



## Reproductive Behavior of Female *Propithecus verreauxi* at Beza Mahafaly, Madagascar

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*Prosimian and anthropoid females are generally thought to have divergent reproductive patterns, characterized by circumscribed and situation-dependent receptivity. This dichotomy underpins the traditional view that nonreproductive mating serves a social function in anthropoid females, distinguishing them from prosimians which, like most other mammals, mate only when conception is most probable. Circumscribed estrous cycles differ from anthropoid menstrual cycles by the presence of menstruation, and greater flexibility in timing and longer duration of receptivity in the latter. The degree to which sexual behavior is tightly synchronized to periovulatory events in *Propithecus verreauxi* was assessed via the behavioral, hormonal, and social correlates of reproduction in a free-ranging population. I collected data from two social groups before and during the 1990–1991 and 1991–1992 breeding seasons at Beza Mahafaly, Madagascar. I also conducted 644 focal-animal hours and collected 485 fecal samples from five marked females in the Vaovao and Vavy Masiaka social groups. Estrus was behaviorally characterized by 0.5–96-h periods of receptivity when females were motivated and willing to mate, the latter not always coincident with periovulatory events. Females exhibited age- and rank-related asynchronous receptivity, and in some cases, periovulatory synchrony within groups. Sifaka were not pair-bonded. Most females mated with multiple males, temporally ordering partners based on male residence and age. Mating was limited by male mate-guarding and sexual aggression by males, female mate competition, and aversions to mating with certain partners. It was facilitated by surreptitious copulations, positive mate choice, and the availability of non-resident mating partners.*

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**KEY WORDS:** Prosimians; sifaka; receptivity; timing of receptivity; reproductive behavior.

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## INTRODUCTION

Two decades of research have produced major advances in our understanding of reproduction in captive female primates (Robinson and Goy, 1986; Ziegler and Bercovitz, 1990; Martin, 1992), and show that prosimian and anthropoid primates have divergent reproductive patterns, characterized by tightly seasonal and less seasonal periods of receptivity, respectively. Like most other mammals, prosimian females exhibit strictly seasonal estrous cycles, during which copulation is tightly synchronized with periovulatory phases of the cycle when fertilization is most probable. Conversely, nonpregnant anthropoid primates, have longer and more variable patterns of receptivity, mating at times other than when ovulation occurs, though seasonal peaks occur (Martin, 1992). This dichotomous view of receptivity as more or less circumscribed has traditionally been used to argue for a social function for nonreproductive mating (Zuckerman, 1932; Sahllins, 1959), an idea that persists today as a major characteristic distinguishing anthropoid from prosimian primates (Martin, 1992). I investigated the degree to which free-ranging *Propithecus verreauxi* conform to the model of circumscribed receptivity and the social factors mediating female reproductive behavior, including female mate competition.

Verreaux's sifaka are 2.5–3.0 kg diurnal prosimian primates indigenous to the riverine and dry forests of south and southwest Madagascar (Pollock, 1979; Tattersall, 1982). Like most other Malagasy primates sifaka exhibit no sexual dimorphism in body size or canine size (Richard, 1992). *Propithecus verreauxi* at Beza Mahafaly Special Reserve (BMSR) live in matrifocal social groups ranging in size from 2 to 13 individuals, in which female philopatry and social dominance is the norm (Richard, 1987; Richard and Nicoll, 1987; Richard *et al.*, 1991, 1993) though Kubzdela (1997) found evidence of female dispersal. Previous studies of captive (Brockman *et al.*, 1995) and free-ranging sifaka (Brockman, 1994; Brockman and Whitten, 1996; Brockman *et al.*, 1998) suggest that *Propithecus verreauxi* have a minimum 3-month breeding season during which most females experience single 0.5–96 hr estrous periods characterized by 10- to 15-day elevations in fecal estradiol (fE<sub>2</sub>) and the absence of vulval indicators of ovulation (i.e., reddening and swelling; Brockman, 1994). Unlike the vulvas of most prosimian females (Hrdy and Whitten, 1987), those of sifaka are not sealed, thus providing no anatomical impediment to the possibility of situation-dependent receptivity. Birth peaks occur from July to September at BMSR (Richard, 1974), during which females give birth to a single infant after a 163-day gestation period (Petter-Rousseaux, 1962). The interbirth intervals yielding the highest infant survival rates are 24 months, although intervals can be reduced to 12 months following the death of a neonate (Richard *et al.*, 1991).

Although previous studies have yielded important new insights into the reproductive biology and mating behavior of captive (Shideler *et al.*, 1983; Pereira, 1991; Perry *et al.*, 1992; Brockman *et al.*, 1995) and free-ranging lemurs (Richard,

1973; Koyama, 1988; Morland, 1991; Sauther, 1991; Brockman, 1994; Brockman and Whitten, 1996; Brockman *et al.*, 1998a, 1998b), no one has examined the demographic, behavioral, and social contexts of reproduction in females. This paper reports on the reproductive behavior of female sifaka at BMSR, focusing on the behavioral and social characteristics of receptivity, female mating behavior, and the factors mediating multiple partner mating.

## METHODS

### Subjects and Data Collection

I collected data from two habituated social groups inhabiting BMSR during two 3- to 3.5-month periods before and during the 1990–1991 and 1991–1992 breeding seasons. I observed them during 644 focal-animal hours (Altmann, 1974) and collected 485 daily fecal samples from five marked females from the Vaovao (VV) and Vavy Masiaka (VM) social groups, composed respectively of one adult male, one subadult male, and three adult females, and of two adult males, one subadult male, one juvenile male, and two adult females. During the 1990–1991 field season, the modal group composition of the 28–30 social groups in the reserve was three adult males and two adult females. Sifaka at this site were typically day-active *sensu* Rasmussen (1998).

### Behavior and Definitions

I collected data on social behavior of focal females six days per week from dawn to dusk, breaking for a 2 h animal rest period, using 15-minute focal-animal (Altmann, 1994), continuous, and ad libitum sampling methods. Exceptions to this regimen occurred when females were in estrus; observations during this time were recorded daily from sunrise to just after sunset. I collected 300 and 344 focal animal hours on VV and VM females, respectively. Ad libitum sampling occurred throughout the day but focused on observations of rare behaviors such as mating. Due to the low frequency of sifaka social interaction, I used continuous sampling methods to record behavioral bouts via a 63-word ethogram. I recorded behavioral data on a check-sheet and subsequently analyzed them to focus on differences in frequencies of behavior over time, partitioned into eight 10-day periods for VV females and seven 14-day periods for VM females. This partitioning tested 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. Before analysis, I checked data for normality, equal variance, and power. Depending upon the results of the tests, I used parametric or nonparametric tests to examine differences and trends in the data. Statistical tests are significant at  $p = 0.05$ .

Behaviorally estrus is a brief period of proceptivity—appetitive responses—and receptivity—consummatory responses (Beach, 1976)—signaling a female's motivation and willingness to mate. Hormonally estrus is characterized by periovulatory increases in ovarian steroids, which indicate circumscribed receptivity. The uncoupling of proceptivity/receptivity from periovulatory events defined situation-dependent receptivity. I quantified receptivity via male Success Ratio, defined as the percentage of all sexual behavior initiated by the male in which the female allows copulation (Michael *et al.*, 1967). The limitation of this measure of receptivity resides in the fact that it is synonymous with mating and thus, is inadequate for assessing a female's motivation and willingness to mate in the absence of male sexual responsiveness. When mating did not occur, I inferred receptivity from solicitation behaviors such as sexual presents.

Reproductive behavior includes all sexual, scent-marking, and aggressive interactions by males and females, the last of which are components of mate competition (Richard, 1992; Brockman *et al.*, 1998b). Sexual behavior includes female receptivity—sexual presents; mating—and male mount and mount attempts and clasps and clasp attempts. Mating refers to copulations in which intromission and thrusting were unambiguously observed. Mounts are defined by their brevity—3–5 sec—and the absence of intromission and thrusting. Clasps were indicated by males securing brief flank contact. Synchrony refers to the complete or partial temporal overlap of receptivity while asynchrony is the temporal nonoverlap of receptivity. Mate preference is indicated by receptive females initiating copulation with some males while rejecting the mating attempts of others. Scent-marking includes anogenital/urine/fecal marking by both sexes and throat-marking by males. Dominance is based on the consistency of submissive and aggressive signals given by an individual (Hausfater, 1975; Sade, 1967). I assessed social relationships via frequencies of submissive (chatter; fear grimace), affiliative (greet, groom; invite to groom; reciprocal groom; play), and aggressive (lunge; cuff; grab; bite) interactions over time (Brockman, 1994).

### Hormonal Data

A field assistant and I collected fecal samples as per Brockman (1994) and Brockman and Whitten (1996). We collected whole daily fecal samples (1–15 g) from each focal female immediately after she voided, then packaged them in foil, labeled them, flattened them to increase surface area, and dried them in a Coleman oven (55°C [solar heat] to 83°C [propane heat] for 2–3 h) within 4 h of collection. After drying, we wrapped the samples in plastic wrap and individually packaged them with indicator silica gel packets in 4 ml zip-lock bags, and labeled, and bagged them again in 2.7 ml 1 gal zip-lock bags with silica gel. At the end of the field season I shipped the samples to P. L. Whitten's laboratory at Emory University for extraction and radioimmunoassay analysis (Brockman and Whitten, 1996).

## RESULTS

## The Demographic Context of Reproduction

Data on the VV and VM groups obtained since 1984 (Richard *et al.*, 1991, 1993; Richard, unpub. data) show that adult membership has fluctuated over time, particularly in the case of males. Neither group has had a high reproductive rate (Table I). In 1989–1990 VV males 10, 29, and 158 transferred into a neighboring group, and males 240 and Fd transferred into VV. Between 1984 and 1990,  $\geq 6$  infants were born in VV and, except for F80, all of them had disappeared from

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

Sex and social group (birth year)	Date (19__)										
	84	85	86	87	88	89	90 <sup>a</sup>	91 <sup>a</sup>	92 <sup>a</sup>	93	94
<i>Vaovao</i>											
F20 (70)	* _____ B <sup>b</sup> (F80) _____ B(D) <sup>c</sup> _____										
F19 (75)	* _____ B(D) _____ B(D) _____ B(D) _____										
M7 (83)	_____ E <sup>d</sup> _____										
M8 (70)	* _____ E _____										
M10 (75)	* _____ E _____										
M29 (78)	_____ I <sup>e</sup> _____ E _____										
M73 (66)	* _____ D _____										
M158 (84)	_____ I _____ E _____										
M240 (84)	_____ I _____ ? _____										
MFd (87?)	_____ I _____ ? _____										
<i>Vavy Masiaka</i>											
F36 (76)	* _____ B(M228) _____ E _____										
F99 (80)	_____ I _____ ? _____										
107 (80?)	* _____ B(D) _____ B(D) _____										
M25 (67)	* _____ E _____										
M29 (78)	* _____ E _____										
M30 (73)	* _____ E _____										
M128 (78)	_____ I _____ D _____										
M140 (82)	_____ I _____ P <sup>f</sup> _____ ? _____										
M146 (80)	_____ I _____ P _____ ? _____										
M243 (83)	_____ I _____ ? _____										
MUC (87?)	_____ I _____ E _____										

<sup>a</sup>This study.

<sup>b</sup>Birth.

<sup>c</sup>Death.

<sup>d</sup>Emigrated.

<sup>e</sup>Immigrated.

<sup>f</sup>Peripheral.

the group at the onset of data collection in November 1990 (Richard, unpub. data). VM showed a similar turnover among males, and in the two-year period from 1990 to 1992, group size also decreased (Table I), F99 having disappeared in mid-1991. Three infants were born into VM between 1985 and 1990, of which only one survived (M228).

Unlike VV whose adult composition remained stable throughout the study, VM experienced a shift in membership in January 1992, a consequence of intense aggression between resident males 146 and 140. Although the factors precipitating the male-male aggression are unknown, just before M146's attack on M140, resident females were maintaining exclusive proximity to the subordinate M140. During two days of bloody fighting and subsequent attempts to expel the loser from the group's home range, an unmarked male (captured and marked 243 in 1993) joined VM and became the central resident male, forcing male 146 and 140 to the group's periphery. Although the resident females did not resist the new male's immigration, M140 and the subadult male, MUC, did so briefly but unsuccessfully. The subadult male eventually ceased his attacks on M243 and transferred into a neighboring group two weeks later.

### Behavioral Characteristics of Reproduction

#### *Receptivity*

Mating occurred during a 2-month period beginning in January during which most females exhibited single 0.5–96-h estrous periods, coincident with 10- to 15-day periovulatory elevations in fecal  $E_2$  (Brockman and Whitten, 1996). However, eight days after her February copulation, VM F36 mated again, unaccompanied by  $fE_2$  elevations, when she presented and copulated with the newly ostracized M146 on the periphery of the social group. Females varied in the degree to which they were receptive to male mating attempts (Table II), alpha F20 copulating most often ( $n = 14$ ), followed by females 19 (beta,  $n = 12$ ), 36 (alpha,  $n = 3$ ), and 107 (beta,  $n = 3$ ).

Although 92% of the matings occurred during periovulatory increases in  $fE_2$  (Brockman and Whitten, 1996), other sexual interactions had broader temporal distributions. In VV (Fig. 1), male sexual interest and female proceptivity coincided with periovulatory receptivity, but in VM (Fig. 2) they peaked before estrus, associated with the immigration of M243. Female sexual presents and male clasp and clasp attempts increased substantially during this time, principally between F107 and M243, though none culminated in an observed mating.

#### *Timing of Receptivity*

Females exhibited age- and rank-related periods of asynchronous receptivity within groups spanning two weeks. VV's alpha F20 was the first to mate (Fig. 3),

Table II. Female receptivity

	Sexual behavior						Total	MSR <sup>a</sup>
	Clasp attempt	Clasp	Mount attempt	Mount	Mt/Introm.	Mate		
VV20	6	2	0	16	1	14	39	.36
VV19	9	6	12	12	0	12	51	.24
VV80	2	11	13	3	0	0	29	.00
VM36	7	7	0	0	0	3	17	.18
VM107	25	5	4	4	0	3	41	.07

<sup>a</sup>Denotes male Success Ratio: the % of all sexual attempts that the female allowed to result in full copulation (Michael *et al.*, 1967).

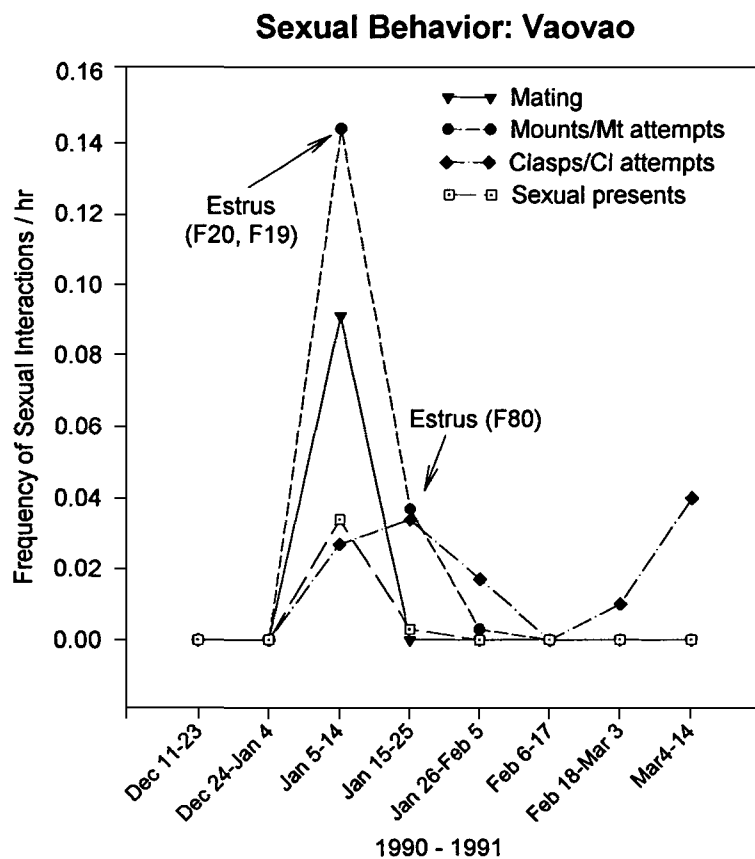


Fig. 1. Temporal variation in the frequency of sexual behavior per hour in the VV group.

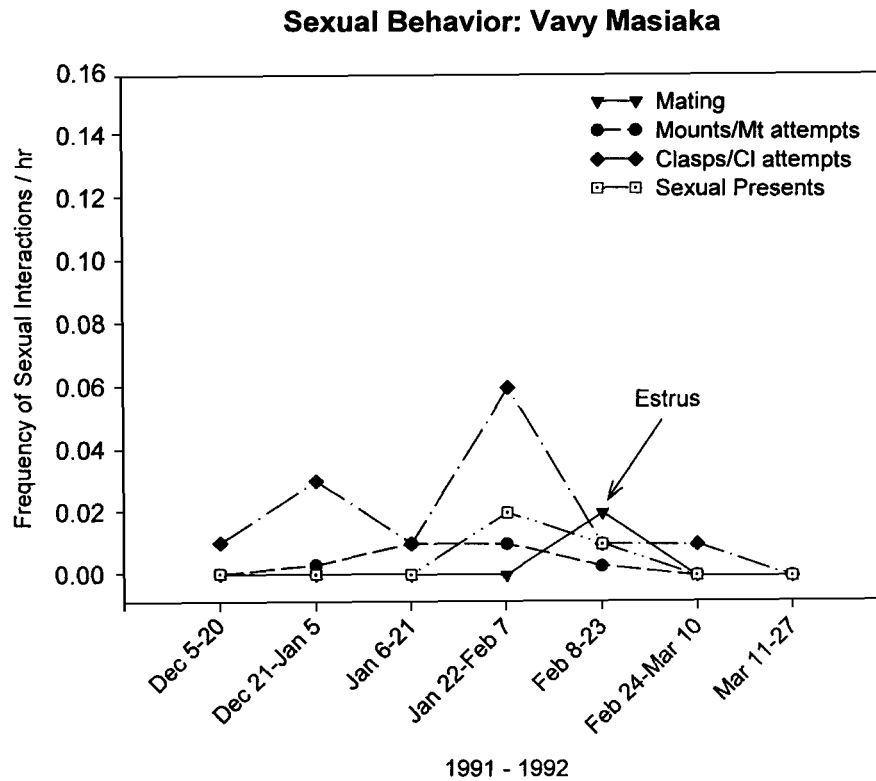


Fig. 2. Temporal variation in the frequency of sexual behavior per hour in the VM group.

followed by beta and gamma females 19 and 80 (F80: mounts only). In VM (Fig. 4), alpha F36 mated first, followed two weeks later by beta F107. Hormonal data (Brockman and Whitten, 1996) showed that VV, but not VM, females had synchronous periovulatory estrous periods, associated with intense female-female competition.

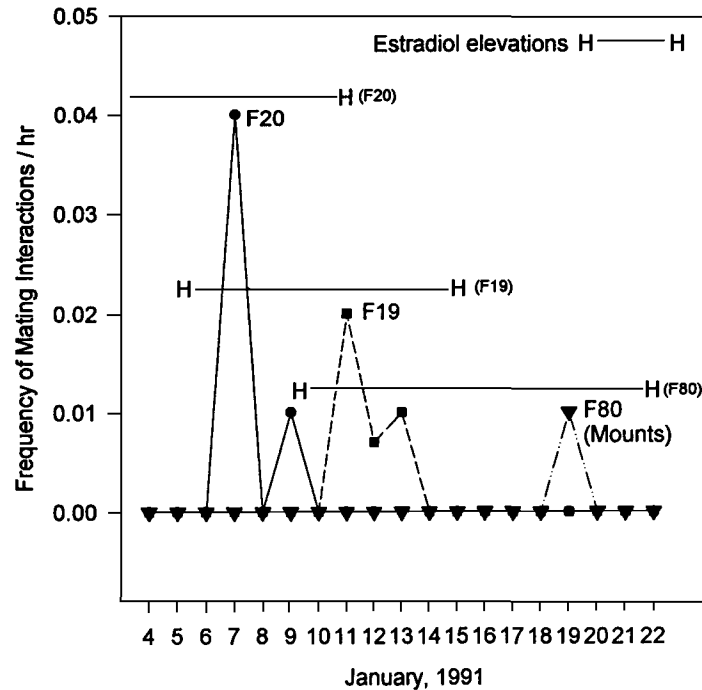
## The Social Context of Reproduction

### *Affiliative Relationships*

VV females were significantly more affiliative than VM females (Mann Whitney Rank Sum Test:  $T = 28$ ,  $p = 0.0003$ ), in large measure due to the close relationship between F20 and her daughter F80. Intergroup differences are reflected in both rates and diversity of behavior: VV females engaged in a wider range of behaviors, including reciprocal grooming, invitations to play, and playing; I



### Estrous Timing: Vaovao



**Fig. 3.** Estrous timing in VV females indicated by the frequency of mating interactions per hour with corresponding duration of fE<sub>2</sub> elevations.

observed no play in VM. Nevertheless, friendly interactions among females increased in both social groups during the mating period. In VV, females were markedly more friendly with other females than they were with males ( $T = 100$ ,  $p = 0.0002$ ), as shown by the 70% affiliative interactions that occurred between females, principally before and during the mating period (Fig. 5). In contrast, there is no difference in rates of affiliation intra- or intersexually in the VM social group. Fifty-four percent of all friendly behaviors occurred between females, primarily during the premating and mating periods (Fig. 6), though male-female interactions rose after group reorganization, associated with increased grooming of females by the newly immigrated M243.

### Scent-Marking Behavior

In the context of mating competition, I predicted that increases in mating-related scent-marking behavior would signal fertility in females, associated with

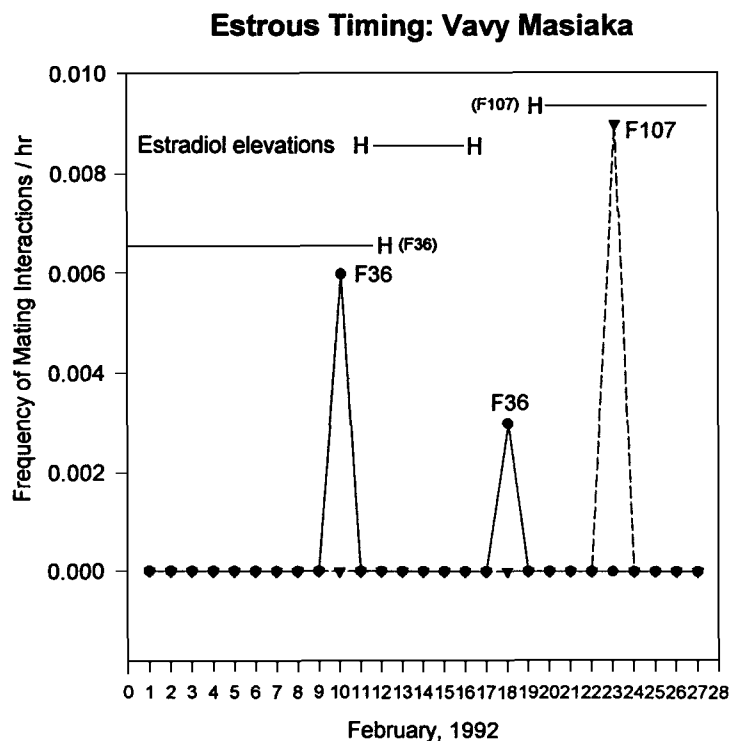


Fig. 4. Estrous timing in VM females indicated by the frequency of mating interactions per hour with corresponding duration of  $fE_2$  elevations.

increased male-male aggressive competition. For the combined groups, mean frequencies of scent marking are significantly higher in females than in males throughout the study period ( $T = 90.0$ ,  $p = 0.02$ , Fig. 7). The temporal patterning of male scent-marking behavior strongly correlates with that of females ( $r_s = 0.90$ ,  $p = 0.0001$ ), increased frequencies being strongly biased toward dominant resident males which were observed depositing 99 and 97% of the scent marks in VV and VM, respectively. With the exception of VV's M240, sifaka scent-marked less often during the mating period than during periods preceding and following estrus (Fig. 7). However, M240 increased scent-marking during female 20 and 19's estrous periods. Thus, although females appeared not to be actively signaling fertility, males may, nevertheless, have received sufficient olfactory cues regarding periovulatory events to stimulate male-male competition for certain preferred females. VM females scent-marked at higher average rates than VV females did ( $t = 84$ ,  $p = 0.003$ ), but dominant males showed no intergroup difference in this behavior ( $T = 55.5$ ,  $p = 0.96$ ), nor did females within groups (Kruskal Wallis One Way ANOVA-VV:  $H = 0.106$ ,  $p = 0.95$ ; VM:  $t = 56$ ,  $p = 0.71$ ).

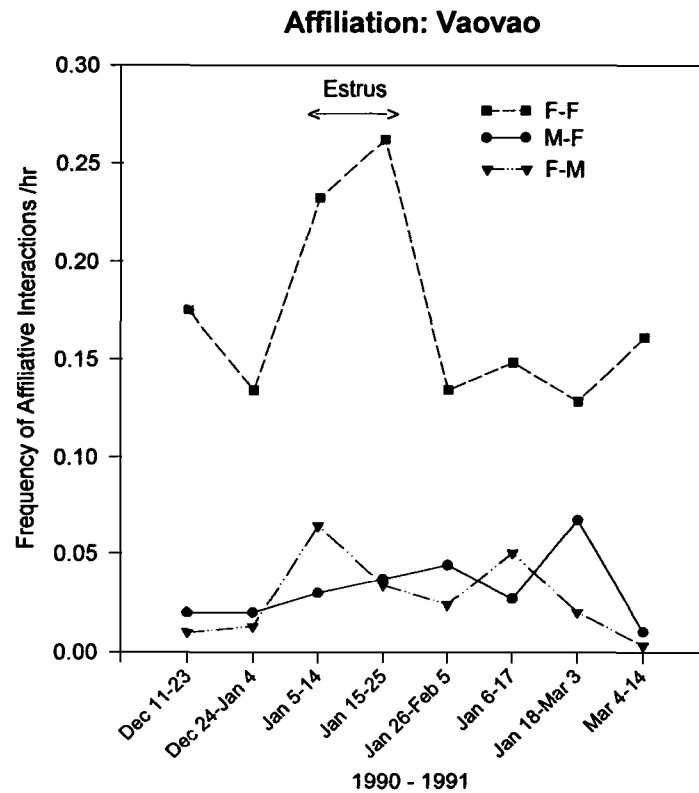
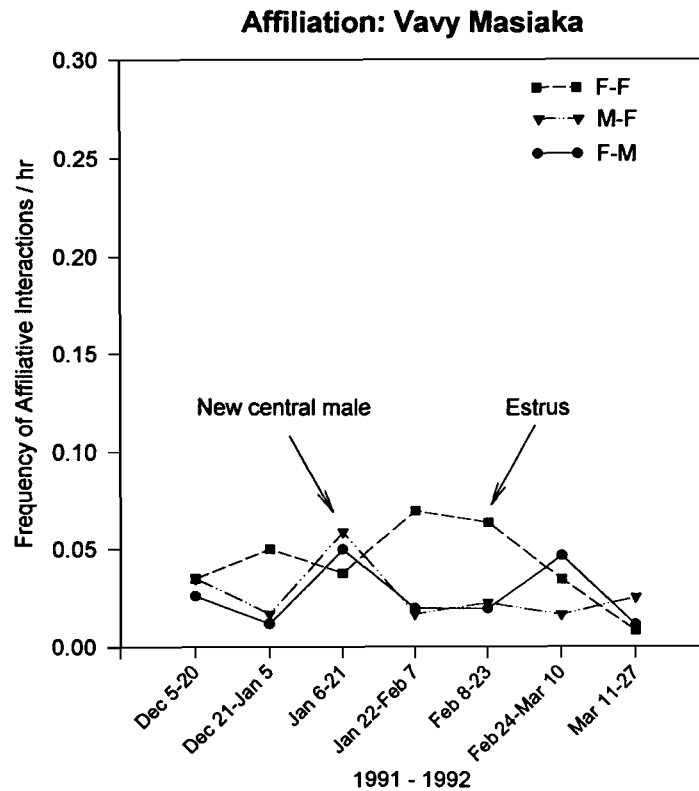


Fig. 5. Temporal variation in frequency of VV affiliative interactions between females (F-F), from males to females (M-F), and from females to males (F-M).

Mean rates of male-female scent marking varied between groups. In contrast to the VM females which scent-marked significantly more often than resident males ( $T = 77$ ,  $p = 0.0006$ ), VV females marked slightly less often than males ( $T = 55.5$ ,  $p = 0.10$ ). Similar intergroup contrasts are apparent in male scent marking over the scent marks of resident females. Dominant VM males scent-marked females at equivalent rates ( $T = 56$ ,  $p = 0.71$ ), whereas VV's dominant M240 showed preferences for certain females, scent-marking females 20 and 19 significantly more often than F80 (Student-Newman Keul's Method: F20 vs. F80:  $p = 3$ ,  $q = 4.68$ ; F19 vs. F80:  $p = 2$ ,  $q = 4.64$ ).

#### *Aggression*

Intergroup comparisons revealed that although VV and VM group members showed no difference in overall rates of aggression ( $T = 60$ ,  $p = 0.69$ ), VV



**Fig. 6.** Temporal variation in frequency of VM affiliative interactions between females (F-F), from males to females (M-F), and from females to males (F-M).

females were markedly more antagonistic toward neighboring groups; mean frequencies of intergroup aggression are significantly higher than those of VM females ( $T = 87$ ,  $p = 0.05$ ). Between-group rates of aggression also varied by sex: VV females exhibited higher rates of female-female aggression than those of VM females ( $T = 28$ ,  $p = 0.0003$ ), and VM females targeted (i.e. marked or selected) group males for aggression substantially more often than VV females did ( $T = 76$ ,  $p = 0.0003$ ). However, within groups, females were significantly more aggressive toward males than they were toward females (VM:  $T = 77$ ,  $p = 0.0006$ ; VV:  $T = 43.5$ ,  $p = 0.007$ , Figs. 8 and 9). Ninety-six percent of all aggression in VM was directed at males by females, which escalated after MUC's departure from the group and M243's successful immigration. Females targeted M243 in particular. He received over 66% of female aggression, principally by F107 when she relentlessly attacked him during her mating period. In VV, intensity of aggression was somewhat less: females targeted resident males and other females in 60 and 33% of the aggressive encounters; the remaining 7% was males targeting females.

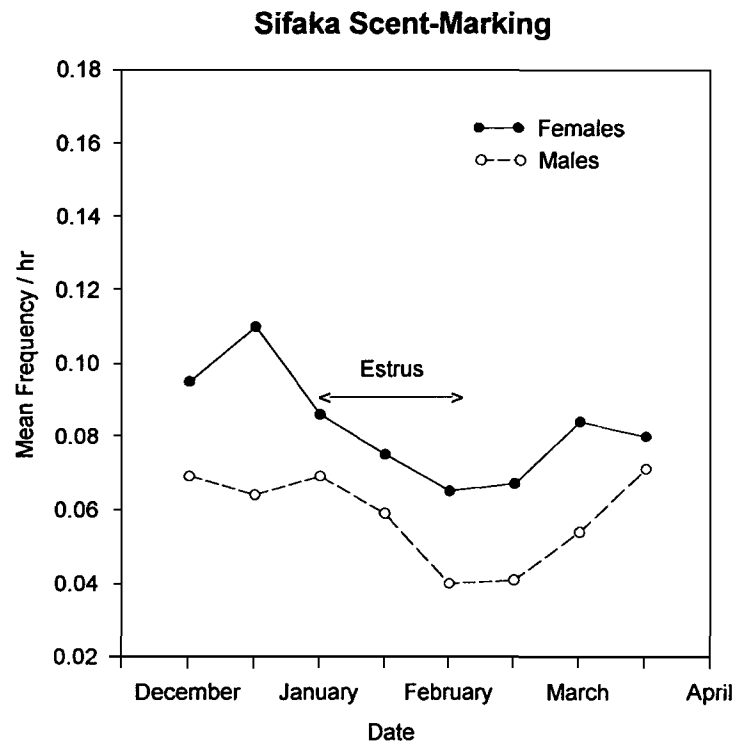
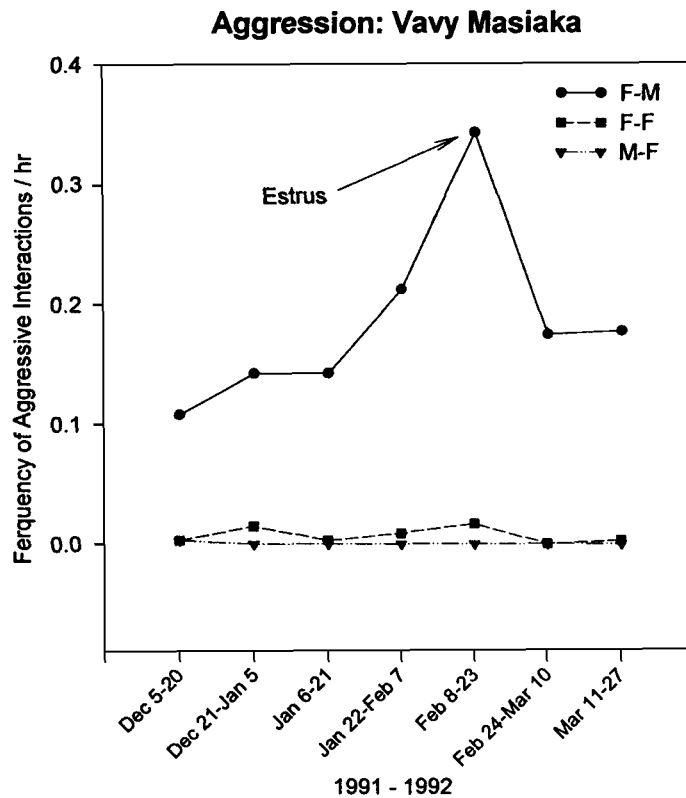


Fig. 7. Temporal variation in frequency of scent-marking behavior per hour in male and female *Propithecus verreauxi*.

Aggressive mating competition—copulatory harassment—occurred only in VV, whose females exhibited periovulatory synchrony but no hormonal evidence of ovulatory suppression (Brockman and Whitten, 1996). Beta F19 attacked alpha F20 whenever she mated with resident, but not nonresident, males. Female 19 and alpha M240 continually harassed F20's copulations with the group's beta MFd, severely limiting his ability to achieve and maintain intromission. This harassment represents a classic example of behavioral reproductive suppression, the behavioral constraints one or more individuals successfully impose on another individual's reproductive efforts. Males rarely initiated conflicts with females, the single exception being VV's M240, which targeted gamma F80 for aggression during her mating period (Fig. 9). Fifty-five percent of male-female aggression occurred during the two-week mating period: females 80 and 19 received 74 and 26% of M240's aggression, respectively. In contrast to F19 which was targeted for aggression in the weeks preceding and following estrus, F80 received 86% of M240's aggression during estrus, a rate that clearly indicates male sexual aggression. The reasons for this are unclear, but F80 was the only female in the group to resist steadfastly M240's mating overtures. Moreover, while he appeared to defer



**Fig. 8.** Temporal variation in frequency of VM aggressive interactions per hour between females (F-F), from males to females (M-F), and from females to males (F-M).

to her reluctance to mate, he nevertheless consistently and aggressively supplanted F80 from preferred feeding sites and harassed her attempted copulations with Fd.

#### *Mating Behavior*

Copulations occurred on arboreal substrates, typically in trees, young saplings, and bushes. Males clasped females with their forelimbs, with one or both feet gripping her ankles or legs. A typical mating sequence, observed at distances of 2–3 m, was composed of 2 to 10 shallow intromissions having rapid and intermittent thrusts followed by a single prolonged intromission with 36 to 156 slow rhythmic thrusts culminating in ejaculation, suggesting that sifaka may be multiple-mount ejaculators. The average mating frequency for the five females was 0.07 copulations per hour, and ranged from 0.15/h (VV F20) to 0.02/h (VM F107). Focal

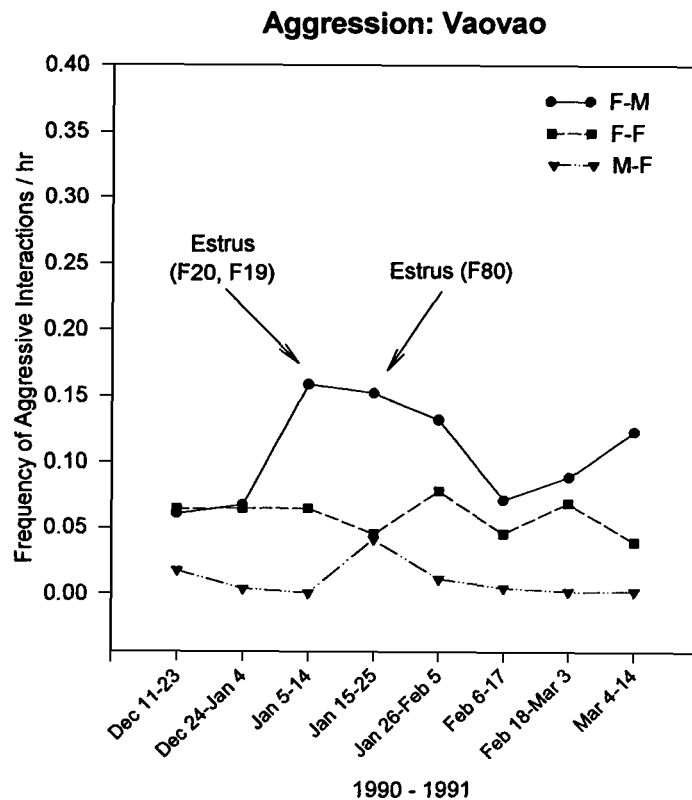


Fig. 9. Temporal variation in frequency of VV aggressive interactions per hour between females (F-F), from males to females (M-F), and from females to males (F-M).

females mated with one or more males during the breeding season, selecting mates from an array of resident, peripheral, and nonresident males. Two females mated with only one male and three females mated with two or three males (Table III). Mating preference was residence- and age-based. Females mated with resident before nonresident males and, in most cases, preferred older dominant males as mates before younger subordinate males.

Female mate preference was constrained by male mate guarding and mating aggression. Males attempted to prevent females from mating with multiple partners by pre- and postcopulatory mate guarding and copulatory harassment. Dominant resident males guarded estrous females and harassed matings involving younger resident and non-resident males. Three females circumvented these male tactics by mating surreptitiously on the periphery of the group and by copulating with non-resident males during intergroup conflicts, or when males made periodic "visits"

Table III. Mating in the Vaovao (VV) and Vavy Masiaka (VM) groups

	Breeding Season									
	1990–1991					1991–1992				
	Males	Date	<i>N</i> <sup>a</sup>	<i>N</i> <sup>b</sup>	Outcome	Males	Date	<i>N</i> <sup>a</sup>	<i>N</i> <sup>b</sup>	Outcome
<i>Vaovao</i>										
F20	VV240	1/7	11	3	Conception	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) <sup>c</sup>	1/19	3		Conception	VM243	1/16	3	0	Infant
<i>Vavy Masiaka</i>										
F36						VM140	2/10	1	1	Infant
						VM146	2/10	1	1	
						VM146	2/18	1	0	
F107						VM243	2/23	3	1	0

*N*<sup>a</sup>: Number of copulations.

*N*<sup>b</sup>: Number of ejaculations.

Mounts<sup>c</sup>: Although intromission was not unambiguously observed, hormonal data indicated F80 conceived at this time (Brockman and Whitten, 1996).

from neighboring groups. These results show that social dominance expressed via female mating preferences may be compromised by the coercive mating strategies of males, but that females can, nevertheless, develop effective counterstrategies which may include elements of opportunism and deception.

Estrous females resisted mating with certain coercive males. In the two cases of monoandrous mating, females rejected the mating attempts of dominant resident males by persistently cuffing and biting them, but with varying degrees of success. In VM, F107's reluctance to mate with the persistent M243 may have been overcome by a lordosis reflex not unlike that seen in other mammals (McClintock, 1981; McClintock and Adler, 1978), including *Varecia variegata* (Shideler *et al.*, 1983). This female fiercely resisted the male's approaches and aggressive clasp attempts in the hours before mating but then immediately ceased all resistance after he was able to secure and maintain flank contact with her via a mount. Female 107, which was slightly wounded, subsequently presented and mated with this male three times. Hormonal evidence (Brockman and Whitten, 1996) showed, however, that this cycle was anovulatory, suggesting that while sexual aggression may have benefited the male by increasing his mating opportunities, but not his reproductive success, it was costly for the female, resulting in reduced mate choice, wounding, and perhaps, disruption of ovulation.

Individual males responded differently to female resistance to mating. In contrast to the case above, VV's dominant M240 acquiesced to F80's reluctance to



mate by ceasing all mating attempts, though his rates of aggression increased. Why he targeted her for aggression is unclear, but in this case, male sexual aggression may have been a male counterstrategy to female mate choice, that is to say the rejected male may have been reacting aggressively to female preferences for mating with other resident males. Having rejected M240's mating attempts, F80 subsequently presented to the subordinate MFd, with whom she apparently conceived (Brockman and Whitten, 1996) in spite of the dominant male's persistent harassment of the pair. These results suggest that differing male mating styles and female mating preferences interact in complex ways to affect mating success and, perhaps, variance in individual reproductive success for both males and females.

## DISCUSSION

### Receptivity

The results of this study support previous findings on reproductive behavior in free-ranging Lemuriformes (Jolly, 1966; Richard, 1974, 1992; Koyama, 1988; Sauther, 1991) and show that female sifaka have a tightly delimited breeding season, spanning the austral summer months of January-March, during which they experience up to two estrous periods when they are sexually motivated and willing to mate. However, in marked contrast to other lemuroids, female sifaka may, on occasion, exhibit nonperiovulatory receptivity, qualitatively indistinguishable from that observed in anthropoid primates. In VM, proceptivity and receptivity were disassociated from periovulatory events, occurring when  $fE_2$  levels were diminished (Brockman and Whitten, 1996). In one case, F36 mated surreptitiously with a peripheral male, presenting to and mating with M146 when hormonal evidence showed (Brockman and Whitten, 1996) that ovulation was unlikely. Likewise, F107's sexual-present interactions increased markedly just after M243 immigrated into the social group, coincident with low  $fE_2$  concentrations (Brockman and Whitten, 1996), indicating that she was motivated and willing to mate when she had no ability to conceive. Similar situation-dependent increases in female sexual motivation and receptivity have been reported for cercopithecine and colobine primates subsequent to male immigration by Cords *et al.* (1984) and Hrdy (1977, 1979) respectively, in the colobine case associated with male infanticide. Infanticide by males also occurs in *Propithecus diadema edwardsi* (Ranomafana: Wright, 1992; Erhart and Overdorff, 1998) and *P. verreauxi* (BMSR: Rigobert, pers. comm.) subsequent to male immigration. These two cases are obviously insufficient to assess the degree to which receptivity is uncoupled from periovulatory events in other prosimians. However, they clearly demonstrate that some degree of socially mediated flexibility in receptivity occurs in *Propithecus*, associated with female preferences for mating with certain males and, perhaps, attempts to socially mediate the threat of male infanticide.

### Timing of Receptivity

*Propithecus* resemble *Lemur catta* (Pereira, 1991; Sauther, 1991) in exhibiting rank- and age-related asynchronous receptivity within groups. Pereira (1991) and Sauther (1991) argued that within-group estrous asynchrony enhances female mate choice through the temporal reduction of competition between females for preferred mates. However, my findings suggest that while in principal female mate choice may be enhanced by rank-related asynchronous receptivity within groups, in practice, male counterstrategies limit female mating preferences. Males effectively mate guard and harass copulating pairs regardless of the degree of receptivity overlap or how socially subordinate they are to females. The fact that female-female competition coincided exclusively with synchronous periovulatory receptivity suggests that assessing the nature, timing, and various functions of receptivity (for them as well as for us) within lemur social groups is complex, requiring hormonal as well as behavioral and demographic information. In this regard, previous studies of free-ranging sifaka (Brockman and Whitten, 1996) show that females living in multifemale groups containing one or two adult males exhibit periovulatory elevations in  $fE_2$  which are three times longer than those living in captive groups containing a single adult pair (Brockman *et al.*, 1995). These results suggest that as with other social mammals (McClintock, 1981), female group size may regulate female reproductive events in sifaka and, in the presence of synchronous ovulation, the intensity of intrasexual competition among subordinate females.

### Social Context of Reproductive Behavior

Receptivity coincided with marked increases in female-female affiliation, reduced scent-marking, and female mating competition (VV) and aggression toward males. Patterns of affiliation among female sifaka differed from those in captive lemurs (Kappeler, 1993) but were consistent with observations of free-ranging *Eulemur fulvus rufus* (Overdorff, 1994) and *Varecia variegata* (Morland, 1991), in which females exhibit higher levels of tactile affiliative behavior toward group females than toward group males. The social significance of these activities is unclear, but they may indicate the quality of female relationships or be mechanisms for enhancing female social bonds or both within groups (Moreland, 1991).

Female-female competition over breeding males increased during the mating period, associated with copulatory harassment of alpha females by unrelated subordinates in the VV group. Although female mate competition over males is widespread in anthropoid primates (Smuts, 1987), this is the first time it has been reported in free-ranging prosimians. The simultaneous mating-related increases in female-female affiliation and aggression among VV females is paradoxical but may result from the coincidental effects of periovulatory synchrony (Brockman and Whitten, 1996) and conflicting social and reproductive imperatives, involving

reassertion of affiliative bonds and competition for preferred mates among unrelated females. Female 19 exhibited remarkable tenacity in her attempts to aggressively disrupt F20's mating opportunities with resident males. While I never saw F20's subordinate daughter, F80, interfere with a dominant female's copulations, beta-ranked F19, joined by M240, was relentless in her attacks on alpha F20 during her copulations with MFd. Female 19's natal group is unknown, but proximity maintenance data (Brockman, 1994) showed that F19 had the highest preference quotient for MFd of all the females of the group, followed by F80. These results suggest that, for unrelated subordinate females, the fitness benefits gained from competing for a particularly desirable male may outweigh the costs of potential wounding, especially in the presence of aggressive coalitions.

The sifaka in this study were not pair-bonded. Social and sexual relationships are characterized by female aggression toward males, mate choice, and polygamous mating patterns. The heightened periovulatory levels of within-group female-male aggression in sifaka resemble those reported for captive (Foerg, 1982; Shideler *et al.*, 1983) and free-ranging *Varecia variegata* (Morland, 1991). Foerg (1982) and Morland (1991) suggest that female aggression is a form of female mate choice. Female *Varecia variegata* approach and attack only males with which they prefer to mate, the idea perhaps being that females are testing their mating resolve. Sifaka females, however, were most aggressive toward males that approached them most frequently during the mating period, a result that was biased by particularly aggressive females exhibiting negative mating preferences—VV's F19/M240—and the actions of sexually coercive males: VM's M243. These data indicate that both sexes evaluate mates and express positive and negative mating preferences: male preferences for certain females through increased approaches and female rejection of certain coercive males through intensity of aggression. Alternatively, the increase of female aggression directed at males during the mating period may be related to both the interval between mounts (without intromission) and to male attempts to elevate the interaction to mating and thus may indicate female arousal. Partial support for this idea comes from the fact that F107 mated cooperatively after aggressively resisting mount attempts.

Male lemurs rarely direct aggression toward females (Richard 1974, 1992; Vick and Pereira, 1989; Sauther, 1991; Morland, 1991; Kappeler, 1993), undoubtedly because adult female lemurs are socially dominant to males (Young *et al.*, 1991; but see Pereira *et al.*, 1990). With the exception of VV's F80, females sifaka were dominant to males based on consistent patterns of male submission to females (Brockman, 1994). However, a marked increase in mating-related aggression directed at females by males occurred in VV, associated with F80's resistance to mating with the group's dominant M240. Similar levels of male aggression toward females occur in free-ranging *Eulemur fulvus rufus*, but in the absence of female social dominance over males (Overdorff, 1994). It could be that male targeting females for aggression indicates relatedness in the species. Aggression increased in proportion to female resistance to mating with close consanguineous kin, implying

that there may be asymmetry in male and female recognition of consanguinity or its importance or both. Although paternity of sifaka is not yet known at this site, captive and free-ranging female ring-tailed lemurs often repel the mating attempts of related natal males (Taylor, 1986; Pereira and Weiss, 1991; Sauther, 1991).

It is unclear to what degree male aggression represents sexual coercion in sifaka (*sensu* Smuts and Smuts, 1993), who define male sexual coercion as male aggression against females that functions to enhance male mating success at some cost to the female. They emphasize that quantifying female costs is extremely difficult, involving evidence of increased energy expenditure, reduced female feeding efficiency or mate choice or both, disruption of ovulation, and wounding (Smuts and Smuts, 1993). In the sifaka case above, it is unlikely that male aggression represented sexual coercion, as it neither increased M240's mating opportunities with F80 (he acquiesced to her reluctance to mate) nor did it appear costly to her in any quantitatively measurable way. Indeed, F80 was able to circumvent M240's sexual aggression, apparently conceiving with her preferred partner, MFd, in spite of M240's harassment (Brockman and Whitten, 1996). This demonstrates that females can develop effective counterstrategies to the aggressive mating tactics of males.

Evidence in support of the hypothesis that male aggression is sexual coercion appears stronger in the case of VM's M243 and F107. Not only did M243's relentless sexual aggression—clasp/mount attempts and biting—against F107 result in a successful copulation (but not fertilization), but also F107's intense and exhausting counterattacks resulted in her being wounded. Although previous hormonal data showed that F107 was anovulatory (Brockman and Whitten, 1996), we have no evidence that anovulation was aggression-related or that M243 was responding to anything other than olfactory cues of follicular phase increases in fE<sub>2</sub>. In the absence of external signs of ovulation and any information regarding a female's fertilization potential, males are better off hedging their reproductive bets by employing every tactic available, including sexual aggression, to enhance their mating opportunities.

### Mating Behavior

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

In contrast to polygamous cercopithecoid primates that mate often during estrus (Hrdy and Whitten, 1987), sifaka copulate infrequently during their 0.5–96 h estrous periods. The female sifaka averaged 0.07 copulations per hour, reflecting the effects of numbers of mating partners, female mate choice, and intrasexual competition on interindividual variation in female mating patterns. In most instances, female sifaka mated with  $\geq 2$  males (Table III), temporally ordering partners based on male residence, age and dominance rank. Asynchronous receptivity *per se* did not affect multiple mating by females. Instead, mating frequency was limited by male mate guarding, copulatory harassment by males and females during estrus, and the reluctance of females to mate with certain males, while it was enhanced by clandestine copulations and the availability of nonresident males. Copulations with nonresident males were associated with a demographic shift in the neighboring VM group during the 1991–1992 breeding season when two VV females mated with three VM males. Alpha F20 mated with the visiting VM peripheral males 146 and 140, while her daughter (F80) mated with the newly immigrated M243. Two of these copulations occurred during intergroup conflicts, showing that females as well as males enhance their mating opportunities through increased contact with neighboring groups during the breeding season.

Finally, although most males attempted to mate with all of their group's estrous females, M243 mated with only one of VM's two resident females (F107) and directed his attentions exclusively to her. Partner preferences may not be mutual and can result in intense intersexual aggression during the mating period, as was the case with this pair. The fact that this sexually coercive male overcame the female's resistance to mating suggests that, in tightly seasonal species with temporally constrained conception periods, some females may have their mating preferences swamped by those of males, with female rejection of certain males being outweighed by the reproductive imperatives of particular males. However, as noted above, F107 showed hormonal evidence of anovulation (Brockman and Whitten, 1996), suggesting that males may incur substantial fitness costs by being too selective in the choice of mates, by making poor choices, or by being too aggressive in the pursuit of copulations so that ovulation is disrupted (Dunbar and Dunbar, 1977), though the latter appeared not to be the case in this instance. Alternatively, facultative anovulation may be a counterstrategy females employ against sexually aggressive males, with the benefits of conceiving during the early austral summer period of food abundance overridden by the costs of mating with an unknown and, perhaps, genetically inferior male.

## CONCLUSIONS

My study demonstrates that (1) sifaka have 0.5 to 96 hr periods of receptivity when they are motivated and willing to mate; (2) receptivity does not always coincide with periovulatory events and is associated with male immigration and female preferences for certain peripheral and nonresident males; (3) sifaka exhibit

age- and rank-related asynchronous receptivity, and in some cases, periovulatory synchrony within groups; (4) sifaka are not pair-bonded; (5) the mating period is characterized by intensified affiliative relationships among females, female-female competition in the presence of periovulatory synchrony, and female aggression toward males; (6) most females mate with multiple males, temporally ordering partners by male residence and age; (7) mating is limited by male mate guarding and sexual aggression by males and females and aversions to mating with certain partners, while it is enhanced by clandestine copulations, positive mate choice, and the availability of nonresident mating partners.

These results indicate that contrary to previous studies of reproduction in captive and free-ranging prosimians (Izard, 1993), the sexual behavior of female *Propithecus verreauxi* is complex and potentially as flexible as that observed in anthropoid primates, being similarly influenced by, among other factors, female-female mate competition, the presence of newly immigrated and potentially infanticidal males, and the availability of extragroup males. The degree to which sifaka may represent the exception to the rule of circumscribed receptivity in prosimians awaits future comparative studies of the socioendocrinology of reproduction in free-ranging populations.

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