

RESEARCH ARTICLE

Mating System of an Exceptional Primate, the Olive Colobus (*Procolobus verus*)

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In the olive colobus (*Procolobus verus*), many groups have multiple males and the males have large testes. This indicates that even though this species lives in small groups, single males do not monopolize the groups. We investigated the strategies employed by males to secure their mating success, and sought to determine whether the lack of male monopolization was a result of female mating strategies, as indicated by the exaggerated sexual swellings of the females. Four study groups were monitored for demographic changes, and group composition was determined in six additional groups in Tai National Park, Ivory Coast, between 1994 and 1999. Social behavior was recorded by scan and focal sampling in the study groups. The almost permanent association of olive colobus with Diana monkeys (*Cercopithecus diana*) in effect provided males a resource at which they could expect females to visit and sometimes even permanently join them, as well as protection from predators. As alternative strategies for obtaining females, one male took over the group of another male and one male immigrated into a bisexual group. Within bi-male groups, dominant males mated most frequently and males defended their groups during intergroup interactions. Lone females that visited groups or solitary males had a swelling more often than expected, and generally mated with the males they visited. Females had long receptive periods, several consecutive receptive cycles, and some overlap in receptive periods within groups. Females mated with extragroup males, and during infertile periods. We concluded that the males used the Diana monkeys for safety reasons and to obtain mating

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partners, and that female reproductive biology and behavior prevented the monopolization of groups of females by single males. Our data were inconclusive as regards the benefits to females of avoiding monopolization by males. *Am. J. Primatol.* 62:261–273, 2004. © 2004 Wiley-Liss, Inc.

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INTRODUCTION

One of the most intriguing mating systems in the primate order is that of the olive colobus (*Procolobus verus*) [Oates, 1994]. In contrast to most other colobines living in similarly sized groups, half of olive colobus groups have multiple breeding males and the males have large testes [Korstjens & Schippers, 2003; Oates, 1994]. These factors are suggestive of limited male monopolization of groups of females, and male investment in sperm competition. The ability of males to monopolize groups of females depends strongly on female reproductive biology and mating behavior, in combination with the distribution of females over the area [e.g., Mitani et al., 1996]. Previous research has shown that females develop large sexual swellings, and that olive colobus mingle with Diana monkeys (*Cercopithecus diana*) on an almost permanent basis [Korstjens & Schippers, 2003; Oates & Whitesides, 1990]. Prompted by these two striking characteristics of the species, we investigated the strategies employed by males to secure mating success, and sought to determine whether the apparent limited monopolization of groups of females by males was a result of female mating strategies.

The almost permanent association of olive colobus with particular Diana monkey partner groups is a unique aspect of the former's natural history [Korstjens & Schippers, 2003; Oates & Whitesides, 1990] that strongly affects the distribution of females over the area. There are several indications that olive colobus benefit from their association with Diana monkeys in that it reduces the risk of predation [Oates & Whitesides, 1990]. First, a similar association of red colobus monkeys with Diana monkeys in the same forest has been related to predator avoidance [Bshary & Noë, 1997]. Second, it has been reported that Diana monkeys are the first to detect predators in polyspecific groups of colobus monkeys and guenons [Bshary, 2001]. Third, the foraging advantages to the olive colobus are minimal, since the olive colobus consume mainly young leaves [Korstjens, 2001; McGraw, 1998] whereas Diana monkeys consume fruits and insects [Wachter et al., 1997]. Therefore, a Diana monkey group may be viewed as a resource that attracts females. As an alternative to direct and indirect male mating competition, the males could therefore use these resources to obtain mating opportunities. We investigated male competition within and between groups, and in this study we present our observations on male and female associations with Diana monkey groups.

Another striking aspect of the olive colobus is the occurrence of large sexual swellings in females [Hill, 1952]. Such swellings can counter male strategies to monopolize females, and they are commonly observed in species that live in much larger groups compared to those of the olive colobus [Sillén-Tullenberg & Møller, 1993]. If these swellings function to allow females to avoid monopolization by single males in this species, we would also expect that other aspects of female reproductive biology (e.g., long receptive periods, mating overlap among females in a group, and female initiated promiscuous mating) would reduce male

monopolization. Therefore, we present data on female reproductive biology and mating behavior, and the possible benefits to females derived from limiting male monopolization.

The avoidance of male monopolization can benefit females in several ways, as described below:

1. *Indirect or direct female mate choice.*

For direct mate choice, females need to create opportunities for choosing between different males. Indirect mate choice is achieved when females can induce or intensify competition among males, in the form of either direct or sperm competition [Clutton-Brock & Harvey, 1976]. If female reproductive biology and mating behavior serve to improve mate choice, one would expect them to mate with multiple males (indirect choice) or preferred males (direct and indirect choice) during their fertile cycles.

2. *Infanticide avoidance.*

Infanticide is likely if a male can accelerate the reproductive cycle of the female and thereby increase his chances to sire her next infant. Accelerating a female's cycle can be achieved if the lactation period is longer than the gestation period [van Schaik & Janson, 2000] and if female reproductive rate is not too strongly constrained by seasonal effects [van Noordwijk & van Schaik, 2000]. Females can reduce the risk of infanticide by mating with many males and becoming receptive and attractive under conditions conducive to infanticide, regardless of whether they are ovulating [van Schaik et al., 2000; Zinner & Deschner, 2000].

3. *Increased paternal care.*

Females may benefit from relatively high male numbers per group if male help is essential for infant survival [Goldizen, 1987]. Only males with a relatively high chance of paternity will provide costly services, because their benefit must outweigh the cost of the provided services. Therefore, females will benefit from a bias in paternity chances toward the males that are most likely to provide services [Noë & Sluijter, 1990]. The importance of males for the survival of offspring may be indicated by the number of offspring per female that survive in a group relative to the number of males per female in that group.

We sought to determine whether 1) females have opportunities to choose between males, 2) female attractiveness is limited to fertile periods, 3) the olive colobus' reproductive biology and social organization render them vulnerable to male infanticide, 4) females use counterstrategies to reduce infanticide risk (following van Noordwijk and van Schaik [2000]), and 5) the adult sex ratio correlated to the number of immatures per female.

MATERIALS AND METHODS

Study Site

This study was carried out from June 1994 to December 1999 in the tropical evergreen, seasonal lowland forest of the Taï National Park (between 5° 10' to 6° 20' N and 4° 20' to 6° 50' W), Ivory Coast [Bshary & Noë, 1997]. Between 1995–1999 we measured an annual rainfall averaging $1,820 \pm 300$ mm, and an average mean temperature of 28.7°C (range=18–34°C) at the study site. The main predators of the olive colobus in Taï are chimpanzees (*Pan troglodytes*), crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), and humans.

Study Animals

The olive colobus is a relatively unknown primate that is endemic to the West African tropical forests [Oates, 1994]. Our study groups spent 90–100% of the observation time within 50 m of Diana monkeys. The home range of each resident olive colobus group (see below for definition) overlapped completely with the home range of its partner Diana monkey group. Five of seven simultaneously monitored Diana monkey groups in the research population had a partner olive colobus group.

Group composition changed regularly in the population as a result of disappearances, migrations, and births (Table I) (for details see Korstjens and Schippers [2003]). The first study group, Ver1, was associated with Diana monkey group Dia2, and was monitored from June 1994 until it dissolved in June 1996. At the same time, a solitary olive colobus male associated with the second Diana monkey study group, Dia1. Data on this male were collected opportunistically during his solitary period. As soon as two adult females joined this

TABLE I. The Composition of Resident (Ver1-11) and Non-resident (VerN1-N5) Groups and Changes Therein During the Research Period

Group name	Month of group count	AM	AF	AFI	JX	IX	AX	XX	Obs. days	Obs. hours
Ver1	June 1994	2	2	1	1	1			137	1000
	June 1995	1	2	1	1	1			46	296
	June 1996	1	1	2	1	2			116	983
	June 1997	1			2				4	29
Ver2	April 1997	1	2		1				76	504
	April 1998	1		3		3			80	647
	April 1999	1	4		2				39	273
Ver3	September 1996	1	2						100	809
	September 1997	1	1		1				75	677
	September 1998	1		1	1	1			63	567
	September 1999	1	1		1				19	171
Ver4	September 1997	3	5		2				56	460
	September 1998	2		1		1			1	7
	August 1999	2	1	1	1	1			1	7
Ver5	February 1998	2	2	1	2	1			2	20
Ver7	February 1998	1		1	1	1	2		2	10
Ver8	February 1998	1	2	2	2	2	1		2	10
Ver9	February 1998	2	4	2	2	2			2	12
Ver10	February 1998	1		1	1	1		2	2	12
Ver11	February 1998	1		1	2	1	1		2	12
VerN1	June 1997	1	1		1				1	n.a.
VerN2	July 1997	2	1						5	24
VerN3	July 1998	1	2		1				2	n.a.
VerN4	April 1999	2	1	1	2	1			1	n.a.
VerN5	September 1999	1	2		1				2	n.a.

Age-sex classes: AM, adult males; AF, adult females without infant; AFI, adult females with infant; JX, juveniles; IX, infants; AX, adult individuals of unknown sex; XX, and individuals of unknown age-sex class. Detailed observation on Ver4 ended in March 1998 and the last annual group count occurred in August 1999. Ver1 was not followed between June–December 1995 due to rebel activity. Obs. days/ Obs. hours: the total number of observation days/hours from the calendar month of the group count on the same line to the next one or the end of the study. n.a. is entered when only group composition was recorded for the group during the observation days. For all study groups annual average and median values for observation hours per day were greater than 71/2 hours.

male in October 1997, they were followed regularly as group Ver3. From April 1997 to December 1999, group Ver2 (which had been briefly contacted in 1996) was monitored. Ver4 was monitored between October 1997 and July 1999 (Table I).

Females were classified as adults when they developed a first sexual swelling, and males were termed adults when their testes became clearly visible. We divided the immatures into two classes: 1) infants (individuals younger than 1 year) and 2) juveniles (all remaining immatures). The sex of the immatures could not be determined. We classified individuals in nonstudy groups by their size and behavior. Demographic and behavioral data were collected in the four study groups. We thus collected data on 16 adult females (23.6 female years), eight adult males (15.8 male years), and 20 immatures (juveniles and infants, 18.4 immature years). The values "female years," "male years," and "immature years" represent the cumulative value of the monitoring period of each individual of the specified age-sex class.

Olive colobus groups or individuals that were associated with one specific Diana monkey group in the research area for at least 3 consecutive months were labeled resident groups and resident individuals, respectively. Apart from the study groups, we determined the composition of six other resident groups in the area (groups Ver5 and Ver7–10; Table I).

In addition to resident groups and individuals, we observed 23 nonresident adult females, 12 nonresident adult males, and six nonresident immatures (Table I). These nonresident groups or individuals were present in the research area for a maximum of 2 months each [Korstjens & Schippers, 2003]. Nonresident individuals were most often females that visited a resident group or a resident solitary male. Nonresident groups (and some nonresident individuals) visited a Diana monkey group that was not associated with a partner olive colobus group at that time. The number of nonresident individuals is a conservative estimate. Individuals of the same age-sex class that were observed <6 months apart were assumed to be the same individual, unless two such individuals could be confidently distinguished on the basis of physical characteristics. The origin and final destination of these nonresidents were unknown to the observers (unless otherwise noted).

Data Collection

The study groups were generally followed from 0700 to 1730 hr for at least 5 days a month. Occasionally a group was followed for half a day (i.e., 0700–1230 or 1230–1730 hr). The number of such early and late follows was equalized each month. Study groups were contacted at least weekly. Under the supervision of the authors, a total of 13 researchers (including A.H.K.) and field assistants collected data on group composition, dispersal events, and female swelling stages. To minimize interobserver effects, we analyzed data from different observers separately. Data on intergroup interactions and intragroup social interactions were collected ad libitum by five observers, each of whom was trained by his predecessor. The analyses were kept very general to minimize interobserver effects. Detailed analyses on social interactions were derived from data collected during focal follows performed by M. Krebs, who followed focal animals for an entire day. The time was recorded as whole minutes during which the animal was in sight and all social interactions could be recorded. F. Bélé collected hourly point samples of the distance between the male of Ver3 and his two females in 1996/1997 when each of the females was cycling.

Group counts of unhabituated groups were performed by A.H.K. and E.P. Schippers. A count of a group was used only when the group had been followed for more than 1 day and the observer was confident that all group members had been seen. We used the first reliable count of a group for the analyses. In analyses in which the composition of the group played a role, we excluded the groups for which not all individuals could be reliably classified into an age-sex class (i.e., Ver7, Ver8, and Ver10; Table I).

The number of days a sexual swelling lasted was based on data collected during a period in which the female was monitored at least every other day by the same observer (M. Krebs or K. Bergman). A female was recorded to have a swelling from the first onset of coloring and swelling of the anogenital region until it had completely disappeared again. In Ver3, 95% of 98 copulations between male Mi and female Li ($\chi^2_1 = 11.96$, $P < 0.001$), and 70% of 13 copulations between male Fa and female Ma occurred while the mating female had a swelling ($\chi^2_1 = 6.5$, $P < 0.02$ (M. Krebs, unpublished results)). Expected values were based on focal observation hours collected on the respective individuals. In accordance with these observations, a "receptive" female was identified as a female with a swelling.

Statistical Analyses

Parametric tests were only used if the chance of a deviation from a normal distribution was < 0.05 . Statistical tests (SPSS 10.1.0) were two-tailed, with the α set at 0.05 unless mentioned otherwise. An α' value was calculated with the "sharper Bonferroni" procedure [Hochberg, 1988] when multiple tests were conducted on the same data set.

RESULTS

Female Reproductive Biology

Females had sexual swellings for 14–20 days (two females were measured during four and three cycles, respectively; median = 17 days for each female;

TABLE II. Distribution of and Overlap in (Ovl) Receptive Periods of Females Li and Ma (Ver3) and Be, Ca, Se and Ni (Ver2) in Particular Calendar Months (Mo)

Ver3 1996–1997				Ver2 1998–1999					
Mo	Ovl	Li	Ma	Mo	Ovl	Be	Ca	Se	Ni
9/96	Y	+(20)	+(17)	8/98	N	– ^b	– ^b	+	
10/96	Y	+(18)	+(14)	9/98	N	– ^b	– ^b	+	
1/97	N	–	+(18)	11/98	N	– ^b	– ^b	+	– ^c
4/97	N	+(17)	–	12/98	Y	– ^b	– ^b	+	+
5/97	N	+(17)	–	3/99	Y	+	–	+	+
6/97	N	–	+(> 14)	4/99	?	?	?	?	+
7/97	N	+ ^a	+(> 14)	6/99	?	?	?	?	+
				7/99	Y	+	+	+	+

Ovl, at least two females of the group had (Y) a swelling on the same day or none of the females had a swelling on the same day during that month (N); ?, no clear information was available for a female's swelling state; + the female had a swelling during that month; –, the female did not have a swelling during that month. In brackets is noted the maximum number of days that a female was observed with swelling. During the monitoring period of Ver3 no swellings were missed. In Ver2 some swellings may have gone unnoticed due to shyness of females and limited observation time. ^aLi disappeared for 11 days. ^bFemale had a lactating infant. ^cFemale immigrated in this month.

Table II). The time between the onsets of the swellings in two consecutive cycles (i.e., the cycle length) of two different females was 27 and 29 days, respectively. The females had two to eight cycles per interbirth interval (Table II). We measured a median time of 3.8 months (2.5–5.5 months, $n = 6$) between the last swelling and birth. Some mating overlap occurred in Ver3 and Ver2 (Table II). In Ver3 and Ver2, more than one female had a swelling simultaneously over a few days during 3 of 6 months, and 3 of 3 months, respectively, in which more than one female had a swelling. We never observed more than one *maximally* swollen female (i.e., with tight sex-skin) in a group at any time. Our limited data showed too much variation among females in the average number of consecutive cycles to determine an expected value for the overlap of receptive periods, or to test whether overlap occurred more often than expected by chance.

Female and Male Mating Behavior

Most sexual interactions with two females in Ver3 followed an approach by the female rather than the male (57% and 65%, respectively, of interactions during focal follows). The alpha male of the bi-male group Ver1 (in 1994) performed 98% of 103 (female To) and 100% of 104 (female Sh) copulations. We recorded more than six copulations by the same couple (max 20 and 23, respectively) on 22% and 18% of observation days in which copulations were observed ($n=49$ and 66 days, respectively) in Ver1 (bi-male group) and Ver3 (one-male group), respectively. Ejaculates that were produced during masturbation coagulated. The male was more often located ≤ 2 m from a female when she had a swelling (for two females of Ver3: 36% and 32%, respectively) than when they did not (16% and 7%, respectively; $\chi^2_1 = 8.85$, $P = 0.004$ and $\chi^2_1 = 17.7$, $P = 0.00003$).

Extragroup Mating

On two occasions a female approached, sexually presented to, and mated with the resident male(s) of a neighboring group shortly after the groups had been at a < 50 -m distance. The male from the female's own group had already moved away with the group. On a third occasion, the receptive female from VerN2 (Table I) that temporarily (10 days) associated with Dia2 presented to the male from Ver3, which refused to mate with her and even chased her away. The latter interaction occurred in the middle of an aggressive intergroup encounter (males from each group were lightly wounded after the interaction). The male of Ver3 did mate with his group's receptive female, and the receptive female of VerN2 mated with one of her group's males during the encounter.

Furthermore, 12 nonresident females visited study groups or solitary males, on average once every 57th observation day [Korstjens & Schippers, 2003]. Ten of these females had a swelling. This is significantly more than expected if females at all reproductive stages were potential visitors (expected rate=0.09–0.23; binomial test: $P < 0.0002$). The expected rate is based on the estimated proportion of an interbirth interval that a female has a swelling (54–136 days), and assumes that a female's life consists of successive interbirth intervals. The observed rate only tends to be higher than the expected rate ($17/28 = 0.61$) if we assume that only cycling females pay visits ($P = 0.069$). We observed copulations between the visiting females and the resident males [Korstjens & Schippers, 2003].

Table III. Monthly Distribution of Births, Observed (Obs.) and Expected (Exp.), Based on the Number of Female-Months Per Calendar Month

Month	Female months	no. births	
		Obs.	Exp.1
January	19	2	1
February	19	1	1
March	18	0	1
April	19	2 (+1) ^b	1
May	22	0	1
June	21	0	1.2
July	20	0	1.1
August	22	0	1.1
September	28	0	1.2
October	29	3	1.5
November	28	5	1.5
December	29	1	1.5
Total	262	14 (+1) ^b	

The expected values were based on the relative number of female-months in each calendar month and the total number of births.

^bThis birth was estimated from observations on the infant in July. It was excluded from the calculations for the expected values.

Vulnerability to Infanticide

Birth seasonality was moderate, and 86% of births occurred between 1 October and 1 February (Table III). The only observed interbirth interval following the loss of an infant (4.5 months old) lasted 19 months, which corresponds to the average interbirth interval (i.e., 19 months) in the population [Korstjens & Schippers, 2003]. The female (AF Se, Table II) reproduced when the other females in her group did, even though they had not lost their infant. The infant that died was born 3 months after its mother immigrated into the group, which means that she conceived the infant before she immigrated. Female Se developed a swelling <10 days after the infant disappeared, and experienced menstrual cycles for 8 months (Table II).

Vulnerability to Infanticide: Social Organization

A change in the dominance hierarchy occurred in Ver1 when it was a bi-male group. Both infants present in the group survived the change. We witnessed a male taking over group Ver3. Ver3 had no infants, and one female in this group had a sexual swelling at the time of the takeover. The other female developed one 49 days later, but she disappeared for 9 days immediately thereafter. She returned without swelling and had no more swellings until the birth of her infant (5.5 mo after the takeover). Both females presented to and mated with the new male the day after the takeover.

Correlates of the Number of Males per Group

The number of immatures per female correlated positively with the adult male to adult female ratio (Pearson correlation: $n = 9$; $r = 0.786$, $P = 0.012$; $\alpha' = 0.05$; two groups without immatures were excluded from the analyses; Fig. 1). The number of males in a group also correlated positively with group size ($n = 11$;

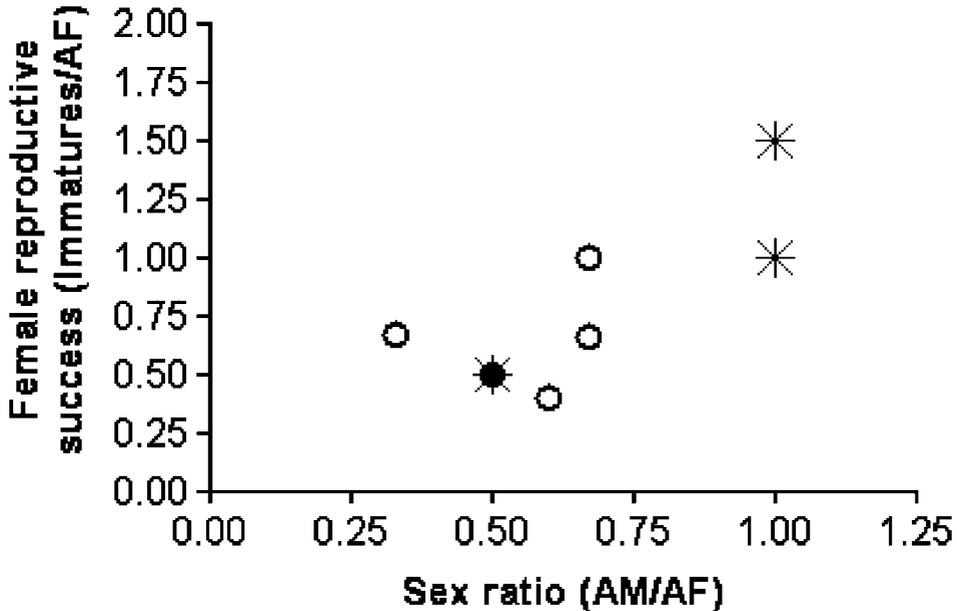


Fig. 1. The number of adult males per female plotted against the number of immatures per adult female for resident groups (M) and nonresident groups (○); a filled circle depicts two identical values.

Table IV. The Number of Particular Types of Inter-group Interactions Relative to the Presence of Females With Swelling in at Least One of the Groups

	Vocal exchange > 50 m	Vocal exchange 50 m	Aggression 0 m	Total
No female with swelling present	15	16	2	33
Females with swelling present	10	5	2	17
Total	25	21	4	50

Vocal exchange >50m/50m, males called at each-other with >50 or ≤50 meters distance between the groups respectively; Aggression 0 m, males chased or even fought each other.

Spearman’s correlation, $r = 0.63$, $P = 0.04$; the term “group size” here excludes adult males and includes immatures).

Male and Female Behavior During Intergroup Encounters

We recorded 50 cases of intergroup vocal exchanges (0–150 m distance between groups) in which the male of at least one of the interacting groups called (Table IV). When groups came within 50 m of each other, females with immatures stayed behind and disappeared into the foliage while males and sometimes females without infants (n=2) interacted. Within 50 m, these interactions entailed vocalizations (100% of cases); in at least 50% of cases, threats (i.e., an individual moved its head and shoulders sideways, with an open mouth) were involved. In the bi-male groups, both males called and threatened the neighbors, and often sat in close proximity to each other. In four cases, the adult males of the two groups also chased each other back and forth. Males used the loudest

vocalization in the olive colobus vocal repertoire, and females uttered a similar but softer and shorter call (M. Krebs, unpublished results). The presence of females with swellings in the group (34% of all interactions) did not affect the chance of male aggression when groups were within 50 m (Table III; $\chi^2_1=0.18$, $P=0.67$).

Male Mating Opportunities and Male Association With Diana Monkey Groups

Two solitary males that remained with one particular Diana monkey group for several months were visited by and mated with solitary females that passed through the area. Eventually, a bisexual group formed around each male. A bisexual nonresident group once joined a solitary male for a day in that male's Diana monkey group. The male avoided the group, and no aggressive or affiliative interactions were recorded. After a group had formed around this male, the typical intermale interactions that occur during intergroup encounters were observed.

Two males of Ver4 remained with their Diana monkey group after all females but one had emigrated; eventually, two new females joined Ver4. The third male of Ver4 left with some of the females. This male and two juvenile group members of his former group immigrated into Ver5, an existing bisexual group, forming a bi-male multifemale group (Table I).

One male (Fa) obtained a group of females by taking over an existing bisexual group (Ver3). He abandoned his last remaining juvenile group member (juvenile male So) and the Dia2 group with which he had associated for ≥ 5 years. The takeover was not directly observed. So joined Fa in Ver3 within a week. The replaced male was observed roaming the area with a solitary male Campbell's monkey the day after the takeover.

DISCUSSION

We investigated male strategies for obtaining mating opportunities in a society in which it apparently was difficult for a single male to monopolize small groups of females that were attached to groups of Diana monkeys. We wanted to know whether female mating strategies limited monopolization by males, and whether Diana monkeys were a resource that provided males with mating opportunities.

We found that male mating competition was characterized by mating competition within groups, resulting in a strong mating bias (current study) [Oates, 1994] and competition between groups. In addition, the relatively large testes (Oates, personal communication) [Hill, 1952], coagulating sperm, and frequent copulations within 1 day by the same males (current study) [Oates, 1994] observed are indicators of sperm competition [Birkhead & Møller, 1998]. Since direct competition appeared to be relatively effective within groups, the adaptation to sperm competition may be a strategy to counter extragroup mating by females.

Males that had no female group could mate with visiting females, and sometimes even obtained a group of females when they associated with Diana monkeys. Our preliminary data did not indicate that males actively defended these resources, as is expected when resource defense is concerned, before they had obtained a group of females. We conclude that the polyspecific association reduces predation risk for solitary males while it also offers a resource that is

frequented by females. Similar polyspecific associations of solitary individuals have been suggested in other species to reduce predation risk during dispersal [Olupot & Waser, 2001].

Males that lost their females through dispersal and disappearance could remain in the old home range with the Diana monkey group and the remaining group members until new females joined them ($n=1$) or until an opportunity to take over a group arose ($n=1$) (current study) [Korstjens & Schippers, 2003]. We conclude from the largely descriptive data we collected that when a male had no opportunity to obtain a group of females directly, he could opt to associate with a Diana monkey group and mate with the females that visited this resource.

The success of male strategies depends on female mating strategies, and in the olive colobus it appeared that the latter reduced the males' ability to monopolize groups of females. We found that the chances for females to escape monopolization by males were high because of long receptive periods during which females were very attractive and proceptive [sensu Dixson, 1998], and the occurrence of several such periods before gestational amenorrhoea set in. These features further limited male control because they increased the chance that more than one female was receptive simultaneously in a group. We investigated whether these characteristics were indicative of female mating strategies to improve mate choice, reduce infanticide, or increase male care.

The limited control of males over females did enable direct female mate choice through visits, and indirect mate choice by mating with multiple males. However, mate choice could not be the sole force behind female sexual swellings, since some swellings occurred after conception. The median time between the last observed swelling and subsequent birth was shorter than the normal gestation time reported for colobines of 5–6 months [Harvey et al., 1987], as confirmed by recent hormone analyses (Noë et al., unpublished results), and female attractiveness lasted longer than the average fertile period in primates (1 week [Dixson, 1998]).

The reproductive biology of the species (i.e., a shorter gestation than lactation period, and moderate breeding seasonality) and the group dynamics (characterized by male immigrations and strong bias in mating success within groups) suggested that, theoretically, the species was vulnerable to infanticide. Indeed, although the only male takeover event observed did not incite a swelling, it did incite proceptive behavior of the female group members, and the only infant that died in the population was conceived before the mother immigrated into the group. However, we observed no actual case of infanticide or a reduction in the interbirth interval after the loss of an infant ($n=1$). Furthermore, postconception swellings were not limited to infanticide-conducive situations.

Males were more active protectors than females against predators, conspecifics, and members of other primate species (this study, personal observations). Males in bi-male groups defended the group cooperatively, and such male alliances may provide better protection than that afforded by single males. In accordance, the immature-to-female ratio was positively related to the adult male-to-female ratio in the group, which suggests that males may be important for the survival of immatures. The advantage of a high male-to-female ratio for infant survival may also reflect an advantage to males, a subject that requires further investigation. In this study, female extragroup mating was not related to increased male care, and more likely even reduced the males' incentive to provide care. Our data indicate that females were more likely to visit bisexual groups or solitary males when they were cycling, which suggests that these visits improved female mate choice.

Our data suggest that female reproductive biology can be explained partially, but not completely, by selective pressure for increased freedom of mate choice, increased paternal care, and a reduction of infanticide risk. Alternatively, reproductive biology and female behavior may be not so much adaptive as they are phylogenetically constrained. Indeed, the most closely related colobine, the red colobus, appears to have a very similar reproductive biology (A.H.K., unpublished results) [Starin, 1988]. However, the detailed data available on red colobus reproductive biology were derived from western populations. These populations differ greatly from eastern populations, which have small or almost no sexual swellings, and (most likely) shorter receptive periods (T.T. Struhsaker, personal communication; A.H.K., personal observation). Considering that this variation evolved after the red and olive colobus split off, we argue that the large sexual swellings and long receptive periods in the olive colobus are not merely a result of phylogenetic inertia.

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REFERENCES

- Birkhead TR, Møller AP. 1998. Sperm competition and sexual selection. London: Academic Press, 826 p.
- Bshary R, Noë R. 1997. Red colobus and diana monkeys provide mutual protection against predators. *Anim Behav* 54:1461–1474.
- Bshary R. 2001. Interactions between red colobus monkeys and chimpanzees. In: Noë R, McGraw WS, Zuberbühler K, editors. *Monkeys of the Taï Forest: an African primate community*. Cambridge: Cambridge University Press. p 251–256.
- Clutton-Brock TH, Harvey PH. 1976. Evolutionary rules and primate societies. In: Bateson PPG, Hinde RA, editors. *Growing points in ethology*. Cambridge: Cambridge University Press. p 195–237.
- Dixon AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings. Oxford: Oxford University Press. 546 p.
- Goldizen AW. 1987. Tamarins and marmosets: communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 112–120.
- Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 181–196.
- Hill WCO. 1952. On the external and visceral anatomy of the olive colobus monkey (*Procolobus verus*). *Proc R Soc Lond Ser B Biol Sci* 122:127–186.
- Hochberg Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75:800–802.
- Korstjens AH. 2001. The mob, the secret sorority, and the phantoms. An analysis of the socio-ecological strategies of the three colobines of Taï. Ph.D. dissertation, Utrecht University, Utrecht, The Netherlands. 174 p.
- Korstjens AH, Schippers EP. 2003. Dispersal patterns among olive colobus in Taï National Park. *Int J Primatol* 24:515–540.
- McGraw WS. 1998. Posture and support use of Old World monkeys (Cercopithecidae): the influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items. *Am J Primatol* 46: 229–250.

- Mitani JC, Gros-Louis J, Manson JH. 1996. Number of males in primate groups: comparative tests of competing hypotheses. *Am J Primatol* 38:315–332.
- Noë R, Sluijter AA. 1990. Reproductive tactics of male savanna baboons. *Behaviour* 113: 117–170.
- Oates JF, Whitesides GH. 1990. Association between olive colobus (*Procolobus verus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. *Am J Primatol* 21:129–146.
- Oates JF. 1994. The natural history of African colobines. In: Davies AG, Oates JF, editors. *Colobine monkeys*. Cambridge: Cambridge University Press. p 75–128.
- Olupot W, Waser PM. 2001. Activity patterns, habitat use and mortality risks of mangabey males living outside social groups. *Anim Behav* 61:1227–1235.
- Sillén-Tullenberg B, Møller AP. 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *Am Nat* 141:1–25.
- Starin ED. 1988. Gestation and birth-related behaviors in Temminck's red colobus. *Folia Primatol* 51:161–164.
- van Noordwijk MA, van Schaik CP. 2000. Reproductive patterns in eutherian mammals: adaptations against infanticide? In: van Schaik CP, Janson CH, editors. *Infanticide by males and its implications*. Cambridge: Cambridge University Press. p 322–360.
- van Schaik CP, Janson CH. 2000. *Infanticide by males and its implications*. Cambridge: Cambridge University Press. 569 p.
- van Schaik CP, Hodges JK, Nunn CL. 2000. Paternity confusion and the ovarian cycles of female primates. In: van Schaik CP, Janson CH, editors. *Infanticide by males and its implications*. Cambridge: Cambridge University Press. p 361–387.
- Wachter B, Schabel M, Noë R. 1997. Diet overlap and polyspecific associations of red colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Ethology* 103:514–526.
- Zinner D, Deschner T. 2000. Sexual swellings in female hamadryas baboons after male takeovers: “deceptive” swellings as a possible female counter-strategy against infanticide. *Am J Primatol* 52: 157–168.