The influence of intergroup competition on the survival and reproduction of female vervet monkeys

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Summary. Primate groups are often larger than might be predicted from a consideration of within-group competition alone. Wrangham (1980) has hypothesized that females live in extended kin groups in order to defend food resources against other groups. In contrast, others have argued that predation pressure, rather than intergroup competition, favors sociality. Data gathered over 10 years on a population of free-ranging vervet monkeys provide more support for the food defense hypothesis than for the predation hypothesis, and suggest than female reproductive success can be influenced strongly by intergroup competition.

1. Of the three groups under intensive study, the smallest experienced the least predation, arguing against the hypothesis that large groups have evolved as a defense against predation.

2. At least three different measures indicated that larger groups experienced slightly greater infant and juvenile female survival than did smaller groups.

3. Larger groups also had larger and better quality ranges than smaller groups. Large groups were more likely to make incursions into the ranges of smaller groups than vice versa, and to expand their ranges at the expense of smaller groups. Perhaps as a result, females in small groups were more aggressive during intergroup encounters than were females in large groups.

4. Within groups, rank reversals were influenced by the presence of female kin, and individuals with female kin were able to rise in rank over those without kin. There was no evidence that high-ranking females attempted to suppress the recruitment of daughters by low-ranking females, however, perhaps because groups with many females had a competitive advantage over groups with fewer females.

5. Data from a small number of group fusions support the hypothesis that small groups benefit from the recruitment of additional females, particularly in populations in which the average group size is small and mortality is high.

Introduction

One current hypothesis concerning the selective pressures favoring female sociality in primates views female kin groups as alliances that maximize individual access to food resources (Wrangham 1980; see also Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Wrangham 1987). According to this hypothesis, females live in extended kin groups in order to defend patchily distributed food resources against other groups of females. Even though sociality forces females to incur some costs in the form of within-group competition for food, these costs are outweighed by the benefits of excluding large numbers of individuals from the group's resources. A primary assumption underlying this hypothesis is that female sociality occurs because between-group competition has a greater effect on fitness than within-group competition.

In contrast, others argue that predation, and not resource competition, is the primary selective factor favoring sociality in primates (van Schaik 1983; Terborgh 1983; Terborgh and Janson 1986). Using data derived from a number of species, van Schaik (1983) has shown that group size is usually negatively correlated with birth rate, and that juvenile survival is often positively correlated with group size only in areas of high predation. These results, it is argued, suggest that feeding competition increases with group size, and that predation

pressure is therefore the primary factor favoring large groups.

Evaluations of these two competing hypotheses have been confounded by a paucity of data on both predation rates (but see Cheney and Wrangham 1987) and the relative severity of within- and between-group competition. Although numerous studies have documented the effects of within-group competition on reproductive success (reviewed by Silk 1987a), almost none have considered the influence of competition between groups. The only study to claim such a comparison (Janson 1985) concluded that intragroup competition was more intense than intergroup competition simply because aggression occurred at higher rates within than between groups. This conclusion is unwarranted, however, unless single acts of intra- and intergroup aggression can be shown to have similar effects on fitness.

Both predation and between-group competition could favor large groups. Unless it can be shown that between-group competition has no effect on female reproductive success, therefore, it is impossible to conclude that large groups have evolved solely as the result of predation pressure. In this paper, we attempt to test the hypothesis that between-group competition favors sociality through an examination of the effects of such competition on female reproduction and survival in free-ranging vervet monkeys (*Cercopithecus aethiops*) living in Amboseli National Park, Kenya. Within-group competition and predation rates in this population are described elsewhere (Cheney et al. 1981, 1987; Wrangham 1981; Cheney and Wrangham 1987) and will therefore only be summarized here.

Vervet monkeys live in social groups in which both within- and between-group competition occur at high rates. Like many other species of Old World Monkeys, females remain in their natal groups throughout their lives, while males transfer to neighboring groups at sexual maturity (Cheney and Seyfarth 1983). Adult females can be ranked in a linear dominance hierarchy which is generally stable over time, and which accurately predicts priority of access to food, water, and social partners (Seyfarth 1980; Wrangham 1981; Whitten 1983; Cheney et al. 1987). Offspring acquire ranks immediately below those of their mothers (Cheney 1983; Lee 1983; Horrocks and Hunte 1983; Fairbanks and McGuire 1984). Although males are dominant to females in dyadic interactions, females regularly form successful coalitions against adult males (Cheney 1983).

In addition to competing with each other with-in social groups, vervets also compete with neighboring groups. In Amboseli, vervet groups inhabit small, relatively stable ranges averaging approximately 23 ha in size that are actively defended against incursions by other groups. Intergroup encounters occur at a mean of one every 1.7 days (Cheney 1987). Many encounters involve simply the exchange of vocalizations between members of the two groups, but 54% escalate to include threats, chases, and even physical contact (Cheney 1981, 1987). Both males and females are aggressive participants in intergroup encounters.

The analysis that follows is limited by a number of methodological constraints. First, like other primates, vervets mature slowly and are long lived, with the result that female lifetime reproductive success can only be estimated indirectly. Second, sample sizes are limited by small group size and the difficulties of observing many groups simultaneously. The problem of sample size is also aggravated by the high rate of mortality in the Amboseli vervet population, which has caused the population to decline dramatically over the past 10 years (Cheney et al. 1987; see also below). Nevertheless, since the population is characterized by high rates of within-group competition, between-group competition, and predation, the sample does permit some preliminary evaluation of the relative importance of each of these selective factors for the survival of females and even for the survival of groups.

Methods

Study area and subjects

Amboseli National Park consists of arid savanna and savanna woodland, dominated by two tree species, *Acacia xanthophloea* and *Acacia tortilis*. Rainfall is light, and averages 300 mm per year. Swamps are the only sources of water during the dry seasons of January–April and June–November.

Vervet monkeys rely heavily on *A. xanthophloea* trees for their food throughout the year (Lee 1981; Wrangham and Waterman 1981; Hauser 1987). Over the past 25 years, however, a rising saline water table has killed most of the mature trees (Western 1983) and elephant damage has prevented recovery. As a result of habitat deterioration, between 1977 and 1986 the vervet population declined by more than 50%. Average group size also declined by approximately 50% (Hauser et al. 1986; Cheney et al. 1987; see also Struhsaker 1973, 1976). This decrease in population density was not accompanied by a concomitant decrease in rates of either within- or between-group aggression. In 1977–78 each female in the three main study groups threatened another female in her group a mean of once every 6.0 h, compared with a mean of once every 6.1 h in 1985–86. Similarly, in 1977–78 the three study groups encountered other groups a mean of once every 1.8 days. In 1985–86, this figure was 1.9.

The data described in this paper are derived principally from three social groups (A, B, and C) with adjacent ranges.

Groups B and C have been observed continuously since 1977, and Group A since 1975. Three additional groups (2, 3, and 4) were added to this intensive study in late 1983, and other groups are censused regularly (Table 1). In this paper, data relying on longitudinal data are restricted to Groups A, B, and C. Data from Groups 2, 3, and 4, however, have been included in some measures of infant survival and most of the analysis of intergroup interactions.

Births in Amboseli are seasonal, with almost all births occurring between October and January (Cheney et al. 1987). Females become sexually mature at approximately 4, and males at 5 years of age. Animals are habituated to observers on foot, and the mothers, offspring, and maternal siblings of almost all females in the study groups are known. Since females remain in their natal groups throughout their lives, and since this paper is concerned primarily with female reproduction and behavior, unless otherwise stated group size throughout this paper is calculated according to the number of adult females in each group. Between 1977 and 1986 the study groups ranged in size from 2–8 adult females and 1–7 adult males (Table 1).

Although all groups in the study population inhabit small, contiguous ranges, there are clear differences across groups in range quality, depending primarily on the proximity of water (Lee 1981; Hauser 1987). Groups that inhabit ranges bordering the permanent swamps have access not only to water throughout the year but also to a larger number of *A. xanthophloea* trees and a greater diversity of plant species than groups that inhabit the drier *A. tortilis* woodlands. Detailed counts made in both 1979 and 1984 of every plant species in each group's range revealed that groups whose ranges bordered the swamps (Groups B and C) had better quality ranges than did the smaller groups found away from permanent water (Group A in 1979 and Groups A, 2, and 3 in 1984).

Definitions and methods

The data in this paper are derived primarily from four discrete time periods: a 14-month period in 1977–78, an 8-month period in 1980, and 8-month period in 1983, and an 8-month period in 1985–86. These were the time periods when the authors themselves were observing the groups, and the same data-gathering techniques were used in each case. Analysis of discrete time periods also facilitates comparisons of changes in range size and location over time, and to some extent reduces the interdependence of data gathered in sequential years. Data on offspring survival and sex ratio are complete as of October 1986.

Range sizes were calculated using a map divided into quadrats measuring 33 × 33 m, on which were located all trees greater than 5 m high. This map was originally constructed by R. Wrangham in 1978, and was subsequently revised in 1983, 1984, 1985 and 1986 by the authors, M. Hauser, and B. Musyoka Nzuma. During 1977 and 1980, precise ranging data were not gathered, and the approximate circumference of each group's range was estimated by drawing boundaries around the quadrats entered by the monkeys during the entire study period. In 1983 and 1986, more precise information on range use was obtained by noting each quadrat occupied by all group members at half hour intervals. Range sizes were then calculated by drawing concave boundaries that minimized the spaces between quadrats. This method may have underestimated range size. Although the two methods are not strictly comparable, they do permit cross-group comparisons of the size of each group's range relative to its neighbors'.

Data on intergroup encounters were gathered on an ad libitum basis. Encounters were defined as any behavioral exchange between the members of two groups, including vocalizations (Cheney 1981). Aggressive encounters were those that in-

Table 1. The number of adult males and females in the study groups and census groups between 1977 and 1986. Groups A, B, and C are the three main study groups, while Groups 2, 3, and 4 were added to the study in 1983. Censuses were taken as close as possible to March in every year except in 1977, when the census was taken in May. Only those census groups with which the study groups interacted at least five times are listed

Year	A (TW1) ♂	A ♀	B (MGR) ♂	B ♀	C (KH5) ♂	C ♀	2 (TW2) ♂	2 ♀	3 (KIT) ♂	3 ♀	4 (BSL) ♂	4 ♀	1 (TW3) ♂	1 ♀	5 (KH4) ♂	5 ♀	BTG ♂	BTG ♀	TW4 ♂	TW4 ♀	KTS ♂	KTS ♀	KWS ♂	KWS ♀	KTW ♂	KTW ♀	ILM ♂	ILM ♀
1977	7	8	3	7	3	8																						
1978	7	8	3	7	2	8									6	8												
1979	3	4	2	7	4 (5)	7	3	7	4 (5)	7	2	5			3	8												
1980	3 (7)	4	1	7	3 (7)	6	3	3	3	3	2	5			1 (3)	6												
1981	1 (2)	4	3 (5)	6	3 (4)	8	3 (6)	3	2	5	1 (3)	3			2 (6)	8												
1982	3 (5)	4	3 (5)	6	3 (4)	7	3	3	4	5	1	3			2 (6)	8	1 (2)	5										
1983	3 (5)	4	3 (4)	5	1 (2)	4	2	2	2	4	1 (2)	3	4	4	4 (7)	10[b]	2	3	4	4								
1984	3	3	3 (4)	6	2	4	1	2	1	4	1	3	4 (5)	3	3 (4)	4	1	2	2 (3)	3								
1985	1	3	3	7	3	5[a]	1 (2)	5[a]	2 (3)	6[a]	1 (2)	3	3	4	3	8	1[b] (3)	5	2	6					3	7	3	3 (4)
1986	1 (2)	3	2	7	1	6	3 (4)	4	3	6	2 (4)	3	2	3	3 (4)	7			3 (5)	5	2	4	2 (4)	3	3		3	3

() indicates total number of males when subadult males are included; blank spaces indicate the group was not censused that year, except in the case of BTG in 1986, which could not be found

a Groups that received female migrants through group fusions (Groups 3 and 4 two females each, Group C one female)
b Group that lost two females through fission

volved the exchange of threats, chases, or bites between the members of different groups. Successive encounters involving the same two groups were always separated by at least 2 h when no behavioral exchanges occurred. The data described here are based on 502 intergroup encounters, of which 271 were aggressive. In some of the analysis of intergroup encounters we have lumped data from the three study groups to increase the sample size. In no case, however, did a single group contribute disproportionately to the pooled results. All tests used in this paper are two-tailed

Results

Within-group competition

A number of studies have documented a positive correlation between dominance rank in female nonhuman primates and one or more measures of reproductive success (see reviews by Cheney et al. 1987; Silk 1987a). Since access to food, water, and social partners is usually positively correlated with rank (see above; see also Silk 1987a), it seems clear that within-group competition for resources can affect female reproductive success. Similarly, several studies of baboons and macaques have found offspring sex ratios among high-ranking females to be female-biased, and have postulated that this bias results from the increased resource competition that occurs when females remain in their natal groups throughout their lives (Silk et al. 1981; Simpson and Simpson 1982; Altmann et al. 1987). Thus, it may be advantageous for high-ranking females to limit the recruitment of daugthers by low-ranking females through selective harassment (Silk 1983).

Contrary to these findings, there is no correlation in the Amboseli vervet population between female rank and any measure of reproductive success. Similarly, the offspring of high- and low-ranking females are not biased toward the members of either sex (Cheney et al. 1987). The lack of a correlation between rank and reproductive success seems to be due primarily to the high rate of predation, which causes over 70% of all deaths and affects females of all ranks (Cheney et al. 1987). Predation is highest in the groups whose ranges border the swamps and permanent waterholes (Group B and especially Group C), where predators occur at high rates (Cheney et al. 1987). Since these groups are larger than groups found in drier areas (Table 1; unpubl. census data), predation tends to occur at higher rates in large groups than in smaller ones.

While predation is the major cause of mortality among Amboseli vervets, high-ranking females do enjoy a competitive advantage over low-ranking

females, and in years of extreme resource scarcity deaths are concentrated primarily among low-ranking individuals (Wrangham 1981; Cheney et al. 1987). It therefore seems probable that, over the long term, there is a reproductive advantage to high rank.

Even though females typically acquire their mother's ranks, they do occasionally rise or fall in rank, and such rank changes seem to be influenced strongly by the presence of kin. Between 1977 and 1986 there were only 11 rank reversals between unrelated adult females in the three study groups. Of these, eight occurred when an individual with living female kin (i.e. mother, daughter, or sister) rose in rank over a female with no such kin. Most of these reversals occurred soon after the death of the losing female's last close female relative. The three other cases all involved females with no known living kin. Similar observations have been made in other species of Old World monkeys (Dunbar 1984; Chapais 1987). Vervet females formed coalitions with other females or juveniles in 22% of their aggressive interactions. Of these coalitions, 65% were formed with close kin (mothers, offspring, or siblings), suggesting that the ability to recruit kin as allies during competitive interactions has a major effect on female dominance rank (data are based on aggressive interactions observed during 1983 and 1985–86, the periods for which kin relations were best known).

These obervations, however, raise a dilemma. If the presence of female kin helps to maintain or even improve dominance rank, why is there no apparent reproductive suppression of low-ranking females? Why is there no evidence that high-ranking females limit the recruitment of daughters by low-ranking females, and selectively harass the daughters of low-ranking females (e.g. Silk 1983)? One possible reason is that mortality in this population is so high, and between-group competition so intense, that it is in the interests of all group members that females be recruited into the group, even if this occasionally has a detrimental effect on an individual's rank and her competitive ability within the group.

Between-group competition

a) The relation between group size and range size. Vervets live in small groups characterized by male dispersal, and mortality is high. As a result, even random fluctuations in either the infant sex ratio or mortality rates strongly influence group size, even to the point of group extinction. For example, in late 1986 Group 4 became extinct after the death
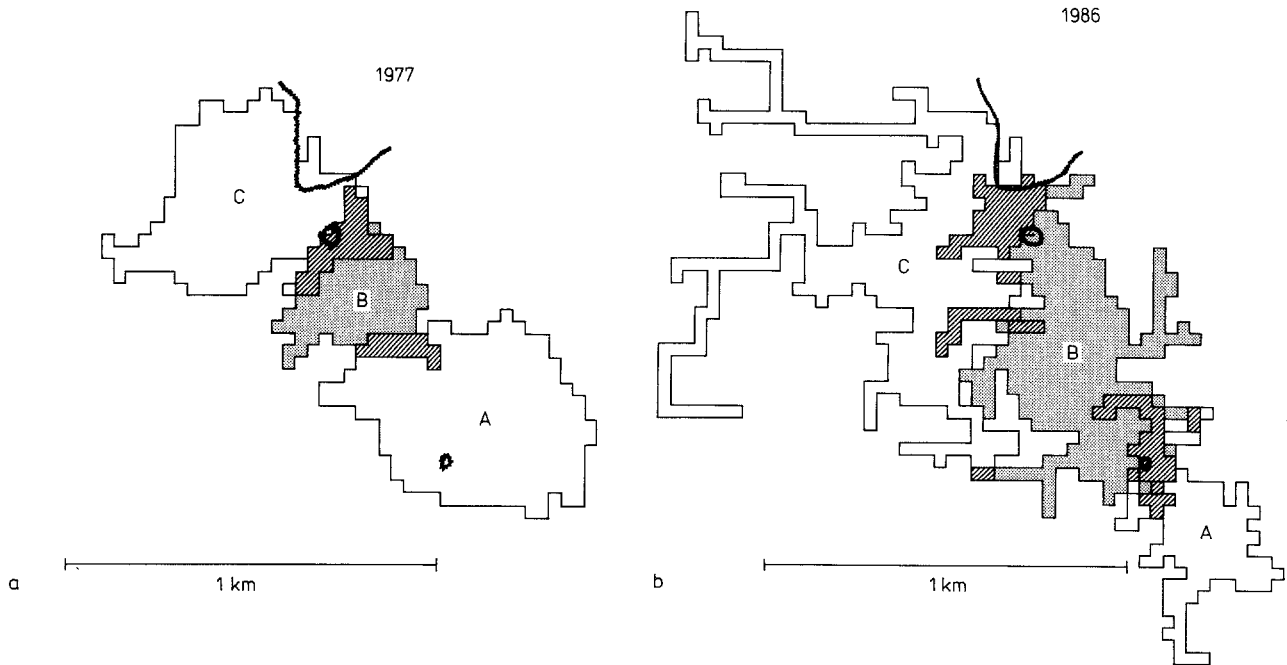
Fig. 1 a, b. The ranges of Groups *A*, *B*, and *C* in 1977 (**a**) and 1986 (**b**). Permanent swamps and a small temporary waterhole in Group *A*'s range in 1977 are outlined in *dark*

of its two adult females. Only one of the seven juveniles who had reached three years of age in this group in the preceding 3 years had been a female, with the result that no breeding females had recently been recruited into the group. In order to compete successfully with other groups, therefore, the steady recruitment of females would appear to be essential.

Although the ranges of vervet groups remain relatively stable from one year to the next, over longer periods of time range size and quality appear to be strongly affected by competition between groups. Figure 1 a illustrates the ranges of the three main study groups in 1977, as well as the location of the two permanent waterholes, where most of the *A. xanthophloea* trees are located. Comparison of the ranges in 1977 with the groups' ranges in 1986 (Fig. 1 b) shows clearly that Group B expanded its range into areas formerly occupied by Groups A and C, particularly in areas near water and *A. xanthophloea* trees. Groups A and C, on the other hand, shifted away from these richer areas into more marginal habitat. For example, although Group C extended its range, it expanded into an area of open savanna where there were few *A. tortilis* trees, only one *A. xanthophloea* tree, and no other vervet groups.

Groups with the greatest number of females relative to other neighboring groups tend to have larger ranges. When the three main study groups
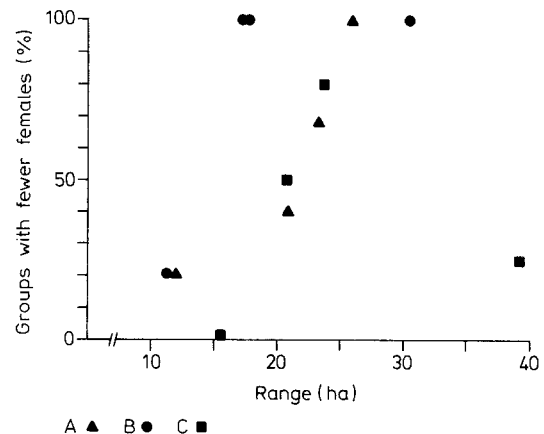
Fig. 2. The correlation between range size and the size of each group relative to its neighbors during four discrete time periods (1977–78, 1980, 1983, and 1985–86). The relative size of each study group was calculated as the proportion of neighboring groups that had fewer females than it did. During each time period, each study group had at least four neighbors

were considered over the four time periods, there was a positive correlation between the size of each group's range during the four time periods and the relative number of females in each group (Fig. 2; $N = 12$, $r_s = 0.467$, $P < 0.15$; the three groups added to the study in late 1983 were excluded from this analysis, because not enough data on changes in range size over time were available). This was also true for the number of males ($N = 12$,

$r_s = 0.416$, $P < 0.20$), possibly because in cercopithecines in general the number of males per group tends to be positively correlated with the number of females (Andelman 1986). The primary exception to this trend was Group C in 1986, which expanded its range tremendously during this year. As noted above, however, the new areas incorporated by this group included few food resources.

Range size is not necessarily correlated with range quality. In Struhsaker's (1967a, b) study of Amboseli vervet monkeys, for example, the smallest group had both the largest and, apparently, the poorest quality range. Indeed, van Schaik et al. (1983) have argued that one of the costs of increasing group size may be the need of large groups to range over larger areas in order to obtain sufficient food. In this study, however, the large groups did appear to have better quality ranges than small groups. Detailed phenological measurements of the three study groups' ranges, made in 1979 (Lee 1981) and 1984 (Hauser 1987), indicated that the largest group (B) had the best habitat and the smallest group (A) the worst, with Group C falling intermediate between these two extremes (see also above; Cheney et al. 1987).

These results suggest that one possible factor influencing range size and quality may be the relative number of females in each group. Indeed, in 1980, 1983, and 1985-86, Group B had more females than any of its five neighbors. What factors might have contributed to the number of females in each group? Below, we discuss some of the reproductive parameters that might have contributed to differential increases in group size. Because the sample sizes involved are small, and the expected effects slight, we cannot expect most intergroup differences to be significant (see e.g. van Schaik 1983). Over time, however, even incremental differences can have potentially strong effects on the relative growth of groups. We therefore present those trends that are evident in the hope that they may stimulate further comparisons and at least partially elucidate some of the factors contributing to differences in group size.

b) Fecundity and survival. Although fecundity varied significantly across groups, it did not account for Group B's greater growth. Females in both Groups B and C had similar interbirth intervals that averaged slightly more than one year. Interbirth intervals were significantly longer in Group A, apparently due to the lack of permanent water in Group A's range (Cheney et al. 1987).

Group B did, however, experience greater survival of females than the other two groups. Fig-
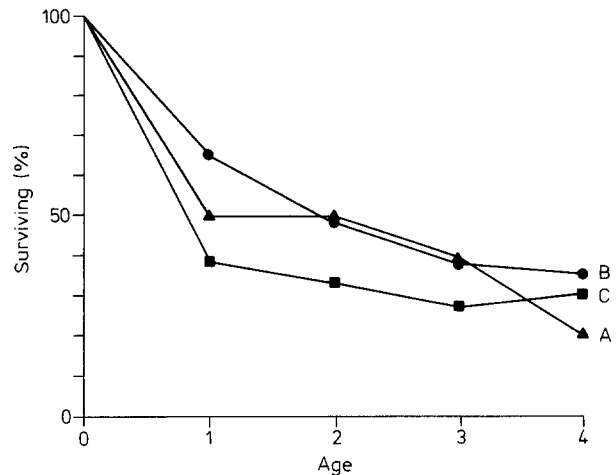

Fig. 3. Age-specific survival curves for all females born into the three study groups between 1977 and 1985. The numbers of females in each age class were: 0–1 year: $A = 6$, $B = 26$, $C = 13$; 1–2: $A = 6$, $B = 23$, $C = 12$; 2–3: $A = 5$, $B = 21$, $C = 11$; 3–4: $A = 5$, $B = 17$, $C = 10$; 4–5: $A = 4$, $B = 14$, $C = 8$; 5–6: $A = 4$, $B = 10$, $C = 4$

ure 3 shows survival curves to four years (or sexual maturity) for all females born in the three study groups (see also Cheney et al. 1987). Although survival in all groups was generally poor, Group B experienced both the highest infant survival and the highest survival to 4 years. While these intergroup differences were not statistically significant, over time such differences could have a strong incremental effect on relative group size.

Mortality in Groups B and C was almost entirely the result of predation (Cheney et al. 1987). In Group A, animals were equally likely to die of illness and predation. It should also be noted that the smallest group (A) did not experience higher juvenile mortality than the larger groups, as would be predicted if smaller groups had been more vulnerable to predation (van Schaik 1983).

c) Offspring sex ratio. The relatively larger number of females in Group B did not appear to be due to differences in the sex ratio of infants across groups. When all births since 1977 were considered, the sex ratio at birth in Group B was skewed slightly toward females (Fig. 4). In Groups A and C, the infant sex ratio was skewed more strongly toward males. The magnitude of the difference approached statistical significance in the case of Group A ($N = 21$, $x = 6$, binomial test, $P < 0.08$).

When the relative survival of males and females in the three groups was considered, inter-group differences became more apparent. Both Groups B and C experienced greater female survival to four years, while there was greater male survival in
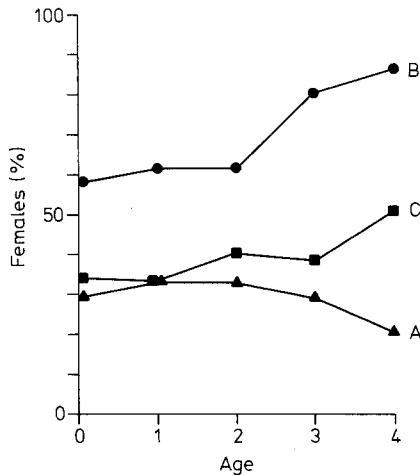
Fig. 4. The infant sex ratio and the relative survival of males and females to sexual maturity. Data are based on all infants born between 1977 and 1985. The number of individuals in each age class were: 0–1 year: $A=21$, $B=45$, $C=38$; 1–2: $A=22$, $B=41$, $C=35$; 2–3: $A=19$, $B=34$, $C=32$; 3–4: $A=17$, $B=28$, $C=30$

Group A. Thus Group B, whose initial sex ratio was skewed slightly toward females, had a sex ratio that was even more strongly skewed toward females at sexual maturity.

At the moment, we have no reason to believe that intergroup differences in infant sex ratio were due to anything more than chance. Previous studies, however, have suggested that competition for food resources may result in higher female mortality after birth, (van Schaik and van Noordwijk 1983; Silk 1983), and it therefore seems worth considering whether the differences in male and female survival might have been at least partially related to inter-group differences in range quality.

Group A had the poorest habitat (see above) and might therefore have been expected to experience both greater intragroup competition for food and reduced female survival. While the relatively greater mortality of juvenile females in Group A supports this hypothesis, there was no behavioral evidence of intensified female-female competition in this group. In 1977–78, for example, each female in Group A threatened another female a mean of once every 6.5 h, compared with once every 5.8 h in Groups B and C. In 1985–86, such threats occurred a mean of once every 9.4 h, compared with once every 4.5 h in the other two groups. Indeed, in 1985–86 (the only time period for which data on the other study groups are available) females in the four groups with no surface water threatened each other at far lower rates than did females in the two groups with surface water (dry groups: a mean of one threat per female every 17.5 h; wet

groups: one threat every 4.5 h), partially because groups in dry habitats were usually more widely dispersed (Hauser 1987, in prep.).

In summary, therefore, it is certainly possible that differences in the intensity of female-female competition contributed to the differential survival of males and females across groups. More long-term data are clearly needed, however, before we can eliminate the hypothesis that these differences were not due simply to chance.

d) The relation between group size, birth rates, and infant survival. The relative importance of within- and between-group competition can also be examined by comparing the number of females in each group with either birth rates or infant survival. A negative correlation might indicate that within-group competition is relatively intense, suggesting a cost to large groups (van Schaik 1983). A positive correlation, on the other hand, might suggest first, that the population is not at carrying capacity, second, that predation pressure is sufficiently intense that large groups are favored over small ones, or third, that between-group competition is greater than within-group competition, with the result that large groups are at a competitive advantage.

Over ten birth seasons, there was no consistent relation between the number of females in the group and the proportion of females giving birth (Group A: $r_s=0.010$; B: $r_s=-0.177$; C: $r_s=0.248$; all tests NS). Similarly, over the 9 year period from 1977 to 1986 there were no significant correlations in any group between the number of females and infant survival to 1 year. The two measures were weakly positively correlated in Group B and C (B: $r_s=0.413$; C: $r_s=0.312$, both tests NS), the larger groups with both richer habitats and greater predation pressure (see above). They were weakly negatively correlated in Group A ($r_s=0.221$; NS), the smallest of the three groups and the one with the poorest habitat.

These weak trends, together with those presented earlier (Figs. 3 and 4) suggest that survival was generally greater in larger groups than in smaller ones. This hypothesis can be tested further by considering whether, on average, infant survival was greater in groups that were larger than the median size than in groups that were smaller than the median size. Using as our sample 9 years of data from Groups A, B, and C and 3 years of data from Groups 2, 3, and 4 survival to one year could be compared against the number of adult females in the group at the time. During this period, the number of females in each group ranged from two to eight, with a median of five females, and the

proportion of infants surviving to one year ranged from 0–100%. In groups that were larger than or equal to the median group size, 55% of infants survived to 1 year. In groups that were smaller than the median size, however, only 32% of infants survived (Mann-Whitney U test, $N_1 = 12$, $N_2 = 19$, $U = 77$, $P = 0.13$). Although this difference was not significant, these data support the other trends described earlier.

It is worth examining these trends in light of previous discussions about the effects of intragroup competition on infant survival. Assuming for the moment that the relatively greater survival of infants in larger groups was not due simply to chance, this difference could have been related either to increased predator detection or to dominance in intergroup competition, since both factors potentially favor large groups (see also below). In this study, there was no evidence that large groups experienced lower predation rates than small ones. A number of factors, however, suggest that the slightly greater survival of infants and females in large groups may have been influenced by intergroup competition. First, large groups dominated smaller ones in intergroup interactions. Second, females in large groups appeared to exert less effort and to incur fewer costs during intergroup interactions than did females in smaller groups.

Behavior during intergroup encounters

a) The relative success of small and large groups. In nonterritorial primates such as baboons, macaques, and capuchins, large groups are almost invariably able to supplant smaller groups from food resources (reviewed in Cheney 1987). It is more difficult to determine the relative success of large and small groups among territorial species such as vervets because single encounters rarely resulted in noticeable boundary changes, and many encounters ended with the retreat of both groups. Struhsaker (1967b), however, observed that large vervet groups were more likely to make incursions into their neighbors' ranges than vice versa. Similarly, in this study females in small groups were consistently more aggressive during intergroup encounters than females in large groups, apparently because they were more often defending their range against an incursion by a larger group.

Since females did not always retaliate against aggression received from the members of other groups, it was possible to determine, for any given group dyad, which was the more hostile. Taking all of the encounters that a given study group had

Table 2. The relative aggressiveness of females toward females in neighboring groups that were larger or smaller than their own. Each cell shows the number of groups in which females either gave or received more aggression when their own group was either larger or smaller than the opposing group. Data are based on encounters involving a total of 14 groups over four different time periods. They include encounters between all of the three main study groups and their neighbors, and, in 1986, the encounters of Groups 2, 3, and 4. Group size was calculated according to the number of females in each group

Did the opposing group have:	In how many groups did females give more aggression to females than they received?	
	Gave more	Received more
Same or fewer females?	6	13
More females?	8	3

$\chi^2 = 4.85$, $P < 0.05$

Table 3. The relative aggressiveness of females toward males in neighboring groups that had fewer or more males than their own. Legend as in Table 2. Data are derived from encounters involving 19 groups over four time periods

Did the opposing group have:	In how many groups did females give more aggression to males than they received?	
	Gave more	Received more
Same or fewer males?	6	16
More males?	12	8

$\chi^2 = 4.51$, $P < 0.05$

with a particular neighbor, we compared the number of encounters in which females gave aggression to females in the other group with the number of encounters in which they received aggression from these same opponents. This comparison allowed us to determine, for each combination of groups in each of the four time periods, which of the two groups was the more aggressive. Results suggested that the group with fewer females was generally more aggressive than the group with more females (Table 2). Similarly, when the aggression that females gave to males in other groups was compared with the aggression that they received from those males, results suggested that females were significantly more aggressive when their own group had fewer males than the opposing group (Table 3).

This was not true for males. Males in small groups were not more or less aggressive to the members of either sex than were males in larger groups (Tables 4 and 5). Indeed, group size had

Table 4. The relative aggressiveness of males toward males in neighboring groups with fewer or more males than their own. Legend as in Table 2. Data are derived from encounters involving 20 groups over four time periods

Did the opposing group have:	In how many groups did males give more aggression to males than they received?	
	Gave more	Received more
Same or fewer males?	12	12
More males?	11	14

$\chi^2 = 0.16$, $P > 0.50$

Table 5. The relative aggressiveness of males toward females in neighboring groups with fewer or more females than their own. Legend as in Table 2. Data are derived from encounters involving 19 groups over four time periods

Did the opposing group have:	In how many groups did males give more aggression to females than they received?	
	Gave more	Received more
Same or fewer females	14	15
More females?	9	8

$\chi^2 = 0.09$, $P > 0.50$

no apparent effect on the behavior of males during intergroup encounters, perhaps because male behavior was related less to range defense than to male-male competition for females (Cheney 1981, 1987).

The heightened aggression of females in small groups may have been due at least in part to the fact that large groups were more often making incursions into the ranges of other groups, whereas small groups were more often defending their range. During 1983 and 1986, the periods for which accurate ranging data were available, there were 56 intergroup encounters in which females were aggressive. 36 (64%) of these encounters occurred in quadrats that were used more by the smaller of the two opposing groups than by the larger group ($\chi^2 = 4.57$, $P < 0.05$).

Such incursions by larger groups appeared to result in increased aggression by females in the smaller, defending group. Females were more likely to be aggressive toward females in other groups when the intergroup encounter took place in their own, rather than in the other group's, range. Of 45 encounters in which females gave more aggression to females in the opposing group than they received, 33 (73%) took place in quadrats that were used more by their own group than by the

other group ($\chi^2 = 9.80$, $P < 0.01$; data are derived from encounters involving the three main study groups and their neighbors, as well as Groups 2, 3, and 4 in 1986). Similarly, of the 51 encounters in which females gave more aggression to males than they received, 41 (80%) took place in the ranges of the females' groups rather than in the ranges of males' groups ($\chi^2 = 18.81$, $P < 0.001$).

These results suggest that small groups not only risk losing parts of their range but that they must also exert greater effort to defend it. This cost may have been particularly high when females fought against males. Females were aggressive to males in other groups primarily when the males' group was making an incursion into their own range. Males have been observed to wound females severely in four intergroup encounters, and two cases of cross-group infanticide have also occurred. Thus, although injuries are rare, the potential costs for females of fighting with larger males may be relatively high. Females appeared to risk these costs primarily when they also risked the loss of their range.

b) Alliances during intergroup interactions. If female-bonded primate groups function at least in part as alliances against other groups, females would be predicted to cooperate with each other during intergroup encounters. Indeed, each female formed an alliance with other females or juveniles in her group in a mean of 84% of her aggressive interactions with members of other groups, compared with 22% of aggressive interactions with members of her own group. Most such alliances occurred with close kin. Considering data from 1983 and 1985-86, the years for which the most accurate kinship data were available, 18 of 19 females who had kin formed alliances with close kin more than would have been expected by chance (two-tailed sign test, $P < 0.001$). The sole exception was a female whose only close relative was a one-year-old son.

Discussion

Almost all of the alliances formed by females during intergroup encounters were formed with kin rather than with less closely related group members, supporting the suggestion (Wrangham 1980) that groups are best regarded as a series of alliances among a number of families that both compete with each other for resources and cooperate in defense of a common range.

One criticism of the hypothesis that female sociality results ultimately from the need to defend

food resources (Wrangham 1980) is that birth rates are often negatively (though rarely significantly) correlated with group size. Thus, unless some other selective pressure like predation favors sociality, within-group competition for food may be too costly to allow sociality to evolve (van Schaik 1983). However, predation pressure alone cannot explain patterns of interactions between groups or the prevalence of female alliances during intergroup encounters. Moreover, in many species female sociality occurs even when predators are rare or absent (Cheney and Wrangham 1987), and, at least in this study, rates of predation were correlated with habitat type rather than group size (Cheney et al. 1987). Predation pressure, therefore, is unlikely to be the only selective factor favoring female sociality. As originally argued by Wrangham (1980), if a female's reproductive success depends at least in part on her groups's ability to compete successfully for resources against other groups, the costs of within-group competition may be outweighed by the benefits that extended kin groups confer in competition against other groups. Both predation and between-group competition, therefore, may favor sociality, and may even act in conjunction to favor large groups.

A number of previous studies of cercopithecine monkeys have suggested that the costs of intragroup competition should usually cause high-ranking females to attempt to limit group size by restricting the recruitment of daughters by lower-ranking individuals (van Schaik and van Noordwijk 1983; reviewed by Silk 1983). In contrast, the data presented here suggest that under some circumstances it may in fact be advantageous for females to recruit additional females into their groups.

Although the costs of within-group competition may rise with increasing group size, the costs of between-group competition appear to decline, both because large groups have a competitive advantage over small groups and because females in large groups may incur fewer costs in intergroup interactions. Numerous studies of nonhuman primates have found that large groups usually dominate small groups during intergroup encounters (reviewed in Cheney 1987; see also Dittus 1986). In Amboseli, large groups were more likely to make incursions into the ranges of smaller groups than vice versa, and perhaps for this reason females in small groups were more aggressive during intergroup encounters than females in larger groups.

In other words, although females in small groups may have experienced reduced intragroup competition for resources, they also incurred se-

vere costs in intergroup competition, both through the loss of their range and through the effort expended in range defense. These results suggest that intergroup competition may sometimes cause females in large groups to experience a reproductive advantage over females in small groups, despite increases in intragroup competition. In this study, for example, the largest group, B, had the greatest female survival. Similar observations have been made for Cebus olivaceus, a species in which large groups not only dominate small groups but also have higher intrinsic growth rates despite high rates of intragroup competition (Robinson in prep.).

At least in some cases, therefore, intergroup competition may influence female reproductive success more strongly than intragroup competition. As a result, the group size that minimizes the costs of within- and between-group competition should always be larger than would be predicted from an analysis only of within-group competition. Furthermore, whenever intergroup competition has any influence on female reproductive success, females should be more cooperative and less aggressive than might be predicted from a consideration of intragroup competition alone (see Boyd 1982).

The recruitment of females, either through birth or through group fusion (see below), should be particularly advantageous whenever ecological conditions result in declining or widely fluctuating population sizes (Boyd 1982; Silk 1987b). For example, when group size is typically small (<10 females), as it is among vervet monkeys and other members of the Cercopithecus genus, high predation rates or random fluctuations in the infant sex ratio can profoundly affect group size, even to the point of group extinction (see also Dunbar 1979 1987). Species such as baboons and macaques, that frequently live in large groups (>10 females), are less likely to be affected by stochastic demographic processes. It is perhaps not surprising that these are the species in which the harassment of low-ranking animals by high-ranking females has most often been reported (reviewed by Silk 1983, 1987).

A consideration of the costs and benefits of living in large and small groups may also clarify the conditions under which groups might be predicted to fission or merge. Previous studies of macaques have suggested that groups fission when group size becomes large, and, by implication, when intragroup competition for resources increases (e.g. Chepko-Sade and Sade 1976; Koyama 1970; Malik et al. 1985). Although these studies have not reported the effects of fissioning on subse-

quent female reproductive success, the fact that fissions occur at all suggests that groups can become so large that the costs of intragroup competition begin to outweigh the benefits of dominance in intergroup interactions. Little is known about the effect of fissioning on competition within and between groups, however, and more data are needed to specify these conditions more precisely.

Similarly, groups may be predicted to merge when they become too small to compete effectively with their neighbors. Although group fusion is rare among nonhuman primates, it does occasionally occur (Dittus 1986; Altmann et al. 1987; reviewed by Pusey and Packer 1987). Four cases of apparent group fusion have been observed among Amboseli vervets. Although the previous ranks and histories of the females were known in only three cases, available data suggest that groups cannot survive after they have been reduced to fewer than two females (Hauser et al. 1986; unpubl. data). They may lose parts of their range to other groups, become more susceptible to predation, and eventually either become extinct or fuse with another group.

In the three cases for which background data on both groups were available, group fusion occurred when a group that had decreased to two juvenile and one or no adult females joined the neighboring group with the fewest resident females (for details see Hauser et al. 1986). Fusion with the smallest neighboring group may have been advantageous for two reasons. First, fusion with a small group may have minimized the aggression received. In fact, although new females assumed lowest ranks, they did not receive more aggression than resident low-ranking females. Second, females in small groups may have been more receptive to new females than females in larger groups, because the recruitment of new females may have improved their ability to compete against neighboring groups. Indeed, for those females for whom data are available, in the 6 months following fusion females in groups that received immigrant females gave more aggression than they received in 48% of their intergroup encounters, compared with 55% in the six months preceding fusion. Moreover, of the two groups for which the ranges of neighboring groups were known, 78% of aggressive intergroup encounters occurred in the groups' own ranges during the six months following fusion, compared with 84% before. Both observations suggest that the addition of females may have lowered the costs of intergroup competition.

In summary, both intergroup competition and predation pressure may cause groups to be larger

than might be predicted from a consideration of the costs of intragroup competition alone. Evidence from vervet monkeys and a variety of other species suggests that groups compete best when group size is relatively large, even if this increases competition within groups. Similarly, although group fusion is rare among nonhuman primates, intergroup competition appears to be an important factor in determining both its occurrence and the distribution of female movement between groups (see also Dittus 1986). Finally, intragroup competition may occur at lower rates in smaller groups not only because competition as a whole is reduced but also because it may be in the interests of all individuals that additional females be recruited into the group. As the vervet monkey data emphasize, random fluctuations in mortality rates and offspring sex ratio in small groups can have important implications for intergroup competition and even the survival of groups.

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