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Sex differences in fitness following a group take-over among Toque macaques: testing models of social evolution

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Summary. A group of toque macaques took-over the home range of one of its subordinate neighboring groups and fused with it to form a larger cohesive group. In the 7 years before the take-over, the dominant group had consistently won all contests at common feeding sites, yet the fitnesses of the females of these two groups did not differ significantly (Fig. 2A). After the take-over the females of the subjugated group occupied the lowest ranks in the combined dominance hierarchy of the merged groups (Fig. 1) and thereby lost the advantages of an own home range, such as priority of access to food. Consequently, in the merged group, survivorship and reproductive success among the subjugated females were significantly less than among the females of the dominant subgroup (Table 2, 4). The dominant matrilines grew numerically and replaced all of the subjugated females, and all but one of their offspring, within 8 years after the take-over (Fig. 2B). These data support the hypothesis that cooperation among female kin in defending resources against strange females is important in the evolution of female-bonded groups. Before the merger all 5 natal males of the subordinate group had transferred to the dominant group, where they occupied high and mid-level dominance ranks (Fig. 1). These males survived at a significantly greater rate than their subordinate female kin. Thus, the cost of group transfer seems to be greater for females than for males, and this may be one reason that females generally do not emigrate or that groups do not fuse. The data suggested three hypotheses. First, since large body size and other adaptations for fighting, giving males an advantage in male-male competition for mates, are also of advantage in resource competition with males *and females*, such male characters may also be favored by non-sexual selection, especially where male reproductive strategy involves group transfer. Second, female bonded groups evolved as female defensive coalitions against not only female but also *male* resource competitors, there having been a mutual influence in the coevolution of large-sized males and female gregariousness. Third, female defensive coalitions against large-sized aggressive males are also advantageous outside the context of food competition, or, independent of foraging strategy.

Introduction

Intragroup competition for limiting food resources often adversely affects the fitness, particularly of low ranking primate individuals that live in social groups (Dittus 1977, 1979, 1980). The amount of food resources that are available to any one group is partly determined by other groups who compete for shared resources in areas of range overlap. In the population of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka, intergroup resource competition has been shown to jeopardize the fitnesses of females of low-ranking groups, and so to limit the growth of such groups, particularly at times of environmental stress (Dittus 1977, 1982).

These kinds of relationships suggest that behaviors such as cooperative defense, which would give an advantage in intergroup competition, should be selected for. Wrangham (1980) has proposed that such cooperation among female kin is the main reason for their living together in female-bonded groups. The evolution of such groups would be favored particularly among those primate species whose diets change seasonally from small dispersed food resources to large defendable

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ones like fruiting trees. The negative effects of intragroup competition are considered as one of the costs that are outweighed by the benefits gained through cooperation in competition with other groups.

The subjects of this paper, toque macaques, have all the ecological and social attributes typical for female-bonded groups. Females breed in their natal groups and rarely transfer between groups, whereas males emigrate out of their natal groups at adolescence. Hence, the adult female members of groups are matrilineally closely related to one another but not to the adult males. Intragroup female relationships, such as grooming, dominance hierarchy and agonistic aids are differentiated and consistent, usually according to matrilineal relationships (Dittus 1975, 1986).

In the population of toque macaques at Polonnaruwa, a subordinate group was no longer able to defend its home range against the incursion of one of its dominant neighboring groups. Consequently, the dominant group took over the subordinate group's home range. In this process the two groups merged to form a new cohesive group even though the natal members of the different groups were not close kin nor had they a shared history of intimate social relationships. Before fusion the sizes of both groups had been less than the median size (in a population of 18 groups). Their fusion created a group of approximately median size. The events which led up to and followed the group fusion have been documented elsewhere (Dittus 1986).

The group fusion is particularly relevant to theories of the evolution of female residence patterns. For example, building on earlier predictions by Crook (1972) and Alexander (1974), van Schaik et al. (1983) have shown that the ability to detect predators increases with group size among forest living primates, and they suggested that predation is the only selective force favoring group living. Terborgh (1983) has argued similarly. Accordingly, one might predict that members of two small groups would cooperate in a merger to form a larger group, and that their fitnesses would be enhanced owing to the larger group's more effective anti-predator defense capability. Group fusion is less readily predicted, however, if gregariousness among female relatives evolved primarily as a strategy of cooperation in the defense of food resources against competing groups. One aim of this paper is to examine the effects of the group fusion on the fitnesses of the individuals of both groups and so to test between these alternative theories. Since both males and females were involved in the group fusion, the data also serve to elucidate sex differences in the ability to survive in a foreign social environment, and hence, to clarify the roles of males and females in the evolution of social groups.

Methods

Study area, period and subjects

Data were recorded between September 1968 and March 1984 as part of a long term study of a population of toque macaques living in the Nature Sanctuary and Archaeological Reserve at Polonnaruwa, Sri Lanka. Observations were continuous between September 1968 and May 1972 and again from March 1975 to March 1984. Intermittent observations were taken between May 1972 and March 1975. The natural dry evergreen forest which the macaques inhabit, as well as several aspects of macaque behavior and socio-demographic relationships, have been described earlier (Dittus 1977a, b, 1985). All macaques in the study groups were individually identified. The macaques were well habituated and could be approached to within 1 to 3 m. The results given here pertain to mainly two groups, labeled A and SG, out of a sample of up to 23 that were under study.

Life-histories, ages and kinship

All groups were censused at least once per month during years of continuous study. During the birth season females were checked every 1–5 days in order to determine neonatal birthdates with accuracy. The demographic fates of all individuals were recorded according to their identity, age, and the range of known dates within which an event occurred.

Following Dittus and Thorington (1981), individuals were classified into broad age-sex classes. A female was adult if she had had an infant, or juvenile if she had not. Most females give birth to their first infant in their sixth year of life. A male was adult if he had acquired the physical size and morphological characteristics typical of adults; subadult if he was as large as or larger than an adult female but physically not as fully developed as a typical adult male; and juvenile if he was smaller than a subadult. Among males the transitions from juvenile to subadult and from subadult to adult occur usually during the 6th and 9th years of life, respectively. Infants of either sex typically were nursing, carried by the mother and less than one year old.

Chronological ages of individuals born after the onset of the study were known, those of individuals born earlier were estimated retrospectively according to known correlations between age and morphological development based on fifteen years of developmental data. Matrilineal relationships were known through birth. Kinship for two individuals was estimated according to morphological traits that were noticeably specific to a known matriline.

Behavioral definitions

An individual was considered *dominant* over another if it consistently supplanted it in contests over food, water, resting and sleeping places, mates, grooming partners or similar resources (Richards 1974). The direction of agonistic signals (threats and appeasement gestures) in all social contexts were in agreement with these measures of dominance. A *group was dominant* over another if it consistently supplanted it from feeding or other sites where the two groups encountered one another.

Statistical analyses

The observed exponential rates of population growth were expressed as regression coefficients (Caughley 1977). In testing whether such growth rates differed significantly from zero or from each other, the standard error of the difference between both coefficients were taken into account as outlined by Stanley (1963). The special case of Student's *t*-test, where a single observed value (of an interbirth interval) was compared with a sample of several such values, follows Sokal and Rohlf (1981). The application of the Mann-Whitney *U*-test and of the Fisher Exact test follows Sokal and Rohlf (1981) and Siegel (1956). All probability values are at the two-tailed level of significance.

Results

Group composition, kinship and dominance

At the time of the group fusion on March 4, 1976, the newly-formed group consisted of twenty animals of varying ages, kinships and origins (Table 1). The five natal males of Group SG had immigrated into Group A between July and December 1975, before the merger. The adult male SY similarly had immigrated into Group A from Group SG where he had been the sole resident male between March, 1970, and December, 1975. SY therefore was the most probable father of all natal juveniles of Group SG that were five years old or less in 1976. Some of the natal males from Group SG therefore shared paternal and maternal genes with the juvenile females of Group SG.

Groups A and SG had had independent but slightly overlapping home ranges since at least October 1968 when observations began. It is unlikely that these two groups were the products of a recent group fission before then because the probability of group fission at Polonnaruwa is low ($P < 0.001$/group/year). Nor were there any male transfers between these groups from 1969 to 1975. The natal animals of the two groups therefore probably were not distant maternal relatives nor did they share recent patrilineal genes.

The dominance rank relationships in March, 1976, following the merger, among the females *within* each subgroup remained the same as they had been in the separate hierarchies before the merger (Dittus 1986). Following the merger, however, all of the natal females of Group SG occupied the lowest ranks in the combined dominance hierarchy of the merged group. And, this rank relationship remained unchanged for as long as a natal female of Group SG survived in the merged group (Fig. 1). Female ranks in general were fairly stable for the eight years after the merger. Changes, such as there were, were owed to deaths and normal processes whereby daughters rose in rank to just below their mothers as they matured to adulthood.

Table 1. The vital statistics, kinships and social histories of all the members of Group A at the time of the fusion of Groups A and SG in March, 1976. Matrilineages are identified by the names of known matriarchs. Parentheses indicate assumed kinship, and * indicates dead matriarchs

Natal group	Matri-line	Name	Age class	Age in years	Social history in Group A
Females					
A	JUDY	JUDY	Ad	>18	native
A	JUDY	LAL	Juv	5.2	native
A	MOLD	MOLD	Ad	>25	native
A	(MOLD)	SAF	Ad	~13	native
A	MOLD	MAG	Juv	6.2	native
SG	TOQ	TOQ	Ad	>15	merged
SG	TOQ	TUP	Juv	~ 2	merged
SG	ONEY*	OBENT	Juv	~ 3	merged
SG	ONEY*	OPI	Juv	~ 2	merged
SG	ONEY*	OFO	Juv	1.3	merged
Males					
?	?	SY	Ad	~17	immigrant
?	?	HEL	Subad	8–9	immigrant
A	JUDY	CAP	Juv	~ 3	native
A	JUDY	JIM	Juv	2.1	native
SG	TOQ	TIM	Subad	6.2	immigrant
SG	TOQ	TRAM	Inf	< 0.2	merged
SG	(ONEY*)	SQN	Subad	7.1	immigrant
SG	ONEY*	OSWALD	Juv	4.1	immigrant
SG	PIN*	PON	Subad	7.1	immigrant
SG	FLAP*	FEL	Juv	4.2	immigrant

Rank changes among the males in the eight years following the merger were few and occurred primarily in relation to the immigration of new males. Although some of the Group SG immigrant males occupied high ranks in Group A for several months after their immigration, they lost rank to a new coalition of immigrant males in October and November of 1976. Thereafter they were mostly mid ranking until their emigration in July 1979 (Fig. 1).

Female survivorship and reproductive success

In comparing the demographic performance of the natal females of Group A with those of Group SG in the merged group, two measures of interest were: first, the survivorship among the original members involved in the merger; and second, their reproductive success in terms of natality and survivorship among offspring that were born after the merger. For Group A this concerned the five females and the two young juvenile males who were alive at the time of the merger plus any new infants born to these females. For Group SG it concerned the five females and one infant male present at

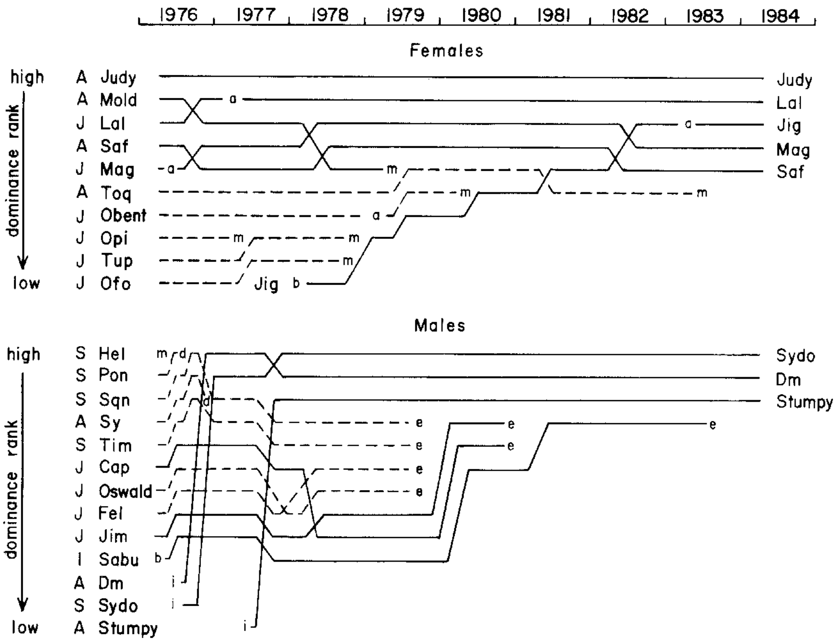

Fig. 1. Changes in dominance ranks and demographic fates, over an eight-year period, among the females and males in Group A following the fusion of Groups A and SG in March, 1976. Natal individuals of Group SG are illustrated with broken lines, others (Table 1) with solid lines. Of individuals born after March 1976, only those which survived to adulthood by March, 1984, are indicated. The names of individuals and their age-classes are shown at left. Age-classes are: *A*, adult; *S*, subadult; *J*, juvenile, *I*, infant. Demographic fates are: *a*, maturation to adulthood as marked by a female's first infant; *b*, birth; *d*, disappearance; *e*, emigration; *i*, immigration; and *m*, death

Table 2. Survivorship after the group merger (March 1976 to March 1984): (a) among the natal adult and juvenile animals of Groups A and SG who participated in the merger on March 4, 1976; (b) among their respective offspring who were born after the merger; and (c) among the total of (a) and (b)

	Number and percent of animals	Adults and juveniles participating in the merger		Offspring born after the merger		All animals	
		Group A	Group SG	Group A	Group SG	Group A	Group SG
Initial cohort size	*n*	7	6	25	5	32	11
	%	100.0	100.0	100.0	100.0	100.0	100.0
Alive on March 5, 1984	*n*	5	0	14	1	19	1
Survivorship	%	71.4	0.0	56.0	20.0	59.4	9.1
Fisher Exact Test, *P*		<0.05		NS		<0.01	

the time of the merger plus any new offspring. The old juvenile and subadult immigrant males from Group SG, who were related to the Group SG females, were not included in this comparison because they generally were independent of these females socially and spatially. That is, these males were subject to a different set of social conditions. The two young males CAP and JIM of Group A were included, however, because they were peers to the Group SG juveniles and they closely associated and interacted with their matrilineal kin.

Survivorships. The overall survivorship (Table 2) among all of the Group A natal animals (59.4%) was significantly greater than that (9.1%) among those of Group SG. The survivorships among only the offspring that were born *after* the merger were 56.0% for subgroup A and 20.0% for subgroup SG, but this difference was not significant. None of the Group SG females that were originally involved in the merger survived, whereas nearly all natal animals from Group A did, at least while being members of Group A. Of the two deaths among the Group A animals, one was of the very old adult female MOLD who had already been postreproductive for 3 to 4 years at the time of the merger. The other was of JIM who died as a 8.6 years old subadult male about two years after he had emigrated from Group A. The deaths of both of these animals was not directly attributable to conditions within the merged group. Nevertheless, including these two deaths as part of the mortality among the Group A natal animals, survivorship among the A subgroup (71.4%) was signifi-

Table 3. The cause of mortality among animals in the merged Groups A and SG between March 1976 and March 1984

Group and age-sex class	Cause of mortality					Total dead	Proportion of deaths by electrocution or automobile
	Perinatal	Old age	Unknown	Electrocution	Automobile		
Group A							
Infant	2		4			6	
Ad Fem and Juv		1	2	2	1	6	3/6
Group SG							
Infant			1			1	
Ad Fem and Juv			5	2	2	9	4/9
Fisher Exact Test, *P*							NS

Table 4. Comparison of interbirth intervals (IBIs) in days among the natal females of Group A and those of Group SG after the merger of these two groups

Name of adult female	Female social rank	Number of IBIs	Range		Mean days	Mann-Whitney *U*	*P*
			Min days	Max days			
JUDY	1	5	312	436	371	1	<0.05
LAL	2	4	363	731	467	8	NS
MAG	3	5	268	606	430		
SAF	4	4	489	829	651	4	NS
Subtotal Group A		18	268	829	471	20	NS
TOQ, Group SG	5	4	423	728	564		

cantly greater than that (0.0%) among the SG subgroup (Table 2). Considering JIM as a survivor of Group A, the survivorship among the A subgroup was 85.7% and differed significantly from that of the SG subgroup (Fisher Exact Test, $P < 0.01$). The greatest difference in survivorship occurred among those individuals which originated from separate groups and that participated in the merger (Table 2).

The home range of Group A/SG was unusual in that a road with electrical poles and wires cut through part of it. During the rice harvest season tiny amounts of rice spilled onto the road from transport vehicles. The macaques foraged for rice along the road sides. Animals generally avoided traffic but when macaque fights occurred, individuals (particularly subordinates) paid less heed to traffic and occasionally used electrical poles as escape routes from aggressors. As these areas of the home range were constantly monitored by local residents and archaeological guards, probably all road kills and electrocutions of macaques were reported to us. Hence, the likelihood of knowing the cause of death was very high when it occurred along the road. The distribution of causes of mortality in Group A/SG after the merger are given in Table 3. About one-half of the deaths among the adults and juveniles of both subgroups A and SG were due to electrocution or automobiles. There was no significant difference between the animals of these subgroups in their susceptibility to this kind of death.

Natality. The interval between successive births is one measure of the rate at which a female gives birth, or, of her natality (Table 4). The interbirth intervals (IBIs) of TOQ of subgroup SG did not differ significantly from those of all of the subgroup A females considered together. TOQ's IBIs were significantly longer, however, than those of the highest ranking female JUDY, but were not significantly different from the mid or low ranking females (Table 4). However, TOQ had had no births for the first two years after the merger (IBI = 728 days) even though her infant had died at the age of only 0.22 years, one month after the merger. Since, in toque macaques as well as in other cercopithecoids, the loss of a young nursing infant generally causes the IBI to shorten (Koford 1966; Tanaka et al. 1970; Angst and Thommen 1977; Altmann et al. 1978), these data suggested an abnormally long IBI for TOQ immediately following the merger. Therefore, a comparison was made with the IBIs of all other females in the Polonnaruwa population whose infants had also died at about the same age as TOQ's infant; that is, at 0.22 years plus or minus 15 days (0.04 years). Among an average of 118 females/year over 10 years, there were 14 such females, the range of their IBIs was 271 to 435 days, mean = 364 days, standard deviation = 52 days. The IBI of TOQ was significantly greater than this subset of IBIs in the population ($t_{13} = 6.75$, $P < 0.001$).

Sex differences in sociodemographic changes

Two of the males from Group SG, SY and PON, disappeared when Group A and the male dominance hierarchy was taken over by two new immigrant males SYDO and DM in October and November 1976. The remaining four natal males (SQN, TIM, FEL and OSWALD) of Group SG, however, survived in the merged group until they emigrated in July 1979 to establish themselves as the sole males in a neighboring Group T (Fig. 1). The 80.0% survivorship among the five natal males of Group SG who had immigrated into Group A before the merger was significantly greater than that (0.0%) among the five natal females of Group SG who merged with Group A (Fisher Exact test, $P < 0.05$).

Population growth rates

The number of survivors among all of the natal animals of Groups A and SG are indicated in Fig. 2. Data were separated so as to distinguish between overall reproductive performance before the merger (Fig. 2A) and thereafter (Fig. 2B). All census totals were taken in March of each year and they exclude infants aged less than six months old. The totals for March 1976 in Fig. 2A include surviving males which were born in 1969 or later but which emigrated from their natal group in 1975. This concerns two natal males of Group A and five natal males of Group SG. These same males cannot be considered as products of their mother's reproductive performances as measured starting *after* the group fusion; therefore, they were omitted from the totals in Fig. 2B. Hence, the totals for March 1976 differ between Figs. 2A and B. Totals in Fig. 2B include natal males which survived to March 1984, but some of which emigrated before then. Thus, totals for Group A include 2 surviving emigrant males in 1981 and 1984, and one in 1982 and 1983.

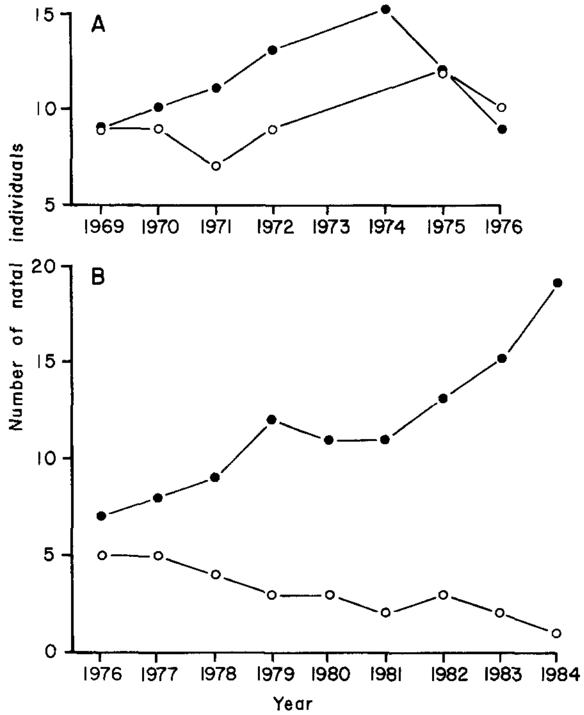

Fig. 2A, B. Cohort growth curves based on the number of natal individuals of Group A (●) and of Group SG (○) that were alive in March of each year: **A** in the seven years (1969–1976) before the fusion of Groups A and SG in March, 1976; and **B** in the eight years (1976–1984) following the group fusion

The mean observed exponential rate of population growth (Caughley 1977) summarizes individual differences in natality, survivorship and reproductive success. It expresses the rate at which a set of one or more individuals grows numerically over time. In the seven years *before* the merger (Fig. 2A), the mean observed exponential rate of growth (r) among the natal animals of Group A ($r = 0.0202$) did not differ significantly from zero growth ($t_5 = 0.65$, $P > 0.50$). That among the natal animals of Group SG ($r = 0.0389$) also did not differ significantly from zero growth ($t_4 = 1.58$, $P > 0.10$). Nor did these rates differ significantly from each other ($t_9 = 0.19$, $P > 0.50$).

In the eight year period after the merger, the Group A females and their offspring increased numerically from 7 to 19 survivors. By March 4, 1984, all of the original Group SG females had died and only TOQ's last infant to be born before she herself died survived as a 2 years old juvenile male (Fig. 2B). The positive rate of growth for subgroup A ($r = 0.1088$) differed significantly from zero growth ($t_7 = 8.82$, $P < 0.001$), as did the negative rate for subgroup SG ($r = -0.1695$) ($t_7 = 5.65$, $P < 0.001$). These rates also differed significantly from each other ($t_{14} = 5.71$, $P < 0.001$).

Discussion

Behavioral asymmetry in the benefit/cost of group fusion

A special relationship had existed between Groups A and SG in the seven years before the merger in that these two groups had contested food resources with each other more frequently than with any one of their other respective neighboring groups. These contests were highly asymmetrical as the dominant Group A had supplanted Group SG on all 41 occasions that an encounter between these groups was observed and resulted in a group supplant. About 95% of the contested resources involved large fruit-bearing trees (Dittus 1986).

This asymmetry was carried over after the merger particularly among the natal females and their juvenile offspring because those of Group SG occupied the lowest ranks in the combined dominance hierarchy of the merged group (Fig. 1). Initially, in the process of the group take-over and for several days thereafter, the Group SG females were frequently harassed by some of the Group A females. Even some time after the merger, when overall aggression towards the Group SG females decreased to normal levels and when affiliative behaviors between the females of the two subgroups increased, the Group SG females were often driven out of or denied access to feeding sites such as fruiting trees. As a consequence the Group SG females occasionally split away from and foraged independently of the rest of Group A in an apparent attempt to avoid resource competition with them. (This behavior would safeguard their threatened fitnesses). These temporary excursions usually did not include any males and continued for three years after the merger by which time three of the natal juvenile females of Group SG had already died (Fig. 1, Dittus 1986).

Before the merger, Group SG was subordinate to its two other neighboring Groups A and 22, so that is mostly relinquished resources when challenged in areas of range overlap. However, in the absence of other groups in such areas, as well as in the exclusive areas of its own home range, Group SG had unrestricted access to resources. The effect of the group take-over was to deprive the Group SG females of such exclusive use of resources in their own range. This occurred because the individuals of Group A could exercise their priority of access to all of Group SG's former resources most of the time, as opposed to only some of them for some of the time. The behavioral data suggested that overall the Group A animals benefited from this take-over at the expense of Group SG (Dittus 1986).

Measured benefit/cost of group fusion

In the seven years that the adult female TOQ of Group SG survived in the merged group, her overall natality was significantly less than that of the alpha female of Group A, but was not significantly different from the birth rates of the mid and low ranking Group A females. Shortly after the merger, however, TOQ had lost her infant and two years passed before she again gave birth. Her interbirth interval was twice that of the mean and significantly greater than the distribution of interbirth intervals of other females in the Polonnaruwa population, whose infants also died at about the same age as TOQ's. Thus TOQ was reproductively inhibited for the first two years following the merger. This inhibition probably was caused by stresses associated with TOQ's sudden drop from high dominance rank in Group SG before the merger to low rank in the merged groups, and with the harassment that she was subject to from the Group A females, particularly shortly after the take-over (Dittus 1986).

All of the Group SG females involved in the merger eventually died, and the order of their death more or less followed their ages and dominance ranks, with the lowest ranking individuals dying first (Fig. 1). TOQ's infant male died first followed by juvenile female OPI. Although OPI dominated the two youngest natal females of Group SG in dyadic relationships, she was often driven to the periphery of the group by an aggressive coalition of the other juvenile females of Group SG. Collectively, the survivorship of the Group SG females was significantly less than that of their higher ranking peers who were native to Group A. With the exception of one of TOQ's sons, all infants born by the Group SG females (TOQ and OBENT) also died. Their mortality was more than twice that of offspring born to the natal females of Group A, but the difference was not statistically significant (Table 2).

Although the cause of mortality for all individuals in the merged group was somewhat confounded by electrocutions and road kills, these artificial agents affected members of both subgroups (A and SG) equally (Table 3). Overall, the data suggest that the differences in survivorship and reproductive success between individuals of subgroups A and SG was attributable, in large part, to factors resulting from the behavioral differences between the members of these subgroups. The most likely factors appear to be nutritional and physiological stresses that are associated with low dominance rank and agonistic harassment.

The combined effects of survivorship and reproductive success (natality plus offspring survivorship) are reflected in the mean observed exponential rate of population growth and in Fig. 2. This rate was positive for the subgroup A animals and differed significantly from the negative rate of subgroup SG. It seems that the natal animals of Group A gained in their fitnesses at the expense of those of the Group SG animals whose home range they took over. Over the seven years before the group merger, however, these rates for the natal animals of Groups A and SG did not differ significantly from each other or from zero growth. That is, the females of Groups A and SG did not differ in survivorship and reproductive performance despite the fact that Group SG was consistently subordinate to Group A. Survivorship and reproductive performance for the Group SG natal females therefore declined as a direct result of the take-over, or, as a consequence of their inability to defend and maintain an independent home range against a dominant competing group.

In the merged group there was a strong tendency among the females and their young to associate spatially with the members of their respective matrilines or groups of origin, especially when foraging (Dittus 1986). Similarly, priority of access to food, as reflected in the hierarchy of dominance ranks, was strongly differentiated by group of origin or kinship. These data support the hypothesis that cooperation among close kin in competition with other less related matrilines is important in the evolution of female residence patterns among female-bonded groups.

By fusing, Groups A and SG increased their group sizes close to the median group size for the population (Dittus 1986). The most frequently observed predators of the macaques at Polonnaruwa were feral dogs, others were jackals, small nocturnal cats, raptors and pythons (Dittus 1975). Although anti-predator defense capabilities may well have been enhanced through group fusion, any benefits that this may have had, appear to have been far outweighed by the negative effects of increased competition, at least for the Group SG females. Thus, while the data in this report do not negate the benefits of gregariousness for defense against predators, they do not support the hypothesis that predation is the sole or principal selective pressure for the evolution of primate social groups as suggested by van Schaik (1983) and Terborgh (1983).

Group fusion in other primates and its relation to female transfer

Altmann (1980) mentions the fusion of two small groups of baboons (*Papio cynocephalus*) in 1972, just after the size of this population had been reduced by 90% (owing to habitat changes and disease between 1963 and 1971). All of the females of the smaller group occupied low ranks in the merged group for at least 10 years after the fusion and their numbers deceased from 6/17 females in 1972–1975 to 3/17 in 1985. After 1982 the ranks of two surviving females (from the original smaller group) and one of their daughters (born after the fusion) rose slightly in the female hierarchy; nevertheless, they still occupied mid and low ranks by 1985 (Samuels et al. 1986). These data suggest that the cost of fusion was higher for the baboon females of the smaller of the two fusion groups, but this cost difference was not as marked as among the two fusion groups of toque macaques at Polonnaruwa.

The transfer of females between groups has been noted in several primates (Moore 1984) and is similar to group fusion insofar as females must cope in a foreign social environment. However, in group fusion, females do not split away from other members of their grown group, and compared to female transfer, group fusion is likely to affect a greater change in range use and intergroup relationships (Dittus 1986). Group fusion also appears to be independent of the factors which influence females to transfer, such as their voluntary transfer to avoid inbreeding [e.g., in gorillas (Harcourt 1978; Pusey 1980)] or infanticidal males (Marsh 1979), and their involuntary expulsion by intragroup competitors (Chivers 1969; Jones 1980; Glander 1980; Crockett 1984).

The evolution of female defensive coalitions against male and female resource competitors and/or male aggressors

In general, group life is thought to be the outcome of male and female reproductive strategies (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). As food mainly limits the reproductive success of females, they distribute themselves in space and time primarily in accordance with ecological factors, i.e., the distribution of food. For males, however, access to females is an additional and overriding factor determining reproductive success. Dispersal therefore is more advantageous for males and they space themselves in relation to female distribution (Trivers 1972; Baker 1978; Clutton-Brock and Harvey 1976; Packer 1979; Greenwood 1980).

Among Old World monkeys and many other mammals, fighting ability, canine teeth, and body size are more developed in males than in females (e.g., Crook 1972; Eisenberg 1981). Such adaptations probably arose primarily through intrasexual selection, whereby physically able males gain an advantage over other males in competition for mates (Trivers 1972; Clutton-Brock et al. 1977; Gaulin and Sailer 1984). But, such traits would also be favored, at least *in part*, by non-sexual selection owing to their advantage in *resource competition* with males *and females*, particularly among primate species where (a) resource competition affects fitness, and (b) male reproductive strategy involves group transfer. Thus, males, owing to their secondary sex characters, are able to rise in status over other individuals more easily than females can. This is true for toque macaques in general (Dittus 1977) and was also the social situation among the males and females from Group SG in the newly formed merged group. As a result, the natal males of Group SG survived at a significantly greater rate than their female kin in the foreign social environment. These data suggest that the costs of group transfer are higher for females than for males among sexually dimorphic species whose individuals compete for resources (food, refuges).

It follows that it would benefit females to cooperate with established allies (male or female) in the defense of resources, not only against other females (or groups), but also against dominant immigrant males. To a certain extent, therefore, female bonding may be a *partial* consequence of the evolution of large sized male competitors. Or, there was a mutual influence in the coevolution of female defensive coalitions and large sized males.

This model differs from Wrangham's (1980) insofar as it considers not only female groups, but also large males and all-male groups as important resource competitors. It underscores the difficulty of identifying which competing sex is more important in promoting female bonding, and takes into account a more realistic social environment confronted by individuals. Furthermore, it predicts that all-male groups too may be selected, at least in part, owing to their worth in resource competition, other advantages relating to male-male competition for mates, and predator defense.

Female bonding also may be beneficial outside the context of resource competition, for example, in coalitions against large males who, in their normal zeal to acquire mates, aggressively herd females away from competing males and often attack and wound females (e.g. Dittus 1977; Whitten and Smith 1984). Infanticide by males would be one special kind of male aggression favoring female bonding (Hrdy 1977) in some species.

As with other models based on cooperation among group members the composition of such groups in primates and other mammals would favor close matrilineal kin for reasons outlined by Hamilton (1964), Eisenberg (1966), and Wrangham (1980, 1983).

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