Causes and Consequences of Differential Reproductive Success in Male White Sifaka (*Propithecus verreauxi verreauxi*)

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ABSTRACT

Causes and Consequences of Differential Reproductive Success in Male White Sifaka
(*Propithecus verreauxi verreauxi*)
RICHARD ROBERTS LAWLER
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Genetic analyses are combined with information on behavior, morphology, and demography, in order to further our understanding of mating and reproductive patterns within a population of wild lemur. Sixteen polymorphic, unlinked, microsatellite loci were isolated from the *P. v. verreauxi* genome. Using these loci, four hundred and ninety-eight animals were genotyped. The average heterozygosity in this population is 0.70 and the combined probability of these loci to exclude a random individual from parentage, when one parent is known, is 0.99.

Thirty-five percent of all adult males in the population-sample sired offspring. Males sire offspring within and outside their resident social group. Reproductive lifespan, fertility, and offspring survival are major components of male fitness. Variance in reproductive lifespan makes the largest percentage contribution to total variation in male fitness, followed by fertility and offspring survival. Factors contributing to extra-group reproduction include female choice, high density of social groups, and seasonal reproduction.

Phenotypic correlates of male reproductive success include larger body mass and larger appendicular muscle mass. Stabilizing selection acts on body mass and directional selection acts on limb muscle mass. The intensity of male-male mate competition in this population ranges from fierce to slight. The pattern of phenotypic variation among sires and non-sires is explained within the context of positive female mate choice, social group composition, and mate competition in an arboreal setting. Implications for sexual monomorphism are discussed.

Genotypic information was analyzed over a 10-year span to ascertain how differential reproduction, dispersal, and philopatry determine genetic population structure. Through time and across the population there is discernable genetic subdivision among social groups. Female relatedness within groups correlates with among-group genetic variation, revealing the matrilineal structure of sifaka. As the number of females in social groups increases, resident males are less able to monopolize reproduction. Offspring genotypes tend towards panmictic proportions when non-resident males obtain fertilizations. Offspring cohorts consist predominantly of males, due to male-biased primary sex ratios. Offspring cohorts retain more genetic subdivision than adult cohorts. However, because male sifaka disperse from their natal group upon reaching reproductive maturity, offspring genetic subdivision is randomized by male natal dispersal.

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TABLE OF CONTENTS

Acknowledgements: v
List of Tables: x
List of Figures: xi

Chapter 1:
Primate mating systems and differential reproductive success in male white sifaka 1

Chapter 2:
Isolation and screening of microsatellite loci in a wild lemur population (*Propithecus verreauxi verreauxi*).
Introduction. 9
Methods. 10
Results. 11
Discussion. 13

Chapter 3:
Reproductive success, reproductive strategies, and fitness in male white sifaka (*Propithecus verreauxi verreauxi*).
Introduction. 18
Methods. 22
Results. 27
Discussion. 30

Chapter 4:
Sexual selection and correlates of reproductive success in male white sifaka (*Propithecus verreauxi verreauxi*).
Introduction. 49
Methods. 51
Results. 55
Discussion. 56

Chapter 5:
Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*), 1992-2001.
Introduction. 74
Methods. 78
Results. 80
Discussion. 84

Chapter 6:
Summary and conclusions 99

References Cited 109

LIST OF TABLES

Table 2.1	Information on primer sequences, sample sizes, reaction conditions, and locus properties, for the 16 microsatellite loci isolated in this study.	15
Table 2.2	Population genetic and genealogical information for the 7 loci genotyped on a minimum of 200 animals.	16
Table 2.3	Mean observed and expected heterozygosities estimated from microsatellites loci for selected wild primate populations	17
Table 3.1	Average values of the within-group and outside-group fitness components.	43
Table 3.2	Decomposition of total fitness into additive and multiplicative components.	44
Table 4.1	The relationship between selected morphological and demographic factors and their expected effect on male mating and/or reproductive success.	70
Table 4.2	The relationship between reproductive status and male morphometric traits when controlling for mass or age.	71
Table 4.3	Selection gradients on body mass and limb shape.	72
Table 4.4	The relationship between reproductive status and adult social group composition.	73
Table 5.1	Yearly census data used in population structure analysis.	92
Table 5.2	θ and f values for adults and offspring in the population by year.	93
Table 5.3	Relatedness (r) of individuals and siring patterns by year.	94

LIST OF FIGURES

Figure 3.1 Distribution of reproductive success among males in the population. 45

Figure 3.2 Distribution of confidence values for paternity assignments. 46

Figure 3.3 Relationship between reproductive lifespan and fertility for males reproducing within their resident group and outside their resident group. 47

Figure 3.4 Relationship between reproductive lifespan and total number of offspring produced by each male in the population. 48

Figure 5.1 Values of F_{IS} (f) and F_{ST} (θ) for adults and offspring by year. 95

Figure 5.2 The relationship between adult F_{ST} (θ) and offspring F_{IS} (f) and the relationship between adult F_{ST} (θ) and relatedness (r) of females within groups. 96

Figure 5.3 The relationship between relatedness (r) of females within groups and offspring F_{IS} (f) and the relationship between relatedness (r) of males within groups and offspring F_{IS} (f). 97

Figure 5.4 The relationship between the percentage of offspring sired by resident males of a group and offspring F_{IS} (f) and the relationship between the percentage of offspring sired by resident males of a group and the adult sex ratio in the population. 98

CHAPTER 1

PRIMATE MATING SYSTEMS AND DIFFERENTIAL REPRODUCTIVE SUCCESS IN MALE WHITE SIFAKA

Knowledge of which individuals contribute genes to subsequent generations is necessary for understanding a variety of questions concerning mating strategies, reproductive success, and mating systems in biological populations. After all, differential reproductive success coupled with offspring viability forms the basis by which much evolutionary change proceeds. Yet in large-bodied, slowly-maturing mammals such as primates, these data are rarely available. For example, in multi-male, multi-female groups of primates it is difficult to accurately measure differences in individual reproductive output. This difficulty arises from the fact that mating is often promiscuous, thereby confusing paternity, and proper assessment of parent-offspring relationships requires continuous, long-term monitoring in the field (cf. Shively and Smith 1985; Nicolson 1987; de Ruiter and van Hooff 1993; de Ruiter and Inoue 1993).

With the advent of cost-effective molecular techniques such as polymerase chain reaction (PCR), it is now possible to obtain genetic information using small amounts of animal material (Woodruff 1993; Morin and Woodruff 1996). PCR, in conjunction with parentage-specific genetic markers, can yield genealogical information on a particular population. This can be achieved without recourse to long-term observations of parent-offspring affiliations and/or indirect behavioral inferences about paternity. In fact, genetic-based genealogical data provide a novel conceptual framework for further behavioral hypotheses. As stated by Martin, "[n]ew techniques, most notably DNA fingerprinting, have opened up revolutionary new possibilities for the interpretation of primate behavior in relation to reproductive success" (1992:vii).

Inferring a mating system simply from observations of adult group composition can be misleading. Individuals within social groups can pursue flexible reproductive strategies, practice exogamy, and/or adopt a variety of "alternative" reproductive strategies (Altmann and Altmann 1979; Dunbar 1983; Davies 1991; Austad and Howard 1984; Andersson 1994; Fleischer 1996). To understand the flexibility underlying individual reproductive strategies long-term data are required, for "...it is clear, especially in species living in complex social groups, a reliable description of mating systems can seldom be achieved unless the breeding careers of recognizable individuals are followed over a substantial proportion of their lifespan" (Clutton-Brock 1989b: 363; also see de Ruiter et al. 1994; Altmann et al. 1996; Weatherhead and Boag 1997). Information on breeding careers, in turn, requires genetic data. Molecular markers track genetic exchanges and reproductive events throughout the population and therefore provide information that is independent of the animals' past and current movements.

While genetic markers give information on reproductive events, the context in which these reproductive events take place is shaped by small-scale demographic and behavioral patterns. Where an animal moves within a population to seek reproductive opportunities depends on the behavior of other reproductively active animals (Altmann and Altmann 1979; Dunbar 1984; 1989; 2000). Animal spatial arrangements are expected to change through time as animals individually readjust their movements or behaviors relative to other animals seeking reproductive opportunities (Wittenberger 1983; Halliday 1983; Clutton-Brock 1989b; Waser 1993; Sutherland 1996). Gregarious animals simultaneously respond to and create the social and demographic context in which reproductive events occur. Therefore, to understand reproductive strategies, it is necessary to understand the mechanisms that underlie the relationship between demographic and genetic structure in a population; that is, where animals move and with whom they mate. Merging genealogical information with long-term demographic data provides a more robust depiction of how shifting social and demographic conditions impinge on individual reproductive strategies.

Reproductive strategies are also contingent on those aspects of the phenotype that aid in mate acquisition and mating competition. Primate males, like other mammals, invest more reproductive resources into behaviors that maximize mate acquisition than into behaviors that contribute to offspring care (Clutton-Brock 1991). This leads to high levels of intrasexual competition. Heritable aspects of the phenotype assisting in competition for mates will be subject to (or have been subjected to) evolutionary modification via sexual selection (Andersson 1994). Therefore, a thorough investigation of the mating system in gregarious primates should also seek to identify which male traits correlate with mate acquisition and reproductive success. Particular phenotypic features such as canine size, body mass, etc., may play crucial roles in male ability to maintain reproductive sovereignty within multi-male, multi-female social groups (cf. Plavcan 2001). Similarly, behavioral factors such as alliances, coalitions, and dominance rank can also influence reproductive control (van Hooff 2000). Integrating information on male morphology and behavior can aid in understanding how reproductive opportunities are differentially exploited given a variable distribution of reproductive partners and sexual rivals within the population.

The degree of bias in male reproductive output, in turn, can significantly influence the genetic and demographic structure of the population (cf. Pope 1996; 1998). When a limited number of males sire the majority of offspring in a population, the population genetic consequences can be far-reaching. High degrees of reproductive skew can simultaneously reduce *variance* effective population size (N_{ev}), increase population subdivision among social groups, enhance the opportunity for sexual selection, and foster kin-selection by uniting cohorts of offspring through paternal alleles (Arnold and Wade 1984a; Nunney 1993; Altmann 1979; Chesser 1991a). In this light, it is important to understand the sources of variation in paternity and what effects this variation has on the genetic constitution of social groups and the population as a whole.

Some efforts have been made in this direction regarding our understanding of primate mating systems (e.g., Pope 1990; 1992; 2000; de Jong et al. 1994; Morin et al. 1994; Altmann et al. 1996; Bercovitch and Nurnberg 1996; Keane et al. 1997). However, these studies encompass only a small portion of primate diversity (i.e., all but one focuses on *Pan* or cercopithecoid species). More recently, genetic and demographic studies focusing on lemur mating systems have emerged (Tomiuk et al. 1997; Feitz et al. 2000; Radespiel et al. 2001; Nievergelt et al. 2002; Wimmer and Kappeler 2002; Wimmer et al. 2002; also see Pereira and Weiss 1991; Merenlender 1993). Taken together, these studies have expanded our understanding of the interplay between genetics, demography, and behavior across the primate order. For example, using genetic and behavioral information, Pope (1990) was able to demonstrate that coalitions of related males outlasted (in years) coalitions of unrelated males among red howler monkey groups. Reproduction in howler groups is skewed, but non-reproductive males who are related to the breeding male can increase their inclusive fitness by cooperatively defending against incursions from non-resident, infanticidal males. Similarly, Feitz et al. (2000) examined the social organization of *Cheirogaleus medius* using genetic and demographic data. This pair-living lemur is characterized by high rates of extra-pair young such that social "fathers" were rearing offspring that were not their own. Feitz et al. (2000) suggest that the mechanism underlying this phenomenon relates to females seeking reproductive partners based on genetic quality—these results show that the social unit (i.e. male-female pair) does not always correspond to the reproductive unit. These studies, and others like them, show how genetic data can be used to corroborate existing hypotheses and/or develop new insights into primate mating systems.

However, out of logistical necessity, many of the studies listed above have focused on one or a few social groups and not on an entire population. Because the *population* is the unit of evolution, it would be helpful to know how individual differences in behavior and morphology translate into population-level phenomena. That is, what factors at the individual-level (e.g., morphological features, mating strategies, dispersal events) determine microevolutionary patterns at the population-level (e.g., genetic diversity, amount of subdivision)? Such knowledge would have propitious implications for a wide range of disciplines including conservation biology, behavioral ecology, and evolutionary demography.

To this end, this dissertation is concerned with how individual differences in behavior, morphology, and reproduction can be collectively summarized for their evolutionary consequence. Specifically, the focus is on male reproductive patterns—especially in terms of how these patterns are created and how they influence genetic population structure. The study group for this dissertation is a population of wild lemur, the white sifaka (*Propithecus verreauxi verreauxi*). *P. v. verreauxi* is a diurnal and gregarious strepsirhine primate that inhabits the south and southwest forests of Madagascar (Tattersall 1982). Data for the present study comes from an on-going study at Beza Mahafaly Special Reserve in southwest Madagascar. Further information on this species is provided in subsequent chapters. The core of the dissertation, chapters 3 through 5, work progressively "outward" from individual variation in reproductive success, to the morphological and social causes of this variation, and finally to how this variation influences the genetic structure of the population. The dissertation is organized as follows. Chapter 2 provides information on the construction and screening of *Propithecus*-specific microsatellite loci and their utility for assessing parentage and kinship in the population. Chapter 3 analyzes male reproductive success with respect to components of fitness—longevity, fertility, offspring survival—and how they contribute to total male fitness. Male sifaka reproduce within and outside their resident social groups. Therefore, this chapter also looks at the consequences and fitness effects of extra-group reproduction. Chapter 4 looks at the causes of variation in male reproductive output by examining associations between reproductive success and various morphological and social factors. The intensity of male mate competition in sifaka varies, and the "expected" correlates of reproductive success (e.g., canine size, body mass, number of adult females in the social group) are obliquely associated with male reproductive output. This chapter provides some context to these findings and interprets the results with respect to sexual monomorphism. Chapter 5 examines the genetic population structure of sifaka over a 10-year period. This chapter determines patterns of relatedness of among males, among females, and among offspring cohorts within and between sifaka social groups. Genetic population structure is interpreted within the context of dispersal and philopatry, reproductive skew, and the sex ratio of offspring cohorts.

This dissertation takes a dynamic approach to the study of mating systems (cf. Clutton-Brock 1989b). Its purpose is not to classify or label the sifaka mating system, but to identify what factors contribute to, and result from, differential patterns of mating and reproduction. Typologically, the sifaka mating system could be called "polygynandrous", indicating the many males mate with many females. However, such a term—while perhaps helpful for comparative studies—does little to advance our knowledge of sifaka reproductive biology. Finer categories or distinctions of mating patterns can be made. For example, it may be helpful to view male and female associations in social groups as the "social" mating system, whereas information on maternity and paternity could be called the "genetic" mating system (cf. Hughes 1998). Determining the relationship between these two types of mating systems can illuminate the conflicts and convergences between male and female reproductive strategies (e.g., Westneat 2000). Males and females have a shared goal in producing viable offspring, but are often in evolutionary conflict about how to achieve this goal (Gowaty 1996; Maynard Smith 1998). When it comes to number of mates, females often weigh costs and benefits of ensuring fertilization versus confusing paternity. Non-cycling females may mate with some males for non-reproductive reasons, for example, as a counter-strategy to infanticide (cf. van Schaik et al. 2000). Males, on the other hand, can almost always benefit by mating with numerous females, even when many of their mating efforts do not result in conception. These observations on mating *behavior* will only show up in the field primatologist's notebook and not on a geneticist's sequencing gel. However, actual *paternity* can be determined through genetic techniques. Assimilating behavioral studies with genetic analyses helps us understand why and how males and females pursue particular mating and reproductive strategies. This dissertation combines genetic information with previous studies on the behavior, demography, and life history of the white sifaka. Integrating this information provides the necessary biological context in which to understand the causes and consequences of differential reproductive success in male sifaka.

Hopefully, this dissertation also is a testament to the power of combining and analyzing different datasets that were all collected on the same primate population. Because this endeavor relies on many previous studies—to which several individuals contributed—this dissertation is really a collective effort.

CHAPTER 2

CHARACTERIZATION AND SCREENING OF MICROSATELLITE LOCI IN A WILD LEMUR POPULATION (*Propithecus verreauxi verreauxi*)

INTRODUCTION

Microsatellites or short, tandem-repeats (STRs) are codominant, highly polymorphic molecular markers that provide information on intra- and interpopulation structure, genetic relatedness and gene location via linkage maps. They consist of a tandemly repeated motif of 1 to 6 nucleotides (e.g., $ATT_{[13]}$ or $CA_{[26]}$ where the bracketed number equals the number of motifs that are repeated) flanked by a non-repetitive sequence of nucleotides. Polymerase chain reaction (PCR) primers may be designed in the flanking regions, allowing one to amplify the polymorphic repeat region. To the extent that the flanking sequences and repeat unit are found in neutral portions of the genome and segregate independently, then microsatellites will act as single, unlinked, neutral loci that are generally 700 base pairs (bp) or less in size (Scribner and Pearce 2000). These properties make microsatellites ideal genetic markers for socio-ecological studies of wild primate populations that require genetic information on population structure and/or kinship.

Microsatellites are increasingly characterized and used in population genetic and behavioral studies of numerous non-human primates (e.g., Constable et al. 2001; Ellsworth and Hoelzer 1998; Jekielek and Strobeck 1999; Von Segesser et al. 1999). Some of these studies have used cross-specific, or heterologous microsatellite loci (loci characterized in a primate species that is different from the one under study), but it has been demonstrated that some cross-specific microsatellite loci show lowered heterozygosities and may yield inaccurate pedigrees (Smith et al. 2000; Vigilant and

Boesch 2001; Vigilant et al. 2001). These phenomena are attributed to mispriming and/or template quality and can lead to potentially serious errors in assigning kin relations and estimating population genetic parameters from cross-specific microsatellite loci (Beaumont and Bruford 1999; Constable et al. 2001; Gagneaux et al. 1997; Pemberton et al. 1995; Smith et al. 2000; Taberlet et al. 1999). Similarly, cross-specific loci will not always amplify in the species under study; in these cases, it is necessary to isolate species-specific microsatellite loci (e.g. Jekielek and Strobeck 1999).

In this chapter, we provide information on microsatellite loci isolated from a wild lemur population, the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar. We were motivated to isolate these loci after having unsuccessfully tested 20 human and 16 *Eulemur*-specific microsatellite loci on the *P. v. verreauxi* genome. Below, we provide information on these *P. v. verreauxi*-specific microsatellite loci and their potential as estimators of genetic diversity and relationships in the Beza Mahafaly *Propithecus* population.

METHODS

Except where noted, we followed the protocol of Hammond et al. (1998). All tissue samples come from individuals captured and released in the wild (Richard et al. 1993; 2002). Approximately 0.3 gms of pinna (ear) tissue from 19 white sifaka were extracted for DNA following the protocol in Strauss (1998). On average, each extraction yielded about 70 ng/ul. The DNA samples were pooled and concentrated, digested, and size-selected for a 350-700 basepair region.

To screen for microsatellites, a 30 base pair oligonucletide consisting of 15 repeat units of CA was used. The enrichment process is different from Hammond et al. (1998; cf., Fischer and Bachmann 1998). Three biotin-tags were attached to the 5' end and the oligo had a 3'chain-terminator to prevent concatamers during subsequent PCR reactions.

The addition of a 3' chain-terminator was a critical component for successful primer design (cf., Koblizkova et al. 1998). The size-selected DNA was added to 30 ul of 20x SSC and 25 ul of H_2O and the mixture was denatured (10 minutes at 95 C) and then placed on ice for 2 minutes. 5 ug of the biotin-labeled CA probes were added and the mixture was put at 65 C for 20 minutes. To capture the portions of DNA containing repeat units, we used Streptavidin-coated magnetic beads (Promega). The entire mixture from above was added to the streptavidin beads (suspended in 0.5x SSC) and put at room temperature for 15 minutes. The beads were separated from the supernatant with a magnetic stand (Promega) and washed three times with 100 ul of 0.1x SSC letting them sit 5 minutes between each wash. The DNA was eluted from the beads by washing two times in 25 ul of ddH_2O. The resulting 50 ul of eluate was concentrated and cleaned using Qiagen purification columns. We performed the enrichment phase two times.

After the enrichment phase, the DNA was ligated and transformed following standard procedures. 212 colonies were screened for an insert via "colony PCR". Forty-six positive clones were identified and sequenced using a Perkin Elmer 377 automated sequencer (Applied Biosystems). Twenty-one of the 46 clones contained a CA repeat. From this, 16 primer pairs were designed using MacVector software. Primer pairs were then tested on the sifaka template. The forward primer was labeled with a fluorescent dye, either 6-FAM, HEX, or TET. A PCR reaction with 1x PCR buffer, 1.5 mM of $MgCl_2$, 80 uM of dNTPs, 20 pmols of forward primer, 20 pmols of reverse primer, and $\approx$100 ng of DNA template was run and analyzed on a 377 automated sequencer for GeneScan analysis (Applied Biosystems) following the prescribed protocols.

RESULTS

We designed 16 primer pairs that yielded easily quantifiable genotypes when visualized on GeneScan software. Initially, we genotyped 16 animals across all loci.

Using information from this initial genotyping, loci that showed high polymorphism were further genotyped on a minimum of 200 animals. For all loci, the primer sequences, number of animals genotyped at the locus, number of alleles, type of repeat unit, and annealing temperature are listed in Table 2.1. The loci ranged in size from ≈ 150-420 base pairs and the number of alleles across all loci ranged from 2 to 11. Ten of the16 loci had pure CA repeat units, while the other 6 had interrupted repeat units. All interrupted repeats contained no more than 1 or 2 nucleotides interspersed within the repeat unit. Across all loci, there was a positive association between number of alleles and number of repeats (Spearman's Rho = 0.67, p = 0.004). In the text below, we refer to each locus by its number only.

Table 2.2 provides population genetic and genealogical data on the 7 loci that were genotyped on a minimum of 200 individuals (Loci 1, 4, 6, 8, 14, 15, 16). This information was generated using the program CERVUS 2.0 (Marshall et al. 1998). All loci except locus 4 conformed to Hardy-Weinberg expectations using the chi-square test and the exact test (Haldane 1954; Raymond and Rousset 1995b). Additionally, two measures that can be used in parentage analysis are provided in Table 2.2. The exclusionary power [Excl (A)] is the average probability of a locus to exclude a randomly chosen individual from parentage of an offspring given only the offspring's genotype. Excl (B) is the average probability of a locus to exclude a randomly chosen individual from parentage, given the offspring's genotype and the genotype of one known parent. Total exclusionary power refers to the combined power of all loci to exclude a random individual from parentage of an offspring (cf., Marshall et al. 1998: 655). Null allele frequency provides a measure of the *potential* for a locus to possess non-amplifying alleles. A large, positive score relative to other loci indicates an excess of homozygotes, but this score does not necessarily imply that null alleles are present (cf., Summers and Amos 1997: 261-262). The mean expected heterozygosity for the population was 0.747 and the total exclusionary power of all 7 loci when neither parent is known is 0.957 and 0.996 when one parent is known.

DISCUSSION

The primary factors contributing to success in microsatellite characterization were the initial isolation of high molecular-weight DNA for subsequent digestion, the use of 3' chain-terminators on the CA biotin-labeled probes during the enrichment phase, and repeating the enrichment phase two times. Six of the 7 loci conformed to Hardy-Weinberg expectations when screened on a minimum of 200 individuals (Table 2.2). This suggests that these 6 loci will be useful for estimating a variety of population-genetic parameters (e.g. population substructure) that require neutral markers. Locus 4 deviates from Hardy-Weinberg expectations. Several factors may account for this: linkage, selection, pooling samples across families or age-cohorts, and/or the presence of null-alleles (the null allele frequency was highest in locus 4, Table 2.2). Interspecific comparative data on microsatellite loci are provided in Table 2.3. Loci isolated in this study have comparable heterozygosities to loci screened in other wild primate populations.

In addition to providing estimates on genetic variability, microsatellite loci can provide a powerful means to assessing parentage and kin relations among individuals (Luikart and England 1999). The method of assigning individuals to parents with exclusion equations is a function of the number and frequency of alleles at a locus (assuming all candidate parents are sampled). While the average exclusion probabilities with or without the genotype of a known parent are calculated differently, (Chakravarkti and Li 1983; Marshall et al. 1998), all exclusion probabilities are generally maximized when there are numerous alleles at relatively equal frequencies at the locus (Evett and Weir 1999). When several unlinked loci are used, the total exclusion probability is the complement of the product of the single-locus inclusion probabilities; that is, the total exclusion probability is one minus (i.e., the opposite of) the combined probability of the set of loci to include a random individual (Evett and Weir 1999; Marshall et al. 1998). Exclusion equations rely on allele frequencies, not genotype frequencies, to assign parents to offspring (Evett and Weir 1999); for this reason, locus 4 can still contribute some information to parent-offspring relationships. As Table 2.2 shows, the exclusion probabilities for locus 4 fall within the range of the other loci, although samples typed at this locus should be checked for the potential for null alleles. The seven loci genotyped above can reliably exclude a random individual from parentage with a probability of 95%, when the other parent is unknown. If there is a known parent that is genotyped, the probability of reliably excluding a random individual from parentage is 99%. Overall, the above data suggest that a number of population genetic (e.g. substructure, effective population size) and genealogical (e.g. reproductive success, kinship) parameters can be reliably estimated from the sifaka population at Beza Mahafaly using these loci.

Table 2.1. Information on primer sequences, sample sizes, reaction conditions, and locus properties for the 16 microsatellite loci isolated in this study.

Primer	Sequence (5' → 3')	(n)	Size (bp)	no. of alleles	no. of repeats (type)	Temp.
P.V. 1 F	GTTTCTTTTTCTTGCAGC	228	156-174	10	CA-17 (P)	54 C
P.V. 1 R	CTTCTCTGGCTTCACATC					
P.V. 2 F	GAAGGTAAGTTTTCTGGCAG	16	273-289	4	CA-15 (I)	58
P.V. 2 R	AGTGTTTTATCGTATGGATGC					
P.V. 3 F	GAAAGAAATGCTAGACCTAGAACGC	16	409-423	9	CA-12 (P)	54 C
P.V. 3 R	GGGATCAGGACTTCAACATACTGC					
P.V. 4 F	TCATTAGTGCCACGCAGTATGG	208	296-339	7	CA-15 (I)	57 C
P.V. 4 R	TGGAAGAACACGCTGACGACAG					
P.V. 5 F	CCCTTCTTCTCTCTGTGAGTGG	16	266-274	5	CA-16 (P)	55 C
P.V. 5 R	TTGGGTTTGCTGCTGTCCTG					
P.V. 6 F	CAAGTGCTAGTCTAAACCTGGGTG	258	260-278	10	CA-21 (P)	55 C
P.V. 6 R	CACAGAAGCCTGATGTAACAACAG					
P.V. 7 F	TTCTCCCACTACTGAGCGAG	16	253-261	4	CA-13 (P)	55 C
P.V. 7 R	TCTGGAGGGCTGGAACAAAG					
P.V. 8 F	CTCAAAGACATTTTCCTTCAGCC	241	211-227	6	CA-16 (I)	53 C
P.V. 8 R	TTTCTACTCACCCCACAGTCATTAG					
P.V. 9 F	TTTCCTCCTCCAGGGAGTCCAAAC	16	222-226	2	CA-12 (P)	58 C
P.V. 9 R	GGACATCTGCACCATTGACCTAAC					
P.V. 10 F	ACGACCAACCCTATCTCTTAAAC	16	237-241	3	CA-11 (I)	50 C
P.V. 10 R	TGTCTTAGGATTGCGTGGG					
P.V. 11 F	GGAAGGGATTTGGGTACACAGAGAG	16	334-338	3	CA-9 (I)	58 C
P.V. 11 R	CATTCGTGGAGGTCAGTTCCATC					
P.V. 12 F	GCCCCTAATAATTTGAGCCAC	16	334-353	6	CA-8 (I)	53 C
P.V. 12 R	ATCAAGCTGCTGTCCAACAAGCCC					
P.V. 13 F	CCTGTGTATGAATCGCAAAGGCAAG	16	229-235	4	CA-15 (P)	57 C
P.V. 13 R	GCAGAGAAGAGTAGGTGAAAGGAAG					
P.V. 14 F	GGCTCAAGACTGATGCTTCAGGTC	241	301-325	11	CA-20 (P)	60 C
P.V. 14 R	GTTTCCAATAGGACAATCACTGGC					
P.V. 15 F	CCTTCATTCCTTTTCATTTCTTGG	227	247-267	11	CA-16 (P)	50 C
P.V. 15 R	TTTTGTATTAGACTAAGCTGCC					
P.V. 16 F	TGAGGGTGGTGAGCTTTAGC	243	270-293	10	CA-15 (P)	55 C
P.V. 16 R	GGGCTGGGGAAAAAATATAAC					

(n) = number of animals genotyped at this locus; (P) = pure repeat; (I) = interrupted repeat.

Table 2.2. Population genetic and genealogical information for the 7 loci genotyped on a minimum of 200 animals.

Locus	k	Het (O)	Het (E)	Excl (A)	Excl (B)	Null alleles
P.V. 1	10	0.706	0.753	0.367	0.550	0.0317
P.V. 4*	7	0.659	0.768	0.367	0.546	0.0715
P.V. 6	10	0.729	0.781	0.401	0.581	0.0322
P.V. 8	6	0.618	0.628	0.219	0.382	0.0095
P.V. 14	11	0.722	0.734	0.348	0.532	0.0072
P.V. 15	11	0.749	0.750	0.365	0.546	-0.0005
P.V. 16	10	0.749	0.814	0.453	0.629	0.0416

Mean number of alleles per locus: 9.29
Mean observed heterozygosity: 0.705
Mean expected heterozygosity 0.747
Total exclusionary power (no parent known): 0.957
Total exclusionary power (one parent known): 0.996

k = number of alleles; Het(O) = observed heterozygosity; Het(E) = expected heterozygosity; Excl (A) = the exclusion probability of the locus when no parents are known; Excl (B) = the exclusion probability of the locus when one parent is known; (*) = deviates from Hardy-Weinberg expectations.

Table 2.3. Mean observed and expected heterozygosities estimated from microsatellites loci for selected wild primate populations.

Species	Het (O)	Het (E)	No. of loci	*n*	Reference
Pan troglodytes spp.	0.73	0.78	8	25-28	Reinartz et al. 2000
Pan paniscus	0.52	0.58	28	14	Reinartz et al. 2000
Gorilla gorilla gorilla	0.41	0.76	8	8-31	Clifford et al. 1999
Macaca sinica	0.76	0.73	4	268	Keane et al. 1998
Macaca sylvanus	0.53	0.65	6	159	Von Segesser et al. 1999
Eulemur rubiventer	0.47	0.64	7	28	Merenlender 1993
Eulemur fulvus rufus	0.64	0.64	9	49	Merenlender 1993
Cheirogaleus medius	0.74	0.77	7	131	Feitz et al. 2000
Propithecus verreauxi	0.71	0.75	7	>200	this study

Het (O) =average observed heterozygosity; Het (E) = average expected heterozygosity; *n* = number of individuals genotyped.

CHAPTER 3

REPRODUCTIVE SUCCESS, REPRODUCTIVE STRATEGIES AND FITNESS IN MALE WHITE SIFAKA (*Propithecus verreauxi verreauxi*)

INTRODUCTION

Group-living is thought to evolve when the fitness of individual animals is enhanced by associating with other conspecifics. For most mammalian species such associations may not be permanent or typical, but for the majority of primate species the stable bisexual social group is a demographically important unit of social organization (cf., Sterk et al. 1997; van Schaik 2000; Cowlishaw and Dunbar 2000). Gregariousness provides collective benefits in terms of safety from predators, resource monopolization, and associations with kin, “friends”, and potential mates (Wrangham 1980; 1987; van Schaik 1983; Janson 1992; Palombit et al. 1997; Silk 2002a;). Nevertheless, despite the benefits to group living, members of social groups must compete with each other for access to mates, fertilizations, and food (Andelmann 1986; Smuts 1987; Janson 1988). It is the distribution and abundance of these fitness critical resources—mates, fertilizations, food—that shape membership and mating patterns within groups. While the etiology of group formation is largely a function of female spatial dispersion, the mating system results from the interaction of male and female reproductive strategies (Clutton-Brock 1989b; Davies 1991). Both sexes are expected to behave in ways that maximize their fitness within a group, yet reproductive strategies differ fundamentally due to differential investment in resources allocated to reproduction (Trivers 1972; Clutton-Brock 1991).

Male primates, like other mammals, have higher rates of gamete production and lower levels of parental care than females (Clutton-Brock and Parker 1992). This means that the number of males ready to mate always exceeds the number of available mates. Because of this, males in most primate species tend to engage in behaviors that maximize mate acquisition rather than offspring care (Clutton-Brock 1991). The lack of available females and surplus of reproductively active males can create potentially high variance in male reproductive success (e.g., elephant seals; Le Boeuf and Reiter 1988). Variance in lifetime reproductive success is a function of a diverse array of selection pressures (and chance events) that act on different periods of the breeding careers of males (Sutherland 1985a; Clutton-Brock 1988). Male mating strategies are thus likely to be adaptively diverse, and observations of males in many primate species indicate that males pursue various behavioral strategies to increase access to mates and to increase exclusivity. These strategies include a variety of direct and indirect mate acquisition tactics, such as physical aggression with rival males, alliances with cooperative males, “friendships” with particular females, consortships, and surreptitious or “sneaky” mating tactics (van Schaik 1996; Kappeler 1999; Pereira et al. 2000). Because individual primate social groups do not exist in isolation, but are parts of a larger network of social groups (i.e., a population), individual males may also seek reproductive opportunities in adjacent groups—that is, males can seek extra-group fertilizations (EGFs). Thus, additional mating opportunities for adult males can be achieved during periods of intergroup contact and solitary visits to neighboring groups (cf., Rowell and Chism 1986; Cheney 1987; Manson 1992; Chism and Rogers 1996; Launhardt et al. 2001).

Extra-group fertilizations have been thoroughly documented for numerous bird species, especially in relation to monogamous social systems (i.e., called "extra-pair fertilizations" or EPFs) (Gowaty 1985; Westneat et al. 1990). However, there has been comparatively little research on the opportunities and genetic consequences of extra-group reproduction in primate species. Studies conducted on gibbons (Palombit 1994) and fat-tailed dwarf lemurs (Feitz et al. 2000) have found high rates of extra-group mating and show how EGFs can strongly influence on variance in male reproductive success in monogamous species. Even fewer studies examine how EGFs influence mating or reproductive success in multi-male, multi-female groups. In these species, resident male reproductive sovereignty can be compromised by influxes of non-resident males (e.g., blue monkeys, Cords et al. 1986; patas monkeys, Ohsawa et al. 1993; rhesus macaques, Berard et al. 1994; patas monkeys, Chism and Rogers 1997; toque macaques, Keane et al. 1997; Hanuman langurs, Launhardt et al. 2001; alaotran gentle lemurs, Nievergelt et al. 2002). EGFs can have different effects on population-wide variance in male reproductive success, but the overall effect for polygynous species is that variance in male reproductive success will be reduced when females mate with non-resident males (Webster et al. 1995). Variation in paternity is a key factor in creating opportunities for sexual selection and influencing effective population size (cf., Arnold and Wade1984a; Nunney 1993); therefore, determining how both within- and between-group reproduction influence variation in male lifetime reproductive success is important.

The behavioral, demographic, and life history factors contributing to the variance in male reproductive output must be determined in order to understand how directional selection has acted, or can act, on male phenotypes. The total amount of variation in fitness is proportional to the total opportunity for selection (Crow 1958; Arnold and Wade 1984a; b). By extension, one can decompose total fitness into components of variation to see how these contribute to total fitness. Those components showing the highest standardized variance present the largest opportunities for directional selection to operate (Crow 1958; Clutton-Brock 1988). Important components of fitness for primates include reproductive life span, fertility, and offspring survival (e.g., Cheney et al. 1988; Altmann et al. 1988).

The objective of this chapter is to determine the relative contribution of different fitness components to total fitness for males in a gregarious primate species. Because social groups in gregarious species often interact—potentially providing an additional source of reproductive opportunities—we partition male fitness into within-group and extra-group components. Our study species is a population of wild lemur, the white sifaka (*Propithecus verreauxi verreauxi*) that inhabits the dry forests of southwest Madagascar. White sifaka form stable social groups of about six animals that contain adult males, females, subadults, and dependent young. This is an ideal study species to investigate the effects of within and extra-group reproductive success on male fitness. Sifaka have a brief, six-to-eight week mating season in which males make forays into adjacent social groups to seek mating opportunities (Richard 1992; Richard et al. 1993; Brockman 1999). Additionally, Lawler et al. (in press) have determined that each year a fraction of the offspring born into social groups are sired by non-resident males.

Drawing on previous studies of paternity, demography, and life history evolution (Richard et al. 1993; 2002; Lawler et al. in press), we investigate the sources of variation that contribute to male fitness. In particular, we examine how reproductive lifespan, fertility and offspring survival contribute to within and extra-group variance in fitness in this population.

METHODS

Population data

The white sifaka population has been studied continuously for the last 18 years at Beza Mahafaly Special Reserve, southwest Madagascar. Information about the study site and regional habitat can be found in Richard et al. (1991; 2002). On-going research focuses on life history, demography, behavior, reproductive endocrinology, and population genetics (Richard 1992; Richard et al. 1991; 1993; 2000; 2002; Kubzdela 1997; Brockman 1999; Brockman et al. 2001; Lawler et al. 2001). Individual animals are captured, individually marked (with numbered tags and color-coded collars), measured, and released back into the wild. During the capture period, morphometric data and tissue samples are collected from each animal (see Richard et al. 1991). As of July 1999 there were 280 animals in the population residing in about 51 social groups. Groups range in size from 2-13 animals with a mean of 6.5 animals. Yearly and monthly census data yield information on population size, numbers of social groups, group composition (sex and age), transfers of individuals, disappearances, deaths, and births.

Parentage analysis

Seven polymorphic microsatellite loci were isolated and screened in this population in order to determine paternity. Chapter 2 gives information on DNA extraction methods, locus characteristics, and genotyping. The probability that these seven loci exclude a random individual from parentage is 99% when one parent is known and 96% when neither parent is known (Lawler et al. 2001). Parentage analysis was performed in Cervus 2.0 (Marshall et al. 1998). We assumed that 90% of all potential sires were sampled and that errors between parent and offspring genotypes at a particular locus occurred at a frequency of 0.015. Confidence levels for paternity assignments were set at 80% and 95%. The youngest age at which male sifaka have been observed to engage in sexual activity is 3 years (Richard et al. 2002). Based on these data and using information on ages of individual animals (known or estimated; Richard et al. 1991; 2002), we analyzed all potential sires against all potential offspring under the restriction that they be separated by at least three years in age. We found no sires that were three or four years old; therefore the data were reanalyzed with a five-year age separation. After paternity was assigned, census data were used to identify the social group in which each sire resided during the time when his offspring was conceived. When the sire's social group matches the social group into which he sired an offspring, we refer to the sire as a *resident* sire. When the sire was not a resident of the social group into which he sired an offspring, we refer to the sire as a *non-resident* sire. In some cases, group membership information for the sire was not available during the exact year in which the offspring was born and thus residency was inferred from subsequent years of census data.

Fitness estimation and components of fitness

Our measure of fitness for this study was lifetime reproductive success (LRS). LRS is widely used as a proxy for fitness in studies of wild populations (e.g., Clutton-Brock 1988). LRS has some limitations (e.g., it is insensitive to the timing of reproduction and also inapplicable under non-equilibrium conditions; Stearns 1992; Caswell 2001). However, for slowly-maturing mammals such as primates, collecting data on age-specific reproduction over many generations and environments can be difficult (cf., Brommer et al. 2002). Additionally, numerous studies have found that LRS is a major determinant of rate-sensitive measures of fitness (McGraw and Caswell 1986; Brommer et al. 2002). In what follows, we equate "total fitness" or "fitness" with LRS.

Following the conventions of Clutton-Brock et al. (1988) and Cheney et al. (1988), we decompose male LRS (i.e., male fitness) into three multiplicative components: reproductive lifespan (R), fertility (F), and offspring survival (S). Reproductive lifespan is defined as the number of years a male has survived past reproductive maturity. Based on paternity data, reproductive maturity begins at age 5. Fertility is calculated as the number of offspring sired by each male divided by his reproductive life span—this can be thought of as the expected number of offspring produced per year by each sire. Offspring survival is the proportion of offspring surviving to the age of 5.

Using the above definitions, total male fitness (T) in a non-subdivided population can be described by the equation,

$$T = R^*F^*S \tag{1}$$

and variation in total fitness can be expressed as the product of its variance components,

$$\mathrm{Var}(T) = \mathrm{Var}(R^*F^*S) \tag{2}$$

Because our sifaka population is divided into social groups, population subdivision adds opportunities for male fitness to be enhanced by mating outside the social group. Males can pursue within group fertilizations and extra-group fertilizations within the same mating season. Therefore, total fitness (*T*) must first be partitioned into two additive components that correspond to reproductive success within a group (*W*) plus reproductive success outside the group (*O*) (Webster et al. 1995). Because these two components do not represent independent episodes of selection, reproduction accrued within and outside the group can be expressed additively as

$$T = W + O \tag{3}$$

and, as in equation 2, variance in total fitness can be expressed as

$$\mathrm{Var}(T) = \mathrm{Var}(W) + \mathrm{Var}(O) + 2\,\mathrm{Cov}(W, O) \tag{4}$$

The variance components of within and outside sources of fitness are determined by the variation in male propensities to survive and sire viable offspring within and outside their own social group, that is, by *R*, *F*, and *S*. Recalling equation 2, we can then write

$$\mathrm{Var}(W) = \mathrm{Var}(R_w{}^*F_w{}^*S_w) \tag{5}$$

and,

$$\mathrm{Var}(O) = \mathrm{V}(R_o * F_o * S_o) \tag{6}$$

and substituting equations 5 and 6 into 4, we get

$$\mathrm{Var}(T) = \mathrm{V}(R_w * F_w * S_w) + \mathrm{V}(R_o * F_o * S_o) + 2\,\mathrm{Cov}(R_w * F_w * S_w\,,\, R_o * F_o * S_o) \tag{7}$$

Equation 7 represents the total decomposition of fitness based on contributions of R, F, and S derived from reproduction within and outside the social group. This approach to fitness decomposition follows that of Webster et al., (1995), who draw from the statistical work of Bohrnstedt and Goldberger (1969). The R, F, and S, components are functions of their mean values, which allows for the use of longitudinal data (Bohrnstedt and Goldberger 1969). For males siring all offspring *within* their social group, variation in R, F, and S contributes only to the $\mathrm{Var}(W)$ and $\mathrm{Cov}(W, O)$ terms. For males siring all offspring *outside* their social group, variation in R, F, and S contributes only to the $\mathrm{Var}(O)$ and $\mathrm{Cov}(W, O)$ terms. For males that sired offspring both within and outside their social group, variation in R, F, and S contributes to both the $\mathrm{Var}(W)$ and $\mathrm{Var}(O)$ as well as $\mathrm{Cov}(W, O)$ terms.

There are some limitations to our use of R, F, and S. Because many of the animals in our sample are still alive, reproductive lifespan and fertility provide an incomplete picture of male survivorship and fertility. In our sample, there are 97 males who were dead in 2001 and 114 males who are alive in 2001. However, there were no significant differences in offspring production between males that were born (or matured during the study) and that died before the study ended (thus encompassing a full lifetime), and those that are still alive (encompassing a portion of their lifetime) (chi-square = 4.884, df = 6, p = 0.5588). This indicates that pooling alive and dead animals will not seriously bias estimations of fertility or a male's opportunity to sire offspring (i.e., his reproductive lifespan). Offspring survival is calculated as the proportion of offspring that survive until age 5. This is an underestimate because offspring mortality is high in the first year of life; on average, 52% of infants survived the first year of life, but there is wide variation from year to year (Richard et al. 2002). Offspring are not captured and collared until after their first year of life. In this regard, "offspring survival" (*S*) actually represents the number of *yearlings* reaching age five, minus the "invisible fraction" that have died prior to capturing (cf., Grafen 1988).

RESULTS

Parentage analysis

The distribution of paternity in the population is given in Figure 3.1. As is evident, the majority of adult males in our sample did not sire offspring (138 non-sires out of 211; it should be kept in mind that some of the "non-sires" may have sired offspring that we died before we could capture them). Mean number of offspring per male was 0.6966 with a variance of 1.56. Among the sires, 29 males sired offspring within their resident group, 24 males sired offspring outside their resident group, and 20 males sired offspring both within and outside their resident group. Confidence values for paternity assignments are presented in Figure 3.2. Confidence in paternity assignments ranged from 83% to 98% with a mean of 86.9%. A t-test on the mean confidence value indicated that it was significantly different from 80%—the lowest conventionally accepted value used in the literature (e.g., Coltman et al. 1999) ($t = 21.83$, $df = 147$, $p = 0.000$). Paternity was checked against census and location data to provide a *post hoc* check of sire-offspring relationships. Sires were either within or adjacent to the social group into which they sired the offspring and no sire was geographically distant from the group at the time of conception. This finding matches behavioral observations of mating behavior and movements of adult males in the population: males tend to mate within their own group and/or in an adjacent group (Richard 1992; Richard et al. 1993).

Components of fitness

Average values of the fitness components are listed in Table 3.1. The average reproductive lifespan of a male in this population is around 8 years. On average, sires produced the equivalent of 0.15 offspring per year. Offspring survival was 0.70 for resident sires and 0.86 for non-resident sires. There were no significant differences between R_w and R_o, between F_w and F_o, or between S_w and S_o.

Variance components of fitness are listed in Table 3.2. Included in this table are the absolute values, standardized values, and percentage contribution to total fitness. Standardized values are the absolute values weighted by specified coefficients (cf. Bohrnstedt and Goldberger 1969) and then divided by the squared mean of total fitness. The percent contribution represents the proportionate amount that the standardized value contributes to total fitness. "D" is a remainder term that captures how the higher order moments of the multivariate distribution contribute to the total variance. D also absorbs any remaining variance because the total variance is not a straightforward sum of component variances and covariances (cf., Webster et al. 1995). Table 3.2 is broken down into "within-group" sources of variation, "outside-group" sources of variation, and "within/outside-group" sources of variation. Variation in within-group fitness components explains 46.29% of the total variation in fitness. Variation in fitness from extra-group components accounts for 36.88% of total fitness. The covariance between these two components accounts for about 8% of total fitness. Fitness components both within and outside the group are further broken down into reproductive lifespan, fertility, and offspring survival. Among these three multiplicative components, variation in reproductive lifespan contributes the most to total fitness for both within and outside sources of variation (R_w = 20.15%, R_o = 33.17%), followed by fertility (F_w = 12.90%, F_o = 19.74%) and offspring survival (S_w = 11.01%, S_o = 13.32%). The percentage effect of a particular component can be thought of as the contribution made to total fitness when all other terms are held constant. For example, R_o contributes 33% to total fitness; therefore, total fitness would have a variance that is only 33% of its total variance if R_o was the sole contributor to fitness (Brown 1988). Covariance terms reflect the joint interaction of the multiplicative components and have a similar interpretation.

Figure 3.3 examines in more detail two of the covariance relationships in Table 3.2. This figure depicts reproductive lifespan plotted against fertility for resident sires (Figure 3.3A) and non-resident sires (Figure 3.3B). The majority of the data points show a significant negative trend in both graphs, indicating that as reproductive lifespan increases reproductive rate decreases. This relationship demonstrates only that the per-year expectation of siring an offspring decreases with age [the same relationship was found for Cov(F_w, R_o)]. Figure 3.4 shows an overall positive relationship between reproductive lifespan and total number of offspring produced by males (F = 29.8446, df = 210, p = 0.0001). This indicates that longer-lived males have, on average, higher fitness than shorter-lived males, even though older males have lower average reproductive rates than younger males. Two outliers in Figure 3.4 influence the slope of the line; however, when excluding these outliers, the overall relationship remains positive and significant (F = 27.0061, df = 208, p = 0.0001). In Figure 3.4, we use the total number of offspring (on the *X*-axis) to predict the *expected* value of reproductive lifespan (on the *Y*-axis). [Normally, one would assume number of offspring to be dependent on reproductive lifespan, in which case the axes should be switched]. In this sense, Figure 3.4 does not reflect the dependence of *Y* on *X*, but gives the expected values for *Y* (those values that fall along the regression line) given the set of *X* values (Sokal and Rohlf 1995). Other relationships among covariance terms were not statistically informative. Offspring survivorship did not depend on a sire's longevity or fertility. The total covariance, Cov(*W*, *O*), is relatively small and therefore the individual "within/outside" terms will not be emphasized below.

DISCUSSION

Reproductive lifespan and the opportunity for selection

A comparison of the relative contributions of fitness components to total fitness can point to those likely to be targets of selection. Within a single episode of selection, those fitness components showing the highest heritable variance provide the greatest opportunity for selection to modify them (Crow 1958). However, when components of fitness are average values taken over a whole lifetime, they only provide a rough approximation to the total opportunity for selection (Brown 1988). This is because chance events (i.e., non-selective forces) also contribute to the variation in fitness components; therefore, the variation exhibited by each component will not be directly proportional to the opportunity for selection (cf. Grafen 1988). Nevertheless, partitioning fitness remains helpful in identifying how much variation characterizes each component and how much each component contributes to total fitness. It also sets up the possibility for future studies to examine the sources of variation for each component. For example, how much of the variation in reproductive lifespan can be related to mortality induced by droughts (i.e., environmental variation) and how much can be related to mortality induced by male-male mate competition (i.e., intrasexual selection)? Also, if we assume that chance events affect each fitness component with equal probability, then we can make comparative statements about the opportunity for selection among them (Clutton-Brock 1988).

Reproductive lifespan contributes a significant proportion of variation to total fitness among male sifaka at Beza Mahafaly. This is the case for males who reproduce within-groups and for males who reproduce outside their resident group. Reproductive lifespan can be viewed as the "per-year opportunity" that a male has to increase his lifetime reproductive success (Clutton-Brock et al. 1988). Reproductive lifespan is positively related to the number of offspring produced in a lifetime, indicating that longevity has an impact on fitness. Figure 3.4 shows a plot of reproductive lifespan plotted against number of offspring produced by males in their lifetime. Recall that reproductive life span plus 5 years equals age (i.e., RLS + 5yrs = age). Values that fall along the regression line can be interpreted as the expected age of those sets of males who have sired zero, one, two, three...nine offspring in their lifetime. For example, those sets of males having sired 1 offspring in their lifetime have an average age of 14 years; those siring 2 offspring during their lifetime have an average age of 15 years, and males having sired 3 offspring have an average age of 17 years. There is much variation around these values, but the overall trend is positive. On average, those males who survive into later years are also expected to sire more offspring. Age-specific mortality rates of males are relatively stable between the ages of 5 and 11 years (about 8%), but after the age of 12, age-specific mortality rates steadily increase (Richard et al. 2002). Every year past the age of 12, a male has an additional opportunity to sire an offspring, but the probability that he will do so declines (i.e., fertility declines with age, see below). The variation in reproductive lifespan and its effect on opportunities for reproduction is captured by the large contributions of R_w and R_0 to total fitness.

In order to interpret reproductive lifespan in terms of the opportunity for selection, we must make some limiting assumptions. If survivorship is highly heritable and the variation we see in the population is entirely due to differential and heritable viability, then selection would favor those individuals who live longest. Successive episodes of selection would act to increase the mean reproductive lifespan of males. However, reproductive lifespan, as used in Table 3.2, is a summary statement of males born at different times and under different climatic conditions. Because of this, reproductive lifespan does not take into account random factors that affect different age cohorts. Cohorts of males born in different years may be subject to differing food availability, predator susceptibility etc. These factors will influence the total variance in reproductive lifespan in our sample. Therefore, in order to view variation in reproductive lifespan in terms of the opportunity for selection, we would further need to show that the differences in male viability are non-random and can be linked to adaptive differences in foraging effort, predator evasion, etc.

Despite the limitations regarding the prospective opportunity for selection, it is possible to interpret the contribution reproductive lifespan makes to total fitness within the context of life history evolution. Richard et al, (2002) have argued that female sifaka experience a "slowing-down" of life history events. They found that when controlling for body size, female sifaka reproduce later in life and live longer than many other mammal species. Additionally, Richard et al. (2002) provided evidence that southwest Madagascar has unpredictable rainfall patterns which impacts female survivorship and fertility. Due to this, they argued that female sifaka are selected to extend their breeding opportunities across numerous years, or follow a "bet-hedging" strategy. It is likely that this argument also applies to male sifaka as they are equal in body mass to females and males have a relatively late age at first reproduction. Similarly, mortality data indicate that males are equally likely to be aversely affected by unpredictable rainfall patterns (Richard et al. 2002). These conditions suggest that selection may have acted to extend the survivorship of male sifaka into later years. If so, it provides an adaptive basis for the large relative contribution of reproductive lifespan to total fitness in male sifaka. Unfortunately, comparative data are lacking on the relationship between reproductive lifespan and age at first reproduction in male primates. If comparative data show that male survivorship is the largest contributor to total fitness across numerous species, then selection for bet-hedging should not be invoked in male sifaka.

Fertility and the trade-off with survivorship

Figure 3.3 indicates that reproductive rate declines with age. This relationship mirrors a basic theoretical principle in life history theory. Because reproduction is assumed to be a costly endeavor, fertility at every age-class cannot be simultaneously maximized; energy that is devoted to immediate reproduction will not be available for future reproduction or survival (Stearns 1992). Figure 3.3 shows a generally negative relationship between reproductive lifespan and fertility. Fertility is defined as the average rate of offspring production per year. If we assume the data in the figures are a complete depiction of the breeding careers of males (as opposed to an incomplete picture that includes males still alive), then the data indicate an average decline in reproductive rate as males get older. This suggests some sort of trade off between survival and reproduction. Nevertheless, for this to qualify as a physiologically-based, life history trade-off, it is necessary to know if the mortality costs are extrinsic or intrinsic (cf., Stearns 1992). That is, it is necessary to show that energy allocated to reproduction is not subsequently available to contribute to survivorship. Such energetic trade-offs are difficult to measure in wild primate populations.

However, the basis for the trade-off may result from agonistic contests among males during the mating season. If the trade-off hinges on yearly costs accrued by males investing in male mate competition, then males who invest more energy in each mating season may suffer from an energy deficit in non-mating season months. If these yearly energy deficits are not recouped after each mating season, they could have negative consequences for future survivorship (cf. Clutton-Brock et al. 1983). To test this possibility it is necessary to demonstrate that, relative to less combative males, aggressive males sire more offspring and die at younger ages. Observations of male behavior during the mating season provide indirect support for this idea. Sifaka males vary in the amount of effort put into intrasexual aggressive mate competition. Aggressive mate competition involves physical combat as well as extended episodes of chasing, lunging, and other activities related to endurance (Richard 1992; Brockman 1999). An analysis of paternity demonstrated that correlates of reproductive success include body size and indices of limb muscle mass. All sires have larger body mass and larger muscle mass in their limbs than non-sires (cf. Chapter 4). If aggressive sires rely on energy reserves stored in muscle tissues, then repeated mating contests will deplete these energy reserves. This phenomenon may provide the proximate mechanism for the trade-off between reproductive effort and survivorship.

Males mating outside their resident groups have a steeper trade-off between reproductive rate and reproductive lifespan than males who mate within groups (Figure 3.3). Two possibilities may account for this result. First, males who mate within their resident group may engage in less contest mating competition due to the operation of female mate choice. In some sifaka groups, females exhibit positive mate choice towards the resident male indicated by proceptive behavior of females toward particular males (Richard 1992; Brockman 1999). Second, males who mate outside the group may engage in more contest competition than males who mate within the group. Behavioral observations have shown that non-resident males attempting to enter an adjacent group are aggressively challenged by resident males (Richard 1992; Brockman et al. 1998; Brockman 1999). Some visiting males fight with resident males and subsequently mate with resident females (Brockman 1999). If males who reproduce outside the group incur greater reproductive costs that affect their future survival, this would explain why the percentage contribution made by R_o to total fitness is larger than the contribution made by R_w. The absolute variance in reproductive lifespan and fertility is similar for males who reproduce within groups and those who reproduce outside of their group (Table 3.2). However, given the more pronounced trade-off in fertility and survivorship in non-resident males, their fitness depends more on their ability to obtain fertilizations outside the group over many years. Figure 3.3 also reveals that a few males "escape" the trade off between longevity and fertility and maintain high reproductive rates to relatively old ages. It would be interesting to investigate how much aggression these males engage in during the mating season. Do these "outliers" represent males who are skillful fighters, males who are always "chosen" by females, males who are intrinsically viable, or some combination of these factors?

Offspring survival, climate, and infanticide

Of the three multiplicative fitness components, offspring survival makes the lowest percentage contribution to total male fitness. Offspring mortality is most likely caused by random climatic factors and differences in maternal experience and condition. Richard et al. (2002) found that, on average, only 52% of infants survived until 1 year of age. There is much variation around this average and a major drought in 1992 reduced infant survival to around 33%. Most infants are weaned after about 6 or 7 months, indicating that for about half of their first year of life, they depend on their mother. Longitudinal records indicate that females who gave birth to surviving offspring in previous birth seasons were as likely to continue to have viable offspring in subsequent birth seasons (Richard et al. 2002). The conditions contributing to successful maternity have been linked to differences in female body mass (Richard et al. 2000). *Male sifaka contribute negligible amounts of paternal care (Richard 1976).* Infanticide has been observed in the sifaka population but it is difficult to reconcile infanticidal behavior with variation in offspring viability (cf. Richard et al. 2002). The relatively small contribution of offspring survival to total male fitness is probably due to the fact that—relative to climactic factors and maternal condition—males play a minimal role in influencing the viability of the offspring they sire. Nevertheless, recent theoretical work indicates that females should choose mates who sire offspring with high reproductive value (Kokko et al. 2002). Females are expected to select mating partners based on their ability to sire offspring of high genetic quality. Further analyses are required to determine how genetic contributions from males influence offspring viability.

The impact of extra-group fertilizations

The distribution of male reproductive output in primate populations is contingent on numerous factors. From the male's perspective, reproductive opportunities are influenced by the number of other adult males and females within the social group, mechanisms maintaining priority-of-access to mates (e.g., fighting ability), and the opportunity for alternative reproductive strategies, including extra-group fertilizations. Genetic studies documenting the impact of EGFs on variance in male reproductive success are scarce for wild primate populations (cf. Keane et al. 1997; Ohsawa et al. 1993; Feitz et al. 2000; Launhardt et al. 2001; Nievergelt et al. 2002; Vigilant et al. 2001). In a study of wild toque macaques (*Macaca sinica*), Keane et al. (1997) found that 11% of the infants born into social groups were sired by non-resident males. Ohsawa et al. (1993) examined paternity in the seasonally breeding patas monkeys (*Erythrocebus patas*) over a two year period. Although their sample size is limited, Ohsawa et al. (1993) determined that during periods of male influxes, 50% of the offspring in some groups were sired by non-resident males. Launhardt et al. (2001) assessed paternity in a wild population of langurs (*Semnopithecus entellus*) in southern Nepal. They found that resident males sired all the offspring within uni-male groups, but that in multi-male groups, 21% of all offspring were sired by non-resident males.

These studies attest to the idea that there is not always a direct correspondence between the social unit and the reproductive unit (cf. Richard 1985b). The socio-sexual and demographic conditions that facilitate EGFs vary between these species. However, variance in male reproductive success clearly can be shaped by males obtaining fertilizations outside their resident group. In our population, resident and non-resident sires were equally likely to sire offspring. We hypothesize that several important factors facilitate the opportunity for EGFs in sifaka. One factor is female mate choice. During the mating season, female sifaka mate with resident and non-resident males. However, individual female mating patterns are not indiscriminate and females exhibit positive and negative mate choice during the mating season (Brockman 1999). Additionally, females have been observed to "call in" males from adjacent groups by lost-calling. Determining which aspects of male behavior and phenotype females use as cues for mate choice is important for understanding why certain males may obtain EGFs and others do not. Females may seek non-resident males to conceal paternity. Such a strategy may preempt non-resident males from entering the female's group and committing infanticide (Brockman and Whitten 1996); this possibility has also been suggested for langurs (Launhardt et al. 2001; cf. Pereira and Weiss 1991). Also, female sifaka precipitate visits and subsequent fights among resident and non-resident males to assess male vigor. Overall, female mating preferences vary from group to group. Some sifaka groups remain stable through out the mating season with no incursions of non-resident males; others are characterized by frequent aggression and are unstable, and often receive visits from non-resident males (Richard 1992; Brockman 1999). The basis for group stability during the mating season is not known, but may relate to females in stable groups directing mating opportunities solely to one or a few "chosen" males (Richard 1992).

A second factor that may facilitate EGFs is the degree of home range-overlap among social groups. If we view extra-group reproduction as a very brief, non-permanent, dispersal event, we can assess the costs and benefits for males who leave their resident group in search of reproductive opportunities. Many studies have documented the costs a resident animal incurs by leaving its resident social unit (cf., Alberts and Altmann 1996 for baboons; Belichon et al. 1996 for general review). Individual dispersers, when away from familiar conspecifics or habitat, suffer from reduced foraging efficiency and increased vulnerability to predation. Additionally, these animals may also sustain injuries when trying to gain residence in a new social group (cf. Pusey and Packer 1987). Isbell and van Vuren (1996) have divided dispersal costs into "locational" and "social" components. Locational costs result from leaving a familiar habitat, while social costs are imposed by leaving a familiar social unit and entering a new one. They examined data on dispersal in primates and found that when home-range boundaries overlap, animals are more likely to incur social costs as opposed to locational costs. In our sifaka population, group density is quite high, home range overlap is considerable, and the habitat is relatively homogenous (Richard et al. 1993). This suggests that males suffer few locational (or "ecological") costs from leaving their current home ranges to visit neighboring social groups. The costs males incur by trying to reproduce outside their resident groups are social, reflected in injuries sustained while trying to enter neighboring groups (Richard 1992; Brockman et al. 1998).

A third component that facilitates EGFs is a restricted mating season. A rapid availability of receptive females is associated with visits by non-resident males in macaques and baboons (e.g., Berenstain and Wade 1983). In hanuman langurs and patas monkey, seasonal influxes of non-resident males occur only during the mating season (Borries 2000; Ohsawa et al. 1993; Chism and Rogers 1996). Borries (2000) found that, contrary to expectation, the number of males visiting a social group was not associated with the number of cycling females in the group. In our sifaka population, groups are relatively small and often only a single male visits a social group during the mating season (Richard 1992; Brockman et al. 1998). The relationship between female reproductive status and male visits is variable in sifaka (Brockman 1999; Brockman et al. 1998). For male sifaka, seasonality of mating restricts the time window that males have to increase their fitness. Any resident male that can visit an adjacent group and mate with a female during the mating season will increase his fitness (assuming he is also able to mate in his resident group) beyond that of a non-visiting male. From the perspective of a male, females coming into estrus within this limited time-window can be thought of as an expanding population of reproductive opportunities during the mating season. The "expansion" is a consequence of the seasonal nature of female reproduction. That is, there can be no "expansion" in reproductive opportunities if females exhibit year-round receptivity. Thus males who exploit these expanding opportunities earlier are likely to leave more offspring than males who do not quickly exploit these opportunities. It is easy to see how this strategy of visitation could get started. If the initial population consisted of non-visiting males, any male who visited a neighboring group would obtain a fitness advantage over non-visiting males. If this strategy were heritable (or even learned), it would quickly spread due to the high fitness it confers. Eventually, an equilibrium would be reached because males engaging in too many visits might have their resident reproductive opportunities co-opted by other visiting males. Estrus asynchrony within and between groups will not necessarily influence this scenario, but will only add a variable "encounter-rate" to those males who opt to visit neighboring groups during this period of increasing mate availability.

In this regard, male influxes may not be predicted by female receptivity or immediate socio-sexual cues. Given the degree of home range overlap and variation in female mating preferences, males may have little to lose in monitoring the reproductive status of females in adjacent groups. This is reflected in the large contribution to total fitness made by reproducing outside the group (the "outside-group" variance in Table

3.2). Although it is less than the "within-group" component, ($W > O$), the conditions outlined above suggest that EGFs are worth pursuing. Across our multi-year sample, the numbers of males who obtain EGFs and those who do not were equal. As discussed above, this does not indicate that there are two fixed strategies in our population. The "decision" to engage in EGFs is likely frequency-dependent and will also depend on male condition and social status. Not all males can concurrently leave their resident group in search of EGFs because any single resident male not choosing to do so will have increased access to the resident females.

Table 3.1. Average values of the within-group and outside-group fitness components.

Component	Term	Average value
Within-group reproductive lifespan	R_w	7.96
Within-group fertility	F_w	0.15
Within-group offspring survival	S_w	0.70
Outside-group reproductive lifespan	R_o	7.92
Outside-group fertility	F_o	0.15
Outside-group offspring survival	S_o	0.86

Table 3.2. Decomposition of total fitness into its various components (see equation 7). Total fitness is partitioned into two additive components (within and outside sources of variation). The two additive components are further decomposed into 3 multiplicative terms. Components of fitness are expressed as a standardized value and as percentage contribution to total fitness.

Source of variation	**Term**	**Value**	**Standardized value**	**Percentage of total variance**
Total variance	Var (T)	1.56	3.20	100.00
Total within-group variance	Var (W)	0.72	1.48	46.29
Total outside-group variance	Var (O)	0.57	1.18	36.88
Total covariance of (W, O)	Cov (W, O)	0.13	0.27	8.38
Within-group components	Var(R_w)	28.44	0.77	20.15
	Var(F_w)	0.01	0.46	12.10
	Var(S_w)	0.12	0.42	11.01
	Cov(R_w, F_w)	-0.08	-0.17	-5.70
	Cov(F_w, S_w)	0.00	-0.04	-1.31
	Cov(R_w, S_w)	0.06	0.03	1.00
Outside-group components	Var(R_o)	29.85	1.27	33.17
	Var(F_o)	0.01	0.76	19.74
	Var(S_o)	0.14	0.51	13.32
	Cov(R_o, F_o)	-0.21	-0.91	-23.74
	Cov(F_o, S_o)	0.00	0.07	1.90
	Cov(R_o, S_o)	0.01	0.01	0.19
Within/Outside components	Cov(R_w, F_o)	-0.07	-0.24	-6.17
	Cov(R_w, R_o)	8.14	0.55	14.45
	Cov(R_w, S_o)	0.03	0.02	0.57
	Cov(F_w, R_o)	-0.09	-0.33	-8.47
	Cov(F_w, F_o)	0.00	0.39	10.18
	Cov(F_w, S_o)	0.00	0.01	0.31
	Cov(S_w, R_o)	-0.28	-0.21	-5.54
	Cov(S_w, F_o)	0.01	0.38	10.02
	Cov(S_w, S_o)	0.04	0.30	7.94
Remainder	D		-0.20	-5.12

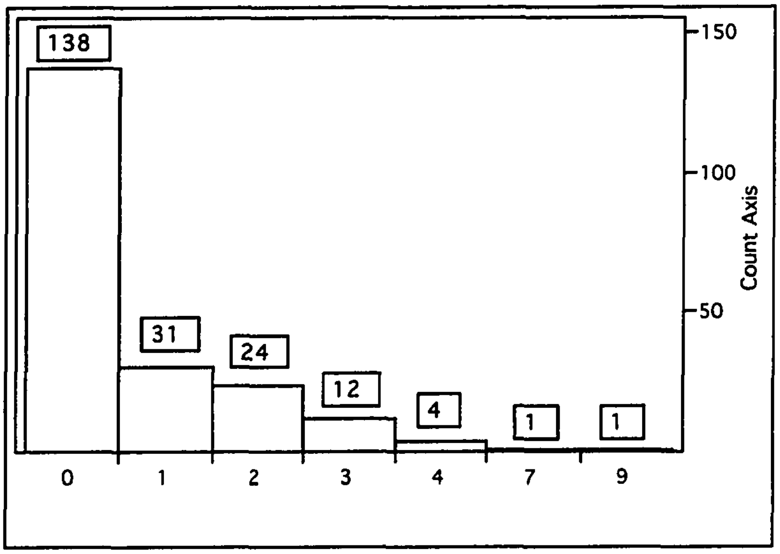


Figure 3.1. Distribution of reproduction among males used in this study. The numbers indicate how many males in our sample sired one offspring, two offspring...nine offspring. Also included is the number of non-reproducing males.

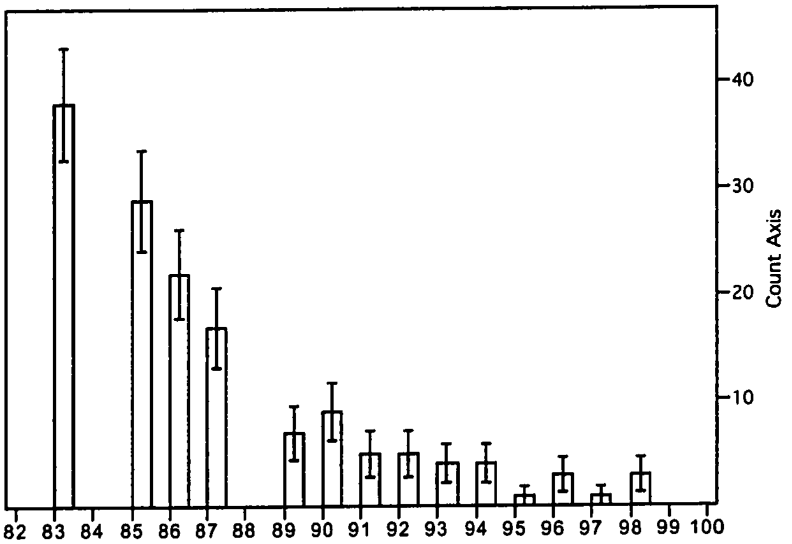
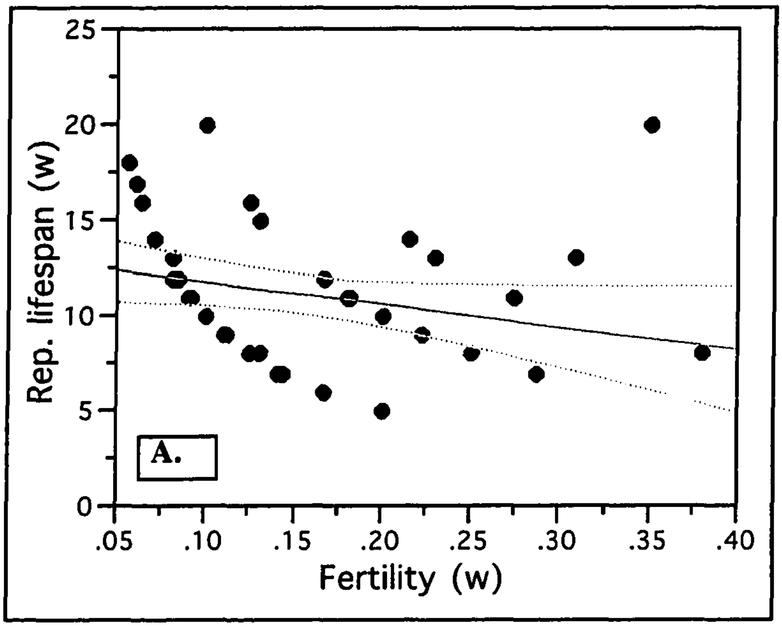


Figure 3.2. Distribution of confidence values for paternity assignments used in this study. The mean confidence value for all assignments was 87%.



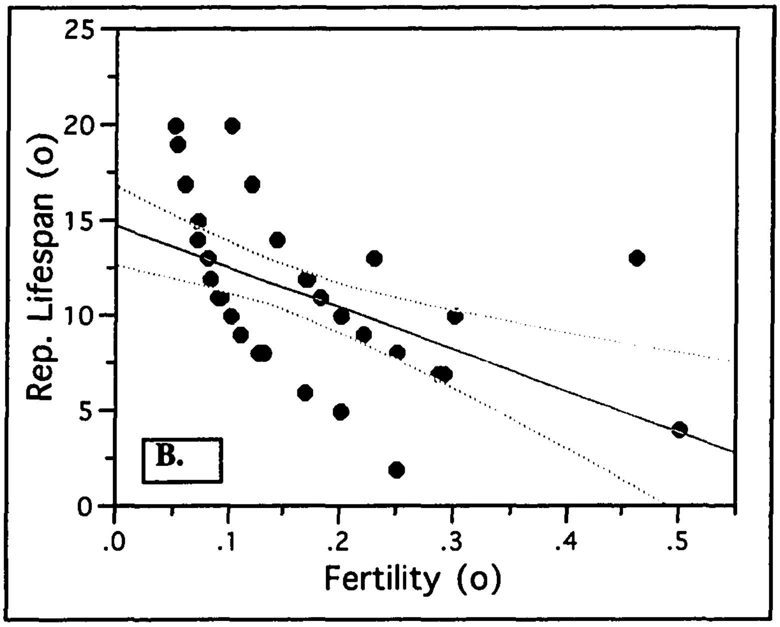


Figure 3.3. The relationship between reproductive lifespan and fertility for males reproducing within groups (A) and males reproducing outside of groups (B). Lines of 95% confidence are shown.

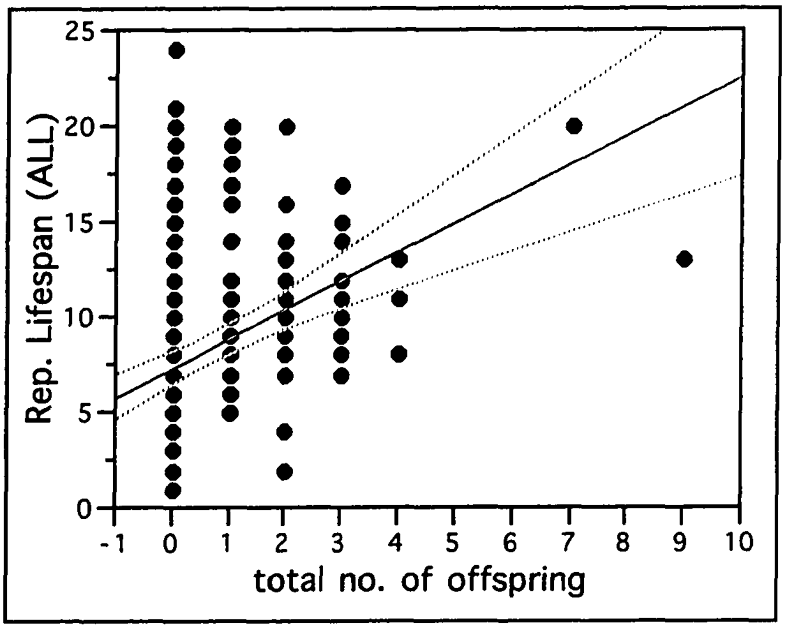


Figure 3.4. The relationship between total reproductive lifespan and total number of offspring produced by males. Lines of 95% confidence are shown. Note the scale on the y-axis starts at negative one.

CHAPTER 4

SEXUAL SELECTION AND CORRELATES OF REPRODUCTIVE SUCCESS IN MALE WHITE SIFAKA (*Propithecus verreauxi verreauxi*)

INTRODUCTION

Because primate males and females differ in physiological investment of reproductive resources, life history schedules, and potential reproductive rates, the manner in which they acquire mates and fertilizations often differs (Dunbar 1983; Smuts 1987; Clutton-Brock 1991; Clutton-Brock and Parker 1992; Plavcan 1999). Reproductive output is a major component of fitness, and much attention has been directed towards understanding the phenotypic factors that affect mating and successful reproduction in males and females. If components of individual fitness are largely determined by conspecifics within the context of mate acquisition and competition then evolutionary change will proceed via sexual selection. Models of sexual selection show that female mating preferences can influence the evolution and expression of male traits and mating strategies (cf. Lande 1981; Kirkpatrick 1982; Iwasa and Pomiankowski 1999). Females are expected to mate with males who possess traits that are linked directly or indirectly to their ability to sire offspring of high reproductive value (Kokko et al. 2002). However, independent of the operation of female choice, particular male features may be differentially selected because they enhance competitive abilities during male-male mate competition. Here, any heritable traits that allow a male to aggressively exclude other males from access to mates will also be subject to selection (cf. Andersson 1994; Maynard Smith and Brown 1986). Taken together, males will compete with other males to increase their access to potential mates, and this can occur separately or commensurately with a female's limited preference for a particular male (Wiley and Poston 1996). Regardless of whether male sexually selected traits are due to female preferences or male mate competition, developing associations between male traits and male reproductive success is an important step in determining the proximate mechanisms of sexual selection.

There is a significant body of theory describing how aspects of the male phenotype influence mate competition and are influenced by mate choice. However, relating particular phenotypes to components of fitness is empirically difficult (cf. Heisler et al. 1987; Price et al. 1987; Andersson 1994). There are several reasons that account for this. First, sexually selected traits—even if one could identify them with certainty—could be variably expressed due to variation in physiological condition and/or seasonal factors. Measuring these variable phenotypes requires long-term information on temporal and/or physiological fluctuations in somatic tissues of individuals. Second, alternative strategies of mate acquisition that bypass overt, aggressive, mate competition can, and often do, evolve (Andersson 1994). Here, even the most obvious and consistently expressed sexually selected phenotypes may not be associated with reproductive output because alternative phenotypes can also reproduce. Third, it is often difficult to isolate sexually selected traits from traits that covary with them. In this case, a trait may not show a strong relationship with fitness because of co-occurring selection pressures. Finally, for long-lived, slow reproducing mammals such as primates, these problems are compounded by the lack of longitudinal data on reproductive success and the factors that determine fitness in wild populations (Wilkinson et al. 1987; Clutton-Brock 1988).

To get around these complications, it helps to have genetic information in conjunction with phenotypic measurements from individually marked animals. With these data, associations can be made between aspects of the phenotype and components of fitness such as survivorship and reproductive success. In this chapter, we examine factors that influence male reproductive success in the Beza Mahafaly sifaka population. Specifically, we test a series of hypotheses regarding the morphological and social factors that show (or are expected to show) a positive or negative correlation with male reproductive success, based on predictions from intra sexual selection theory as it pertains to primates (cf. Plavcan 1999, 2001; van Schaik et al. 1999; Paul 2002). These hypotheses are derived from both comparative and intraspecific studies and are listed in simplified form in Table 4.1. This list is not exhaustive. In particular, it omits social rank and testicular volume, which we will consider in another study. To test these hypotheses, we examine the association between reproductive output and numerous somatic and socio-demographic factors in our population. We show that while there are significant differences between sires and non-sires for particular factors, female choice can dilute intrasexual selection pressures on male phenotypes.

METHODS

Information on the study population and parentage analysis is given in chapter 3. As in chapter 3, we use the parentage data to determine the reproductive status of males in the population—either *sire* or *non-sire*. Our sample size in this chapter is 128 adult male animals, consisting of 82 sires and 46 non-sires. As in Chapter 3, sires are further divided into two classes. Sires that were members of the social group into which they sired an offspring are called *resident sires*, and sires that were not members of the social group into which they sired an offspring are called *non-resident sires*.

Morphometric analysis and reproductive status

Besides body mass, we assessed the effects of eighteen linear somatic measurements and one composite measure derived from these linear measurements on male reproductive status (Table 4.2). Bilaterally symmetric measurements were taken on the left side. The composite measure is *limb shape*, defined as the geometric mean of the circumferences of the upper and lower arms and legs divided by the cube root of body mass. The geometric mean is a standard size proxy; dividing by body mass (devalued by the appropriate root to keep the scales the same) provides a good estimate of shape (cf. Jungers et al. 1995). Body mass fluctuates seasonally in sifaka and certain somatic measurements covary with body mass. To eliminate any biases brought in by seasonal effects, we only used animals captured in November through May. These months correspond to the full wet season (Nov.—Feb.) and most of the early dry season (Mar.—Jun.). Our sample had significantly higher than average body mass in November through May than animals caught in the remaining months (F = 77.36, df = 1, 553, p = 0.0001; also see discussion in Richard et al. 2000). Eliminating samples from the "boundary months", November and/or May, did not alter the results.

Prior to testing for their effect on reproductive status, we performed several transformations on the somatic data to reduce heteroscedascity. Box-Cox transformations proved to be most effective when visualized using normal quantile plots ("Q-Q plots") and are used in all analyses (cf. Sokal and Rohlf 1995). We used analysis of covariance (ANCOVA) to control for confounding variables when examining the relationship of a somatic measurement to reproductive status. We use ANCOVA to develop associations between reproductive status and phenotype. Because both age and body mass covary with the somatic measurements (even in our restricted sample), we used a correlation matrix to determine whether either age or mass had the greater confounding effect based on its correlation score with the somatic measure. For brevity, we will refer to body mass and all linear and composite somatic measures as *traits* or *characters.* ANCOVAs were performed on sires and non-sires as well as on resident and non-resident sires.

Selection gradient analysis

We use ANCOVA to ask the question: Are there differences among sires and non-sires for each character when the differences among sires and non-sires in the confounding variable are taken into account (cf. Sokal and Rohlf 1995: 513)? ANCOVA tells us only about the influence of a trait on a reproductive status (i.e., sire versus non-sire), it does not tell us the influence the trait has on differences in reproductive output among all males (i.e., those males who've sired 2 offspring, those who've 3 offspring, etc.). To assess the effects of male traits on reproductive output, we estimated the gradient or strength of directional and curvilinear selection acting on each trait (cf. Weatherhead et al. 2002). Curvilinear selection can be seen as a proxy of stabilizing or disruptive selection (Brodie et al., 1995). Within a multivariate regression of male traits (z_i) on relative fitness (ω), the standardized partial least-squares regression coefficients provide estimates of selection gradients (Lande and Arnold 1983). We only calculated selection gradients for those traits that were significant in the ANCOVA. They are body mass and limb shape (the latter captures many significant linear measurement from the ANCOVA).

Relative fitness was calculated by dividing each male's reproductive output by the average reproductive output in the entire sample. Body size and limb shape were transformed to have a mean of 0 and a standard deviation of 1. We estimated directional and curvilinear selection gradients from the coefficients in the equation:

$$\omega = \text{intercept} + \sum \beta_1 z_i + \beta_2 z_i^2 \qquad (1)$$

β_1 represents the strength of directional selection after correcting for the correlation between traits. β_2 represents the strength of curvilinear selection. Stabilizing selection is assumed to be operating when the sign (- or +) of β_2 is opposite of β_1. We estimated directional selection coefficients and then added in the quadratic terms in order to estimate curvilinear selection (cf. Lande and Arnold 1983). Our estimates of selection gradients suffer from the fact that we pooled males across years and only have measurements from one or two capture periods. Ideally, to assess a trait's effect on reproductive success, we would want to measure each animal during each mating season. For these analyses, we assume that the measurements taken from each animal give some indication of genetic quality and that male phenotypes remain relatively constant throughout their breeding career. In this regard, we assume that the variation observed in the population is due to heritable differences in phenotype on which selection acts. Investigations into the heritability of phenotypic components can confirm this assumption.

Socio-demographic factors

We also examined whether adult social group composition had an effect on reproductive status. Using longitudinal census data on sires and non-sires in our sample, we compared the social composition of a group into which an offspring was born against the social composition of a group into which no offspring were born. Thus, *sire group* refers to any group into which an offspring was born and *non-sire group* refers to any group in which no offspring were born. We tested for differences in the group composition (i.e., number of adult males, number of adult females, group size, and adult sex ratio) among sire groups and non-sire groups using logistic regression. The motivation for this test was to determine whether a male's reproductive status was facilitated or hindered by aspects of social group composition.

We did not calculate the operational sex ratio (OSR) for sire and non-sire groups because some of the variables required to calculate OSR (e.g., number of estrous cycles prior to conception, duration of estrous; Sutherland 1985b) are not available for individual groups and using population-wide average values would not provide any contrast. Group composition information was determined from census data. Sex ratio data was not available for some years for every group, so in these cases we used data from the subsequent year. To avoid double-counting, we omitted any groups that could be classified as both a sire-group and non-sire group within the same year.

RESULTS

Morphological factors and selection gradient analysis

Table 4.2 provides results of the ANCOVA. Body mass showed a marginally significant association with paternity ($F = 3.88$, $df = 1$, $p = 0.0510$). Three out of eighteen linear measurements showed significant associations with reproductive status ($p = < 0.05$): lower arm length, lower arm circumference, and upper leg circumference. One measure (base of skull to base of tail) was close to significance ($p = 0.0517$). For marginally significant variables, power tests that solve for the least significant sample size number indicated that only 1 to 2 more animals need be added to the sample to get an alpha level of $p = 0.05$. Only one factor (lower arm length) showed a significant interaction between reproductive status and the cofactor ($p = 0.0198$). With age controlled, the correlation with limb shape was significant ($F = 8.122$, $df = 1$, $p = 0.0055$). Coefficients of determination accounted for 5 to 22 percent of the variation in the statistically significant male traits. There were no significant differences for any of these measurements in terms of whether the sire was a resident or non-resident.

Table 4.3 provides estimates of directional and curvilinear selection gradients acting on body mass and limb shape. There is no directional selection acting on body mass ($\beta_1 = 0.09$, $p = 0.3536$). There is evidence of stabilizing selection acting on body mass, indicated by the negative selection coefficient ($\beta_2 = -0.12$, $p = 0.0489$). Limb shape is subject to strong directional selection ($\beta_1 = 0.79$, $p = 0.0001$) but there is not evidence of stabilizing selection as indicated by the positive sign of β_2 ($\beta_2 = 0.16$, $p = 0.0001$).

Socio-demographic factors

Table 4.4 lists summary statistics of group composition for sire groups and non-sire groups. Among sire and non-sire groups, there were significant differences in the average number of females (Chi-square = 14.76, df = 1, p = 0.0001), average group size (Chi-square = 8.29, df = 1, p = 0.0040), and sex ratio (Chi-square = 5.22, df = 1, p = 0.0223). On average, sire groups had more females, larger group sizes, and female-biased sex ratios when compared to non-sire groups. There were no significant differences in number of males among sire groups and non-sires groups (Chi-square = 2.68, df = 1, p = 0.1015).

DISCUSSION

Patterns of male mate competition

Sifaka are characterized by a restricted breeding season that lasts from January through early March. During this time, female estrus periods are asynchronous within and between groups (Brockman and Whitten 1996). The mating season in sifaka is distinguished from other periods in the year due to the breakdown of social group boundaries and social positions of individual animals within groups. Such conditions facilitate (or result from) incursions from non-resident males into neighboring social groups, presumably to monitor the reproductive status of females (Richard 1985b; Brockman et al. 1998). In a detailed study of mating behavior, Brockman (1999: 396) has documented that sifaka females tend to mate with multiple males both within and outside their own social group and that "mating is limited by male mate guarding and sexual aggression by males and females and aversions to mating with certain partners, while it is enhanced by clandestine copulations, positive mate choice, and the availability of non-resident mating partners."

Female variation in mating preferences, timing of receptivity, and number of mates can create potentially high variance in male reproductive success. In this context, any heritable morphological or behavioral factor that would enhance a particular male's mating success would be favored by selection. Observations of sifaka during the mating season indicate that male mating behavior and ability to obtain mates vary widely. Males engage in contest and scramble competition for mates, as well as something akin to endurance rivalry (cf. Andersson 1994). To summarize this diversity, we describe three categories of male mate competition that encompass the variation in our population. They represent composite situations (i.e., each episode can include aspects of other events) that are based on several thousand hours of behavioral observations (Richard 1974; 1978; 1992; Brockman 1994; 1999; Brockman and Whitten 1996; Brockman et al. 1998; Kubzdela 1997; also see Jolly 1966).

1). *Agonistic episodes.* These episodes involve contest competition between two or more animals. Sifaka primarily bite, cuff, or grab their opponents during combat and this is accompanied by lunging, threat displays, and a variety of dominant and submissive gestures between interactants. Fighting takes place on tree branches of all orientations as well as the ground. The most serious wounds are inflicted by biting with the incisors and canines. Fighting can be fierce with animals suffering open wounds and gashes. Agonistic episodes often arise when non-resident and resident males compete for mates although there can be considerable agonistic contests within a single group. Females sometimes mate with the winner of the agonistic contest, but this is not always the case.

2). *Endurance episodes.* These episodes include sustained periods of chasing and lunging, often accompanied by aggressive and submissive displays. Typically competitors will run towards each other and veer away at the last moment. Animals mostly use their typical mode of locomotion, vertical clinging and leaping (cf. Napier and Walker 1967)—although they may also rely on other forms of locomotion. Chasing and lunging episodes can last several hours until the competitors are visibly exhausted. They are often between resident and non-resident males. There is no clear association with female mating preference: sometimes a female mates with the chasing male or the chased-away male.

3). *Passive episodes.* These situations do not show any particular evidence of overt male mate competition (here, the males are *passive*, although females may be *active* in choosing mates). Quite often a particular female will mate with a resident male in view of other group males or the female will engage in extra-group copulations with a non-resident male while not in view of other males. Passive mating occurs in groups that generally do not experience incursions from non-resident males and there is no observable aggression among resident males. In passive situations, females sometimes exhibit mate preference, mating with older, resident males before young males.

From these descriptions, factors such as body size, agility, and canine size ought to be important in male contest competition. Nevertheless, the above descriptions also suggest that these traits may not have a corresponding influence on reproductive success because of female choice (e.g., Richard 1992). Some male sifaka do compete quite fiercely during the mating season, relying on their canines and agility to overpower or chase away another male. If features such as canine size and body mass significantly affect male reproductive success, then presumably selection would favor modifications to these traits. Across primates and other mammals, a conventional hypothesis is that selection has acted to increase the size of canine teeth and body mass of species where males compete with each other for chances to mate with females (e.g., Plavcan 2001). Males with larger canines and body mass can use these traits to fend off sexual rivals during mate competition thereby increasing their chances for mating exclusivity. In our population, body mass and limb shape and size were significantly associated with reproductive success, but canine height was not.

Morphological factors

Body mass is likely to fill two roles in overt mate competition. Because overall body mass is strongly correlated with muscle mass and adipose deposits in primates (Grand 1977; Zilhman 1984), one role is simply that a larger male can overpower an assailant by force. For combative sifaka, this can include forceful cuffing, grabbing, and biting as discussed above. Secondly, greater adult body mass may enable a male to out-last an opponent in endurance rivalries because the capacity for energy storage also increases as body mass increases. This occurs because larger animals have decreased metabolic needs per unit tissue than smaller animals, but any increase in size primarily adds either skeletal muscle or body fat, both of which store energy sources over the short or long-term (cf. Calder 1984). Significant fluctuations in body mass, apparently entrained to seasonal factors, occur in lemurs. The largest increase in body mass happens just before the onset of the mating season (Pereira 1993; Richard et al. 2000) and the body tissue likely responsible for this fluctuations is white adipose tissue (Pereira and Ponds 1995). Adipose tissue is a major source of energy for metabolism during physical activity (Calder 1984). The increased levels of physical activity during the mating season are likely supplemented by energy derived from adipose deposits acquired during the late dry season (Richard et al. 2000). It is possible that the most successful males are the ones that can out-last opponents throughout the mating season, and this ability may be linked to the ability to draw from relatively larger energy reserves than their rivals.

Limb shape also correlates with reproductive success. Because male sifaka engage in extended episodes of chasing as well as fighting during mate competition, aspects of limb shape that favor agility, endurance, or strength may be selected for. In Table 4.2, many of the circumferences of arm and leg dimensions are significant or approach significance. Similarly, Table 4.3 shows that strong directional selection is acting on limb shape. Sifaka rely on a unique form of locomotion in which the animal propels itself from one vertical substrate to another via the propulsive muscles of the thigh. The animal lands feet first and the arms of sifakas play a role in guiding and stabilizing the take-off and landing motions as well as a providing a leading weight during mid-air rotation (Anemone 1993; Demes et al. 1996). Sifaka rely on vertical clinging and leaping during endurance episodes of mate competition. Our measure of limb shape captures the physiologically important aspects of this type of locomotion because it is a composite of the circumferences of the upper and lower arms and legs. Muscle force is proportional to the cross-sectional area of the muscle, so long as all muscle fibers are oriented in the same direction and fire simultaneously (Swartz 1993). In this regard, measures of limb form that take into account muscle circumference (c) provide an approximation of muscle cross-sectional area (a) (noting that $c^2/4\pi = a$, and assuming all adult males have equal bone mass) and—by extension—muscle force. Directional selection pressures act on limb shape, particularly limb circumferences. Because so much male competition involves extended periods of aggression, chases, and acrobatic movements—many of which are on vertical substrates—limb shape likely captures the overall physical ability of the animal. Successful males are those that can outlast or out-compete other males for access to mates (cf. Clutton-Brock and Harvey 1976; Clutton-Brock 1985; Kappeler 1990; Richard 1992). This conclusion also explains why stabilizing selection acts on body mass. On the whole, sires are larger than non-sires, but given that the majority of male mating competition takes place in an arboreal setting, directional selection to increase body mass may ultimately compromise a male's competitive ability in the trees.

Studies of canine dimorphism in relation to the intensity of male-male competition across anthropoid species have found a positive relationship (Plavcan 2001). Lemurs stand out against this pattern by showing relatively little canine dimorphism despite strong male-male competition in some species (Kappeler 1996a). Plavcan and van Schaik (1992; 1997; Plavcan 1999) have formalized male-male competition levels among primate species. Intrasexual mate competition in sifaka during the breeding season corresponds to their level 4 (Plavcan 1999), defined by both high intensity and high frequency of male-male aggression. Given this, sifaka, like other lemurs, prove the exception to the general rule that intensity of male-male competition is associated with canine dimorphism.

However, intensity of mate competition and canine dimorphism are not always correlated. It has been noted that selection for increased canine height may actually be a mechanism that forestalls agonistic encounters among competing males (Leutenegger and Kelly 1978). This type of signaling system invokes facial expressions as a means to signal aggressive intent thereby allowing one of the competitors an opportunity to defer without physical harm. In many cercopithecoid species, dominant males can keep subordinate males at a distance by signaling a threat with their canines (Crook 1972). Here, canine dimorphism may result from selection for mating exclusivity without agonism and therefore a positive correlation between canine size and male-male physical combat may not be found (cf. Plavcan 2001).

For selection to act on canine size, canines must be advantageous in maintaining differential reproductive success among males, either through agonistic signaling or overt, physical combat. Although contests between sifaka males can be fierce and often involve biting with the canines, canine height was not significantly related to reproductive status in our population (measures of canine shape and size, not presented here, were also not significantly related to reproductive status). Also, sifaka do not use their teeth to signal agonistic intent (Richard 1978). Canines may be a factor in agonistic contests in terms of short-term access to mates or incursions into non-resident space, but because victors do not always sire offspring (i.e. there is no correlation between canine size and reproductive status), there is little selection for canine modification. Selection for increased canine size may be offset by female choice and/or genetic correlations between the sexes (Richard 1992; Kappeler 1996a).

Socio-demographic factors

The key male "competitive traits" should be advantageous in male-male mating contests. However, coefficients of determination show that there is a lot of variation in sire versus non-sire traits (Table 4.2). The advantage these morphological traits provide to a particular male are only one of many factors contributing to reproductive success. For sifaka, the distribution of values for body mass, limb shape, and other morphological variables is not wholly explained by differential reproductive success in this population. Permanent, gregarious, male-female groups characterize most primate species; therefore, much attention has focused on socio-demographic factors affecting reproductive success (e.g., Mitani et al. 1996b; 1996b). Comparative and longitudinal studies have shown that as the number of other males in a social group increases, a particular male's reproductive opportunities are compromised, whereas if the number of females in the social group increases, a particular male's mating opportunities are enhanced (e.g., Andelmann 1986). The number of males and females in a population is often expressed as a ratio, either the adult sex ratio or the operational sex ratio (OSR). The latter is a more meaningful measure of potential male-male competition because it measures the temporal availability of receptive females, but we could not calculate the OSR because it relies on population-wide averages and individual values for particular females in groups are not available. Instead we used the adult sex ratio, which gives an approximation of the number of potential mates and sexual rivals for each group.

In the population, males were more likely to sire offspring in groups that had greater proportions of females. On average, sire-groups contained relatively more females, fewer males, and a greater ratio of females to males, than non-sire groups. This suggests that sires either reside in, or visit, social groups that have a greater proportion of females. Non-sires reside in groups that had relatively fewer females. Although it seems likely, we cannot say whether non-sires visit adjacent social groups during the mating season because we infer "visits" based on the perspective of the offspring; that is, visits are deemed to occur when the offspring born into a group has a father who resides in an adjacent group. Because of this, we can only suggest that within the operation of male-

male competition and female choice, those males who are able to reside in, or visit groups with a greater proportion of females are those who will be successful in reproduction.

Sexual dimorphism, climate, and honest signaling

Clutton-Brock (1985) has argued that sexual dimorphism will not evolve unless there is a comparative difference between the sexes in reproductive success based on body size (or any other feature). When there is an equal and positive effect of a particular trait on reproductive success in both sexes, the sexes will remain monomorphic. In sifaka, body mass apparently influences reproduction in *both* male and female sifaka. Richard et al. (2000) found that females that were heavier during a given mating season were more likely to give birth in the following birth season than lighter females. These results mirror the ones presented above for males: heavier males are more likely to be sires. These findings suggest that the effect of body mass on reproductive success is equivalent in sifaka males and females. We should also note that mortality rates of adult males and females in this population are similar; therefore it is difficult to attribute sexual monomorphism to viability costs males would incur by being larger than females (cf. Promislow 1992).

Sexual selection relies on variance in male reproductive success to determine the course of sex-specific phenotypic evolution. Any particular feature of a male that allows him to be chosen by females or out-compete other males for mating opportunities falls under the rubric of sexual selection (Arnold 1983). Because body mass and/or canine size tend be targeted by selection during male-male mate competition, sexual dimorphism is a powerful cue to the operation of intrasexual selection. Most lemurs show little or no sexual dimorphism, unlike most anthropoids. Results presented here suggest why this is the case for sifaka. Male sifaka show high levels of mating competition during the mating season, but there is only a limited association between body mass and reproductive success. Because so much mating competition occurs in the trees, stabilizing selection influences body mass more so than directional selection. Also, based on the result from Richard et al. (2000), selection for increased male body mass—while a factor in determining paternity—is matched by selection on female body mass. Additionally, the existence of female choice dilutes directional selection pressures on male "competitive" traits (i.e., large canines, large body mass). A genetic correlation between the sexes can also hinder the evolution of sexual dimorphism (Lande 1980); this hypothesis will be examined in a future study. Below, we consider two further possibilities that may contribute to sexual monomorphism in sifaka.

First, southwest Madagascar is distinguished from many other tropical regions by having an extremely unpredictable annual rainfall (Dewar and Wallis 1999; Richard et al. 2002). Based on 40 years of rainfall data from 1492 weather stations, a major drought is expected to hit this region at least once every decade (Dewar and Wallis 1999). Richard et al. (2002) have argued for the evolutionary consequences of this climate on sifaka life history strategies, which is associated with high and unpredictable infant mortality. This type of environmental variation selects for a life history strategy known as "bet-hedging" where animals are selected to extend their reproductive efforts across numerous years. Sifaka females live longer and reproduce later in life for their size than mammals in other orders (Richard et al. 2002). This type of climate also has implications for the evolution of sexually selected traits.

Recurrent population bottlenecks can preclude a sexually selected trait from reaching fixation (Otto and Whitlock 1997). Here, our point is heuristic and not exact. We suggest the possibility that sexual monomorphism in sifaka could be due to recurrent population bottlenecks that prevent an advantageous trait from becoming established in the population. If we assume that a sexually selected trait, for example canine size, is controlled by a single advantageous allele (carried by both sexes and expressed only in males, cf. Kirkpatrick 1982), we can ask: what is the probability of fixation of an advantageous allele initially present in a single heterozygous individual in a population that undergoes fluctuations in population numbers? Ewens (1967; Otto and Whitlock 1997) showed that the probability of fixation (P) is approximately equal to two times the selective coefficient (*s*) multiplied by the ratio of the effective population size (N_e) to initial population size when the allele is introduced (N_t):

$$P \approx 2s \cdot N_e/N_t \qquad (2)$$

For example, based on a survey of natural populations, we assume a selective coefficient of 0.2 (Endler 1986). Effective population size can be estimated from census data. Here, we assume that the lowest size of the population during a drought is 100 animals and the population increases by 75 each year to a maximum of 400. Thus, in a ten-year span—the period encompassing a major drought—the population reaches a low (the bottleneck) of 100 and grows each year to 175, 250, 325, 400, remaining at 400 for six years before another drought occurs. The harmonic mean of these values provides a good approximation of the size of a fluctuating population (Wright 1931); in this case, $N_e = 264$. If the initial allele is introduced when the population is at 400, then $N_t = 400$. Putting these values into equation 2, the probability of fixation is 0.26. Obviously, this is a simplified exercise and purely heuristic, but the resulting probability indicates that advantageous traits may have difficulty reaching fixation given the recurrent population bottlenecks. Past population sizes may have been much larger (although still subject to fluctuations) due to more available habitat (Richard and Dewar 1991). The conditions and assumptions going into the above exercise are strict and include non-overlapping generations (Otto and Whitlock 1997). Because sifaka have overlapping generations, the loss of an advantageous allele due to sampling error is mitigated by the potential for animals to reproduce across years. Incorporation of the potential for multi-year reproduction into a single measure of a fluctuating population requires knowledge of how variance in reproduction changes as a function of population size (e.g., Clutton-Brock et al. 1997).

Our second point concerns the role of female choice in maintaining sifaka monomorphism. Although behavioral observations indicate that female sifaka can offset intrasexual selection pressures by mating with non-combative males, we would like to explore female mate choice in more detail. In 1992 Richard proposed that male submissiveness to females in sifaka can provide long-term enhancement of reproductive success that outweighs any short-term aggression towards other males. Many lemur species, including sifaka, are unique among mammals in that females are dominant to males during all times of the year. Females are almost always able to displace a male at a feeding site or other location via threats and/or outright aggression (Richard 1987). Males do not always unconditionally relinquish food items, but the consistent pattern is male deference to females at feeding sites (cf. Kappeler 1993; Richard 1987). This runs contrary to the pattern seen in other mammal species (including monomorphic ones) where males can dominate females. The observation that females are behaviorally dominant to males in many lemur species has led researchers to focus predominantly on aspects of female physiology that could potentially differ with non-female dominant primate species (e.g., Richard and Nicoll 1987; Young et al. 1990; Kappeler 1996b). However, focusing on female dominance as the phenomenon to be explained has directed disproportionate attention to finding behavioral or metabolic idiosyncrasies in females that require adaptive interpretation. The relevant trait may be *male deference*, not *female dominance*.

Richard's hypothesis can be subsumed within a broader theoretical framework of honest signaling by males (Zahavi 1975). We propose that males in the sifaka population are honest signalers. Grafen (1990a; 1990b) has modeled the evolution of honest signaling with regard to mate choice. His model has four conditions that must be satisfied for a system of honest signaling to be maintained in a population: 1) the signal must be costly to males; 2) for any level of investment in a signal, the fitness costs must be lower for a higher quality male than for a lower quality male; 3) female perceptions of high quality males increase those males' chances for mating; and, 4) females do not alter their mating preferences based on a deceptive signal sent by a low quality male. Grafen assumed that differences among males were entirely environmentally driven (1990b); however, similar conditions obtain when variation in male quality is genetic (Grafen 1991).

As with other indicator models, we assume that a male signal corresponds to a heritable component of fitness; for example, high quality males have high quality offspring. Females who mate with a lower quality male (as in point 4) have offspring with a lower viability. Hence, at equilibrium, female fitness is highest when they can accurately perceive and mate with the highest quality males, thereby maintaining a cost to deception. The male signal is *deference* or *submissiveness.* That is, the signal males are sending to females is high viability via submission or relinquishment of food. Only high quality males can afford to give up food to females. Their handicap is an honest signal of robust viability; that is, they can honestly afford to relinquish a food item in comparison to lowly viable males who cannot afford to give up a food item. The opposite behavioral response to passive relinquishment of a valued resource is resistance. We expect that lower quality males are less likely to defer to females and more likely to contend for the resource. Because high quality males have high and heritable viability, they are preferred by females for mating. Low quality males, even when investing in high quality signals (i.e., deferring beyond their means), incur lower survivorship, making it difficult to send a dishonest signal of quality.

This scenario provides a theoretical framework to the observation that male reproductive success is played out "...in an arena of competitive submission to females..." (Richard 1992: 403). Relinquishing a food source could have negative physiological consequences for adult male body size, making it difficult for males to attain a larger body mass than females. This phenomenon might hinder sexual dimorphism in this population. We have framed the above scenario in terms of a *strategic-choice* handicap model (Grafen 1990b), where males can control the intensity in the signal they send to females. However, this model could also be framed in terms of a *revealing* handicap model (Maynard Smith 1976). In this model, males cannot control the level of display or investment in a signal. A possible example of this is the inverse correlation between bright breast plumage and parasite load in male birds; it is assumed that males with a high parasite load cannot manipulate (i.e., make brighter) the color intensity of their plumage (Hamilton and Zuk 1982). Male deference under a revealing handicap model in sifaka would require that males are unable to control their ability to defer at a food source; that is, low quality males would be expected to resist giving up food to females.

Various extensions and alterations are possible. Fitness itself need not be heritable in our scenario, so long as high quality males provide direct benefits to females and their offspring (i.e., "direct benefit" models; Price et al. 1993). In this case, deferential males are chosen by females not for the high quality offspring they sire, but for the immediate benefits they provide to females in terms of paternal care or protection (cf. Pereira and Weiss 1991). By assuming that there is no heritable variation in fitness, we can bypass the sundry problems associated with determining how heritable variation in fitness is maintained in populations (cf. Charlesworth 1987). However, it is worth pointing out that heritable variation in fitness is more likely to be preserved in fluctuating environments (Gillespie 1973).

If we assume a heritable variation in fitness among male sifaka, the honest signaling scenario makes several predictions: 1) deferential (i.e., high quality) males live longer than non-deferential males; 2) deferential males have deferential sons; 3) female mating preferences during the mating season will be directed to those males who have deferred at feeding sites throughout the year; and, 4) non-deferential males are more combative than deferential ones and do not engage in paternal care. Regarding point 4, lower quality males are expected to engage in more intrasexual contest competition for mates, whereas high quality males are expected to engage in relatively less intrasexual contest competition. Naturally, casting female-dominance in terms of male handicaps does not *explain* the evolution of female dominance; however, shifting the perspective from the female to the male allows for different predictions to be formulated and tested.

Table 4.1. The relationship between selected morphological and demographic factors and their expected effect on male mating and/or reproductive success (M/RS).

Morphological or social factor	Expected effect on male M/RS	Examples	Study type	Ref
increased body mass[1]	Positive	baboons	L	1
		many anthropoids	C	2
increased canine size	Positive	rhesus macaques	L	1
		many anthropoids	C	3
factors relating to endurance[2]	Positive	rhesus macaques	L	1
		many anthropoids	C	4
no. of males per group	Negative	vervets	L	6
		many anthropoids	C	7
no. of females per group	Positive	patas monkeys	L	9
		many anthropoids	C	7
seeks extra-group mating	Positive	gibbons	L	10
		dwarf lemurs	L	11
coalitions/mating cooperation	Positive	chimpanzees	L	12
		howlers	L	8

Study type: C = comparative (interspecific); L = longitudinal (intraspecific). Notes: 1-increased body mass tends to correlate with age and rank in many primates; 2-this is specific to the biology of the mating system as it can include things like large or small body size, agility, and aspects of body shape. Refs: 1 Becovitch and Nurnberg 1996; 2 Plavcan and van Schaik 1997; 3 Plavcan and van Schaik 1992; 4 Clutton-Brock and Harvey 1976; 5 Andelmann 1986; 7 Mitani et al. 1996a; 8 Pope 1990; 9 Ohsawa et al. 1993; 10 Palombit 1994; 11 Feitz et al. 2000; 12 Watts 1998.

Table 4.2. The relationship between reproductive status and male morphometric traits when controlling for age or body mass. The coefficient of determination (R^2) is also given for the bold entries.

Male trait	Significance	R^2 (sig. only)	Confounding variable	Interaction with confounding variable
Pelvic width	$p = 0.8486$		mass	NO
Biacromial width	$p = 0.0918$		age	NO
Base of skull to base of tail	**$p = 0.0517$**	**0.05**	age	NO
Tail length	$p = 0.3425$		mass	NO
Chest circumference	$p = 0.8153$		mass	NO
Upper arm length	$p = 0.8147$		age	NO
Upper arm circumference	$p = 0.1565$		mass	NO
Lower arm length	**$p = 0.0229$**	**0.22**	mass	YES
Lower arm circumference	**$p = 0.0215$**	**0.22**	mass	NO
Hand length	$p = 0.1246$		mass	NO
Upper leg length	$p = 0.1270$		mass	NO
Upper leg circumference	**$p = 0.0102$**	**0.22**	mass	NO
Lower leg length	$p = 0.1058$		mass	NO
Lower leg circumference	$p = 0.0779$		mass	NO
Ankle + foot length	$p = 0.1209$		mass	NO
Skull length	$p = 0.7194$		mass	NO
Skull breadth	$p = 0.4917$		age	NO
Canine height	$p = 0.2809$		mass	NO
Body mass	**$p = 0.0510$**	**0.11**	age	NO
Limb shape	**$p = 0.0055$**	**0.13**	age	NO

Limb shape = geometric mean of circumferences of upper and lower arms and legs divided by cube root of body mass.

Table 4.3. Selection gradients on body mass and limb shape.

Trait	Directional Selection Gradient	Curvilinear Selection Gradient
Body mass	0.09	−0.12
(significance)	$p = 0.3536$	$p = 0.0489$
Limb shape	0.79	0.16
(significance)	$p = 0.0001$	$p = 0.0001$

Table 4.4. The relationship between reproductive status and adult group composition.

	Sire Groups (n = 10)	Non-sire Groups (n = 9)	Significance
Mean number of females	2.76	1.55	**p = 0.0001**
Variance in females	0.88	0.47	
Mean number of males	2.88	2.36	p = 0.1015
Variance in males	0.55	0.88	
Mean sex ratio	1.01	0.74	**p = 0.0223**
Variance in sex ratio	0.14	0.07	
Mean males + females	6.55	4.64	**p = 0.0040**
Variance males + females	2.63	5.85	

Sex ratio = (number of adult females divided by number of adult males)

CHAPTER 5

GENETIC POPULATION STRUCTURE OF THE WHITE SIFAKA (*Propithecus verreauxi verreauxi*), 1992-2001

INTRODUCTION

Natural populations typically have some amount of genetic subdivision that can be arranged hierarchically (Wright 1978). Depending on the population size and range, the degree to which the population subunits will genetically differentiate is contingent on a variety of factors including gene flow, mutation, regional adaptation, and drift. Although modeling the interplay among all these factors is complex, it is possible to gain insight into population structure by focusing solely on how genetic variation is apportioned among population levels under localized panmictic mating and drift (Wright 1969). Wright developed several *F*-statistics that measure the genotypic deviations from panmictic proportions among population levels. In order to increase their generality, *F*-statistics were derived within the framework of an idealized population (Wright 1921). *F*-statistics have been widely used to study geographic population structure (cf. Wright 1978). However, as many researchers have noted, *F*-statistics do not take into account several behavioral and demographic features that are typical of socially structured populations (e.g., Sugg et al. 1996; Balloux et al. 1998). These factors include sex-specific dispersal and philopatry, socially-stratified reproductive opportunities, and the presence of reproductive and non-reproductive members within social units. Chesser (1991a; 1991b) derived explicit formulations of gene dynamics for socially structured populations that determined the transitional and asymptotic values of genetic variation among different population levels. Chesser's work made clear two issues that were implicit in early studies of socially structured populations (e.g., Long 1986; Melnick et al. 1984). First, care must be taken in defining geographic or demic population levels so as not to overlook hidden reproductive structure within demes. Second, significant gene correlations can accrue from sex-biased dispersal and polygyny without needing to invoke inbreeding.

Although derived for any type of socially structured species, the genetic consequences of social structure are often studied in mammalian species (cf. Dobson 1998; Storz 1999). Storz (1999) has noted that mammal populations were previously assumed to be organized into small, semi-isolated, panmictic social units that retain high levels of inbreeding due to limited dispersal (e.g., Bush 1977; White1978; Chepko-Sade and Shields 1987). These assumptions were based precisely on the issues Chesser sought to rectify: inbreeding, subpopulation divergence, and coancestry are not always causally linked. More recent mammalian studies have applied *F*-statistics at the level of social group—the lowest level at which random mating may prevail—and reveal a different partitioning of genetic variation within the population (e.g., Pope 1992; 1996; 1998; Dobson et al. 1997; Dobson 1998; Dobson et al. 2000; Storz 1999; Storz et al. 2001; Richardson et al. 2002). These values are more credibly interpreted with respect to the socio-demographic factors mediating gene flow and reproduction within and among breeding groups rather than invoking drift, restricted dispersal, and random mating (Chesser 1991a, 1991b; Sugg et al. 1996; Storz 1999). Examining the relationship between social and genetic structure has become known as the "social structure" view of population genetics (cf. Sugg et al. 1996; Balloux et al. 1998).

Primate species would appear to be ideal taxa with which to test the predictions of the social structure view of population genetics. Relative to other mammalian orders, primate social systems are very well-studied (cf. Richard 1985a; Strier 2000). Further, most primate species are gregarious and characterized by female philopatry, male dispersal, and different degrees of mating competition (cf. Smuts et al. 1987; Lee 1999; Kappeler 2000). However, despite their well-characterized social systems, there are few available data sets that contain reproductive information on an entire primate population; therefore, the apportionment of genetic diversity in primate populations is not well understood. Out of logistical necessity, many long-term primate studies focus on one or a few social groups instead of an entire population (but see, for example, Altmann et al. 1996; Keane et al. 1997; Sauther et al. 1999). The population-levels parameters determining gene dynamics in the population are determined by intra- and intergroup membership and mating. In order to understand how gene correlations change through time as a function of group membership and mating, longitudinal data collected from numerous social groups are required. In this chapter, we analyze the genetic structure of a wild population of lemur, the white sifaka (*Propithecus verreauxi verreauxi*) using longitudinal genetic and demographic data sets. Sifaka live is spatially and socially cohesive groups that contain from 2-14 animals (mean = 6.5). Females are generally philopatric, although females born into groups with several older females may disperse (unpub. data). In contrast, all males disperse from their natal group usually around the age of five years (Richard et al. 1993). However, unlike many anthropoid primates, sifaka have a restricted breeding season that lasts about 6-8 weeks. The mating season disrupts the spatial and social cohesion of some groups in the population (Richard 1992; Brockman 1999). Observations during the mating season indicate that some sifaka males make forays into neighboring groups to seek reproductive opportunities. An analysis of paternity on this population confirmed these observations. Across several groups, males sired offspring in social groups other than their own (see chapter 3).

The objective of this chapter is to test several predictions of the social structure view of population genetics. First, under the conditions of sex-biased dispersal, the degree of among-group genetic variation in adults should be proportional to the relatedness of the philopatric sex within groups; for sifaka, female relatedness within groups should be positively related to adult F_{ST} (Chesser 1991a). Second, when breeding groups are properly defined, offspring should have negative F_{IS} values; therefore, if the sifaka social group corresponds to a reproductive unit, offspring cohorts within groups should show negative F_{IS} values (Cockerham 1969; Chesser 1991a). Third, reproductive skew within social groups is expected to increase F_{ST} values and decrease F_{IS} values in offspring. We approximate reproductive skew as the proportion of resident males siring offspring. We expect that when a single resident male, or several related resident males, sire the majority of offspring within groups, offspring cohorts will be characterized by increasingly negative F_{IS} values (Chesser 1991b). Fourth, under female philopatry and polygyny, offspring cohorts are expected to have F_{ST} values that are relatively equal to adults, because female offspring cohorts—united by a subset of paternal alleles—are recruited into their natal group (Chesser 1991a;

Storz et al. 2001). We estimate F_{IS} and F_{ST} values at the level of the social group and interpret them with respect to mating and dispersal patterns in this population. We analyze offspring and adult cohorts separately. This separation is the most effective way to operationalize expectations from theoretical models using genetic data (Spielman et al. 1977; Storz et al. 2001).

The motivation for this study is straightforward: how genetic variation is apportioned within a population determines the distribution of kinship ties. Relatedness among individuals is one condition that can foster the evolution of altruism and cooperation (cf., Trivers 1985; Silk 2002b). In this regard, demographic factors that affect gene correlations among individuals could have potentially important consequences for how cooperative and agonistic behaviors are manifested in different primate species.

METHODS

This chapter analyzes data collected over the last ten years. Information on genetic loci, population characteristics, and parentage analysis are provided in chapters 2 and 3. In this chapter, all analyses are conducted on groups of four or more individuals. Data used in this study come from 10-28 core social groups censused since 1992. This is not an exhaustive set of social groups, there are "buffer zone" groups whose home ranges lie partially within the Beza Mahafaly reserve (cf. Richard et al. 2002). The demographically important features of core groups are the following: 1) the home range of each core group lies entirely within the protected reserve; 2) core groups contain individually marked animals; 3) core groups have been censused monthly since

1992; and, 4) more animals are born into, or transfer between, core social groups than migrate into these groups from outside the protected sector (Richard et al. 2002; unpub. data). Following analyses in earlier chapters, we divide sires into *resident* and *non-resident* sires. Table 5.1 gives the yearly data on number of females and males, number of groups, and average adult population sex ratio.

Analysis of population structure and parentage

Tests for deviations from Hardy-Weinberg equilibrium among the loci were determined within each yearly population using an exact test (Raymond and Rousset 1995a). Tests for gametic phase disequilibrium among the loci were determined using the permutation tests. Using a G-test, we tested for difference in allele frequencies between males and females in the population. To measure genetic variation within and between groups, we used two *F*-statistics: F_{IS} represents the correlation of alleles in individuals relative to the breeding group and F_{ST} represents the correlation of alleles in breeding groups relative to the total population. *F*-statistics for adults and offspring each year were estimated using FSTAT 2.8 (Goudet 1995). This program calculates Weir and Cockerham's (1984) estimators of genetic variance ($f = F_{IS}$, $\theta = F_{ST}$) and each subgroup is weighted by sample size. Despite overlapping generations, a year-by-year analysis is appropriate as animals enter and leave groups each year through birth, death, immigration, and emigration. R_{ST} values were not used in the analysis as not all of our microsatellite markers followed a stepwise mutational pattern and furthermore, *F*-statistics are not generally contingent on mutation rates when applied at small spatial scales (Rousset 2001). Significance tests were determined using randomization procedures that calculated significant departures away from zero. *F*-statistics from offspring cohorts were calculated by pooling offspring into groups spanning 4-year intervals. This interval maximizes the sample size of the offspring cohort but precludes those female offspring coming into reproductive maturity (at age 5) within the social group. In this sense, *offspring cohort* is synonymous with *sibship*. All offspring cohorts contain infants born over the last four years; for example, the 1992 offspring cohort contains infants born in 1989, 1990, 1991, and 1992. Because offspring cohorts have adjacent (i.e., non-independent values) for each year, a Durbin-Watson test was used to test for first-order autocorrelation. Under Model I regression, this test determines whether adjacent values have correlated errors through time (Chatfield 1975).

Average relatedness (*r*) of adult females to each other within a group, relative to the total population, was estimated using the coefficient of relatedness derived by Queller and Goodnight (1989). Relatedness was calculated using the program RELATEDNESS 5.08, correcting for bias within groups (Goodnight and Queller 1999). This same definition of relatedness was used to characterize adult males and offspring. Associations between variables were tested using parametric and non-parametric tests. Because both were significant, we only present non-parametric results.

RESULTS

Hardy-Weinberg, gametic phase disequilibrium, and *F*-statistics

Deviations of genotypic proportions from Hardy-Weinberg equilibrium were assessed for the population. When the entire sample of genotypes was pooled across years, one locus (Locus 4) deviated from Hardy-Weinberg (Lawler et al. 2001). However, an exact test (with $p = 0.05$) of expected genotypic proportions within the population for each year revealed no significant deviations. For each year in our analysis, a test of gametic phase disequilibrium was performed. Using a resampling test with 3000 permutations, these tests detected no significant gametic phase disequilibrium (with $p < 0.01$) between all pairwise combinations of loci. There were no significant differences in allele frequencies between males and females at each locus (p-values ranged from $p = 0.17$-0.28).

The values of f and θ for adults and offspring cohorts are listed in Table 5.2. Figure 5.1 shows θ values for adults versus offspring and adult females versus adult males. Overall, the results in Table 5.2 indicate that for each year included in the study, offspring show a greater degree of heterozygote excess and a greater degree of between-group differentiation than do adults. The mean θ across years for adults was 0.052 (range 0.024 to 0.075) and for offspring it was 0.108 (range 0.074 to 0.127). Adult female values of θ were consistently larger than adult males values of θ. The mean value of θ for adult females was 0.098 (range 0.056 to 0.147) whereas for adult males it was 0.046 (range 0.023 to 0.077). The mean degree of deviations from expected heterozygosity (f) across years for adults was 0.003 (range –0.04 to 0.047) and for offspring it was –0.068 (range –0.13 to –0.02).

Relatedness and siring patterns.

Relatedness (r) and siring patterns within the population by year are presented in Table 5.3. Offspring had a higher level of relatedness within a group than did adults (mean adults: 0.098, range: 0.047 to 0.144; mean offspring: 0.2063, range: 0.142 to 0.255). Similarly, females were more related to each other than males within groups (mean females: 0.186 range: 0.106 to 0.278; mean males: 0.086 range: 0.045 to 0.148). Using parentage data, Table 5.3 also presents data on whether offspring within a group were sired by resident or non-resident males. The percentages refer to the proportion of offspring born into groups that were sired by resident males of that group (versus males from another group) each year. In all years but one, a majority of offspring (> 50%) were sired by resident males within groups. The lowest percentage of infants sired within a group by resident males is 35% (1993), one year after there was a major drought at Beza Mahafaly that reduced the population size and altered the population structure (see discussion in Richard et al. 2002). Nineteen-ninety eight showed the highest percentage of resident-sirings with 83% of all infants born into groups sired by resident males. Based on yearling censuses, the majority of offspring born in the population were males. Across years, the average percentage of male offspring born into the population is 61% (range of 17% to 77%).

Interactions between variables.

There is a significant negative relationship between adult θ values and offspring f values (Figure 5.2A) (Spearman Rho = -0.648, p = 0.0426). This indicates that as adults among social groups become more genetically differentiated, offspring cohorts show a greater degree of heterozygote excess (f). Genetic differentiation of adults among social groups (θ) shows a positive association with relatedness of females (r) within groups (Figure 5.2B) (Spearman Rho = 0.701, p = 0.0239). The relationship between male relatedness and adult group differentiation did not show a significant relationship. Relatedness of adult females and males within a group is significantly associated with offspring heterozygosity. As relatedness of females within a group increases, offspring have increasingly negative *f* values (Figure 5.3A) (Spearman Rho = -0.898, p = 0.0004). This relationship does not have significant autocorrelation (p = 0.322). A similar negative relationship obtained for males and offspring *f* values but the association was not as strong (Figure 5.3B) (Spearman Rho = -0.687, p = 0.0282). However, this relationship has significant positive autocorrelation (p = 0.022).

Patterns of siring by resident and non-resident males influence genetic variation within offspring cohorts (Figure 5.4A). There is a negative relationship between heterozygote excess in offspring cohorts and the percentage of offspring sired by resident males (Spearman Rho = -0.910, p = 0.0017); there is a significant amount of positive autocorrelation for this relationship (p = 0.041). However, there is no significant relationship between percentage of infants sired by resident males and adult group genetic differentiation (θ). There is a significant negative association between adult sex-ratio within a group and the percent of offspring sired by resident males (Figure 5.4B). As the number of females within a group increases (sex ratio >1), the number of offspring sired by resident males decreases (Spearman Rho = -0.905, p = 0.0020).

DISCUSSION

Philopatry, dispersal and heterozygosity

Across all years, there is a negative relationship between adult social group differentiation (θ) and offspring within-group heterozygosity (f). We attribute this excess heterozygosity in offspring cohorts to differences in dispersal in adult males and females. Each year, a minority of the offspring are female and there is considerable female philopatry such that daughters are recruited into their natal social groups (Richard et al. 1993; Kubzdela 1997). As daughters reach sexual maturity and join the adult breeding pool, this creates the opportunity for gene correlations to build up among female sifaka within groups. As Table 5.3 shows, females are more related to each other within groups than are males. Through time, each matriline becomes genetically distinct due to factors such as drift and mutation. Figure 5.2A shows that as female relatedness (r) within groups increases, so does the genetic subdivision among adult social groups. Relatedness (r) can be linked to population structure through the equation $r = 2F_{ST}/(1 + F_{IT})$ (Hamilton 1971), and because r is proportional to F_{ST}, it is evident that female relatedness within groups drives the genetic differentiation of adult social groups. Vitalis (2002) has derived equations to calculate the sex-specific dispersal rates using pre- and post-reproductive values of θ. In our population, adult female θ values were consistently larger than adult male θ values—a pattern consistent with female philopatry and male dispersal. Male relatedness within groups is lower than that of females. It does not show a significant relationship with adult group subdivision. Therefore, female philopatry and the coancestry that builds up within matrilines strongly influences the degree of genetic structure in adult sifaka groups.

Female philopatry is often associated with male dispersal (Smale et al. 1997) and a seven-year study of dispersal and transfer found that all male sifaka disperse from their natal groups (n = 191 cases of transfer) (Richard et al. 1993). Males tend to transfer into neighboring groups; for example, in a 5-year census period, all males transferred no more than two home ranges away from their natal group (n = 19). The pattern of adjacent (and secondary) transfers among core social groups causes some groups to have related males (Table 3), resulting in a "neighborhood-like" social organization (Richard 1985b; Richard et al. 1993). Within social groups, breeding females represent a subset of the total female gene pool. When these females mate with a subset of adult males, a Wahlund-effect occurs (cf. Pope 1992; Storz et al. 2001). We interpret the heterozygote excess in offspring to be a consequence of consolidating gene pools that are from different maternal lineages (Chesser 1991a). Effectively, so long as males eventually transfer into unrelated matrilines, the differences in allelic combinations that characterize breeding males and females will produce a heterozygote excess in the first filial generation (cf. Cockerham 1973; Long 1986).

The pattern of female philopatry and male dispersal observed in this population is similar to that seen in other mammalian species. As predicted from theoretical studies by Prout (1981) and Chesser (1991a; 1991b), female relatedness within breeding groups is proportional to adult θ. This finding has been recorded in diverse taxa such as howling monkeys (Pope 1992), white tailed-deer (Mathews et al. 1997), soay sheep (Coltman et al. 2003), Indian fruit bats (Storz et al. 2001), black-tailed prairie dogs (Dobson et al. 1997), rabbits (Richardson et al., 2002), and Alpine marmots (Goosens et al. 2001). Further, many of these studies found different degrees of heterozygote excess within the reproductively delineated sampling units (e.g., breeding group, coterie, etc.). The negative correlation of uniting gametes results from parents derived from different maternal lineages within the population and it is enhanced by reproductive skew (cf. de Jong et al. 1994; Storz et al. 2001).

Male reprodution in social groups and inbreeding.

Sifaka are seasonal breeders and have a mating season that lasts for about 6 to 8 weeks. Social group boundaries tend to break down during the mating season, and some males will make forays into neighboring groups, possibly to assess the reproductive status of neighboring females (Richard 1985b). Male-male interactions within and between groups can be quite aggressive during the mating season (Richard 1992; Brockman et al. 1998). Females exhibit estrous asynchrony within the breeding season and show positive mate choice toward resident and non-resident males (Brockman and Whitten 1996). Both male mate competition and female mate choice can lead to high variance in male reproductive success. This skew in male reproduction will further contribute to heterozygote excess in offspring because only a small portion of the total paternal gene pool is used to start the next generation. Polygyny enhances sampling error of adult gametes leading to deviations from random mating. The consequences of related males reproducing in social groups leads to a similar phenomena of complete polygyny: only a subset of male alleles are represented in the offspring generation. As discussed above, the pattern of transfers among adult males results in some groups containing related males. When related males (or a single male) sire the offspring in groups, this causes a heterozygote excess in offspring cohorts because of sampling error. We interpret the relationship in Figure 5.4A to be the result of either a single resident or related resident males siring the majority of offspring in groups. As additional males contribute to the progeny gene pool, the variance in alleles donated from adult males decreases, resulting in smaller departures from panmictic expectations in offspring genotypes (Figure 5.4A). However, increased offspring subdivision may result from offspring united by maternal alleles, independent of the degree of polygyny (Chesser 1991a; 1991b; Balloux et al. 1998). We are currently investigating the variance in paternity and maternity on a finer spatial scale. Within groups, we expect that as the proportion of offspring sharing the same father increases, offspring subdivision (θ) will also increase. Behaviorally, the potential for reproductive skew can be approximated by adult sex ratios within groups. In Figure 5.4B, we divide the number of adult females by number of adult males within groups and plot this ratio against resident siring patterns. As expected, the percentage of offspring sired by resident males decreases when the number of adult females in a group increases (cf. Andelmann 1986; Altmann 1990). We note that this longitudinal, intraspecific data—which measures the reproductive outcome of male dispersion and not just a mating opportunity—supports the general pattern found using interspecific data sets: as the number of females within a group increases, males apart from resident males are also able to mate (cf. Mitani et al. 1996a).

Avoidance of inbreeding within these groups increases the heterozygote excess in offspring cohorts. Median tenure length of males in sifaka groups is about 3 years and this is shorter than the average age of reproductive maturity of female sifaka. This suggests that breeding males will disperse (or be evicted by adult females; cf., Richard et al. 1993) prior to the age that their female offspring reach sexual maturity. Such conditions would decrease the probability of father-daughter matings (Clutton-Brock 1989a; Richard et al. 1993; also see Pereira and Weiss 1991). Thus, in sifaka offspring cohorts, significant heterozygote excess is related to sex-biased dispersal and is also likely enhanced by the timing of adult male dispersal. This dispersal reduces the chances for close consanguineous matings and keeps homozygosity among offspring to a minimum. However, it is important to note that considerable amounts of inbreeding may occur before a heterozygote deficit will be observed (cf. Pope 1992).

Genetic subdivision in adults and offspring.

Offspring cohorts consistently show more genetic variation between groups than adult cohorts. Up to 13% of the genetic variation is found between groups of offspring cohorts, whereas this value is only about 8% for adults. This pattern can be illuminated by considering variation in reproduction and yearling sex-ratio. A long-term analysis of fecundity and mortality shows that within the sifaka population there is a yearling sex ratio bias towards males (Richard et al. 1991; 2002). This sex ratio bias may be related to adult female competition for breeding opportunities within groups; selection may favor male offspring, which—unlike females—do not have to compete for breeding opportunities in their natal group (Richard et al. 2002). Cohorts of young males outnumber cohorts of young females and male yearlings make up a greater proportion of the offspring cohort every year in this study except for one (cf. Richard et al. 2002).

Average offspring relatedness in groups is high, approaching the half-sib value of 0.25 in some years. However, birthrates in sifaka groups are low, with no more than two surviving infants per group, per year (Richard et al. 2002). To increase the sample size, offspring cohorts were pooled such that each yearly sample could contain offspring born across four years (i.e., offspring cohorts are sibships; see methods). High relatedness among offspring cohorts (which can contain individuals born in sequential years) suggests offspring are united by subsets of paternal (and maternal) alleles. By definition, closely related offspring cohorts are likely to share alleles identical-by-descent from only a subset of individuals in the total parental gene pool. If there is high reproductive variance across numerous social groups then such non-random sampling of the adult gamete pool will increase the rate that certain alleles are differentially lost between groups. These conditions will enhance the genetic differentiation of offspring cohorts among groups.

Female philopatry and male natal dispersal breaks up the average relatedness of offspring cohorts. As sifaka primary and secondary sex ratios are skewed towards males, a majority of the related offspring cohorts—young males—transfer out of their natal group. Approximately thirty-five percent of all young males transfer each year and there are no clear patterns of kin-based immigration (Richard et al. 1993). Although dispersing males generally transfer into a neighboring group, a single group range boundary in this population can overlap with up to six other groups. Distantly related adult males (i.e., a pairwise relationship of 0.10 or less) may end up in the same group together (as discussed above); however, pairs of males from the same offspring cohort have never been observed to transfer together (Richard et al. 1993). These data suggest that the genetic structure of the offspring cohort is rearranged—via male dispersal—prior to recruitment into adult social groups. Thus, offspring cohorts united by maternal and paternal alleles, as well as sex-ratios biased towards males within groups accounts for why genetic structure of offspring cohorts exceeds that of adults each year: cohorts of young males within groups disperse randomly into adult breeding groups. This may explain why our results differ with the predictions of Chesser (1991a). "Breeding group" models assume a female-biased adult sex-ratio within lineages and equal sex-ratios among progeny (Chesser 1991a; 1991b).

Relevance for the study of social behavior in primates.

Linking demographic and reproductive factors to the distribution of gene correlations within and between social groups has implications for kin selection. Simply knowing if there is a continuity (due to natal recruitment) or disjunction (due to natal dispersal) between the genetic structure of offspring cohorts and the genetic structure of adults can assist in understanding whether kin-selected social behaviors are likely to evolve (Storz et al. 2001). For example, among many group-living primates, same-sex related animals are characterized by dominance hierarchies that appear to mediate disputes over resources; this is particular true of matrilineal societies in macaque species (Gouzoules and Gouzoules 1987). Here, female coancestry provides the impetus for one mechanism through which dominance hierarchies can evolve. This mechanism pertains to maternal investment in future reproductive value. In establishing dominance ranks, mothers often intervene in daughter conflicts on behalf of the youngest daughter. Implicitly, this is a maximization of inclusive fitness for the mother because she is supporting the daughter most likely to have the highest expected future reproduction (Chapais and Schulmann 1980; but see Horroks and Hunt 1983). This behavioral mechanism is more likely to evolve in female philopatric societies because the opportunity for selection to maximize inclusive fitness is prolonged if daughters remain in the same group as their mothers; that is, if matrilines are not randomized by female dispersal.

Recognizing such patterns may help to explain divergent systems of agonistic behavior in lemur species (e.g., between *L. catta* and *E. fulvus rufus*; cf. Pereira and Kappeler 1997). It is illuminating to think about how genetic correlations of same-sexed offspring cohorts relate to the genetic structure of adults in social groups. With regard to the ontogenetic development of adult social behaviors (Pereira 1995), genetic correlations in offspring cohorts that are preserved into adulthood could facilitate the evolution of complex kin-based social behaviors in adults. However, if both sexes of offspring disperse, then adult social groups may not retain evolutionary significant genetic correlations and kin-selected behaviors may not be favored by selection (cf., Pope 2000; Storz et al. 2001). In specifying the relationship between demographic and genetic structure in adults and offspring, the analyses presented above help identify when such conditions are likely to be met.

Table 5.1. Census data by year used in population structure analysis.

Year	*n* total	adult females	adult males	*n* groups	sex ratio (female/males)
1992	77	31	37	13	0.84
1993	79	28	28	10	1.00
1994	93	30	39	12	0.77
1995	147	57	81	22	0.70
1996	122	49	62	27	0.79
1997	105	40	58	21	0.69
1998	178	63	109	27	0.58
1999	191	77	106	28	0.73
2000	148	51	52	25	0.96
2001	131	48	48	22	1.00

Table 5.2. θ and *f* values for adults and offspring by year.

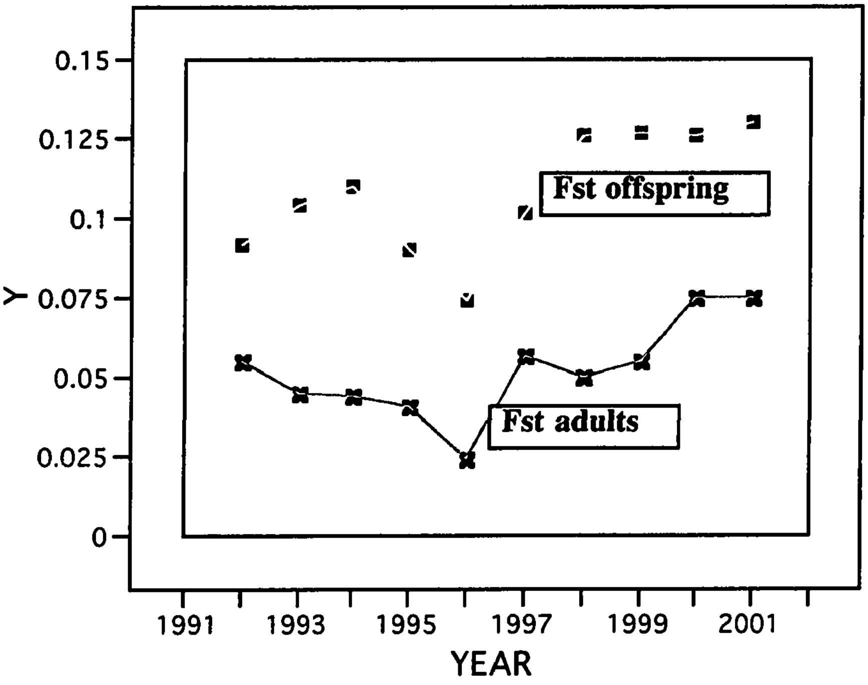
Year	θ adults	θ offspring	θ adult females	θ adult males	*f* adults	*f* offspring
1992	0.055*	0.092*	0.062*	0.025*	0.047	-0.020
1993	0.045*	0.104*	0.056*	0.023	0.017	-0.026
1994	0.044*	0.110*	0.082*	0.047*	0.013	-0.051
1995	0.041*	0.090*	0.068*	0.057*	0.005	-0.051
1996	0.024*	0.074*	0.093*	0.043*	0.019	-0.038
1997	0.057*	0.102*	0.112*	0.034*	-0.025	-0.064
1998	0.050*	0.126*	0.109*	0.049*	0.013	-0.091*
1999	0.055*	0.127*	0.110*	0.031*	-0.001	-0.097*
2000	0.075*	0.126*	0.145*	0.077*	-0.040	-0.116*
2001	0.075*	0.130*	0.147*	0.071*	-0.011	-0.130*

(* = $p < 0.05$)

Table 5.3. Relatedness (*r*) of individuals and siring patterns by year.

Year	(*r*) females	(*r*) males	(*r*) adults	(*r*) offspring	% of infants sired by resident male	*n* offspring	*n* male offspring
1992	0.11	0.04	0.10	0.17	44.0	9	7
1993	0.10	0.04	0.08	0.19	35.0	23	13
1994	0.15	0.08	0.08	0.20	46.0	24	16
1995	0.12	0.10	0.07	0.17	66.0	9	7
1996	0.17	0.08	0.04	0.14	63.0	11	6
1997	0.21	0.06	0.11	0.19	71.0	7	5
1998	0.20	0.09	0.09	0.24	83.0	6	1
1999	0.20	0.05	0.10	0.24	75.0	8	5
2000	0.27	0.14	0.14	n.d	n.d.	n.d.	n.d.
2001	0.27	0.13	0.14	n.d	n.d.	n.d.	n.d.

n.d. (no data): offspring captured in 2000 and 2001 were not analyzed.



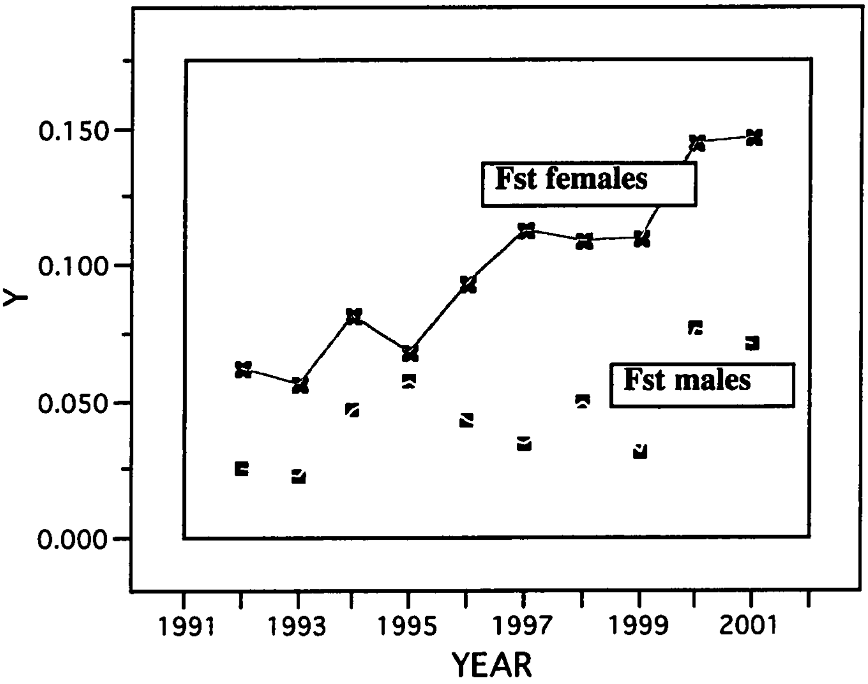


Figure 5.1. Values of *F*ST (θ) for adults and offspring (top) and adult females and adult males (bottom) by year. Y-axis is *F*ST value (see Table 5.2).

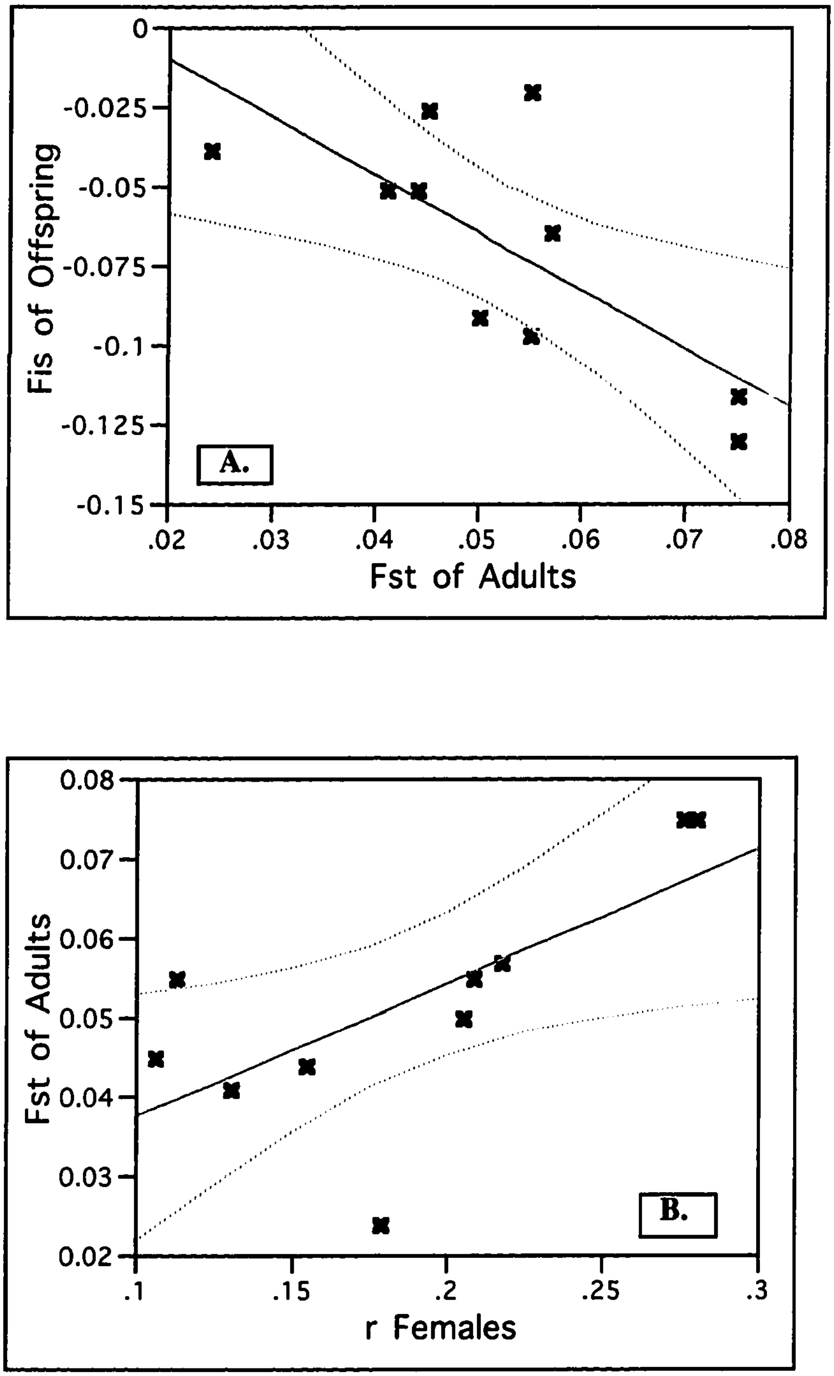
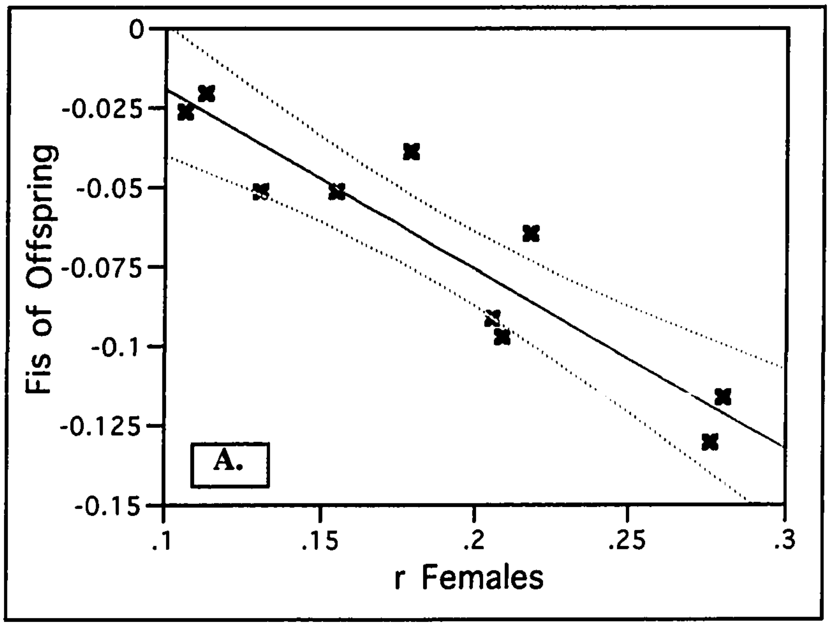


Figure 5.2. The relationship between adult *F*ST (θ) and offspring *F*IS (*f*) (A) and the relationship between adult *F*ST (θ) and relatedness (*r*) of females within groups (B). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.



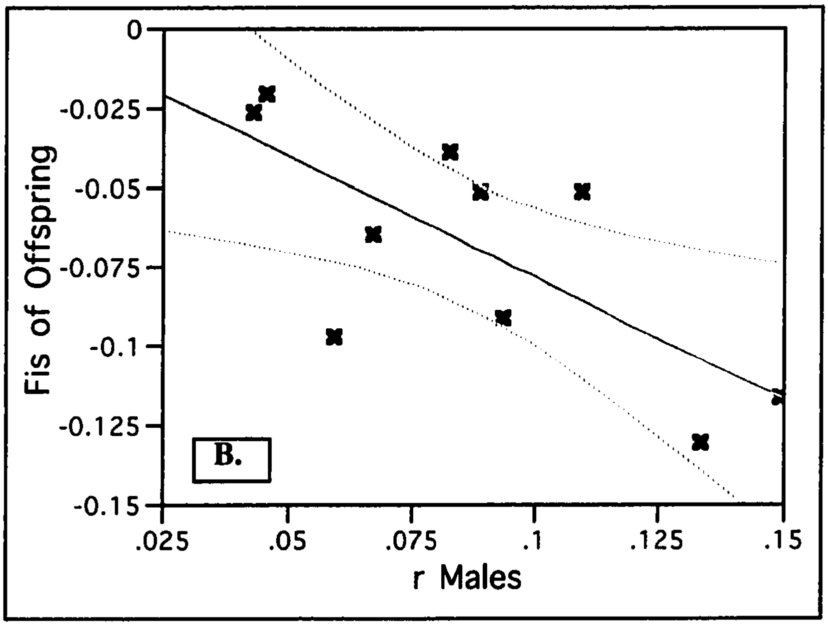


Figure 5.3. The relationship between relatedness (*r*) of females within groups and offspring *F*IS (*f*) (A) and the relationship between relatedness (*r*) of males within groups and offspring *F*IS (*f*) (B). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.

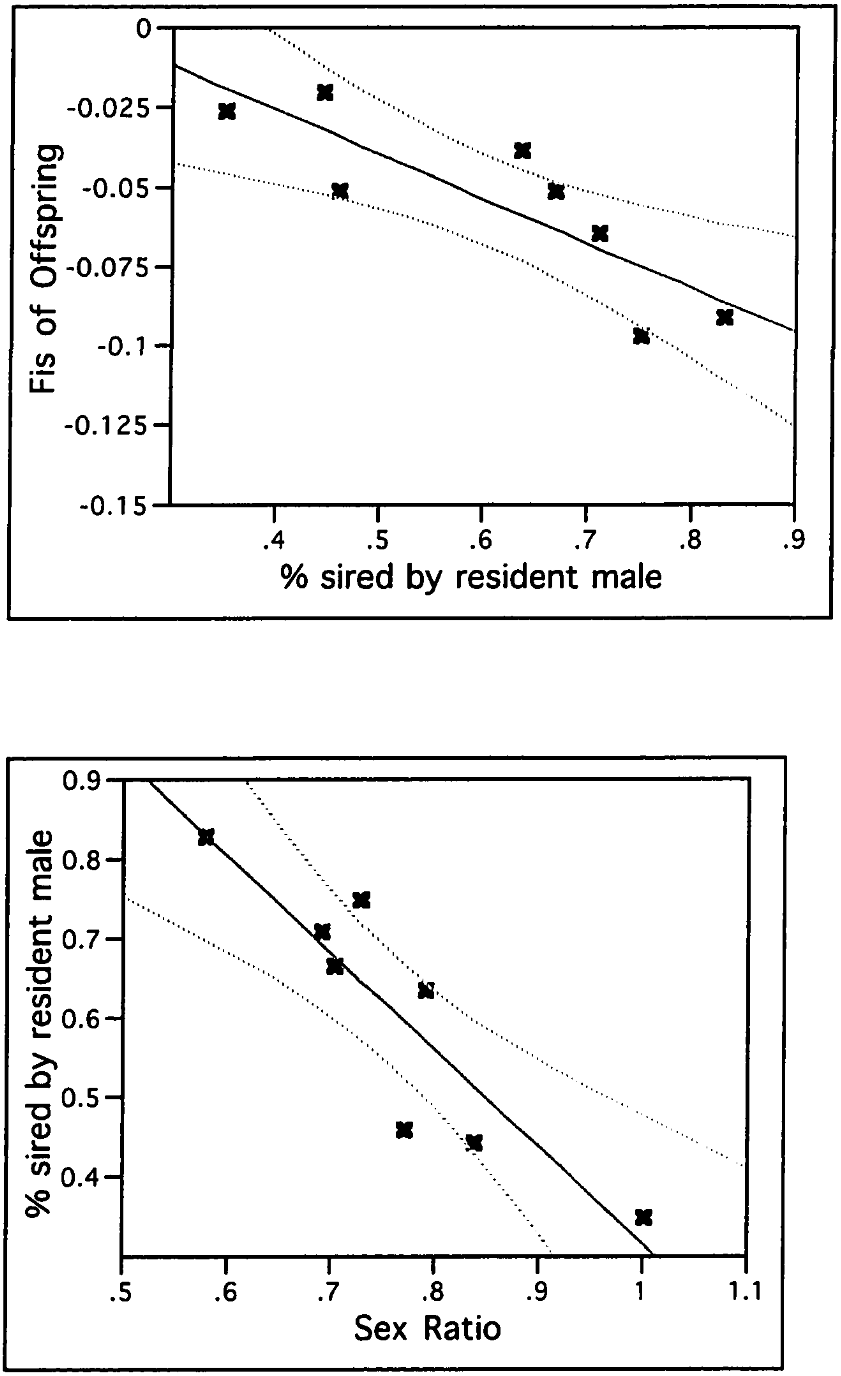


Figure 5.4. The relationship between the percentage of offspring sired by resident males of a group and offspring *F*IS (*f*) (A) and the relationship between the percentage of offspring sired by resident males of a group and the adult sex ratio (females/males) in the population (B). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.

CHAPTER 6

SUMMARY AND CONCLUSIONS

This chapter provides a summary of the major results and conclusions presented in this dissertation. The overall goal of this dissertation was to investigate the causes and consequences of differential reproductive success in male sifaka. This dissertation is part of a larger, on-going, study of white sifaka, and various data sets all collected on this same population were integrated and analyzed for their evolutionary consequence. This study focused on an entire population of wild primates, not just on a few social groups; therefore, differences in individual reproductive output were linked to their population-level effects. To this end, this dissertation analyzed components of male fitness, their phenotypic correlates, and how differential reproductive success and dispersal patterns influence genetic population structure. Results and interpretations are summarized below.

Chapter 2

Chapter 2 is a methods chapter. The major contribution of this chapter is that it presents primer sequences for microsatellite loci isolated in *Propithecus verreauxi verreauxi*. Microsatellite are versatile genetic markers. They have been used in parentage analyses, population genetic studies, and genetic mapping. They have high mutation rates (caused by slippage during DNA replication), which render them sufficiently variable to detect genetic and genotypic differences among individuals, groups, populations, and sometimes between species. The loci isolated in this study were highly polymorphic and proved to be effective for determining parentage in the sifaka population. Although we did not screen these primers on closely related species, (e.g., *P. v. coronatus, P. diadema*), it is possible that the primer sequences provided in Chapter 2 may also be of some use to other on-going field studies of *Propithecus* species. We note this only because isolating new microsatellite loci *de novo* can be costly and time consuming.

Chapter 3

Chapter 3 examines how major components of fitness contribute to total fitness in male sifaka. The approach taken in this chapter was motivated by the results from the parentage analysis. These results indicated a skewed distribution of paternity in the population; further, among the sires, many were not residents of the social group into which they sired offspring. That is, many sires in the population visited adjacent social groups for reproductive opportunities. Due to this, sires were divided up into *resident* and *non-resident* sires. Based on this pattern of reproduction, total fitness (T) was first partitioned into two additive components: a resident-group component (or *within* component, W) and a non-resident component (or *outside* component, O, denoting males who reproduce in social groups other than their own). Once the two additive components were defined, three multiplicative fitness components were further defined: reproductive lifespan (R) (number of years each adult male lived past five), fertility (F) (average number of offspring sired per year), and offspring survival (S) (offspring who lived at least until age 5). These three multiplicative components contribute to either the within and/or outside fitness components (because males can switch from resident to non-resident during their breeding careers). Variation in fitness components were analyzed for their contribution to variance in total fitness (Var *T*).

Results revealed that only 35% of all males sired offspring in the population and most sires only produced one offspring. When expressed as a percentage contribution to total fitness, reproductive lifespan made the greatest contribution for both resident and non-resident sires, followed by fertility and offspring survival. There is a positive relationship between total number of offspring sired by each male (ranging from 0 to 9) and reproductive lifespan. However, there was a trade off between reproductive lifespan and fertility among resident and non-resident males, the latter having a steeper trade off. Owing to sampling methods and high levels of maternal care, infant survival was the lowest contributor to total male fitness.

The large contribution to total fitness made by reproductive lifespan suggests that males who live longer have more opportunities to sire offspring. Reproductive lifespan reflects the per-year opportunity for siring an offspring. If lifespan itself is heritable, then selection will act to increase lifespan, given the constraints and trade offs imposed by physiology. Selection may be more likely to modify reproductive lifespan and not factors such as fertility. This occurs because fertility is dependent on yearly rate of reproductive performance, which may vary due to female choice, male-male competition, and nutritional status relating to seasonal affects. In short, reproductive lifespan is subject to viability selection, whereas fertility is subject to viability selection as well as sexual selection. In seeking outside-group fertilizations, young non-resident males may experience more aggression from resident males. This strategy increases the reproductive rate of non-resident males, but has negative consequences for their long-term survivorship. Factors contributing to males seeking reproductive opportunities outside their resident group are linked to seasonal reproduction, low environmental risks associated with "visits", and female preferences for mating with non-resident males. If the variation in reproductive lifespan is heritable, then selection has the greatest opportunity to act on this variation. Even without considering the prospective effects of selection, knowing which components show the greatest variation is useful for designing future studies. For example, demographic studies can focus on the causes of mortality among males, perhaps giving some insight into how climate and other stochastic factors create variation in cohorts of males independent of genetic quality.

Chapter 4

Chapter 4 examines the phenotypic and socio-demographic correlates of reproductive success in male sifaka. For this analysis, paternity data were combined with longitudinal morphometric and census data. Controlling for seasonal effects and phenotypic covariates, analysis of covariance (ANCOVA) established the association between several somatic measurements and reproductive status (sire versus non-sire). Based on significant results from the ANCOVA, selection gradients were estimated for body mass and limb shape. Logistic regression was used to determine whether sires were more likely to sire offspring in groups with more females, more males, and/or with adult sex ratios skewed toward females.

Results revealed that body mass and limb shape (a composite estimate of limb circumferences) were significantly different among sires and non-sires, with sires being larger and having more robust limbs than non-sires. Canine size does not show a significant association with reproductive status. There was some overlap in phenotypic variation among sires and non-sires; that is, not all sires were larger than non-sires. Body mass was under the influence of stabilizing selection and limb shape was subject to strong directional selection. Sires were more likely to sire offspring into groups that contained absolutely more females and a greater proportion of females relative to males. These results are interpreted within the context of male mating competition and female choice.

The intensity of male-male competition during the mating season varies. Some males engage in fierce fighting while others do not. There is no clear-cut pattern between the victor and whether or not he mates with a female. Male-male mating competition involves a combination of aggression, endurance without physical contact, and non-confrontational episodes where females may simply "choose" a particular male. These behavioral patterns show why the theoretically expected male "competitive" traits (e.g., canine size, body mass) do not increase with increasing reproductive success—such traits only constitute one of many factors that positively influence male reproduction. Because much of the aggressive and endurance-based male mating competition occurs in the trees, selection cannot act to increase body mass indefinitely without compromising efficient arboreal locomotion. Sires were significantly larger than non-sires, but stabilizing selection limits the variance in overall body mass and does not act to increase body mass. Limb shape correlates with reproductive success and it was found that directional selection acts on limb shape to increase muscle mass in the limbs. This result is also related to mate competition within an arboreal setting. Sires either resided in, or visited, social groups with greater numbers of females.

Larger body mass correlates with reproductive success in *both* males and females. Because there are comparable influences of body mass on reproduction, sex-specific selection for increasing body mass does not occur. This result helps explain why sifaka are sexually monomorphic. Additionally, two other factors could contribute to sexual monomorphism. First, fluctuating population numbers caused by living in a stochastic climate, can prevent an advantageous allele from reaching fixation. In this regard, any sexually selected trait that increases reproductive success in males (and is carried but not expressed in females), could fail to fix in the population due to recurrent population bottlenecks. Second, male deference to females at feeding sites (i.e., female dominance) may have negative implications for male adult body mass, thereby precluding the potential for sexual dimorphism to evolve in this population. This second point is cast in terms of a "handicap" scenario, where males (honestly) signal their viability to females by the degree to which they defer to females at a food source.

Chapter 5

Chapter 5 examines the population genetic consequences of differential reproductive success in this population. Longitudinal demographic data pertaining to transfers and reproduction were combined with information on reproductive success in order to determine how these factors affect genotypic distributions within and among social groups. Several measures of population structure were employed. These include F_{IS} (the correlation of alleles within social groups), F_{ST} (the correlation of alleles between social groups), and r (the relatedness of individuals). Different classes of individuals (i.e., offspring, adults, females, males) were analyzed separately in order to determine which classes had the most influence on population structure. By analyzing genetic structure at the level of the social group, information on transfers and reproduction can be linked to genotypic patterns. Additionally, because males seek reproductive opportunities outside their resident group, the genetic consequences of this phenomenon can be examined for its influence on the genetic structure of the social group.

Results revealed considerable subdivision among social groups in the population. Data reveal that, across years, offspring are consistently more heterozygous than expected from panmictic proportions within groups (mean $F_{IS} < 0$), while adults show both positive and negative deviations from panmictic proportions within groups (mean $F_{IS} \approx 0.003$). Adult females are more related than adult males within groups ($r_{\text{females}} > r_{\text{males}}$). Among groups, offspring cohorts are more genetically subdivided than adult cohorts ($F_{ST\,\text{offspring}} > F_{ST\,\text{adults}} > 0$). The probability that resident males sire offspring in their groups decreases as the proportion of females in their groups increases. Offspring cohorts within groups retain more heterozygosity as fewer resident males sire offspring within groups.

The genetic structure of the population corresponds to the demographic and reproductive patterns in the population. Females generally remain in their natal group while males disperse from their natal group upon reaching sexual maturity. The high relatedness of adult females within groups captures the matrilineal organization of sifaka social groups. As female relatedness within groups increases, genetic subdivision between groups increases. This indicates that matrilines retain different alleles, likely due to mutation and drift. Male relatedness within groups does not have a significant association within among group genetic subdivision. Offspring cohorts within groups were more heterozyogous than expected from random mating within social groups. This suggests that males and female parents in the population are unrelated because they consistently donate different alleles to offspring genotypes. This corresponds to the demographic observation that sexually mature males leave their natal group to preclude mating with female kin. When resident males sired the majority of offspring in social groups, offspring were more heterozygous. However, as the number of females in a social group increased, more non-resident males were able to obtain fertilizations. This decreased the variance in alleles donated by males and resulted in smaller departures from panmictic expectations in offspring genotypes within social groups. Because these offspring cohorts within groups often share a common father, mother, or both, they are united by paternal and/or maternal alleles. Therefore, the relatedness among offspring cohorts is high and this creates substantial subdivision among offspring cohorts in different groups. Offspring cohorts are comprised primarily of males, owing to biased sex ratios at birth. Males, as noted above, leave their natal group upon reaching sexual maturity. Dispersing males transfer randomly into adjacent groups, and this breaks up the genetic relatedness within offspring cohorts. This pattern reveals why offspring cohorts are more subdivided than adults.

Major results and conclusions

The key findings of this study are the following:

- The distribution of reproductive success in the population is uneven. Only 35% of all males sired offspring.
- Reproductive success in male sifaka is dependent primarily on how long they live past sexual maturity. There is a positive relationship between reproductive lifespan and total reproductive output.
- There is an inverse relationship between the expected number of offspring produced per year and reproductive lifespan.
- Sifaka males pursue a flexible reproductive strategy in which they reproduce both within their own resident group and in groups other than in which they are members. About half of all sires reproduced in adjacent social groups.
- Factors facilitating reproduction in non-resident social groups are seasonal reproduction, home range overlap, habitat familiarity, and female choice.
- Sires have larger body mass and greater limb muscle mass than non-sires. Canine size does not distinguish sires from non-sires.
- Stabilizing selection acts on body mass and directional selection acts on limb muscle mass.
- Mate acquisition in males is dependent on factors such as male-male aggressive contests, endurance contests, and female choice.
- Selection on body mass and limb muscle mass are likely related to extended bouts of arboreal mate competition.
- Resident and non-resident sires reproduce in groups that had greater numbers of females.
- Sexual monomorphism in sifaka is likely due to a combination of factors including similar body mass requirements for successfully reproducing males and females, genetic correlations between the sexes, low fixation probabilities of beneficial alleles due to population bottlenecks, and female dominance.

- Social groups of sifaka are genetically subdivided. Within groups, females are more related to each other than males. Female relatedness within social groups drives the genetic differentiation between social groups.
- Offspring cohorts within groups retain more heterozygous genotypes than would be expected from random mating in the population. This indicates that offspring have parents that are unrelated.
- Offspring genotypes approach panmictic proportions within groups as more males contribute to the paternal genepool.
- Resident males were less likely to sire offspring in their own group when adult sex ratios became female biased.
- Offspring cohorts were more genetically subdivided than adult cohorts. Natal male dispersal randomizes the genetic structure of offspring cohorts.

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