved in this process, as has been shown in some species (Sun & Muller-Schwarze 1997, Todrank et al. 1998, Knapp et al. 2006).

In her 1994 synthesis, Strier noted that prosimians were perhaps the only primate taxa besides the cercopithecines (baboons and macaques), in which the sex-biased dispersal phenomenon was truly occurring. This study shows that even prosimians may not hold to this paradigm and suggests a model to explain the pattern of unbiased dispersal and complicated breeding dispersal patterns seen in this lemur and potentially other group-living animals. This model is related in concept to those developed by Waser (Waser 1985, Waser and Elliott 1991, Waser 2004) in which he considers the effect of resource vacancies on dispersal. I believe that the Local Mate Availability Model may be useful for explaining population dynamics in a variety of social species with "non-typical" patterns of dispersal.

Understanding dispersal is critical to the conservation and management of natural populations (Verhulst et al. 1997, Caswell et al. 2003, Fraser et al. 2004, Thomas et al. 2004, Lecomte et al. 2008).  Recent acceptance of the reality of anthropogenic climate change has led policy makers to search for solutions to manage and mitigate its effects on natural populations (Wright 2006, Dunham et al. 2008, Kremen et al. 2008); information on the function and mechanism of animal dispersal will be critical to accomplishing this.  Changes in landscapes and habitat heterogeneity have been shown to affect dispersal rates and thus will be a crucial focus for conserving species living in patchy habitats and/or with small populations.

This study shows that behaviors regularly considered rare in a polygynous primate, such as unbiased dispersal and female infanticide, are occurring regularly and predictably in sifakas.  The Local Mate Availability Model clearly elucidates this simple yet remarkable life history pattern; future studies will determine whether the LMA is more broadly informative.

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**Chapter 4**
**The Genetic Structure of *Propithecus edwardsi***
**in Ranomafana National Park**


**INTRODUCTION**

Habitat fragmentation is a central topic for conservation biologists. It is important to understand how animals move through the landscape in order to conserve endangered species in the face of habitat degradation. Madagascar presents a particularly good environment for studying the effects of fragmentation on populations. It is estimated that natural habitat has been lost across 90% of the island (Lowry et al. 1997). However, a recent report by Conservation International (March 2008) indicated that this rate is slowing in the country's nature reserves (0.1%/year from 0.8%/year in the 1990s). Effective management of Madagascar's protected areas is believed to be critical to maintaining viable populations of the island's remarkable endemic biodiversity (Van Vuren 1998, Ganzhorn et al. 2001). The study of the impact of geographic and man-made barriers on dispersal may be particularly appropriate (Forman et al. 2003); recent analyses have shown that river catchments have historically acted as barriers to gene flow, isolating populations and resulting in the remarkable species diversity found in Madagascar (Wilmé et al. 2006, Kremen et al. 2008). These barriers occur around as well as within Madagascar's protected areas.

With the accelerating habitat destruction that is occurring in the biodiversity hotspots of the world (Myers et al. 2000), conservation programs must optimize limited resources in order to maximize results. Management decisions need to be made quickly, with realistic goals to implement effective plans. Thus, information that will help to direct resources where they will be most useful is a top priority. Genetic analyses can provide just this type of information (Haig 1998, Hedrick 2001). Besides the basic ecological, evolutionary, and behavioral questions that these analyses can readily answer, genetic data can provide input to supplement population surveys. This added dimension can aid research and policy and thus maximize conservation efforts.

In this study, I sought to understand the population dynamics of sifakas in southeastern Madagascar. I focused on Ranomafana National Park (RNP), a particularly successful example of a protected area (Wright and Andriamihaja 2002, 2003). RNP is divided into three parcels: Parcel II is north of the national highway Route Nationale 25 (RN 25) and north of the Namorona River, Parcel I is south of RN 25 and the Namorona River, and Parcel III is a western fragment isolated from the rest of the park by the river and road (Figure 1).

RNP contains remarkable biological diversity, including at least 12 lemur species; this study focused specifically on the largest of these lemurs, *Propithecus edwardsi*. *P. edwardsi* is a diurnal, folivorous/frugivorous lemur that lives in multi-male, multi-female groups of two to nine individuals (Mittermeier et al. 1990, Wright 1995). Recent surveys (Irwin et al. 2000, Lehman and Wright 2000, Irwin et al. 2001, Lehman 2002) indicated that the range of *P. edwardsi* may be much more limited than previously thought and that RNP may enclose one of the few remaining viable populations of this sifaka.
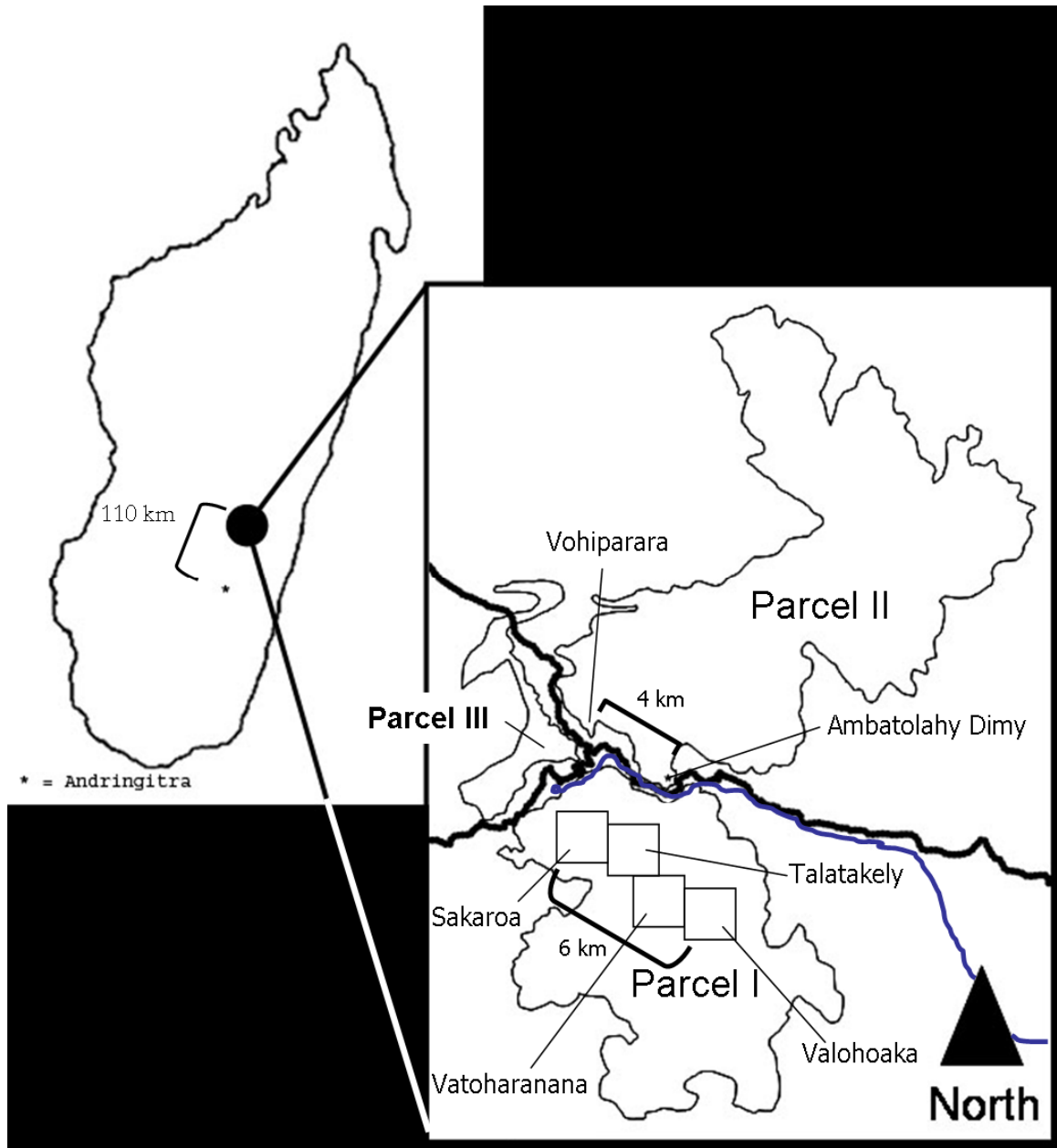
**Figure 1.** Map of parks, parcels, and sites. Inset outlines the three parcels that encompass Ranomafana National Park with the national highways (thick black lines) and the Namorona River (blue line) that intersect the park. Modified from Kightlinger 1993.

The river/road complex that intersects RNP may be acting as a barrier to gene flow for the terrestrial fauna protected there. To test this, I focused on 98 Milne-Edwards' sifakas (*Propithecus edwardsi*) within 12 social groups at six sites: four within Parcel I and two others across the road/river barrier within Parcel II. In addition, a population of *P. edwardsi* was sampled at Andringitra National Park, located 110 kilometers to the south of RNP (Figure 1).

These seven sites encompass areas of varying degrees of disturbance. The Andringitra site was nearly undisturbed forest, lying approximately 110 kilometers to the south of RNP. Vohiparara and Ambatolahy Dimy are sites in Parcel II on the other side of the road/river, sampled by E. E. Louis and colleagues; they were fairly disturbed with some recent logging by hand. Sakaroa was previously a rice paddy in some parts and encompassed the territory of recent immigrants from the adjacent site Talatakely. The main study population Talatakely, with 34 individuals, was where most of my dissertation research focused. This site was used extensively by villagers as recently as the 1950s and, like Sakaroa, was selectively logged by hand from 1986 to 1989. There was little human disturbance of Vatoharanana, e.g., single trees occasionally felled by hand for local honey gathering, whereas Valohoaka was undisturbed forest; these sites are the deepest into the forest of RNP.

*Objectives*

The objective of this study was to investigate the genetic composition of a population of an endangered primate in order to determine whether it was genetically divided by barriers running through its protected habitat. I hypothesized that gene flow would be disrupted most between the two national parks and further between the parcels, separated by geographic barriers.

I also determined the genetic composition and reproductive skew of groups of sifakas in RNP. Based on behavioral observations, I hypothesized that group males would father the majority of offspring in the group.

**Table 1.** List of sites by park, parcel, site, disturbance level, genetic sample size, years that samples were collected from each site, and distance to nearest site (measured from center point of locations where individuals were captured).  Sample sites are listed in adjacent order.

| Location | Parcel | Site | Disturbance Level | N | Date of Sample Collections | Distance to Next Site (km) |
|---|---|---|---|---|---|---|
| ANP | NA | Andringitra | Little | 12 | 2004 | 110 |
| RNP | II | Vohiparara | Moderate | 10 | 2002-2003 | 5 |
| RNP | II | Ambatolahy Dimy | Moderate | 9 | 2003-2004 | 2 |
| RNP | I | Sakaroa | Moderate | 12 | 2002-2005 | <1 |
| RNP | I | Talatakely | Moderate | 34 | 1994-2004 | 5 |
| RNP | I | Vatoharanana | Little | 12 | 2002 | 3 |
| RNP | I | Valohoaka | None | 9 | 2002-2004 | - |
| ANP = Andringitra National Park; RNP = Ranomafana National Park. | | | | | | |

## METHODS

*Field Methods*

This study focused on sifakas, *Propithecus edwardsi*, at six sites inside Ranomafana National Park (RNP), located at 12°16' S latitude and 47°20' E longitude in southeastern Madagascar. RNP ranges in elevation from 500 to 1500 m. This 43,500-ha submontane rainforest was declared a national park in 1991 (Wright 1992) and a UNESCO World Heritage site in 2007. A description of the study site and behavioral data collection methods can be found in Chapter 2: Methods. The population of *P. edwardsi* in RNP occupying the Talatakely Trail System is one of the best studied wild mammal populations; P. C. Wright and colleagues have followed them for more than 9,792 animal days since 1986 (Wright 1995, Wright et al. 2008, In Press).

In addition, E. E. Louis and colleagues collected samples of *P. edwardsi* in Andringitra National Park (ANP). ANP is located in the Andringitra Massif in Fianarantsoa Province, between 22° 7' and 22° 21' S and between 46° 47' and 47° 2' E. It is 31,160 ha and ranges in elevation between 650 and 2658 m (Goodman 1996).

Blood samples were collected from 34 of the main study animals in Talatakely, with an additional 52 genetic samples captured from sifakas at the other five RNP sites: Vohiparara, Ambatolahy Dimy, Sakaroa, Vatoharanana, and Valohoaka (Table 1, Figure 1). In addition, 12 individuals were sampled at a site in ANP. To collect genetic samples, our darting team used a $CO_2$ rifle, which launched light-weight 9-mm darts, to tranquilize adult and juvenile sifakas. Darts injected Telazol® (a combination of the dissociative anesthetic drug tiletamine and the benzodiazepine anxiolytic drug zolazepam) at 10 mg/kg of body weight intramuscularly. The team caught the animals with large nets as they fell. Infants were carried down with their mothers. Each animal was weighed and measured and, when conditions allowed, 1-6 cc of blood was extracted from its femoral vein (amounts have been deemed safe by two different veterinarians). Each animal received a tracking microchip (AVID Friendchip) after being checked to prevent duplicates. All animals in Talatakely, Sakaroa, and Valohoaka older than 2 years also received a dog collar/tag combination to be used to identify for ongoing behavioral studies. The animals were allowed to recuperate in light-weight sacks (recovery time ≈ 3 hours) before release back to the darting site and were followed to ensure successful recovery. The blood samples were kept at room temperature in a blood storage solution until returned to the United States for analysis (Longmire et al. 1992) and then frozen at -80°C until extraction. Most samples were collected from individuals that were present at the sites from 2000-2006 ($N = 87$); some individuals ($N = 11$) were sampled between 1987-2000.

*Primer optimization*

I isolated genomic DNA from these samples according to standard procedures (Sambrook et al. 1989). Primer pairs (Table 2) were optimized from *Propithecus verreauxi* (Lawler et al. 2001), *Propithecus coquereli* (Rakotoarisoa et al. 2006), *Propithecus diadema* (unpublished, developed by E.E. Louis and colleagues), and generalized *Propithecus* primers (Mayor et al. 2002). PCR amplification was carried out in a 25 μL reaction volume using an ABI 480 thermocycler (Perkin-Elmer) with approximately 25 ng of genomic DNA as

**Table 2.** List of primers used, their sequences, repeat motifs, GenBank accession numbers, annealing temperatures used in PCR, and range in allele size.

| Primer Name | Sequence (5'-3') | Repeat Motif | GenBank Accession No. | Annealing Temp. | Size (bp) |
|---|---|---|---|---|---|
| 47HDZ215 F | CTAACCAAAAAGGCTGACAGTG | $(CA)_{10}$ | AY045554[1] | 58 | 149-163 |
| 47HDZ215 R | TCCCAGAAGCAAAAGTCCTAC | | | | |
| 47HDZ236 F | AGGTCCTGTTGCTGCTGG | $(CA)_9TACT(CA)_7$ | AY045556[1] | 58 | 290-294 |
| 47HDZ236 R | GGGAGGGGTCTGCTTCAG | | | | |
| 47HDZ422 F | TCATGTTCATTGTAGCATTATTCAC | $(CA)_{19}$ | AY406741[1] | 56 | 245-267 |
| 47HDZ422 R | TGCAAAACCTACTGATATGGAAG | | | | |
| 47HDZ470 F | CCATTTGCTTTTAAGTTGAGG | $(GT)_{14}$ | AY045555[1] | 52 | 187-195 |
| 47HDZ470 R | GTCTAAGAAGCCTGTTATTGACTG | | | | |
| 47HDZ682 F | GGGGAAGGTTGTTGAAAGC | $(GT)_{15}$ | AY045557[1] | 58 | 209-217 |
| 47HDZ682 R | GGGAAAGGGAGAAGGAAGAG | | | | |
| 47HDZ712 F | AATCCAACTTAGCACTTCTTTCAA | $(GT)_{10}$ | AY045559[1] | 54 | 173-175 |
| 47HDZ712 R | GAAAAAGTTCCTGAGGTAAAAGAGA | | | | |
| 47HDZ720 F | CCAGGTTGATTTCTGTGAGGT | $(CA)_{13}$ | AY045558[1] | 52/56 | 166-174 |
| 47HDZ720 R | AGTGGTGGTTGGCTAAGTTG | | | | |
| 88HDZ10 F | GAAAAAAAAGTAAAACACAGTAGTAAGC | $(CA)_8CG(CA)_6$ | DQ453551[2] | 56 | 195-213 |
| 88HDZ10 R | ATAGACACACACAGGGACCATC | | | | |
| P.V. 1 F | GTTTCTTTTTCTTGCAGC | $(CA)_{17}$ | NA[3] | 54 | 149-181 |
| P.V. 1 R | CTTCTCTGGCTTCACATC | | | | |
| P.V. 3 F | GAAAGAAATGCTAGACCTAGAACGC | $(CA)_{12}$ | NA[3] | 54 | 387-405 |
| P.V. 3 R | GGGATCAGGACTTCAACATACTGC | | | | |
| P.V. 7 F | TTCTCCCACTACTGAGCGAG | $(CA)_{13}$ | NA[3] | 55 | 265-271 |
| P.V. 7 R | TCTGGAGGGCTGGAACAAAG | | | | |
| P.V. 8 F | CTCAAAGACATTTTCCTTCAGCC | $(CA)_{16}$ | NA[3] | 53 | 208-214 |
| P.V. 8 R | TTTCTACTCACCCCACAGTCATTAG | | | | |
| P.V. 9 F | TTTCCTCCTCCAGGGAGTCCAAAC | $(CA)_{12}$ | NA[3] | 61 | 242-258 |
| P.V. 9 R | GGACATCTGCACCATTGACCTAAC | | | | |
| P.V. 12 F | GCCCCTAATAATTTGAGCCAC | $(CA)_8$ | NA[3] | 60 | 342-344 |
| P.V. 12 F | ATCAAGCTGCTGTCCAACAAGCCC | | | | |
| P.V. 15 F | CCTTCATTCCTTTTCATTTCTTGG | $(CA)_{16}$ | NA[3] | 50/52 | 249-263 |
| P.V. 15 R | TTTTGTATTAGACTAAGCTGCC | | | | |
| P.V. 16 F | TGAGGGTGGTGAGCTTTAGC | $(CA)_{15}$ | NA[3] | 55 | 274-286 |
| P.V. 16 R | GGGCTGGGGAAAAAATATAAC | | | | |
| PROPD291 F | ACGGCTGAGGCAAAACC | $(GT)_{17}$ | NA[4] | 54/56 | 277-283 |
| PROPD291 R | CAATGCTAAATGAGAAAACACAC | | | | |
| PROPD40 F | TCTCTCTCTCTATCTTTCTCTCCCTC | $(CA)_{16}GA(CA)_2$ | NA[4] | 54 | 121-123 |
| PROPD40 R | GGTGTTGCATTACTATTACAGTTTCAG | | | | |
| PROPD74 F | GGAGTGTTCATTGCTATTGGG | $(CA)_6CG(CA)_8$ | NA[4] | 60 | 230-238 |
| PROPD74 R | GATGGAGAAGGCAGTCACAAA | | | | |
| PROPD86 F | AATCAAATGTGAGAAATAAGCCC | $(GT)_{14}(CT)_2(GT)_5$ | NA[4] | 58 | 191-205 |
| PROPD86 R | TGGAAAACTCCCCAGGTTAG | | | | |

[1]=Mayor et al. 2003; [2]=Rakotoarisoa et al. 2006; [3]=Lawler et al. 2001; [4]=unpublished primers developed by E. E. Louis and colleagues.
Discarded alleles (with ≤ 2 alleles) shaded in gray.

template.  Final amplification conditions consisted of 12.5 pmol unlabelled reverse primer, 12.5 pmol fluorescently-labeled forward primer, 1.5 mM $MgCl_2$, 200 µM each dNTP, and 0.5 U of *Taq* DNA polymerase (Promega) in 0.5 M KCl Tris buffer.  The thermal profile for PCR amplification was 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, a primer-specific annealing temperature for 30 s, 72°C for 30 s, and ending with a single extension of 72°C for 10 min.  To ensure accuracy, I extracted DNA from each individual 1-4 times and amplified each sampled 1-7 times (mean = 2.3).

I determined allele sizes by separation of the PCR products on a 7% polyacrylamide gel run on an ABI 377 DNA Analyser (Applied Biosystems) and assigned fragment length using the Genescan software (Applied Biosystems) and Genescan-500 [Tamra] size standard. I carefully checked allele sizes by comparing locus-specific patterns across individuals within each locus.

*Summary Statistics*

I gathered population genetic information on the dataset of 97 to 98 sifakas (one individual was only typed at fewer than eight loci and thus was dropped from some analyses).  I analyzed the dataset for errors using MICRO-CHECKER (van Oosterhout et al. 2004) and MSA (Dieringer and Schlotterer 2003).  Using GENEPOP 3.3 (Raymond and Rousset 1995), I performed exact tests (using default parameters: dememorization number = 1000, number of batches = 100, number of iterations per batch = 1000) for genotypic linkage disequilibrium between all pairs of loci within all populations to evaluate the independence of loci and whether the gene pool was subdivided in each population.  I also ran a Hardy-Weinberg test for excess heterozygotes through ML-RELATE (Kalinowski et al. 2006) to identify null alleles (alleles that were not amplified by the PCR process) using a Monte Carlo test set to 10,000 randomizations (Guo and Thompson 1992) and the *U* test statistic described by Rousset and Raymond (1995).  $F_{IS}$ was calculated to test Hardy-Weinberg expectations in each population as per Weir and Cockerham (1984) using exact tests available in GENEPOP (using default parameters as above).

Deviations from Hardy-Weinberg indicate an excess of heterozygotes or homozygotes in the population.  $F_{IS}$ ranges from -1 to 1.  Positive $F_{IS}$ indicates an excess of homozygotes/deficiency of heterozygotes in that subpopulation, possibly due to inbreeding, assortative mating, or small population size.  Excess homozygotes could also indicate the presence of allelic dropout, possibly due to null alleles, a problem that arises when alleles are not correctly amplified during PCR (Pemberton 1995).  Negative $F_{IS}$ indicates an excess of heterozygotes/deficiency of homozygotes in that subpopulation, due to outbreeding, disassortative mating, or the mating of individuals from distant populations.

I estimated gene diversity and allelic richness using FSTAT 2.9.3.2 (Goudet 1995, 2001) and GENEPOP (using default parameters as above).  I estimated $F_{ST}$ by a weighted analysis of variance (Weir and Cockerham 1984) using GENEPOP.  $F_{ST}$ ranges from 0 to 1. It is a measure of genetic differentiation between groups and thus increases as gene flow between populations decreases, e.g., as a result of a barrier.  Zero indicates a panmictic population; one represents complete reproductive isolation between the subpopulations, possibly indicating the mixing of samples from two discrete non-interbreeding populations (the Wahlund effect).

*Spatial genetic structure*

      To estimate the amount of variability between populations, I calculated allele frequencies and degree of heterozygosity.  I used the Bayesian clustering method through STRUCTURE (Pritchard et al. 2000, Falush et al. 2003) to estimate genetic structure in the populations.  STRUCTURE assigns individuals probabilistically to $K$ populations.  After a preliminary run with 100,000 burnin period, 1,000,000 MCMC reps after burnin, $K = 1\text{-}10$ for 1 iteration, I ran a full model with 100,000 burnin period and 1,000,000 MCMC reps after burnin, $K = 3\text{-}8$ for 10 iterations each.  Results were visualized using *distruct* version 1.1 (Rosenberg 2004).

      To estimate the effective number of migrants ($N_m$), I used the private allele method through GENEPOP (according to Slatkin 1985), where relatively high levels of gene flow are indicated by $N_m > 2$.  I examined an isolation by distance effect using a Mantel Test (10,000 permutations; Mantel 1967, Sokal and Rohlf 1995) through GENEPOP.  This one-tailed test used a Spearman Rank correlation coefficient.  I also tested for sex bias in dispersal using a two-tailed T-test through FSTAT based on 10,000 randomizations.

*Group structure*

      To determine relatedness within the Talatakely groups, I used CERVUS (Marshall et al. 1998).  I verified relatedness results with ML-RELATE (Kalinowski et al. 2006) and also used this program to identify null alleles.  CERVUS was set to the following conditions: 100 offspring, 20 candidate fathers, prop. sampled = 0.3 sampled, prop. loci typed = 0.9, prop. loci mistyped = 0.1, minimum typed loci = 8.  These parameters represent a conservative analysis that will identify any potential fathers in the population.  The results of this analysis are particularly robust because all individuals were genotyped from blood samples and all individuals, and their corresponding samples, were known, avoiding complications of pseudoreplication.  Differences between groups were considered significant at $P < 0.05$.

# RESULTS

*Summary statistics*

I originally typed 98 individuals at 20 loci. However, 4 loci were discarded due to low allelic diversity (47HDZ236, 47HDZ712, PROPD40, and P.V. 12 each showed only 2 alleles; Table 2). Most of the remaining 16 loci displayed moderate levels of allelic variation, ranging from two to nine alleles in 9-34 individuals/site (Table 3). Allele size differed according to the repeat length as expected (e.g., alleles from dinucleotide markers were two nucleotides apart). Linkage disequilibrium tests indicated linkage at only 4/121 combinations of loci (47HDZ720/88HDZ10, $P < 0.01$; 47HDZ215/PROPD74, $P = 0.011$; 47HDZ470/ 47HDZ682, $P = 0.012$; and 47HDZ470/P.V.1, $P = 0.028$). Allelic richness, the number of alleles per locus at each site, averaged 1.64, with little variance across sites (range = 1.48-1.70; Table 3).

Mean expected heterozygosity ($H_e$) ranged from 0.08 to 0.88 (Table 3). Although there were individual differences between expected heterozygosity and observed heterozygosity ($H_o$) between loci within sites, there was no overall difference across sites within loci (mean range in difference = -0.24-0.099) or across loci within sites (mean range = 0.00-0.03). When averaged across sites within loci, there was no deficiency of heterozygotes (all $P > 0.072$) or excess of heterozygotes (all $P > 0.15$), except for P.V. 3, which had an excess of heterozygotes ($P = 0.0060$). These values indicate a lack of allelic dropout among the loci, with the possible exception of P.V. 3. When averaged across loci within sites, there was no deficiency of heterozygotes (all $P > 0.13$) or excess of heterozygotes (all $P > 0.20$), except for Sakaroa, which showed an excess of heterozygotes ($P = 0.044$). A global test using the Markov chain method across all loci and all sites was not significant for heterozygote deficiency ($P = 0.87$, SE = 0.0076) or heterozygote excess ($P = 0.13$, SE = 0.0069). These values indicate a lack of inbreeding or assortative mating; however, the excess of heterozygotes found in the population of Sakaroa may indicate sampling of two separate subpopulations.

$F_{ST}$ values were highest (0.095-0.20) between Andringitra and the six sites in RNP (Table 4). The next highest values occurred between Parcel I and Parcel II sites (0.062-0.16). Between sites within each parcel, values were much lower (Parcel I: -0.019-0.074; Parcel II: 0.053), with the lowest of these values between the least disturbed sites of Vatoharanana and Valohoaka. These low values (negative values considered equivalent to values of zero) indicate that these sites were not genetically differentiated. Within parcel comparisons (mean = 0.027) differed significantly from between park (mean = 0.152) and between parcel (mean = 0.110) comparisons (Tukey test: P<0.0001); there was no significant different between comparisons of sites between parks and between parcels.

*Spatial genetic structure*

A test using the Markov chain method and Fisher exact test indicated strong allelic differentiation in the distribution of alleles between each pair of sites (all $P < 0.005$ except Vatoharanana/Sakaroa at $P = 0.049$; Vatoharanana/Valohoaka were not significantly different at $P = 0.052$). Similarly, a test using the same methods revealed strong genotypic differentiation between all site pairs (all $P < 0.001$ except Vatoharanana/Sakaroa at $P = 0.013$) except Vatoharanana/Valohoaka, which did not differ significantly ($P = 0.078$).

**Table 3.** Summary statistics for each of 16 microsatellite loci. Populations are abbreviated. Summary table of averages follows.

| | | Andring | Vohi | Ambat Dimy | Saka | Tala | Vato | Valo | | Andring | Vohi | Ambat Dimy | Saka | Tala | Vato | Valo |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $n$ | | 12 | 10 | 9 | 12 | 34 | 12 | 9 | $n$ | 12 | 10 | 9 | 12 | 34 | 12 | 9 |
| $N$ | 44HDZ215 | 3 | 6 | 2 | 4 | 6 | 6 | 7 | P.V. 7 | 2 | 3 | 1 | 3 | 4 | 2 | 3 |
| $A$ | | 1.594 | 1.732 | 1.325 | 1.574 | 1.562 | 1.684 | 1.879 | | 1.228 | 1.279 | 1 | 1.392 | 1.505 | 1.173 | 1.56 |
| $H_o$ | | 0.83 | 0.60 | 0.33 | 0.58 | 0.56 | 0.50 | 0.78 | | 0.25 | 0.30 | NA | 0.33 | 0.44 | 0.17 | 0.33 |
| $H_E$ | | 0.59 | 0.73 | 0.29 | 0.48 | 0.53 | 0.57 | 0.68 | | 0.23 | 0.28 | NA | 0.29 | 0.37 | 0.16 | 0.44 |
| $F_{IS}$ | | -0.429 | 0.188 | -0.167 | -0.235 | -0.058 | 0.129 | -0.151 | | -0.1 | -0.08 | NA | -0.143 | -0.192 | -0.053 | 0.25 |
| $N$ | 44HDZ422 | 5 | 6 | 7 | 5 | 6 | 5 | 3 | P.V. 8 | 4 | 4 | 5 | 2 | 3 | 3 | 3 |
| $A$ | | 1.766 | 1.778 | 1.842 | 1.805 | 1.681 | 1.747 | 1.56 | | 1.649 | 1.689 | 1.726 | 1.091 | 1.403 | 1.481 | 1.242 |
| $H_o$ | | 0.83 | 0.80 | 0.78 | 0.83 | 0.59 | 0.58 | 0.56 | | 0.75 | 0.60 | 0.78 | 0.08 | 0.41 | 0.50 | 0.22 |
| $H_e$ | | 0.70 | 0.70 | 0.94 | 0.74 | 0.60 | 0.62 | 0.44 | | 0.65 | 0.69 | 0.81 | 0.08 | 0.40 | 0.44 | 0.21 |
| $F_{IS}$ | | -0.198 | -0.153 | 0.176 | -0.136 | 0.021 | 0.067 | -0.304 | | -0.165 | 0.136 | 0.038 | 0 | -0.021 | -0.143 | -0.037 |
| $N$ | 44HDZ470 | 1 | 3 | 2 | 4 | 4 | 3 | 2 | P.V. 9 | 5 | 6 | 6 | 8 | 8 | 7 | 6 |
| $A$ | | 1 | 1.833 | 2 | 2 | 1.258 | 1.833 | 2 | | 1.793 | 1.705 | 1.817 | 1.892 | 1.825 | 1.84 | 1.8 |
| $H_o$ | | NA | 0.20 | 0.11 | 0.17 | 0.15 | 0.08 | 0.11 | | 0.67 | 0.70 | | | | 0.75 | 0.78 |
| $H_e$ | | NA | 0.17 | 0.11 | 0.17 | 0.19 | 0.14 | 0.11 | | 0.79 | 0.71 | | 0.82 | 0.80 | 0.77 | 0.71 |
| $F_{IS}$ | | NA | -0.333 | NA | 0 | 0.228 | 0.5 | NA | | 0.166 | 0.008 | -0.094 | -0.128 | -0.029 | 0.027 | -0.101 |
| $N$ | 44HDZ682 | 3 | 6 | 5 | 4 | 7 | 7 | 5 | P.V. 15 | 4 | 5 | 6 | 4 | 5 | 5 | 5 |
| $A$ | | 1.467 | 1.758 | 1.795 | 1.537 | 1.624 | 1.749 | 1.791 | | 1.435 | 1.706 | 1.779 | 1.659 | 1.577 | 1.784 | 1.708 |
| $H_o$ | | 0.42 | 0.80 | 0.67 | 0.50 | 0.53 | 0.67 | 0.78 | | 0.50 | 0.50 | 0.89 | 0.50 | 0.41 | 0.58 | 0.67 |
| $H_e$ | | 0.47 | 0.68 | 0.88 | 0.45 | 0.55 | 0.69 | 0.79 | | 0.43 | 0.64 | 0.82 | 0.38 | 0.44 | 0.65 | 0.63 |
| $F_{IS}$ | | 0.113 | -0.185 | 0.255 | -0.125 | 0.039 | 0.03 | 0.018 | | -0.158 | 0.223 | 0.371 | -0.333 | 0.068 | 0.113 | -0.063 |
| $N$ | 44HDZ720 | 2 | 5 | 4 | 4 | 4 | 4 | 5 | P.V. 16 | 3 | 6 | 4 | 5 | 7 | 6 | 5 |
| $A$ | | 1.29 | 1.641 | 1.684 | 1.675 | 1.738 | 1.747 | 1.791 | | 1.467 | 1.789 | 1.634 | 1.784 | 1.658 | 1.762 | 1.667 |
| $H_o$ | | 0.33 | 0.60 | 0.78 | 0.75 | 0.68 | 0.75 | 0.56 | | 0.33 | 0.90 | 0.67 | 0.83 | 0.71 | 0.58 | 0.56 |
| $H_e$ | | 0.29 | 0.58 | 0.76 | 0.62 | 0.63 | 0.62 | 0.62 | | 0.47 | 0.79 | 0.63 | 0.72 | 0.64 | 0.70 | 0.67 |
| $F_{IS}$ | | -0.158 | -0.043 | -0.024 | -0.224 | -0.076 | -0.218 | 0.104 | | 0.296 | -0.149 | -0.055 | -0.17 | -0.107 | 0.172 | 0.175 |
| $N$ | 44HDZ291 | 4 | 3 | 3 | 4 | 4 | 4 | 4 | PROPD74 | 3 | 5 | 4 | 4 | 4 | 3 | 5 |
| $A$ | | 1.699 | 1.621 | 1.647 | 1.768 | 1.664 | 1.784 | 1.786 | | 1.518 | 1.805 | 1.721 | 1.766 | 1.697 | 1.589 | 1.813 |
| $H_o$ | | 0.50 | 0.50 | 0.56 | 0.67 | 0.53 | 0.58 | 0.44 | | 0.33 | 0.80 | 0.78 | 0.67 | 0.76 | 0.42 | 0.67 |
| $H_e$ | | 0.70 | 0.56 | 0.65 | 0.64 | 0.57 | 0.65 | 0.35 | | 0.52 | 0.81 | 0.80 | 0.70 | 0.59 | 0.54 | 0.63 |
| $F_{IS}$ | | 0.294 | 0.111 | 0.149 | -0.043 | 0.066 | 0.113 | -0.333 | | 0.367 | 0.007 | 0.031 | 0.053 | -0.293 | 0.237 | -0.059 |
| $N$ | P. V. 1 | 3 | 6 | 7 | 4 | 6 | 5 | 6 | PROPD86 | 5 | 5 | 4 | 3 | 4 | 4 | 4 |
| $A$ | | 1.366 | 1.742 | 1.81 | 1.689 | 1.609 | 1.632 | 1.562 | | 1.66 | 1.758 | 1.739 | 1.595 | 1.718 | 1.619 | 1.747 |
| $H_o$ | | 0.25 | 0.60 | 0.78 | 0.50 | 0.53 | 0.75 | 0.67 | | 0.50 | 0.90 | 0.78 | 0.58 | 0.53 | 0.75 | 0.67 |
| $H_e$ | | 0.37 | 0.74 | 0.81 | 0.57 | 0.54 | 0.53 | 0.56 | | 0.50 | 0.76 | 0.74 | 0.50 | 0.57 | 0.57 | 0.58 |
| $F_{IS}$ | | 0.327 | 0.2 | 0.043 | 0.136 | 0.015 | -0.459 | -0.2 | | -0.011 | -0.2 | -0.057 | -0.189 | 0.073 | -0.343 | -0.161 |
| $N$ | P.V. 3 | 2 | 3 | 3 | 2 | 3 | 2 | 3 | PROPC10 | 3 | 6 | 6 | 7 | 7 | 9 | 7 |
| $A$ | | 1.228 | 1.595 | 1.679 | 1.189 | 1.344 | 1.091 | 1.392 | | 1.475 | 1.811 | 1.763 | 1.842 | 1.801 | 1.84 | 1.892 |
| $H_o$ | | 0.25 | 0.90 | 1.00 | 0.17 | 0.38 | 0.08 | 0.44 | | 0.50 | 0.80 | 0.89 | 0.75 | 0.71 | 0.92 | 0.78 |
| $H_e$ | | 0.23 | 0.59 | 0.75 | 0.16 | 0.32 | 0.08 | 0.39 | | 0.47 | 0.81 | 0.85 | 0.70 | 0.66 | 0.77 | 0.79 |
| $F_{IS}$ | | -0.1 | -0.558 | -0.35 | -0.059 | -0.185 | 0 | -0.143 | | -0.056 | 0.014 | -0.051 | -0.073 | -0.071 | -0.202 | 0.02 |

| Multilocus | Andringitra | Vohiparara | Ambatolahy Dimy | Valohoaka | Vatoharanana | Sakaroa | Talatakely |
|---|---|---|---|---|---|---|---|
| $N$ | 5 | 6 | 7 | 7 | 9 | 8 | 8 |
| $A$ | 1.48 | 1.70 | 1.69 | 1.70 | 1.65 | 1.64 | 1.60 |
| $H_o$ | 0.483 | 0.656 | 0.698 | 0.563 | 0.542 | 0.528 | 0.527 |
| $H_e$ (SE) | 0.494 (0.0044) | 0.639 (0.010) | 0.703 (0.0073) | 0.538 (0.0091) | 0.531 (0.0097) | 0.501 (0.0037) | 0.525 (0.0098) |
| $F_{IS}$ | 0.02 | -0.046 | 0.034 | -0.063 | 0.022 | -0.103 | -0.038 |
| $P$ | 0.86 | 0.25 | 0.81 | 0.27 | 0.20 | 0.044 | 0.23 |

$n$ = Sample size per population; $N$ = Number of alleles; $A$ = Allelic richness; $H_o$ = Observed heterozygosity; $H_e$ = Expected heterozygosity; SE = Standard error; $P$ = Probability of heterozygote excess.

**Table 4.** $F_{ST}$ values between site pairs. Higher values indicate greater differentiation between subpopulations. Within parcel comparisons (mean = 0.027) differed significantly from between park (mean = 0.152) and between parcel (mean = 0.110) comparisons (P < 0.0001).

| Site | Andringitra | Vohiparara | Amb Dimy | Sakaroa | Talatakely | Vatoharanana | |
|---|---|---|---|---|---|---|---|
| Vohiparara | 0.177 | | | | | | |
| Ambatolahy Dimy | 0.178 | 0.053 | | | | | |
| Sakaroa | 0.136 | 0.107 | 0.089 | | | | |
| Talatakely | 0.202 | 0.164 | 0.133 | 0.042 | | | |
| Vatoharanana | 0.095 | 0.103 | 0.103 | -0.011 | 0.044 | | **Average** |
| Valohoaka | 0.124 | 0.079 | 0.099 | 0.009 | 0.074 | -0.019 | 0.094 |

These results support the $F_{IS}$ values showing that there was genetic differentiation between the sites except for the site pair Vatoharanana and Valohoaka.

When considering all sites, the average frequency of private alleles was calculated as 0.096 (Table 5). The estimated number of migrants ($N_m$) across sites based on private alleles (corrected for size) was fairly high at 1.11. When excluding Andringitra, the average frequency of private alleles was 0.075. The estimated $N_m$ across the six sites (corrected for size) was 1.83. This result supports the genetic separation of Andringitra National Park from Ranomafana National Park and further suggests historical gene flow among the RNP sites. I also looked at whether there was a difference between the movement of females and males across the sites; I found no sex-bias (female $N = 41$, male $N = 56$; $P = 0.88$).

Clustering analysis in STRUCTURE indicated that the highest probability occurred at $K = 5$ clusters. The slope of $q$, the mean confidence assignment of all individuals to their most probable cluster, minimized after $K = 5$ (Figure 2). Thus, cluster analysis indicated that the 98 individuals separated genetically into 5 populations. Figure 3 shows the seven sites separated into these 5 populations, which broke up further into three clusters: the outgroup in Andringitra National Park separated distinctly from the RNP sites, the two Parcel II sites clustered together, and the four Parcel I sites formed a third grouping. Moreover, the STRUCTURE output indicated gene introgression among the Parcel I sites overall, with Vatoharanana and Valohoaka most similar.

I analyzed the data for a correlation of geographic distance on genetic difference using a Mantel test. When all seven sites were analyzed, there was a slightly significant effect of genetic distance on genetic differentiation (Spearman Rank correlation: $P = 0.046$). However, I found no isolation by distance effect when I excluded the outgroup site at ANP (Spearman Rank correlation: $P = 0.26$; Figure 4).

*Group structure*

Using CERVUS and ML-RELATE, I also examined the relatedness found between individuals within groups, focusing on the well-studied Talatakely site. Thirty-three individuals were included in this analysis, distributed between the four groups that compose the Talatakely population (see Chapter 3: Figure 1). All genetic relationships were ascertained and compared to behavioral observations of family dynamics and mating behavior. No extra-group mating has ever been observed, although mating observations were rare (< 10 observations) due to the brevity of the sifaka estrus (12-48 hours).

All genetic results followed Mendelian patterns of inheritance for known mother/offspring and sibling pairs (Table 6). I tested whether the breeding males in the group, and not floater or other group males, were the fathers of the group offspring. In five cases there were potentially two breeding males present, in all other cases there was only one unrelated adult male present at conception. In all 19 sampled cases, the group breeding male received the highest probability (LOD score) as the father. Relatedness analysis including siblings supported these results. LOD scores ranged from 0.66 to 8.58 with 14/19 showing over 95% confidence in the paternity assignment (Table 6). Thus, group males were indicated as fathers in 14 of 19 cases. In two other cases (NCNTf and INFGS04), relationships with siblings (Pu, PuPu, YR and GR, PO, RP, respectively) supported the group breeding male (B) as the father. In one of the remaining three cases (YS), the mother was not sampled, reducing the power of the analysis.

**Table 5.** Private (unique) and shared (found in only two sites) alleles found at each locus and at each site. Totals across all loci within each population are listed at the bottom of the table.

| | | Andringitra | Vohipara | Ambatolahy Dimy | Sakaroa | Talatakely | Vatoharanana | Valohoaka |
|---|---|---|---|---|---|---|---|---|
| 44HDZ215 | Private | | 1 | | | 1 | | |
| | Shared | | 1 | | | 1 | 1 | 1 |
| 44HDZ422 | Private | 1 | 1 | 1 | | | | |
| | Shared | | 1 | 1 | | | | |
| 44HDZ470 | Private | | | | 1 | | | |
| | Shared | | 1 | | | 1 | | |
| 44HDZ682 | Private | | | 1 | | | 1 | |
| | Shared | | | | | | | |
| 44HDZ720 | Private | | 1 | | | | | 1 |
| | Shared | | | | | | | |
| 44HDZ291 | Private | 0 | | | | | | |
| | Shared | | | | | | | |
| P. V. 1 | Private | | | 2 | | 1 | | |
| | Shared | | | | | | | |
| P.V. 3 | Private | | | | | | | |
| | Shared | | 1 | 1 | | 1 | | 1 |
| P.V. 7 | Private | | | | | | | |
| | Shared | | | | 1 | 1 | | |
| P.V. 8 | Private | 2 | | 1 | | | | |
| | Shared | | | | | | | |
| P.V. 9 | Private | | | 1 | | | | |
| | Shared | | 1 | | | | 1 | |
| P.V. 15 | Private | | 1 | 1 | | 1 | | |
| | Shared | 2 | 1 | 2 | | | 1 | 2 |
| P.V. 16 | Private | | 1 | | | 1 | 1 | |
| | Shared | | | | | | | |
| PROPD74 | Private | 0 | | | | | | |
| | Shared | | | | | | | |
| PROPD86 | Private | | 1 | | | | | |
| | Shared | | | | | | | |
| PROPC10 | Private | 0 | | | | | | |
| | Shared | | 1 | | | | | 1 |
| TOTAL | Private | 3 | 6 | 7 | 1 | 4 | 2 | 1 |
| | Shared | 2 | 7 | 4 | 1 | 4 | 3 | 5 |
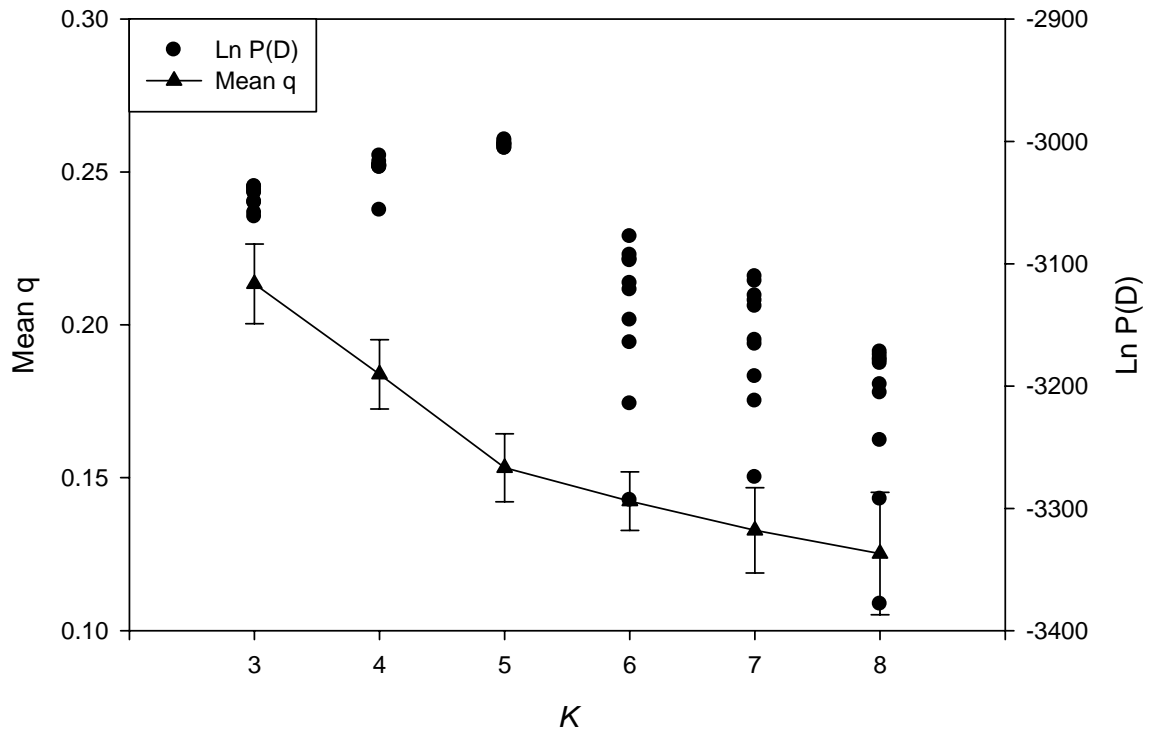
**Figure 2.** Likelihood plot of STRUCTURE results (10 runs for each value of *K* and MCMC with 1,000,000 repetitions). *q* (mean ± SE; left y-axis) is the mean confidence assignment of all individuals to their most probable cluster, indicating robustness of assignment. LnP(D) (right y-axis) is the log likelihood for each value of *K*, the number of simulated clusters. LnP(D) maximized (was most probable) at *K* = 5.
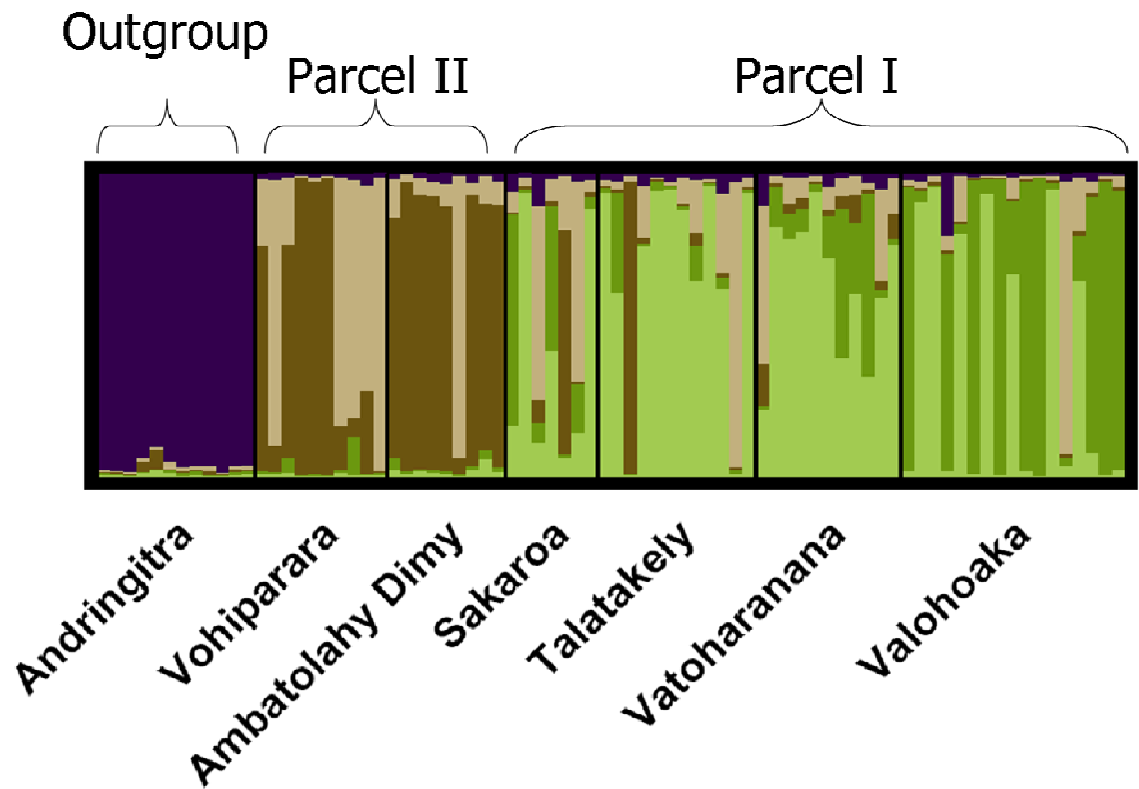
**Figure 3.** Histogram of genetic clusering analysis results for the seven sites. Each column represents an individual and its probabilistic assignment into each of $K = 5$ genetic clusters, represented by five random colors. Shared colors represent similar genotypes. Populations are separated by black lines and labeled above (area) and below (site) the figure.
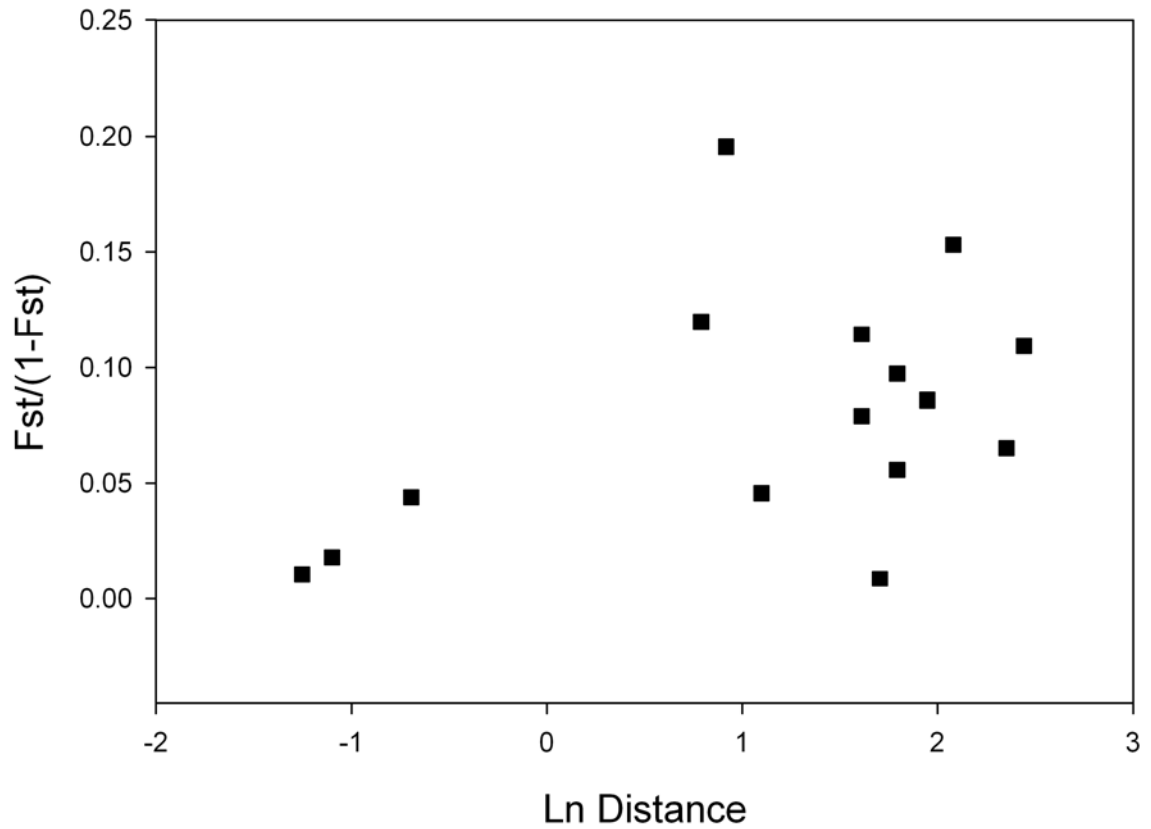
**Figure 4.** Correlation between the ln geographic distance and genetic distance, represented conventionally as $F_{ST}/(1-F_{ST})$, for the six sites sampled in Ranomafana National Park (excluding the outgroup site in Andringitra National Park). There was no effect of distance on genetic differentiation ($P = 0.29$).

**Table 6:** Relationship analysis from CERVUS comparing offspring with their mothers, if known, and the group male. Last columns compare mother, group male, and offspring in combination. LOD scores indicate the likelihood of the relationship being real; higher numbers are more likely. The numbers in ( ) indicate mismatches.

| | Offspring | | Offspring-Mother Dyad | | | | | Offspring-Group Male Dyad | | | | | Triad | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | ID | Loci typed | ID | Loci typed | Loci compared[a] | LOD score | Non-exclusion probability | ID | Loci typed | Loci compared[a] | LOD score | Non-exclusion probability | Loci compared[a] | LOD score |
| 1 | Br | 16 | BB | 16 | 16 | 6.48 | 1.21E-02 | R | 16 | 16 | 4.49* | 2.34E-04 | 16 | 6.69** |
| 1 | BrBl | 8 | BB | 16 | 8 | -0.31 | 3.92E-01 | R[b] | 16 | 8 | 2.39 | 6.90E-03 | 8 | 4.09** |
| 1 | PB | 8 | BB | 16 | 8 | 2.04 | 2.77E-01 | R[b] | 16 | 8 | 1.38 | 4.03E-03 | 8(1) | 0.61 |
| 1 | YS | 12 | Y | NA | NA | NA | 1.45E-02 | R[b] | 16 | 12 | 0.85 | 1.45E-02 | NA | NA |
| 1 | PuS | 15 | TS | 14 | 13 | 10.33 | 2.63E-03 | Br[b] | 16 | 15 | 3.82* | 1.42E-03 | 15 | 5.44** |
| 1 | P3 | 11 | GO | 14 | 11 | 3.40 | 2.24E-02 | OB | 15 | 11 | 6.37** | 3.32E-04 | 11 | 8.58** |
| 2 | B | 15 | PY | 9 | 8 | 2.54 | 7.30E-03 | Y | 10 | 9 | 1.57 | 3.93E-04 | 9(2) | 0.66 |
| 2 | BS | 14 | RS | 14 | 13 | 7.63 | 1.05E-02 | P | 16 | 14 | 5.62** | 1.20E-04 | 14 | 8.53** |
| 3 | NCNTm | 14 | BB | 16 | 14 | 4.56 | 1.95E-02 | BP | 16 | 14 | 2.24 | 2.41E-04 | 14 | 5.99** |
| 3 | RG2 | 16 | BB | 16 | 16 | 3.17 | 3.61E-02 | BP | 16 | 16 | 4.52* | 2.04E-05 | 16 | 7.89** |
| 3 | BP | 16 | BY | 13 | 13 | 7.32 | 1.16E-02 | P[b] | 16 | 16 | 3.22* | 9.48E-05 | 16 | 8.15** |
| 4 | NCNTf | 15 | BG | 15 | 14 | 2.26 | 1.03E-01 | B | 15 | 14 | 2.23 | 1.17E-04 | 14 | 5.90 |
| 4 | Pu | 16 | BG | 16 | 15 | 2.49 | 5.50E-02 | B | 15 | 15 | 3.1* | 1.60E-04 | 15 | 6.23** |
| 4 | PuPu | 16 | BG | 16 | 15 | 4.24 | 3.64E-02 | B | 15 | 15 | 1.98 | 8.04E-04 | 15 | 5.27** |
| 4 | YR | 15 | BG | 15 | 15 | 1.14 | 4.77E-02 | B | 15 | 14 | 3.56* | 6.23E-06 | 14 | 8.37** |
| 4 | GR | 16 | GS | 16 | 16 | 4.40 | 2.87E-02 | B | 15 | 15 | 3.95 | 2.96E-05 | 15 | 7.99*** |
| 4 | INFGS04 | 14 | GS | 16 | 14 | 3.93 | 3.01E-02 | B | 15 | 13 | 1.66 | 3.58E-03 | 13 | 3.67* |
| 4 | PO | 14 | GS | 16 | 14 | 2.00 | 4.73E-02 | B | 15 | 14 | 2.96 | 2.96E-03 | 14 | 4.62** |
| 4 | RP | 16 | GS | 16 | 16 | 6.91 | 2.82E-02 | B | 15 | 15 | 2.22 | 3.56E-04 | 15 | 6.56** |

[a] = no loci mismatching unless noted in parentheses; [b] = 1 of 2 group males

* = 80% confidence; ** = 95% confidence

Table 7 delineates pairwise relatedness between all 34 Talatakely sifakas and uses these maternity and paternity assignments, along with pedigree information known from behavioral follows, to group dyads into relationship categories.  Dyads are color-coded by relationship: parent/offspring dyads in red; dyads colored orange shared the same father (half-siblings) and their mothers were related (aunt-niece/nephew); full-sibling dyads (same mother and father) are colored pink; half-sibling (same mother, different father or same father, different mother), grandparent/grandchild, and aunt or uncle/niece or nephew dyads in yellow; green colors the dyads that were cousins and nephew or niece/mother's halfsister; dark blue represents male-female breeding pairs, adults that shared the same group and produced offspring; and light blue indicates all other combinations, mostly immigrants and their new groupmates.  The inset shows that most related dyads shared fewer alleles on average than expected due to their relationships.  Unrelated dyads, representing a sampling of the population, were slightly higher than 0 at 0.4, and mates were slightly higher at 0.7.

Overall, the results from CERVUS and ML-RELATE were consistent and supported behavioral observations.  Furthermore, the group breeding male sired the majority, and perhaps the entirety, of group offspring.

**Table 7.** r values for Talatakely study animals. Internal table lists the expected r between these relationships and the observed r averaged within the categories.

| RELATIONSHIPS | R_EXP | R_OBS |
|---|---|---|
| PARENTS-OFFSPRING | 0.5 | 0.51 |
| SIBLINGS | 0.5 | 0.33 |
| HALFSIB+AUNT-NIECE | 0.36 | 0.20 |
| HALFSIB-GRAND-AU-NI | 0.25 | 0.17 |
| COUSINS-AUNT-NIECE* | 0.13 | 0.10 |
| MATE | 0 | 0.07 |
| UR | 0 | 0.04 |
| Site Average | | 0.095 |

Pink = Parent/offspring dyads; Red = Full-sibling dyads; Orange = Dyads related as half-siblings through their mothers; Yellow = Half-sibling dyads or grandparent/grandchildren dyads or aunt/niece, uncle/niece, aunt/nephew, or uncle/nephew dyads; Green = Cousin dyads or half-aunt/niece, half-uncle/niece, half-aunt/nephew, or half-uncle/nephew dyads; Dark blue = Male/female breeding pairs; Light blue = Dyads of unknown or unrelated individuals.

## DISCUSSION

Results of this research elucidate the genetic flow of the lemur *Propithecus edwardsi* at the regional, population, site, and group level.

The sifaka population in Ranomafana National Park (RNP) appears to be genetically diverse and viable. Allelic diversity was moderate and heterozygosity did not differ from expected across the population. $F_{IS}$ and relatedness values indicated a lack of inbreeding. $F_{ST}$ values did show some differentiation between the groups in Parcel I found south of the river/road barrier and those groups in Parcel II north of the barrier. These results were substantiated by the STRUCTURE analysis, which indicated the Parcel II sites as a separate cluster. Although there has been introgression, especially compared to the outgroup over 100 km away at Andringitra National Park (ANP), gene flow has been somewhat impeded. The isolation by distance analysis did not reveal a correlation between genetic and geographic distance except for the outgroup site ANP.

In this study, several different measures of genetic differentiation, including $F_{ST}$, private alleles, and genetic clustering analysis, showed that RNP and ANP are at least partly genetically isolated. These two parks enclose rainforest fragments that were part of the same contiguous habitat until recent deforestation. However, although these habitats were undisturbed by human development only centuries ago, they have been divided by natural barriers for much longer. Specifically, two large rivers divide the 110 km stretch of land between RNP and ANP. River systems throughout Madagascar have been implicated as the source of much of the island's endemic regional diversity (Wilmé et al. 2006).

The barrier that intersects RNP is actually composed of two very different obstacles. The Namorona River is an old, natural geographic barrier, whereas RN 25 developed in the 1930s and 1940s and was not paved until the 1960s. However, the river itself is not very wide except in some stretches and in some seasons and may not have been a rigid obstacle for large, mobile organisms; this study indicates that moderate level of migrants have moved between the northern and southern parcels of the park. On the other hand, the recent paving of the road and the subsequent deforestation around its edges may have greatly increased its obstruction (Trombulak and Frissell 2000, Ortega and Capen 2002, Forman et al. 2003, Riley et al. 2006). Moreover, as the road closely parallels the river, this double barrier may be acting synergistically to erect an insuperable barrier to gene flow for the fauna of RNP.

In such a long-lived species as *P. edwardsi*, the impact of a recent barrier may take a substantial amount of time to observe, especially in contrast to an ancient one (Coulon et al. 2008). Nevertheless, it is important to monitor populations and understand the effects of development before negative impacts have been experienced too widely, especially when dealing with endangered species. If this barrier is now insurmountable, mechanisms for promoting dispersal between the parcels could be considered. Possibilities to promote safe animal crossing include traffic management techniques such as occasional speed bumps to slow traffic, road diversions such as underpasses or overpasses, or even simply retaining large canopy trees on either side of the road at intermittent distances (Jimba et al. 1998, Mumme et al. 2000, Forman et al. 2003). Further studies are being conducted to determine whether these patterns of gene flow are similar for other species in RNP, focusing on a number of lemur species that encompass a diversity of locomotor abilities and behavior.

Too often species are judged as viable simply on density estimates, yet these statistics can mask the reality at the population level. It is important to have a true measure of the size of a population in order to understand its condition, predict its status, and, if necessary,

manage it appropriately. This includes understanding the dynamics of populations within groups as well. This study revealed that mating opportunities appear to be limited to group membership in *Propithecus edwardsi*. Moreover, only one and rarely two males are breeding within *P. edwardsi* groups. Adult sex ratios in lemur groups are roughly equal, unlike most primate taxa (Nunn 1999, Wright 1999), increasing the effective population size. However, a single breeding male with a long tenure increases the reproductive skew for males and reduces the effective population size of the species, potentially causing uninformed censuses to overestimate the viability of the population (Creel 1998).

Inbreeding is a concern to populations that exist in fragmented habitats. The result can be population crashes from a sudden environmental disturbance, such as an introduced pathogen or a cyclone. These are real threats in Madagascar, given its relatively recent global market, its escalated habitat destruction, and its extreme weather; it is crucial that these issues are addressed. As one of the top biodiversity hotspots (Mittermeier et al. 1998), we need to understand the population dynamics within the protected areas of Madagascar so that we can maximize the effect of limited resources and effect an optimal conservation strategy there.

There were potential problems with this analysis. The microsatellites, though developed in *Propithecus*, did not contain very high allelic richness, even after discarding four of the original 20 microsatellites. Further, most microsatellites used in this study were dinucleotide markers, potentially creating problems when determining allele sizes, e.g., due to stutter bands. Future analyses will incorporate species-specific, non-dinucleotide markers to confirm the results of this study. However, the great number of microsatellites used, their development from closely related species, the multiple PCR amplification and careful scoring of results, the lack of homozygote excess, the sampling of known individuals, and the comparison of results to known pedigrees provide confidence in the results.

Data like these, which are obtained at a high cost in terms of financial and human resources, can be used as indicators for other, lesser known species in a habitat. This analysis should now be expanded to other species in Ranomafana National Park to understand how these barriers are affecting other taxa.

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**Chapter 5**
**Conclusion**

In this dissertation, I sought to understand the population dynamics of the Milne-Edwards' sifaka, *Propithecus edwardsi*, from the perspective of social interactions, reproduction, relatedness, dispersal, and gene flow. I first investigated the social dynamics of sifakas, using the Evolutionary Theory of the Family to examine kinship effects and adult interactions. I then looked at the interactions between groups in the form of dispersal, developing a model to explain the circumstances that lead to dispersal. Finally, I considered the broader context of the population as a whole, exploring the effect of geographic barriers on the genetic structure of sifakas in a protected area.

*Social Dynamics in Sifakas*

In Chapter 2, I examined sifaka social interactions using the framework of Emlen's Evolution Theory of the Family (ETF). Specifically, I examined the effect of kinship, reproductive skew, and ecological constraints on grooming, aggression, and proximity to test whether the ETF explained group dynamics in sifakas. Results supported some, but not all, of the predictions of the ETF.

Kinship and sex affected the frequency that adults and juveniles initiated grooming and aggression. Specifically, female adults and juveniles allogroomed group young more often and longer and aggressed against them less often if they were relatives. However, male adults and juveniles social interactions did not show a significant effect of relatedness. Moreover, adult females, dominant in sifaka species, allogroomed adult males much less and were much more frequently aggressive toward them than vice versa. However, females initiated mutual grooming bouts with adult males and non-relatives initiated many more and longer mutual grooming bouts than relatives.

Although social interactions do appear to be partially driven by relatedness in sifakas, there may be an equally important effect of reciprocal altruism in grooming interactions. Sifakas may groom and avoid aggressing against relatives for the indirect fitness benefits, whereas they may groom and avoid aggressing against non-relatives for immediate benefits through reciprocal grooming and perhaps commodity exchange. Females are clearly dominant in this species and may only groom when they receive indirect fitness benefits (e.g., by grooming offspring). However, male adult sifakas are subordinate and may attempt to exchange grooming for tolerance at feeding sites and future mating opportunities.

The ETF is an excellent synthesis of behavioral ecology theory but seems neither to describe accurately nor sufficiently the social dynamics of sifakas. An updated model could incorporate reciprocal altruism. Future studies should more closely examine the effect of ecology, as well as test for a correlation between grooming given and benefits received, such as tolerance.

*Dispersal in Sifakas*

In Chapter 3, I explored the dispersal behavior of sifakas inhabiting Ranomafana National Park (RNP). After determining that there was no sex bias in dispersal in this population, I developed a model to understand what predicts dispersal in sifakas and potentially other species. The Local Mate Availability Model (LMA) focuses on a single predictor, the presence of an unrelated, sexually mature opposite sex individual ("mate") in the group. With this single factor, LMA predicted the breeding and dispersal behavior of the majority of known cases among the Talatakely groups. I then considered the effect of takeovers by unrelated same-sex adults and found that each immigration event, whether by a male or a female, was associated with the disappearance of the resident breeder's infant. Subsequently, the resident female would disperse, if the immigrant was female, or come into estrus the following season, significantly more quickly than if her offspring had survived, if the immigrant was male. A sex ratio of more breeding males than breeding females in the group predicted several more of the male dispersals. When accounting for sex ratio and forced dispersal associated with same-sex takeovers, I found that LMA predicted almost all dispersal events.

Thus, I found that unbiased sex dispersal behavior in sifakas was being driven by accessible mate availability as well as these takeover events, which were also greatly increasing infant mortality rates. LMA may be useful in predicting dispersal behavior in other species that do not show sex-biased dispersal.

*Genetic structure of Sifakas*

In Chapter 4, I analyzed the genetic structure of *P. edwardsi* in southeastern Madagascar. Although the sites appeared to have moderate allelic diversity and heterozygosity, I found differentiation between sites located in different parcels of RNP. These sites are separated by a river which was made a more substantial boundary over the last half century, when a road was paved alongside the river and the traffic and cutting along its edges increased. Results of this analysis indicated that the sifaka population in RNP, protected by legal enforcement and good management, has been healthy and viable historically in this area. However, the road/river barrier that has recently expanded could potentially block gene flow between the northern and southern parcels of the park. Because *Propithecus edwardsi* are endangered, with the sifakas in RNP representing one of the few remaining viable populations, this could have a substantial detrimental effect on the species. Moreover, smaller and/or less mobile animals, including other lemur species as well as other taxa, may be greatly affected by these developments. This analysis is currently being expanded to include other taxa to determine whether there is variation in gene flow across these barriers due to behavioral, morphological, and locomotor differences between species.

*General Conclusions*

In conclusion, this dissertation examined the population dynamics of a primate from the individual, group, population, and metapopulation perspective. At every stage, kinship and dispersal had a major impact on *Propithecus edwardsi*. Kinship and dispersal drove social interactions, group composition, genetic viability, and potentially the conservation status of this lemur. For example, the presence of a single male breeder and closely related female breeders in each group, combined with inbreeding avoidance, potentially led to the dispersal

of both male and female subadults from the group, which in turn affected gene flow and genetic variation at the population level.  Thus, performing detailed behavioral and genetic analyses with a broad perspective has revealed much about sifakas and increased our understanding of population dynamics in other social species.

*Future Directions*

This research has answered some questions and raised many.  The complete avoidance of breeding between relatives within sifaka groups suggests an effective mechanism for kin recognition.  I am currently conducting chemical analyses with collaborators to investigate the potential for the use of olfaction for recognizing relatedness.

Another unresolved issue is what causes sifakas to delay dispersal past sexual maturity.  This study revealed great variation in this characteristic.  Future research can explore the fitness consequences of foregoing reproduction temporarily in order eventually to inherit a breeding spot in the natal group or an adjacent territory.

Microsatellite analyses revealed the effects of genetic structuring in sifakas in southeastern Madagascar.  I am currently examining variation at a set of genes, the Major Histocompatibility Complex (MHC), to determine whether these patterns hold in a coding region.  I am also analyzing the effects of the river/road barrier on population structuring in other lemur species in Ranomafana National Park, specifically exploring the effects of different behavioral and locomotor tendencies.

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