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Group Fission in a Semifree-ranging Population of Barbary Macaques (*Macaca sylvanus*)

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ABSTRACT. During a 16-month study of semifree-ranging Barbary macaques (*Macaca sylvanus*) the group under observation divided into two groups. Observations were carried out in 1987–1988, at "La Montagne des Singes," Kintzheim, France. A subgroup of monkeys, which was already cohesive at the beginning of the study, became progressively autonomous in relation to the rest of the main group, during the mating season. Overt aggression between the males of the two groups during this period brought about the fission. Only low-ranking genealogies left their group of origin. Dominance relations between females remained identical in both groups except for one lineage. The alpha male and the alpha female of the subgroup had a close relationship before the fission occurred. The sequence of agonistic intergroup relations is described and analyzed in relation to male sexual competition and female alliance power. The results suggest that: (1) the males of the subgroup instigated the fission because it was the best strategy for them to counter sexual competition; and (2) the females followed the males in order to maintain their alliance network, necessary to insure their dominance status over subordinate females.

Key Words: Group fission; Barbary macaque; *Macaca sylvanus*; Sexual competition; Female dominance; Alliance network.

INTRODUCTION

In the course of a study of the social development of female Barbary macaques (*Macaca sylvanus*), carried out at "La Montagne Des Singes," Kintzheim, France, between March 1987 and June 1988, and during May 1989, the main group under observation divided into two autonomous groups. Previous studies of group fissions focused on cercopithecines species, particularly on Japanese macaques (*Macaca fuscata*) (SUGIYAMA, 1960; FURUYA, 1969; KOYAMA, 1970; NISHIMURA, 1973; YAMAGIWA, 1985) and rhesus macaques (*Macaca mulatta*) (DRICKAMER & VESSEY, 1973; MISSAKIAN, 1973; CHEPKO-SADE & SADE, 1979; MALIK et al., 1985). Although group fissions have been observed in Barbary macaques (*Macaca sylvanus*) in the colony of Salem (FDR) (PAUL & KUESTER, 1985) and in the colony of Kintzheim (ELLEN MERZ, pers. comm.) they have never been described in detail. The present paper does so, and attempts to delineate the factors that contributed to the process.

Two main hypotheses have been proposed to account for a group fission. The first hypothesis relates to an overgrowth of the population which would tend to intensify male sexual competition (SUGIYAMA, 1960; FURUYA, 1969; KOYAMA, 1970; YAMAGIWA, 1985); this in turn would tend to prevent some young adult males from achieving a higher rank. These males would become peripheral, and would develop affiliative relations with a certain number of subordinate females of the group. Males and females would eventually leave their group of origin.

The second hypothesis relates to resource competition in female-bonded groups which are typical of the genus *Macaca*. It proposes that if the benefits of group-living, such as defence against predators (van Schaik, 1983) or female cooperation in the competition for resources (Wrangham, 1980), were outweighed by the costs of intragroup competition for food, then females from the low-ranking matrilines should be the first to suffer the burden. Such intragroup competition may be due, to ecological stress (Dittus, 1982) or to population overgrowth among other factors. The subordinate females would tend to separate from the group, creating a new one, when the cost for their fitness becomes too great. This hypothesis accounted for the group fissions that Dittus (1988) observed among feral toque macaques (*Macaca sinica*).

MATERIAL AND METHODS

Study Site

The Kintzheim colony includes approximately 250 Barbary macaques living in a semifree-ranging condition in an enclosure of 24 ha (enlarged in 1986). Details on the vegetation and climate of this enclosure have been previously described (de Turkheim & Merz, 1984). Food is scattered on a daily basis in a geographical pattern which varies according to the groups' movements. This is done in order to minimize aggression and to insure an adequate distribution of food to all animals.

Subjects

Four distinct groups of animals are known to exist in this enclosure (Table 1). The age grouping for males used in this study has been described by Kuester and Paul (1988). The genealogical bonds of each female born after 1974 are known. Thirteen females, whose age varied between 3 and 4 years in 1987, were the focus of the study.

Data Collection

All animals are tattooed, which allows the recognition of individuals. A total of 1,604 hr of observation was recorded. Twenty-minute focal samples (Altmann, 1974) were car-

Table 1. Composition of the groups of the Kintzheim colony before and after the fission of the main group.

Groups	Sex	Infant	Juvenile	Subadult	Adult	Total
Pre-fission:						
Main group	Male	7	18	15	12	132
	Female	15	14	23	28	
Group B	Male	5	6	4	3	38
	Female	1	6	3	10	
Group 112	Male	4	11	5	4	64
	Female	10	8	6	16	
Post-fission:						
Main group	Male	5	15	10[1)]	9	94
	Female	11	10	16	18	
Subgroup	Male	2	3	4	3	37
	Female	4	4	7	10	
Group B	*idem*					
Group 112	*idem*					

1) Male *F59* died during the mating season from a wound inflicted in an inter-male fight.

ried out every day on each of the 13 females. The order of observation was randomized on a daily basis. A 10-min search period was devoted to finding the next focal animal. When one was not found after this time, then the first focal female seen was observed. This was done to insure that every focal subject was observed daily. Three measures of proximity to the focal female were taken, at the beginning, middle, and end of each focal period, in order to collect data on her social network. Animals within a radius of 0 to 0.5 m, 0.5 to 2 m, and 2 to 5 m were identified.

Agonistic and affiliative events implicating other animals were recorded *ad libitum* (ALTMANN, 1974) concurrently with focal sampling, and during the 10-min search for the next focal female.

The mating season extended from September 4, 1987 to April 10, 1988. It was delimited by the first and the last sexual mount with intromission recorded.

BEHAVIORAL CATEGORIES AND DEFINITIONS

Dominance relationships were determined by the direction of displacements and by the outcome of dyadic agonistic conflicts. "Peanut tests" were performed at the end of the study for certain adult males, when the direction of dominance within dyads had not been clearly determined. Aggressive behavior included open-mouth threat, charging, chasing, hitting, and biting.

Affiliation refers to non-agonistic contact such as grooming, mutual perineal inspection, and sleeping or sitting in full or partial body contact. A new grooming bout was recorded whenever the direction of grooming changed in a dyad or when partners began to groom each other simultaneously. If the groomer stopped for more than 30 sec or performed any action other than looking around, the bout was considered to be completed. Grooming dyads observed *ad libitum* were scored only once, unless the direction of grooming had changed.

Three kinds of intergroup encounters were observed. The approach-retreat type of encounter refers to a group retreat which occurs when members from another group approach without emitting any threats. The chase type refers to a rapid submissive flight of one group as another approaches and/or charges. Finally, a counter-attack refers to a conflict between one or more members of two distinct groups, resulting in one group being pursued by the other.

The moment of fission and the end of the fission process were determined using three criteria, as described by CHEPKO-SADE and SADE (1979): (1) the maintenance of spatial separation between the two groups; (2) the stabilization of adult female membership of the two groups; and (3) the occurrence of intergroup agonistic encounters between the two groups.

In this study the term "main group" refers to the original group that divided into two; the term "subgroup" refers to the unit that left the main group. For the sake of simplicity, the two terms will be used when describing events that took place before and after the fission.

RESULTS

COMPOSITION OF GROUPS

The subgroup was already identified within the main group, at the early stage of the study, although its composition was not yet stable. Figure 1 presents the composition of

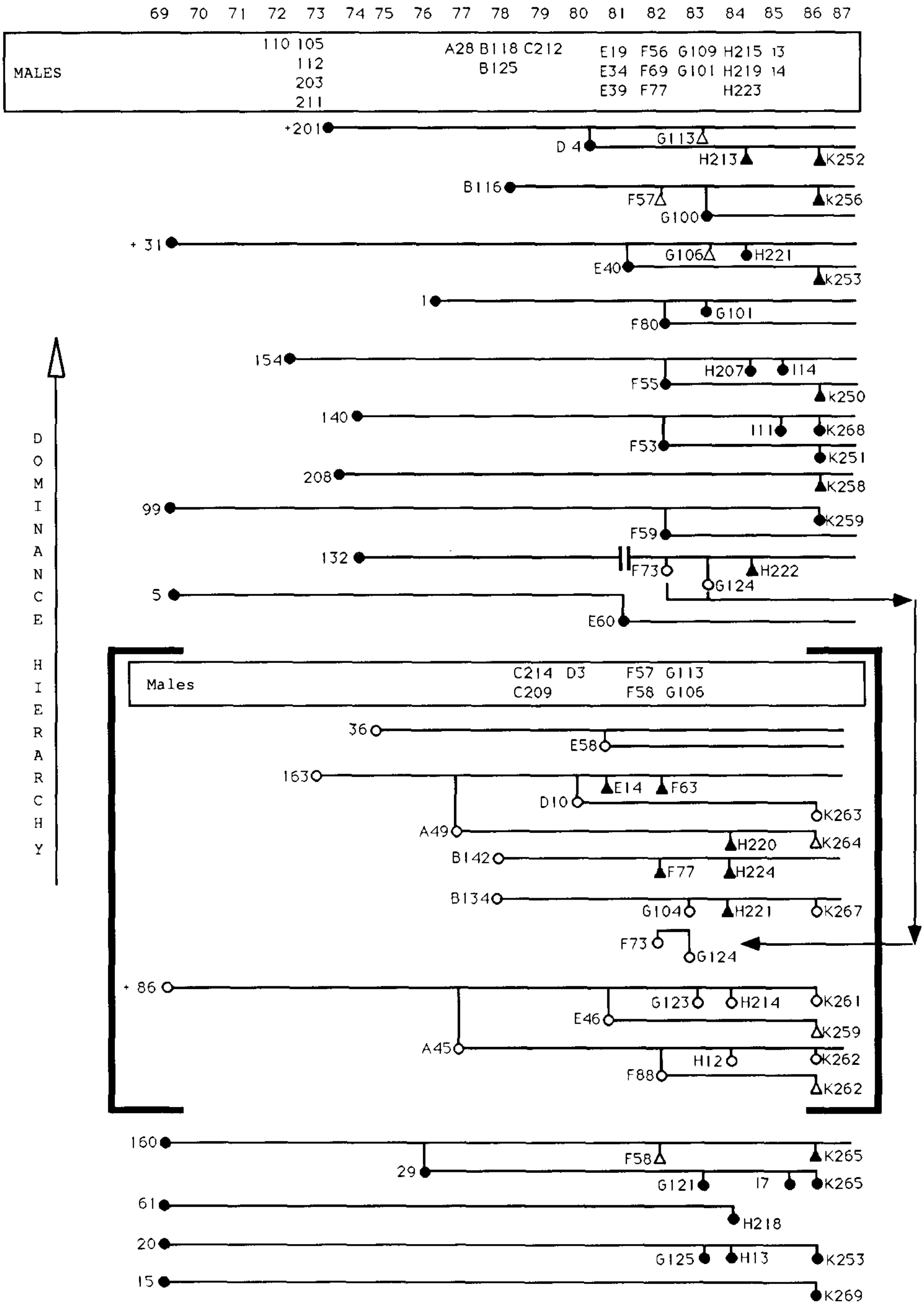

Fig. 1. Date of birth and genealogical relations through the maternal line of the main group animals prior to the fission. ▬ Delineations of the subgroup genealogies; + animals who died; ▲ main group males; △ subgroup males; -||- point of fission; ● main group females; ○ subgroup females; → rank reversal.

Table 2. Monthly affiliation frequencies for the focal females of the main group and subgroup, each compared to its intergroup monthly frequencies for the pre-fission period.

Months	Main group	Intergroup	Subgroup	Intergroup
July 1987	150	11	55	12
August	128	13	55	9
September	102	13	108	9
October	154	16	114	10
November	79	0	73	2
Mann & Whitney test (two-tailed)	$U=0$, $Z=2.611$, $p<.008$		$U=0$, $Z=2.627$, $p<.008$	

Table 3. Frequencies of presence of focal animals during scan samplings for the main group and the subgroup females, each compared to its intergroup frequencies for pre-fission period.

Months	Main group	Intergroup	Subgroup	Intergroup
July 1987	203	47	136	64
August	163	48	131	65
September	220	43	164	64
October	278	32	199	63
November	241	10	120	18
Mann & Whitney test (two-tailed)	$U=0$, $Z=2.611$, $p<.008$		$U=0$, $Z=2.611$, $p<.008$	

the two groups as they appeared at the end of the fission process (five mid-ranking females of the main group, with no kin, are not represented in the figure).

The data on affiliation and the data on spatial proximity between the focal females indicate the formation of the subgroup within the main group. Eight focal females were members of the main group while five were members the subgroup. From July 1987 to the moment of fission in December (Table 2), the monthly frequencies of intragroup affiliation for focal females are significantly higher than those of intergroup affiliation; this is true for both groups.

The second indication of the formation of the subgroup refers to the spatial distribution of the groups (Table 3). It is assumed that the physical proximity of the focal females to each other is representative of that of the other females of their group. The measure of proximity is based on the scans performed during the focal sampling. From July to the end of November 1987, 3,639 proximity scans were done. A focal female, belonging to the same group as the female observed, was in the vicinity of this female significantly more often than she was in the vicinity of a focal female of the other group.

THE FISSION PROCESS

The data presented above reveal that the subgroup was already distinct from the main group in July 1987. However, one cannot conclude from this that a fission had already taken place. Until October 1987, agonistic events between members of the two groups were mostly dyadic. They never consisted of a coordinated action by many animals of the main group that would have triggered a group displacement or a flight (Table 4).

The mating season began in early September 1987. As it intensified, the distance between the subgroup and the main group increased. From October 1987 on, although some females from the two groups continued to affiliate with one another, the first intergroup encounters of the type approach-retreat were observed. In all cases the main group displaced the subgroup. Yet, the subgroup was not independent of the main group. On November 16, females of the subgroup had an agonistic encounter with the females of a third group, Group 112.

Table 4. Evolution of the main group and the subgroup relationship.

Months	Groups1)	Number of episodes	Type of interaction
July 1987 – September	—	—	—
October	MG-SG	2	Approach/Retreat
November	MG-SG	2	Approach/Retreat
	MG-SG	1	Chase
	Gr.112-SG	1	Fight2)
November 25	MG-SG	Inter-males	Counter-attack
······	······	······	······
December	MG-SG	1	Approach/Retreat
	Gr.B-SG	1	Chase3)
January	MG-SG	4	Chase
January 8	MG alpha male-SG	# 3 male	Counter-attack
February	MG-SG	5	Chase
March	MG-SG	2	Chase
April	MG-SG	4	Chase

1) MG: Main group; SG: subgroup; 2) males *118*, *112*, *F69*, *E39*, and *G109* from the main group support subgroup members; 3) males *118* and *112* from the main group chase subgroup members. In all intergroup encounters the subgroup retreated. ···: Moment of fission.

Females assaulted and inflicted serious wounds on each other. Two high-ranking males (*118* and *112*) and three mid-to-low-ranking males (*E39*, *F69*, and *G109*) belonging to the main group ran to the site and supported the subgroup, resulting in the flight of Group 112.

On the morning of November 25, for the first time, males of the subgroup retaliated upon the main group for a charge. The alpha male of main group, *203*, two other adult males, the beta female, *B116*, and a few mid-ranking females charged the subgroup animals who were foraging. The alpha male of the subgroup, *C214*, and the subadult male, *G113*, charged and threatened some main group males. Additional animals of the main group joined and pursued the subgroup members. Following this incident, the encounters between the two groups were always of the chase or counter-attack types, except for one occasion. This indicates that the two groups were becoming autonomous. During the following year the subgroup was constantly chased by members of the main group, and subgroup animals were individually attacked and/or pursued (ELLEN MERZ, pers. comm.).

On the basis of the criteria of CHEPKO-SADE and SADE (1979), a fission is considered to be completed when female transfer has ceased. This took place at the end of April 1988 when female *G124*, whose mother (*132*) had stayed in the main group, returned to this group (N.B.: In the analysis, she is considered to be a member of the subgroup, having spent all the process of fission with this group).

During observations in May 1989 (one year later) no affiliative contact was recorded between individuals of the two groups. No male or female transfer had taken place and the hierarchy was still the same for both males and females. The subgroup was found to be a cohesive group living at the northern end of the enclosure and avoiding the main group. It was once seen to "displace at a distance" some members of the main group including two mature males.

The foregoing description shows that the fission process was not a discrete incident, but rather a continuum of events that ultimately led to the splitting of the original social network into two autonomous groups. However, in order to analyze the social interaction with respect to the fission, a line had to be drawn which would allow the comparison of pre-fission and post-fission behavior. December 1, 1987 was considered to be the beginning of the post-fission period for three reasons: (1) the subgroup had retaliated for the approaches of the main group for the first time around mid-November; (2) in December, males *118* and *112*, who had supported the subgroup in a previous intergroup encounter, pursued the subgroup, during an intergroup chase involving the subgroup and a third party (group-B); and (3) from December on, all intergroup encounters except for one, happened at a higher level of aggression.

MALE AND FEMALE RANK RELATIONS FOLLOWING THE FISSION PROCESS

No rank reversal was observed in the main group after the fission. The lineages that left the main group were mid-to-low-ranking (Fig. 1). All related females and infants followed their matriarch in the transfer, except for the lineage of female *132*. The fission occurred within her lineage.

Female *132* was often seen in affiliation with subgroup members during the pre-fission period. Nevertheless, she did not transfer to the subgroup, as did her daughters. She was attacked and wounded in August 1987, probably during a conflict with the subgroup members, although the attack was not observed. This would explain the fact that following this incident, she was seen rarely in the vicinity of the subgroup. This incident had a direct consequence on the dominance rank of her daughters, females *F73* and *G124*. These females were outranked by females who were previously subordinate. Table 5 presents the dominance relationships between female *132* and her daughters, and the dominant females of the subgroup, before August 1987. One may see from this matrix, that female *132* and her daughters were dominant over all females of the subgroup before this date (neither displacement nor agonistic interaction was observed between the future alpha female *36* and female *132*).

Table 6 presents the dominance relations of *132*'s daughters after she was attacked. The

Table 5. Dominance matrix for the lineage of female *132* in relation to the subgroup dominant females, before August 1987.*

	132	*F73*	*G124*	*36*	*E58*	*163*	*A49*	*D10*	*B142*	*B134*	*G104*
132	—	1	1		1	1		1		1	
F73		—	4							2	2
G124			—								4
36				—							
E58					—						1
163						—					
A49							—				
D10								—			
B142									—		
B134										—	
D104											—

*Frequencies of threats and aggressions received by the females in the top line, from animals in the left column.

Table 6. Dominance matrix of sisters *F73* and *G124* in relation to the subgroup dominant females, after August 1987.

	36	*E58*	*163*	*A49*	*D10*	*B142*	*B134*	*G104*	*F73*	*G124*
36	—								1	
E58		—							1	8
163			—							6
A49				—					1	11
D10					—				4	7
B142						—			1	8
B134							—		7	5
G104								—		18
F73								4	—	12
G124										—

Conventions as in Table 5.

oldest daughter *F73* (aged 5 years) was able to maintain her rank over her last challenger (*G104*) until the end of September 1987, while her younger sister *G124* (aged 4 years) was able to do so until her mother stopped affiliating on a continuous basis with the subgroup. Both sisters dropped in rank ending subordinate to the matriline of female *B134* (arrows in Fig. 1).

No male over 3 years of age and related to the females of the subgroup transferred with his kin. On the other hand, four males unrelated to the subgroup (mean age 5 years) joined the three central adult males during the mating season (Fig. 1). These four males maintained the same relative rank among themselves as they had had when they were members of the main group, in spite of the fact that each male transferred at a different time. Three of them, *G113*, *F57*, and *G106*, were sons of the most dominant females of the main group, *D4*, *B116*, and dead female *31*, respectively.

The alpha male of the subgroup, *C214*, maintained a preferential relationship with the alpha female *36* during the entire study period. He was repeatedly seen in affiliation with her. Although measures of proximity were carried out only on focal females, *ad libitum* data on affiliation reveal that *C214* was in contact with this female four times more often than was any other adult male (68 times, versus 12 for male *D3*, and 15 for male *C209*). Moreover this frequency of affiliation is the highest recorded for any male-female relationship in the subgroup.

EFFECTS OF THE FISSION ON REPRODUCTIVE ACTIVITY

The fission occurred within the largest group of the Kintzheim colony (Table 1). The difference in size between the population of the main group and that of the two others, Groups B and 112, was statistically significant ($\chi^2=21.26$, $df=2$, $p<.05$).

Table 7 presents the ratio of sexually active males to sexually active females, before and after the moment of fission, for each group. The comparison of these ratios during the pre-fission period (the subgroup population is thus included in the main group) shows that the main group had the lowest ratio of all groups. In the post-fission period, the sex-ratios increased in the subgroup and decreased in the main group.

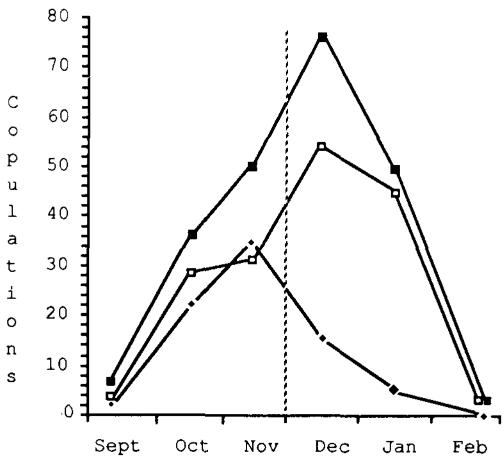

Fig. 2. Copulation frequencies within and between the two groups. -■- Main group; -□- subgroup; -◆- intergroup; ----- Delineation of pre-fission and post-fission periods (December 1, 1987).

Table 7. Reproductive population and sex-ratio.

Group	Male	Female	Sex-ratio
Main group (pre-fission)	27	48	1:1.78
Group B	7	13	1:1.86
Group 112	6	17	1:2.83
Main group (post-fission)	19	32	1:1.63
Subgroup	7	16	1:2.29

The male to female ratio is evaluated including 4.5-year-old males and 3.5-year-old females.

Data on copulations within the main group, within the subgroup, and between the two are presented in Figure 2. The intergroup copulations declined drastically in December despite the fact that this month coincided with the peak of the mating season for both groups. It is noteworthy that the males from the main group were responsible for 86.4% of all intergroup copulations recorded.

DISCUSSION

Role of Males in the Fission Process

The fission took place in the largest group of the Kintzheim's population (132 animals). Malik et al. (1985) reported that when their groups of feral rhesus monkeys grew larger than 120 animals they tended to lose their internal cohesiveness, which led eventually to a group fission. Previous studies of group fissions among Japanese macaques have demonstrated that a fission tends to occur when there is an overgrowth in the population. Sugiyama (1960), Furuya (1969), and Koyama (1970) stated that their populations were all larger than 100 animals. It is also generally admitted for Japanese macaques that a lack of cohesion appears within social relationships when groups become too large; a condition which would favor the creation of subgroups (and eventually a fission between these units) (Sugiyama, 1960; Furuya, 1968). In such a context, dominance relations between males would become very unstable. The greater number of young adult males would prevent certain males from achieving the dominance rank that they would normally attain in a smaller population. Yamagiwa (1985) suggests that a rise in the number of males contributes to the increase of intra-sexual competition, which in turn, raises the probability of a fission.

The conditions which existed in the main group prior to the fission conform well to the ones described in the above studies. The main group had the lowest ratio of females per male of all the groups in Kintzheim. In addition, data on the demography of the main group also support the hypothesis that turmoil in the male dominance order, before observations had begun, could have caused the adult males of the subgroup to become peripheral, while they were members of the main group. The dominance rank of these males within the main group could not be assessed at the beginning of the study.

Data on intergroup encounters and copulations also support the hypothesis that males initiated the fission process. The subgroup males tended to break off relations with individuals of the main group during the pre-fission period. This is indicated by the fact that the subgroup as a whole began to avoid the main group approaches in October 1987, when the mating season intensified. Moreover, the males began to retaliate for charges of the main group at the end of November, and in December there was a rapid decrease in intergroup copulations. Finally, males of the subgroup were involved in less than 15% of the total number of the intergroup copulations, while females of the subgroup continued to be in affiliation with males of the main group, participating in more than 85% of the intergroup copulations.

These results show that the subgroup males refrained from interacting, with the main group when the mating season intensified. On the one hand, the sex-ratio in the subgroup indicates a clear advantage for these males to mate with the subgroup females. By keeping their distance from the main group, and on condition that the subgroup females followed, the subgroup males could copulate while minimizing the risk of conflicts with the males of the main group. The agonistic responses to the main group approaches prevented the main group males from copulating with the subgroup females. On the other hand, from the point of view of the males of the main group, the fact that they were at a disadvantage regarding the sex-ratio is illustrated by the observation that they tried to maintain relations with subgroup females until the onset of conflicts between males. It is also highlighted *a posteriori* by the fact that the main group underwent a second fission during the fall and winter of 1989–1990 (ELLEN MERZ, pers. comm.).

If one interprets the data on intergroup copulations as an indication of the willingness of the subgroup females to continue to associate, at least partly, with the main group, then the following question is raised: what were the advantages for the females of the subgroup to follow the males in the fission process?

ROLE OF FEMALES IN THE FISSION PROCESS

DITTUS (1988) showed that in four fissions which took place in groups of feral toque macaques, the cost to the females of competition for food outweighed the benefits of group living, causing a group of females to become peripheral, and eventually to leave their group of origin. In the present case, however, socioecological factors are probably of minimal importance because the population is fed. Data on female copulations also indicate that the subgroup females did not initiate the fission process. Thus, food competition was probably of minimal importance in the case of this fission.

The reason for the willingness of females to follow the males in the process of fission may be explained by their need to maintain affiliation with females of their immediate social network, in order to secure their social position. In the species that form matrilineal hierarchies, such as the Barbary macaque, rank reversals among unrelated females do happen occasionally and appear to be the result of support interventions and coalitions among unrelated females. Research by CHAPAIS and SCHULMAN (1980), WALTERS (1980), DATTA (1983), CHAPAIS (1983), CHENEY (1983), NETTO and VAN HOOFF (1986), HUNTE and HORROCKS (1986), and PEREIRA (1988) on baboons, macaques, and vervets, revealed that non-kin females do support each other during agonistic conflicts. The direction of aid always favors the dominant opponent. The supporter may be dominant to both animals in conflict, but is always dominant to its target. In this way, the supporter and the recipient reinforce their own rank and reaffirm their power of alliance against the target. In other words, the aid flows downward in the female dominance order. This pattern would explain why female hierarchies are stable and rank reversals infrequent. CHAPAIS (1988, in press) induced rank reversals experimentally among Japanese macaques by manipulating the composition of the group. His results indicate that the status of high-ranking females depends strongly on their having a more powerful alliance network than that of the subordinate females.

The necessity to have and to maintain an alliance network, even for dominant females, could explain why females followed males in the process of fission. The alpha female (*36*) of the subgroup was in constant affiliation with the alpha male (*C214*). This type of longterm association (not confined to the mating season) between an adult male and an adult female is frequent in cercopithecines and well documented (see SMUTS, 1985 for a review). Such a female may benefit from the support of her male associate in case of conflict (SEYFARTH, 1978; SMUTS, 1983; CHAPAIS, 1986). One can therefore presume that female *36*, benefited from a powerful alliance by maintaining a preferential relationship with male *C214*.

The finding that females need their alliance network to maintain their position, and the above argument, could explain why the females of the subgroup proceeded with the fission. When the alpha female *36* decided to follow male *C214* during the fission, the females immediately subordinate to her followed her, so as to not weaken their network of alliances which could have put them in jeopardy of a rank reversal with respect to lower ranking females.

The need to maintain a network of alliances could also explain why female *132* did not transfer into the subgroup and why her daughters were outranked. One effect on the females of the subgroup of being peripheral, was to restrain them from affiliating with the higher ranking females of the main group, who were potential allies in case of conflict with more subordinate females. It is thus suggested that female *36* counterbalanced the loss of these potential supporters by affiliating with male *C214*, while female *132* had weakened her potential support. This unequal power of alliance of female *132*, compared to that of female *36*, may have permitted the attack suffered by female *132*; attack which probably caused the cessation of her association with the subgroup females in August 1987. At least three cases of rank reversal between unrelated females have been reported in Japanese and crab-eating macaques (KOYAMA, 1970; CHANCE et al., 1977; GOUZOULES, 1980), in which a male was considered to have a determinant role. In the present case, female *36* may have become the subgroup alpha female because of her relationship with male *C214*.

The younger daughter of female *132*, *G124*, stayed in the subgroup until April 1988. She later returned to the main group. Following the attack on her mother, she was immediately outranked by the females of the subgroup of matrilines *36*, *163*, *B142*, and *B134*. Female *132*'s eldest daughter, *F73*, was slowly outranked, and by October 1987 was clearly subordinate to these females. CHEPKO-SADE and SADE (1979) suggested that if a fission occurs within a matriline, it will probably happen between the eldest daughter and her mother, because this daughter is subordinate to her younger sisters (KAWAMURA, 1958–65) and therefore is the most peripheral female of her matriline. In the light of PAUL and KUESTER's (1987) study of female rank relations in Barbary macaques, this hypothesis seems improbable. They showed that the pattern of "age-inverse hierarchy" between sisters is not as clear-cut in this species as it is in rhesus or Japanese macaques. One hypothesis, as to why female *F73* did transfer into the subgroup, is that the costs associated with a low rank in the main group exceeded those associated with a middle rank in the smaller subgroup.

MALE AND FEMALE SOCIAL NETWORKS IN BARBARY MACAQUES

The importance of an affiliative network may also be illustrated by two points. First, the four lowest ranking matrilineages of the main group did not leave with the subgroup. All four matriarches were old (Fig. 1), socially peripheral, and approaching senescence, while none had mature daughters through whom to maintain active social bonds, except for female *160* (in prep.). To maintain affiliative bonds with dominant allies was probably less important to them, which could explain why they did not join the subgroup.

The second point concerns the six juvenile and subadult males who did not follow their kin in the fission. KUESTER and PAUL (1988) showed that Barbary macaque males, in order to acquire their rank, are not as directly dependent on their mother's rank, as are rhesus macaques (LOY & LOY, 1974; SADE, 1967) or Japanese macaques (KOYAMA, 1967). The rank of a young Barbary macaque male is influenced by the timing of his birth relative to other males of the same age, and by the existence of a brother. Sons of subordinate females may outrank daughters of higher ranking females during the 2nd year of life. Accordingly, it may be inferred that these males did not depend on their female kin to establish or maintain their own rank; consequently they had no need to follow them in the fission.

INTERGROUP RELATIONS IN BARBARY MACAQUES

No study has ever described a group fission in Barbary macaques, but DEAG and CROOK (1971) and DEAG (1973, 1974) reported that independent groups were sometimes seen affiliating or joining. WRANGHAM (1980) hypothesized that this apparently non-competitive behavior of the Barbary macaque groups would differentiate them from other female-bonded groups. MEHLMAN and PARKHILL (1988) discussed this question in the light of WRANGHAM's model, and concluded that the behavior of Barbary macaques did indeed conform to the predictions inferred from the study of female-bonded group. The general pattern of fission observed in this study is very similar to the known pattern for Japanese or rhesus macaques. Once the fission had occurred, in early December 1987, intergroup encounters became essentially agonistic, and remained so during the following year. In May 1989, the subgroup was living in the northern sector of the enclosure and avoiding the main group. No affiliative contact was recorded between any of the animals in either group. All of this appears to demonstrate the xenophobic character of Barbary macaque groups, and supports MEHLMAN and PARKHILL's (1988) conclusion that this species behaves as a typical female-bonded society.

CONCLUSION

The observed group fission involved the formation of a cohesive subgroup composed of several females and three adult males within the main group. With the beginning of the mating season of 1987, this subgroup became more and more distant from the main group. The fission took place when the subgroup males retaliated for charges by the main group. From this time on, relations became essentially aggressive and the two groups became autonomous. It is suggested that the behavior of the subgroup males had the effect of diminishing sexual competition with the males of the main group. However it does not explain the motivation of the females to follow them in the fission process. Having discarded the explanation of food competition because this population is fed, it is suggested that females left the main group because they needed to stay in affiliation with females forming their network of alliances, in order to counter more subordinate females in the competition for rank. Finally the general pattern of fission and the type of agonistic intergroup interaction observed in this study conform well to the overall pattern known for other species of cercopithecines, suggesting that Barbary macaques behave as do other female-bonded groups.

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