ANIMAL BEHAVIOUR, 1999, **57**, 1013–1020
Article No. anbe.1998.1063, available online at http://www.idealibrary.com on IDEAL

Male mating patterns in wild multimale mountain gorilla groups

MARTHA M. ROBBINS
Department of Zoology, University of Wisconsin–Madison

(Received 25 August 1998; initial acceptance 25 August 1998;
final acceptance 3 December 1998; MS. number: A7827R)

Although mountain gorillas, *Gorilla gorilla beringei*, are classified as having a one-male mating system, approximately 40% of the social units are multimale groups. I observed two multimale groups of mountain gorillas at the Karisoke Research Center, Rwanda, Africa, for 17 months to determine male mating patterns and male–male mating harassment in relation to both male dominance rank and female reproductive status. Dominant males mated significantly more than did individual subordinate males, and dominant males mated more with cycling adult and pregnant females. The dominant males participated in 47 and 83% of observed matings in the two groups. Subordinate males were more likely than dominant males to mate with subadult females. Eleven of 14 females were observed to mate with more than one male, and multiple males mated with three of the five females observed at the probable time of conception. Mating harassment was initiated and received by both dominant and subordinate males. Mating harassment occurred infrequently (during 30 and 22% of matings in each group), usually consisted of mild aggression, and usually terminated copulations by subordinate males, but not those by dominant males. These results suggest that multimale mountain gorilla groups can be favourable environments for subordinate males to obtain mating opportunities. Dominant males may be unable or unwilling to prevent subordinate males from mating. Based on behavioural observations, mountain gorillas can have a multimale mating system but further research on the role of females in male mating success and paternity determination is needed to understand fully this species' mating system.

© 1999 The Association for the Study of Animal Behaviour

The mating system of a species does not always mirror its social system and there can be extensive intraspecific variation in a mating system with individual strategies to maximize fitness (Rowell 1988, 1991; Clutton-Brock 1989; Lott 1991). In multimale groups, the type of mating system may be viewed as a continuum with complete monopolization of fertilizations by the dominant male on one end and equally shared fertilizations by all males on the other (Stacey 1982; Vehrencamp 1983). Although it has been suggested that one of the benefits of high dominance status is exclusive or high reproductive success through the monopolization of females (Altmann 1962; Cowlishaw & Dunbar 1991), a direct relationship between dominance rank, mating success, and reproductive success may not always exist (Fedigan 1983; Bercovitch 1991; deRuiter & van Hooff 1993). A dominant male may be tolerant of some mating and reproduction by subordinate males to gain the benefits of subordinate males remaining in the group (Vehrencamp 1983). Dominant males also may not be able to prevent subordinate males from mating due to habitat type or group size (van Hooff & van Schaik 1992). Examining the mating patterns of males is particularly important to determine the costs and benefits of a multimale group structure to both dominant and subordinate males, which in turn can influence the social system of the species (Wrangham & Rubenstein 1986; Dunbar 1988; van Hooff & van Schaik 1992).

Mountain gorillas are considered to have a one-male mating system (Harcourt 1981; Yamagiwa 1987), although approximately 40% of all groups are multimale (Schaller 1963; Weber & Vedder 1983). The harem-type grouping pattern of mountain gorillas is hypothesized to provide protection for females against potentially infanticidal outsider males and represents a form of long-term mate guarding of females by males (reviews in Harcourt 1981; Wrangham 1986; Watts 1989; Brereton 1995). Intergroup competition between males for access to females is considered to be high (Harcourt 1981; Watts 1989, 1994, 1996; Sicotte 1993). Gorilla groups containing only one adult male (silverback) probably do have a one-male mating system because extragroup copulations have never been reported and intergroup encounters are infrequent (Watts 1989, 1990; Sicotte 1993). In multimale groups, however, subordinate males have been observed mating and there is male–male competition for

Correspondence and present address: M. M. Robbins, Max Planck Institute for Evolutionary Anthropology, Inselstrasse 22, 04103 Leipzig, Germany (email: robbins@eva.mpg.de).

Table 1. Adult and old adolescent males in each study group

Name	Age*	Natal group	Time observed (h)	Focal periods	Dominance rank
Group 5					
ZZ	20.5	5	116.7	32	1
PB	17	5	102.3	28	2
SH	14	5	108.8	28	3
CA	12.5	5	92.8	25	4
Beetsme's group					
TI	17	4	169.8	39	1
BM	26†	?	176.0	39	2

*Reflects age of each subject at the midpoint of the study (July 1991).
†Estimated age.

reproductive opportunities within groups (Harcourt 1981; Fossey 1982; Watts 1990, 1991, 1992, 1996; Sicotte 1994). Early studies of mountain gorillas suggested that subordinate males mated only with infertile, nulliparous females, and never attempted to mate with a potentially fertile female (e.g. Harcourt 1981). More recent observations indicate that dominant males will tolerate matings between their putative daughters and subordinate males, and that these subordinate males may mate successfully with other fertile females when not in proximity to the dominant male (Watts 1990, 1991).

The aim of this study was to examine male mating behaviour and male–male mating harassment in relation to male rank and female reproductive status in two multimale mountain gorilla groups. Other factors, such as female choice, may affect the relationship between male rank and mating success, but these were not considered in this study. Based on priority of access models, the ability of a dominant male to monopolize matings should correlate negatively with the number of competitors and mating opportunities (Hausfater 1975; Berenstein & Wade 1983; Cowlishaw & Dunbar 1991; Bulger 1993). If males can detect the reproductive condition of females, possibly through behavioural cues (Watts 1990, 1991), dominant males may be tolerant of subordinate males mating with infertile, subadult females and pregnant females and only interfere with matings involving fertile females. Additionally, mating harassment is expected to occur mainly by dominant males towards subordinate males and it should serve as a method of preventing subordinate males from mating.

METHODS

Study Site and Study Groups

This study was conducted at the Karisoke Research Center, located in the Virunga Volcanoes of Rwanda, Africa during March–October 1990 and March–December 1991. The two groups of mountain gorillas observed were fully habituated to human observers and life histories were known for nearly all individuals (Karisoke Research Center long-term records, unpublished data). Adult males (silverbacks) were males 14 years of age or older, and old adolescent males were between 11 and 13 years of age (after Watts & Pusey 1993). Adult females were more than 8 years of age, and subadult females were between 6 and 8 years of age. Group 5 consisted of three silverbacks (adult males), one old adolescent male, 11 adult females, two subadult females, and 14 immature individuals. Beetsme's group consisted of two silverbacks, seven adult females and seven immature gorillas. The only changes in adult group composition during the course of this study were that one female transferred into and one female emigrated out of group 5 during an interaction with a neighbouring group in February 1991.

The three adult males in group 5 were born in that group when it was a multimale group so they may or may not have been paternal half-siblings (Table 1). Two of these adult males (ZZ and SH) were known to be maternal half-siblings. Of the nine females observed mating, seven emigrated into the group and were known not to be mothers, daughters, or siblings to the adult males. One adult female was a maternal sibling, and putative paternal sibling, to ZZ and SH. One subadult female was a putative paternal half-sibling to all three adult males. In Beetsme's group, it was highly unlikely that the two silverback males were related because they were born in different groups. All the adult females emigrated into Beetsme's group and were believed to be unrelated to the adult males (Karisoke Research Center long-term records, unpublished data).

Behavioural Observations

I used focal animal sampling (Altmann 1974) of the adult males and the old adolescent male to collect 420 h of behavioural observations on group 5, and 345 h on Beetsme's group (Table 1). I established a fixed rotating schedule to determine the order in which the six males were observed. I could follow a given individual for several hours at a time so usually only one male was followed per day.

During observations, I recorded all agonistic and sexual interactions between the males and other group members. I determined dominance relationships between the males independently of aggressive behaviour by observing patterns of displacements (Robbins 1996). A displacement was defined as an approach–retreat interaction in which one animal approached another, causing the first animal to move away from the second (Watts 1995).

A copulation was defined as a male mounting a female accompanied by pelvic thrusts (after Harcourt et al. 1980, 1981; Nadler 1989; Watts 1991). I recorded copulations during both focal animal sampling of the male gorillas and on an ad libitum basis because of the infrequent occurrence of the behaviour. Additionally, I used copulations recorded in the study groups by other researchers during the time of my observations as part of the data set. Although this sampling method does not represent 'all occurrence sampling' (Altmann 1974), which would be nearly impossible to do in the field conditions, the data set is believed to be representative of the proportion of mating activity by all group members. Within each group, roughly the same proportion of matings by each male was observed during focal sampling (group 5: ZZ=56.4%, PB=25%, SH=48.6%, CA=100%, but CA was observed to mate only once; Beetsme's group, TI=35%, BM=37.5%).

I also conducted analysis of harassment during matings (participants, type, and reaction). A harassed mating was one in which aggression directed towards the male performing the copulation either did or did not result in disrupting the mating. I also considered situations to be harassed matings when the copulating male behaved aggressively towards another male nearby (which was harassing the pair due to his presence or perhaps some subtle behavioural cue). Aggressive behaviour consisted of cough grunting, screaming, chest beating, any part of the strut-walking sequence, hits, bites, or kicks (Schaller 1963; Fossey 1972; Harcourt et al. 1993).

All statistical analyses performed were nonparametric and two-tailed.

Reproductive Status of Females

I classified females into three groups based on their reproductive status: cycling subadults, pregnant adults and cycling adults. The age of first observed full copulation for female mountain gorillas is between 5.8 and 7.1 years (median 6.33 years) and the median age for first birth is 10 years (range 8.7–12.8 years; Harcourt et al. 1980; Watts 1991). Therefore females between 6 and 8 years of age were considered subadults (Watts & Pusey 1993).

Female gorillas show no external signs of ovulation and therefore oestrus is inferred by behavioural cues such as proceptivity and receptivity of females (Harcourt et al. 1980; Nadler 1989, 1992; Watts 1991). Proceptivity is defined as a female's behaviour to attract a male for mating, receptivity refers to females that are willing to copulate with certain males, and both can be reliable indicators of oestrus (Nadler 1992). Females are typically proceptive to copulations only for a few days during the 28-day cycle, which is presumed to be around the time of ovulation, but females also show postconception proceptivity at irregular intervals (Stewart 1977; Harcourt et al. 1980, 1981; Nadler 1989; Watts 1991; Martin 1992). Forced matings have been observed in captivity but not in the wild (Nadler 1989). The median duration of oestrus is 1 day (maximum 4 days), although some longer periods are probably missed due to breaks in observation (Harcourt et al. 1981; Watts 1991). In this study an 'oestrus day' was a day when at least one mating was observed.

In this study, the probable time of conception was estimated by counting back 255 days from date of birth and included any matings observed within 10 days before or after this time. Gestation length for gorillas is estimated to be between 250–260 days based on both captive lowland gorillas and wild mountain gorillas (Tijskens 1971; Harcourt et al. 1980; Cross & Martin 1981; Fossey 1982). Gorillas have one of the lowest coefficients of variation (3.0%) for recorded gestation lengths in simian primates (Martin 1992), and their short oestrus period (1–2 days) increases the reliability of estimating time of conception. Cycling adult females were non-pregnant, nonlactating adults. Mating did not occur while females were lactating. Four females in group 5 and two females in Beetsme's group were lactating during the entire study period and were not observed copulating.

RESULTS

Male Dominance Rank

Dominance relationships existed between the males in both groups (Robbins 1996; Table 1). In group 5, the dominance hierarchy was ZZ, PB, SH and CA in descending order of dominance. In Beetsme's group, TI was dominant over BM.

Mating Behaviour

I observed 115 matings between nine females and the three adult males in group 5. The matings in group 5 were not evenly distributed between the three males; ZZ, PB and SH performed 48, 21 and 31% of the matings, respectively (chi-square test: $\chi^2_2=12.76$, $P<0.01$; Fig. 1a). Because CA, the old adolescent male, was observed mating only once with a subadult female (and this copulation was harassed), he was not considered in analyses.

Five females and the two adult males were observed mating 54 times in Beetsme's group. TI performed significantly more matings than BM, 83% versus 17% (binomial test: $z=4.627$, $P<0.001$; Fig. 1b).

Reproductive Status of Female

In both groups, cycling adult females mated more with the dominant male than with subordinate males (group 5: $\chi^2_1=19.64$, $P<0.001$; Beetsme's group, binomial test: $z=4.47$, $P<0.0001$; Fig. 1a, b). Only 37 (32%) of the 115 matings were with cycling adult females in group 5. ZZ, PB and SH performed 25 (68%), three (8%), and nine (24%) of these copulations, respectively. In Beetsme's group, 48 (89%) of the 54 observed copulations were with cycling adult females; TI and BM performed 40 (83%) and eight (17%) copulations, respectively.

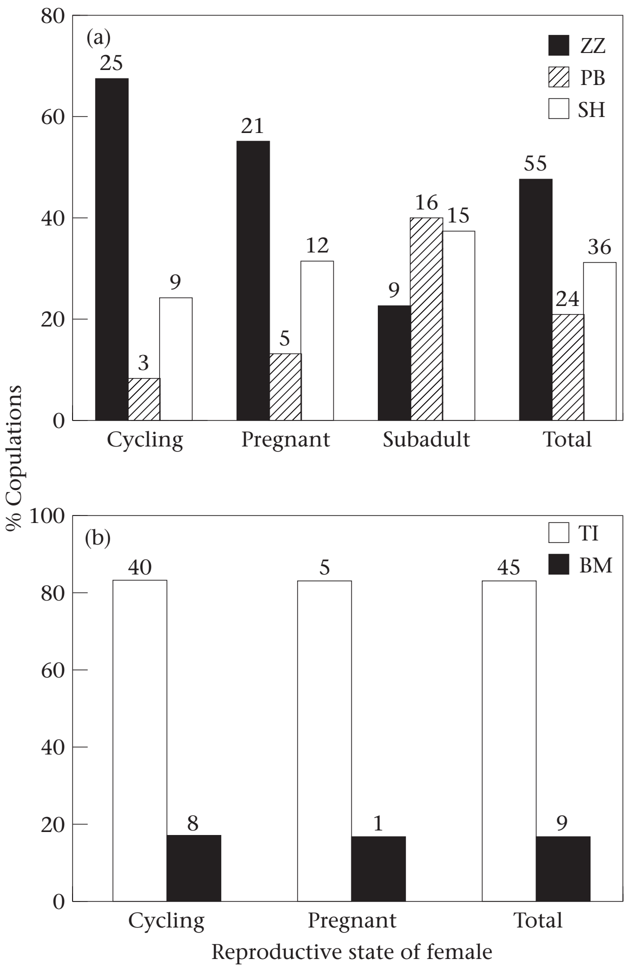

Figure 1. Percentage of copulations peformed by each male with females of different reproductive status. Numbers above bars are the number of copulations performed by each male. (a) Group 5. (b) Beetsme's group.

Forty matings (35%) occurred with cycling subadult females in group 5. Cycling subadult females were equally likely to mate with dominant and subordinate males (χ^2_1=2.12, P<0.20; Fig. 1a). ZZ, PB and SH performed nine (23%), 16 (40%) and 15 (37%) of these copulations, respectively. Beetsme's group did not contain any subadult females.

In group 5, pregnant females were more likely to mate with the dominant male than with the subordinate males and there was a similar trend in Beetsme's group (group 5: χ^2_1=8.22, P<0.01; Beetsme's group, binomial test: P=0.09; Fig. 1a, b). Thirty-eight of the 115 (33%) matings observed in group 5 were with pregnant females. ZZ, PB and SH performed 21 (55%), five (13%) and 12 (32%) of these copulations, respectively. In Beetsme's group, six (11%) of the 54 observed copulations were with cycling adult females; TI and BM performed five copulations (83%) and one copulation (17%), respectively.

From the perspective of males, in group 5 the matings with the three classes of females were not evenly distributed between the dominant and subordinate males (χ^2_2=16.82, P< 0.001), with the dominant male mating proportionately more with cycling adult females and subordinate males mating proportionately more with cycling subadult females. Forty-six per cent of the dominant male's (ZZ) matings were with cycling adult females, but only 13% of PB's and 25% of SH's matings were with cycling adults. Only 16% of the dominant male's (ZZ) copulations were with cycling subadult females, whereas 67 and 42% of PB's and SH's matings, respectively, were with cycling subadults. Matings with pregnant females consisted of 38, 20 and 33% of all matings for ZZ, PB and SH, respectively.

In Beetsme's group, TI and BM were equally likely to mate with females of differing reproductive status (Fisher's exact test: P=0.99), with TI and BM participating in 89 and 11%, respectively, of the matings with both cycling adult and pregnant females.

Matings during probable time of conception

Five females were observed copulating during the probable time of conception. Matings were observed within an average of 4.2 days of the estimated 255-day gestation length (N=9 oestrus days; median=5; range 1–8; SD=2.7).

Two females (SIM, FU) were observed mating only with the dominant male of the group during the likely time of conception. Three females (KB, WAL, PAP) were observed mating with multiple males at the probable time of conception. KB was observed mating with three males on the same day. WAL was observed copulating 10 times during her presumed conceptive period, eight times with ZZ, the dominant male. PAP was observed mating with TI twice and BM once during her conceptive period. The timing of PAP's conception was confirmed with urinary hormone data (Czekala & Sicotte 1992).

Mating Harassment

In group 5, harassment by adult males occurred during 35 of 115 (30%) of the observed matings (Table 2). Although there was a significant difference between the number of harassed matings involving the three adult males (χ^2_2=7.72, P=0.021), there was no clear trend; ZZ, PB and SH were harassed during 26, 13 and 50% of their overall matings, respectively. If matings only with cycling females were considered, there still was a significant difference (χ^2_2=10.53, P=0.005). Males ZZ, PB and SH were harassed during 27, 5 and 50% of their matings with cycling females, respectively. Only seven (20%) harassed matings were with cycling adult females and 12, 0 and 44% of matings with cycling adult females were harassed for ZZ, PB and SH, respectively (χ^2_2=5.18, P=0.075).

In Beetsme's group, 12 of the 54 (22%) copulations were harassed by adult males (Table 3). No difference was found in the ocurrence of harassment between the two males (Fisher's exact test: P=0.665). TI and BM harassed each other during one (11%) and 11 (24%) of their matings, respectively. No harassment occurred during matings with pregnant females in Beetsme's group.

The dominant male was the harasser in 43% of the harassments in group 5 and 8% in Beetsme's group. Most

Table 2. Number (percentages) of observed matings that were harassed in the two groups of mountain gorillas studied

Male	Harassed matings	Harasser			Reproductive state of female		
					Subadult	Pregnant	Cycling adult
Group 5		ZZ	PB	SH			
ZZ	14* (26)	—	9	4	6	5	3
PB	3 (13)	3	—	0	1	2	0
SH	18† (50)	12	7	—	10	4	4
Total	35	15 (43)	16 (46)	4 (11)	18 (50)	11 (30)	7 (20)
Beetsme's group		TI	BM				
TI	11 (24.4)	—	11		0	0	11
BM	1 (11.1)	1	—		0	0	1
Total	12	1	11		0	0	12 (100)

Reproductive state of females was categorized as subadult, pregnant, or cycling adult.
*Includes one case by an unknown harasser.
†Both ZZ and PB harassed SH in one incident.

Table 3. Type of mating harassment and reaction to harassment in the two groups of mountain gorillas studied

Male	Type of harassment received			Reaction to harassment		
	CG/Run	Attack	Proximity	Stop	Continue	Aggression
Group 5						
ZZ	6	0	8	6	2	6
PB	2	1	0	3	0	0
SH	18	0	0	13	5	0
Total	26 (74)	1 (3)	8 (23)	22 (63)	7 (20)	6 (17)
Beetsme's group						
TI	9	2	0	1	9	1
BM	0	1	0	0	0	1
Total	9 (75)	3 (25)	0	1 (8)	9 (75)	2 (17)

Type of harassment includes cough grunting (CG) and/or running at (CG/run), physical aggression (attack), or the proximity of a male causing the copulating male to react with aggression (proximity). Reactions included ending the mating ('stop'), the mating continued ('continue'), or aggression from the mating male directed at the harasser ('aggression'). Numbers in parentheses are percentages.

harassment (about 75% in both groups) consisted of mild aggression (cough grunting and/or running) directed at the mating pair (Table 3). Very few harassments involved physical aggression ($N=1$, 3% in group 5; $N=3$, 25% in Beetsme's group). The dominant male in group 5 was harassed by the close proximity of subordinate males for eight (57%) of his harassed matings. These events were included as harassment because it appeared that the subordinate males were subtly inducing male–male aggression and had a negative impact on the dominant male's mating behaviour.

The most frequent reaction to mating harassment was to stop the copulation in group 5 (63%), but only 8% of harassed copulations were terminated in Beetsme's group (Table 3). All subordinate males stopped mating when harassed except for SH, who continued mating during five (28%) of his harassed matings. ZZ, the dominant male, was the only male to respond to harassment with aggression in group 5 ($N=6$; 43% of his harassed matings). In Beetsme's group, TI and BM each responded once to harassment by attacking each other.

Harassment was less likely to occur during matings with cycling adult females than with cycling subadult or pregnant females ($\chi^2_2=5.787$, $P<0.05$; Table 2). Only 19% of the matings with cycling adult females were harassed compared with 44 and 41% of matings with cycling subadult and pregnant females. This difference may reflect the fact that subordinate males were more likely to mate with subadult females than adult females and that the dominant male, ZZ, performed 68% of the matings with cycling females. All of the harassed matings in Beetsme's group were with cycling females.

DISCUSSION

Male Rank, Female Reproductive Status and Mating Behaviour

Although the dominant males in both groups participated in the largest proportion of matings (48 and 83%), they may not monopolize mating behaviour as much as previously thought (Harcourt 1981; Watts 1990, 1991).

There was less variation in mating success between the males in group 5, which contained more males and females than in Beetsme's group. This result is consistent with the prediction that the ability of a dominant male to monopolize matings should correlate negatively with the number of competitors and mating opportunities (Hausfater 1975; Berenstein & Wade 1983; Cowlishaw & Dunbar 1991; Bulger 1993). Results of this study confirm earlier reports that dominant males participate in more matings with cycling adult and pregnant females and that subordinate males mate primarily with subadult females (Harcourt 1981; Fossey 1982; Watts 1990, 1991). In many primate species, it has been hypothesized that adult males prefer adult females over adolescent females as mating partners because of their proven reproductive abilities (Anderson 1986). The observed patterns of mating behaviour suggest that partner preference may also be influenced by the strength of social relationships between the individuals; dominant males and adult females are more likely to have strongly developed social relationships with each other than are dominant males and subadult females or subordinate males and adult females (Watts 1992).

To ensure fertilization, the reproductive state of the female at the time of mating may be as important to a male as the overall number of matings. In many species, dominant males concentrate their matings around the time of presumed ovulation (e.g. brown capuchin monkey, *Cebus apella*: Janson 1986; mandrill, *Mandrillus sphinx*: Wickings et al. 1993; longtailed macaque, *Macaca fascicularis*: deRuiter et al. 1994). In this study, multiple males were observed mating during the probable time of conception for three of five females. This indicates that subordinate, as well as dominant, males can obtain matings at the likely time of conception and that there is the possibility of a multimale mating system at the genetic level.

Mating Harassment

Mating harassment may be seen as a form of male mating competition (Niemeyer & Anderson 1983). There has been great variation in the amount of mating interference observed in different primate species; nearly 80% of mating attempts in langurs, *Presbyis entellus* (Sommer 1989) and 68% of attempts in Japanese macaques, *Macaca fuscata* (Inoue et al. 1993) are harassed compared with only 2% in chimpanzees, *Pan troglodytes* (Hasegawa & Hiraiwa-Hasegawa 1990). In this study, mating harassment occurred in 33% of the matings in group 5 and 22% of matings in Beetsme's group. Mating harassment may have occurred relatively infrequently because males may have been too far away from one another to interfere effectively before a copulation was completed. Males in both groups spent less than 10% of the time within 5 m of each other (Robbins 1996), and they were often separated by as much as 50 m or more (personal observation).

Aggression during mating harassment followed a pattern similar to overall male–male aggression (Robbins 1996); it was usually mild aggression with infrequent contact. Mild harassment was usually enough to stop a copulation but one subordinate male sometimes continued to mate. In Beetsme's group, harassment of the dominant male was usually ineffective and in group 5, the presence of nearby subordinate males interrupted several of the matings by the dominant male.

Matings with subadult females were harassed more than matings with pregnant or cycling females in group 5. This may be more a reflection of which males participated in the matings than the reproductive state of the female. Most matings with subadult females were performed by subordinate males and dominant males were more likely to challenge subordinate males than vice versa. Copulations with cycling females were rarely harassed, perhaps because most copulations with cycling females in both groups were performed by the dominant males.

Mating System of Mountain Gorillas

According to early studies, male gorillas do not mate-guard or form consort relationships with females (Harcourt et al. 1980), but more recent observations suggest that mate guarding may occur (Sicotte 1994; Watts 1996). Female choice also probably influences male mating patterns (Small 1989). Interestingly, all 11 female gorillas that were observed to copulate more than twice in this study mated with more than one male. Additionally, it has been hypothesized that male mountain gorillas use two opposing, but not mutually exclusive, mating strategies with females, coercion (aggression) and affiliation (Watts 1992; Smuts & Smuts 1993). Further examination of male–female relationships during oestrous periods is necessary to understand strategies used by males and females to obtain mates in multimale groups.

What influence does mating behaviour have on the costs and benefits of a multimale group structure to dominant and subordinate male mountain gorillas? Paternity determination studies are necessary to fully ascertain the reproductive costs and benefits to dominant and subordinate males. Kin selection may be operating because in most cases males in multimale groups are closely related, although Beetsme's group is an exception (Stewart & Harcourt 1987; Yamagiwa 1987). Dominant male mountain gorillas may benefit from the presence of subordinate males through assistance given during intergroup encounters (Watts 1989; Sicotte 1993), and through the reduced risk of infanticidal attacks on his offspring if he dies (Robbins 1995). These benefits to the dominant male may be great enough to outweigh the loss of reproductive opportunities.

For younger subordinate males, the strategy of remaining in a multimale group to wait for reproductive opportunities can result in higher lifetime reproductive success than emigrating and attempting to form a new social unit (waterbuck, *Kobus ellipsiprymnus*: Wirtz 1981; howler monkey, *Alouatta seniculus*: Pope 1990; golden lion tamarin, *Leontopithecus rosalia*: Baker et al. 1993; savanna baboon, *Papio cynocephalus*: Alberts & Altmann 1994; mountain gorilla: Robbins 1995). Results of this study show that subordinate males may be siring offspring. The mating opportunities in these multimale groups may, in part, keep subordinate males from emigrating.

What is the mating system of mountain gorillas? Part of the difficulty of classifying a species by mating system is that the classification can be made on the basis of group composition, behaviour and/or genetics (Baker et al. 1993). This study provides another example of the influence of demography on mating systems (e.g. black-tailed prairie dog, *Cynomys ludovicianus*: Hoogland & Foltz 1982; redtail monkey, *Cercopithecus ascanius*: Cords 1984; patas monkeys, *Eurythrocebus patas*: Chism & Rowell 1986, Ohsawa et al. 1993; chimpanzee: Sugiyama et al. 1993; blue monkey, *Cercopithecus mitis*: Rowell 1994). In the 60% of mountain gorilla groups that are one-male, the mating system probably is one-male. Results of this study indicate that in multimale gorilla groups, the mating system should be considered multimale.

Acknowledgments

I thank l'Office Rwandais du Tourisme et des Parcs Nationaux and l'Institute Zairois pour la Conservation de la Nature for permission to work at the Karisoke Research Center in the Virunga Volcanoes. I thank the Dian Fossey Gorilla Fund for permission to conduct this research project at Karisoke. Special thanks to the entire Karisoke staff and particularly L. Munyanshoza, S. Kwiha, F. Barabgiriza, E. Rukera, A. Nemeye, A. Banyangandora, K. Munyanganga, F. Ntantuye and J. Mpiranya for their gorilla-tracking skills and patience. I thank D. Doran, A. Fletcher, A. McNeilage, P. Sicotte and D. Watts for their contributions of observed gorilla copulations to the Karisoke long-term records. This research and paper was greatly improved from comments and discussions with D. Abbott, P. Arcese, K. Strier, P. Waser, C. Snowdon and three anonymous referees. This work was supported by a research assistantship from the Dian Fossey Gorilla Fund and a NSF predoctoral fellowship. This is publication no. 141 of the Karisoke Research Centre.

References

Alberts, S. C. & Altmann J. 1994. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist*, **145**, 279–306.

Altmann, S. A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Science*, **102**, 338–435.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–265.

Anderson, C. M. 1986. Female age: male preference and reproductive success in primates. *International Journal of Primatology*, **7**, 305–326.

Baker, A. J., Dietz, J. M. & Kleiman, D. G. 1993. Behavioural evidence for monopolization of paternity in multimale groups of golden lion tamarins. *Animal Behaviour*, **46**, 1091–1103.

Bercovitch, F. B. 1991. Social stratification, social strategies, and reproductive success in primates. *Ethology and Sociobiology*, **12**, 315–333.

Berenstein, L. & Wade, T. D. 1983. Intrasexual selection and male mating strategies in baboons and macaques. *International Journal of Primatology*, **4**, 201–235.

Brereton, A. R. 1995. Coercion-defense hypothesis: the evolution of primate sociality. *Folia Primatologica*, **64**, 207–214.

Bulger, J. 1993. Dominance rank and access to estrous females of male savanna baboons. *Behaviour*, **127**, 67–100.

Chism, J. B. & Rowell, T. E. 1986. Mating and residence patterns of male patas monkeys. *Ethology*, **72**, 31–39.

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

Cords, M. 1984. Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). Zeitschrift für Tierpsychologie, **64**, 313–329.

Cowlishaw, G. & Dunbar, R. I. M. 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, **41**, 1045–1056.

Cross, J. F. & Martin, R. D. 1981. Calculation of gestation period and other reproductive parameters for primates. *Dodo, Jersey Wildlife Preservation Trust*, **18**, 30–43.

Czekala, N. M. & Sicotte, P. 1992. *Urinary Analysis of Free-ranging Female Mountain Gorillas*. Strasbourg, France: XIV Congress of the International Primatological Society.

Dunbar, R. I. M. 1988. *Primate Social Systems*. Princeton, New Jersey: Princeton University Press.

Fedigan, L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology*, **26**, 91–129.

Fossey, D. 1972. Vocalizations of the mountain gorilla *(Gorilla gorilla beringei)*. *Animal Behaviour*, **20**, 36–53.

Fossey, D. 1982. Reproduction among free-living mountain gorillas. *American Journal of Primatology*, **1** (Supplement), 97–104.

Harcourt, A. H. 1981. Intermale competition and the reproductive behavior of the great apes. In: *Reproductive Biology of the Great Apes* (Ed. by C. E. Graham), pp. 301–318. New York: Academic Press.

Harcourt, A. H., Fossey, D., Stewart, K. J. & Watts, D. P. 1980. Reproduction in wild gorillas and some comparisons with chimpanzees. *Journal of Reproduction and Fertility* (Supplement), **28**, 59–70.

Harcourt, A. H., Stewart, K. J. & Fossey, D. 1981. Gorilla reproduction in the wild. In: *Reproductive Biology of the Great Apes* (Ed. by C. E. Graham), pp. 265–279. New York: Academic Press.

Harcourt, A. H., Stewart, K. & Hauser, M. 1993. Functions of wild gorilla 'close' calls. I. Repertoire, context, and interspecific comparison. *Behaviour*, **124**, 91–122.

Hasegawa, T. & Hiraiwa-Hasegawa, M. 1990. Sperm competition and mating behavior. In: *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies* (Ed. by T. Nishida), pp. 115–132. Tokyo: University of Tokyo Press.

Hausfater, G. 1975. *Dominance and Reproduction in Baboons (Papio cynocephalus): A Quantitative Analysis*. Basel: Karger.

van Hooff, J. A. R. A. M. & van Schaik, C. P. 1992. Cooperation in competition: the ecology of primate bonds. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 357–389. Oxford: Blackwell Scientific.

Hoogland, J. L. & Foltz, D. W. 1982. Variance in male and female reproductive success in a harem-pologynous mammal, the black-tailed prairie dog. *Behavioral Ecology and Sociobiology*, **11**, 155–163.

Inoue, M., Mitsunaga, F., Nozaki, M., Ohsawa, H., Takenaka, A., Sugiyama, Y., Shimizu, K. & Takenaka, O. 1993. Male dominance rank and reproductive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. *Primates*, **34**, 503–511.

Janson, C. H. 1986. The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: *Primate Ecology and Conservation* (Ed. by J. G. Else & P. C. Lee), pp. 169–179. Cambridge: Cambridge University Press.

Lott, D. F. 1991. *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.

Martin, R. D. 1992. Female cycles in relation to paternity in primate societies. In: *Paternity in Primates: Genetic Tests and Theories*

(Ed. by R. D. Martin, A. F. Dixson & E. J. Wickings), pp. 238–274. Basel: Karger.

Nadler, R. D. 1989. Sexual initiation in wild mountain gorillas. *International Journal of Primatology*, **10,** 81–92.

Nadler, R. D. 1992. Sexual behavior and the concept of estrus in the great apes. In: *Topics in Primatology. Vol. 2* (Ed. by N. Itoigawa, Y. Sugiyama, G. P. Sachett & R. K. R. Thompson), pp. 191–206. Tokyo: University of Tokyo Press.

Neimeyer, C. L. & Anderson, J. R. 1983. Primate harassment of matings. *Ethology and Sociobiology*, **4,** 205–220.

Ohsawa, H., Inoue, M. & Takenaka, O. 1993. Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates*, **34,** 533–544.

Pope, T. R. 1990. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioural Ecology and Sociobiology*, **27,** 439–446.

Robbins, M. M. 1995. A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour*, **132,** 21–47.

Robbins, M. M. 1996. Male–male interactions in heterosexual and all-male wild mountain gorilla groups. *Ethology*, **102,** 942–965.

Rowell, T. E. 1988. Beyond the one-male group. *Behaviour*, **104,** 189–201.

Rowell, T. E. 1991. What can we say about social structure? In: *The Development and Integration of Behavior: Essays in Honour of Robert Hinde* (Ed. by P. Bateson), pp. 255–270. Cambridge: Cambridge University Press.

Rowell, T. E. 1994. Choosy or promiscuous: it depends on the time scale. In: *Current Primatology. Vol. 2: Social Development, Learning and Behaviour* (Ed. by J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt), pp. 11–18. Strasbourg: Universite Louis Pasteur.

deRuiter, J. R. & van Hooff, J. A. R. A. M. 1993. Male dominance rank and reproductive success in primate groups. *Primates*, **34,** 513–523.

deRuiter, J. R., van Hooff, J. A. R. A. M. & Scheffrahn, W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour*, **129,** 203–224.

Schaller, G. B. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.

Sicotte, P. 1993. Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. *American Journal of Primatology*, **30,** 21–36.

Sicotte, P. 1994. Effect of male competition on male-female relationships in bi-male groups of mountain gorillas. *Ethology*, **97,** 47–64.

Small, M. F. 1989. Female choice in nonhuman primates. *Yearbook of Physical Anthropology*, **32,** 103–127.

Smuts, B. B. & Smuts, R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, **22,** 1–63.

Sommer, V. 1989. Sexual harassment in langur monkeys (*Presbytis entellus*): competition for ova, sperm, or nurture? *Ethology*, **80,** 205–217.

Stacey, P. B. 1982. Female promiscuity and male reproductive success in social birds and mammals. *American Naturalist*, **120,** 51–64.

Stewart, K. J. 1977. The birth of a wild mountain gorilla *(Gorilla gorilla beringei)*. *Primates*, **18,** 965–976.

Stewart, K. J. & Harcourt, A. H. 1987. Gorillas: variation in female relationships. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. M. Wrangham & T. T. Struhsaker), pp. 155–164. Chicago: University of Chicago Press.

Sugiyama, Y., Kawamoto, S., Takenaka, O., Kumazaki, K. & Miwa, N. 1993. Paternity discrimination and inter-group relationships of chimpanzees at Bossou. *Primates*, **34,** 545–552.

Tijskens, J. 1971. The oestrous cycle and gestation period of the mountain gorilla. *International Zoo Yearbook*, **11,** 181–183.

Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, **31,** 667–682.

Watts, D. P. 1989. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology*, **81,** 1–18.

Watts, D. P. 1990. Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zoo Biology*, **9,** 185–200.

Watts, D. P. 1991. Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology*, **24,** 211–225.

Watts, D. P. 1992. Social relationships of immigrant and resident female mountain gorillas. I. Male–female relationships. *American Journal of Primatology*, **28,** 159–181.

Watts, D. P. 1994. The influence of male mating tactics on habitat use in mountain gorillas (*Gorilla gorilla beringei*). *Primates*, **35,** 35–47.

Watts, D. P. 1995. Post-conflict social events in wild mountain gorillas (Mammalia, Hominoidea). I. Social interactions between opponents. *Ethology*, **100,** 139–157.

Watts, D. P. 1996. Comparative socioecology of gorillas. In: *Great Apes Societies* (Ed. by W. C. McGrew, T. Nishida & L. Marchant), pp. 16–28. Cambridge: Cambridge University Press.

Watts, D. P. & Pusey, A. E. 1993. Behavior of juvenile and adolescent great apes. In: *Juvenile Primates* (Ed. by M. E. Pereira & L. A. Fairbanks), pp. 148–172. Oxford: Oxford University Press.

Weber, A. W. & Vedder, A. 1983. Population dynamics of the Virunga gorillas: 1959–1978. *Biological Conservation*, **26,** 341–366.

Wickings, E. J., Bossi, T. & Dixson, A. F. 1993. Reproductive success in the mandrill, *Mandrillus sphinx*: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. *Journal of Zoology, London*, **231,** 563–574.

Wirtz, P. 1981. Territorial defence and territory take-over by satellite males in the waterbuck *Kobus ellipsiprymnus* (Bovidae). *Behavioral Ecology and Sociobiology*, **8,** 161–162.

Wrangham, R. W. 1986. Ecology and social relationships in two species of chimpanzee. In: *Ecological Aspects of Social Evolution: Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 352–378. Princeton, New Jersey: Princeton University Press.

Wrangham, R. W. & Rubenstein, D. I. 1986. Social evolution of birds and mammals. In: *Ecological Aspects of Social Evolution: Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 452–470. Princeton, New Jersey: Princeton University Press.

Yamagiwa, J. 1987. Male life history and the social structure of wild mountain gorillas (*Gorilla gorilla beringei*). In: *Evolution and Coadaptation in Biotic Communities* (Ed. by S. Kawano, J. H. Connell & T. Hidaka), pp. 31–51. Tokyo: University of Tokyo Press.