

BRIEF REPORT

Group Fusions and Minimum Group Sizes in Vervet Monkeys (*Cercopithecus aethiops*)

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Six unequivocal cases of group fusion occurred between 1984 and 1988 in a declining population of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. In each case, the remaining group members abandoned their territory and joined a neighboring group shortly after the group lost its penultimate adult. Because the number of juveniles did not appear to influence the timing of fusion, only adults (both males and females) appear able to maintain vervet groups as cohesive units. After examining the relative contributions of adults and juveniles to group-living, we infer that intergroup competition may be more important than predation avoidance in determining the timing of fusions.

Key words: Amboseli National Park, Kenya; juveniles, fusion, resource competition

INTRODUCTION

In an 11 year study of a population of vervet monkeys (*Cercopithecus aethiops*) undergoing decline [Struhsaker 1973, 1976; Cheney & Seyfarth 1987; Isbell et al., 1990], we and our colleagues observed six unequivocal cases of fusion in which groups became so small that the remaining members joined neighboring groups. Primate group fusions are rarely observed, and have been reported in only two other species, once in toque macaques (*Macaca sinica*) [Dittus 1986, 1987] and once in savannah baboons (*Papio cynocephalus*) [Altmann, 1980]. The six group fusions observed in the Amboseli vervet population thus represent the largest number of fusions known in a primate population.

We describe the fusions in detail here and note patterns that have emerged from them. They are generally consistent with the patterns reported in a previous paper on a smaller number of fusions from the same population [Hauser et al., 1986], i.e., fusions occur when the number of adult females in the group declines to one or none, groups fuse with the smallest neighboring group, and the immigrating adult female assumes the lowest rank in the dominance hierarchy. However, data from the subsequent fusions suggest that 1) the presence of adult males can also influence the timing of fusions, and 2) fusions occur when group sizes are reduced from two adults to one, with varying numbers of accompanying juveniles. We discuss these findings in relation to ultimate causes of group-living in primates.

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METHODS

Study Site and Subjects

This study was conducted in Amboseli National Park, Kenya (2° 41'S, 37° 10' E). Vervets in Amboseli live in small, multi-male, multi-female groups. Vervet groups are associations of individuals that travel and feed together. Females typically remain in their natal groups throughout their lives while males emigrate to neighboring groups around sexual maturity, and may transfer between groups repeatedly throughout their lives [Cheney & Seyfarth, 1983]. Vervet groups in the study area are territorial and their home ranges are defended by both males and females against incursions from neighboring groups [Cheney, 1981; Cheney & Seyfarth, 1987].

In Amboseli, two species of trees predominate: *Acacia xanthophloea*, or fever trees, found along waterways and swamps, and *A. tortilis*, found in drier soils away from water. In the mid-1950s the fever trees began to die [Western, 1983]. By the early 1970s the die-off was occurring in the southwestern part of Amboseli where the vervet study area is located [Struhsaker, 1973, 1976]. The decline of the fever tree population has been attributed to a combination of short-term climatic change, stand senescence, and elephant browsing [Western & van Praet, 1973; Young & Lindsay, 1988].

When fever trees still occurred in groves in the study area, vervets slept and fed in them year-round [Struhsaker, 1967]. As of 1990, however, only one fever tree was still alive in the main study area (Isbell, pers. obs.). As the fever trees declined, vervets relied more heavily on *A. tortilis* for food and refuge, although the proportion of *A. tortilis* in their diet was less than that previously contributed by fever trees [Wrangham & Waterman, 1981; Cheney & Seyfarth, 1987; Cheney et al., 1988]. Vervet groups whose home ranges did not include fever trees had lower reproductive rates than groups whose home ranges had fever trees, which suggests that fever trees are important food plants for vervets [Cheney et al., 1988]. The decline of the fever tree population is the probable ultimate cause of the continuing decline of the vervet population [Struhsaker 1973, 1976; Cheney et al., 1988].

While the loss of food resources is responsible for the long-term decline of the vervet population, predation has also contributed in important ways to the population decline. For example, during 1987, the vervet population suffered significantly higher mortality than in past years. Evidence suggests that a majority of vervets died of predation [Isbell, 1990]. This sudden, short-term increase in mortality exacerbated the effects of reduced food resources by causing several smaller groups to disappear through fusion while larger groups declined to sizes comparable to those of smaller groups that existed before 1987. A fusion was said to have occurred when all members of one group began traveling and feeding with another group.

Data Collection

Three social groups of vervets were studied intensively beginning in 1977, and intensive study of three additional groups was begun in 1983. Observations continued until August 1988. All demographic events, i.e., births, deaths, immigrations, emigrations, and disappearances, were recorded for each of the six main study groups during the periods of intensive study. Between June 1986 and January 1988 when four of the six fusions occurred, each main study group was censused on average eight times per month (range: 4–22). In addition, up to eight groups surrounding the main study groups were censused semi-annually every year except 1981.

Age classes of vervets follow those of Seyfarth et al. [1980]. Immature monkeys under 1 year old are classified as infants. Females between 1 and 4 years and males between 1 and 5 years are classified as juveniles. Females 4 years and older and males 5 years and older are classified as adults.

Intergroup encounters were defined as any behavioral interaction between members of two groups, including vocalizations [Cheney, 1981; Cheney & Seyfarth, 1987]. Aggressive intergroup encounters were limited to those encounters in which members of a group chased, hit, or bit members of another group. Occurrences of intergroup encounters were recorded whenever they were observed during 1,187 hours of observation from June 1986 through January 1988 and in May and June 1988. The identities of individuals that were involved in intergroup encounters were recorded and the nature of their involvement described.

RESULTS

Fusions

Six unequivocal cases of fusion occurred between 1984 and 1988. Information on group membership during the process of group decline and fusion exists for five of these groups. Most losses in membership resulted when animals "disappeared." These disappearances have been attributed to predation [Isbell, 1990; Isbell et al., 1990]. Since infants are not independent of their mothers and only one infant lived in one group that fused, this infant has been omitted from the description of its group's fusion. Below are the demographic histories of the six fusions.

1. In June 1983, group 11, consisting of two adult females and two juvenile females, separated from group 5 to form their own group. In early January 1984, one of the adult females and one of the juveniles disappeared. Within 5 days, the remaining adult female and 3 year-old juvenile female abandoned their home range and joined group C [see Hauser et al., 1986 for a more detailed description].

2. In December 1985, group 4 consisted of four adults (two females and two males) and six juveniles. In February 1986, two juveniles disappeared. In April, one adult male transferred into the group while one juvenile male was reclassified as an adult. In July, adult female SN and juvenile female SY disappeared, leaving one adult female among the seven remaining in the group. In August, adult male ND disappeared and in September, adult female AJ and her juvenile son, HH, disappeared, leaving three adult males and a juvenile male. After AJ disappeared, the group continued to exist as an all-male group, traveling and feeding together, for about 2 months. Between 9 and 11 November, adult male IS disappeared. The group split up between November 23 and December 8, when one of the remaining two adult males, HK, transferred to neighboring group TW4. The other adult male (GY) and 4 year-old juvenile male PR joined group 2, another neighboring group.

3. In March 1986, group A consisted of five adults (three females and two males) and four juveniles. In July, juvenile male GO disappeared, and in November adult female LS disappeared while adult male TT transferred to a neighboring group. In February 1987, adult female ES disappeared, leaving one adult male, one adult female, two juvenile males (4 and 3 years old) and one 3 year-old juvenile female. In March, the adult male (GC) transferred to group TW3, a neighboring group that had recently lost its adult male but which still included three adult females and one juvenile female. Five days later, adult female BA and the three juveniles abandoned their home range and began traveling and feeding with group TW3.

4. In October 1986, group 2 consisted of six adults (four females and two males) and one juvenile. In November or December, adult male GY and juvenile male PR

joined group 2 from group 4, which then ceased to exist (see above). In January 1987, adult female LI disappeared and in March, adult female JR and juvenile female NS disappeared. In May, adult males KJ and GY transferred to neighboring group B and juvenile male PR disappeared, leaving two adult females and one adult male. In June, one adult male (SK) transferred into the group while the other adult male (BN) transferred to group B. In July, adult female BE disappeared, leaving one adult female and one adult male. In September, adult female BT's 1 year-old son (LJ) was reclassified as a juvenile. In October, BT disappeared. Within 4 days, juvenile LJ joined neighboring group TW3 while the adult male, SK, remained on the periphery for 1 month before becoming incorporated into the group.

5. In May 1987, group 5 consisted of eight adults (five adult females and three adult males) and three juveniles. By November, censuses revealed that the group had undergone a reduction to six individuals: two adults (one female and one male) and four juveniles. The study was interrupted from February to May 1988, but limited censuses during that time indicated that between February 1 and March 23, the adult male transferred to neighboring group C. Between March 24 and April 19, the remaining adult female and four juveniles (exact ages unknown) abandoned their home range and began traveling and feeding with group C.

6. Information on the sixth group (group 10) is less clear. Hauser et al. [1986] reported that in June 1984 group 10 consisted of three adults (two females and one male) and two juvenile females aged 3.5 and 1.5 years. Sometime within the next 2 months, all adults disappeared and by August, the two juveniles joined a neighboring group (group 2). It is not known whether the last two adults disappeared separately or simultaneously. If the adults disappeared separately, this fusion would be inconsistent with the pattern of the other fusions unless the older juvenile female, who was almost adult, influenced the timing of fusion. On the other hand, if the adults disappeared simultaneously, this fusion would be consistent with the general pattern of the other fusions regardless of the behavior of the older juvenile. Because this case is unclear, however, it is not included in the following discussion.

It might be argued that since males typically transfer between groups, movements of males that resulted in the disappearances of groups should be considered male transfers rather than group fusions. However, the two male transfers that resulted in the disappearances of groups were accompanied by juveniles whereas only 3 of 51 male transfers between January 1984 and June 1988 that did not result in group disappearances were possibly accompanied by juveniles. Male transfers that resulted in disappearances of groups can therefore be distinguished from male transfers that occurred at other times.

Four consistent patterns emerge from the details of the fusions. First, all groups continued to feed and travel together as long as at least two adults were present in the group (Table I). Second, once the penultimate adult disappeared or left the group, fusion occurred almost immediately. Data from the groups whose fusions were documented in sufficient detail indicate that the length of time that groups persisted with two adults was significantly longer than their persistence with one adult (Wilcoxon signed ranks test: $n = 4$, $P < .02$; Fig. 1). Third, all groups fused when they were reduced to one adult and a variable number of juveniles. Fourth, groups existed before fusion in all combinations of two adults, i.e., two males, two females, and one male and one female. The patterns were consistent regardless of whether the last adult was male or female.

TABLE I. Numbers of Adults and Juveniles Left in Vervet Groups Immediately Before Fusion and at Fusion*

Group	Before fusion				At fusion			
	Number of adults		Numbers of juveniles		Numbers of adults		Numbers of juveniles	
	M	F	M	F	M	F	M	F
11	0	2	0	1	0	1	0	1
4	2	0	1	0	1	0	1	0
A	1	1	2	1	0	1	2	1
2	1	1	1	0	1	0	1	0
5	1	1	2	2	0	1	2	2
Range	2		1-4		1		1-4	

*M, males; F, females.

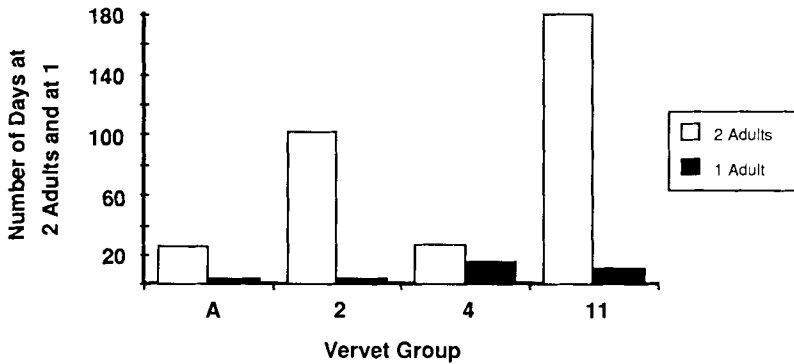


Fig. 1. The number of days that groups had two adults is significantly greater (Wilcoxon signed ranks test: $n = 4$, $P < .02$) than the number of days that they remained at one adult before fusion occurred.

Intergroup Encounters

From June 1986 through January 1988, when four of the six fusions occurred, the six main study groups were involved in 47 intergroup encounters with groups whose individuals were recognized by observers. Intergroup encounters occurred at much lower rates than in previous years [see Cheney, 1981] and reflects a lower density of vervet groups [Isbell et al., 1990]. Adult males were aggressive in 26 of the 47 (55%) intergroup encounters and were aggressive toward both adult males and adult females. Adult females were aggressively involved in 12 of the 47 (26%) encounters. Juveniles were aggressive in only four of the 47 (8%) encounters.

DISCUSSION

Adult vervets appeared to be willing to remain as a group as long as at least one other adult was present in the group. This suggests that 1) there is an advantage in living with other adults that does not exist in their absence, and 2) juveniles do not compensate for the absence of adults. We consider here adaptive reasons for these patterns of fusion and do not address proximate explanations. Two possible explanations for the apparent ability of adults to maintain groups as

cohesive units are that adults alone improve competition against others for food resources [Wrangham, 1980, 1987] or reduce predation [Alexander, 1974; van Schaik, 1983; Terborgh & Janson, 1986].

Adult and Juvenile Contributions to Predation Avoidance

Because of their small size, vervets do not actively defend themselves from predators [Cheney & Wrangham, 1987], so cooperative defense is not an advantage of group-living in vervets. However, group-living in vervets might minimize predation by dilution [Pulliam & Caraco, 1984] or by enhancing predator detection [van Schaik, 1983; van Schaik et al., 1983].

In order for adults to benefit from dilution, the probability that a given adult would be killed would depend largely on how many others are in the group and whether others are at least as vulnerable to attack. In fact, juveniles appear to be more vulnerable to predation than adults. For example, half of the adult females (12 of 24) but three-fourths of the juveniles (16 of 22) disappeared from the five main study groups in 1987. Evidence suggests that most of these disappearances were caused by predation [Isbell, 1990]. At fusion, the number of adults and juveniles equalled total group size in all groups except one, which also included one infant. If the dilution effect were primarily responsible for maintaining vervet groups as cohesive units, the number of juveniles in groups would have been expected to influence the timing of fusions. This, however, was not the case.

Fundamental to the issue of ultimate causes of group-living is the relation between group size and frequency of alarm calls. In 1987, a year of unusually high predation, monthly alarm call rates did not vary with monthly group sizes, suggesting that small vervet groups are as likely as large groups to detect predators [Isbell, 1990]. There is also evidence that juveniles [but not infants: Seyfarth et al., 1980] are at least as effective as adults in detecting predators and in giving alarm calls: 1) juveniles are as likely as adults to give alarm calls first when predators are present despite the fact that they make up a smaller proportion of the group [Cheney & Seyfarth, 1981], and 2) playbacks of alarm calls of juveniles are as likely to elicit responses from others as are alarm calls of adults [Seyfarth et al., 1980]. If predator detection were primarily responsible for maintaining vervet groups as cohesive units, total group size, including juveniles, would have been expected to influence the timing of fusions. Again, however, this was not the case.

Adult and Juvenile Contributions to Intergroup Resource Competition

Although it is difficult to determine winners and losers during particular intergroup encounters, there is evidence that larger groups can and do supplant smaller groups over longer time periods [Cheney & Seyfarth, 1987; Isbell et al., 1990]. However, despite the potential of juveniles to contribute by their presence to their groups' success in intergroup competition, they seem actually to contribute relatively little. While juveniles and adult females appear to vocalize equally during intergroup encounters [Cheney, 1981], juveniles are aggressively involved in a much smaller proportion of intergroup encounters than adults. Between June 1986 and January 1988, adult females were aggressively involved in three times as many intergroup encounters as were juveniles. Cheney [1981, Table VII] also reports that adults were aggressive in three times as many intergroup encounters as were juveniles. Similarly, data from Hauser et al. [1986] show that females were aggressively involved in intergroup encounters on average 25 times more often than juvenile females (adult females: 12%; juveniles: 0.5%) (from Table VII, p. 72). If intergroup competition were primarily responsible for maintaining vervet groups as cohesive units, the number of juveniles in groups would not have been

expected to influence the timing of fusions. In fact, this was the case. This implies that intergroup competition is more important than predation avoidance in determining the timing of fusions [see also Hauser et al., 1986].

The Importance of Males in Intergroup Competition

Because fusions occurred when groups were reduced to one adult regardless of the sex of that adult, adult males appear to be as important as adult females in maintaining group integrity when groups are reduced to the minimum number required for maintaining groups. The numbers of males that live in groups and male aggression toward other groups are generally believed to be associated with male-male competition for access to potential mates [Clutton-Brock & Harvey, 1977; Andelman, 1986; Altmann, 1990]. This may be an oversimplification for vervets. If male-male competition in vervets is primarily related to gaining access to females, a male would be expected to transfer to another group when the adult sex ratio in his current group becomes biased toward males, or at the very latest, when the last female in his group disappears. However, one of the vervet groups consisted of males who traveled and fed together for 2 months without females before they moved to other groups. Since male vervets normally live in groups with females year-round, and do transfer between groups outside the breeding season, it is unlikely that they remained together because there were no receptive females elsewhere. Moreover, they did not appear to be excluded from other groups by resident males, nor were they observed to approach or interact with other groups, a behavior typical of males in the process of transfer. This is consistent with the idea that males gain more from living in groups than just access to females.

That fusion occurred shortly after each group was reduced to one male or one female from various pair-wise combinations of sexes suggests that both sexes may live in groups for the advantage that it provides in intergroup resource competition. Among wedge-capped capuchins (*Cebus olivaceus*), the number of males in groups appears to influence the outcome of intergroup encounters [Robinson, 1988] and Robinson argues that because of their potential contributions during intergroup encounters, males should also be considered in future analyses of intergroup resource competition in other species. There are obvious benefits that a male might gain by defending food resources as well as defending females. A male might benefit by defending resources for his offspring or for females that will produce his offspring. In addition, a male that helps in resource competition against other groups is likely to increase his own access to food resources and thereby improve his physical condition. This may translate ultimately into improved competitive abilities against other males for access to mates.

CONCLUSIONS

1. Six unequivocal cases of group fusion occurred between 1984 and 1988 in a declining population of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya.

2. While several patterns were consistent with those reported previously from a smaller sample of fusions, other patterns emerged, including the importance of adult males in determining the timing of fusions and the relative unimportance of juveniles in the timing of fusions.

3. The importance of adults but not juveniles in determining the timing of fusions suggests that adults alone are responsible for maintaining vervet groups as cohesive units.

4. Juveniles and adults appear to be similar in their contributions to predation avoidance but not intergroup competition.

5. These results imply that the advantage of group-living in vervets is more likely to be related to intergroup competition than to predation avoidance.

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