INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road. Ann Arbor. MI 48106-1346 USA
313/761-4700 800/521-0600

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Order Number 9430260

Reproduction and mating system of Verreaux's sifaka, *Propithecus vereauxi*, at Beza Mahafaly, Madagascar

Brockman, Diane Katherine, Ph.D.

Yale University, 1994

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

Reproduction and Mating System of Verreaux's Sifaka, *Propithecus verreauxi,* at Beza Mahafaly, Madagascar

A Dissertation
Presented to the Faculty of the Graduate School
of
Yale University
in Candidacy for the Degree of
Doctor of Philosophy

by
Diane Katherine Brockman

May 1994

ABSTRACT

Reproduction and Mating System of Verreaux's Sifaka *Propithecus verreauxi* at Beza Mahafaly, Madagascar

Diane Katherine Brockman
Yale University
1994

Field work was conducted on the mating patterns of Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly, Madagascar, prior to and during the breeding season from November 1990 - March 1991 and from November 1991 - April 1992. Data on the behavioral, hormonal, and social correlates of reproduction were collected in order to examine adaptive explanations for multiple mating by females.

Verreaux's sifaka are 2.5-3.0 kg diurnal strepsirhine primates inhabiting riverine and dry forests of south and southwest Madagascar. Sifaka have a minimum 3-month breeding season. July - September births occur in the south during which a single infant is born after a 162-day gestation. Infants are weaned 5 months later coincident with the onset of austral summer rains.

Over 644 focal animal hours and 485 daily fecal samples were collected on 5 marked females in the Vaovao and Vavy Masiaka social groups composed of 2 males and 3 females, and 3 males and 2 females, respectively. Solid phase extraction and radioimmunoassay techniques were used to measure fecal estradiol and progesterone levels. Sifaka are not pair-bonded. Social and sexual relationships were characterized by female-female affiliation and female-directed agonism toward males. Females mated with multiple resident and non-resident males during the breeding season. In most cases, mating was associated with elevated estradiol levels. Although the timing of hormonal estrus varied between groups, estrous synchrony/asynchrony did not determine whether multiple mating by females occurred. Rather, mating was limited by intrasexual competition associated with guarding and copulatory harassment, aversions to mating with certain males, and aggressive mating tactics by individual males. Seven to 15-day hormonal estrous periods and demographic shifts in and increased contacts with neighboring groups enhanced the opportunity to mate with more than one male. Ejaculation frequency did not affect females' conception rate. Multiple ejaculations resulted in conception in three polyandrous matings, while a single ejaculation resulted in conception in one monoandrous pair. It is argued that three selective factors underlie multiple mating in females: increased insurance against male infertility, increased indirect male parental care, and increased reproductive success through reduced inter-group agonism with related neighboring males.

ACKNOWLEDGMENTS

A dissertation is a journey that one does not take alone. In my case, it begins and ends with Dr. Alison Richard. She not only provided me the opportunity to explore a new direction in life, but she was also a teacher, mentor, and friend. I feel privileged to have studied sifaka at Beza Mahafaly. I am deeply grateful for the discussions we had about my work and for Dr. Richard's careful attention to my writing. Dr. Richard will remain for me a model of what it means to be a teacher and an anthropologist.

I am also indepted to another member of my committee, Dr. Pat Whitten, who patiently taught me the laboratory skills necessary to complete this project. The many hours we spent in the lab and on the phone were instructive, stimulating, and enjoyable. I have gained a real appreciation for the insights to be derived from fecal steroid analysis. My perspective on the importance of this material will never be quite the same.

My thanks extend as well to Dr. Steve Beissinger who was a source of much encouragement and who provided helpful and detailed readings of this dissertation.

Permission was granted to conduct research in Madagascar by the Direction des Eaux et Forêts de Ministère de la Production Animale (Élevage et Peche) et des Eaux et Forêts, Ministère des Affaires Étrangerès, Ministère de l'Enseignement Supérieur, and Ministère de la Recherche Scientifique et Technologique pour la Developpement.

The research was conducted under the auspices of an accord between Ecole Superieure des Sciences Agronomiques (ESSA), Yale University, and Washington University. Mme. Berthe Rakotosamimanana and M. Pothin Rakotomanga were instrumental in providing logistical support for this research. The care, dedication, and commitment M. Pothin Rakotomanga extends to Beza Mahafaly Special Reserve makes working there possible.

I am particularly grateful to my research assistants, Alison Hurley, Bram Gunther, and Paige McCurdy for the enthusiasm with which they expertly and carefully collected the sifaka fecal samples. The dissertation would have been much less substantial without these sources of data.

Life in New Haven would not have been as comfortable as it was without the enjoyable hours spent in conversation with colleagues and fellow students. Besides being a good friend, Marian Schwartz was instrumental in helping me navigate the Yale University system. Her cheerful phone calls during the long hours of writing will be remembered with fondness. Her home was always open to me, and for that I am especially grateful.

Finally, this rich and challenging journey would not have been possible without the love, encouragement, and support of my family. To Alex, Blaise, and Jim, thank you from the bottom of my heart.

This project was generously supported a Grant-in-Aid of Research from Sigma Xi, grants from The Williams Fund of

Yale University, The Conservation Fund of the American Society of Primatologists, Chicago Zoological Society, Jersey Wildlife Preservation Trust International, The Boise Fund of Oxford University, National Science Foundation (#SBR-3903531), and fellowships from Yale University and the American Association of University Women.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I. INTRODUCTION

A. The Research Goal and Its Context

For the last several decades, anthropologists have employed evolutionary theory to explain intersexual differences in primate mating behavior (Dunbar, 1984; Clutton-Brock & Harvey, 1977; Wilson, 1975). Originally proposed by Darwin (1859, 1871) to explain the evolution of morphological and behavioral differences between males and females, sexual selection theory posits that intrasexual competition and mate choice differentially characterize male and female reproductive efforts in most species (Trivers, 1972).

Modern interpretations of sexual selection theory, however, have focused on the relationship between pre- and post-zygotic investment of resources in gametes and sexual competition, and the latter's effect on lifetime reproductive success (Trivers, 1972). Male and female mating patterns are presumed to differ because they have competing reproductive priorities. Males are assumed to have unlimited supplies of sperm and are expected to compete for and acquire as many matings as possible, with the corollary expectation that they will therefore exhibit greater variance in lifetime reproductive success. Females, having finite supplies of eggs, are expected to be highly selective in choosing mates and to exhibit negligible variance in lifetime reproductive success (Bateman, 1948). In short, males are supposed to behave largely competitively and with little discrimination, whereas females are expected to behave noncompetively and be discriminating in their selection of mates.

Recent studies of mating in free-ranging primates have shown that male and female mating patterns are much less divergent than predicted by modern interpretations of sexual selection theory. Not only are males highly selective in their choice of mates (Chapais, 1983; Hausfater, 1975; Smuts, 1985; Tutin, 1979), but females compete for access to males (Dunbar, 1984; Lindburg, 1971; Seyfarth, 1976; Young, 1981) and mate with multiple males during a breeding season (Cords et al., 1984; Koyama, 1988; Pereira & Weiss, 1991; Sauther, 1991; Small, 1990). Moreover, while the degree of variance in male reproductive success has yet to be demonstrated, females in at least some species are now known to exhibit marked variation in lifetime reproductive success (Altmann et al., 1988; Fedigan et al., 1986; Gouzoules et al., 1982). Explanations for why females mate with several males include: (1) they are seeking to confuse paternity to forestall male infanticide (Collins, et al., 1985; Goodall, 1977; Hrdy, 1979; Rudran, 1979; Sugiyama, 1965) and/or ensure male infant care (Garber et al., 1984; Goldizen, 1987; Taub, 1980, but see Ménard et al., 1992), or (2) they are ensuring fertilization (Milton, 1985; Sauther, 1991; but see Bercovitch, 1987).

Exploration of these alternative explanations requires information about paternity and the temporal relationship between mating behavior and gonadal hormones, and also about the social factors influencing that relationship. The relationship between mating and gonadal hormones in free-ranging primates is pertinent to questions about the possible effects of socially mediated estrous asynchrony, mating frequency, and mate preference on conception and paternity. These questions must be answered if we are to estimate the relative contributions of fecundity and social factors to lifetime reproductive success in female primates. While major studies have been made in recent years on paternity (Curie-Cohen et al., 1983; Melnick & Kidd, 1981; Melnick et al., 1984; Martin et al., 1992; Paul et al. 1992), there have been few studies of the socioendocrinology (Ziegler & Bercovitch, 1992) of mating behavior in free-ranging primates (Andelman et al., 1985; Clarke et al., 1991; Strier & Ziegler, 1994).

The goal of this study was to investigate mating patterns in Verreaux's sifaka (*Propithecus verreauxi*) at Beza Mahafaly, Madagascar via behavioral, hormonal, and social correlates of reproduction. Mating refers to copulatory behavior in which intromission and thrusting have occurred. Mating pattern denotes the characteristics of mating behavior based on the numbers of partners involved during a single breeding season. Polygyny is defined as a male mating with more than one female; polyandry is when a female mates with more than one male; monogamy (or monoandry) occurs when a female mates with only one male, and promiscuity characterizes a pattern in which a female mates with all available adult males (Clutton-Brock, 1989). Mate preference refers to either the differential solicitation and acceptance of some individuals for mating while rejecting others, or the differential temporal ordering of solicitation and acceptance of some individuals before others. Synchrony refers to the complete or partial temporal overlap of estrus while asynchrony is the temporal non-overlap of estrus. Behavioral estrus refers to mating behavior and hormonal estrus refers to the duration of estradiol elevations associated with mating.

Verreaux's sifaka are diurnal strepsirhine primates inhabiting riverine and dry forests of south and southwest Madagascar (Pollock, 1979; Tattersall, 1982). Sifaka live in social groups ranging in size from two to thirteen individuals, in which female philopatry and social dominance appear to be the rule (Richard, 1987; Richard & Nicoll, 1987; Young et al., 1990; but see Pereira et al., 1990). Although *Propithecus verreauxi* is one of the more studied of the endangered Malagasy lemurs (Jolly, 1966, 1967, 1984; Jolly et al., 1982; Richard, 1974, 1976, 1977, 1978, 1985, 1987, 1992; Richard & Heimbuch, 1975; Richard & Nicoll, 1987; Richard et al., 1991), its reproductive physiology and mating system remain poorly documented. Sifaka have a minimum breeding season of three months (Jolly, 1966;

Richard, 1974) during which individual females are receptive to males for up to 72 hrs no more than twice per year (Brockman et al., submitted). A "pseudo-estrus" characterized by vulval pinkening and an increase in male "visiting" and scent-marking behavior has been observed one month prior to copulation (Richard, 1974). A July through September birth peak occurs in southern populations (Jolly, 1967; Richard, 1974), during which a single infant is born after a 162 day gestation (Petter-Rousseaux, 1962). Infants are weaned five months later coincident with the onset of austral summer rains (Richard, 1974).

B. Background

1. Mating Typologies and Primate Mating Patterns

The categories most commonly used to describe the mating patterns of mammals are "monogamy," "polygyny," "polyandry," and "promiscuity" (Clutton-Brock, 1989). Primate species have commonly been assigned to one of these categories on the basis of social group composition rather than observations of mating. Species in which groups contain a single male and female are presumed to be monogamous, those with a single male and several females are designated polygynous, groups containing a single female and several males are inferred to be polyandrous, and those with several males and females are characterized as promiscuous (Clutton-Brock, 1989). Recent studies (Cords, 1984; Ruth, 1991; Tsingalia & Rowell, 1984;) have shown, however, that social group composition is often a poor predictor of mating patterns in primates even among monogamous species where extra pair copulations are known to occur among single male-female pairs (Mason, 1966). Similarily, social group composition cannot readily be used to infer mating patterns among sifaka because sifaka social groups vary in composition from a stable group of females and one or more males to one female and one or several males.

Research over the last twenty years suggests that sifaka mating relationships are extremely flexible. Mating flexibility may represent alternating patterns in mating which are situation-dependent incorporating monogamy (O'Connor, pers. comm.) and female-controlled polygyny (Richard, 1992). Rather than a typological approach to mating patterns (Clutton-Brock, 1989), this study took a dynamic approach rooted in the recent recognition of the importance of small-scale demographic effects on primate social organization. The dynamic demographic qualities of social groups have long been recognized in the study of primates (Carpenter, 1940; Cohen, 1969; Dunbar & Dunbar, 1974), but the contributions of small-scale demographic changes to mating flexibility have been under-emphasized (but see Dunbar, 1984).

The flexibility of mating relationships found among sifaka is not unique or even, perhaps uncommon among primates. Rather, the categories frequently used to describe species-wide primate mating patterns have served to normalize behavior and mask real variability. Recent studies of wild callitrichids, for example, show that some *Callithrix* and *Saguinus* species, which were previously thought to live in monogamous family groups, have highly variable social groups (Dawson, 1978; Garber et al., 1984; Hubrecht, 1984; Sussman & Garber, 1985; Terborgh & Goldizen, 1985) in which monogamy, polyandry, polygyny and/or polygyandry occur (Garber et al., 1984; Goldizen, 1987, 1989, 1990; Rylands, 1982, 1986; Terborgh & Goldizen, 1985; Ruth, 1991). In forest *Cercopithecus* primates, polygyny and promiscuity occur in *Cercopthecus ascanius* and *Cercopithecus mitus* groups, the latter associated with the breakdown of the one-male group structure (Butynski, 1982; Cords, 1984, 1988; Tsingalia & Rowell, 1984), and coinciding with multimale influxes and increased sexual activity among synchronously mating females (Cords, 1984; Cords et al., 1984).

2. Strepsirhine Reproduction and Mating Patterns

a. The Behavioral and Hormonal Characteristics of Strepsirhine Primates. Previous studies suggest that with few exceptions, strepsirhines are seasonally polyestrous with females being receptive to males during brief periods each year (Hrdy and Whitten, 1987). Estrus coincides with ovulation and is behaviorally defined by an increase in attractivity (female stimulus value to males), proceptivity (female sexual initiating behavior), and receptivity (copulation willingness; Beach, 1976), communicated to males via visual and olfactory cues. This brief, seasonal estrous period distinguishes strepsirhine from catarrhine primates; most catarrhine primates have year round reproduction (but with seasonal birth peaks) characterized by menstruation and a longer and more flexible period of sexual activity not strictly confined to ovulation (Hrdy and Whitten, 1987).

This transition from estrus to menstrual cycle has been described in terms of "loss of estrus" during primate evolution. However, recent studies of captive primates suggest that it may be more productive to investigate the difference between strepsirhines and catarrhines by studying the hormonal basis of receptivity and the social contexts in which it becomes circumscribed or situation dependent (Hrdy & Whitten, 1987; Dixson & Lloyd, 1988). For example, female attractivity and proceptivity coincide with rising estrogen levels in *Varecia variegata* (Shideler et al., 1983), *Callithrix jacchus* (Dixson, 1986), *Miopithecus talapoin* (Dixson & Herbert, 1977), and *Macaca mulatta* (Michael & Bonsall, 1979; Johnson & Phoenix, 1976; Wallen & Goy, 1977; Dixson, 1983). But estrogen withdrawal prior to or at ovulation coincides with female receptivity in *Lemur catta* (Van Horn & Resko, 1977), *Varecia variegata* (Shideler et al., 1983), *Galago crassicaudatus* (Eaton et al., 1973), *Macaca mulatta* (Parkin & Hendrickx, 1975), and *Macaca silenus* (Shideler & Lasley, 1982). Consequently, it has been suggested that a prolonged follicular phase may be responsible for the expanded period of attractivity and proceptivity that distinguishes female catarrhine primates (Shideler & Lasley, 1982).

Evidence of spermatogenic seasonality in male strepsirhines comes primarily from studies of variations in testicular size between the breeding and non-breeding seasons (Bogart et al., 1977; Perry et al., 1992; Petter-Rousseaux, 1964; Petter-Rousseaux & Picon, 1981). Although breeding season increases in testicular size have been assumed to be an accurate predictor of spermatogensis (de Krester, 1984), and thus fertility in males, testes size appears to be unrelated to reproductive fitness in some captive strepsirhines (Perry et al. 1992). Moreover, laboratory studies of seasonal variation in sperm morphology of *Eulemur fulvus mayottensis* suggest that while continuous spermatogenesis occurs throughout the year, seasonal variations occur in sperm count and motility, and monthly variations occur in numbers of abnormal sperm (i.e. teratospermia) produced by each male (Brun & Rumpler, 1990). Significant differences in percentage of teratospermia were found between seasons and among individuals ranging from 23.7% to 56.7% among breeding season males to 49.5% to 88.5% among non-breeding season males. Finally, although all males were found to produce a high percentage of normal-appearing, motile sperm "at some point during the breeding season" (Brun & Rumpler, 1990:5), there was marked individual variation in the time of onset of effective spermatozoa production. Teratospermia is also known to occur in captive gorillas (Seuanez et al., 1977), free-ranging rhesus macaques (Zamboni et al., 1974) and humans (Schwartz et al., 1984) but its potential effects on male (and female) lifetime reproductive success are unknown.

b. Social Influences on Reproduction and Implications of Estrous Synchrony and Order. The study of social influences on strepsirhine reproduction focuses on factors inhibiting male and female reproductive function (Izard, 1990) and on factors regulating estrous synchrony. Inferred social factors inhibiting strepsirhine reproductive function are of two kinds: female-female and male-male competition, and the reproductive consequences for females of the presence of dependent offspring.

Modifications in the captive social environment (e.g. changing group membership) have been found to result in female reproductive abnormalities in several species (Table 1.1). Although none of these studies experimentally investigated the mechanisms of social inhibition, Izard (1990) suggested that olfactory communication is the most likely explanation based on morphological, neural, and chemical characteristics of strepsirhines.

While evidence is mounting that social mechanisms regulate estrous cycles (Izard, 1990), the effects of environment on estrous synchrony have yet to be evaluated. Pereira (1991) has argued that both photoperiodic and social

Table 1.1. Social influences on strepsirhine reproduction (Izard, 1990).

Species	Among Females	Outcome	Females/ Offspring	Outcome	Among Males	Outcome	Reference
Microcebus murinus	Yes	P			Yes	T	Perret, 1982,1985
	Yes	E					Petter-Rousseaux, 1962, 1964 Andriantsiferana et al., 1974 Glatston, 1979
	Yes	U					Glatston, 1979 Perret, 1982
	Yes	A,F					Glatston, 1979
Lemur catta	Yes	I					Taylor, 1986
Varecia variegata					Yes	T	Foerg, 1982
Galago senegalensis			Yes	O			Izard and Simons, 1987

Note: Consequence of social influences:

P - Inhibits pituitary function
E - Estrous cycle aberrations
U - Uterine abnormalities
A - Abortions
F - Fetal resorptions
I - Decreases infant survival
O - Ovarian function inhibited when lactating
T - Testicular function inhibited in presence of breeding male

entrainments lead females within *Lemur catta* groups to experience 7- to 20-day estrous periods. A single pheromone-based signal response system was hypothesized to mediate (i.e. shorten and lengthen) estrous cycles within the social group, thus facilitating the development of estrous asynchrony and female mate choice.

Laboratory investigations of mechanisms influencing reproduction in male strepsirhines suggest that both environment and social milieu affect seasonal changes in male reproductive capacity. In studies of captive lemurs increased testes size was associated with decreased day length (Foerg, 1982; Kappeler, 1987; Perry et al., 1992; Vick et al., 1989). In studies of laboratory *Microcebus murinus,* pheromone-like signals from dominant males lead to sexual inhibition in subordinate males (Schilling et al., 1984). In the latter case, the inhibitory effects of dominance were hypothesized to be modulated by photoperiodicity and reproductive physiology associated with andrenocortical activation (Schilling et al., 1984). Although the effects of social dominance on male reproduction in sifaka have yet to be demonstrated, potential seasonal and rank-dependent variations in sperm quantity and quality may influence female reproductive success via constraints on fertility and lifetime reproductive rate.

In sifaka, within-group temporal patterning of estrus may have implications for the mating system as it relates to the ability of males to monopolize females and to the ability of females to select mates. If all of the females in a group are tightly synchronous (i.e. behavioral estrus occurs on the same day), then it is difficult for males to monopolize females and polygyny is constrained. If a group's females are not simultaneously in estrus, then a male may be able to monitor and copulate with all of the females in his group and with females in other groups as well, thus enhancing polygyny. The implications of estrous synchrony for females include the possibility of monopolization of a preferred male by one presumably dominant female, an increase in female-female competition (i.e. copulatory harassment), and a reduction in opportunities for subordinate females to select preferred mates. On the other hand, if females cycle asynchronously, female-female competition for a preferred male may be reduced and opportunities for polyandrous mating would be enhanced. Each female would have the potential to mate with a preferred male as well as with other males. The greater the level of between- and within-group estrous asynchrony, the easier it is for males to monopolize mates, and the greater the opportunity for males and females to select multiple mates. Thus, estrous asynchrony affects mating diversity in *Propithecus verreauxi*, enhancing the development of polygyny in males, polyandry in females, and conflict between males and females.

Within-group temporal ordering of estrus may influence conception and infant survival. This occurs by affecting the ability of females to select multiple mates with sufficient high quality sperm to conceive early enough in the breeding season for weaning to occur during the period of seasonal food abundance. The likelihood of conception would be increased among asynchronous females, regardless of rank, because female-female competition for multiple mates would be reduced and the opportunity for polyandrous mating would be enhanced for all females. However, in the presence of rank-dependent estrous order, dominant females would be able to conceive earlier in the breeding season, give birth prior to the austral winter period of food scarcity, and wean infants at the onset of the subsequent breeding season's food abundance in time to cycle and conceive again. Subordinate females, on the other hand, would conceive later in the breeding season and give birth during the winter when food resources would be only marginally adequate to support lactation, thereby increasing the likelihood of infant mortality. Thus, a testable, though as yet untested, proposition results wherein rank-dependent estrous order increases variance in lifetime reproductive success by enhancing reproductive rate and infant survival among high-ranking females.

c. Strepsirhine Mating Patterns. Our understanding of strepsirhine mating patterns is based on inferences from social group composition and size and rarely observed instances of mating. Based on group size, monogamy has been reported for *Phaner furcifer* (Petter et al., 1971), *Avahi laniger* (Martin, 1972; Petter, 1962: Pollock, 1979), *Indri indri* (Petter, 1962; Pollock, 1975), *Eulemur mongoz* (Schaaf & Stuart, 1983; Tattersall & Sussman, 1975; Tattersall, 1976; Tilson, 1986; Wright, 1990), *Eulemur rubriventer* (Overdorff, 1988; Pollock, 1979), *Varecia variegata* (Iwano, 1989; Petter et al., 1977; White, 1989), and *Hapilemur griseus* (Petter & Peyrieras, 1975). Polygynous groups include *Eulemur macaco* (Petter, 1962) and *Eulemur fulvus* (Petter, 1962). Polygyny is also inferred for some solitary species as *Microcebus murinus* (Martin, 1972, 1973), *Lepilemur mustelinus* (Charles-Dominique & Hladek, 1971), and *Galago moholi* (Harcourt & Bearder, 1989).

Data on mating behavior show that monogamous mating occurs in *Eulemur rubriventer* (Overdorff, 1988) and polyandrous mating patterns (i.e. serial matings with a select group of males by a single female) occur in *Lemur catta* (Budnitz & Dainis, 1975; Jolly, 1966; Koyama, 1988; Sauther, 1991) and *Daubentonia madagascariensis* (Sterling, 1993). Variable patterns of mating occur in wild *Varecia variegata* during a single breeding season, suggestive of monogamy, polygyny and polyandry (Morland, 1993).

3. Sifaka Reproduction and Mating Patterns

Data on *Propithecus verreauxi* reproduction and mating come from captive and wild populations. These studies show that sifaka have a three month breeding season (Haring, 1988; Jolly, 1966; Richard, 1974) during which females are receptive to males for up to three days no more than twice per breeding season (Brockman, et. al., submitted). Postpartum estrus has been reported in one captive female over an intermittent three year period after the death of her infants (Haring, 1988). Data on estrous synchrony come from birth data and infrequent observations of female mating. They suggest that females appear to be asynchronous within groups (Jolly, 1967; Richard, 1974). Data on the hormonal basis of mating behavior come from a preliminary study of two captive female Verreauxi's sifaka at Duke University Primate Center, Durham, NC. Copulations occurred on the day of elevated estradiol levels, but not all estradiol peaks were associated with mating (Brockman et al., submitted).

Sifaka have rarely been seen mating even in groups in which births occur subsequently. Perhaps this is because most copulations occur at night, and/or they are brief and cryptic. Most previous observations of mating in wild sifaka come from groups apparently undergoing transition. In these groups "either resident and non-resident males engaged in extended battles (involving fights and chases) and the estrous female mated with the winner or, if no clear winner emerged, [she mated] with a non-resident and non-combatant male" (Richard 1992:5). In one group of three males and two females at Hazafotsy, one female copulated with two non-resident males sequentially over a two day period and subsequently conceived, while the other female mated with one of the resident males but produced no offspring (Richard, 1974). In another similarily composed group at Beza Mahafaly, a female mated with two non-resident males from different neighboring groups on the same day (Richard, 1992), but no offspring resulted from these matings (Richard, pers. comm.). Apart from the results of this study, the only other observed sifaka copulation occurred as a "quiet copulation" between a female and resident male at Berenty (O'Connor, pers. comm.). This copulation occurred on the periphery of the group and was apparently undetected by other group members.

C. Specific Aims of This Study

It has been suggested in previous studies of primate mating patterns (see above) that females mate with multiple males to confuse paternity and thereby forestall infanticide by males, ensure male parental care, and ensure fertilization. Although data are lacking on paternity and reproductive endocrinology in free-ranging strepsirhines, multiple matings among high-ranking female *Lemur catta* have been argued to enhance the likelihood of fertilization

(Sauther, 1991). Without data on paternity, the temporal relationship between mating behavior and gonadal hormone levels, the timing of estrus among females, and the demographic and social factors affecting mating, we cannot measure the effects of multiple matings on conception or the contributions of fertility and social factors to female reproductive success.

Although estrous timing and female mate preference are theoretically important in sifaka mating (see above; Brockman et al., submitted), several issues remain unexamined. Three are addressed thematically in this study, based on their hypothesized effects on conception and mating behavior:

1. Specific Aim 1. To Describe the Behavioral and Hormonal Characteristics of Seasonal Reproduction

The first objective was to characterize estrus, pseudo-estrus, and anestrus as behavioral and hormonal events. Based on knowledge of the reproductive biology of other strepsirhines (see above), I expected to find that: (1) estrus (defined by an increase in female attractivity, proceptivity, and receptivity [Beach, 1976]) occurs for up to 72 hours no more than twice per breeding season; (2) pseudo-estrus occurs for two to three days one month prior to estrus and is characterized by females being attractive but not receptive to males, receptivity being definitive of behavioral estrus; and (3) anestrus temporally brackets pseudo-estrus and estrous and is defined by the lack of attractivity, proceptivity, and receptivity. With respect to the hormonal correlates of reproduction, I expected to find that: (1) female attractivity and proceptivity are characterized by elevated estrogen levels; (2) receptivity coincides with, or just follows, most estrogen peaks; (3) pseudo-estrus is defined by a two to three day period of increased estrogen levels one month prior to estrus; and (4) anestrus is defined by consistantly low estrogen and progesterone levels, unless there is a pregnancy, in which case progesterone levels are consistantly elevated followed by elevated estradiol levels 40+ days post-mating until just before parturition.

2. Specific Aim 2. To Determine the Degree of Reproductive Synchrony

The second objective was to determine the degree of within- and between-group reproductive synchrony. Based on preliminary data concerning estrous synchrony in female strepsirhines (see above), I expected to find that: (1) most females are asynchronous; (2) estrous asynchrony is age- and rank-dependent, affording dominant females temporal priority of access to preferred resident (and non-resident) males; (3) in the event of complete estrous synchrony, dominant females mate during the first estrous cycle, and subordinate females mate during the second estrous cycle; and (4) in the event of partial estrous synchrony, dominant females mate first when estrogen levels are at their peak and conception is most likely, and subordinate females mate second when estrogen levels are diminished and conception is less likely, and/or they mate during the second estrous cycle.

3. Specific Aim 3. To Determine the Social Correlates of Reproduction

The third objective was to determine the social correlates of female mating patterns. Based upon previous data on sifaka mating patterns (see above), I expected that most females: (1) mate with more than one male; (2) mate with some males before others; (3) do not mate with all of the males that solicit them; (4) mate preferentially with older resident and non-resident males when they are most likely to conceive and then mate with younger males; (5) are more likely to conceive if they have mated with two or more males than if they have confined their mating to one male; and (6) if subordinate, compete for access to preferred males by harassing copulating pairs.

D. Field Site and Study Population

1. Field Site

Propithecus verreauxi at Beza Mahafaly Special Reserve occupy one of the driest regions of Madagascar. Annual rainfall averages only 720 mm and is concentrated during the summer months of October through March. Day time and evening temperatures during the austral summer range from 51°C to

21°C (Brockman, pers. obser.), while winter temperatures range between 36°C and 3°C (Richard et al., 1991).

Beza Mahafaly Special Reserve is divided into two non-contiguous sections: Sector 1 (100 ha) situated along the Sakamena River and Sector 2 (500 ha) located 5 km west of the Sakamena River (Figure 1). The reserve has a rich array of fauna composed of more than 68 bird, 10 mammal, and 18 reptile species. Sector 1 is a low gallery forest, with a vegetative gradient ranging from xerophtic plants to a riverine forest dominated by *Tamarindus indica* along the river. Sector 2 is largely spiny forest dominated by *Alluanudia procera* along with members of the Didiereacae and Euphorbiacae (Richard et al., 1991).

Established as a reserve in 1979, Sector 1 has been protected from cattle and goat herds by a barbed-wire fence. Sector 2 has been delimited by a three meter wide cleared path bounded by an *Opuntia* barrier. A grid trail system has been established for both sectors. Sector 1 has a 100m-to-a-side grid and Sector 2 has a 500m-to-a-side. Since its inception, Beza Mahafaly has been the focus of collaborative botanical and zoological research under an Accord between the University of Antananarivo, Yale University, and Washington University (Richard et al., 1991).

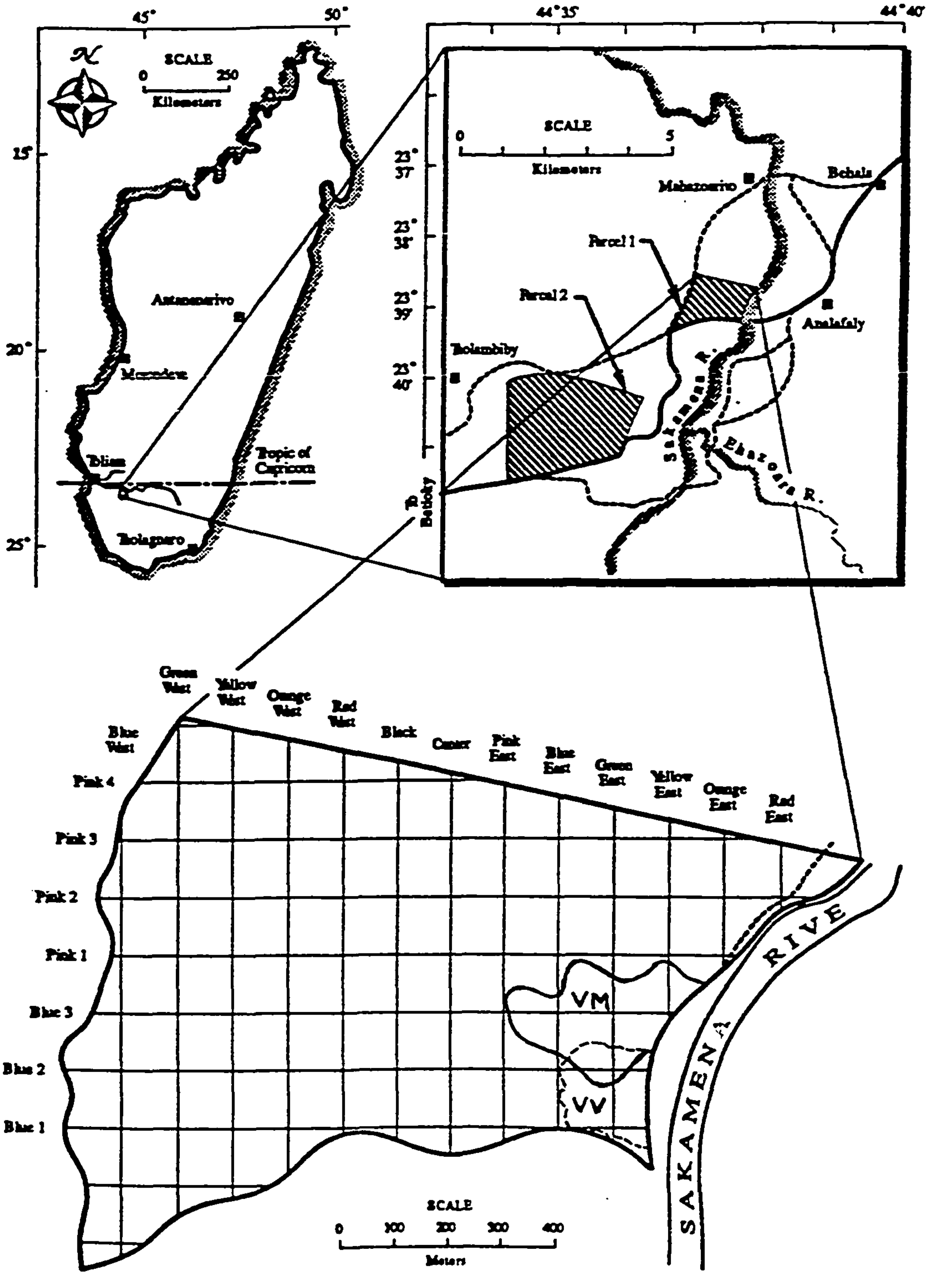


Figure 1. Map of location of Beza Mahafaly Special Reserve in Madagascar (after Sauther, 1991).

2. Study Population

At the time of this study there were about 170 sifaka living in 28-30 groups in the reserve. Eighty-two individuals were marked with ear notches, and colored and numbered collars and tags. Home ranges of these groups are completely encompassed by the boundaries of Sector 1. Study population members move freely between the reserve and the unprotected forest and were part of a larger biological population inhabiting the surrounding forest. The study population has been censused annually since 1984, as part of a long-term demographic study (Richard et al., 1991). Social groups are composed of between 2 and 13 individuals, and in 1991 had a modal group composition of 3 males and 2 females. Home ranges of the social groups vary from 4 to 6 ha with considerable overlap between ranges of neighboring groups. The diet of sifaka at Beza Mahafaly is composed primarily of young leaves and shoots, supplemented by seasonally available fruits and flowers (Richard et al., 1991).

Two habituated social groups from Sector 1 were studied for 5 months each during the 1990-91 and 1991-92 field seasons. *Propithecus verreauxi* at Beza Mahafaly were particularily conducive to studies of mating diversity, because individuals were well habituated and had detailed demographic and social group histories spanning seven years (Richard et al., 1991). This high visibility facilitated the collection of continuous focal animal samples (Altmann,

1974) and daily fecal samples from known individuals prior to and throughout the breeding season. Data obtained on the behavioral, hormonal, and social correlates of reproduction in free-ranging *Propithecus verreauxi* were crucial for assessing intersexual mating patterns in this species and for examining adaptive explanations for multiple mating by females.

CHAPTER II. THE SOCIAL AND SEXUAL RELATIONSHIPS OF MALE AND FEMALE SIFAKA

A. Introduction

Two decades of research have produced major advances in our understanding of the reproductive biology of female primates (Robinson and Goy 1986; Ziegler and Bercovitz, 1990). These studies show that strepsirhine and catarrhine primates have divergent reproductive patterns characterized by estrous cycles in the former and menstrual cycles in the latter associated with flexible periods of sexual activity not confined to ovulation. Strepsirhine primates are, with few exceptions, seasonally polyestrous. Females are receptive to males one to three times per breeding season depending on when conception occurs (reviewed in Hrdy and Whitten, 1987).

Although captive studies have yielded important new insights into the reproductive biology and mating behavior of female Malagasy primates (Brockman et al., submitted; Eaton et al., 1973; Kappeler, 1993; Pereira, 1991; Pereira & Weiss, 1991; Perry et al., 1992; Shideler et al., 1983; Shideler & Lindburg, 1982; Van Horn & Resko, 1977; van Schaik & Kappeler 1993), few studies have examined the behavioral and social correlates of mating in free-ranging populations (Koyama, 1992; Morland, 1991; Richard, 1992; Sauther, 1991).

In this chapter, reproduction and mating in free-ranging *Propithecus verreauxi* were examined with the following specific aims: (1) to describe the behavioral characteristics of seasonal reproduction; (2) to determine the degree of within-group estrous asynchrony and order; and (3) to describe the social correlates of estrus associated with female mate preference and multiple mating patterns.

Previous studies of captive sifaka (Brockman et al., submitted) have suggested that females experience up to two 1- to 2-day estrous periods 27 days apart if conception does not occur during the first estrus. In the five observations of mating in free-ranging sifaka prior to this study, females were in estrus for up to 48 hrs once per breeding season (O'Connor, pers. comm.; Richard 1974, 1992). In the single instance in which more than one female in a group was observed to mate (Richard, 1974), estrus appeared to be asynchronous (i.e. non-overlapping). Sifaka mating patterns have been previously described as incorporating monogamy (O'Connor, pers. comm.) and female-controlled polygyny (Richard, 1992).

1. The Mating Context

Mating in female Verreaux's sifaka occurs in varying life history, demographic, and social contexts. Demographic studies of sifaka at Beza Mahafaly, Madagascar spanning 9 years (Richard et al., 1991, pers. comm.) show that in most cases, females live out their reproductive lives in their natal groups among matrilineal kin. Age at first reproduction occurs at 5 years of age at Beza Mahafaly and infants are born at 2-year intervals on average. With an estimated longevity of 20+ years (Richard et al., 1991), an adult female could potentially give birth to 5 to 7 infants in her lifetime. However, most females do not experience such fecundity as older more fertile females have a higher mortality rate than younger less fertile females (Richard et al., 1991). Unlike most other primates, female sifaka are dominant to males. This is hypothesized to provide reproductively stressed females priority of access to food resources (Richard & Nicoll, 1987; Young et al. 1990; but see Pereira et al., 1990).

Male sifaka reach sexual maturity at or before 3 years of age, after which they emigrate from their natal groups into neighboring social groups. Males subsequently transfer several times during their lifetimes depending upon their age, previous experience, and the female composition of social groups. Young males (3- to 6-year olds) emigrate into groups with a higher proportion and number of adult females while older males transfer into groups with a lower proportion and number of adult females. New groups consisting of an older male and a nulliparous female are occasionally formed. Group tenure lengths of older males are longer than those for younger males, averaging 5 years, coinciding with the age at first reproduction for females (Richard et al., 1993).

An important consequence of male dispersal patterns is the development of male-female social relationships which extend beyond the confines of the social group into the sifaka neighborhood (Jolly, 1966; Jolly et al., 1982; Richard et al., 1991). These relationships are maintained through regular encounters, both peaceful and agonistic, between neighboring groups in areas of their homes ranges which overlap. For females, maintaining familiarity with neighboring males throughout the year may be crucially important during the breeding season when conception could depend upon mating with more than one resident and/or non-resident males.

B. Materials and Methods

1. Subjects

Behavioral data were collected from 2 social groups (Vaovao [VV] and Vavy Masiaka [VM]) prior to and during the 1990-1991 and 1991-1992 breeding seasons at Beza Mahafaly, Madagascar. During the 1990-1991 field season, the modal group composition of the 28-30 social groups in the reserve was 3 adult males and 2 adult females. Data on the Vaovao social group, composed of 2 adult males and 3 adult females, were collected from early November 1990 through mid-March 1991. Data on the Vavy Masiaka social group, composed of 3 adult males, 1 juvenile male, and 2 adult females, were obtained between mid-November 1991 and late March 1992. These groups occupied neighboring home ranges in Sector 1's riverine gallery forest region of Beza Mahafaly Special

Reserve. The demography and reproductive histories of the groups are given below (Results).

2. Behavioral Sampling and Statistics

Focal animal (Altmann, 1974) and ad libitum sampling methods were used to collect data 6 days per week. A total of 644.25 focal animal hours was collected on five females in the Vaovao and Vavy Masiaka social groups. Just over 300 focal animals hours were collected on the Vaovao females (F20: 94.0 hrs; F19: 101.75 hrs; F80: 101.75 hrs), while slightly less than 343 focal animals hours were collected on the Vavy Masiaka females (F36: 171.87 hrs; F107: 171.87 hrs). The Vaovao and Vavy Masiaka females were out of view 7.72% and 10.64% of the time, respectively.

Ad libitum sampling occurred throughout the day but focused on observations of rare behaviors such as mating. Observations began at dawn (0600 hr), and terminated at dusk (when the animals retired at 1800 hr), and broke for 2 hours mid-day coincident with the animals' rest period. Exceptions to this regimen occurred when females were in estrus; observations during this time period were recorded from sunrise to just after sunset. Due to the low frequency of sifaka social interaction, both continuous and instantaneous sampling methods were used to record behavioral bouts using a 63-word ethogram (Appendix A). Grooming, reciprocal grooming, genital grooming, and playing were scored as states, and all others were recorded as events. A bout was defined by a 4-sec interval between behaviors. In the instance when unilateral grooms transformed into reciprocal grooms, the reciprocal groom bout was scored at the onset of mutuality. Dominance was determined based on the consistency of submissive and agonistic signals given by an individual (Hausfater, 1975; Sade, 1967). Fifteen-minute focal animal samples were evenly distributed among three 2-hour morning time blocks (to accommodate fecal collections) and four 1-hour afternoon/evening time blocks. Behavioral data were recorded on a check-sheet (Appendix B) and subsequently analyzed to focus on differences in frequencies of behavior over time. The latter were partitioned into eight 10-day and seven 14-day time periods for the Vaovao and Vavy Masiaka females, respectively. This was done to test the consistency of directional change in rates of behavior across time periods. Thus, it was possible to derive large enough samples of behaviors for statistical analysis without sacrificing the resolution needed to detect more subtle changes in behavior.

Prior to analysis, the data were checked for normality and equal variance. Depending upon the results of these tests, parametric (e.g. Student's t Test, One Way ANOVA, Pearson Product-Moment Correlation Coefficient) or nonparametic tests (e. g. Mann-Whitney Rank Sum, Kruskal-Wallis One Way ANOVA by Ranks, Spearman Rank-Order Correlation Coefficent) were used to examine differences and trends in the data. Statistical tests were considered significant at $p = <.05$.

C. Results

1. The Demographic Context of Sexual Relationships

Data on the Vaovao and Vavy Masiaka social groups obtained since 1984 (Richard et al., 1991, pers. comm.) show that their adult membership has fluctuated, particularily in the case of males. Neither group has had a high reproductive rate (Table 2.1). In 1989-90 Vaovao males 10, 29, and 158 transferred into a neighboring social group and males 240 (M240) and Fd (MFd) transferred into Vaovao. Between 1984 and 1990, 6 infants were born in Vaovao and. Except for F80, all these offspring had disappeared from the group at the onset of data collection in December 1990 and are known or presumed dead (Table 2.1).

Vavy Masiaka showed a similar turnover among males. In the two year period from 1990 to 1992, group size also decreased (Table 2.1). Three infants were born in Vavy Masiaka between 1985 and 1990, of which only one survived (M228).

Unlike the Vaovao social group whose composition remained stable throughout my study, the Vavy Masiaka social group experienced a shift in membership in January 1991 (Table 2.1) after intense agonism between resident males 146 and 140. During 2 days of bloody fighting an unmarked adult male (captured and marked 243 in 1993) immigrated into Vavy

Table 2.1. Vaovao (VV) and Vavy Masiaka (VM) social group histories, including group members' sexes, ages, births, and group tenure lengths (Richard, unpubl. data).

```
                             Date (19__)

             84   85   86   87   88   89   90#   91#  92#  93

 Sex and
 Social Group
 (Birth Year)

  Females

   VV19(75)  *-----------------------------------------------
                       B(D) B(D) B(D)
   VV20(70)  *-----------------------------------------------
                  B(F80)-------------------------------------
                                          B(D)
   VM36(76)  *-----------------------------------------------
                                          B(M228)------------

   VM99(80)                           I-----------?

   VM107(80?)*-----------------------------------------------
                   B(D)     B(D)

  Males

   VV7(83)   *---------E
   VV8(70)   *----E
   VV10(75)  *---------------------------E

   VV29(78)       I----------------------E
   VV73(66)  *---------D
   VV158(84)                          I--E
   VV240(84)                               I-----------------
   VVFd(87?)                               I-----?
   VM25(67)  *----------E
   VM29(78)  *----E
   VM30(73)  *--------------E

   VM128(78)                          I----D
   VM140(82)                          I-------------------E
   VM146(80)                          I-------------------E
   VM243(83)                                          I------
   VMUC(87?)                          *---------------E

# This study
B Birth
D Death
E Emigrated
I Immigrated
```

Masiaka and became the central resident male moving males 146 and 140 to the group's periphery (i.e. M146 and M140 shadowed the group's movements, fed near group members, but did not sleep with the group). Although the group's females did not resist the new male's transfer, the younger uncollared male of this group (MUC) did so briefly, but unsuccessfully. This uncollared male transferred into a neighboring social group 2 weeks later.

The change in membership in the Vavy Masiaka social group is pertinent to the analysis of social behavior below. Because the number of resident males in the group was halved, frequencies of social interactions between females and males were constant or declined in contrast to the increased rates of social interactions associated with mating in the Vaovao social group. Comparison of social behavior between these 2 social groups is therefore problematic and differences may be the result of sampling effects or reflect real differences in behavior and demographic context.

2. The Social Context of Sexual Relationships

Social relationships among adult sifaka were assessed via frequencies of submissive (i.e. chatter, fear-grimace), agonistic (i.e. displace, nose-jab, lunge, attempt-to-cuff, faint-to-cuff, cuff, grab, bite), and affiliative (i.e. greet, invite-to-groom, groom, reciprocal groom, invite-to-play, play) interactions over time.

a. Agonism and Dominance. Using the criteria established by Hausfater (1975) and Sade (1967) adult females were typically dominant to males (Tables 2.2-5; Appendices C-F). In three instances, females were observed to give submissive signals to males. These were when females 20 and 19 fear-grimaced/chattered once and twice at M240 and MFd respectively (Tables 2.2, 2.3). Females directed substantially higher levels of agonism toward males than females, reaching significance in Vavy Masiaka (Mann-Whitney test, $T = 28$, $p < 0.001$, Appendices E,F).

The intensity of female agonism varied according to the sex of the targeted animal (Tables 2.6-9). Females more frequently displaced and attempted to bite other females (Tables 2.8,2.10), but they were much more inclined to nose-jab, lunge at, feint-to-cuff, attempt-to-cuff, cuff, grab, and bite males (Tables 2.6-14; Appendices G-O). Female 19 was particularily antagonistic toward males while F80 was the least antagonistic, M240 receiving substantially more aggression from females than MFd (Tables 2.6-14). On the rare occasions when a Vaovao male directed aggression at a female, most of it was directed by M240 toward F80 (Table 2.4).

Dominance relationships were clearly linear among the Vaovao females. Female 20 was the most dominant followed by F19 and F80. The highest frequency of submission was observed in F80, who directed most of her submissive signals

Table 2.2. Matrix of submissive interactions in the Vaovao social group.

Received Submission	*Exhibited Submission*					Total Received
	F20	F19	F80	M240	MFd	
F20	-	11	5	6	10	32
F19	4	-	39	13	17	74
F80	2	0	-	5	8	15
M240*	1	1	0	-		2
MFd*	0	1	0		-	1
Total Given	*7*	*13*	*44*	*24*	*35*	**124**

Table 2.3. Matrix of submissive interactions in the Vavy Masiaka social group.

Received Submission	*Submission Exhibited*						Total Received
	F36	F107	M146	M140	MUC	M243	
F36	-	4	11	8	14	27	64
F107	0	-	8	4	3	45	60
M146*	0	0	-				0
M140*	0	0		-			0
MUC*	0	0			-		0
M243*	0	0				-	0
Total Given	*0*	*4*	*19*	*12*	*17*	*72*	**124**

* Non-focal animal whose submissive interactions were recorded only when the focal animal was involved.

Table 2.4. Matrix of agonistic interactions in the Vaovao social group.

Exhibited Aggression			Received Aggression			*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	28	19	47	18	*112*
F19	3	-	85	92	39	*219*
F80	0	2	-	37	19	*58*
M240*	0	5	14	-		*19*
MFd*	1	1	1		-	*3*
Total Received	4	36	119	176	78	**411**

Table 2.5. Matrix of agonistic interactions in the Vavy Masiaka social group.

Exhibited Aggression			Received Aggression				*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	6	36	16	42	123	*223*
F107	11	-	28	10	18	174	*241*
M146*	0	0	-				*0*
M140*	1	0		-			*1*
MUC*	0	0			-		*0*
M243*	0	0				-	0
Total Received	12	6	64	26	60	297	**465**

Note: In this and all subsequent matrices' figures are based on frequencies of behaviors directed toward and received by group members. Left-hand column shows sex and I.D. number (or name) of group members who directed the interaction.

* Non-focal animal whose behavioral interactions were recorded only when the focal animal was involved.

Table 2.6. Matrix of grab interactions in the Vaovao social group.

Exhibited Grabb	Received Grab					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	6	6	12	7	*31*
F19	1	-	25	31	16	*73*
F80	0	0	-	13	5	*18*
M240*	0	3	5	-		*8*
MFd*	1	0	1		-	*2*
Total Received	2	9	37	56	28	**132**

Table 2.7. Matrix of bite interactions in the Vaovao social group.

Exhibited Bite	Received Bite					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	6	2	5	2	*15*
F19	0	-	10	21	13	*44*
F80	0	2	-	12	8	*22*
M240*	0	0	2	-		*2*
MFd*	0	0	0		-	*0*
Total Received	0	8	14	38	23	**83**

Table 2.8. Matrix of displacement interactions in the Vaovao social group.

Exhibited Displacement	Received Displacement					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	7	10	8	1	*26*
F19	2	-	37	10	0	49
F80	0	0	-	2	0	2
M240*	0	1	2	-		2
MFd*	0	0	0		-	0
Total Received	2	8	49	20	1	**80**

Table 2.9. Matrix of lunge interactions in the Vaovao social group.

Exhibited Lunge	Received Lunge					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	3	0	8	4	*15*
F19	0	-	8	8	5	*21*
F80	0	0	-	7	5	*12*
M240*	0	0	2	-		*2*
MFd*	0	0	0		-	*0*
Total Received	0	3	10	23	14	**50**

Table 2.10. Matrix of attempt-to-bite interactions in the Vaovao social group.

Exhibited Attempt-to-Bite	Received Attempt-to-Bite					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	1	1	0	0	*2*
F19	0	-	1	0	0	1
F80	0	0	-	0	1	*1*
M240*	0	0	1	-		*1*
MFd*	0	0	0		-	*0*
Total Received	0	1	3	0	1	**5**

Table 2.11. Matrix of nose-jab interactions in the Vaovao social group.

Exhibited Nose-jab	Received Nose-jab					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	0	0	0	0	*0*
F19	0	-	1	2	0	*3*
F80	0	0	-	0	0	*0*
M240*	0	0	0	-		*0*
MFd*	0	1	0		-	*1*
Total Received	0	1	1	2	0	**4**

Table 2.12. Matrix of cuff interactions in the Vaovao social group.

Exhibited Cuff	Received Cuff					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	3	0	10	1	*14*
F19	0	-	0	12	2	*14*
F80	0	0	-	1	1	*2*
M240*	0	0	2	-		*2*
MFd*	0	0	0		-	*0*
Total Received	0	3	2	23	4	**32**

Table 2.13. Matrix of feint-to-cuff interactions in the Vaovao social group.

Exhibited Feint-to-cuff	Received Feint-to-Cuff					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	1	0	3	3	*7*
F19	0	-	3	8	2	*13*
F80	0	0	-	1	0	*1*
M240*	0	1	0	-		*1*
MFd*	0	0	0		-	*0*
Total Received	0	2	3	12	5	**22**

Table 2.14. Matrix of attempt-to-cuff interactions in the Vaovao social group.

Exhibited Attempt-to-Cuff	Received Attempt-to-Cuff					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	1	0	1	0	*2*
F19	0	-	0	0	1	*1*
F80	0	0	-	0	0	*0*
M240*	0	0	0	-		*0*
MFd*	0	0	0		-	*0*
Total Received	0	1	0	1	1	3

toward F19. She was followed by F19, who fear-grimaced/chattered exclusively to F20 (Table 2.2). Female 20 was the target of the fewest agonistic interactions from group females, while F80 received the most. Female 19 was the most intensely agonistic, directing almost all of her aggression toward F80 (Table 2.4).

Vavy Masiaka females showed similar agonistic patterning, targeting males over females for intense aggression (Table 2.15-19; Appendix F, P-W). Female 107 was responsible for over half of all female agonism directed at males. She targeted much of it at M243, who was the most frequent recipient of female agonism overall (Tables 2.15-23). Male aggression toward females was negligible (Table 2.16).

In contrast to Vaovao females, dominance relations among Vavy Masiaka females were unclear. The only submissive gestures observed were directed at F36 by F107 (Table 2.3), but F107 was more aggressive toward F36 than vice versa (Table 2.5).

b. Affiliation. Females showed much more affiliative behavior toward other females than toward males (Student Newman Keuls test, $q = 6.2$, $p < 0.05$; Tables 2.24,2.25; Appendices X, AE). In Vaovao, most of the friendly interactions involved grooming and greeting among females (Tables 2.26,2.27; Appendices AB, AC). Females played with males more often, but they more frequently groomed, greeted,

Table 2.15. Matrix of lunge interactions in the Vavy Masiaka social group.

Exhibited Lunge	Received Lunge						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	1	8	3	9	39	*60*
F107	0	-	5	2	1	49	*57*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	0	1	13	5	10	88	**117**

Table 2.16. Matrix of grab interactions in the Vavy Masiaka social group.

Exhibited Grab	Received Grab						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	1	4	3	9	25	*42*
F107	0	-	5	3	6	56	*70*
M146*	0	0	-				*0*
M140*	1	0		-			*1*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	1	1	9	6	15	81	**113**

Table 2.17. Matrix of bite interactions in the Vavy Masiaka social group.

Exhibited Bite	Received Bite						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	1	2	7	9	22	*41*
F107	0	-	9	3	5	52	*69*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	0	1	11	10	14	74	**110**

Table 2.18. Matrix of cuff interactions in the Vavy Masiaka social group.

Exhibited Cuff	Received Cuff						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	0	13	1	9	16	*39*
F107	1	-	0	2	2	11	*16*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	1	0	13	3	11	27	**55**

Table 2.19. Matrix of displacement interactions in the Vavy Masiaka social group.

Exhibited Displacement	Received Displacement						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	2	1	1	1	3	*8*
F107	6	-	2	0	0	0	*8*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		0
M243*	0	0				-	*0*
Total Received	6	2	3	1	1	3	**16**

Table 2.20. Matrix of attempt-to-cuff interactions in the Vavy Masiaka social group.

Exhibited Attempt-to-Cuff	Received Attempt-to-Cuff						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	0	7	1	1	13	*22*
F107	0	-	2	0	2	4	*8*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	0	0	9	1	3	17	**30**

Table 2.21. Matrix of nose-jab interactions in the Vavy Masiaka social group.

Exhibited Nose-jab	Received Nose-jab						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	3	1	0	2	3	*9*
F107	1	-	2	0	1	0	*4*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	1	3	3	0	3	3	**13**

Table 2.22. Matrix of attempt-to-bite interactions in the Vavy Masiaka social group.

Exhibited Attempt-to-Bite	Received Attempt-to-Bite						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	1	0	0	2	0	*3*
F107	0	-	3	0	1	2	*6*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	0	1	3	0	3	2	**9**

Table 2.23. Matrix of feint-to-cuff interactions in the Vavy Masiaka social group.

Exhibited Feint-to-Cuff	Received Feint-to-Cuff						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	0	0	0	0	2	*2*
F107	0	-	0	0	0	0	*0*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	0				-	*0*
Total Received	0	0	0	0	0	2	**2**

Table 2.24. Matrix of affiliative interactions in the Vaovao social group.

Exhibited Affiliation	Received Affiliation					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	44	82	6	4	*136*
F19	88	-	33	12	12	*145*
F80	96	66	-	6	25	*193*
M240*	6	15	10	-		*31*
MFd*	5	17	23		-	*45*
Total Received	195	142	148	24	41	**550**

Table 2.25. Matrix of affiliative interactions in the Vavy Masiaka social group.

Exhibited Affiliation	Received Affiliation						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	57	10	2	6	18	*93*
F107	46	-	2	3	6	17	*74*
M146*	13	5	-				*18*
M140*	6	3		-			*9*
MUC*	8	7			-		*15*
M243	12	13				-	*25*
Total Received	85	85	12	5	12	35	**234**

invited to groom, and reciprocally groomed other females (Table 2.26-31; Appendices Y-AD).

Dominant females received more grooming than subordinate females in Vaovao. Subordinate F80 groomed most often, distributing her grooming bouts between F20 and F19 (Table 2.26). Female 19 groomed the least and confined her grooming bouts almost exclusively to F20, while over half of F20's grooming was directed toward her daughter, F80. Female 19 was the greeter of the group, equally distributing her greets between F80 and F20. Mother and daughter greeted each other more often than they greeted F19 (Table 2.27). Female 20 rarely solicited grooming from other females, but when she did, it was from F19 (Table 2.28). Female 19 invited the most grooms, 60% from F80, while the latter solicited most of her grooming bouts from her mother. Reciprocal grooming occurred most frequently between mother and daughter (Table 2.29). Play among Voavao group members was rare, involving only the youngest group members, MFd and F80, usually at F80's initiation (Tables 2.30,2.31).

Most friendly interactions between males and females involved grooming (Appendices Y, AF). Male Fd groomed females twice as often as M240, directing over half of his grooming toward F80. Male 240 groomed F19 most often (Table 2.26).

Although affiliative interactions were less frequent and less intense in Vavy Masiaka than in the Vaovao, their pattern was similar. Females directed 54% of their

Table 2.26. Matrix of groom interactions in the Vaovao social group.

Exhibited Groom	Received Groom					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	29	61	0	1	*91*
F19	63	-	6	1	0	*70*
F80	68	49	-	5	4	*126*
M240*	3	10	7	-		*20*
MFd*	2	16	22		-	*40*
Total Received	136	104	96	6	5	**347**

Table 2.27. Matrix of greet interactions in the Vaovao social group.

Exhibited Greet	Received Greet					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	6	18	6	3	*33*
F19	13	-	14	6	4	*37*
F80	10	7	-	1	4	*22*
M240*	3	4	3	-		*10*
MFd*	3	1	1		-	*5*
Total Received	29	18	36	13	11	**107**

Table 2.28. Matrix of invite-to-groom interactions in the Vaovao social group.

Exhibited Invite-to-Groom	Received Invite-to-Groom					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	4	2	0	0	*6*
F19	4	-	9	0	2	*15*
F80	6	1	-	0	1	*8*
M240*	0	0	0	-		*0*
MFd*	0	0	0		-	*0*
Total Received	10	5	11	0	3	**29**

Table 2.29. Matrix of reciprocal groom interactions in the Vaovao social group.

Exhibited Reciprocal Groom	Received Reciprocal Groom					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	5	1	0	0	*6*
F19	5	-	2	1	1	*9*
F80	9	3	-	0	0	*12*
M240*				-		-
MFd*					-	-
Total Received	14	8	3	1	1	**27**

Table 2.30. Matrix of play interactions in the Vaovao social group.

Exhibited Play	Received Play					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	0	0	0	0	*0*
F19	3	-	2	4	4	*13*
F80	2	5	-	0	15	*22*
M240*	0	0	0	-		*0*
MFd*	0	0	0		-	*0*
Total Received	5	5	2	4	19	**35**

Table 2.31. Matrix of invite-to-play interactions in the Vaovao social group.

Exhibited Invite-to-Play	Received Invite-to-Play					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	0	0	0	0	*0*
F19	0	-	0	0	1	*1*
F80	1	1	-	0	1	*3*
M240*	0	1	0	-		1
MFd*	0	0	0		-	*0*
Total Received	1	2	0	0	2	**5**

affiliative interactions towards one another, while male-to-female and female-to-male affiliative interactions were evenly distributed (Appendix AE). Grooming and greeting interactions made up most of the friendly interactions in Vavy Masiaka (Appendices AF-AG).

Affiliative interactions in Vavy Masiaka were less diverse than in Vaovao, and no play was seen at all (Tables 2.32-35). The ambiguous relationship between females 36 and 107 was evident again in their equally distributed greet (Table 2.32) and invite-to-groom interactions (Table 2.33). Asymmetry was more apparent in their grooming interactions, where F107 received 61.5% of all grooming bouts initiated by F36 (Table 2.34).

As in Vaovao, most of the affiliative behaviors directed by males toward females involved grooming (Table 2.34). Male 243 groomed females most often. Male 146 showed a strong grooming preference for F36 while the other males divided their grooming equally between the females.

3. The Dynamics of Social Interaction

Sifaka interact at low rates and in this study two approaches were used to assess social dynamics: Hinde and Atkinson's (1970) formula for the maintenance of spatial proximity based upon approaches and leavings (% Leavings - % Approaches) and Rowell and Olson's (1983) method of recording glance rate as the basis for inferring frequencies and patterns of monitoring among individuals.

Table 2.32. Matrix of greet interactions in the Vavy Masiaka social group.

Exhibited Greet	Received Greet						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	21	4	2	3	8	*38*
F107	21	-	1	2	3	11	*38*
M146*	1	2	-				*3*
M140*	2	0		-			*2*
MUC*	1	0			-		*1*
M243*	0	1				-	*1*
Total Received	25	24	5	4	6	19	**83**

Table. 2.33. Matrix of invite-to-groom interactions in the Vavy Masiaka social group.

Exhibited Invite-to-Groom	Received Invite-to-Groom						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	4	6	0	3	10	*23*
F107	5	-	0	1	3	5	*14*
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	1	0				-	*1*
Total Received	6	4	6	1	6	15	**38**

Table 2.34. Matrix of groom interactions in the Vavy Masiaka social group.

Exhibited Groom	Received Groom						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	32	0	0	0	0	*32*
F107	20	-	1	0	0	0	*21*
M146*	12	3	-				*15*
M140*	4	3		-			*7*
MUC*	7	7			-		*14*
M243*	11	12				-	*23*
Total Received	54	57	1	0	0	0	**112**

Table 2.35. Matrix of reciprocal groom interactions in the Vavy Masiaka social group.

Exhibited Reciprocal Groom	Received Reciprocal Groom						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	0	0	0	0	0	*0*
F107	0	-	0	0	0	1	*1*
M146*			-				-
M140*				-			-
MUC*					-		-
M243*						-	-
Total Received	0	0	0	0	0	1	**1**

The relative contributions males made to maintaining proximity at 1 m or less were determined for each pair of animals (Table 2.36,2.37). The intensity of the interaction is shown in the strength of the quotient derived from the formula:

$$\frac{[L(\text{female}) - App(\text{female})] \times 100}{App(\text{female}) + App(\text{male})}$$

Where: L = Leavings
App = Approaches

The results of this analysis reveal interesting associations between males and females of differing age and dominance status. Among the Vaovao dyads, resident males were primarily responsible for maintaining proximity to the most dominant female (F20; Table 2.36). Subordinate females F19 and F80 exhibited stronger proximity to both males and for MFd in particular. The overall intensity of association between the dyads was weak (not more than +12% or less than -16%). The strongest proximity associations were directed by MFd toward F20 (+11.48%) and by F19 toward MFd (-16.13%).

In Vavy Masiaka, prior to the shift in group composition, the oldest resident male 146 maintained proximity to both females (Table 2.37), and to F107 in particular. Male 243 maintained proximity to F107 while F36 showed a stronger proximity value for M243. The younger males 140 and MUC showed proximity preferences for both females, M140 showing a particular interest in F36.

Table 2.36. Relative contributions Vaovao females (-) and males (+) made to maintaining proximity at 1 m or less (calculated as the difference between % approaches due to male and % leavings due to male per male/female pair. Statistical tests compared differences in proximity values for each male/female pair across 8 time periods).

	Male		**Student's t Test**	
	240	Fd	*t*	*p*
Female				
20	+2.16	+11.48	-0.557	0.586
19	-7.69	-16.13	0.317	0.756
80	-3.13	- 8.86	-0.441	0.666

Table 2.37. Relative contributions Vavy Masiaka females (-) and males (+) made to maintaining proximity at 1 m or less (calculated as above. Statistical tests compared differences in proximity values among 4 male/female pairs across 7 time periods).

	Male				**ANOVA/KW ANOVA**	
	146	140	UC	243	*F/H*	*p*
Female						
36	+ 1.67	-31.58	-22.22	-6.60	0.830	0.49
107	+10.42	-24.24	- 5.13	+4.98	5.223	0.16

The individuals maintaining proximity during estrus varied. Proximity intensities were age- and rank-related. Oldest resident males showed a stronger tendency to be near dominant females during estrus (i.e. M240/F20, M243/107 Figures 2,3; Appendices AJ, AK). Subordinate females maintained spatial proximity to younger (i.e. F19/MFd, Figure 4) and older males (i.e. F36/M146, Figure 5). Although F80 was not observed to mate, she was mounted by MFd, and during that time she exhibited a higher proximity value for MFd over M240 (Figure 6).

It is of interest to note, female-maintained proximity to M140 just prior to his fight with M146. Although the factors precipitating M146's attack of M140 are not known, the females' preference for M140 may have played a role. Additional support for this idea is provided by an increase in female approaches to males at less than 1 meter, and increased male guarding at this time (see below).

Relationships between rate of female monitoring of male conspecifics and changes in frequency of distancing and social behaviors were examined via glance rate. A vertical or horizontal glance directed at an individual was distinguished from visual foraging by the lateral weaving of the head and shoulders which characterized the latter behavior.

Female glance rates were not significantly different across all time periods in either social group (Vaovao: One-Way ANOVA, $F(2,23) = .84$, $p > .05$; Vavy Masiaka: *t*-test,

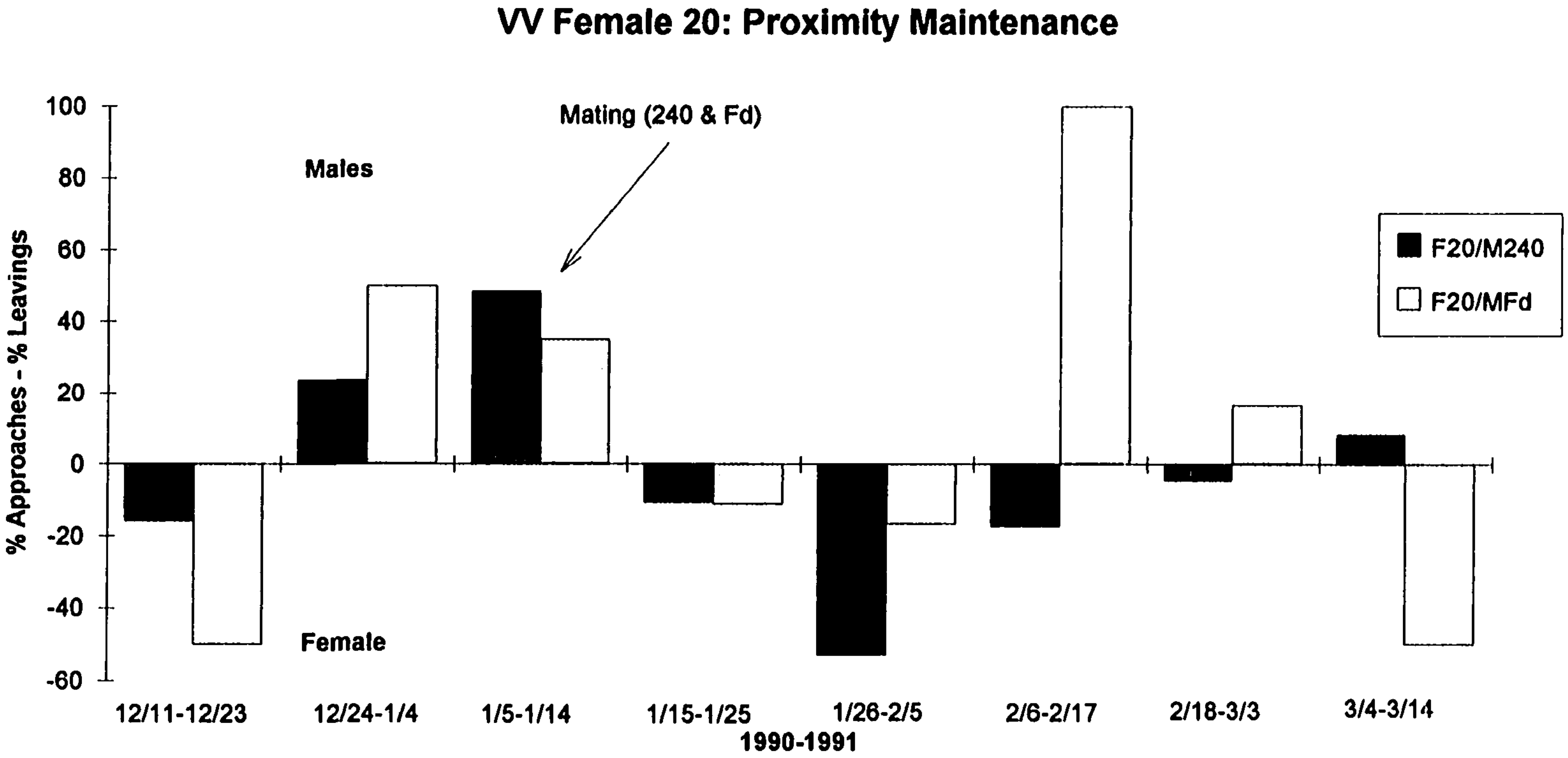


Figure 2. Relative contributions Vaovao F20 (-) and males (+) made to maintaining proximity to one another over time per male/female pair.

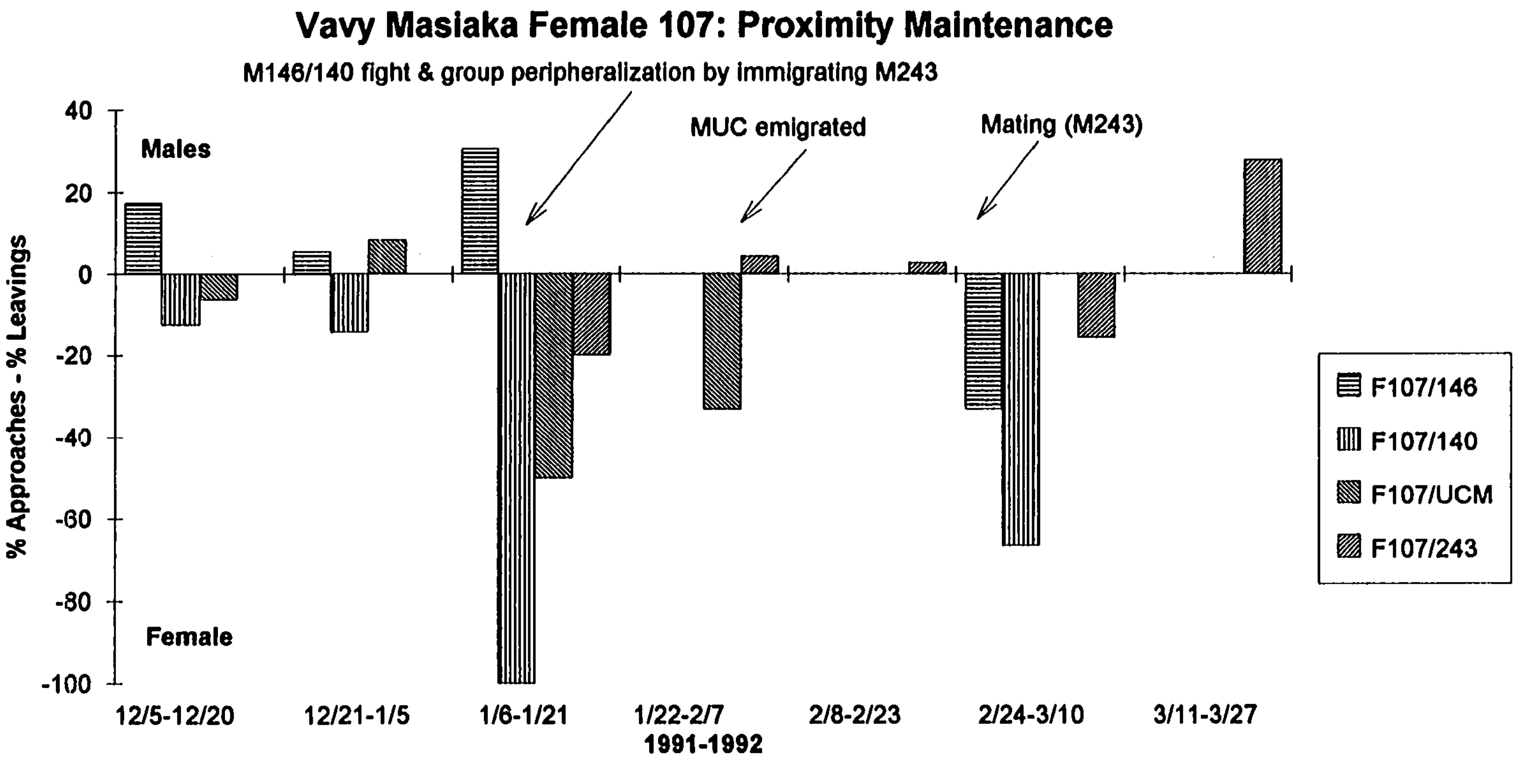


Figure 3. Relative contributions Vavy Masiaka F107 (-) and males (+) made to maintaining proximity to one another over time per male/female pair.

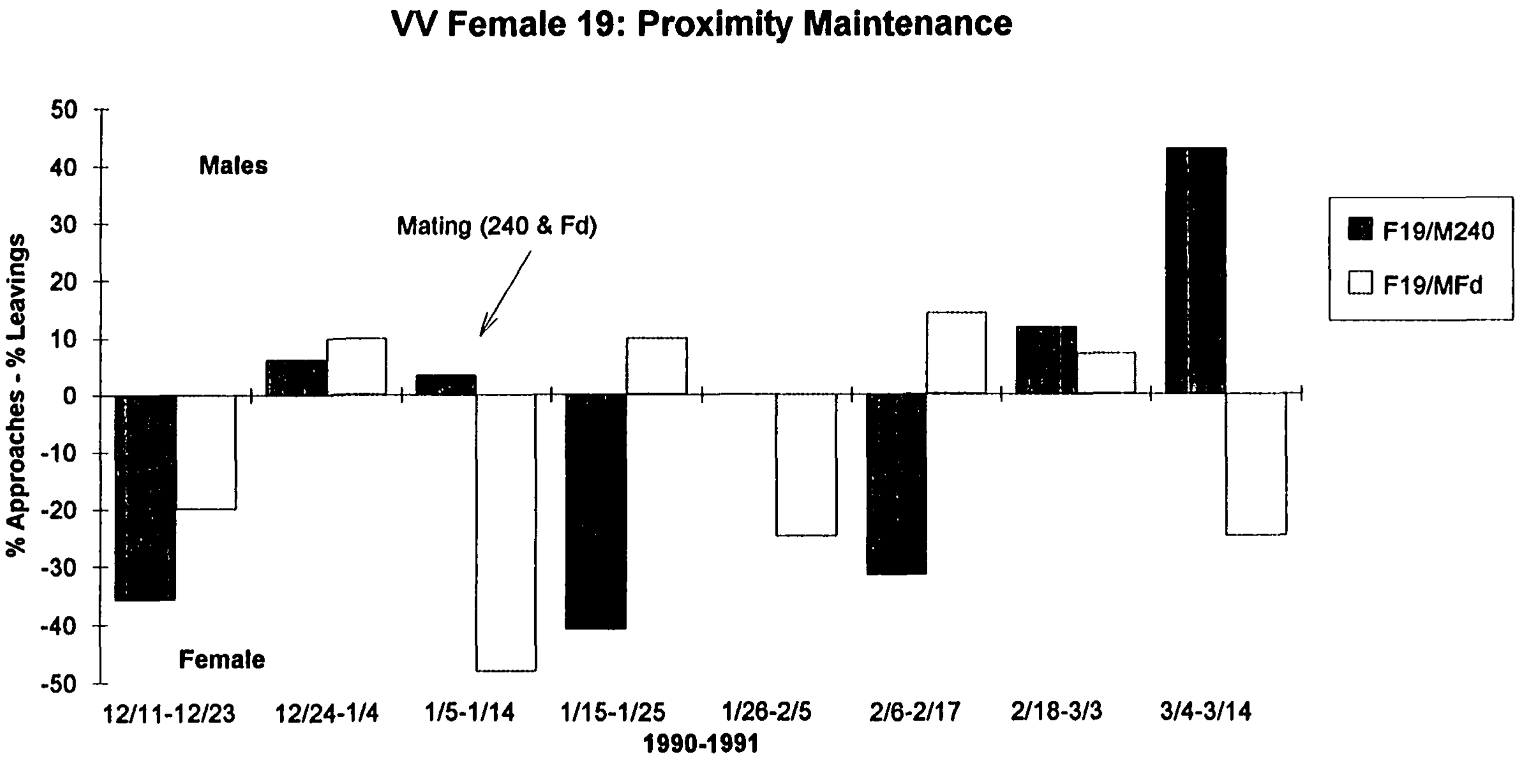


Figure 4. Relative contributions Vaovao F19 (-) and males (+) made to maintaining proximity to one another over time per male/female pair.

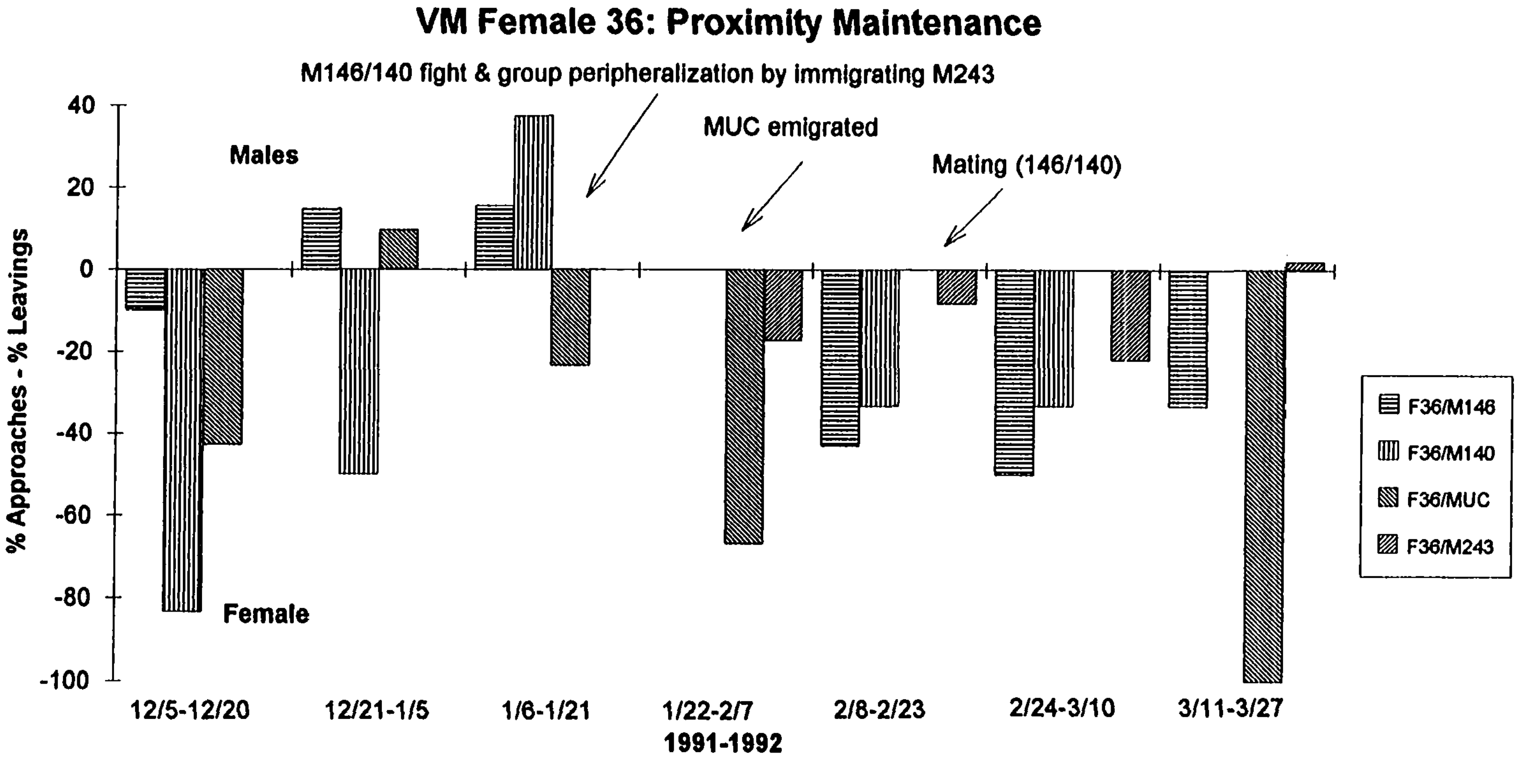


Figure 5. Relative contributions Vavy Masiaka F36 (-) and males (+) made to maintaining proximity to one another over time per male/female pair.

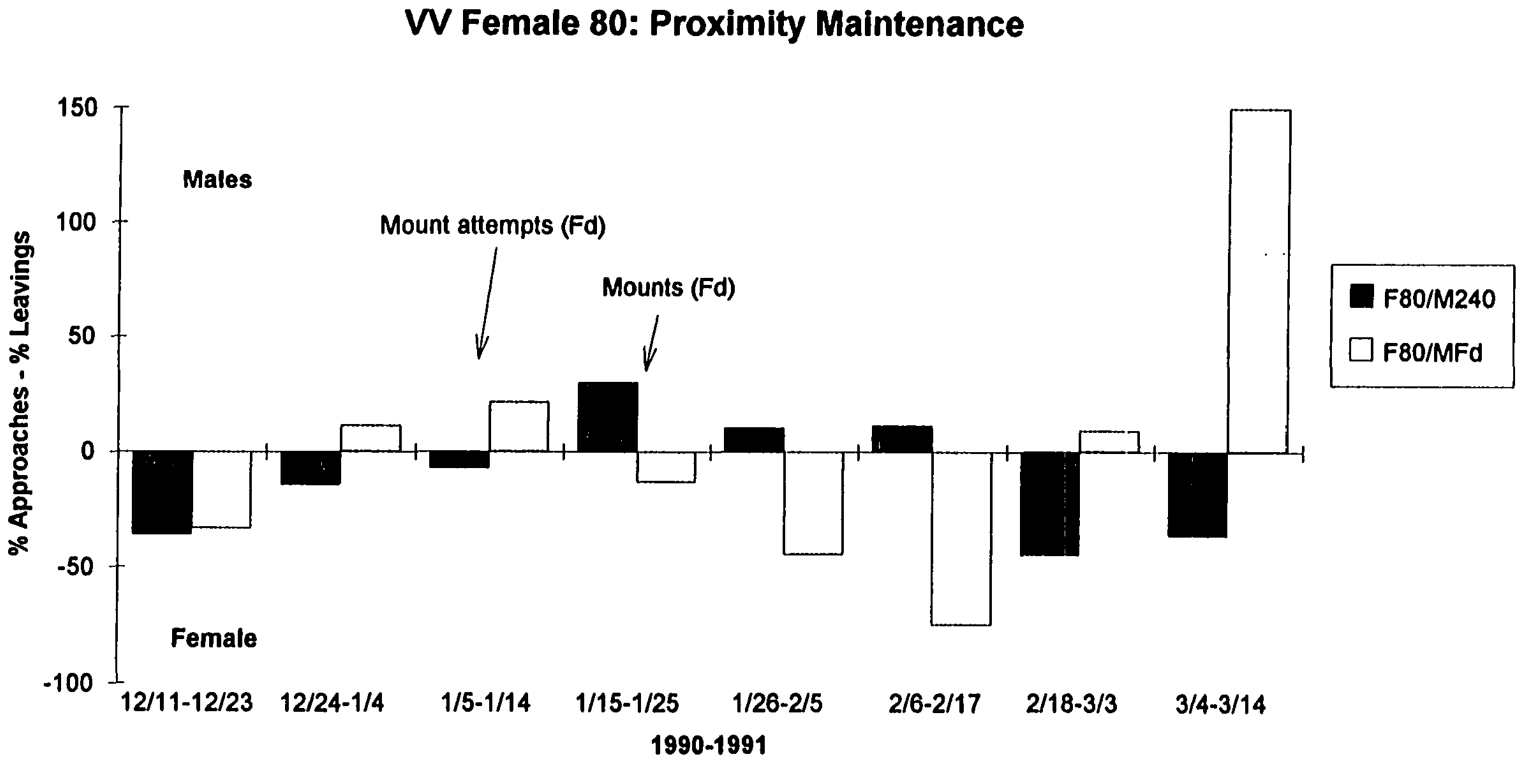


Figure 6. Relative contributions Vaovao F80 (-) and males (+) made to maintaining proximity to one another over time per male/female pair.

$t(12) = .02$, $p > 0.05$). Inter-individual variation in glance rates was minimal, ranging from 24.76 (F36) to 28.99 (F80) glances per hour. Glance rates over time remained relatively constant in both social groups (Appendices AL, AM).

In Vaovao, female glance rates were moderately, but insignifantly, associated with frequency of male withdrawals ($r_s = 0.53$, $n = 8$, $p = 0.17$) whereas in Vavy Masiaka they were associated to the same degree way with frequency of male approaches ($r_s = 0.61$, $n = 7$, $p = 0.14$). Glance rates in Vaovao females were strongly associated with frequency of male grooming of females ($r_s = 0.83$, $n = 8$, $p = 0.01$), while in Vavy Masiaka females they were negatively associated with frequency of female to male agonism ($r = -0.41$, $n = 7$, $p = .37$).

4. Sexual Relationships Between Male and Female Sifaka

a. Estrus. Estrus was behaviorally defined as an increase in the frequency of attractivity, proceptivity, and receptivity (Beach, 1976). Attractivity, defined as females' stimulus value to males, was assessed through increases in male approaches, guarding, and affiliative behaviors (Beach, 1976). Male approaches to (Appendix AN) and guarding of (Appendix AO) Vaovao females were moderately (but insignifcantly) correlated with estrus (male approach: $r_s = 0.58$, $n = 8$, $p = 0.13$; male guarding: $r_s = 0.62$, n = 8, $p = 0.10$). There were only slight associations between these behaviors and estrus in the Vavy Masiaka females (male approach: $r_s = 0.31$, $n = 7$, $p = 0.44$; male guarding: $r_s = 0.52$, $n = 7$, $p = 0.23$; Appendices AP, AQ). The highest frequencies of male approaches to females were at 1 m, <1 m, and contact (Appendices AR-AW). There was no association between estrus and affiliative interactions directed by males toward in either group (VV: $r_s = 0.08$, $n = 8$, $p = 0.84$; VM: $r_s = 0.00$, $n = 7$, $p = 0.97$, Appendices X, AE). Estrus was moderately associated with male submission in Vavy Masiaka ($r_s = 0.62$, $n = 7$, $p = 0.14$) and negatively correlated with male submission in Vaovao ($r_s = -0.50$, $n = 8$, $p = 0.19$; Appendices C, D).

Vaovao's M240 approached females more than twice as often as MFd, with the highest frequency directed at F20, and male guarding followed the same pattern (Table 2.38, 2.39). In Vavy Masiaka, in contrast, males distributed their approaches between females equally (Table 2.40). Prior to M243's transfer into the group, M146 most frequently approached the females. Thereafter, M243 had an approach frequency to females twice that of M146. Females were guarded exclusively by the older resident males (M146, M243, Table 2.41).

Proceptivity, defined as female sexual initiation behavior, was determined through increases in the frequency of female approaches, present, and affiliative behaviors toward males (Beach, 1976). There were substantial significant correlations between frequencies of present

Table 2.38. Matrix of approach at 1 m interactions at 1 m or less in the Vaovao social group.

Exhibited Approach	Received Approach					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-	148	110	95	21	*374*
F19	162	-	185	75	42	*464*
F80	116	71	-	46	38	*271*
M240*	136	96	81	-		*313*
MFd*	41	50	39		-	*130*
Total Received	455	365	415	216	107	**1552**

Table 2.39. Matrix of male guard interactions in the Vaovao social group.

Exhibited Guarding	Received Guarding					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	11	10	8	-		*29*
MFd*	0	0	0		-	*0*
Total Received	11	10	8	-	-	**29**

Table 2.40. Matrix of approach interactions at 1 m or less in the Vavy Masiaka social group.

Exhibited Approach	Received Approach						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-	171	45	27	32	98	*373*
F107	177	-	35	20	18	85	*335*
M146*	71	60	-				*131*
M140*	11	10		-			*21*
MUC*	31	21			-		*52*
M243*	101	137				-	*238*
Total Received	391	399	80	47	50	183	**1150**

Table 2.41. Matrix of male guard interactions in the Vavy Masiaka social group.

Exhibited Guarding	Received Guarding						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	3	16	-				*19*
M140*	1	0		-			*1*
MUC*	0	0			-		*0*
M243*	12	20				-	*32*
Total Received	16	36	-	-	-	-	**52**

behaviors and estrus in Vaovao females ($r_s = 0.76$, $n = 8$, $p = 0.03$; Appendix AX). Approaches and affiliative interactions were only moderately (and insignificantly) correlated with estrus (approaches: $r_s = 0.58$, $n = 8$, $p = 0.13$; Appendix AN; affiliative interactions: ($r_s = 0.58$, n = 7, $p = 0.13$; Appendix X). A moderate, but insignificant, association occurred between frequencies of present behaviors and estrus in the Vavy Masiaka females ($r_s = 0.51$, $n = 7$, $p = 0.23$, Appendix AY). No correlations were found between estrus and rates of affiliative interactions ($r_s = -0.10$, $n = 7$, $p = 0.78$; Appendix AE) or frequency of female approaches to males ($r_s = 0.00$, $n = 7$, $p = 0.97$; Appendix AP).

Female approach and affiliative patterns varied between groups. In Vaovao, females were more likely to approach and affiliate with M240 than with MFd (Tables 2.38, 2.24). Vavy Masiaka females, likewise, approached the oldest resident males (M243, M146) two to three times more often than the younger males (Table 2.40). However, no association was found between estrus and the rate at which Vavy Masiaka females directed affiliative behavior at males, although M243 received a much greater increase in female-directed affiliation than did males M146 and M140 (Appendix AE).

Female present behavior also varied between groups. Vaovao F20 and Vavy Masiaka females 36 and 107 presented exclusively to the oldest resident males. Vaovao females 19 and 80 presented exclusively to the younger resident male (Table 2.42, 2.43).

In contrast to the Vaovao females, whose presents occurred only during estrus, females in Vavy Masiaka presented to males prior to and during estrus (Appendix AY). Pre-estrous presents (i.e. Period 4) coincided with M243's transfer into the group and were significantly correlated with increased rates of mounts ($r_s = 0.82$, $n = 7$, $p = 0.03$) and attempts to clasp ($r_s = 0.75$, $n = 7$, $p = 0.05$) principally by M243. The rate of pre-estrous presents were also significantly associated with frequencies of female-female affiliation ($r_s = 0.81$, $n = 7$, $p = 0.03$; Appendix AE).

Receptivity, defined as female willingness to copulate, was assessed by male "Success Ratio" defined as the percentage of all sexual behavior which the female allows to result in copulation (Michael et al., 1967). The highest male Success Ratio occurred in F20, followed by F19, F36, and F107 (Table 2.44).

The onset of estrus in Vaovao females occurred during the first month of the breeding season on 7 January and terminated 13 days later on 19 January. Each female was observed to have only one estrous period during the breeding season lasting from 0.5 hrs to 50 hrs. Estrus in the Vavy Masiaka females began during the second month of the breeding season on 10 February and ended 13 days later on 23

Table 2.42. Matrix of present interactions in the Vaovao social group.

Exhibited Present			Received Present			*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-			2	0	*2*
F19		-		0	7	*7*
F80			-	0	1	*1*
M240*				-		-
MFd*					-	-
Total Received	-	-	-	2	8	**10**

Table 2.43. Matrix of present interactions in the Vavy Masiaka social group.

Exhibited Present			Received Present				*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-		1	0	0	2	*3*
F107		-	1	0	0	4	*5*
M146*			-				-
M140*				-			-
MUC*					-		-
M243*						-	-
Total Received	-	-	2	0	0	6	**8**

Table 2.44. Female receptivity in the Vaovao and Vavy Masiaka social groups.

	Sexual Behavior							
Female	Clasp Attempt	Clasp	Mount Attempt	Mount	Mt/Intro.	Mate	Total	MSR*
20	6	2	0	16	1	14	39	.36
19	9	6	12	12	0	12	51	.24
80	2	11	13	3	0	0	29	.00
36	7	7	0	0	0	3	17	.18
107	25	5	4	4	0	3	41	.07

* Denotes male Success Ratio, defined as the % of all sexual attempts which the female allows to result in a full copulation (Michael et al., 1967).

February. Female 107 had a single 1-hr estrous period while F36 had a second estrous period 8 days after her estrous period of 10 February.

Estrus in sifaka occurred in the context of the following male sexual behaviors: attempts to clasp, clasp, attempts to mount, mount, mount with intromission, and mount with intromission and thrusting (i.e. mating). In Vaovao, mounts, mating, attempts to mount, and clasps were the most frequently occurring sexual behaviors, making up 85% of all sexual interactions between males and females (Table 2.45-50; Appendices AZ-BC). Attempts to clasp, clasp, and mating made up 86% of the sexual interactions between males and females in Vavy Masiaka (Tables 2.51-55; Appendices BF-BH).

Analysis of sexual behavior over time showed that while mating was, in most cases, temporally limited to 7- to 15-day periods of elevated estradiol levels, sexual behaviors occurred during the entire pre-breeding and breeding season. There were substantial relationships between frequency of mating behavior and rates of mounts ($r_s = 0.66$, $n = 8$, $p = 0.07$), and attempts to mount ($r_s = 0.66$, $n = 8$, $p = 0.07$) in Vaovao dyads. Mating was only weakly correlated with frequency of mounts ($r_s = 0.34$, $n = 7$, $p = 0.40$) and attempts to mount ($r_s = 0.24$, $n = 7$, $p = .604$) in the Vavy Masiaka dyads. The lack of association between mating and mounts and mount attempts in Vavy Masiaka most

Table 2.45. Matrix of mount interactions in the Vaovao social group.

Exhibited Mount	Received Mount					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	8	5	0	-		*13*
MFd*	8	7	3		-	*18*
Total Received	16	12	3	-	-	**31**

Table 2.46. Matrix of mate interactions in the Vaovao social group.

Exhibited Mating	Received Mating					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	11	7	0	-		*18*
MFd*	3	5	0		-	*8*
Total Received	14	12	0	-	-	**26**

Table 2.47. Matrix of attempt-to-mount interactions in the Vaovao social group.

Exhibited Attempt-to-Mount	Received Attempt-to-Mount					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	0	5	0	-		*5*
MFd*	0	7	13		-	*20*
Total Received	0	12	13	-	-	**25**

Table 2.48. Matrix of clasp interactions in the Vaovao social group.

Exhibited Clasp	Received Clasp					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	2	4	0	-		*6*
MFd*	0	3	11		-	*14*
Total Received	2	6	11	-	-	**20**

Table 2.49. Matrix of attempt-to-clasp interactions in the Vaovao social group.

Exhibited Attempt-to-Clasp	Received Attempt-to-Clasp					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	6	2	1	-		*9*
MFd*	0	7	1		-	*8*
Total Received	6	9	2	-	-	**17**

Table 2.50. Matrix of mount with intromission interactions in the Vaovao social group.

Exhibited Mt/Intromission	Received Mount/Intromission					*Total Exhibited*
	F20	F19	F80	M240	MFd	
F20	-					-
F19		-				-
F80			-			-
M240*	1	0	0	-		*1*
MFd*	0	0	0		-	*0*
Total Received	1	0	0	-	-	**1**

Table 2.51. Matrix of attempt-to-clasp interactions in the Vavy Masiaka social group.

Exhibited Attempt-to-Clasp	Received Attempt-to-Clasp						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	1	5	-				*6*
M140*	0	4		-			*4*
MUC*	6	5			-		*11*
M243*	0	11				-	*11*
Total Received	7	25	-	-	-	-	**32**

Table 2.52. Matrix of clasp interactions in the Vavy Masiaka social group.

Exhibited Clasp	Received Clasp						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	2	0	-				*2*
M140*	0	2		-			*2*
MUC*	5	3			-		*8*
M243*	0	0				-	*0*
Total Received	7	5	-	-	-	-	**12**

Table 2.53. Matrix of mate interactions in the Vavy Masiaka social group.

Exhibited Mating	Received Mating						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	2	0	-				*2*
M140*	1	0		-			*1*
MUC*	0	0			-		*0*
M243*	0	3				-	*3*
Total Received	3	3	-	-	-	-	6

Table 2.54. Matrix of attempt-to-mount interactions in the Vavy Masiaka social group.

Exhibited Attempt-to-Mount	Received Attempt-to-Mount						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	0	0	-				*0*
M140*	0	0		-			*0*
MUC*	0	0			-		*0*
M243*	0	4				-	*4*
Total Received	0	4	-	-	-	-	4

Table 2.55. Matrix of mount interactions in the Vavy Masiaka social group.

Exhibited Mount	Received Mount						*Total Exhibited*
	F36	F107	M146	M140	MUC	M243	
F36	-						-
F107		-					-
M146*	0	0	-				*0*
M140*	0	1		-			*1*
MUC*	0	1			-		*1*
M243*	0	2				-	*2*
Total Received	0	4	-	-	-	-	4

likely reflects the increase in sexual behavior coinciding with M243's transfer into the group noted above (Appendices BF-BL). The moderate correlation between mating and mount attempts and mounts in Vaovao, on the other hand, suggests that while F80 was never observed to mate, she did conceive (Chapter 3) probably as a consequence of an unobserved mating that coincided with MFd's mounts and mount attempts.

b. Pseudo-estrus. Pseudo-estrus has been observed to occur in some lemurs one month prior to estrus (Perry et al., 1992; Richard, 1974; Vick, 1977), indicated by increased indices of female attractivity and male scent-marking behavior. Pseudo-estrus was assessed in sifaka using these criteria (Appendices X, AE, BK, BL). A moderate but insignificant increase in male affiliative interactions toward F36 in the month preceding estrus (Appendix AE) was the only indication that pseudo-estrus occurred in these sifaka.

c. Anestrus. Anestrus was assessed by the absence of female attractivity, proceptivity, and receptivity (Beach, 1976). Females remained attractive to males throughout the study (male approach: Appendices AN, AP; male guarding: Appendices AO, AQ; male affiliation: X, AE). Thus, by the criteria used above, anestrus occurred in the month preceding estrus. The sampling regimen did not permit assessment of anestrus after the breeding season.

5. The Social Correlates of Estrus

The kinds of social behavior associated with estrus differed in the two groups studied. In Vaovao, frequency of estrus behavior was moderately, but not significantly, correlated with rate of male guarding (r_s, = *0.62,* $n = 8$, $p = 0.10$), male approaches at all distances ($r_s = 0.60$, $n = 8$, $p = 0.13$), and greeting behavior (female to female: $r_s = 0.60$, $n = 8$, $p = 0.11$; female to male: $r_s = 0.60$, $n = 8$, $p = 0.11$). The rate of cuffing of males by females was the only agonistic behavior moderately associated with frequency of estrus behavior ($r_s = 0.60$, $n = 8$, $p = .11$).

In Vavy Masiaka, there were moderate, but insignifanct, associations between rate of male submission and guarding and frequency of estrus behavior (submission: $r_s = 0.62$, $n = 7$, $p = 0.14$; guarding: $r_s = 0.52$, $n = 7$, $p = 0.23$). Rate of female approaches to males at <1 m was weakly associated with frequency of estrus ($r_s = 0.20$, $n = 7$, $p = 0.60$), while female approaches to females had a moderate negative association with estrus ($r_s = -0.62$, $n = 7$, $p = 0.64$). Frequency of estrus behavior was moderately correlated with rates of female-female greeting ($r_s = 0.62$, $n = 7$, $p = 0.14$) and female-male lunging ($r_s = 0.64$, $n = 7$, $p = 0.11$), cuffing ($r_s = 0.62$, $n = 7$, $p = 0.14$), and biting behavior ($r_s = 0.62$, $n = 7$, $p = 0.14$).

6. Estrous Synchrony and Mating

Behavioral estrous periods were asynchronous in both social groups. The interval between estrous periods ranged from 24 hrs (F20/F19) to 5.25 days (F19/F80) among Vaovao females. It was 12 days and 17 hrs between the Vavy Masiaka females. In Vaovao estrous order followed female age and dominance.

Copulations occurred on vertical and semi-vertical branches of trees, young saplings, and low bushes. Males clasped females with their arms, one or both feet gripping the females' feet or legs. A typical mating sequence was composed of a single prolonged mount with 36-156 slow rhythmic thrusts culminating in ejaculation preceded by 2 to 10 mounts having rapid and intermittent thrusts. Extensive genital grooming followed several of the copulations and, in the absence of visable ejaculate, ejaculation was inferred to have taken place. Females mated with one or more resident and/or non-resident males but not with all available males.

Female 20 was the first to mate, mating with M240 on 7 January and then with MFd on 9 January. Male 240 copulated with F20 11 times in 1 hr while 10 m up in a dense *Tamarindus indica* tree, but only a few of these copulations resulted in ejaculation. Copulations varied in duration from 2 sec to 3 minutes. Three copulations lasting from 1 to 3 mins each were characterized by slow rhythmic thrusts followed by ejaculation. Initially, MFd and F19 repeatedly lunged at, grabbed, and attempted to bite the mating pair while F80 remained out of sight. Subsequently, when F19 briefly contacted MFd on the group's periphery, M240 interrupted his mount to chase MFd. During the remainder of that and the following 3 days, M240 was not seen to mate. Instead, he continually shadowed females 20 and 19, jumping between the females and MFd whenever the latter approached the females. Female 20's typical post-mating response to M240's attempts to approach her were hissing lunges, cuffs and grabs.

After 3 hrs of Herculean effort MFd finally completed three successful copulations with F20 on the morning of 9 January. These copulations were composed of 8, 36, and 43 thrusts each, and were preceded by eight 2- to 7-sec mounts without thrusts. During this time, M240 and F19 engaged in relentless and intense harassment of the mating pair, pursuing them from tree to tree, jumping at and grabbing and biting them. On three occasions F20 cuffed and grabbed M240 in a effort to fend off the harassment, but to no avail as M240 continued his assault even while fear-grimacing and chattering at F20. Male Fd was equally unrelenting in his efforts to maintain contact with F20, often hanging precariously from her back suspended from tree limbs and struggling against falling from the trees. These copulation attempts were further complicated by an encounter with another social group. Twice F20 attempted to throw off MFd by biting him in an effort to join F80's chase of the other group, but she, too, failed to dislodge the persistent MFd.

By mid-morning all mating attempts had ceased and everyone rested in a large *Tamarindus indica* tree. The remainder of that day was chiefly characterized by quiet feeding and grooming between the males. The Vaovao social group spent the bulk of 10 January feeding and resting without incident.

Female 19 mated with both resident males over her 50-hr estrous period between January 11 and 13. Male 240 copulated with her seven times over a 30 min period in a dense thicket. Cooperative copulations were composed of from 3 to 117 thrusts, the 14- and 117-thrust copulations resulting in ejaculation. These copulations had been immediately preceded by two mounts without intromission. They were strongly resisted by F19, who wrestled with and bit M240, in one instance struggling with him for as long as 13 seconds. These copulations occurred without harassment from other group members; MFd was observed quietly watching the mating from a 4 m distance. In the 30 min preceding and following mating, MFd attempted to mount F19 three times but was cuffed and bitten by her and then chased away by M240. The remainder of that day was spent resting.

January 12 was marked by F19's continual attempts to approach MFd and her prolonged "gazing" at him. Male Fd's two 3-thrust copulations with F19 (without ejaculation) occurred that morning, preceded by four brief mount attempts interrupted by M240 who repeatedly tried to jump between the pair. The 15-min period of copulation attempts by MFd were recorded as follows:

> 0926-0947hr: Female 19/Fd copulations occurred with few sustainable mounts due to 240's continual harassment of the pair. Although 19 continually approached and presented to Fd while cuffing and biting 240, 240 was successful in preventing Fd from maintaining a mount for more than 8 sec. Mounts with intromission and thrusting were few (2) and of short duration (3 sec).
> 0958hr: Fd and 240 stick close to 19, 240 shadowing her every move while Fd keeps his distance 2-3 m away. Twice it seemed Fd was trying to lure 19 away by approaching her and then quickly jumping away while staring at her. There was no response by 19.

The remainder of that day was characterized by intense guarding of F19 by M240 and protracted glances between MFd and F19.

In the late morning of January 13 MFd copulated with F19 three times high up in a *Tamarindus indica* tree out of M240's sight. These copulations occurred over a 4 min period and were composed of 3, 6, and 82 thrusts. Ejaculation was inferred from the 82-thrust mating based on extensive post-copulatory genital grooming. The matings were in stark contrast to the previous day's mating attempts in their lack of urgency. The pair had numerous opportunities to mate for 20 min undetected by group members, but except for the copulations noted above, they spent most of the time licking themselves and grooming one another. The only other sexual activity recorded that day was a mount attempt of F80 by MFd which was rebuffed. The balance of 13 January was spent voraciously consuming ripe berries, M240 shadowing F19's every move.

Although F80 was never observed to mate, she was mounted by MFd four times over a 3-day period between 16 January and 19 January. On 16 January MFd approached and mounted F80 for 2 sec before she successfully cuffed him off. Later that day M240 approached to within a meter of F80 on a low limb. Female 80 subsequently backed down the limb into his lap, afterwhich, seemingly startled, he urinated and withdrew several meters. Male Fd again mounted F80 later that afternoon. This mount was vigorously resisted by F80, being able to break the mount only after dropping to the ground from a 3 m high limb. January 17 and 18 were noteworthy for F80's "ambivalence" toward M240. It was marked by her continual approaches and withdrawals and his guarding of her from MFd, who, on one occasion, attempted to clasp F80. Ad libitum notes for the morning of 18 January are typical of M240/F80's interactions during that time period:

> 1148hr: The morning has been pregnant with sexual possibilities for 80 and 240. Male 240 has not only guarded 80 intensively, but he has been an attentive companion often resting in close contact with 80 and, on one occasion, maintaining an erection for 5-8 min. On two occasions he attempted to clasp her from the rear and was cuffed. After that he only attempted to maintain close proximity which was well tolerated by her.

During the late afternoon (1725 hr) of 19 January, F80 was observed to be finally receptive to mating attempts, the event recorded as follows:

> 1725hr:80, Fd and 240 were being noisy 3 m up in a low branching tree. I heard chattering and found 80 backing into and presenting to Fd and Fd attempting to mount 80. Male 240 continually interfered in the mount attempts by grabbing at Fd while he was being grabbed and bitten by 80. Fd continued to fear-grimace/chatter at 240 while trying to clasp and mount 80. Two mounts occurred (8 and 11 sec), but neither with intromission although Fd did have an erection.

Although a subsequent MFd mount attempt was met with a bite by F80, a half hour later F80 again approached MFd who then attempted to mount F80, only to have it broken up by M240. The following is typical of the remainder of the day's interactions among F80, MFd and M240:

> 1832hr:Fd is sitting behind 80 clasping her. Male 240 sits right in front of 80 looking at Fd.
> 1833hr:Fd grooms 80 for 49 sec and then licks his penis.
> 1835hr:80 withdraws several meters from Fd/240 and is followed by them. Fd attempts to mount 80 twice and 240 interrupts them Fd fear-grimacing and chattering at 240.
> 1838hr:Fd withdraws several meters from 80 and 240 who remain in the top a Euphorbia tree.
> 1840hr:80 withdraws a couple of meters from 240 to feed. Both 240 and Fd are now feeding within 3 m of 80, 240 feeding in closer proximity to 80 than Fd.

Mating in the Vavy Masiaka social group occurred in February of the 1991-92 breeding season. Female 36 was the first to mate, copulating with males 146 and 140 during her

2-hr estrous period the afternoon of 10 February. Female 36 mated first with M140, the copulation occurring immediately after M243, M107, and M228 had moved to an adjoining feeding site 10-20 m away. Female 36 was still feeding when M140, who had been feeding on the periphery of the group 5 to 10 meters away, dashed up F36's tree and mounted her. The 23-thrust copulation (ejaculation inferred from extensive genital grooming) lasted approximately 30 sec before it was broken up by M243, who dashed up the pair's sapling and bit M140 hard on the tail. Male 140 screamed, breaking his contact with F36, thereby allowing F36 to leap to a neighboring tree 2 m away. Female 36 was immediately joined by M243, who stared at M140 while placing himself between M140 and F36. Very soon thereafter, F36 joined F107 and JR to feed, followed closely by M243 and distantly shadowed by males 146 and 140.

Over the next 1.5 hrs Vavy Masiaka group members dispersed. Male 243, F107, and M228 gradually moved west feeding on the ground, while F36 drifted north 12-15 m out of sight of the group feeding alone. In late afternoon, F36 began the first of a series of very low lost calls while sitting in a small tree. She continued her "whispered" lost calls over the next 7 min, in full view of M140, who was feeding alone 10 m south. At 1756 hr M146 dashed toward F36, having emerged from a nearby dense thicket. Female 36 immediately presented to him and they copulated. This single copulation had 153 slow, rhythmic thrusts lasting just over

3 min and ejaculation was inferred based on extensive post-copulatory genital grooming by both animals. Two minutes into the copulation they were joined by the juvenile male 228, who sat in a tree 3 m away intensely watching the mating activity. At 1759 hr M146 dismounted and both animals licked their genitals. They then moved to a nearby bush and fed on berries. At 1818 hr M243 and F107 approached within 8 m of the pair, M243 staring at M146. Five minutes later M146 dashed away, moving toward M140 who was approximately 12 m from the group. For the balance of that afternoon M243 and the females fed on the ground while the males 146, 140 and 228 fed 12-15 m east.

Female 36 was again observed to mate briefly with M146 during the afternoon of 18 February. As before, the mating occurred as F36 lagged behind the core group who had moved off to feed some 10 m away. Male 146, who had been moving with the group all day, dashed to the top of F36's sapling. Female 36 presented to him, and they copulated for 8 sec before F36 dislodged M146 by biting him.

Female 107 mated with M243 on 23 February. The copulation occurred during the late morning and was preceded by intense agonism between the pair. Every attempt M243 made to approach to within 3 m of F107 was met by "glares" and repeated hissing attacks, F107 lunging at, grabbing and biting M243 while backing him down trees. Male 243, however, was unrelenting in maintaining his proximity. Shortly before 1120 hr, M243 again attempted to approach

F107 and was met with lunges, grabs, and bites. Female 107 chased him 1.5 m down a tree before leaping to a bush 3 m away. At 1133 hr the first mount occurred (without intromission) and was recorded as follows:

> 1133hr:107 and 243 sit 1 m apart in a low bush, 243 licking his penis. Male 243 approaches <1 m of 107, greets her and is immediately attacked. During the attack 243 is able to move behind 107 and quickly mounts her (without intromission), 107 immediately assuming a stationary posture for 15 sec before moving away.

Male 243 followed F107, she presented to him, and he accomplished the first of three copulations, characterized by 10 uneven and intermittent thrusts while hanging from a moving F107. Thirty seconds into the copulation, F107 bit M243 and he fell off. Male 243 sat next to her fear-grimacing and chattering. Within a minute M243 and F107 again mated briefly for approximately 30 seconds. The third and most sustained copulation occurred at 1137 hr. This copulation lasted 3 min and was characterized by 75 slow, rhythmic thrusts terminating in ejaculation. Following dismount, the pair then sat quietly together for 5 min grooming the ejaculate from their hair. These copulations occurred in clear view of the other napping group members. The remainder of the day was marked by frequent friendly interactions between M243 and F107. Female 107 permitted M243's close proximity while feeding and even occasionally grooming him.

Opportunistic observations of the Vaovao females during the 1991-92 breeding season revealed F20 to have a 96 hr estrous period beginning on exactly the same day as in the previous breeding season's estrous period. During one 30-min period F20 copulated with both resident M240 and the Vavy Masiaka M140. Male 140 had been absent from the Vavy Masiaka group the early afternoon of 7 January and was found on the periphery of Vaovao. Female 20 approached M140 from approximately 15 m away, greeted him, and was immediately mounted (without apparent ejaculation). The 2-min copulation occurred in full view of Vaovao groups members without incident. It was only after M140 attempted a second copulation with a resistant F20 that he was driven away by M240. Within minutes of M140's departure F20 presented to M240, and she copulated five times over a 40-min period. The 107-thrust copulation that ended in ejaculation had been preceded by four brief 3- to 5-thrust copulations. These matings were interspersed with two mount attempts which were met with cuffs by F20.

Two days later on 9 January, F20 was observed mating with Vavy Masiaka M146 (53 thrusts with inferred ejaculation) in full view of Vaovao group members, but no harassment occurred. On 10 January F20 and Vavy Masiaka M140 copulated briefly for 8 sec (no ejaculation) before their copulation was broken up by M146. This copulation occurred at the end of a Vaovao-Vavy Masiaka inter-group encounter as the two groups were dispersing. Female 20 approached M140, presented to him, and was immediately mounted.

Female 80 was also observed mating on 16 January at precisely the same time of year as in the previous breeding season. Vavy Masiaka M243 mated with F80 three times in 10 minutes during an inter-group encounter, the copulations occurring only four days after M243's transfer into Vavy Masiaka. The first copulation lasted 3 minutes and was accompanied by intense harassment by M140 and F36. It was followed by a brief 5 sec copulation and then a 4 min copulation with ejaculation, the latter accompanied by harassment from Vaovao's resident M240. The Vaovao females 20 and 80, but not the Vavy Masiaka females, were observed with infants the following birth season.

D. Discussion

The results of this study show that while sifaka resemble other lemurs in their estrous characteristics, female social relationships differ in important ways from those previously described in Lemuridae (Kappeler 1993; Morland, 1991; Sauther, 1991). These inter-specific differences may have profound implications for characterizations of lemur mating systems and social structure (Chapter 4).

Observations of reproductive seasonality in this study accord with previous reports of mating in free-ranging sifaka (Jolly, 1966; Richard, 1974, 1992). Females had a minimum 3-month breeding season during which they experience up to three 0.5- to 96-hr estrous periods, characterized by increases in attractivity, proceptivity, and receptivity (Beach, 1976).

In Vavy Masiaka, the frequency of proceptivity and recptivity (i.e. present behavior) increased prior to estrus associated with high rates of clasps and mount attempts by the newly immigrated M243. Similar situation-dependent increases in proceptivity and receptivity have been reported for cercopithecine and colobine primates subsequent to male immigration (Cords et al., 1984; Hrdy, 1977). This suggests that some degree of socially mediated flexibility in sexual behavior may occur in strepsirhines.

Pseudo-estrus, reported to occur in four Malagasy primates (*Lemur catta*: Jolly, 1967; *Lemur mongoz*: Perry et al., 1992; *Lemur fulvus*: Vick, 1977; *Propithecus verreauxi*: Richard, 1974), has been characterized by increased female attractivity (but not receptivity) and male scent-marking behavior one month prior to estrus. Pseudo-estrus was not evident in this study. The only possible behavioral indicator being a moderate, but insignificant, increase in male affiliative interactions directed toward a single female. These results suggest that what was previously called pseudo-estrus in sifaka may have been estrous behavior unaccompanied by observations of mating. Anestrus occurred in Vaovao and Vavy Masiaka females in the month prior to mating, based on the absence of attractivity, proceptivity and receptivity (Beach, 1976).

Sifaka resemble other Malagasy strepsirhines in exhibiting rank- and age-related estrous asynchrony within groups (*Lemur catta*: Pereira, 1991; Sauther, 1991; *Propithecus verreauxi*: Jolly, 1967; Richard, 1974: *Varecia variegata*: Morland, 1991). It has been argued that within-group estrous asynchrony enhances female mate choice through the temporal reduction of competition between females for preferred mates (Pereira, 1991). However, results from this study suggest that while in principle female mating choice may be enhanced by rank-related estrous asynchrony within groups, in practice intrasexual competition may circumvent female mate choice through effective guarding by males, and harassment of copulating pairs by other females. Male 240's guarding of F80, and M240's and F19's harassment of the MFd/F80 dyad had profoundly negative effects on MFd's mating success based on numbers of mounts (F80) and copulations (F20) observed (but see Chapter 3)

Estrus was associated with increases in affiliative interactions between females and female agonism directed toward males. Heightened peri-estrous levels of female agonism directed toward males has also been reported for captive (Foerg, 1982; Shideler et al., 1983) and free-ranging *Varecia variegata* (Morland, 1991). Foerg (1982) and Morland (1991) have suggested that female agonism represents a form of female mate choice. Females approached and attacked only those males with whom they prefer to mate. In contrast, sifaka females were most aggressive toward males who approached them most frequently during estrus. These data suggest that both sexes may have been expressing mating preferences. Male preferences were expressed through approach interactions and females' rejection of (not preference for) certain males being expressed through intensity of female agonism.

Alternatively, the increase of female agonism directed at males during estrus may be related to the interval between mounts (without intromission) and male attempts to elevate the interaction to mating, and be indicative of female arousal. Partial support for this idea comes from the fact that some females (e.g. F19, F107) mated cooperatively immediately after aggressively resisting mating.

Social relationships between male and female lemurs vary with respect to the intensity of female-directed aggression toward males (Kappeler, 1993; Morland, 1991; Sauther, 1991; Vick and Pereira, 1989). Female sifaka in this study were often aggressive toward males, especially the oldest resident males. Particular females (e.g. VV:F19, VM:F107) targeting particular males (VV:M240, VM:M243) for assault. High rates of female-male agonism have also been observed in captive *Eulemur coronatus* male-female pairs (Kappeler, 1993) and in free-ranging *Varecia variegata* (Simons Morland, 1991) and *Lemur catta* (Sauther, 1991) social groups, the latter in the context of feeding.

On the other hand, captive *Eulemur fulvus* and *Lemur catta* females were reported to target males for aggression only rarely, usually during the birth season (Vick and Pereira, 1989). It is unclear why sifaka females target certain males for aggression. Pereira and Weiss (1991) have suggested that female-directed agonism toward males socially mediates the potentially lethal effects of newly immigrated infanticidal males among captive *Lemur catta*. However, Sauther and Sussman (1993) find no support for this idea in free-ranging ringtailed lemurs. Male infanticide has been observed twice in free-ranging *Propithecus diadema edwardsii* (Wright, pers. comm.). Males killed infants following their transfer into the social group, but no such data exist for *Propithecus verreauxi* social groups.

Male lemurs rarely direct agonism toward females (Kappeler, 1993a; Richard, 1974, 1992; Sauther, 1991; Simons Morland, 1991; Vick and Pereira, 1989), most likely because adult female lemurs are socially dominant to males (Young et al., 1991, but see Pereira et al., 1990). In this study, female sifaka were dominant over males based on consistent patterns of submission directed at females by males. However, Vaovao's oldest resident male (F240) directed a substantial amount of agonism at the group's youngest female (F80), particularily during estrus. Similar levels of male-directed agonism toward females have been observed in free-ranging *Eulemur fulvus rufus*, but in the absence of female social dominance over males (Overdorff, 1994). (Pereira at al. (1990) and Sauther and Sussman (1993) have suggested that in *Lemur catta* groups, female social dominance over males develops gradually over time. Young females do not acquire their full dominance status until after their first estrus. Partial support for this idea was found in captive, but not free-ranging sifaka. A father and his 1-year-old daughter were observed lunging at, cuffing, and chasing one another in a captive group of *Propithecus verreauxi* at the Duke Univrsity Primate Center in Durham, NC. (Brockman, unpub. data). Although Vaovao's F80 was a relatively young female (i.e. 5 years old), she experienced her second breeding season in 1991, after producing her first infant in 1990.

Social relationship among female lemurs appear to differ inter-specifically more than previously recognized. Patterns of affiliation between female sifaka differ from those seen in captive lemurs (Kappeler, 1993) but resembled those seen in free-ranging *Eulemur fulvus rufus* (Overdorff, 1994) and *Varecia variegata* (Morland, 1991). In *Eulemur fulvus rufus* (Overdorff, 1994), *Varecia variegata* (Morland, 1991) and *Propithecus verreauxi* social groups, females were much more affiliative with other group females than they were with group males. In sifaka, most friendly interactions involved greeting and grooming, the recipients of the latter based on dominance rank. High levels of tactile affiliative behaviors have also been observed in *Eulemur fulvus rufus* (Overdorff, 1994) and *Varecia variagata* (Morland, 1991). The social significance of these activities is unclear and may be a manifestation of close female relationships. Alternatively, Morland (1991) has suggested that they may enhance female social bonds within groups. In contrast, captive studies of female *Lemur catta*, *Eulemur fulvus*, and *Eulemur coronatus* showed that within-group social interactions were predominantly characterized by competitive relations among females even of the same matriline (Kappeler, 1993). Sauther and Sussman (1993) observed female competition occurring between, but not within, matrilines in free-ranging *Lemur catta* groups.

These data show that sifaka social relationships affected and were affected by small scale demographic effects and suggest that strepsirhine social dynamics may approach the complexity of those observed in catarrhine primates (Altmann and Altmann, 1979; Dunbar, 1984). Proximity data indicate that females' association preference for certain males may have precipitated the demographic shift that occurred in Vavy Masiaka. Just prior to M146's attacks on M140, both females were maintaining exclusive proximity to M140. Male 243's successful immigration into Vavy Masiaka coincided with the battling males' absence from the group thus enhancing his subsequent mating opportunities with females in his own and a neighboring group.

Females in this study mated with one or more males during the breeding season, selecting mates from an array of resident, peripheral, and non-resident males. Two females mated with only one male, and three females mated with either two or three males. In most instances (4 of 6) females confined their mating to resident males, in all but one case (F36) mating with the older male before the younger male. In one instance a female (F80) was never observed to mate. She rejected all mating attempts by the oldest resident male and seemingly having her attempts to copulate with the younger male thwarted by a constantly guarding older male. Female 80, nevertheless, conceived (Chapter 3), probably mating at night with MFd undetected by other group members and the observer. Undetected copulations have been inferred in free-ranging *Lemur catta* females from the presence of vaginal semen plugs (Sauther, 1991).

Copulations with non-resident males were associated with demographic shifts in neighboring social groups which occurred during the 1991-92 breeding season. In the two instances in which extra-group mating occurred, Vaovao females mated with three newly immigrated and peripheral males who were members of the neighboring Vavy Masiaka social group. Dominant F20 mated with the peripheral males 146 and 140, while her daughter (F80) mated with the recently immigrated M243. Two of these copulations occurred during inter-group encounters, suggesting females may enhance their mating opportunities through increased contact with neighboring groups during the breeding season.

Previous studies of female mate choice suggest that female mating preferences in captive and free-ranging *Lemur catta* are based upon relatedness (Periera and Weiss, 1991; Taylor and Sussman, 1985) and dominance status of males (Sauther, 1991). However, in free-ranging *Varecia variegata,* females prefer to mate with familiar males (Morland, 1991, 1993). Sauther (1991) indicated that in her study of free-ranging *Lemur catta* groups, female mate choice affected mate order, the group's preferred central male having mating priority over subordinate males (Sauther, 1991). Sauther (1991) does not make clear, however, how she differientated central male mating priority based on female mate choice from that based on male-male competition.

Female sifaka exhibited age-related mating preferences which, in most cases, affected male mating order. Dominant females (VV:F20) mated with older resident males (VV:M240) before younger males (VV:MFd) and subordinate females (VV:F19,F80; VM:F36) accepted both younger (VV:MFd) and older (VM:M146) resident males as mates. In the case of the Vaovao and Vavy Masiaka females 19 and 36, however, mating preference did not affect mating order as both females mated with the "less-preferred" (based on "present" behavior) males M240 and M140 before mating with their preferred mates, MFd and M146 respectively. The reasons for this are unclear, but may reflect the swamping of female mating preferences by those of males and/or temporally constrained conception imperatives, the benefits of conception outweighing the costs of resisting the mating efforts of persistent males.

Male responses to a female's reluctance to mate varied between groups. Vavy Maisaka's persistant M243 was able to overcome F107's fierce resistance to mating. Vaovao's M240 was never observed to mate with F80, appearing to have acquiesced to F80's reluctance to mate by diminishing his mating efforts and increasing his guarding efforts of F80. The sharply contrasting behaviors exhibited by these two males in response to female reluctance to mating suggest that differing male mating styles could have profound effects on male copulatory success and long term reproductive fitness (but see Chapter 3).

The small sample size of social groups and females reported here prevents broad generalizations about the social and behavioral correlates of estrus and mating in free-ranging female Verreauxi's sifaka, particularily in view of the diverse and complex patterns of behavior found even in this small sample. Nevertheless, sifaka in this study exhibited affiliative relationships between females, female-directed agonism toward males, female mate choice and multiple mating patterns. Multiple mating was affected by intrasexual competition and diverse mating styles among males. These results show the dynamic and complex nature of social and sexual relationships possible even in these small brained, energetically challenged strepsirhines (Richard and Nicoll, 1987).

CHAPTER III. HORMONAL CORRELATES OF MATING IN SIFAKA

A. Introduction

Female sifaka mate with one or more males during a 0.5- to 96-hr estrous period and are selective in their mating preferences (Chapter 2). It has been suggested that in other primates females mate with several males to confuse paternity and forestall male infanticide (Collins et al., 1984; Goodall, 1977; Hrdy, 1979; Pereira and Weiss, 1991; Rudran, 1979; Sugiyama, 1965), ensure male care by males (Garber et al., 1984; Goldizen, 1987; Taub, 1980; but see Menard et al., 1992), or ensure fertilization (Milton, 1985; Sauther, 1991; Sauther and Sussman, 1993; but see Bercovitch, 1987). This study assesses the proposition that female *Propithecus verreauxi* increase their probability of fertilization through estrous asynchrony, increased mating frequency, and mate choice. Determining how these behavioral components affect conception in sifaka requires information on the temporal relationship between mating and ovarian hormones.

The hormonal correlates of mating in free-ranging *Propithecus verreauxi* were investigated using fecal steroids as indices of reproductive state. Fecal gonadal steroids accurately reflect ovarian function in various primates including *Propithecus verreauxi* (Brockman et al., 1993; submitted), *Nycticebus coucang* (Perez et al., 1988), *Callithrix jacchus* (Heistermann et al., 1992), *Alouatta* *palliata* (Clarke et al., 1991), *Brachyteles arachnoides:* Strier & Ziegler, 1994; *Macaca nemestrina* (Risler et al., 1987), *Papio cynocephalus* (Stavisky et al., submitted; Wasser et al., 1991), and *Homo sapiens* (Aldercreutz and Jarvenpaa, 1982). Apart from the data presented here, only one other study has investigated the relationship between fecal steroid levels and mating in free-ranging primates. In Clarke et al.'s (1991) study of nine female *Alouatta palliata* in northwestern Costa Rica, multiple copulations were associated with elevated estrogen levels, but no information was provided regarding conception or mate preference.

The endocrinology of reproduction in *Propithecus verreauxi* was preliminarily investigated in a captive study sifaka at Duke University Primate Center (Brockman et al., 1993; submitted). Cyclic changes in estradiol (E_2) and progesterone (P_4) were observed in two females spanning four months. The 5-day luteal and 24- to 27-day follicular phases observed in these 2 females were similar to results obtained from serum and urinary studies of other species of *Lemur* and *Varecia* (Shideler et al., 1983; Perry et al., 1992). The female who conceived experienced two putative cycles unaccompanied by observations of mating, while the female who failed to conceive had two discrete periods of mating separated by 30 days. Profiles of E_2 and P_4 levels concorded with observations in other primates in that E_2 was elevated during estrus and mid-pregnancy and P_4 was low at estrus and increased during early pregnancy. Although mating behavior was associated with elevated E_2 levels, not all E_2 peaks were associated with observed copulations (Brockman et al., submitted).

Pseudo-estrus has been reported to occur in some strepsirhines, indicated by vulval pinkening and swelling (*Lemur catta*: Jolly, 1967; Vick, 1977; *Propithecus verreauxi*: Haring, 1988; Richards, 1974; *Eulemur mongoz*: Perry et al., 1992; *Varecia variegata*: Shideler and Lindburg, 1982) and increased E_2 levels one month prior to estrus (Perry et al., 1992). Although no hormonal evidence of pseudo-estrus has been observed in captive sifaka (Brockman et al., submitted), this study assessed the relationship between E_2 levels and cyclic changes in vulval morphology indicating pre-mating ovarian activity.

B. Material and Methods

1. Subjects

Daily serial fecal samples were collected from Vaovao females 20 (F20), 80 (F80), and 19 (F19) and Vavy Masiaka females 36 (F36) and 107 (F107). Collections were made prior to and during the breeding season (January through March) at Beza Mahafaly, Madagascar.

2. Fecal Sample Collection and Preservation

Fecal samples were collected from December 10, 1990 through March 14, 1991 for the Vaovao females and December

5, 1991 through March 27, 1992 for the Vavy Masiaka females. This collection period was determined from existing information about the time of mating and births in the study population.

A total of 485 fecal samples were collected from females (F20: 79; F19: 86; F80: 86; F36: 112; F107: 112). Morning fecal samples (1-15 gm) were collected in entirety immediately after voiding, packaged in foil, flattened to increase surface area, and dried in a Coleman oven (temperatures ranging from 55°C [solar heat] to 83°C [propane heat] for 2-3 hours) within 4 hrs of defecation. After drying, the fecal samples were wrapped in plastic wrap and individually packaged with indicator silica gel packets in 4 ml zip-lock bags, labeled, and bagged again in 2.7 ml zip-lock bags with silica gel. The samples were carried back to the U.S. at the end of the field season and shipped to Dr. P.L. Whitten's laboratory at Emory University for analysis.

Fecal desiccation was used as an alternative to freezing and chemical preservation because electricity and chemical preservatives were not readily available at Beza Mahafaly. The effectiveness of this preservation method was evaluated in a laboratory study assessing steroid degradation over time in desiccated sifaka feces. Fecal E_2 and P_4 were measured in fresh frozen fecal samples using radioimmunoassay techniques. The samples were subsequently dried and additional measurements were taken immediately after desiccation, and then again at one, two, and three week intervals.

Diurnal variation in fecal E_2 excretion was investigated in serial fecal samples collected from two female sifaka on several sample days. No significant difference in E_2 excretion was found according to time of day the fecal sample was collected (One-Way ANOVA, $F = .076$, N.S., N = 6).

3. Behavior and Vulval Morphology

A total of 644.25 focal animal hours of observation (Altmann, 1974) were carried out on 5 females (Vaovao F20, F19, F80; Vavy Masiaka F36, F107) using a 63-word ethogram (Appendix A). Observations were collected 6 days per week beginning at dawn, terminating at dusk, and breaking for two hours mid-day coincident with the animals' rest period. The only exception to this regimen occurred when females were in estrus; observations during this time were recorded from sunrise to just after sunset. Fifteen-minute focal animal samples were evenly distributed among three 2-hr morning time blocks (to accommodate fecal collections) and four 1-hr afternoon/evening time blocks. Behavioral samples were randomized across females using a lottery technique. Pieces of paper inscribed with female I.D. numbers were mixed and then drawn from an enclosed container. The behaviors of interest in this chapter were mating (i.e. mounts with intromission and thrusting), mounts, and attempts to mount.

Behavioral data were recorded and analyzed as described in Chapter 2.

Vulval morphology was visually assessed daily for all females and recorded using the 0-3 scale (0 = black; 1 = pale pink dot; 1.5 = bright pink dot; 2 = swollen pink slit; 2.5 = swollen pin-head opening; 3 = swollen pink opening) to evaluate potential relationships between changes in hormone level and external signs of estrus and pseudo-estrus.

4. Hormone Assay

Dried fecal samples were pooled and pulverized into a fine powder from which 0.1 gm sample was measured out for hormone analysis. Conjugated fecal estradiol (E_2) and progesterone (P_4) were quantified using solid phase extraction and radioimmunoassay (RIA) procedures previously validated for this species (Brockman et al., submitted).

a. Fecal steroid extraction. A 0.1 gm (dry wt) sample was homogenized in 2 ml methanol:acetone (8:2, v/v) for 30 sec 1300 rpm. The homogenate was filtered by layering onto a 0.2 μm G Prep PTFE filter (Gelman Sciences, Ann Arbor, MI) and centrifuged at 1500 x g for 5 min. The filtrate was solid phased extracted on small columns of reversed-phase octadecylsilane (C18) bonded to silica (Burdick and Jackson), using the methods of Shackleton and Whitney (1980). The column was primed with 2 ml of methanol, followed by 5 ml deionized water. The sample was then layered onto the column, and the column washed with 5 ml water. The steroid extract was then diluted with 3 ml methanol. Recovery experiments indicated that an average of 65% of estradiol and progesterone were eluted in the first 2 ml of methanol.

b. Estradiol radioimmunoassay. The estradiol radioimmunoassay procedures followed the microassay procedures developed by Worthman et al. (1990). This protocol was a modification of the Pantex Direct ^{125}I Estradiol Test kit (Santa Monica, CA). Working buffer was 0.1% gelatin phosphate buffered saline (pH 7.4) achieved by heating 0.1 gm gelatin in 100 ml Dulbecco's Buffer (Gibco, Grand Island, NY) at 45°C. The estradiol antiserum, containing rabbit anti-estradiol-17α-6-oxime-BSA in 0.01M phosphate buffer, 0.25% BSA, 1.0 mg/ml lipase, and 0.1% sodium azide, exhibited cross-reactivities of 1.4% (estradiol-17α), 0.018% (estriol), and less than 0.001% for other related compounds. The antisera was diluted 1:4 with working buffer. Estradiol standards were diluted 1:5 with working buffer to give concentrations of 0, 2, 4, 8, 16, 32, 64, 128, 256, 512, and 1024 pg/ml. Additional controls containing estradiol (Bio-Rad, ECS Division, Anaheim, CA) in human serum base were also diluted 1:5 in working buffer. The PEG second antibody solution for the estadiol assay containing polyethylene glycol 6% w/v and goat anti-rabbit, 0.05% BSA and 0.1% sodium azide as preservative was diluted 1:2 with working buffer.

An aliquot of fecal extract was evaporated under nitrogen and reconstituted in working buffer. ^{125}I estradiol tracer (50 μl), containing 0.025M phosphate buffer, estradiol binding inhibitor with 0.05% sodium azide as preservative, and diluted antiserum (300 μl) were added to aliquots (200 μl) of standards, samples, and controls. Each was vortexed and incubated overnight at room temperature. The following morning, diluted second antibody (500 μl) was added, incubated an additional 20 minutes at room temperature, and centrifuged at 1500 x g for 60 minutes at 4 °C. The supernatant was decanted and the radioactivity of the precipitate was determined by ten minute counts in a gamma counter.

c. Progesterone radioimmunoassay. The progesterone radioimmunoassay procedures are as previously described above.

The hormone data from the five sifaka females were grouped into 10-day intervals in order to determine trends in steroid values over time. One 10-day interval incorporated the days of estrus, determined by observations of mating (or mounts in the absence of mating), with the first day of estrus being day 0, and the additional 10-day intervals incorporated pre- and post-estrous days. Means for 10-day intervals of E_2 and P_4 were calculated, and Mann Whitney rank sum tests were used to assess differences between the estrous interval and the two 10-day intervals bracketing it. Tests were considered statisticall significant at .05.

C. Results

1. Sample Preservation

Radioimmunoassay results assessing steroid degradation over time in desiccated feces showed that the greatest loss in E_2 and P_4 occurred immediately after drying, and then stabilized (Table 3.1). Less loss occurred in E_2 than in P_4. Overall, the change in steroid levels from the post-dry period to week three was not significantly different (One-Way RM ANOVA, E_2: $F = 3.42$, $N = 16$, $p = 0.07$; P_4: $F = 2.26$, $N = 16$, $p = 0.15$).

2. Fecal Steroid Profiles

Estradiol and P_4 were quantified spanning a 146 day period from 80 days prior to estrus (F107) to day 66 post-estrous (F20). Figures 7-11 show E_2 and P_4 profiles for the 5 females in this study. Although it would have desirable to have used the same scale for each graph so that E_2 and P_4 values would be comparable, to do so would have eliminated the scale necessary to properly interpret females 36, 19, and 107's graphs.

Estradiol and P_4 profiles of F80 are shown in Figure 7. A marked 7-fold, 7-day E_2 elevation is seen on 9-15 January followed by a substantial rise in P_4 beginning on January 18. A large elevation in E_2 and P_4 occurred 42 days later in

Table 3.1. Progesterone (P_4) and estradiol (E_2) recoveries over time in desiccated sifaka fecal samples.

	Fresh Frozen (ng/gm)	Post-Dry(%) (ng/gm)	1 Week(%) (ng/gm)	2 Weeks(%) (ng/gm)	3 Weeks(%) (ng/gm)
P_4					
Low*	8.0	4.4(55)			
	8.0	5.6(70)			
	12.0	5.4(45)	7.3(61)	4.7(39)	3.3(28)
	17.0	5.6(33)	4.7(28)	2.7(16)	5.0(29)
Rec.# (SE)		*50.7±6.8*	*44.2±11.8*	*27.6±8.3*	*29.0±0.3*
High*	47.0	12.6(27)	5.3(11)	2.7(06)	11.0(23)
	20.5	14.4(80)	5.7(28)	3.7(18)	9.0(44)
Rec.# (ES)		*53.4±18.9*	*19.6±5.8*	*11.8±4.4*	*33.6±7.3*
E_2					
Low	122.0	81.6(67)	40.0(33)	45.3(37)	142.0(116)
	93.0	74.4(80)	58.7(63)	64.0(69)	97.3(105)
	64.0	48.8(76)			
	54.0	54.8(100)			
Rec.# (SE)		*80.8±6.0*	*48.0±10.7*	*53.0±11.2*	*1.10±0.04*
High	937.0	659.6(70)	1290.7(138)	604.0(65)	886.7(95)
	801.0	631.2(79)	1036.0(129)	626.0(78)	1300.0(162)
Rec.# (SE)		*74.6±3.0*	*133.5±3.0*	*71.4±4.8*	*128.4±24.0*

#	Mean recoveries in percent ± standard error
(%)	Percentage of steroid recovered
Low*	Samples with lowest steroid levels
High*	Samples with highest steroid levels

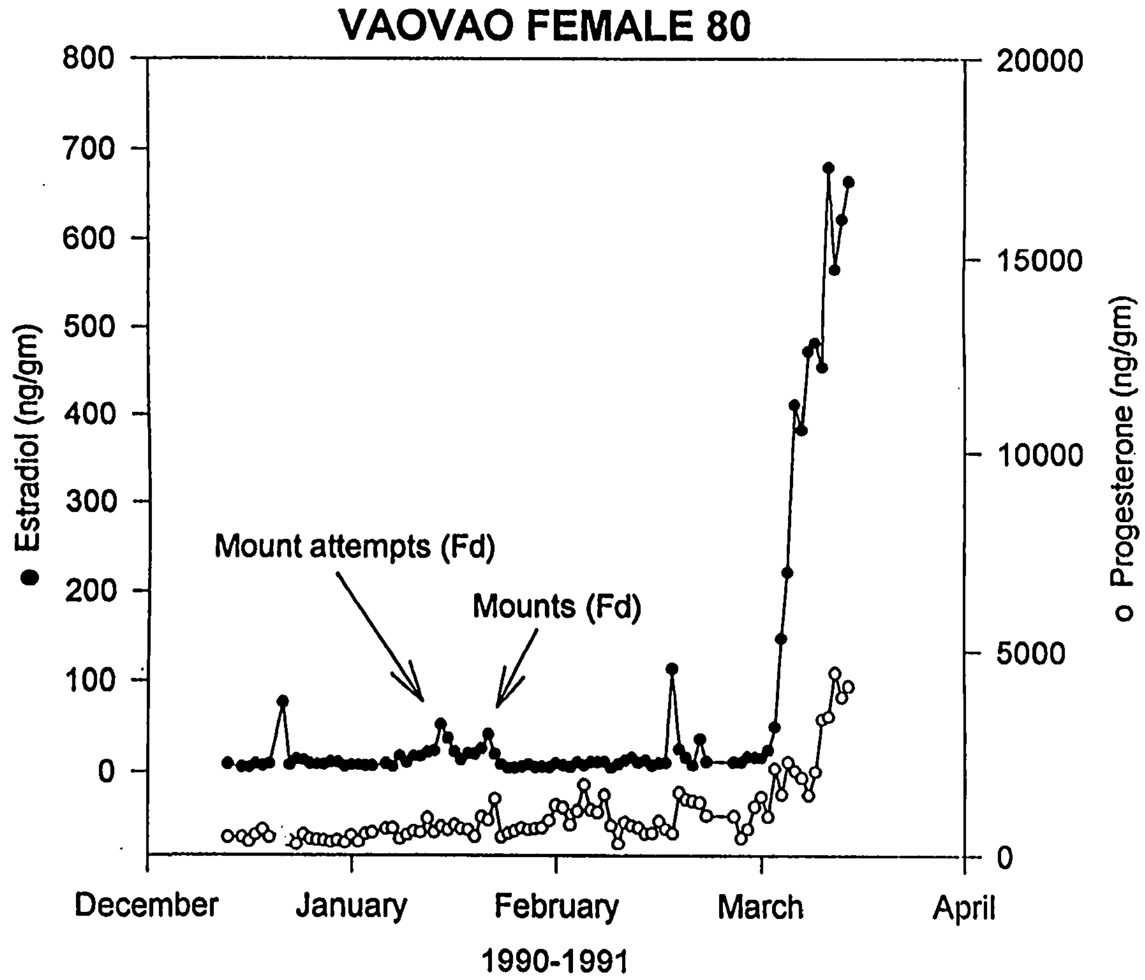


Figure 7. Estradiol and progesterone profiles for Vaovao F80.

late-February. Baseline levels of E_2 were 62% of the values reported for non-breeding season females (mean = 8.53 ng/gm, sd = 2.45, n = 16; Brockman et al., submitted [published wet weight values were converted to dry weight values for comparison]), while peak values were 50-fold higher. Another, more moderate, rise in E_2 took place 7 days after the 12 January elevation on January 19. This "estrous" elevation (behaviorally defined by observations of male mounts) in E_2 was characterized by a gradual 3-fold increase lasting six days. A third and fourth 1-day elevation in E_2 occurred 31 and 28 days prior to and after estrus on 20 December 20 and 16 February. Estradiol values twice that of estrous levels.

Elevations in P_4 began within 3 days of the rapid January 12 rise in E_2 and lasted 53 days when sampling terminated (Figure 7). Baseline P_4 levels were almost three times higher than those reported for non-breeding season females (mean = 401.74 ng/gm, sd = 88.67, n = 17; Brockman et al., submitted), while peak values were 18-fold higher. The late-February E_2 and P_4 levels were three and almost twice as high as captive pregnancy levels (Brockman et al., submitted) suggesting F80 conceived during her first estrous period.

Figure 8 depicts the E_2 and P_4 profiles of F20. A gradual 10-day elevation in fecal E_2 is seen in early January, followed by a gradual rise in P_4. A more dramatic

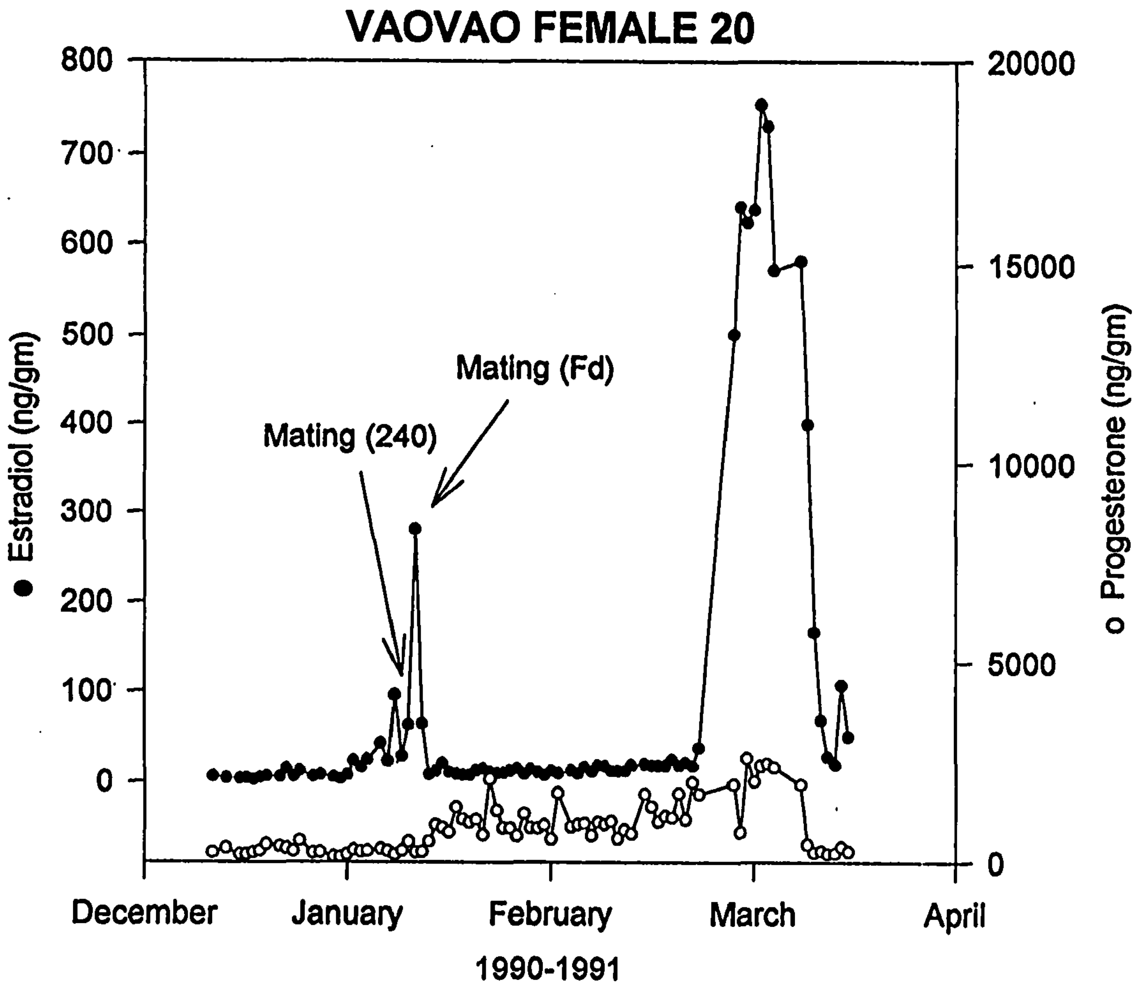


Figure 8. Estradiol and progesterone profiles for Vaovao F20.

rise in E_2 and P_4 occurred 42 days post-estrous in the third week of February. Baseline levels of E_2 were 50% of the values observed in non-breeding season females (mean = 6.51 ng/gm, sd = 3.02, n = 16; Brockman et al., submitted), while peak values were 133-fold higher. Estrous elevations of E_2 were characterized by a gradual 14-fold rise lasting 10 days. A second E_2 elevation occurred 42 days after estrus, was 133-fold above baseline levels, and lasted 14 days before dropping precipitously to pre-estrous levels.

Elevations in P_4 began immediately after the sharp 9 January rise in E_2 and lasted 54 days before returning to pre-estrous levels (Figure 8). Baseline levels of P_4 were equal to the levels reported for non-breeding season females (mean = 276.8 ng/gm, sd = 107.98, n = 17; Brockman et al., submitted) while peak values were 10-fold higher. The late-February elevations in E_2 and P_4 observed in this profile were three times and 67% the pregnancy levels previously reported for captive sifaka (Brockman, et al., submitted) showing that F20 also conceived during her first estrous period. The precipitous drop in steroid levels in early March, however, suggests that this conception may have aborted 58 to 61 days post-conception.

Figure 9 depicts the E_2 and P_4 profiles of F19. A gradula 11-day, 5-fold E_2 increase is seen on 12 January followed by two marked E_2 peaks on 19 February and 13 March, representing 11- and 9-fold increases above baseline levels.

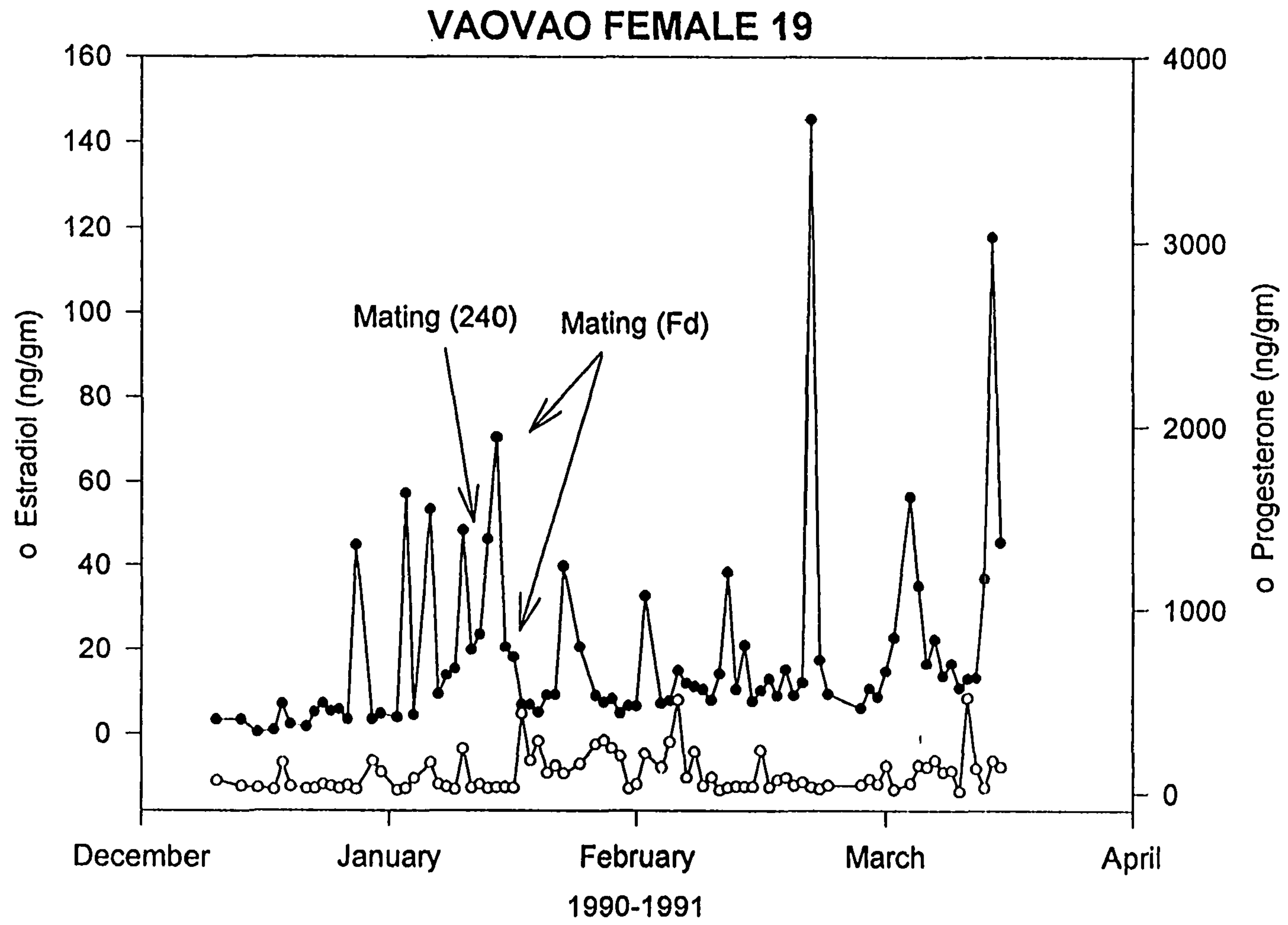


Figure 9. Estradiol and progesterone profiles for Vaovao F19.

Baseline levels of E_2 were within the range of values reported for non-breeding season females (mean = 3.96 ng/gm, sd = 2.2, n = 13; Brockman et al., submitted), while the peak value was 11-fold higher and occurred 35-days post-estrous. Estrous elevations of E_2 (January 5-15) were characterized by a gradual 5-fold rise lasting 11 days. Several additional, but more abbreviated, pre- and post-estrous elevations occurred which represented 2- to 4-fold increases over baseline values but lasted only one to two days.

Elevations in P_4 began immediately after the sharp January rise in E_2 and lasted 23 days, before resuming pre-estrous levels (Figure 9). Baseline levels were 20% of those reported for non-breeding season females (mean = 47.5 ng/gm, sd = 36.1, n = 13; Brockman et al., submitted), while peak values were twice as high. Although longer and less elevated than estrous E_2 levels, the 12-day March 13 elevation in E_2 , 46 days later, was immediately followed by a P_4 elevation and may be indicative of the beginning of an additional "cycle."

In F36's steroid profiles (Figure 10), a gradual and variable 15-day E_2 elevation occurred between 29 January and 12 February, followed by a gradual rise in P_4. Baseline levels of E_2 were 66% of those observed in non-breeding season females (mean = 8.0 ng/gm, sd = 3.02, n = 27; Brockman et al., submitted), while peak values were five

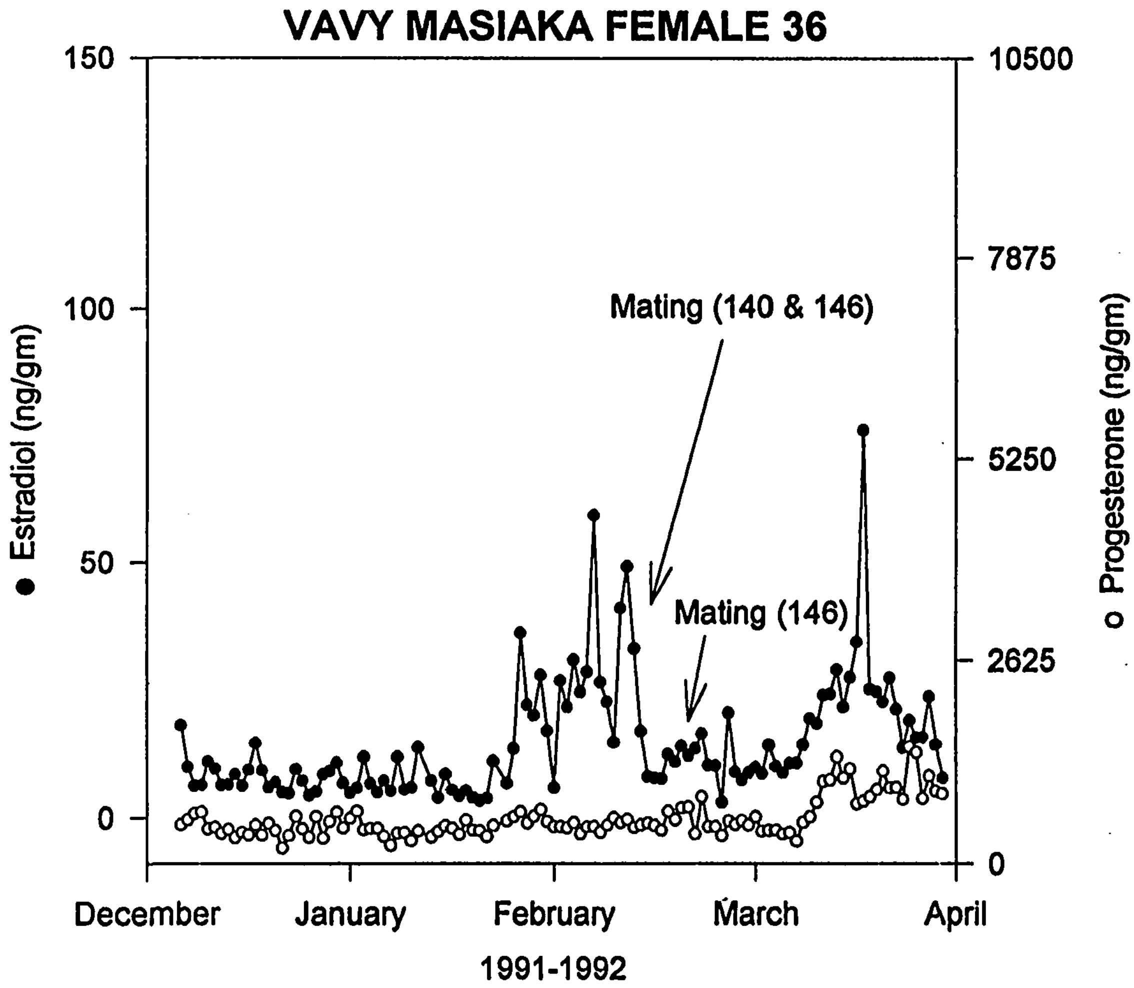


Figure 10. Estradiol and progesterone profiles of Vavy Masiaka F36.

times higher. The estrous E_2 elevation on 9 February exhibited a rapid 3-fold rise lasting 7 days. Six days prior to this estrous elevation a 10-day, 4-fold increase on 4 February occurred and was followed 36 days later by a 7-day, 17-fold rise in E_2 on 15 March.

Progesterone elevations began 2 days after the 9 February E_2 rise and lasted 43 days when sampling terminated (Figure 10). Baseline levels of P_4 were almost twice as high as non-breeding season levels (mean = 478.66 ng/gm, sd = 120.12, n = 27; Brockman et al., submitted), while peak levels were more than five times higher. The 7-day E_2 and 23-day P_4 elevations observed in mid-March were 30% of those reported for pregnant captive sifaka (Brockman et al., submitted) although the E_2 levels were not sustained. These data suggest that like females 20 and 80, F36 conceived during her first estrous period.

Female 107's E_2 profile (Figure 11) closely resembles the mid-December through late-February profile of F80 (Figure 7), except for the second 1-day E_2 elevation on 11 January and the unsustained rise in that steroid on 21 March. Baseline levels of E_2 were 30% of those reported for non-breeding season females (mean = 4.5 ng/gm, sd = 1.5, n = 21; Brockman et al., submitted), while peak values were 14-fold higher. Four 4- to 10-day E_2 elevations occurred on 26 December, 24 January, 24 February, and 21 March representing 2-, 4-, 3-, and 14-fold increases above

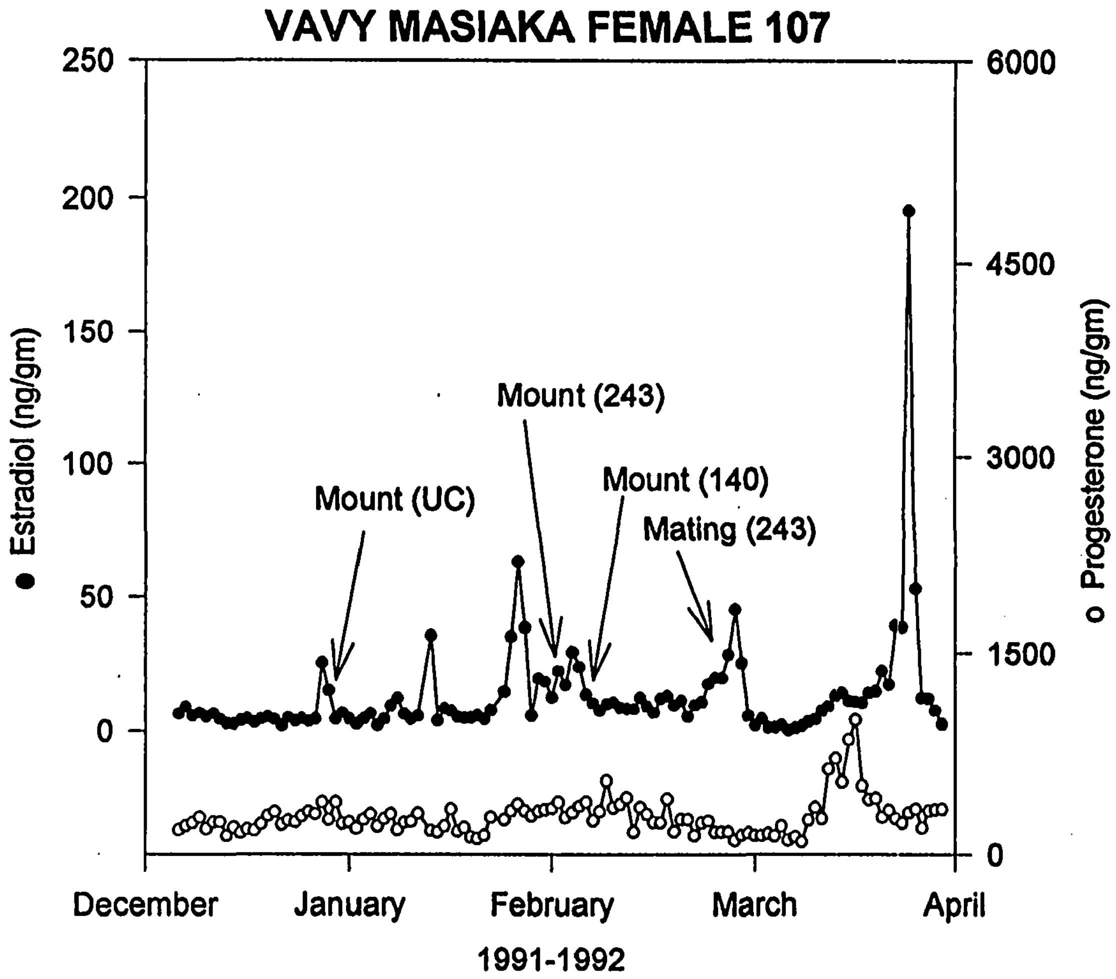


Figure 11. Estradiol and progesterone profiles of Vavy Masiaka F107.

baseline. Estrous elevations in E_2 were characterized by a gradual 3-fold rise on 24 February lasting 10 days but they were unaccompanied by elevations in P_4. Two additional E_2 elevations occurred on 26 December and 24 January associated with male mounts, suggesting that cyclic ovarian activity was occurring prior to estrus.

Female 107's P_4 profile (Figure 11) remained fairly constant throughout the sampling period with baseline levels equal to those reported for non-breeding season females (mean = 241.1 ng/gm, sd = 57.6, n = 27; Brockman et al., submitted). A single 42-fold increase in P_4 lasting 19 days occurred on 14 March following the 24 February E_2 rise by eight days and preceding the March 21 E_2 elevations by 18 days.

3. Estradiol Levels and Mating

For all 5 females combined, mean E_2 and P_4 values were significantly different between the estrous and post-estrous 10-day intervals (Mann Whitney rank sum test, E_2: $T = 1874$, $p < 0.001$, N(small) = 50, N(big) = 54; P_4: $T = 2349$, $p < 0.004$, N(small) = 54, N(big) = 48), but were not significantly different between the pre-estrous and estrous 10-day intervals (Table 3.2). Estrous levels of E_2 and P_4 were also significantly different among the 5 females (Kruskal-Wallis one-way ANOVA on ranks, E_2: $H = 9.81$, df = 4, $p < 0.04$: P_4: $H = 24.88$, df = , $p < 0.05$, N = 5). Females 80 and 107 exhibited an elevation in E_2 one cycle length

Table 3.2. Mean fecal estradiol and progesterone concentrations of free-ranging female *Propithecus verreauxi* for 10-day intervals during the estrous cycle, where estrus = day 0.

	Estradiol (ng/gm)				**Progesterone (ng/gm)**			
Sample Interval	Mean	SD	N«	N»	Mean	SD	N«	N»
-76 to -80	6.46	1.21	1	5	217.96	33.27	1	5
-66 to -75	4.11	1.10	1	10	215.97	52.32	1	10
-56 to -65	7.34	6.80	1	10	286.37	57.47	1	10
-46 to -55	5.59	2.83	1	10	240.80	37.15	1	10
-36 to -45	7.09	4.00	3	13	345.03	42.52	3	13
-26 to -35	10.46	10.84	4	29	335.82	69.32	4	29
-16 to -25	9.50	5.68	5	40	325.56	126.06	5	40
- 6 to -15	18.28	10.57	5	48	348.07	151.60	5	48
- 5 to + 5*	29.01	26.49	5	54	395.30	190.75	5	54
+ 6 to +15*	9.49	4.71	5	48	617.03	216.77	5	48
+16 to +25	12.00	4.58	5	49	574.26	200.63	5	49
+26 to +35	26.30	24.65	5	44	655.00	167.23	5	44
+36 to +45	40.88	45.89	4	36	976.13	295.53	4	36
+46 to +55	317.71	122.00	4	26	1546.30	413.06	4	26
+56 to +65#	117.79	117.71	2	13	350.72	376.59	2	13
+66°	50.90	---	1	1	272.70	---	1	1

« Number of females sampled per interval.
» Total number of fecal samples per interval.
* Mann-Whitney rank sum test: $T = 1874$, $p < 0.001$.
# Post-abortion and cycling steroid values.
° Post-abortion steroid values.

prior to estrus similar to the pseudo-estrous elevations in E_2 seen in *Eulemur mongoz* (Perry et al., 1992).

Sifaka resemble captive *Eulemur mongoz* (Perry et al., 1992), *Varecia variegata* (Shideler et al., 1983) and *Propithecus verreauxi* (Brockman et al., submitted) in the fact that mating occurred when estrogen levels were elevated. Four of the 5 female sifaka mated when E_2 levels were substantially increased above baseline levels. Although F80 was never seen mating, she was mounted (without intromission and thrusting) by MFd when E_2 was elevated, suggesting that an undetected copulation may have occurred at this time.

Mating was associated with rising (F20, F19, F107), peak (F20, F19), and diminishing (F19, F36) E_2 levels. Serum studies of ovarian hormone levels in primates show that ovulatory levels of lutenizing hormone (LH) peak within 24 hrs of the estrogen peak (Robinsaon & Goy, 1986). Wasser et al. (1988) investigated the excretion rate of ovarian hormones in free-ranging yellow baboons and found that there was a 1-day lag between serum and fecal concentrations of estrogen. The results of these studies suggest that elevations in fecal E_2 may approximate elevations of ovulatory LH. Support for this is shown by the fact that in F20's and F36's pregnancy profile, mating occurred when E_2 was at peak levels or diminishing.

Female 20 mated with two resident males during the 10-day E_2 peak (Figure 8). She copulated with the older adult male 240 (M240) 7 days after when E_2 was beginning to rise on 7 January and then mated with the younger male Fd (MFd) at the E_2 estrus peak of 9 January. The F20/M240 copulations spanned 1 hr and were composed of 11 copulations lasting from 2 to 122 seconds. Three copulations, lasting from 1- to 3-mins each, were characterized by slow rhythmic thrusts followed by ejaculation. These serial mounts were preceded by several brief non-ejaculatory copulations lasting only a few seconds, the latter accompanied by harassment from F19 and MFd. Three copulations occurred with MFd on January 9 lasting 8, 36, and 43 sec, preceded by eight 2- to 7-sec mounts. The 36 and 43 sec copulations were composed of slow rhythmic thrusts. Although ejaculate was not observed following the dismount, ejaculation was inferred based upon the rapid increase in thrusting (e.g. "quiver thrusts") and then a pause just prior to the dismount and intense post-coital genital grooming. The brief copulations preceding the ejaculatory copulations occurred during a three-hour period of intense harassment by F19, F80, and M240. The latter pursued the copulating pair from tree to tree, jumping at and grabbing and biting them. These copulations were separated by a day when no sexual activity was observed.

Female 19 copulated with M240 seven times (lasting 3 sec to 2 min) on 11 January when E_2 was increasing (Figure 9). Vulval ejaculate was observed subsequent to one 14- and 117-thrust mating. Female 19 subsequently copulated twice with male Fd (three seconds) on 12 January at peak E_2 elevations and then again on 13 January for 3, 6, and 82 secs when E_2 was diminishing. The 12 January copulations, but not those of 13 January, were accompanied by guarding and harassment from M240.

Female 36 mated briefly with male 140 (M140, 23 thrusts with ejaculation [inferred from extensive genital grooming]) on the morning of 10 February 10 when E_2 elevations were diminishing (Figure 10). This copulation was interruped by male 243 (M243) when the latter bit M140 on the tail thus forcing him to break contact with F36. Later that day F36 mated with M146 on the periphery of the social group undetected by other adult group members. This single copulation, lasting just over 3 mins, was characterized by 153 slow rhythmic thrusts followed by "ejaculatory" quivering thrusts, pause, dismount, and intensive genital grooming. An additional 8-sec non-ejaculatory copulation occurred with M146 8 days later when E_2 levels were slightly above baseline values.

Female 107 copulated with M243 three times on 23 February when E_2 levels were increasing (Figure 11). The first two copulations lasted 8 and 10 secs each and were characterized by brief and uneven thrusts, while the third lasted approximately 1.5 mins and was noteworthy for its 75 slow and rhythmic thrusts culminating in ejaculation. Single 3- to 4-sec mounts occurred with males UC (MUC), M243, and M140 on 25 December, 31 January, and 3 February respectively, and were associated with low E_2 values (E_2 mean = 7.1 ng/gm, sd = 7.1, n = 3).

Female 80 was mounted three times by MFd over a 7-day period when E_2 levels were elevated (Figure 7). These mounts were unaccompanied by observations of thrusting and ejaculation. One 2-sec mount occurred on 16 January while an 8- and 11-sec mount occurred on 19 January, the latter marked by intense guarding and harassment by M240. Male Fd attempted to mount F80 five times during the 9-15 January peak elevations in E_2 6 days previous to the "estrous period" of male mounts. The rapid and sustained increase in P_4 on January 15 followed by a rapid E_2 elevation 42 days later suggests that conception occurred during the January 10-14 period of mount attempts.

4. Estrous Synchrony

Hormonal data from this study showed that within-group estrous synchrony varied between groups. Vavy Masiaka females exhibited no temporal overlap in E_2 peaks or in sexual activity (i.e. mounts and mating). While there was some overlap in E_2 elevations, estrous elevations in E2 were not-overlapping, suggesting that estrus was asynchronous in this social group (Table 3.3). In contrast, the Vaovao females exhibited temporal overlap in E_2 elevations and, in the case of females 19 and 80, E_2 peaks occurred on the same day. Although mounts and copulations were not observed to overlap, male attempts to mount F80 coincided with F19's mating activity (Table 3.4).

Behavioral data from studies of captive (Pereira, 1991) and free-ranging (Sauther, 1992) *Lemur catta* suggest that females exhibit estrous asynchrony within groups, the latter determined by vulval morphology and mating behavior (Pereira, 1991; Sauther, 1991). Pereira (1991) argues that social entrainments and pheromone-based signal-response systems mediate estrous cycles in ringtailed lemur social groups. This argument is based on McClintock's (1978, 1981, 1984) studies of female *Rattus norvegicus*. She showed that synchronization of ovarian cycles results from estrous-related chemosignals coupling ovarian cycles within social groups, thereby altering estrous timing. Estrous cycles were shortened or lengthened within groups based on the duration and patterning of exposure to follicular or ovulatory ordors respectively and the numbers of females present (McClintock, 1984). Social signals exchanged among females living in a group affected ovarian cyclicity, social interactions and social isolation enhancing and suppressing cyclicity, respectively, via exposure to estrous pheromones (McClintock, 1981). Ovarian synchrony within *Rattus*

Table 3.3. Estradiol peaks, elevation durations, and sexual behavior in Vavy Masiaka females.

```
                               Date (December 1991 - February 1992)

      25 26 27 28 29..1/31 2/1 2 3 4 5 6 7 8 9 10 11 12 13...18 19 20 21 22 23 24 25 26 27

Female

 F107  *--^------*(4)*----^--------*(6)                     #------------------^--------#
              Mt       Mt                                                    MT       (10)

 F36              #-------------------------^-----------#(15)
                                                MT
```

#	Estrous-related elevations
^	E_2 peak
MT	Mating
Mt	Mount
( )	E_2 elevation in days

Table 3.4. Estradiol peaks, elevation durations, and sexual behavior in Vaovao females.

```
                        Date (January, 1991)

        1...5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Female

 F20    #-------^-----#(11)
            MT  MT

 F19        #---------------^------#(11)
                         MT MT MT

 F80                *-------^--------*(7)#-------^--------#
                           Mt Att.....   Mt      Mt       (6)
```

#	Estrous-related elevations
^	E_2 peak
MT	Mating
Mt Att	Mount attempt
Mt	Mount
( )	E_2 elevation in days

norvegicus social groups could be induced either by mutual entrainment (i.e. the interaction of equally potent chemosignals from several individuals in a group) or by the *Zeitgeber* effects of a dominant female (McClintock, 1978, 1981, 1984).

The results from this study of sifaka show that the criteria used to measure estrous synchrony are crucial to its diagnosis. Vulval morphology and mating behavior alone may not be adequate for its determination. While the behavioral data suggested that estrus was asynchronous in both social groups based on observations of mating, the hormonal data obtained from Vaovao females clearly showed that estrous elevations in E_2 were synchronous (Table 3.4). Not only were these females a very cohesive group and frequently in close proximity, but their social relationships were hierarchical. This latter affected estrous order - dominant F20 cycled first. The hormonal data from Vavy Masiaka, on the other hand, showed that estrous elevations in E_2 were asynchronous. In contrast to Vaovao females, female relationships in Vavy Masiaka were much less cohesive. The two females occasionally spent entire days moving and feeding independently of one another some 50 to 100 m apart. Dominance was also less clear, and although F107 appeared to be dominant to F36, she was the second to cycle, suggesting that dominance did not affect estrous order. These results suggest that while estrous timing is strongly tied to environmental cues associated with seasonal reproduction, variability can occur as a consequence of the numbers of females living in a group, female spatial and pheromonal proximity, and the cohesiveness of female social relationships (McClintock, 1981).

5. Estradiol Levels and Vulval Morphology

Previous reports suggest that some lemurs undergo estrous-related changes in genital morphology indicated by vulval swelling and pinkening (*Cheirogalus*: Foerg, 1982; Petter-Rousseaux, 1964; *Microcebus*: Andriantsiferana et al., 1974; Martin, 1972; Petter-Rousseaux, 1962; *Propithecus*: Haring, 1988; Richard, 1974; Petter-Rousseaux, 1962; *Lemur*: Bogart et al., 1977; Koyama, 1988; Van Horn and Resko, 1977; Cranz et al., 1986; *Varecia*: Foerg, 1982; Shideler and Lindburg, 1982). In urinary studies of captive *Varecia vareigata* changes in vulval morphology were associated with elevated estrogen levels and mating (Shideler et al., 1983). Results of fecal steroid analysis of free-ranging sifaka showed only slight associations between estrous-related changes in genital morphology and E_2 elevations (Table 3.5).

D. Discussion

The data presented here suggest that reproductive states (i.e. estrus and pregnancy) of free-ranging female sifaka can be determined using radioimmunoassay techniques in conjunction with observations of sexual behavior. Hormonal data obtained from desiccated feces showed that this method

Table 3.5 Correlations between estrous-related changes in vulval morphology and E_2 concentrations.

Female	r_s	N	*p*
F20	0.01	57	0.92
F80	0.27	60	0.04
F19	0.13	58	0.34
F36	0.28	53	0.12
F107	.27	66	0.03

preserved sufficient levels of E_2 and P_4 to make biologically meaningful assessments of ovarian activity in free-ranging sifaka.

The steroid profiles in this study exhibited more day to day fluctuation in values than those in captive sifaka (Brockman et al., submitted). Previous studies suggest that some of this variation may be due to the cross-reactivity of the estradiol antibody with a catechol estrogen. This estrogen is a direct metabolite of estradiol present in fecal extracts which is unstable, varies with reproductive state, and shows inter-individual variation in its expression. (Brockman et al., submitted).

The hormone data from the 5 females showed cyclic changes in E_2 and P_4 which varied, in some cases, from that typically seen in other primates. The primate ovarian cycle begins with a rapid rise in E_2, indicating folliculogensis, followed by a decline, in association with an ovulatory rise in luteinizing hormone. Ovulation is verified by a sustained increase in P_4 indicating the development of a functioning corpus luteum (Robinson and Goy, 1986). Female 19's profile diverged from this pattern as seen in the gradual 5-fold increase in E_2 lasting 11 days followed immediately by a 2-fold increase in P_4 lasting 23 days. The length and magnitude of these changes in ovarian steroids were longer (E_2) and shorter (P_4) than the 5-day follicular and 25- to 28-day luteal phases reported for other strepsirhines, including sifaka (Bogart et al., 1977; Van Horn and Resko, 1977; Shideler et al., 1983; Perry et al., 1992; Brockman et al., submitted).

Three females (F20, F80, and F36) experienced gradual 3- to 14-fold increases in E_2 over a 7- to 15-day period followed by immediate and sustained elevations in P_4 lasting 54, 53, and 43 days, respectively. Although more gradual, similar elevations in E_2 followed by sustained elevations in P_4 have been observed in captive pregnant sifaka (Brockman et al., submitted) suggesting that two of these profiles represent later gestational stages of conception, as indicated by extremely elevated steroid values 42 (F20) and 47 (F80) days after estrous elevations in E_2. Female 36's P_4 profile resembles F80's early conceptive profile before gestational increases in E_2 and P_4 levels might be expected to occur. Although the early March precipitous drop in F20's ovarian steroid resembles the abortion profiles of other primates (Diamond et al., 1985), this one case is not sufficient to generate definitive conclusions regarding abortion in sifaka.

Female 107's steroid profiles present a different endocrine response from other free-ranging females. While 27- to 32-day cycles in E_2 secretion occur, suggestive of adequate follicular function, they are unaccompanied by P_4 cyclicity and may be indicative of anovulation.

Previous studies suggest that pseudo-estrus occurs in some strepsirhines. It is behaviorally characterized by increased female attractivity (but not receptivity), male scent-marking behavior, and vulval pinkening and swelling one month prior to behavioral estrus (Jolly, 1967; Vick, 1977; Richard, 1974). Hormonal characteristics of pseudo-estrus have been observed in captive *Lemur mongoz* showing E_2 elevations occurring one cycle length prior to ovulatory cycles unaccompanied by behavioral estrus (Perry et al., 1992). In this study, F80 and F19 exhibited hormonal profiles consistant with the hypothesis of pseudo-estrus while slight, but significant, correlations were found between changes in vulval morphology and E_2 elevations (e.g. Vavy Masiaka females 36 and 107).

Mating, mounts, and mount attempts in these sifaka females were associated with elevated and peak levels of E_2 .In one instance (i.e. F36), however, mating occurred 9 days after the estrus E_2 peak when E_2 levels were only slightly above baseline levels. Not all E_2 elevations were associated with observations of sexual behavior. This concords with data from captive sifaka (Brockman et al., submitted) and might be the result of copulations occurring at night or ovarian cyclicity occurring in the absence of sexual activity due to the mediating effects of environmental or social cues (Crews and Moore, 1986). Additional data from free-ranging sifaka are required to identify the specific hormonal, environmental, and social contraints affecting reproduction in sifaka. None of these females was observed with infants the following August, one month after the infants' expected birthdates in late June (F80) and late July (F36).

Hormonal data from this study show that within-group timing of estrus varied between groups. It has been suggested in previous studies of *Lemur catta* (Periera, 1991; Sauther, 1992) that estrous asynchrony characterizes most ringtailed lemur social groups, reducing female-female competition and enhancing mate choice. The results from this study show, however, that the criteria used to measure synchrony are crucial to its determination and that hormonal data may more accurately reflect timing of estrus than vulval morphology and/or observations of mating. This study also suggests that estrus may have a stochastic component, social factors associated with female group size, spatial proximity, and female-female interactions influencing estrous timing within groups (McClintock, 1981).

In this study female-female competition was most evident in Vaovao females wherein copulatory harassment coincided with estrous synchrony. Although such within-group intrasexual competition has potentially negative reproductive consequences for subordinate females, F80, who was subordinate to F19, appeared to avoid the problem by copulating "discreetly" undetected by the observer and perhaps, by other group members which resulted in conception (Chapter 2).

The potentially negative reproductive consequences of within-group competition between females may be compounded by those of intergroup agonism. Female 20's steroid profile appears to show that an abortion occurred in early March 54 days after estrus. Ad libitum behavioral data recorded for that period showed a substantial increase in intergroup encounters coincident with the dramatic drop in F20's steroid levels. A particularly aggressive individual during the breeding season, F20 frequently took the lead in encounters with neighboring groups and was observed, on more than one occasion, to be the solitary combatant in altercations with members of the neighboring Sakamena Sud social group. Although circumstantial, this finding suggests additional avenues of inquiry for identifying specific social constraints affecting female reproduction in sifaka.

Finally, the evidence does not support fertilization insurance as an explanation for multiple mating in females. Two of the three females (F20 and F36) who copulated two or more times with more than one male conceived, while one female (F80) conceived after having apparently been mounted by a single male. In the latter case, the hormonal evidence suggests that F80 conceived during F19's mating period when MFd was observed to make five attempts to mount F80 over a four day period. As previously indicated (Chapter 2), F80 consistently rejected M240's attempts to clasp her, thereby suggesting that she most likely conceived with MFd.

The small sample size of females and cycles reported here preclude broad generalizations about the endocrinology of reproduction and mating in free-ranging Verreauxi's sifaka. The results of this study do, however, concord with captive studies of *Propithecus verreauxi* and suggest that (1) female sifaka have a 30 to 32 day estrous cycle; (2) conception occurs during the first behavioral estrous cycle (i.e. associated with mating); (3) if females fail to conceive during the first estrous cycle, they may have an additional 2 or even 3 (F36) estrous cycles; (4) within-group estrous asynchrony varies between groups; (5) mating coincides with elevated and peak E_2 levels, and low P_4 levels; (6) gestational phase elevations of ovarian steriods are apparent 40 to 45 days post-estrus; (7) perinatal loss may be an important conception component of low fertility (3 of 5 females conceived but none was observed with infants the following birth season); and (8) between-group agonism may have negative reproductive consequences for pregnant female sifaka.

CHAPTER IV.

SIFAKA MATING PATTERNS AND THEIR IMPLICATIONS FOR LEMUR SOCIAL STRUCTURE

A. Introduction

Integrating the results of the previous two chapters, this chapter summarizes data on the behavioral, hormonal, and social correlates of sifaka reproduction and examines the effects of multiple mating on conception as well as the implications of these effects for lemur social structure.

Sexual selection theory posits that intrasexual competition and mate choice differentially characterize male and female reproductive efforts in most species (Darwin, 1871). Contemporary applications of this idea focus on the relationship between investment of resources in gametes and sexual competition (Trivers, 1972). Male and female mating patterns are expected to differ because of competing reproductive priorities: males, having unlimited supplies of sperm, are expected to compete for and acquire as many matings as possible, while females, having finite supplies of eggs, are expected to be selective in choosing mates.

Recent studies of mating in free-ranging Malagasy primates have shown, however, that male and female mating patterns are much less divergent than predicted by sexual selection theory (see Fedigan, 1982 for a general critique). Not only are males selective in their choice of mates (this study), but males and females compete for access to preferred mates (Koyama, 1988; Sauther, 1991) and females as well as males mate with multiple partners during a breeding season (Colquhoun, 1987; Koyama, 1988; Simons, 1991; Sauther, 1991; Sterling, 1993).

B. Toward a Behavioral and Endocrinological Synthesis

Behavioral and hormonal results from Chapters 2 and 3 are integrated here in order to explore the following questions: 1) What are the behavioral, hormonal, and social correlates of seasonal reproduction? 2) To what degree are females' estrous cycles synchronous within and between groups and what effect does estrous synchrony/asynchrony have on the ability of females to choose mates? 3) What are the mating patterns of sifaka, how are they affected by female dominance rank, mate choice, and intrasexual competition and what effect do they have on conception?

1. Behavioral, Hormonal, and Social Correlates of Estrus

Observations of reproductive seasonality in this study concord with previous reports of mating in captive (Brockman et al., submitted) and free-ranging sifaka (Jolly, 1966; Richard, 1974, 1992) and show that females have a minimum 3 month breeding season during which they experience up to three estrous periods.

Estrus was behaviorally characterized by 0.5- to 96-hr periods of attractivity, proceptivity and receptivity (Beach, 1976) and hormonally characterized by 7- to 15-day elevations in estradiol (E_2). In Vavy Masiaka, non-estrus-related (i.e. behavioral) proceptivity occurred associated with high rates of clasp and mount attempts by the group's newly immigrated male. Situation-dependent sexual behavior has been previously reported to occur only in catarrhine primates (Hrdy and Whitten, 1987).

The average 10-day estrous E_2 elevations observed in free-ranging sifaka diverge from the 5- to 7-day E_2 elevations reported for captive *Eulemur mongoz* (Perry et al., 1992), *Varecia variegata* (Shideler et al., 1983), and captive sifaka (Brockman et al., submitted), suggesting that prolonged hormonal estrus periods may facilitate multiple mating by females in the wild.

In previous studies of captive and free-ranging lemurs it has been proposed that pseudo-estrus occurs one month prior to estrus, characterized by increased female attractivity and male scent-marking behavior (Jolly, 1967; Perry et al., 1992; Richard, 1994; Vick, 1977). No behavioral and scant hormonal evidence (i.e. "pseudo-estrus" elevations in E_2 seen in females 80 and 107) of pseudo-estrus was found in this study, suggesting that what was previously called pseudo-estrus in sifaka was estrous behavior unaccompanied by observations of mating.

Anestrus occurred in the month preceding estrus and was characterized by the absence of attractivity, proceptivity, and receptivity (Beach, 1976) and low E_2 levels. The data collection regimen did not permit the assessment of anestrus after the 3-month breeding season.

Estrus was associated with increases in affiliative interactions between females and female agonism directed toward males (Chapter 2). Female-female affiliative interactions were principally composed of greeting and grooming and female-male agonism involved cuffs, grabs and bites. Similar peri-estrous levels of female-directed agonism toward males have been reported for captive and free-ranging *Varecia* (Foerg, 1982; Morland, 1991) associated with female mate choice. Sifaka females were most aggressive toward males who approached them most frequently, suggesting that both sexes were exhibiting mating preferences: males through approach interactions, and females through intensity of agonism. Estrus was also correlated with male guarding behavior, older resident males attempting to prevent younger males from copulating with estrous females.

2. Estrous Synchrony

Behavioral and hormonal data yielded differing conclusions with respect to estrous synchrony. Behavioral data suggest that sifaka resemble other lemurs in exhibiting rank- and age-related estrous asynchrony within groups (*Lemur catta*: Pereira, 1991; Sauther, 1991; *Varecia variegata*: Morland, 1991). Dominant females mated before subordinate females, mating with various resident and non-resident males over their non-overlapping 1- to 3-day behavioral estrous period.

In contrast, hormonal estrus was asynchronous and synchronous in the Vavy Masiaka and Vaovao social groups respectively. Estradiol elevations were non-overlapping in Vaovao females while the Vavy Masiaka females exhibited temporal overlap in E_2 elevations. In the case of two Vavy Masiaka females, E_2 peaks occurred on the same day, but only one female was observed to mate. These results suggest that estrous timing may be more stochastic than previously recognized and not solely governed by social factors (McClintock, 1981; Pereira, 1991).

In his study of captive *Lemur catta* Pereira (1991) argued that estrous asynchrony was a consequence of social entrainments and pheromone-based signals shortening and lengthening cycles, the latter enhancing mate choice by reducing temporal competition between females for preferred mates. The results from this study of sifaka show, however, that not only can intrasexual competition override female mate choice, but that estrus timing is a function of whether hormonal, morphological, or behavioral criteria are used to define it.

These results further suggest that between-group variation in the timing of hormonal estrus had equivocal effects on multiple mating patterns within groups. Estrous asynchrony was associated with polyandry, monoandry, and polygyny, while estrous synchrony was associated with polyandry and polygyny. Although intense intrasexual competition and avoidance of mating with certain males constrained polandrous mating in the synchronous group's subordinate female, multiple matings nevertheless occurred. Several factors appear to affect mating patterns, including estrous timing, mate choice, intrasexual competition, and male mating styles (see below).

3. Sifaka Mating Patterns

Previous studies of mating in Malagasy primates show that, contrary to predictions of mating asymmetry in males and females (Trivers, 1972), Lemuriformes exhibit an array of mating patterns including monogamy (*Varecia variegata*: Morland, 1993), polygyny (*Eulemur fulvus:* Colquhoun, 1987; *Lemur catta*: Koyama, 1988; Sauther, 1991; *Varecia variegata*: Morland, 1993), scramble competition polygyny (*Daubentonia madagascariensis:* Sterling, 1993), and polyandry (*Varecia variegata*: Morland, 1993).

In these studies, female lemurs mated with one or more males, mating with resident and non-resident males according to relatedness (Pereira and Weiss, 1991; Taylor and Sussman, 1985), dominance status of males (Sauther, 1991), and familiarity (Morland, 1993). Mating patterns in free-ranging *Lemur catta* have been characterized in terms of competing mating strategies: females mate with multiple males, enhancing mate choice through estrous asynchrony (Pereira, 1991; Pereira and Weiss, 1991; Sauther, 1991; Sauther and Sussman, 1993), while males compete for central male breeding priority and try to circumvent multiple mating by females through pre- and post-copulatory guarding and harassment of copulating pairs (Sauther, 1991; Sauther and Sussman, 1993). Sauther and Sussman (1993) suggest that multiple mating and mate choice ensure fertilization by high quality sperm at first estrus, but no data are provided regarding how this association was determined.

Mating patterns observed in free-ranging *Propithecus verreauxi* resembled those previously reported in the Lemuridae, particularly *Varecia variegata* (Morland, 1993). Individuals living in social groups containing several males and females mated with one or more, but not all, available mates. Richard (1992) has characterized the sifaka mating system as one of female-controlled polygyny, wherein a single resident male has copulatory access to group females over several mating seasons, his reproductive success being dependent upon submission to females rather than male-male competition. The data from this study do not support this characterization but rather indicate that a resident male may have his "exclusive" mating status compromised by female mate choice and the availability of non-resident males.

In most instances (4 of 6) female sifaka mated with two or more males, temporally ordering partners based on male residence and age. Females mated with resident before non-resident males and preferred older males as mates before younger males. Most females mated with each male only once, these single mating bouts being composed of from 3 to 11 copulations spanning a .5- to 3-hr period.

Rank- and age-related estrous order afforded dominant sifaka females priority of access to preferred mates. Female mate choice, however, was affected by female-female competition in the form of copulatory harassment, the latter coinciding, in some cases, with synchronous estradiol elevations within groups. Clearly, the temporal overlap of estrus within lemur social groups is a more complex phenomenon than previously recognized, its clarification requiring hormonal as well as morphological and behavioral information.

Female mate choice was affected by male efforts to prevent females from mating with other males by pre- and post-copulatory guarding and harassment of copulating pairs. Older resident males guarded estrous females and harassed copulations involving younger resident males and non-resident males. Some females, however, managed to mate unseen on the periphery of the social group, copulating with certain peripheral and younger resident males undetected by the older resident male.

Females resisted mating with certain males. In two cases, females rejected older resident males as mates by cuffing or biting them. In one case, however, a female's resistance to mating may have been overcome by a lordosis reflex resembling that seen in some mammals (McClintock, 1981; McClintock and Adler, 1978) including lemurs (*Varecia* *variegata*: Shideler et al., 1983). In this case, she fiercely resisted the male's approaches and clasp attempts in the hours prior to mating, but then immediately ceased all resistance after he was able to secure and maintain flank contact with her via a mount. The female subsequently presented and mated with this male three times.

Individual males responded differently to females' reluctance to mate. In one pair, the resident male overcame the female's reluctance to mate and successfully copulated with her, while in the other pair, the resident male acquiesced to the female's preference against mating. The female in the latter case subsequently presented to the group's younger resident male and apparently conceived in spite of the older resident male's persistent guarding and harassment of the pair. These results suggest that differing male mating styles may affect their copulatory success and fitness.

The effects of multiple mating by females on their conception rate were assessed through hormonal correlates of mating and, in the absence of hormonal data, the presence of infants the following birth season. During the seven estrous periods observed, monoandrous and polyandrous matings occurred 43% and 57% of the time respectively. Sixty-seven percent of the monoandrous and 75% of the polyandrous pairings resulted in conception. However, 60% of these conceptions failed for unknown reasons. In one case, an apparent abortion coincided with an increase in intergroup encounters. These results suggest that conception was not a consequence of ejaculation frequency. Conception resulted from single ejaculations in one monoandrous mating and from 1 to 3 ejaculations in three polyandrous matings (Table 4.1).

Male sifaka mated with more than one female including resident and non-resident females. Older males had priority of access to estrous females within their own group. Although most resident males attempted to mate with all the estrous females in their group, one male mated with only one of the group's two available females, directing his approaches and sexual behavior exclusively to this female. As noted above, mating preferences may not be mutual and can result in intense male-female agonism during estrus as was the case in this pair. The fact that this male overcame the female's fierce resistance and copulated with her suggests that, in seasonally breeding species with temporally constrained conception periods, some females may have their mating preferences swamped by those of males, the benefits of fertilization by particular males being outweighed by the costs of resisting the mating efforts of persistent males.

Competition between males was associated with within-group hormonal estrous synchrony and females' mating with non-resident males. Although mating was associated with E_2 elevations, not all copulations occurred when ovulation was likely (i.e. when E_2 levels were slightly above baseline

Table 4.1. Mating in Vaovao (VV) and Vavy Masiaka (VM) social groups at Beza Mahafaly: 1990-92.

	Breeding Season									
	1990-91					1991-92				
	Males	Date	No. of Copul.	No. of Ejacul.	Result	Males	Date	No. of Copul.	No. of Ejacul.	Result
Vaovao										
F20	VV240	1/7	11	3	Concep.	VM140	1/7	1	?	Infant
	VVFd	1/9	3	2		VV240	1/7	5	1	
						VM146	1/9	1	1	
						VM140	1/10	1	0	
F19	VV240	1/11	7	1	0					
	VVFd	1/12	2	0						
		1/13	3	1						
F80	VVFd (mounts)	1/19	3		Concep.	VM243	1/16	3	1	Infant
Vavy Masiaka										
F36						VM140	2/10	1	1	Concep
						VM146	2/10	1	1	
						VM146	2/18	1	0	
F107						VM243	2/23	3	1	0

levels). These results show that, while in principal hormonal estrous synchrony constrains male-male competition and multiple mating in males, in practice, 7- to 15-day estrous periods, female mate choice, and tendency to mate once with several males facilitates intrasexual competition and polygyny in males and polyandry in females.

It is unclear to what extent multiple mating in females confuses paternity and/or guards against male infertility. Although males provide no direct parental care, they do provide agonistic support in defense of home ranges during breeding season, the latter coinciding with seasonal food abundance and weaning of infants. The fertilizing abilities of male sifaka are unknown, but previous laboratory studies of variation in *Eulemur fulvus mayottensis* sperm morphology (Brun and Rumpler, 1990) show that seasonal variations occur in sperm count and motility and monthly variations occur in number of abnormal sperm (i.e. teratospermia). Assessing fertility insurance as an explanation for multiple mating in females requires additional studies on the reproductive biology of male sifaka.

In one social group females mated with the same two resident males thereby increasing the likelihood that their infants would be related. Males typically transfer out of their natal groups and into neighboring social groups when they reach sexual maturity (Richard et al., 1991). It could be argued that a neighboring related male might be less inclined to engage in inter-group encounters if he were related to members of the opposing group. Circumstantial evidence suggests that abortion and increased infant mortality may be associated with increased encounters during the breeding season. Hormonal data (Chapter 3) show that Vaovao F20's dramatic decline in pregnancy levels of estradiol and progesterone coincided with increased encounters with the neighboring Sakamena Sud social group. Vaovao F80's 5-month-old infant was found dead/abandoned in the area of their home range which overlapped that of Sakamena Sud, suggesting that the infant may have fallen from his mother during a chase. Infants have been observed falling from distances of up to 15 m when dislodged from their mothers during high speed chases between neighboring social groups. These data suggest that by mating with identical resident males, females could enhance their reproductive success as a consequence of reduced inter-group agonism with neighboring related males.

Mating opportunities for males and females were enhanced as a consequence of increased contact between groups and changes in group composition in resident and neighboring groups. In the group experiencing the change in membership, the newly immigrated male copulated with both resident and non-resident females, the latter during an inter-group encounter. In the neighboring group, females copulated with newly resident and peripheralized males residing in the group undergoing the change in group membership. These data show that the effects of small, "localized" shifts in group composition resonate out into the sifaka neighborhood (Richard et al., 1991) affecting male and female mating patterns within and between groups.

For multiple mating patterns to predominant within sifaka social groups the latter must be minimally composed of two males and two females in order for each male and each female to mate with more than one member of the opposite sex. A analysis 35 sifaka social groups residing at Beza Mahafaly from 1989 to 1993 (Richard, unpubl. data; N = 128 non-independent observations) shows that 58% of these 35 groups at Beza Mahafaly met or exceeded the minimum group composition required for polyandry and polygyny to occur (Figure 12). Between 1989 and 1993 average group compositions ranged from two males and two females (1991) to three males and three females (1990), while the modal group composition was three males and two females (Table 4.2).

The composition of the two social groups studied during the 1990-91 and 1991-92 breeding seasons ranged from two adult males and three adult females in Vaovao (i.e. 2.3 individuals, group sex ratio: .60) to three adult males, two adult females, and one juvenile male in Vavy Masiaka (i.e. 3.2.1 individuals, group sex ratio: .33). Vavy Masiaka experienced a change in membership in 1992 just prior to mating wherein female proximity preferences for a particular resident male may have precipitated a two-day fight between this male and an older resident male. During these males'

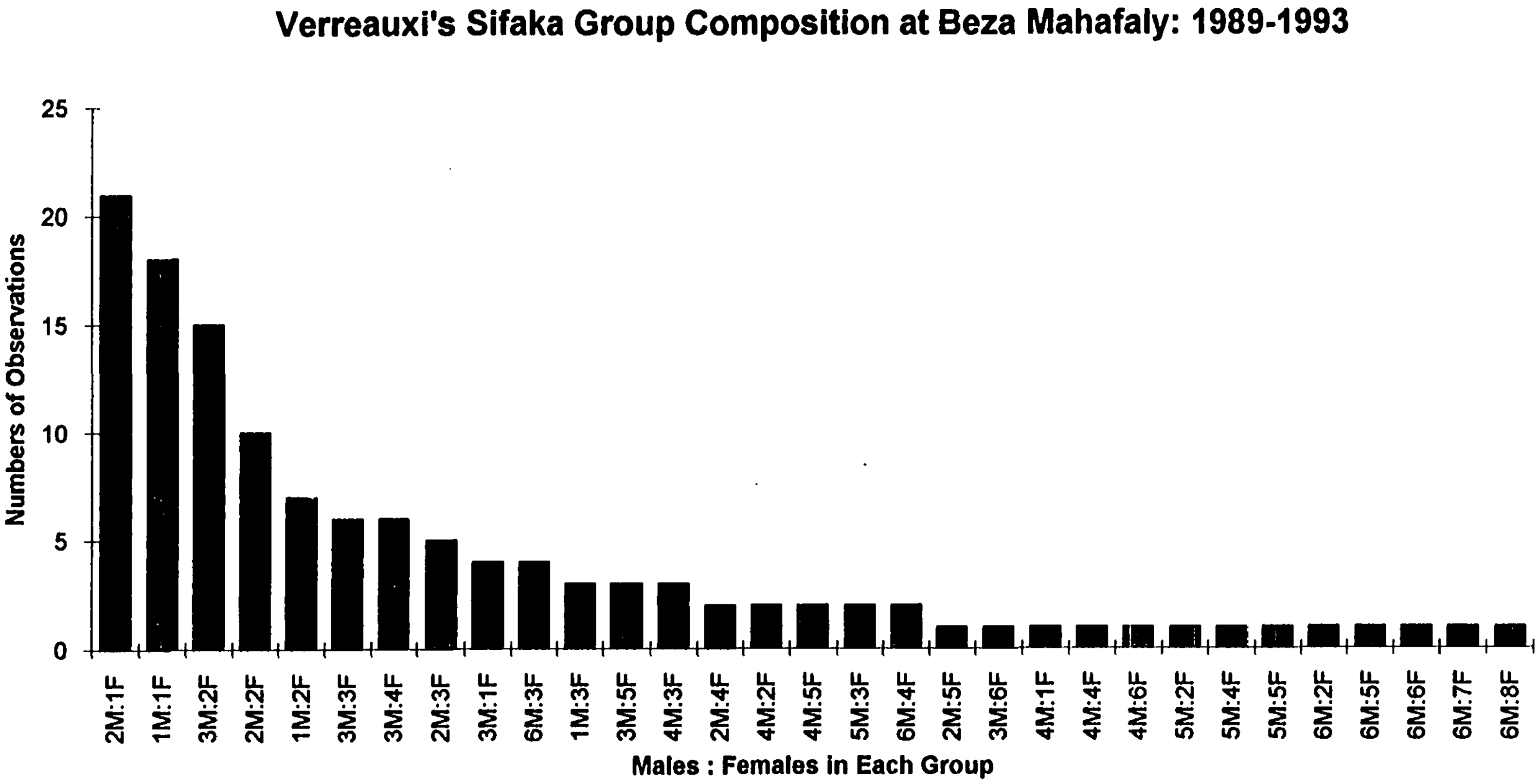


Figure 12. Composition of 35 sifaka social groups at Beza Mahafaly: 1989-1993 (N = 128 independent observations).

Table 4.2. *Propithecus verreauxi* group composition and sex ratios(#) in 35 social groups at Beza Mahafaly: 1989-1993 (N = 128 non-independent observations; Richard, unpubl. data).

	Mean (sex ratio)	**Numbers of Groups**	**Mode (sex ratio)**	**Numbers of Groups**	**Range**
Date (Aug)					
1989	*3.2(.40)	24	1.1(.50)	5	1.1-6.6
1990	3.3(.50)	24	3.2(.40)	4	1.1-6.7
1991	2.2(.50)	23	1.1(.50)	4	1.1-6.3
			2.2(.50)	4	
1992	3.2(.40)	27	2.1(.33)	7	1.1-6.5
1993	3.2(.40)	30	2.1(.33)	6	1.1-6.8

* Denotes 3 males and 2 females

\# Refers to the proportions of group members that were female.

8-hr absence from the group, a new unmarked male immigrated into the group spatially peripheralizing the resident males and facilitating the emigration of the group's younger male. While this demographic shift did not change the group's overall numerical composition, male-female proximity and social relationships were affected between the peripheralized males and resident females.

C. The Components of Lemur Social Structure

Recently, it has been argued that permanent male-female pair bonds form the fundamental social unit in lemurs, having evolved as a deterrent to male infanticide (van Schaik and Kappeler, 1993). In a study examining published and unpublished data on 30 lemur species, Van Schaik and Kappeler (1993) suggest that lemur social systems differ in fundamental ways from other prosimians and anthropoids, particularly with respect to social organization and social structure.

Lemur social organization is characterized as having three grouping patterns (i.e. solitary, pair-bonded, and large gregarious groups) which correlate with activity period (i.e. solitary nocturnal species vs. pair-bonded and gregarious cathemeral and diurnal species) and vary interspecifically. Bonded pairs are suggested to predominate, however, even among *Propithecus*, inferred from equal sex ratios and the existence of variable grouping patterns (although it is unclear to this author why the latter represent evidence of pair-bonding [van Schaik and Kappeler, 1993]).

Van Schaik and Kappeler (1993) use bonding patterns in *Eulemur fulvus*, *Eulemur coronatus*, *Lemur catta*, *Varecia variegata*, and *Propithecus tattersalli* as additional support for their argument that large lemur groups are composed primarily of multiple pairs. Measures of bonding were similar to those used in studies of anthropoid primates and focused on affiliative and proximity interactions.

The authors suggest that in most gregarious lemurs, bonding patterns differ from those found in female-bonded and non-female-bonded anthropoid primates. Female-bonded anthropoids exhibit strong bonds between females and between females and a small number of adult males, while non-female-bonded anthropoids have weak female bonds, strong male bonds, and strong bonds between females and the group's dominant male (Harcourt, 1979; Watts, 1990 in van Schaik and Kappeler, 1993).

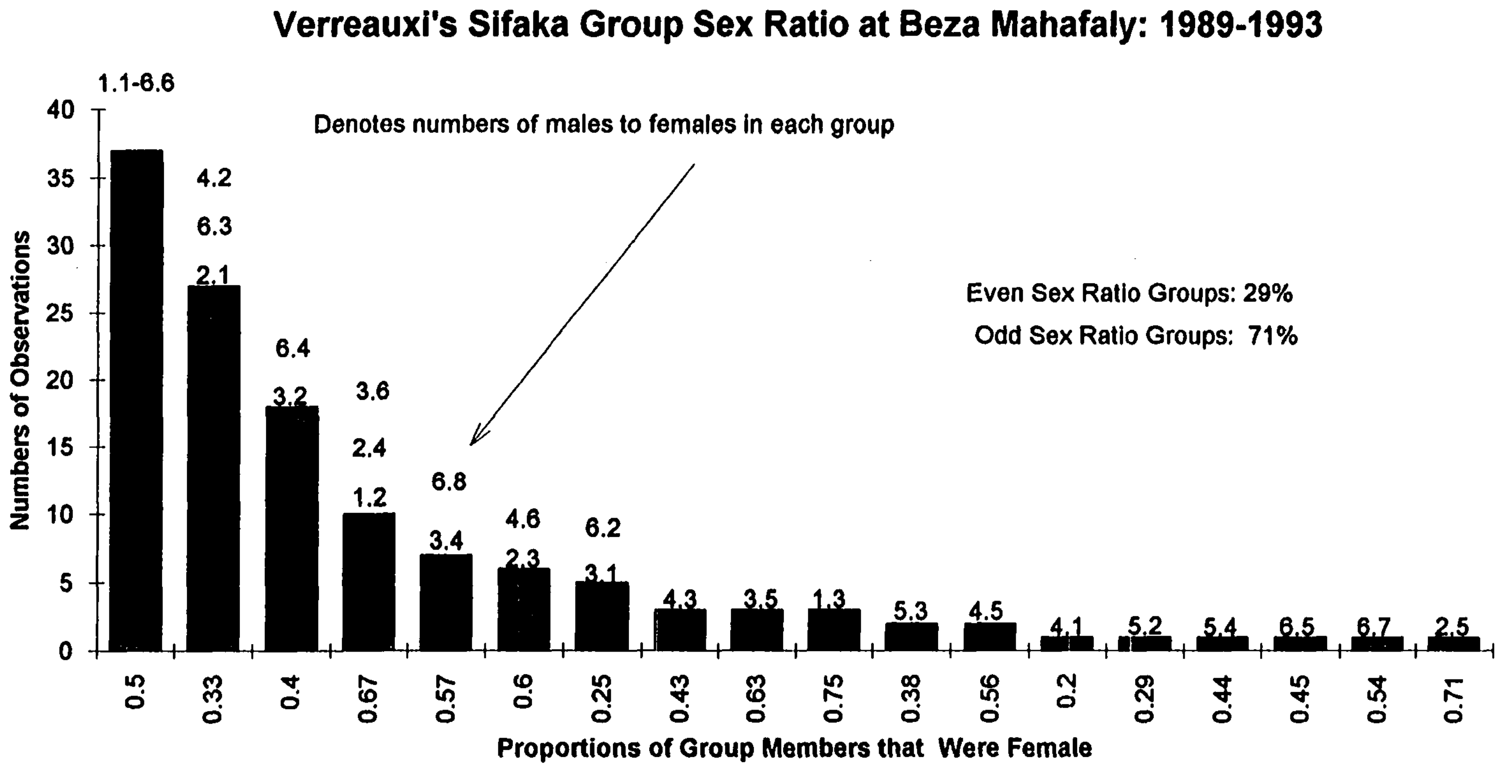
Van Schaik and Kappeler (1993) suggest that *Lemur* and *Propithecus* resemble female-bonded anthropoids in their strong bonds between females and between females and a single male, but that *Eulemur fulvus*, *Eulemur coronatus*, and *Varecia variegata* exhibit contrasting bonding patterns based on strong male-female bonds. A close examination of these data show, however, that the pair-bonded gregarious lemur argument rests principally on proximity interactions observed in 3 species: *Eulemur fulvus*, *Eulemur coronatus*, and *Varecia variegata*. *Propithecus* is portrayed as an exception to the pair-bonded pattern according to nearest neighbor data obtained from one *Propithecus tattersalli* social group (van Schaik and Kappeler, 1993).

This study supports the idea that *Propithecus* are not pair-bonded, and suggests that observations of mating, agonism, and group sex ratio may be better indicators of social structure than spatial proximity and species-specific sex ratio. Polyandry and polygyny were the predominant mating patterns within and between sifaka social groups. There were two instances in which pair-bonds might be inferred from monogamous matings. In one, mating occurred between individuals of neighboring social groups during a brief intergroup encounter. In the other case, mating was associated with intense male-female agonism, the resident male having to overcome the resident female's fierce resistance to mating by being persistent in his approach interactions and clasp attempts. Spatial proximity may be a less reliable predictor of mating patterns in lemurs than the social indicators associated with intersexual agonism and mating.

Sifaka resemble female-bonded anthropoid primates living in multimale social groups (van Schaik, 1989; Wrangham, 1980) in that females exhibited strong affiliative relationships with one another. Unlike anthropoids, however, female relationships with males were not weak, but instead were very antagonistic. Female relationships with other females were characterized by high levels of greeting and grooming interactions while their relationships with males were marked by frequent lunges, grabs and bites (Chapter 2).

Van Schaik and Kappeler (1993) use species-specific equal sex ratios to infer that most gregarious diurnal lemurs are pair-bonded. Analysis of sex ratios in 35 sifaka social groups at Beza Mahafaly between 1989 and 1993 (Richard, unpubl. data) shows, however, that most groups were composed of unequal proportions of males and females, representing 71% of the study population (Figure 13). These results suggest that sex ratios within groups may be better indices of the potential for pair-bonding in lemurs than species-wide sex ratios.

Sifaka social structure and social relationships among females do not concord with characterizations of lemur societies as pair-bonded (van Schaik and Kappeler, 1993). Sifaka social groups are most often composed of groups with unequal sex ratios wherein females direct intense agonism toward males. The multiple mating patterns and close affiliative relationships among females, on the other hand, resemble those found in polygynous female-bonded anthropoid primates (van Schaik, 1989; Wrangham, 1980). These results suggest that lemurs and anthropoid primates may be less divergent in their social relationships and mating patterns than previously recognized.



Verreauxi's Sifaka Group Sex Ratio at Beza Mahafaly: 1989-1993

Denotes numbers of males to females in each group

Even Sex Ratio Groups: 29%

Odd Sex Ratio Groups: 71%

Figure 13. Sex ratios of 35 sifaka social groups at Beza Mahafaly: 1989-1993 (N = 128 independent observations).

Chapter V.
Multiple Mating Patterns in Female Sifaka: Mammalian Contexts and Adaptive Explanations

A. Introduction

This chapter explores the selective mechanisms underlying the mating patterns of female sifaka. It examines evidence from a range of mammals assessing adaptive explanations for why females mate with multiple males. Reproductive consequences of disassociating mating from ovulation are discussed relative to the evolution of concealed ovulation and situation-dependent receptivity in human and nonhuman primates.

In most female mammals mating is tightly synchronized with seasonal estrous periods when ovulation is most likely to occur (Bronson, 1989; Sadler, 1967). Catarrhine primates diverge from this mammalian pattern. Mating occurs not only when fertilization is possible, but, in some cases, it occurs throughout the menstrual cycle and during pregnancy, although there are seasonal peaks (Hrdy and Whitten, 1987; Martin, 1992).

Multiple mating in male and female primates is associated both with circumscribed seasonal estrous periods and with menstrual cycles (Hrdy and Whitten, 1987). In contrast to other mammals who are receptive only during estrus, simian primates and humans exhibit varying degrees of concealed ovulation and continuous receptivity. In the latter, morphological cues are often absent and libidinous behavior may or may not signal ovulation (reviewed in Hrdy and Whitten, 1987; Martin, 1992).

Seasonal estrous synchrony may be expected to constrain multiple mating patterns in females by temporally limiting sexual behavior to brief periods of mating once or twice per year (Bronson, 1989; Sadler, 1967). However, the results of this and similar studies of mating in free-ranging mammals, including Lemuriformes (Calquhoun, 1987; Koyama, 1988; Morland, 1991; Richard, 1974, 1992; Sauther, 1991; Sterling, 1993), show that this is not the case.

B. Multiple Mating by Female Mammals

Over the last decade, behavioral observations of several species of free-ranging mammals have shown that females mate polyandrously and promiscuously during the breeding season (Polyandry: *Lemur catta:* Koyama, 1988 Sauther, 1991; *Eulemur fulvus*: Calquhoun, 1987; *Varecia variegata*: Morland, 1993; *Saguinus fuscicollis*: Goldizen, 1989; Terborgh & Goldizen, 1985; *Saguinus mystax:* Garber et al., 1993; Ruth, 1991; *Brachyteles arachnoides*: Strier & Ziegler, 1994; *Macaca sylvanus*: Ménard et al., 1992; *Spermophilus beldingi*: Hanken & Sherman, 1981; *Callosciurus erythraeus thaiwanensis:* Tamura et al., 1988; *Hyaena brunnea*: Mills, 1982; *Panthera leo*: Packer & Pusey, 1983; *Mirounga angustirostris*: LeBoeuf, 1972; *Lycaon pictus:* van Lawick-Goodall & van Lawick-Goodall, 1970; *Loxodonta africana*: Moss, 1983; *Equus grevyi*: Ginsberg & Rubenstein, 1990; *Equus asinus*: Moehlman, 1974; *Kobus ellipsiprymnus*: Wirtz, 1983; *Ovus canadensis*: Hogg, 1988; Promiscuity: *Saguinus mystax*: Garber et al., 1984; *Cercopithecus ascanius*: Struhsaker, 1977; Cords et al, 1986, 1988; *Cercopithecus mitis*: Cords et al., 1986; Tsingalia & Rowell, 1984; *Macaca sylvanus*: Small, 1990; *Cervus elephas*: Clutton-Brock et al., 1982).

Various selective factors have been advanced to explain why female mammals mate with multiple males (Table 5.1), but empirical evidence permitting tests or even assessments of plausibility is rare (e.g. paternity exclusion tests or reproductive endocrinology). As a consequence, most of these functional explanations remain highly speculative, inferred from little more than observations of mating frequency.

In three studies, copulation/ejaculation frequency was used to infer that females derived fertilization and genetic benefits from mating with more than one male. In each case, the arguments are unsubstantiated by empirical evidence (e.g. hormonal indices of ovarian or testicular function, population genetics, etc.). In Milton's (1985) study of promiscuous mating in free-ranging *Brachyteles arachnoides*, single ejaculations from multiple males was suggested to ensure fertilization by high quality sperm. In Ginsberg & Rubenstein's (1990) study of 33 *Equus grevyi* mares 73% of the matings were polyandrous while 23% were monoandrous. Stallions mating with polyandrous mares mated significantly

Table 5.1. Adaptive explanations for multiple mating patterns in females.

Explanation	Species	Evidence	Reference
1. Fertilization insurance	*Lemur catta*	No. of partners	Sauther, 1991
	Brachyteles arachnoides	Copulation frequency	Milton, 1985
	Macaca sylvanus	No. of partners	Small, 1988
	Mirounga angustirostris	No. of partners	LeBoeuf, 1972
	Kobus ellipsiprymnus	No. of partners	Wirtz, 1983
2. Guard against male infertility	*Loxodonta africana*	No. of partners	Moss, 1983
3. Confuse paternity to deter infanticide	*Lemur catta*	Paternity tests	Pereira & Weiss, 1991
	Panthera leo	No. of partners	Packer & Pusey, 1983
	Cercopithecus aethiops	Ovarian hormones	Andelman, 1985; Andelman et al., 1987
4. Confuse paternity to ensure male care	*Saguinus mystax*	No. of partners	Garber et al., 1984
	Saguinus fuscicollis	No. of partners	Terborgh & Goldizen, 1984
	Macaca sylvanus	No. of partners	Taub, 1980 (but see Ménard et al., 1992)
5. Reduce male-male competition	*Macaca sylvanus*	No. of partners	Small, 1988

Table 5.1. Adaptive explanations for multiple mating in female mammals (continued).

Explanation	**Species**	**Evidence**	**References**
6. Increase genetic relatedness	*Spermophilus beldingi*	Paternity tests	Hanken & Sherman, 1981
	Panthera leo	Computer modeling	Davies & Boersma, 1984
7. Promote sperm competition	*Lemur catta*	No. of partners	Sauther, 1991
	Equus grevyi	Copulation frequency	Ginsberg & Rubenstein, 1984
	Ovis canadensis	Copulation frequency	Hogg, 1988

more frequently than did stallions mating with monoandrous mares, suggesting that differences in female mating behavior generated variability in the potential for sperm competition and enhanced fertility. Hogg (1988) used copulation frequency to argue that *Ovis canadensis* ewes derived genetic benefits from dominant defending rams. While defending and coursing (i.e. males without territories) rams copulated at equally high rates, ewes provided prolonged copulatory access to defending rams after forced copulations with coursing rams. The author suggested that ewes gained genetic benefits for their offspring from dominant defending rams, but these benefits are not identified, nor are other equally plausible explanations proposed.

In the few cases in which testable evidence is used to assess the adaptiveness of multiple mating, the selective arguments are underdeveloped or questionable. Paternity tests were used in three studies to assess kinship benefits, male infanticide, and male parental care as selection mechanisms for multiple mating in female squirrels, lemurs, and macaques. Paternity exclusion tests of 27 *Spermophilus beldingi* showed that while litters were sired by multiple males, paternal representation was unequal. In one litter of six, one male fathered five young and a second male fathered one offspring. In another litter of four, two males sired two young each and a third fathered none (Hanken & Sherman, 1981). Hanken and Sherman (1981) suggested that multiple mating in Belding's ground squirrels increased kinship in offspring, but the supposed adaptive function of increased kinship in offspring is not, itself, explained (Hanken & Sherman, 1981).

In Pereira & Weiss's (1991) study of captive *Lemur catta*, DNA fingerprinting was used to determine the paternity of offspring born after multiple matings. Females preferred to mate with unrelated immigrant males but, after conception, they targeted unrelated immigrating males for aggression. In previous years, newly immigrated males had been observed attempting to kill infants, suggesting that female targeting of non-fathers for aggression deters male infanticide in this species (Pereira & Weiss, 1991). The frequency with which infanticide occurs in ringtailed lemurs, however, is in dispute as male killing of infants has never been observed in free-ranging populations (Sauther & Sussman, 1993).

Ménard et al.'s (1992) study of male paternal care in Barbary macaques is an exception to the studies previously mentioned. Paternity was determined in free-ranging polyandrous *Macaca sylvanus* females using restriction fragment length polymorphisms (Ménard et al., 1992). In previous studies of mating in Barbary macaques, it has been suggested that females mate with more than one male to ensure male parental care (Taub, 1980). In this study, however, no relationships were found between paternity certainty and male investment in infants. Among the males which were excluded from having sired infants, 30% cared for those infants while 70% did not. In one instance, a father ignored his own infant, while caring for 2 infants he had not sired. The authors suggest that paternity may be a factor influencing male investment patterns in this species, and that male investment in infants may be affected by other kinds of relationships, such as those between brothers or cousins (Ménard et al., 1992).

Recently, the hormonal correlates of mating have been investigated in free-ranging primates using excreted steroid techniques (Andelman et al, 1985; Clarke et al., 1991; Strier & Ziegler, 1994). The quality of these studies vary with respect to the evidence gathered and evolutionary questions asked or not asked. Nevertheless, determining the relationship between mating and gonadal hormones has been shown to be a promising method for assessing fertilization insurance as a selective mechanism for multiple mating patterns in female mammals (see below).

Urinary and fecal steroid techniques were used to assess the hormonal correlates of mating in free-ranging *Alouatta palliata* (Clarke et al., 1991), *Brachyteles arachnoides* (Strier & Ziegler, 1994), and *Cercopithecus aethiops* (Andelman et al., 1985), but only one of these studies evaluated the adaptive consequences of multiple mating in females. In Clarke et al.'s (1991) study of 9 female *Alouatta palliata* in northwestern Costa Rica, multiple copulations were associated with elevated (i.e. above baseline) fecal estrogen levels, but the authors provide no information regarding mate choice or conception.

In a study of *Brachyteles arachnoides* (Strier & Ziegler, 1994), a female was observed copulating with 4 males coincident with elevations in fecal estradiol and estrone levels. However, the sampling regimen was not long enough to determine whether pregnancy occurred, and no infant was born the following birth season.

In studies of free-ranging *Cercopithecus aethiops* females (Andelman, 1985, Andelman et al., 1987), multiple copulations were unrelated to ovulatory increases in urinary pregnanediol-3α-glucuronide levels. Mating was most frequent during pregnancy and during the 2 months preceding ovulation. Females were found to successfully conceal ovulation from males by continuing to mate through the first half of pregnancy and not just when they were fertile. Andelman (1985) suggested that in light of her own observations of attempted infanticide by incoming males, concealed ovulation and multiple mating patterns in vervet monkey females probably functioned to reduce the potential for male infanticide in this species.

These studies show that the evidence used to assess multiple mating in females is highly variable and, in most cases, it provides little information regarding the various selective mechanisms underlying mating patterns in mammals. Insights into the adaptive consequences of multiple mating in free-ranging mammals will begin to emerge only when genetic and/or endocrinological data are combined with data on mating behavior, the latter framed in the context of specific evolutionary questions.

C. Multiple Mating by Female Sifaka

The behavioral, hormonal, and social correlates of mating in sifaka was examined to examine adaptive explanations for multiple mating in females. Females mated with multiple males, selecting mates from an array of resident and non-resident males. In most cases, mating was associated with elevated estradiol levels, although copulations also occurred when estradiol levels were just above baseline levels. Although the timing of hormonal estrous varied between groups, estrous synchrony/asynchrony had no effect on multiple mating patterns. Hormonally synchronous females mated with more than one resident male.

In some cases, multiple mating by females was limited by intrasexual competition associated with guarding and copulatory harassment, preferences against mating with certain males, and aggressive mating tactics by individual males. It was enhanced, on the other hand, by 7- to 15-day hormonal estrous periods and demographic shifts in and increased contacts with neighboring social groups. In the 5 females studied here, ejaculation frequency had no affect on conception rate. Multiple ejaculations resulted in conception in three polyandrous matings, while a single ejaculation resulted in conception in one monoandrous pair.

It is unclear to what extent multiple mating in females enhances paternity and/or guards against male infertility. Previous studies of seasonal variation in sperm morphology and motility in *Eulemur fulvus* (Brun & Rumpler, 1990) show that while spermatogenesis is continuous throughout the year in captive males, there is marked seasonal variation in the numbers of abnormal sperm (i.e. teratospermia), ranging from an average of 72.7% in the non-breeding season to 36.3% during the breeding season. Teratospermia has also been reported for free-ranging *Macaca mulatta* (non-breeding season; Schwartz et al., 1984), captive gorillas (Seuanez & Carothers, 1977) and humans, (Ewing, 1982), but similar studies are lacking for *Propithecus*. Preliminary data on breeding season testosterone levels in free-ranging *Propithecus verreauxi*, suggest, however, that fecal testosterone levels vary inter-individually and with age (Brockman, unpubl. data).

Offspring relatedness may be a factor in multiple mating patterns in female sifaka associated with enhanced reproductive success and indirect male parental care. In two instances of polyandrous matings, females mated with the same two resident males, thereby increasing the likelihood that their offspring would be related. Sifaka social groups are characterized by female philopatry, male transfer, and defense of home ranges (Richard et al., 1991). Inter-group encounters are frequent during the breeding season coincident with seasonal food abundance (Brockman, unpubl. data).

Hormonal data show that embryonic loss may be associated with increased inter-group encounters, suggesting that increased reproductive success could accrue to females through the reduction of inter-group agonism with related neighboring males. Although males do not take an active role in infant care, they do provide agonistic support during inter-group encounters. Fathers--and mothers--may increase their reproductive success by defending seasonally abundant food resources while infants are being weaned.

Finally, female sexual behavior was not strictly confined to estrus but was associated with changes in resident male membership. In one social group, higher frequencies of non-estrous-related present behaviors occurred in 2 females coinciding with the immigration of an unmarked male into the social group. Although this one instance is not sufficient to assess the degree to which receptivity diverges from circumscribed estrus in strepsirhines, it does suggest that sifaka sexual behavior may be more flexible than previously recognized.

The results of this, and those few empirical studies preceding it, suggest that female primates exhibit enormous behavioral flexibility in their mating behavior in spite of the "constraints" imposed by their reproductive biology. It is also apparent, however, that the adaptive consequences of this flexibility are largely unknown.

D. Adaptive Explanations for Multiple Mating in Females

Human females have been described as uniquely able to exercise flexible sexual behavior by virtue of their ability to conceal ovulation and be continuously receptive to males (Symons, 1979). As a consequence, various sociobiological arguments have been proposed regarding the evolution of these traits (Alexander and Noonan, 1979; Etkin, 1963; Hrdy, 1977; Symons, 1979) based on the perceived dichotomy between simian and human menstrual cycles. Catarrhine and anthropoid menstrual cycles have been described as having morphological and behavioral indicators of ovulation and receptivity. Human menstrual cycles are "unique" by having no external signs of ovulation and sexual behavior is not tied to ovulation but, rather, occurs throughout the menstrual cycle and during pregnancy (reviewed in Hrdy and Whitten, 1987).

It has been argued that concealed ovulation and "continuous" receptivity evolved in humans, to: 1) enhance pair-bonding (Benshoof & Thornhill, 1979; Morris, 1967; Etkin, 1954), 2) promote male parental care (Alexander & Noonan, 1979; Strassmann, 1981), 3) reduce male-male competition and enhance cooperation between males (Etkin, 1963; Hrdy, 1979), and 4) promote self deception thereby preventing females from avoiding conception in biologically non-adaptive ways (Burley, 1979; Daniels, 1983).

These explanations rely on the assumption that women are, by necessity, completely unaware of ovulation. They ignore the potential of hominid sexual behavior to evolve from the more obvious "primate" libidinous signals of ovulation to the more subtle "human" expressions of sexual interest associated with verbal and nonverbal cues (Moore, 1985).

Previous studies suggest that human reproductive success has been dependent upon the lack of external signs of ovulation and the psychological awareness of its occurrence (Benshoff & Thornhill, 1979; Daniels, 1983). Daniels (1983) has argued that concealed ovulation evolved to strengthen intragroup bonds, and that self-deception of ovulation evolved so that selfish interests (e.g. propagation of one's genes) would be secondary to group survival interests such as monogamy and cooperation. In the same vein, Benshoof and Thornhill (1979) argued that a woman who was able to deceive herself about her motivations for extra-pair copulations (e.g. superior genes) would be better able to deceive her mate about her infidelity. Furthermore, since "maximizing the benefit/cost ratio associated with extra-bond copulations by females would require *sophisticated deception* [emphasis mine]...selection for deception associated with successful infidelity could lead to the evolution of self-deception" (Benshoof & Thornhill, 1979:103). It appears, based on these studies, that ovulatory self-deception evolved so that females could not control their reproduction and act in their own self interest.

Alternatively, it could be argued that, in the presence of variation in ovulation awareness, selective advantages might have accrued to those early hominid females most aware of their ovulatory cycles and able to exercise mate choice unimpeded by competition from other females and males. Awareness of ovulation and behavioral flexibility could have allowed females to control the circumstances of conception thereby affording them the opportunity to assess the fertilizing and parental abilities of males. Support for this idea is found in the physiological correlates of ovulation observed in some women today, associated with cervical secretions and the hormonal effects on the central nervous system and sensory sensitivity (Stassmann, 1981).

Research over the last decade suggests that the assumptions underlying adaptive scenarios for the evolution of sexual behavior in hominid females are not robust. Comparative reviews of simian and human reproductive physiology and behavior (Hrdy and Whitten, 1987; Martin, 1993) show that, while the strepsirhine-catarrhine reproduction dichotomy (i.e. estrus vs. menstrual cycles) may be valid, that between simians and humans is not.

Humans are not unique in exhibiting sexual behavior during pregnancy and at times other than when ovulation occurs. Copulation during pregnancy occurs in various mammals, including carnivores, ungulates, and primates (Kleiman & Mack, 1977 in Martin, 1992) although the reasons for it are unclear. Likewise, free-ranging catarrhine primates have been observed to diffuse their copulations throughout their reproductive cycle and not limit them to fertile periods (e.g. *Cercopithecus aethiops*: Andelman, 1985; Andelman et al., 1985, 1987; Gartland, 1969; *Cercopithecus ascanius*: Cords, 1984; *Papio ursinus*: Saayman, 1975, 1970; *Pan troglodytes*: Tutin & McGinnis, 1981; Goodall, 1986).

Recently, it has been suggested that an examination of the reproductive consequences of disassociating mating from conception may provide insights into its adaptive function (Martin, 1992). Synchronizing copulation with conception has obvious reproductive advantages associated with increased fitness; Martin (1992) suggests that the disassociation of mating from ovulation has little or no reproductive value given recent laboratory studies on gamete aging in small mammals. In these studies gamete aging was associated with increased embryonic loss following fertilization (Austin, 1970; Blandau, 1975; Blandau & Jorden, 1941). These studies show that there are two "danger zones" associated with reproductive failure: when fresh eggs are fertilized by aging sperm prior to ovulation and when aging eggs are fertilized by fresh sperm after ovulation (Martin, 1992).

Martin (1992) argues that for the desynchronization of mating with ovulation to evolve in primates, the reproductive benefits of flexible receptivity must have outweighed the fitness consequences of reproductive failure. He suggests that these reproductive benefits were associated with increased investment in single offspring and the evolution of extended reproductive cycles (Martin, 1992). Obviously, the affects of flexible receptivity on lifetime reproductive success have not been sufficiently explored in extant primates to identify potential benefits for the evolving human. However, recent studies of paternity in males (Ménard et al., 1992) and of the endocrinology of concealed ovulation and multiple mating in female primates (Aldelman, 1985; Andelman et al., 1987) suggest that paternity may be an important factor for females who mate with multiple males when they are not likely to conceive.

Although it is clear we will never be able to determine the mating patterns of early hominids, studies of male reproductive physiology suggest that females may have enhanced their probability of conception by mating with more than one partner. These studies show that compared to other primates, human ejaculate has many abnormal sperm (Bedford, 1974; Seuanez et al., 1977), much variation in sperm morphology (Zamboni et al., 1971), and low motility (Afzelinus, 1981). Semen volume and sperm density are also known to decline in humans if ejaculation occurs more than once every two to three days (Freund, 1963 in Allen & Lemmon, 1982). In addition, studies of contemporary marriage patterns suggest that women who marry polygynously have lower fertility than those who marry monogamously (Gomilia, 1975; Isaac, 1980), although there may be other reasons for reduced fertility (e.g. nutrition). If one accepts the possibility that fertility in hominid males was variable, then low levels of sexual activity and poor sperm quality in some males may have been an inducement for hominid females to consort with multiple males in order to conceive.

This idea is partially supported by a recent study (Baker & Bellsi, 1989) of sperm count variability in humans. In this study, copulatory and masturbatory ejaculates, and behavioral data were collected from 15 couples with average sexual activity (i.e. 1 to 3 copulations per week) for 7 months. The copulatory results showed that the number of sperm in ejaculate was significantly associated with the percentage of time a couple spent together since their last copulation, while the masturbatory samples showed no correlation. Regression analysis indicated that the time a couple spent together was a strong predictor of number of sperm ejaculated during copulation, while time since last ejaculation was a weak predictor. Numbers of sperm ejaculated during copulation decreased over time the longer a couple spent together after copulation, although the mechanism of adjustment was not known (Baker & Bellis, 1989). It is unclear from the study, however, if the authors controlled for the potential confounding effects associated with age, health, temperature, and proximity.

These results suggest that variable reproductive potential associated with sperm count, sperm morphology and motility, and male-female bonding patterns may have been important factors in the evolution of mating patterns in female primates, including humans.

The study of the behavioral, hormonal, and social correlates of mating is a powerful tool for examining postulated selective mechanisms underlying multiple mating patterns in free-ranging primates. Three selective mechanisms appear to underlie multiple mating in sifaka: increased insurance against male infertility, increased indirect male parental care, and enhanced reproductive success through reduced inter-group agonism with neighboring related males. In contrast to previous studies of mating in free-ranging Lemuriformes (Koyama, 1988; Morland, 1991; Sauther, 1991; Sterling, 1993), sexual behavior in female sifaka appears to be more flexible than previously recognized making the dichotomy between estrus and menstrual cycles in primates less clear.

APPENDIX A. BEHAVIORAL ETHOGRAM

I. Static/Spatial

01. Rest: Any form of inactivity.
02. Feed: Food in mouth, food being pulled to mouth; must be chewing or harvesting; if not, then 01.
03. Move: Any form of movement.

II. Food Part

54. Mature leaf: Based on color: younger ones are paler.
55. Young leaf: As above.
56. Unripe fruit: For example, little green berries that would change in color at some point to red.
57. Flower, flower bud.
58. Vine leaf: Generic for all vine leaves.
59. Ripe fruit: See 43.
60. Seeds: Opening fruit and just eating seeds.
61. Wood/Bark: Licking scarred or dead trees, eating tree bark.
62. Leaf buds/shoots
63. Leaf stems

III.Monitor/Adjust

04. Glance (G): X's eyes (face) oriented toward Y for 2 sec. or less.
05. Approach/Contact (A/C): X moves toward and contacts Y.
06. Approach/1m (A/1M): X approaches within 1 m of Y.
07. Approach/1m> (A/1m>): X approaches more than 1 m of Y.
08. Approached By/Contact (ABy/C): Y moves toward and contacts X.
09. Approached By/1m (ABy/1m): Y approaches within 1 m of X.
10. Approached By/1m> (A/1m>): Y approaches more than 1 m of X.
11. Withdraw/Contact (W/C): X breaks contact with Y.
12. Withdraw/1m (W/1m): X moves 1 m away from Y.
13. Withdraw/1m> (W/1m>): X moves more than 1 m from Y.
14. Is Withdrawn From/Contact (IsW/C): Y breaks contact with Y, but less than 1 m.
15. Is Withdrawn From/1m (IsW/1m): Y moves 1 m away from X.
16. Is Withdrawn From/1m> (IsW/1m>): Y moves more than 1 m from X.
17. Follow (F): X moves in the same direction as Y, X initiating movement after Y's move, but not later than 5 sec. after Y stops.
18. Lost Call (LC): A contact call occurring during separation; high pitched wail.

IV. Social Interaction

A. Affectional

19. Greet (Gr): X touches Y's nose.
20. Is Greeted By (IsGr): Y touches X's nose.
21. Invite to Groom (I/Gm): X exposes body part to Y for grooming.
22. Groon (Gm): X's oral contact with Y involving licking of body part.
23. Is Groomed (Is/Gm): Y's oral contact with X involving licking of body part.
24. Reciprocal Grooming (R/Gm): X and Y groom one another simultaneously.

B. Agonism

25. Nose Jab (N/J): X quickly pushes her nose into Y's face resulting in Y looking or moving away from X.
26. Is Nose Jabbed (Is/NJ): Y quickly pushes his nose into Y's face resulting in X looking or moving away.
27. Lunge At (L): In a seated position, X's upper body moves toward Y quickly while maintaining eye contact.
28. Is Lunged At (Is/L): Receiver of 27.
29. Cuff (Cu): X manually strikes Y.
30. Is Cuffed (Is/Cu): Receiver of 29.
31. Feint-to-Cuff (FT/Cu): X rapidly lifts her hand in preparation to strike Y.
32. Grab (Gb): X's manual seizure of Y's hair or body.
33. Is Grabbed (Is/Gb): Receiver of 32.
34. Bite (B): X's oral seizure of Y, or canine slash.
35. Is Bitten (Is/B): Receiver of 34.

C. Dominance/Submission

36. Displace (D): X moves toward Y, Y immediately moves away and X occupys the location previously held by Y.
37. Is Displaced (Is/D): X immediately moves away when Y moves toward X, occupying X's location.
38. Chatter/Grimace (Cht/Grm): Low level, repeated vocalization by Y when approached by X accompanied by lips retracted and teeth bared.
39. Is/Chattered/Grimaced At (Is/Cht/Grm): low level, repeated vocalization accompanied by lips retracted and teeth bared that is received by X.
40. Ano-gentital mark (GenMr): X presses or rubs genital region on tree trunk previously occupied by Y.
41. Is/Ano-genitally marked (Is/Gen/Mr): Receiver of 40.
42. Throat Mark (Th/Mr): X presses his throat gland on tree previously occupied by Y.
43. Is Throat Marked (Is/Th/Mr): Receiver of 42.
44. Ano-genital/throat mark (Gen/Th/Mr):40 and 42 occur in sequence (can occur in reverse sequence).

45. Is Ano-genitally/throat marked (Is/Gen/Th/Mr): Receiver of 44.

D. <u>Sexual</u>

46. Present (P): female approaches male, orients her hindquarters to him with her tail deflected.
47. Is/Attempted to be Clasped (Is/At/Cl): X is approached by Y from behind, Y only briefly touching X's flank before X moves away from Y.
48. Is/Clasped (Is/Cl): X is approached by Y from behind, Y clasps X's flank with both arms while Y's feet remain in contact with the substrate.
49. Is Attempted to be Mounted (Is/At/Mt): X is approached from behind by Y, Y attempts to make ventro-dorsal contact with X, but fails to clasp X's legs with his feet.
50. Is Mounted (Is/Mt): X is approached by Y from behind, Y assumes a ventro-dorsal position on X, Y's feet clasping X's legs with his foot or feet.
51. Is Mounted With Intromission (Is/Mt/Int): #49 with penile penetration.
52. Is Mounted With Intromission and Thrusting (Is/Mt/Int/Th): #50 with thrusting.
53. Is Dismounted (Is/D/Mt); Y breakes genital contact with X.

APPENDIX B. DATA COLLECTION CHECK-SHEET.

DATE_______ TIME_______ TEMP/HUM/LITE________ SHEET______
FOCAL ID_______ GROUP ID___________ VUL. MORPH.___________

ACTIVITY

TIME	QUADRATE	REST	MOVE	FEED	FOOD/PART.	FOOD/SP.	NN ID

MONITOR/ADJUST

APPROACH/Con______________________________

W/In 1m______________________________

APPROACH BY/Con______________________________

W/In 1m______________________________

WITHDRAW/Con______________________________

1m or <______________________________

WITHDRAW FROM/Con______________________________

1m or <______________________________

FOLLOW______________________________
LOST CALL______________________________
GLANCE______________________________

SOCIAL INTERACTIONS

APPENDIX C. FREQUENCY OF SUBMISSION INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total Submission									
F:F	4	10	11	2	15	10	7	2	61(20.33)
F:M	2	0	1	0	0	0	0	0	3(1.00)
M:F	4	5	4	16	10	5	6	9	59(29.50)
Total	10	15	16	18	25	15	13	11	*123(50.83)*
B. F:F (40%) Submission									
20	0	2	3	0	1	0	0	0	6
19	1	1	2	0	3	2	2	0	11
80	3	7	6	2	11	8	5	2	44
Total	4	10	11	2	15	10	7	2	*61*
C. F:M (2%) Submission									
20	0	0	1	0	0	0	0	0	1
19	2	0	0	0	0	0	0	0	2
80	0	0	0	0	0	0	0	0	0
Total	2	0	1	0	0	0	0		*3*
D. M:F (58%) Submission									
20	1	1	2	7	2	2	0	1	16
19	2	4	2	6	5	2	2	7	30
80	1	0	0	3	3	1	4	1	13
Total	4	5	4	16	10	5	6	9	*59*

In this and all subsequent tables the following indicate:
^ 14-day period
* Mating period (or in the case of Period 4, mounts)
\# Interactions per female or male

APPENDIX D. FREQUENCY OF SUBMISSION INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. <u>Total Submission</u>								
F:F	1	0	0	1	0	1	1	4(2.00)
F:M	0	0	0	0	0	0	0	0
M:F	15	19	14	11	34	17	10	120(40.00)
Total	16	19	14	12	34	18	11	*124(42.00)*
B. <u>F:F</u> (5%) <u>Submission</u>								
36	0	0	0	0	0	0	0	0
107	1	0	0	1	0	1	1	4
Total	1	0	0	1	0	1	1	*4*
C. <u>M:F</u> (95%) <u>Submission</u>								
36	7	15	7	7	17	1	6	60
107	8	4	7	4	17	16	4	60
Total	15	19	14	11	34	17	10	*120*

In this and all subsequent tables the following indicate:
^ 10-day periods
* Mating period
# Interactions per female or male

APPENDIX E. FREQUENCY OF AGONISTIC INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total Agonism									
F:F	19	19	19	13	23	13	20	11	137(46.00)
F:M	18	20	47	45	39	21	26	36	252(84.00)
M:F	5	1	0	12	3	1	0	0	22(11.00)
Total	42	40	66	70	65	35	46	47	*411(141.00)*
B. F:F (33%) Agonism									
20	7	6	7	2	8	4	8	5	47
19	11	13	12	11	14	9	12	6	88
80	1	0	0	0	1	0	0	0	2
Total	19	19	19	13	23	13	20	11	*137*
C. F:M (60%) Agonism									
20	3	3	8	12	12	2	7	8	66
19	14	16	32	13	22	15	10	9	131
80	1	1	7	20	5	4	9	9	56
Total	18	20	47	45	39	21	26	36	*252*
D. M:F (7%) Agonism									
20	1	0	0	0	0	0	0	0	1
19	3	0	0	0	2	1	0	0	6
80	1	1	0	12	1	0	0	0	15
Total	5	1	0	12	3	1	0	0	*22*

APPENDIX F. FREQUENCY OF AGONISTIC INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total Agonism								
F:F	1	5	1	3	6	0	1	17(9.00)
F:M	37	49	49	73	118	60	61	447(149.00)
M:F	1	0	0	0	0	0	0	1(.33)
Total	39	54	50	76	124	60	62	*465(158.33)*
B. F:F (4%) Agonism								
36	0	2	0	2	2	0	0	6
107	1	3	1	1	4	0	1	11
Total	1	5	1	3	6	0	1	*17*
C. F:M (96%) Agonism								
36	25	33	30	34	55	13	27	217
107	12	16	19	39	63	47	34	230
Total	37	49	49	73	118	60	61	*447*
D. M:F Agonism								
36	1	0	0	0	0	0	0	1
107	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	0	0	*1*

APPENDIX G. FREQUENCY OF GRAB INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total</u> <u>Grab</u> (32%)									
F:F	7	6	6	3	9	1	3	3	38(13.00)
F:M	6	11	11	16	16	5	10	9	84(28.00)
M:F	2	0	0	6	2	0	0	0	10(5.00)
Total	15	17	17	25	27	6	13	12	*132(46.00)*
B. <u>F:F</u> (28%) <u>Grab</u>									
20	4	2	2	0	3	0	1	0	12
19	3	4	4	3	6	1	2	3	26
80	0	0	0	0	0	0	0	0	0
Total	7	6	6	3	9	1	3	3	*38*
C. <u>F:M</u> (61%) <u>Grab</u>									
20	0	2	2	4	5	0	1	5	19
19	5	8	7	6	9	4	5	3	47
80	1	1	2	6	2	1	4	1	18
Total	6	11	11	16	16	5	10	9	*84*
D. <u>M:F</u> (11%) <u>Grab</u>									
20	1	0	0	0	0	0	0	0	1
19	1	0	0	0	2	0	0	0	3
80	0	0	0	6	0	0	0	0	6
Total	2	0	0	6	2	0	0	0	*10*

APPENDIX H. FREQUENCY OF BITE INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total Bite (20%)									
F:F	4	5	0	1	4	1	3	2	20(7.00)
F:M	4	4	12	14	9	3	4	11	61(20.00)
M:F	0	0	0	2	0	0	0	0	2(.67)
Total	8	9	12	17	13	4	7	13	*83(27.67)*
B. F:F (25%) Bite									
20	2	4	0	0	0	0	1	1	8
19	1	1	0	1	3	1	2	1	10
80	1	0	0	0	1	0	0	0	2
Total	4	5	0	1	4	1	3	2	20
C. F:M (72%) Bite									
20	0	0	1	2	2	0	0	2	7
19	4	4	9	2	5	2	3	5	34
80	0	0	2	10	2	1	1	4	20
Total	4	4	12	14	9	3	4	11	*61*
D. M:F (3%) Bite									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	0	0	0	2	0	0	0	0	2
Total	0	0	0	2	0	0	0	0	*2*

APPENDIX I. FREQUENCY OF DISPLACEMENT INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (19%) Displace.									
F:F	7	7	9	7	5	10	7	4	56(19.00)
F:M	3	4	3	2	1	4	1	3	21(7.00)
M:F	1	0	0	1	1	0	0	0	3(1.00)
Total	11	11	12	10	7	14	8	7	*80(27.00)*
B. F:F (70%) Displace.									
20	1	0	3	1	2	3	3	4	17
19	6	7	6	6	3	7	4	0	39
80	0	0	0	0	0	0	0	0	0
Total	7	7	9	7	5	10	8	4	56
C. F:M (26%) Displace.									
20	2	1	1	1	1	1	1	1	9
19	1	3	2	1	0	3	0	0	10
80	0	0	0	0	0	0	0	2	2
Total	3	4	3	2	1	4	1	3	21
D. M:F (4%) Displace.									
20	0	0	0	0	0	0	0	0	0
19	1	0	0	0	0	0	0	0	1
80	0	0	0	1	1	0	0	0	2
Total	1	0	0	1	1	0	0	0	*3*

APPENDIX J. FREQUENCY OF LUNGE INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (12%) Lunge									
F:F	0	0	2	2	2	1	2	2	11(4.00)
F:M	1	0	7	5	8	3	9	4	37(12.00)
M:F	0	0	0	2	0	0	0	0	2(1.00)
Total	1	0	9	9	10	4	10	4	*50(17.00)*
B. F:F (24%) Lunge									
20	0	0	0	1	1	1	0	0	3
19	0	0	2	1	1	0	2	2	8
80	0	0	0	0	0	0	0	0	0
Total	0	0	2	2	2	1	2	2	*11*
C. F:M (70%) Lunge									
20	0	0	2	2	3	0	3	2	12
19	1	0	2	1	4	2	2	1	13
80	0	0	3	2	1	1	4	1	12
Total	1	0	7	5	8	3	9	4	*37*
D. M:F (6%) Lunge									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	0	0	0	2	0	0	0	0	2
Total	0	0	0	2	0	0	0	0	*2*

APPENDIX K. FREQUENCY OF CUFF INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total</u> (8%) <u>Cuff</u>									
F:F	0	0	1	0	0	0	2	0	3(1.00)
F:M	2	0	10	2	1	4	0	8	27(9.00)
M:F	1	0	0	1	0	0	0	0	2(1.00)
Total	3	0	11	3	1	4	2	8	*32(11.00)*
B. <u>F:F</u> (9%) <u>Cuff</u>									
20	0	0	1	0	0	0	2	0	3
19	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0
Total	0	0	1	0	0	0	2	0	*3*
C. <u>F:M</u> (82%) <u>Cuff</u>									
20	0	0	2	0	0	1	0	8	11
19	2	0	8	1	1	2	0	0	14
80	0	0	0	1	0	1	0	0	2
Total	2	0	10	2	1	4	0	8	*27*
D. <u>M:F</u> (9%) <u>Cuff</u>									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	1	0	0	1	0	0	0	0	2
Total	1	0	0	1	0	0	0	0	*2*

APPENDIX L. FREQUENCY OF FEINT-TO-CUFF INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total</u> (5%) <u>Fe/Cuff</u>									
F:F	1	1	0	0	1	0	1	0	4(1.33)
F:M	1	0	4	6	4	1	1	0	17(5.70)
M:F	1	0	0	0	0	0	0	0	1(.50)
Total	3	1	4	6	5	1	2	0	*22(7.53)*
B. <u>F:F</u> (18%) <u>Fe/Cuff</u>									
20	0	0	0	0	1	0	0	0	1
19	1	1	0	0	0	0	1	0	3
80	0	0	0	0	0	0	0	0	0
Total	1	1	0	0	1	0	1	0	*4*
C. <u>F:M</u> (75%) <u>Fe/Cuff</u>									
20	1	0	0	3	1	0	1	0	6
19	0	0	4	2	3	1	0	0	10
80	0	0	0	1	0	0	0	0	1
Total	1	0	4	6	4	1	1	0	*17*
D. <u>M:F</u> (7%) <u>Fe/Cuff</u>									
20	0	0	0	0	0	0	0	0	0
19	1	0	0	0	0	0	0	0	1
80	0	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	0	0	0	*1*

APPENDIX M. FREQUENCY OF ATTEMPT-TO-BITE INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (1%) At/Bite									
F:F	0	0	1	0	2	0	0	0	3(1.00)
F:M	0	0	0	0	0	0	0	1	1(.33)
M:F	0	1	0	0	0	0	0	0	1(.33)
Total	0	1	1	0	2	0	0	1	*5(1.66)*
B. F:F (60%) At/Bite									
20	0	0	1	0	1	0	0	0	2
19	0	0	0	0	1	0	0	0	1
80	0	0	0	0	0	0	0	0	0
Total	0	0	1	0	2	0	0	0	*3*
C. F:M (20%) At/Bite									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	1	1
Total	0	0	0	0	0	0	0	1	*1*
D. M:F (20%) At/Bite									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	0	1	0	0	0	0	0	0	1
Total	0	1	0	0	0	0	0	0	*1*

APPENDIX N. FREQUENCY OF NOSE-JAB INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (1%) Nose-jab									
F:F	0	0	0	0	0	0	1	0	1(.33)
F:M	1	0	0	0	0	1	0	0	2(.67)
M:F	0	0	0	0	0	1	0	0	1(.33)
Total	1	0	0	0	0	2	1	0	*4(1.33)*
B. F:F (25%) Nose-jab									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0	1
80	0	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	0	1	0	*1*
C. F:M (50%) Nose-jab									
20	0	0	0	0	0	0	0	0	0
19	1	0	0	0	0	1	0	0	2
80	0	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	1	0	0	*2*
D. M:F (25%) Nose-jab									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	1	0	0	1
80	0	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	1	0	0	*1*

APPENDIX O. FREQUENCY OF ATTEMPT-TO-CUFF INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total</u> (1%) <u>At/Cuff</u>									
F:F	0	0	0	0	0	0	1	0	1(.33)
F:M	0	1	0	0	0	0	1	0	2(.67)
M:F	0	0	0	0	0	0	0	0	0(.00)
Total	0	1	0	0	0	0	2	0	*3(1.00)*
B. <u>F:F</u> (33%) <u>At/Cuff</u>									
20	0	0	0	0	0	0	1	0	1
19	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	1	0	0
Total	0	0	0	0	0	0	0	0	*1*
C. <u>F:M</u> (67&) <u>At/Cuff</u>									
20	0	0	0	0	0	0	1	0	1
19	0	1	0	0	0	0	0	0	1
80	0	0	0	0	0	0	0	0	0
Total	0	1	0	0	0	0	1	0	*2*

APPENDIX P. FREQUENCY OF LUNGE INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (25%) Lunge								
F:F	0	0	0	0	1	0	0	1(.50)
F:M	8	8	8	17	38	19	18	116(56.00)
M:F	0	0	0	0	0	0	0	0
Total	8	8	8	17	39	19	18	*117(56.50)*
B. F:F (1%) Lunge								
36	0	0	0	0	1	0	0	1
107	0	0	0	0	0	0	0	0
Total	0	0	0	0	1	0	0	*1*
C. F:M (99%) Lunge								
36	5	7	4	11	17	7	8	59
107	3	1	4	6	21	12	10	57
Total	8	8	8	17	38	19	18	*116*

APPENDIX Q. FREQUENCY OF GRAB INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (24%) Grab								
F:F	0	0	0	0	1	0	0	1(.50)
F:M	5	8	13	21	32	17	15	111(55.50)
M:F	1	0	0	0	0	0	0	1(.50)
Total	6	8	13	21	33	17	15	*113(56.33)*
B. F:F (1%) Grab								
36	0	0	0	0	1	0	0	1
107	0	0	0	0	0	0	0	0
Total	0	0	0	0	1	0	0	*1*
C. F:M (98%) Grab								
36	3	6	6	8	12	1	5	41
107	2	2	7	13	20	16	10	70
Total	5	8	13	21	32	17	15	*111*
D. M:F (1%) Grab								
36	1	0	0	0	0	0	0	1
107	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	0	0	*1*

APPENDIX R. FREQUENCY OF BITE INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (24%) Bite								
F:F	0	0	0	0	1	0	0	1(.50)
F:M	8	11	14	20	31	14	11	109(54.50)
M:F	0	0	0	0	0	0	0	0
Total	8	11	14	20	32	14	11	*110(55.00)*
B. F:F (1%) Bite								
36	0	0	0	0	1	0	0	1
107	0	0	0	0	0	0	0	0
Total	0	0	0	0	1	0	0	*1*
C. F:M (99%) Bite								
36	4	8	7	6	11	0	4	40
107	4	3	7	14	20	14	7	69
Total	8	11	14	20	31	14	11	*109*

APPENDIX S. FREQUENCY OF CUFF INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. <u>Total</u> (12%) <u>Cuff</u>								
F:F	0	0	0	0	1	0	0	1(.50)
F:M	9	8	7	7	11	3	9	54(27.00)
M:F	0	0	0	0	0	0	0	0
Total	9	8	7	7	12	3	9	*55(27.50)*
B. <u>F:F</u> (2%) <u>Cuff</u>								
36	0	0	0	0	1	0	0	1
107	0	0	0	0	0	0	0	0
Total	0	0	0	0	1	0	0	*1*
C. <u>F:M</u> (98%) <u>Cuff</u>								
36	8	7	6	4	10	0	4	39
107	1	1	1	3	1	3	5	15
Total	9	8	7	7	11	3	9	*54*

APPENDIX T. FREQUENCY OF ATTEMPT-TO-CUFF INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. <u>Total</u> (7%) <u>At/Cuff</u>								
F:F	0	0	0	0	0	0	0	0
F:M	3	6	3	6	4	5	3	30(15.00)
M:F	0	0	0	0	0	0	0	0
Total	3	6	3	6	4	5	3	*30(15.00)*
B. <u>F:M</u> (100%) <u>At/Cuff</u>								
36	2	3	3	3	4	5	2	22
107	1	3	0	3	0	0	1	8
Total	3	6	3	6	4	5	3	*30*

APPENDIX U. FREQUENCY OF DISPLACEMENT INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (3%) Displace.								
F:F	1	1	1	2	2	0	1	8(4.00)
F:M	4	0	1	0	1	1	1	8(4.00)
M:F	0	0	0	0	0	0	0	0
Total	5	1	2	2	3	1	2	*16(8.00)*
B. F:F (50%) Displace.								
36	0	0	0	1	1	0	0	2
107	1	1	1	1	1	0	1	6
Total	1	1	1	2	2	0	1	*8*
C. F:M (50%) Displace.								
36	3	0	1	0	1	0	1	6
107	1	0	0	0	0	1	0	2
Total	4	0	1	0	1	1	1	*8*

APPENDIX V. FREQUENCY OF NOSE-JAB INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (3%) Nose-jab								
F:F	0	3	0	1	0	0	0	4(2.00)
F:M	0	4	2	2	0	0	1	9(4.50)
M:F	0	0	0	0	0	0	0	0
Total	0	7	2	3	0	0	1	*13(6.50)*
B. F:F (31%) Nose-jab								
36	0	3	0	0	0	0	0	3
107	0	0	0	1	0	0	0	1
Total	0	3	0	1	0	0	0	*4*
C. F:M (69%) Nose-jab								
36	0	1	2	2	0	0	1	6
107	0	3	0	0	0	0	0	3
Total	0	4	2	2	0	0	1	*9*

APPENDIX W. FREQUENCY OF ATTEMPT-TO-BITE INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (2%) At/Bite								
F:F	0	1	0	0	0	0	0	1(.50)
F:M	0	4	1	0	1	1	1	8(4.00)
M:F	0	0	0	0	0	0	0	0
Total	0	5	1	0	1	1	1	*9(4.50)*
B. F:F (11%) Att/Bite								
36	0	1	0	0	0	0	0	1
107	0	0	0	0	0	0	0	0
Total	0	1	0	0	0	0	0	*1*
C. F:M (89%) At/Bite								
36	0	1	1	0	0	0	0	2
107	0	3	0	0	1	1	1	6
Total	0	4	1	0	1	1	1	*8*

APPENDIX X. FREQUENCY OF AFFILIATION INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total Affiliation									
F:F	52	40	69	78	40	44	38	48	409(136.33)
F:M	3	4	19	10	7	15	6	1	65(21.70)
M:F	6	6	9	11	13	8	20	3	76(38.00)
Total	61	50	97	99	60	67	64	52	*550(196.03)*
B. F:F (70%) Affiliation									
20	15	9	24	35	9	7	10	17	126
19	8	14	17	28	17	13	15	9	121
80	29	17	28	15	14	24	13	22	162
Total	52	40	69	78	40	44	38	48	*409*
C. F:M (11%) Affiliation									
20	1	0	3	3	0	2	1	0	10
19	0	0	11	2	3	6	2	0	24
80	2	4	5	5	4	7	3	1	31
Total	3	4	19	10	7	15	6	1	*65*
D. M:F (19%) Affiliation									
20	1	1	1	0	1	2	3	2	11
19	1	2	6	5	4	2	11	1	32
80	4	3	2	6	8	4	6	0	33
Total	6	6	9	11	13	8	20	3	*76*

APPENDIX Y. FREQUENCY OF GROOM INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (63%)									
Groom									
F:F	37	23	45	57	23	29	26	36	276(92.00)
F:M	3	2	2	1	1	1	0	1	11(3.67)
M:F	5	4	7	10	9	6	17	2	60(30.00)
Total	45	29	54	68	33	36	43	39	*347(125.67)*
B. F:F (73%)									
Groom									
20	11	6	10	26	8	6	8	15	90
19	6	5	15	22	6	5	7	3	69
80	20	12	20	9	9	18	11	18	117
Total	37	23	45	57	23	29	26	36	*276*
C. F:M (3%)									
Groom									
20	1	0	0	0	0	0	0	0	1
19	0	0	1	0	0	0	0	0	1
80	2	2	1	1	1	1	0	1	9
Total	3	2	2	1	1	1	0	1	*11*
D. M:F (24%)									
Groom									
20	0	0	1	0	0	1	2	1	5
19	1	1	4	5	3	2	9	1	26
80	4	3	2	5	6	3	6	0	29
Total	5	4	7	10	9	6	17	2	*60*

APPENDIX Z. FREQUENCY OF GREET INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (19%) Greet									
F:F	7	9	17	11	9	4	7	4	68(22.67)
F:M	0	0	13	6	2	2	1	0	24(8.00)
M:F	1	2	1	1	4	2	3	1	15(7.50)
Total	8	11	31	18	15	8	11	5	*107(38.17)*
B. F:F (59%) Greet									
20	2	3	10	7	1	0	1	0	24
19	1	5	2	2	6	4	4	3	27
80	4	1	5	2	2	0	2	1	17
Total	7	9	17	11	9	4	5	4	*68*
C. F:M (21%) Greet									
20	0	0	3	3	0	2	1	0	9
19	0	0	7	1	2	0	0	0	10
80	0	0	3	2	0	0	0	0	5
Total	0	0	13	6	2	2	1	0	*24*
D. M:F (20%) Greet									
20	1	1	0	0	1	1	1	1	6
19	0	1	1	0	1	0	2	0	5
80	0	0	0	1	2	1	0	0	4
Total	1	2	1	1	4	2	3	1	*15*

APPENDIX AA. FREQUENCY OF PLAY INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
	1	2	3*	4*	5	6	7	8	Total(#)
Dyad									
A. Total (6%) Play									
F:F	0	1	3	1	1	4	2	0	12(4.00)
F:M	0	2	3	2	3	11	2	0	23(7.70)
M:F	0	0	0	0	0	0	0	0	0
Total	0	3	6	3	4	15	4	0	*35(11.70)*
B. F:F (34%) Play									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	1	0	2	2	0	5
80	0	1	3	0	1	2	0	0	7
Total	0	1	3	1	1	4	2	0	*12*
C. F:M (66%) Play									
20	0	0	0	0	0	0	0	0	0
19	0	0	2	1	0	5	0	0	8
80	0	2	1	1	3	6	2	0	15
Total	0	2	3	2	3	11	2	0	*23*

APPENDIX AB. FREQUENCY OF INVITE-TO-GROOM INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total</u> (5%) <u>In/Groom</u>									
F:F	1	4	4	4	5	3	0	5	26(8.67)
F:M	0	0	1	0	1	0	1	0	3(1.00)
M:F	0	0	0	0	0	0	0	0	0
Total	1	4	5	4	6	3	1	5	*29(9.67)*
B. <u>F:F</u> (90%) <u>In/Groom</u>									
20	0	0	3	0	0	1	0	2	6
19	0	3	0	2	4	2	0	2	13
80	1	1	1	2	1	0	0	1	7
<u>Total</u>	1	4	4	4	5	3	0	5	*26*
C. <u>F:M</u> (10%) <u>In/Groom</u>									
20	0	0	0	0	0	0	0	0	0
19	0	0	1	0	1	0	0	0	2
80	0	0	0	0	0	0	1	0	1
Total	0	0	1	0	1	0	1	0	*3*

APPENDIX AC. FREQUENCY OF RECIPROCAL GROOM INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (5%) Rec/Groom									
F:F	7	3	2	3	1	3	3	3	25(8.33)
F:M	0	0	0	0	0	1	1	0	2(.67)
M:F	0	0	0	0	0	0	0	0	0
Total	7	3	2	3	1	4	4	3	*27(9.00)*
B. F:F (93%) Rec/Groom									
20	2	0	1	2	0	0	1	0	6
19	1	1	0	1	1	0	2	1	7
80	4	2	1	0	0	3	0	2	12
Total	7	3	2	3	1	3	3	3	*25*
C. F:M (7%) Rec/Groom									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	1	1	0	2
80	0	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	1	1	0	*2*

APPENDIX AD. FREQUENCY OF INVITE-TO-PLAY INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (1%) In/Play									
F:F	0	0	0	1	0	1	0	0	2(.67)
F:M	0	0	0	1	0	0	1	0	2(.67)
M:F	0	0	1	0	0	0	0	0	1(.50)
Total	0	0	1	2	0	1	1	0	*5(1.84)*
B. F:F (36%) In/Play									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
80	0	0	0	1	0	1	0	0	2
Total	0	0	0	1	0	1	0	0	*2*
C. F:M (36%) In/Play									
20	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0	1
80	0	0	0	1	0	0	0	0	1
Total	0	0	0	1	0	0	1	0	*2*
D. M:F (28%) In/Play									
20	0	0	0	0	0	0	0	0	0
19	0	0	1	0	0	0	0	0	1
80	0	0	0	0	0	0	0	0	0
Total	0	0	1	0	0	0	0	0	*1*

APPENDIX AE. FREQUENCY OF AFFILIATION INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A.<u>Total Affiliation</u>								
F:F	12	17	13	24	22	12	3	103(51.3)
F:M	9	4	17	7	7	16	4	64(21.3)
M:F	12	6	20	6	8	6	9	67(22.3)
Total	33	27	50	37	37	34	16	*234(94.9)*
B.<u>F:F</u> (54%) <u>Affiliation</u>								
36	6	10	9	11	10	8	3	57
107	6	7	4	13	12	4	0	46
Total	12	17	13	24	22	12	3	*103*
C.<u>F:M</u> (22%) <u>Affiliation</u>								
36	6	1	12	3	4	8	2	35
107	3	3	5	4	3	8	2	28
Total	9	4	17	7	7	16	4	*64*
D.<u>M:F</u> (22%) <u>Affiliation</u>								
36	6	3	15	3	4	3	5	39
107	6	3	5	3	4	3	4	28
Total	12	6	20	6	8	6	9	*67*

APPENDIX AF. FREQUENCY OF GROOM INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. <u>Total</u> (48%) <u>Groom</u>								
F:F	8	8	6	15	7	7	1	52(26.00)
F:M	1	0	0	0	0	0	0	1(.50)
M:F	12	4	19	6	6	6	6	59(19.67)
Total	21	12	25	21	13	13	7	*112(46.17)*
B. <u>F:F</u> (56%) <u>Groom</u>								
36	6	5	4	6	5	5	1	32
107	2	3	2	9	2	2	0	20
Total	8	8	6	15	7	7	1	*52*
C. <u>F:M</u> (2%) <u>Groom</u>								
36	0	0	0	0	0	0	0	0
107	1	0	0	0	0	0	0	1
Total	1	0	0	0	0	0	0	*1*
D. <u>M:F</u> (42%) <u>Groom</u>								
36	6	2	14	3	3	3	3	34
107	6	2	5	3	3	3	3	25
Total	12	4	19	6	6	6	6	*59*

APPENDIX AG. FREQUENCY OF GREET INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (36%) Greet								
F:F	4	9	5	6	12	4	2	42(21.00)
F:M	3	3	7	6	5	9	1	34(17.00)
M:F	0	2	1	0	2	0	2	7(2.33)
Total	7	14	13	12	15	13	5	*83(40.33)*
B. F:F (52%) Greet								
36	0	5	4	3	4	3	2	21
107	4	4	1	3	8	1	0	21
Total	4	9	5	6	12	4	2	*42*
C. F:M (42%) Greet								
36	2	0	5	2	3	5	0	17
107	1	3	2	4	2	4	1	17
Total	3	3	7	6	5	9	1	*34*
D. M:F (6%) Greet								
36	0	1	1	0	1	0	1	4
107	0	1	0	0	1	0	1	3
Total	0	2	1	0	2	0	2	7

APPENDIX AH. FREQUENCY OF INVITE-TO-GROOM INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (16%)								
In/Groom								
F:F	0	0	2	3	3	1	0	9(4.50)
F:M	5	1	10	1	2	6	3	28(14.00)
M:F	0	0	0	0	0	0	1	1(.33)
Total	5	1	12	4	5	7	4	*38(18.83)*
B. F:F (24%)								
In/Groom								
36	0	0	1	2	1	0	0	4
107	0	0	1	1	2	1	0	5
Total	0	0	2	3	3	1	0	*9*
C. F:M (74%)								
In/Groom								
36	4	1	7	1	1	3	2	19
107	1	0	3	0	1	3	1	9
Total	5	1	10	1	2	6	3	*28*
D. M:F (2%)								
In/Groom								
36	0	0	0	0	0	0	1	1
107	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	0	0	*1*

APPENDIX AI. FREQUENCY OF RECIPROCAL GROOM INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (.4%) Rec/Groom								
F:F	0	0	0	0	0	0	0	0
F:M	0	0	0	0	0	1	0	1(.50)
M:F	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	1	0	*1(.50)*
B. F:M (100%) Rec/Groom								
36	0	0	0	0	0	0	0	0
107	0	0	0	0	0	1	0	1
Total	0	0	0	0	0	1	0	*1*

APPENDIX AJ. PROXIMITY MAINTENANCE OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^							
	1	2	3*	4*	5	6	7	8
Dyad								
F20:								
M240	-15.79	23.81	48.48	-10.53	-52.94	-17.39	-4.55	8.33
MFd	-50.00	50.00	35.00	-11.11	-16.67	100.00	16.67	-50.00
F19:								
M240	-35.71	6.25	3.45	-40.91	00.00	-31.58	11.76	42.86
MFd	-20.00	10.00	-48.15	10.00	-25.00	14.29	7.14	-25.00
F80:								
M240	-36.00	-14.29	-7.14	29.73	10.00	11.11	-44.44	-36.36
MFd	-33.33	11.11	21.43	-13.33	-44.44	-75.00	9.09	150.00

APPENDIX AK. PROXIMITY MAINTENANCE OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^						
	1	2	3	4	5*	6	7
Dyad							
F36:							
M146	-10.00	14.89	15.79	00.00	-42.86	-50.00	-33.33
M140	-83.33	-50.00	37.50	00.00	-33.33	-33.33	00.00
MUC	-42.86	9.52	-23.53	-66.67	00.00	00.00	-100.00
M243	00.00	00.00	00.00	-17.14	- 8.47	-21.88	2.08
F107:							
M146	17.50	5.56	30.70	00.00	00.00	-33.33	00.00
M140	-12.50	-14.29	-100.00	00.00	00.00	-66.67	00.00
MUC	- 6.25	8.33	- 50.00	-33.33	00.00	00.00	00.00
M243	00.00	00.00	- 20.00	4.35	2.70	-15.69	27.94

APPENDIX AL. FREQUENCY OF GLANCE INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
	1	2	3*	4*	5	6	7	8	Total(Per/Hr)
Female									
20	293	282	285	352	292	350	351	266	2471(25.6)
19	294	331	431	381	308	340	385	256	2726(26.8)
80	337	275	253	384	306	291	411	310	2567(25.2)
Total	924	888	969	1117	906	981	1147	832	*7764*
%	12	11	12	14	12	13	15	11	100

APPENDIX AM. FREQUENCY OF GLANCE INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

				Period^				
	1	2	3	4	5*	6	7	Total(Per/Hr)
<u>Female</u>								
36	546	554	641	472	566	493	560	3832(22.3)
107	566	575	576	617	482	476	536	3828(22.3)
Total	1112	1129	1217	1089	1048	969	1096	*7660*
%	14	15	16	14	14	13	14	100

APPENDIX AN. FREQUENCY OF APPROACH INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. <u>Total Approach</u>									
F:F	92	101	121	103	104	106	108	57	792(264.00)
F:M	36	31	58	55	43	26	38	30	317(105.70)
M:F	30	44	129	76	41	39	48	36	443(222.00)
Total	158	176	308	234	188	171	194	123	*1552(591.70)*
B. <u>F:F</u> (44%) <u>Approach</u>									
20	34	31	37	33	38	28	40	17	258
19	41	42	51	46	45	55	45	22	347
80	17	28	33	24	21	23	23	18	187
Total	92	101	121	103	104	106	108	57	*792*
C. <u>F:M</u> (18%) <u>Approach</u>									
20	14	6	11	25	20	12	14	14	116
19	13	13	36	19	10	9	9	8	117
80	9	12	11	11	13	5	15	8	84
Total	36	31	58	55	43	26	38	30	*317*
D. <u>M:F</u> (38%) <u>Approach</u>									
20	12	20	62	22	9	13	15	24	177
19	8	13	49	13	18	17	21	7	146
80	10	11	18	41	14	9	12	5	120
Total	30	44	129	76	41	39	48	36	*443*

APPENDIX AO. FREQUENCY OF GUARD INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

				Period^					
	1	2	3*	4*	5	6	7	8	Total(%)
A. <u>Total Guard</u>									
M240	0	0	19	8	0	1	0	1	29
MFd	0	0	0	0	0	0	0	0	0
Total	0	0	19	8	0	1	0	1	*29*
B. <u>M240:</u>									
20	0	0	9	0	0	1	0	1	11(38)
19	0	0	10	0	0	0	0	0	10(34)
80	0	0	0	8	0	0	0	0	8(28)
Total	0	0	19	8	0	1	0	1	*29*

APPENDIX AP. FREQUENCY OF APPROACH INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

				Period^				
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total Approach								
F:F	46	50	44	72	49	42	45	348(174.00)
F:M	60	53	57	45	51	50	44	360(180.00)
M:F	59	77	61	54	60	48	83	442(147.33)
Total	165	181	162	171	159	140	171	*1150(501.33)*
B. F:F (35%) Approach								
36	24	27	22	40	20	22	16	171
107	22	23	22	32	29	20	29	177
Total	46	50	44	72	49	42	45	*348*
C. F:M (36%) Approach								
36	32	29	36	24	35	23	23	202
107	28	24	21	21	16	27	21	158
Total	60	53	57	45	51	50	44	*360*
D. M:F (29%) Approach								
36	24	46	38	19	38	17	32	214
107	35	31	23	35	22	31	51	228
Total	59	77	61	54	60	48	83	*442*

APPENDIX AQ. FREQUENCY OF GUARD INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total
A. <u>Total Guard</u>								
M146	4	11	4	0	0	0	0	19
M140	0	0	1	0	0	0	0	1
MUC	0	0	0	0	0	0	0	0
M243	0	0	2	10	11	8	1	32
Total	4	11	7	10	11	8	1	*52*
B. <u>F36</u>:								
M146	0	3	0	0	0	0	0	3
M140	0	0	1	0	0	0	0	1
M243	0	0	1	5	4	1	1	12
Total	0	3	2	5	4	1	1	*16*
C. <u>F107</u>:								
M146	4	8	4	0	0	0	0	16
M243	0	0	1	5	7	7	0	20
Total	4	8	5	5	7	7	0	*36*

APPENDIX AR. FREQUENCY OF APPROACH 1 m INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (33%) App/1m									
F:F	13	32	41	33	36	29	38	18	240(80.00)
F:M	5	10	16	21	20	5	12	9	98(32.67)
M:F	4	23	47	25	10	17	27	19	172(86.00)
Total	22	65	104	79	66	51	77	46	*510(198.67)*
B. F:F (40%) App/1m									
20	4	11	14	14	14	6	11	3	77
19	6	14	15	11	15	17	19	8	105
80	3	7	12	8	7	6	8	7	58
Total	13	32	41	33	36	29	38	18	*240*
C. F:M (17%) App/1m									
20	0	4	6	11	10	4	7	7	49
19	3	2	8	8	4	1	2	0	28
80	2	4	2	2	6	0	3	2	21
Total	5	10	16	21	20	5	12	9	*98*
D. M:F (43%) App/1m									
20	4	12	21	7	3	10	8	11	76
19	0	6	21	6	3	3	12	5	56
80	0	5	5	12	4	4	7	3	40
Total	4	23	47	25	10	17	27	19	*172*

APPENDIX AS. FREQUENCY OF APPROACH <1 m INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (52%) App/<1m									
F:F	52	50	61	55	51	48	59	35	411(137.00)
F:M	21	17	37	26	16	16	20	16	169(56.33)
M:F	20	20	63	44	27	16	18	16	224(112.00)
Total	93	87	161	125	89	80	97	67	*804(305.33)*
B. F:F (45%) App/<1m									
20	21	16	16	14	17	14	25	13	136
19	25	18	29	28	24	24	21	13	182
80	6	16	16	13	10	10	13	9	93
Total	52	50	61	55	51	48	59	35	*411*
C. F:M (18%) App/<1m									
20	11	2	5	10	8	7	6	5	54
19	4	8	24	8	4	5	4	5	62
80	6	7	8	8	4	4	10	6	53
Total	21	17	37	26	16	16	20	16	*169*
D. M:F (37%) App/<1m									
20	8	8	34	13	5	3	6	13	90
19	6	7	19	7	12	11	7	2	71
80	6	5	10	24	10	2	5	1	63
Total	20	20	63	44	27	16	18	16	*224*

APPENDIX AT. FREQUENCY OF APPROACH CONTACT INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total (15%) App/Contact									
F:F	27	19	19	15	17	29	11	4	141(47.00)
F:M	10	4	5	8	7	5	6	5	50(16.67)
M:F	6	1	19	7	4	6	3	1	47(23.50)
Total	43	24	43	30	28	40	20	9	*238(87.17)*
B. F:F (54%) App/Contact									
20	9	4	7	5	7	8	4	1	45
19	10	10	7	7	6	14	5	1	60
80	8	5	5	3	4	7	2	2	36
Total	27	19	19	15	17	29	11	4	*141*
C. F:M (19%) App/Contact									
20	3	0	0	4	2	1	1	2	13
19	6	3	4	3	2	3	3	3	27
80	1	1	1	1	3	1	2	0	10
Total	10	4	5	8	7	5	6	5	*50*
D. M:F (27%) App/Contact									
20	0	0	7	2	1	0	1	0	11
19	2	0	9	0	3	3	2	0	19
80	4	1	3	5	0	3	0	1	17
Total	6	1	19	7	4	6	3	1	*47*

APPENDIX AU. FREQUENCY OF APPROACH <1 m INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (47%) App/<1m								
F:F	17	24	20	31	32	22	20	166(83.00)
F:M	25	20	29	19	28	32	23	176(88.00)
M:F	22	34	19	27	32	21	38	193(32.16)
Total	64	78	68	77	92	75	81	*535(203.16)*
B. F:F (41%) App/<1m								
36	8	14	9	17	14	11	6	79
107	9	10	11	14	18	11	14	87
Total	17	24	20	31	32	22	20	*166*
C. F:M (43%) App/<1m								
36	15	13	18	9	19	13	13	100
107	10	7	11	10	9	19	10	76
Total	25	20	29	19	28	32	23	*176*
D. M:F (16%) App/<1m								
36	11	17	15	10	21	8	14	96
107	11	17	4	17	11	13	24	97
Total	22	34	19	27	32	21	38	*193*

APPENDIX AV. FREQUENCY OF APPROACH 1 m INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total
A. Total (36%) App/1m								
F:F	13	18	15	19	8	15	21	109(54.50)
F:M	16	21	12	12	11	11	11	94(47.00)
M:F	29	31	37	20	25	25	43	210(70.00)
Total	58	70	64	51	44	51	75	*413(171.50)*
B. F:F (32%) App/1m								
36	8	8	8	11	2	8	9	54
107	5	10	7	8	6	7	12	55
Total	13	18	15	19	8	15	21	*109*
C. F:M (27%) App/1m								
36	5	11	9	7	10	7	6	55
107	11	10	3	5	1	4	5	39
Total	16	21	12	12	11	11	11	*94*
D. M:F (41%) App/1m								
36	11	23	18	6	16	9	17	100
107	18	8	19	14	9	16	26	110
Total	29	31	37	20	25	25	43	*210*

APPENDIX AW. FREQUENCY OF APPROACH CONTACT INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. Total (18%)								
App.Contact								
F:F	16	8	9	22	9	5	4	73(36.50)
F:M	19	12	16	14	12	7	10	90(45.00)
M:F	8	12	5	7	3	2	2	39(13.00)
Total	43	32	30	43	24	14	16	*202(94.50)*
B. F:F (38%)								
App/Contact								
36	8	5	5	12	4	3	1	38
107	8	3	4	10	5	2	3	35
Total	16	8	9	22	9	5	4	*73*
C. F:M (48%)								
App/Contact								
36	12	5	9	8	6	3	4	47
107	7	7	7	6	6	4	6	43
Total	19	12	16	14	12	7	10	*90*
D. M:F (14%)								
App/Contact								
36	2	6	5	3	1	0	1	18
107	6	6	0	4	2	2	1	21
Total	8	12	5	7	3	2	2	*39*

APPENDIX AX. FREQUENCY OF PRESENT INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total
20	0	0	2	0	0	0	0	0	2
19	0	0	8	0	0	0	0	0	8
80	0	0	0	1	0	0	0	0	1
Total	0	0	10	1	0	0	0	0	*11*

APPENDIX AY. FREQUENCY OF PRESENT INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total
36	0	0	0	1	2	0	0	3
107	0	0	0	4	1	0	0	5
Total	0	0	0	5	3	0	0	*8*

APPENDIX AZ. FREQUENCY OF MOUNT INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total(%)
20	0	0	16	0	0	0	0	0	16
19	0	0	11	0	1	0	0	0	12
80	0	0	0	3	0	0	0	0	3
Total	0	0	27	3	1	0	0	0	*31(26)*

APPENDIX BA. FREQUENCY OF MATE INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total(%)
20	0	0	14	0	0	0	0	0	14
19	0	0	12	0	0	0	0	0	12
80	0	0	0	0	0	0	0	0	0
Total	0	0	26	0	0	0	0	0	*26(22%)*

APPENDIX BB. FREQUENCY OF ATTEMPT-TO-MOUNT INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total(%)
20	0	0	0	0	0	0	0	0	0
19	0	0	11	0	0	0	1	0	12
80	0	0	5	8	0	0	0	0	13
Total	0	0	16	8	0	0	1	0	*25(21%)*

APPENDIX BC. FREQUENCY OF CLASP INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
	1	2	3*	4*	5	6	7	8	Total(%)
Female									
20	0	0	0	0	0	0	0	2	2
19	0	0	5	0	1	0	1	0	7
80	0	0	3	8	0	0	0	0	11
Total	0	0	8	8	1	0	1	2	*20(16%)*

APPENDIX BD. FREQUENCY OF ATTEMPT-TO-CLASP INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total(%)
20	0	0	0	0	0	0	0	6	6
19	0	1	0	0	2	0	2	4	9
80	0	0	0	2	0	0	0	0	*2*
Total	0	1	0	2	4	0	2	10	*17(14%)*

APPENDIX BE. FREQUENCY OF MOUNT WITH INTROMISSION OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Female	1	2	3*	4*	5	6	7	8	Total(%)
20	0	0	1	0	0	0	0	0	1
19	0	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0
Total	0	0	1	0	0	0	0	0	*1(1%)*

APPENDIX BF. FREQUENCY OF ATTEMPT-TO-CLASP INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total(%)
36	2	3	1	0	1	0	0	7
107	0	1	1	17	3	3	0	25
Total	2	4	2	17	4	3	0	*32(55%)*

APPENDIX BG. FREQUENCY OF CLASP INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total(%)
36	0	2	2	3	0	0	0	7
107	0	3	0	2	0	0	0	5
Total	0	5	2	5	0	0	0	*12(21%)*

APPENDIX BH. FREQUENCY OF MATE INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total(%)
36	0	0	0	0	3	0	0	3
107	0	0	0	0	3	0	0	3
Total	0	0	0	0	6	0	0	*6(10%)*

APPENDIX BI. FREQUENCY OF ATTEMPT-TO-MOUNT INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total(%)
36	0	0	0	0	0	0	0	0
107	0	0	2	1	1	0	0	4
Total	0	0	2	1	1	0	0	*4(7%)*

APPENDIX BJ. FREQUENCY OF MOUNT INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Female	1	2	3	4	5*	6	7	Total(%)
36	0	0	0	0	0	0	0	0
107	0	1	0	2	1	0	0	4
Total	0	1	0	2	1	0	0	*4(7%)*

APPENDIX BK. FREQUENCY OF MALE SCENT-MARKING INTERACTIONS OVER TIME IN THE VAOVAO SOCIAL GROUP.

	Period^								
Dyad	1	2	3*	4*	5	6	7	8	Total(#)
A. Total Scent/Mr									
M240	26	19	24	13	7	16	14	20	140
MFd	0	0	0	0	0	0	0	1	1
Total	26	19	24	13	7	16	14	21	*141(70.00)*
B. F20:(51%)									
M240	16	7	11	7	3	7	6	13	70
MFd	0	0	0	0	0	0	0	1	1
Total	16	7	11	7	3	7	6	14	*71(35.50)*
B. F19:(34%)									
M240	8	7	10	3	2	7	6	4	47
MFd	0	0	0	0	0	0	0	0	0
Total	8	7	10	3	2	7	6	4	*47(23.50)*
C. F80:(16%)									
M240	2	5	3	3	2	2	2	3	22
MFd	0	0	0	0	0	0	0	0	0
Total	2	5	3	3	2	2	2	3	*22(11.00)*

APPENDIX BL. FREQUENCY OF MALE SCENT-MARKING INTERACTIONS OVER TIME IN THE VAVY MASIAKA SOCIAL GROUP.

	Period^							
Dyad	1	2	3	4	5*	6	7	Total(#)
A. <u>Total Scent/Mr</u>								
M146	33	43	12	0	0	0	0	87
M140	0	0	1	1	1	0	0	3
MUC	1	1	2	0	0	0	0	4
M243	0	0	23	49	37	19	42	170
Total	34	44	38	50	38	19	42	*265(88.33)*
B. <u>F36:</u>(56%)								
M146	12	28	7	0	0	0	0	47
M140	0	0	1	0	1	0	0	2
MUC	0	1	1	0	0	0	0	2
M243	0	0	15	30	25	11	16	97
Total	12	29	24	30	26	11	16	*148(49.30)*
C. <u>F107:</u>(44%)								
M146	21	15	5	0	0	0	0	41
M140	0	0	0	1	0	0	0	1
MUC	1	0	1	0	0	0	0	2
M243	0	0	8	19	12	8	26	73
Total	22	15	14	20	12	8	26	*117(39.00)*

LIST OF REFERENCES

Adlercruitz, H., & Jarvenpaa (1982). Assay of estrogens in human feces. *Journal of Biochemistry, 17,* 639-645.

Afzelius, B.A. (1981). Abnormal human spermatozoa including comparative data from apes. *American Journal of Primatology 1,* 175-182.

Alexander, R.D., & Noonan, K.M. (1979). Concealment of ovulation, parental care, and human social evolution. In N.A. Chagnon & W. Irons (Eds.), *Evclutionary biology and human social behavior* (pp. 436-453). North Scituate: Duxbury Press.

Allen, M.L., & Lemmon, W.B. (1981). Orgasm in female primates. *American Journal of Primatology 1,* 15-34.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour 49,* 227-267.

Altmann, S.A., & Altmann, J. (1979). Demographic constraints on behavior and social organization. In I.S. Bernstein & E.O. Wilson (Eds.), *Primate ecology and human origins: Ecological influences on social organization* (pp. 47-63). New York: Garland STMP Press.

Altmann, J., Hausfater, G., & Altmann, S. (1988). Determinates of reproductive success in savannah baboons, *Papio cynocephalus*. In T.H. Clutton-Brock (Ed.), *Reproductive success, studies of individual variation in contrasting breeding systems* (pp. 403-418). Chicago: university of Chicago Press.

Andelman, S.J. (1987). Evolution of concealed ovulation in vervet monkeys (*Cercopithecus aethiops*). *The American Naturalist 129,* 785-799.

Andelman, S.J., Else, J.G., Hearn, J.P., & Hodges, J.K. (1985). The non-invasive monitoring of reproductive events in wild vervet monkeys (*Cercopithecus aethiops*) using urinary pregnanediol-3α-glucuronide and its correlation with behavioral observations. *Journal of Zoology (London) A 205,* 467-477.

Andriantsiferana, R., Rarijanona, Y., & Randrianaivo (1974). Observations sur là reproduction du microcebe (*Microcebus, murinus,* Miller, 1777) en captivite à Tananarive. *Mammalia 38,* 234-243.

Austin, C.R. (1970). Aging and reproduction: Post-ovulatory deterioration of the egg. *Journal of Reproduction and Fertility (Supplement)* 39-53.

Baker, R.R., & Bellis, M.A. (1989). Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Animal Behaviour 37*, 867-869.

Beach, F. (1979). Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior 20*, 105-138.

Bedford, J.M. (1974). Biology of primate spermatozoa. *Contributions to Primatology 3*, 97-139.

Benshoof, L., & Thornhill, R. (1979). The evolution of monogamy and concealed ovulation in humans. *Journal of Social and Biological Structures 2*, 95-106.

Bercovitch, F.B. (1987). Reproductive success in male savanna baboons. *Behavioral Ecology and Sociobiology 21*, 163-172.

Blandau, R.J. (1975). *Aging gametes*. Basel: S. Karger.

Blandau, R.J., & Jordon, E.S. (1941). The effect of delayed fertilization on the development of the rat ovum. *American Journal of Anatomy 68*, 275-291.

Bogart, M.H., Kumamoto, A., & Benirschke, K. (1977). A comparison of the reproductive cycles of three species of *Lemur*. *Folia Primatologica 28*, 134-143.

Brockman, D.K. Whitten, P.L., Russell, E., Richard, R.F., & Izard, M.K. (1993). Measuring gonadal fecal steroids in female sifaka, *Propithecus verreauxi*. *American Journal of Physical Anthropologists (Supplement) 16*, 63.

Brockman, D.K., Whitten, P.L., Russell, E., Richard, R.F., & Izard, M.K. (submitted). Application of fecal steroid techniques to the reproductive endocrinology of female Verreauxi's sifaka, *Propithecus verreauxi*. *American Journal of Primatology*.

Bronson, F.H. (1989). *Mammalian reproductive biology*. Chicago: University of Chicago Press.

Brun, B., & Rumpler, Y. (1990). Seasonal variation of sperm morphology in the Mayotte brown lemur (*Eulemur fulvus mayottensis*). *Folia Primatologica 55*, 51-56.

Budnitz, N., & Dainis, K. (1975). Lemur catta: Ecology and behavior. I. Tattersall & R.W. Sussman (Eds.), *Lemur biology* (pp. 219-235). New York: Plenum Press.

Burley, N. (1979). The evolution of concealed ovulation. *The American Naturalist 114*, 835-858.

Butynski, T.M. (1982). Harem male replacement and infanticide in the blue monkey (*Cercopithecus mitus stuhlmanni*) in the Kabale Forest, Uganda. *American Journal of Primatology 3*, 1-22.

Carpenter, C.R. (1940). A field study in Siam of the behavior and social relations of the gibbon, *Hylobates lar*. *Comparative Psychological Monographs 16*, 1-212.

Chapais, B. (1983). Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. *Behavioral Ecology and Sociobiology 12*, 215-228.

Charles-Dominique, P., & Hladik, C.M. (1971). Le lepilemur du sud de Madagascar: Ecology, alimentation et vie social. *Terre et Vie 25*, 3-66.

Clarke, M.R., Zucker, E.L., & Harrison, R.M. (1991). Fecal estradiol, sexual swelling, and sociosexual behavior in free-ranging female howling monkeys in Costa Rica. *American Journal of Primatology 24*, 93.

Clutton-Brock, T.H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London B 236*, 339-372.

Clutton-Brock, T.H., & Harvey, P.H. (1977). Primate ecology and social organization. *Journal of Zoology (London) 183*, 1-39.

Clutton-Brock, T.H., Guinness, F.E., & Albon, S.D. (1982). *Red deer: Behavior and ecology of the two sexes*. Chicago: Chicago University Press.

Cohen, J.E. (1969). Natural primate troops and a stochastic population model. *The American Naturalist 103*, 455-477.

Collins, D.A., Busse, C.D., & Goodall, J. (1984). Infanticide in two populations of savannah baboons. In G. Hausfater & S.B Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 193-215). Hawthorne, N.Y.: Aldine.

Colquhoun, I.C. (1987). Dominance and "fall fever": The reproductive behavior of male brown lemurs (*Lemur fulvus*). *Canadian Review of Physical Anthropology 6*:10.

Cords, M. (1984). Mating pattern and social structure in redtail monkeys (*Cercopithecus ascanius*). *Zeitschrift Fur Tierpsychologie 64*, 313-329.

Cords, M. (1988). Mating systems of forest quenons: A preliminary review. In A. Gautier-Hion, F. Bourliere, J-P. Gautier, & J. Kingdon (Eds.), *A primate radiation:*

Evolutionary biology of the African guenons (pp. 232-339). Cambridge: Cambridge University Press.

Cords, M, Mitchell, B.J., Tsingalia, H.M., & Rowell, T.E. (1984). Promiscuous mating among blue monkeys in the Kakamega Forest, Kenya. *Ethology 72*, 214-226.

Cranz, C., Ishak, B., Brun, B., & Rumpler, Y. (1986). Study of the morphological and cytological parameters indicating oestrus in *Lemur fulvus mayottensis*. *Zoo Biology* 5, 379-386.

Crews, D., & Moore, M.C. (1986). Evolution of mechanisms controlling mating behavior. *Science 231*, 121-125.

Curie-Cohen, M. Yoshirara, D., Luttrepp, L., Bentorado, K., MacCluer, J., & Stone, W.H. (1983). The effects of dominance on mating behavior and paternity in a captive troop of rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology 5*, 127-138.

Daniels, D. (1983). The evolution of concealed ovulation and self-deception. *Ethology and Sociobiology 4*, 69-87.

Darwin, C. (1859). *The origin of species by means of natural selection*. London: J. Murray.

Darwin, C. (1871). *The decent of man and selection in relation to sex*. London: J. Murray.

Davies, E.M., & Boersma, P.D. (1984). Why lionesses copulate with more than one male. *The American Naturalist 123*, 594-611.

Dawson, G. (1978). Composition and stability of social groups of the tamarin, *Saguinus oedipus oedipus*, in Panama. In D.G. Kleiman (Ed.), *Biology and conservation of the Callitrichidae*, (pp. 23-38). Washington: Smithsonian Institution Press.

Diamond, E.J., Aksel, S., Hazelton, J.M., Barnet, S.D., Williams, L.E., & Abee, C.R. (1985). Serum hormone patterns during abortion in the Bolivian squirrel monkey. *Laboratory Animal Science 35*, 619-623.

Dixson, A.F. (1983). Observations on the evolution and behavioral significance of "sexual skin" in female primates. *Advancement in the Study of Behavior 13*, 63-106.

Dixson, A.F. (1986). Proceptive displays of the female common marmoset (*Callithrix jacchus*): Effects of ovariectomy and oestradiol 17β. *Physiology and Behavior 36*, 971-973.

Dixson, A.F. & Herbert, J. (1977). Gonadal hormones and sexual behavior in groups of adult talapoin monkeys (*Miopithecus talapoin*). *Hormones and Behavior 8*, 141-154.

Dixson, A.F. & Lloyd, S.A.C. (1988). The hormonal and hypothalamic control of primate sexual behavior. *Symposium of the Zoological Society of London 60*, 91-117.

Dunbar, R.I.M. (1984). *Reproductive decisions*. Princeton: Princeton University Press.

Dunbar, R.I.M. & Dunbar, P. (1974). Ecology and population dynamics of *Colobus guereza* in Ethiopia. *Folia Primatologica 21*, 188-208.

Eaton, G.G., Slob, A. & Resko, (1973). Cycles of mating behaviour, oestrogen and progesterone in the thick-tailed bushbaby (*Galago crassicaudatus crassicaudatus*) under laboratory conditions. *Animal Behaviour 21*, 309-315.

Etkin, W. (1963) Social behavioral factors in the emergence of man. *Human Biology 35*, 299-310.

Evans, C.S., & Goy, R.W. (1968). Social behavior and reproductive cycles in captive ring-tailed lemurs (*Lemur catta*). *Journal of Zoology (London) 156*, 181-197.

Ewing, L.L. (1982). Seasonal variation in primate fertility with an emphasis on the male. *American Journal of Primatology (Supplement) 1*, 145-160.

Fedigan, C. (1982). *Primate paradigms: Sex roles and social bonds*. Montreal: Eden Press.

Fedigan, L.M., Fedigan, L., Gouzoules, S., Gouzoules, H. & Koyama, N. (1986). Lifetime reproductive success in female Japanese macaques. *Folia Primatologica 47*, 143-157.

Foerg, R. (1982). Reproductive behavior of *Varecia variegata*. *Folia Primatologica 38*, 108-121.

Freund, M. (1963). Effect of frequency of emission on semen output and an estimate of daily sperm production in man. *Fertility and Sterility 6*, 269-286.

Garber, P.A., Moya, L., & Malaga, C. (1984). A preliminary field study of the mustached tamarin monkey (*Saguinus mystax*) in northeastern Peru: Questions concerned with the evolution of a communal breeding system. *Folia Primatologica 42*, 17-32.

Garber, P.A., Encarnación, F., Moya, L., & Pruetz, J.D. (1993). Demographic and reproductive patterns in mustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *American Journal of Primatology 29*, 235-254.

Gartlan, J.S. (1969). Sexual and maternal behaviour of the vervet monkey, *Cercopithecus aethiops*. *Journal of Reproduction and Fertility (Supplement) 6*, 137-150.

Ginsberg, J.R., & Rubenstein, D.I. (1990). Sperm competition and variation in zebra mating behavior. *Behavioral Ecology and Sociobiology 26*, 427-434.

Glatston, A.R.H. (1979). *Reproduction and behavior of the lesser mouse lemur* (*Microcebus murinus*, Miller 1777) *in captivity*. Unpublished doctoral dissertation, University of London, London.

Goldizen, A.W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-backed tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology 20*, 99-109.

Goldizen, A.W. (1989). Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology 24*, 79-89.

Goldizen, A.W. (1990). A comparative perspective on the evolution of tamarin and marmoset social systems. *International Journal of Primatology 11*, 63-81.

Gomila, D.J. (1975). Fertility differentials and their significance for human evolution. In F.M. Salzano (Ed.), *The role of natural selection in human evolution*. Amsterdam: North-Holland.

Goodall, J. (1977). Infant killing and cannibalism in free-living chimpanzees. *Folia Primatologica 28*, 259-282.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge: Belknap Press.

Gouzoules, H., Gouzoules, S., & Fedigan, L. (1982). Behavioral dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). *Animal Behaviour 30*, 1138-1150.

Hanken, J., & Sherman, P.W. (1981). Multiple paternity in Belding's ground squirrel litters. *Science 212*, 351-352.

Harcourt, A.H. (1979). Social relationships between adult male and female mountain gorillas. *Animal Behaviour 27*, 325.

Harcourt, C.S., & Bearder, S.K. (1989). A comparison of *Galago moholi* in South Africa with *Galago zanzibaricus* in Kenya. *International Journal of Primatology 10*, 35-44.

Haring, D. (1988). Natural history and captive management of Verreauxi's sifaka. *International Zoo Yearbook 27*, 125-134.

Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*): A quantitative analysis. In A.H. Schultz, D. Starck & F.S. Szalay (Eds.). *Contributions to primatology (Vol.7)* (pp. 1-150). Basel: S. Karger.

Heistermann, M., Tari, S., & Hodges, J.K. (1992). Monitoring ovarian function in Callitrichidae by faecal steroid analysis. *Biology of Reproduction 46*, 30.

Hinde, R.A., & Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Animal Behaviour 18*, 169-176.

Hogg, J.T. (1988). Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology 22*, 49-59.
Hrdy, S.B. (1977). *The langurs of Abu*. Cambridge: Harvard University Press.

Hrdy, S.B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology 1*, 13-40.

Hrdy, S.B., & Whitten, P.L. (1987). Patterning of sexual activity. In BB. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies* (pp. 370-384). Chicago: University of Chicago Press.

Hubrecht, R.C. (1984). Field observations on group size and composition of the common marmoset (*Callitrix jacchus jacchus*) at Tapacura, Brazil. *Primates 25*, 13-21.

Iwano, T. (1989). Some observations of two kinds of Lemuridae (*Varecia variegata variegata* and *Lemur fulvus albifrons*) in the reserve of Nosy Mangabe. *Primates 25*, 13-21.

Izard, M.K. (1991). Social influences on the reproductive success and reproductive endocrinology of prosimian primates. In T.E. Ziegler & B.F. Bercovitch (Eds.), *Socioendocrinology of primate reproduction, monographs in primatology (Vol.13)* (pp. 159-186). New York: Wiley Press.

Izard, M.K., & Simons, E.L. (1987). Lactation and interbirth interval in the Senegal galago (*Galago senegalensis moholi*). *Journal of Medical Primatology 16*, 323-332.

Isaac, B. (1980). Female fertility and marital form among the Mende of the rural Upper Bambara chiefdom, Sierra Leone. *Ethology 19*, 297-313.

Johnson, D.F., & Phoenix, C.H. (1976). Hormonal control of female sexual attractiveness, proceptivity, and receptivity in rhesus monkeys. *Journal of Comparative Physiology and Psychology 90*, 473-484.

Jolly, A. (1966). *Lemur behavior: A Madagascar field study*. Chicago: University of Chicago Press.

Jolly, A. (1967). Breeding synchrony in wild *Lemur catta*. In S.A. Altmann (Ed.), *Social communication among primates* (pp. 3-14). Chicago: University of Chicago Press.

Jolly, A. (1984). The puzzle of female feeding priority. In M. Small (Ed.), *Female primates: Studies by women anthropologists* (pp. 197-215). New York: Alan R. Liss.

Jolly, A., Gustafson, H., Oliver, W.L.R., & O'Connor, S.M. (1982). *Propithecus verreauxi* population and ranging at Berenty, Madagascar, 1975 and 1980. *Folia Primatologica 39*, 124-144.

Kappeler, P.M. (1987). Reproduction in the crowned lemur (*Lemur coronatus*) in captivity. *American Journal of Primatology 12*, 497-503.

Kappeler, P.M. (1993). Variation in social structure: The effects of sex and kinship on social interactions in three lemur species. *Ethology 93*, 125-145.

Koyama, N. (1988). Mating behavior in ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates 29*, 163-175. LeBoeuf, B.J.

LeBoeuf, B.J. (1972). Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. *Behaviour 41*, 1-26.

Lindburg, D.G. (1971). The rhesus monkey in northern India: An ecological and behavioral study. In L.A. Rosenblum (Ed.), *Primate behavior (Vol. 2)* (pp. 2-106). New York: Academic Press.

Martin, R.D. (1972). Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London B 264*, 295-353.

Martin, R.D. (1992). Female cycles in relation to paternity in primate societies. In R.D. Martin, A.F. Dixson, & E.J. Wickings (Eds.). *Paternity in primates: Genetic tests and theories* (pp. 238-274). Basel: S. Karger.

Martin, R.D., Dixson, A.F., & Wickings, E.J. (Eds.). (1992). *Paternity in primates: Genetic tests and theories*. Basel: S. Karger.

Mason, W.A. (1966). Social organization of the South American monkey, *Callicebus moloch*: a preliminary report. *Tulane Studies of Zoology 13*, 265-270.

McClintock, M.K. (1978). Estrous synchrony in the rat and its mediation by airborne chemical communication (*Rattus norvegicus*). *Behaviour 67*, 67-96.

McClintock, M.K. (1981). Social control of the ovarian cycle and the function of estrous synchrony. *American Zoologist 21*, 243-256.

McClintock, M.K. (1984). Estrous synchrony: Modulation of ovarian cycle length by female pheromones. *Physiology & Behavior 32*, 701-705.

McClintock, M.K., & Adler, N.T. (1978). Induction of persistent estrus by airborne chemical communication among female rats. *Hormones and Behavior 11*, 414-418.

Melnick, D.J., & Kidd, K.K. (1981). Social group fission and paternal relatedness. *American Journal of Primatology 1*, 333-343.

Melnick, D.J., Pearl, M.C., & Richard, A.F. (1984). Male migration and inbreeding avoidance in wild rhesus monkeys. *American Journal of Primatology 7*, 229-243.

Ménard, N., Scheffrahan, W., Vallet, D., Zidane, C., & Reber, C. (1992). Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics of wild Barbary macaques. In R.D. Martin, A.F. Dixson, & E.J. Wickings (Eds.), *Paternity in primates: Genetic tests and theories* (pp. 155-174). Basel: S. Karger.

Michael, R.P., & Bonsall, R.W. (1979). Hormones and the sexual behavior of rhesus monkeys. In C. Beyer (Ed.), *Endocrine control of sexual behavior* (pp. 279-301). New York: Raven Press.

Mills, M.G.L. (1982). The mating system of the Brown hyaena, *Hyaena brunnea*, in the southern Kalahari. *Behavioral Ecology and Sociobiology 10*, 131-136.

Milton, K. (1985). Mating patterns of woolly spider monkeys, *Brachyteles arachnoides*: Implications for female choice. *Behavioral Ecology and Sociobiology 17*, 53-59.

Moehlman, P.D. (1974). *Behavior and ecology of feral asses.* Unpublished doctoral dissertation, University of Wisconsin, Wisconsin.

Moore, M.M. (1985). Nonverbal courtship patterns in women: Context and consequences. *Ethology and Sociobiology 6*, 237-247.

Moss, C.J. (1983). Oestrous behaviour and female choice in the African elephant. *Behaviour 86*, 167-186.

Morland, H.S. (1991). *Social organization and ecology of black and white ruffed lemurs* (*Varecia variegata variegata*) *in lowland rain forest, Nosy Mangabe, Madagascar.* Unpublished doctoral dissertation, Yale University, New Haven.

Morland, H.S. (1993). Reproductive activity of ruffed lemurs (*Varecia variegata variegata*) in a Madagascar rain forest. *American Journal of Physical Anthropology 11*, 63-81.

Overdorff, D. (1988). Preliminary report on the activity cycle and diet of the redbellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology 16*, 143-153.

Overdorff, D. (1994). Social organization in *Eulemur fulvus rufus* in Madagascar. *American Journal of Physical Anthropology (Supplement) 18*, 156.

Packer, C., & Pusey, A.E. (1983). Adaptations of female lions to infanticide by incoming males. *The American Naturalist 121*, 716-728.

Packer, C., & Pusey, A.E. (1984). Infanticide in carnivores. In G. Hausfater & S.B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 31-42). New York: Aldine Publishing Company.

Parkin, R.F., & Hendrickx, A.G. (1975). The temporal relationship between the periovulatory estrogen peak and the optimal mating period in rhesus and bonnet monkeys. *Biology of Reproduction 13*, 610-616.

Paul, A, Kuester, J., & Arnemann, J. (1992). Maternal rank affects reproductive success of male Barbary macaques (*Macaca sylvanus*): Evidence from DNA fingerprinting. *Behavioral Ecology and Sociobiology 30*, 337-341.

Pereira, M.E. (1991). Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). *Psychology & Behavior 49*, 47-52.

Pereira, M.E., & Weiss, M.L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology 28*, 141-152.

Pereira, M.E., Kaufmann, R., Kappeler, P.M., & Overdorff, D. (1990). Female dominance does not characterize all the Lemuridae. *Folia Primatologica 55*, 96-103.

Perez, L.E., Czekala, N.M., Weisenseel, K.A., & Lasley, B.L. (1988). Excretion of radiolabeled estradiol metabolites in the slow loris (*Nycticebus coucang*). *American Journal of Primatology 16*, 321-330.

Perry, J.M., Izard, M.K., & Fail, P.A. (1992). Observations on reproduction, hormones, copulatory behavior, and neonatal mortality in captive *Lemur mongoz* (mongoose lemur). *Zoo Biology 11*, 81-97.

Perret, M. (1982). Stress-effects in *Microcebus murinus*. *Folia Primatologica 39*, 63-114.

Perret, M. (1985). Influences of social factors on seasonal variation in plasma testosterone levels in *Microcebus murinus*. *Zeitschrift Fur Tierpsychologie 69*, 265-280.

Petter, J.-J. (1962). Recherches sur l'écologie et l'éthologie des lemuriens malgaches. *Mémoire du Muséum National d'Histoire Naturelle de Paris 27*, 1-146.

Petter, J.-J., & Peyrieras, A. (1975). Preliminary notes on the behavior and ecology of *Hapalemur griseus*. In I. Tattersall & R.W. Sussman (Eds.), *Lemur biology* (pp. 281-286). New York: Plenum Press.

Petter, J.-J., Schilling, A., & Pariente, G. (1971). Observations écoethologiques sur deux lemuriens malagaches nocturnes: *Phaner fucifer* et *Microcebus coquereli*. *Terre et Vie 25*, 287-327.

Petter, J.-J., Albignac, R., & Rumpler, Y. (1977). *Faune de Madagascar: Mammiferes lemuriens (Primates, Prosimians)*. Paris, OSTOM/cnrs.

Petter-Rousseaux, A. (1962). Recherches sur la biologie de la reproduction des primates inférieurs. *Mammalia 26*, 1-88.

Petter-Rousseaux, A. (1964). Reproductive physiology and behavior of the Lemuroidea. In J. Buettner-Janusch (Ed.), *Evolutionary and genetic biology of primates (Vol.II)* (pp. 92-132). New York: Academic Press.

Petter-Rousseaux, A., & Picon, R. (1981). Annual variation in the plasma testosterone in *Microcebus murinus*. *Folia Primatologica 36*, 183-190.

Pollock, J.I. (1975). Field observations on *Indri indri*: A preliminary report. In I. Tattersall & R.W. Sussman (Eds.), *Lemur biology* (pp. 287-311). New York: Plenum Press.

Pollock, J.I. (1979). Spatial distributions and ranging behavior in lemurs. In G.A. Doyle & R.D. Martin (Eds.), *The study of prosimian behavior* (pp. 359-409). New York: Academic Press.

Richard, A.F. (1974). Patterns of mating in *Propithecus verreauxi*. In R.D. Martin, G.A Doyle, & A.C. Walker (Eds.), (pp. 49-75). London: Duckworth Press.

Richard, A.F. (1976). Preliminary observations on the birth and development of *Propithecus verreauxi* to the age of six months. *Primates 17*, 357-366.

Richard, A.F. (1977). Feeding behavior of *Propithecus verreauxi*. In T.H. Clutton-Brock (Ed.), *Primate ecology* (pp. 72-96). London: Academic Press.

Richard, A.F. (1978). *Behavioral variation: Case study of a Malagasy lemur*. Lewisburg: Bucknell University Press.

Richard, A.F. (1985). Social boundaries in a Malagasy prosimian, the sifaka (*Propithecus verreauxi*). *International Journal of Primatology 6*, 553-568.

Richard, A.F. (1987). Malagasy prosimians: Female dominance. In B.B. Smuts, D.1. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies* (pp. 25-33). Chicago: University of Chicago Press.

Richard, A.F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution 22*, 395-406.

Richard, A.F., & Heimbuch, R. (1975). An analysis of the social behavior of three groups of *Propithecus verreauxi*. In I. Tattersall & R.W. Sussman (Eds.), *Lemur biology* (pp. 313-333). New York: Plenum Press.

Richard, A.F., & Nicoll, M.E. (1987). Female dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology 12*, 309-314.

Richard, A.F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex ratio, survival, and fertility, 1984-1988. *American Journal of Physical Anthropology 84*, 307-322.

Risler, L., Wasser, S.K., & Sackett, G.P. (1987). Measurement of excreted steroids in *Macaca nemestrina*. *American Journal of Primatology 12*, 91-100.

Robinson, J.A., & Goy, R.W. (1986). Steroid hormones and the ovarian cycle. In W.R. Dukelow & J. Erwin (Eds.), *Comparative primate biology (Vol. 3)* (pp. 63-91). New York: Alan R. Liss.

Rowell, T.E., & Olson, D.K. (1983). Alternate mechanisms of social organization in monkeys. *Behaviour 86*, 31-54.

Rudran, R. 1979. The demography and social mobility of a red howler (*Alouatta seniculus*) population in Venezuela. In J.F. Eisenberg (Ed.), *Vertebrate ecology in the northern Neotropics* (pp. 107-126). Washington, D.C.: Smithsonian Institution Press.

Ruth, B. (1991). Observations of polyandrous mating in wild-living callitrichid *Saguinus mystax*. *American Journal of Physical Anthropologists (Supplement) 12*, 156.

Rylands, A.B. (1982). *The behaviour and ecology of three species of marmosets and tamarins (Primates, Callitrichidae) in Brazil*. Unpublished doctoral dissertation, University of Cambridge, Cambridge.

Rylands, A.B. (1986). Infant-carrying in a wild marmoset group, *Callithrix humeralifer*: Evidence of a polyandrous mating system. In M.T. de Mello (Ed.), *A primatologia no Brazil (Vol. 2)* (pp. 131-144), Brasilia: Sociedade Brasileira de Primatologia.

Saayman, G.S. (1970). The menstrual cycles and sexual behaviour in a troop of free-ranging chacma baboons (*Papio ursinus*). *Folia Primatologica 12*, 81-110.

Saayman, G.S. (1975). The influence of hormonal and ecological factors upon sexual behavior and social organization in Old World primates. In R.H. Tuttle (Ed.), *Socioecology and psychology of primates* (pp. 181-204). The Hague: Mouton.

Sade, D.S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In S. Altmann (Ed.), *Social communication among primates* (pp. 99-114). Chicago: University of Chicago Press.

Sadlier, R.M.F.S. (1969). *The ecology of reproduction in wild and domestic mammals*. London: Methuen & Co Ltd.

Sauther, M.L. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology 84*, 463-477.

Sauther, M., & Sussman, R.W. (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In P.M. Kappeler & J.U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 111-122). New York: Plenum Press.

Schaaf, C.D., & Stuart, M.D. (1983). Reproduction in the mongoose lemur (*Lemur mongoz*) in captivity. *Zoo Biology* 2, 23-38.

Schilling, A., Perret, M., & Predine, J. (1984). Sexual inhibition in a prosimian primate: A pheromone-like effect. *Journal of Endocrinology 102*, 143-151.

Schwartz, D., Mayaux, M.S., & Guihard-Moscato, M.L. (1984). Study of sperm morphologic characteristics in a group of 833 fertile men. *Andrologia 16*, 423-428.

Seuanez, H.N., Carothers, A.D., Martin, D.E., & Short, R.V. (1977). Morphological abnormalities in spermatozoa of man and great apes. *Nature 270*, 57-85.

Seyfarth, R.M. (1976). Social relationships among adult female baboons. *Animal Behaviour 24*, 917-938.

Sackelton, C.H.L., & Whitney, J.O. (1980). Use of Sep-pack cartridges for urinary steroid extraction: evaluation of the method for use prior to gas chromatographic analysis. *Clinica Chimica Acta 107*, 231-243.

Shideler, S.E., & Lasley, B.L. (1982). A comparison of primate ovarian cycles. *American Journal of Primatology (Supplement) 1*, 171-180.

Shideler, S.E., & Lindburg, (1983). Selected aspects of *Lemur variegatus* reproductive biology. *Zoo Biology 1* 127-134.

Shideler, S.E., Lindburg, D.G., & Lasley, B.L. (1983). Estrogen-behavior correlates in the reproductive physiology and behavior of the ruffed lemur (*Lemur variegatus*). *Hormones and Behavior 17*, 249-263.

Small, M.F. (1988). Female primate sexual behavior and conception: Are there really sperm to spare? *Current Anthropology 29*, 81-100.

Small, M.L. (1989). Female choice in nonhuman primates. *Yearbook of Physical Anthropology 32*, 103-127.

Small, M.L. (1990). Promiscuity in Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology 20*, 267-282.

Smuts, B.B. (1985). *Sex and friendship in baboons.* New York: Aldine.

Sterling, E.J. (1993). *Behavioral ecology of the Aye-Aye (Daubentonia madagascariensis) on Nosy Mangabe.* Unpublished doctoral dissertation, Yale University, New Haven.

Strassmann, B.I. (1981). Sexual selection, parental care, and concealed ovulation in humans. *Ethology and Sociobiology 2,* 31-40.

Strier, K.B., & Ziegler, T.E. (1994). Insights into ovarian function in wild Muriqui monkeys (*Brachyteles arachnoides*). *American Journal of Primatology 32,* 31-40.

Struhsaker, T.T. (1977). Infanticide and social organization in the redtail monkey (*Cercopithecus ascanus schmidti*) in the Kibale Forest, Uganda. *Zeitschrift Fur Tierpsychologie 45,* 75-84.

Sugiyama, Y. (1965. On the social change of hanuman langurs (*Presbytis entellus*) in their natural conditions. *Primates 6,* 213-47.

Sussman, R.W., & Garber, P.A. (1987). A new interpretation of the social organization and mating system of Callitrichidae. *International Journal of Primatology 8,* 73-92.

Symons, D. (1979). *The evolution of human sexuality.* New York: Oxford University Press.

Tamura, N., Hayashi, F., & Miyashita, K. (1988). Dominance hierarchy and mating behavior of the Formosan squirrel, *Callosciurus erythraeus thaiwanensis. Journal of Mammalogy 69,* 320-331.

Tattersall, I. (1976). Group structure and activity rhythm in *Lemur mongoz* (Primates, Lemuriformes) on Anjouan and Moheli Islands, Comoro Archipelago. *Anthropological Papers of the American Museum of Natural History 53,* 367-380.

Tattersall, I. (1982). *The primates of Madagascar.* New York: Columbia Press.

Tattersall, I., & Sussman, R.W. (1975). Observations on the ecology and behavior of the mongoose lemur, *Lemur mongoz mongoz* Linnaeus, (Primates, Lemuriformes) at Ampijoroa, Madagascar. *Anthropological Papers of the American Museum of Natural History 52,* 193-216.

Taub, D.M. (1980). Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus*). In D. Lindburg

(Ed.) *The Macaques: Studies in ecology, behavior and evolution* (pp 287-345). New York: Van Norstrand Reinhold.

Taylor, L. (1986). *Kinship, dominance, and social organization in a semi-free ranging group of ringtailed lemurs* (*Lemur catta*). Unpublished doctoral dissertation, Washington University, St. Louis.

Taylor, L.L., & Sussman, R.W. (1985). A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *International Journal of Primatology 6*, 601-614.

Terborgh, J., & Wilson Goldizen, A. (1985). On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology 16*, 293-299.

Tilson, R.L. (1986). Primate mating systems and their consequences for captive management. In K. Benirschke (Ed.), *Primates: The road to self-sustaining populations* (pp. 361-373). New York: Springer-Verlag.

Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136-179). Chicago: Aldine Press.

Tsingalia, H.M., & Rowell, T.E. (1984). The behavior of adult male blue monkeys. *Zeitschrift Fur Tierpsychologie 64*, 253-268.

Tutin, C.E.G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*) *Behavioral Ecology and Sociobiology 6*, 29-38.

Tutin, C.E.G., & McGinnis, P.R. (1981). Chimpanzee reproduction in the wild. In C.E. Graham (Ed.), *Reproductive biology of the great apes* (pp. 239-264). New York: Academic Press.

Van Horn, R.N., & Easton, G.G. (1979). Reproductive physiology and behavior of prosimians. In G.A. Doyle & R.D. Martin (Eds.), *The Study of prosimian biology* (pp. 79-122). New York: Academic Press.

Van Horn, R.N. & Resko, J.A. (1977). The reproductive cycle of the ring-tailed lemur (*Lemur catta*): Sex steroid levels and sexual receptivity under controlled photoperiods. *Endocrinology 101*, 1579-1586.

Van Lawick-Goodall, H., & van Lawick-Goodall, J. (1970). *Innocent killers*. New York: Ballantine Books.

Van Schaik, C.P., & Kappeler, P.M. (1993). Life history, activity period and lemur social systems. In P.M. Kappeler & J.U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 241-260). New York: Plenum Press.

Vick, L.G. (1977). *The role of interindividual relationships in two troops of captive Lemur fulvus.* Unpublished doctoral dissertation, University of North Carolina, Chapel Hill.

Vick, L.G., & Pereira, M.E. (1989). Episodic targeting aggression and the histories of *Lemur* social groups. *Behavioral Ecology and Sociobiology 25*, 3-12.

Wallen, K., & Goy, R.W. (1977). Effects of estradiol benzoate, estrone, and propinates of testosterone or dihydrotestosterone on sexual and related behaviors of ovariectomized rhesus monkeys. *Hormones and Behavior 9*, 228-248.

Wasser, S.K., Risler, L., & Steiner, R.A. (1988). Excreted steroids in primate feces over the menstrual cycle and pregnancy. *Biology of Reproduction 39*, 862-872.

Wasser, S.K., Monfort, S.L. & Wildt, D.E. (1991). Rapid extraction of faecal steroids for measuring reproductive cyclicity and early pregnancy in free-ranging yellow baboons (*Papio cynocephalus cynocephalus*). *Journal of Reproduction and Fertility 92*, 415-423.

Watts, D.P. (1990). Ecology of gorillas and its relation to female transfer in mountain gorillas. *International Journal of Primatology 11*, 21.

White, F.J. (1989). Diet, ranging behavior and social organization of the black and white ruffed lemur, *Varecia variegata variegata*, in southwestern Madagascar. *American Journal of Physical Anthropology 87*, 323.

Wilson, E.O. (1975). *Sociobiology: The new synthesis.* Cambridge: Harvard University Press.

Wirtz, P. (1983). Multiple copulations in the Waterbuck (*Kobus ellipisiprymnus*). *Z. Tierpsychologie 61*, 78-82.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour 75*, 262-300.

Wright, P.C. (1990). Patterns of paternal care in primates. *International Journal of Primatology 11*, 89-102.

Young, A.L., Richard, A.F., & Aiello, L.C. (1990). Female dominance and maternal investment in strepsirhine primates. *The American Naturalist 135*, 473-488.

Zamboni, L., Conaway, C.H., & van Pelt, L. (1974). Seasonal changes in production of semen in free-ranging rhesus monkeys. *Biology of Reproduction 11*, 251-267.

Zamboni, L., Zemjanis, R., & Stefanini, M. (1971). The fine structure of monkey and human spermatozoa. *Anatomical Record 169*, 129-154.

Ziegler, T.E., & Bercovitch, F.B. (Eds.). (1990). *Socioendocrinology of primate reproduction*. New York: Wiley-Liss.