

Behavioral Correlates of Non-Random Mortality Among Free-Ranging Female Vervet Monkeys

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Summary. Over a 3.5 year period, illness and predation operated in a non-random manner on free-ranging vervet monkeys in Amboseli National Park. As a result, there was no correlation among adult females between dominance rank and reproductive success. Deaths due to illness were concentrated among low-ranking individuals, and appeared to occur as a result of restricted access to food and water during the dry season. In contrast, deaths due to predation were concentrated among high-ranking individuals. The precise cause of such increased vulnerability could not be determined.

High-ranking females alarm-called at higher frequencies than low-ranking females, and were also more aggressive than low-ranking females during intergroup encounters. In contrast, low-ranking females were more likely to initiate friendly interactions with the members of other groups. The non-random distribution of causes of mortality suggests that individuals living in the same social group may confront different selective pressures. Perhaps as a result, individuals appear to respond differently to similar social and environmental variables.

Introduction

Numerous theories have been proposed to explain the evolution of female sociality in birds and mammals, as well as the costs and benefits of group life (see e.g. Bradbury and Vehrencamp 1977; Clutton-Brock and Harvey 1977; Emlen and Oring 1977; Warner 1980; Wrangham 1980). While these functional models often offer plausible explanations for the evolution of species-typical behavior, such as cooperation among related females, they are not always useful in making precise, quantitative predictions

about individual differences in the behavior of animals living in highly variable social groups (Chase 1980). Sociality may impose variable constraints on individuals, even when such individuals are of the same sex, inhabit the same range, and compete for the same resources. For example, females in many species of Old World Monkeys form linear dominance hierarchies in which related individuals occupy adjacent ranks (Kawai 1958; Koyama 1967; Sade 1967; Missakian 1972; Cheney 1977 and in prep.; Chapais and Schulman 1980). Because a female usually assumes her mother's dominance rank, each individual is confronted from a very early age with a different social environment to which she must adapt her behavior. This paper considers the costs and benefits of high and low rank to free-ranging female vervet monkeys (*Cercopithecus aethiops*), and discusses some behavioral adaptations related to minimizing those costs and maximizing potential benefit.

A number of studies of captive and semi-captive groups of macaques have suggested that high-ranking females are able to raise more offspring than are low-ranking females (Drickamer 1974; Sade et al. 1976; Wilson et al. 1978; Silk et al. 1981). Two factors appear to contribute to the differential reproductive success of high-ranking females: harassment of low-ranking females (see Discussion below) and priority of access to food and water (Dittus 1977; Wrangham 1981; see also below).

All previous studies documenting a positive relation between female rank and reproductive success have been conducted either on captive, provisioned populations (see references above) or in areas where predators are rare (Dunbar and Dunbar 1977). In contrast, the vervet monkeys described here confronted predators regularly. Deaths due to predation and those due to illness during periods of food scarcity were non-randomly distributed with reference to dominance rank, and individuals appeared to adopt

different behavioral strategies depending upon their susceptibility to different kinds of mortality. In describing the behavior of high- and low-ranking females, we do not propose to offer a definitive analysis of the relation between behavior and individual reproductive success, which in any primate species would take years of observation. Instead, our aim is to provide some examples of the ways in which the social environment places different selective pressures on individuals, even though such individuals live in the same group, confront the same predators, and utilize the same food resources.

Materials and Methods

The three vervet groups discussed in this paper have been studied continuously since at least 1977 in Amboseli National Park, Kenya. The park lies in an area of semi-arid acacia savanna that has been described by Struhsaker (1967a), Altmann and Altmann (1970), and Western and Van Praet (1973). Between March 1977, and September 1980, the period examined in this paper, the three study groups ranged in size from 11 to 28 individuals. Births, deaths, immigrations, and emigrations were monitored throughout this period. Although the ages and genetic relations among adults could not be determined, the mothers and siblings of almost all juveniles were known, either through birth dates or through prolonged nipple contact with a particular adult female. In two cases maternity was inferred through grooming and the maintenance of spatial proximity (see Walters 1981). A 'family' was defined as an adult female and her immature offspring. A family's dominance rank was defined in terms of each adult female's rank relative to other females. This definition was adopted because in all cases when an adult female died her offspring retained their mothers' rank (unpublished data). Thus for purposes of analysis each family retained the same absolute rank even after the death of its adult female.

The study groups inhabited contiguous home ranges, averaging approximately 0.4 km² in size (Lee, in prep.). The areas incorporated by each group's home range remained stable throughout the study period. Each group actively defended its range against incursions by other groups (Struhsaker 1976b; Cheney 1981). Of the three study groups, Groups B and C had unrestricted access to permanent water holes. In contrast, no pools of water were available to Group A during the dry seasons, which extend from between February and March and between June and November of each year.

The study groups were observed by Cheney and Seyfarth in 1977, 1978, and 1980, and by Lee during 1978 and 1979. Because the scientific aims of our research varied, some behavioral measures were not gathered continuously. As a result, many of the behavioral data we present do not incorporate the entire period between 1977 and 1980. In addition, some data described in this paper have already been published elsewhere. In some cases we therefore summarize our findings from other works.

Data were gathered using focal animal, behavior-dependent, and *ad libitum* sampling techniques (Altmann 1974). In the following analysis, data from each group have been presented separately. In the case of Spearman correlations, we present separate correlations for each group, as well as an overall correlation coefficient ($\hat{\rho}$) (Kraemer 1975) whenever statistical tests revealed no significant heterogeneity across group. All tests are two-tailed.

Results

A. Competition Among Females

Like baboons and macaques, female vervets remain in their natal groups throughout their lives, while males emigrate to neighboring groups at around sexual maturity (Cheney 1981). Within the group, adult females can be ranked in linear dominance hierarchies, based on the direction of approach-retreat interactions (Seyfarth 1980). Table 1 shows the distribution of approach-retreat interactions among adult females during a 14 month period in 1977 and 1978. In Groups A and C, female ranks remained stable through 1980, with daughters assuming ranks similar to those of their mothers (Cheney, in prep.; Lee, in prep.). In Group B, two pairs of adjacently-ranked females switched ranks in 1978. In both cases, formerly lower-ranking individuals were subadult females who rose one place in the rank order after the female ranked immediately above them had given birth. In each case, physical resemblance suggested that the females who switched ranks may have been sisters, but lack of long-term data preclude any definitive statements regarding their genetic relationships (see Chapais and Schulman 1980).

High-ranking females in each of the study groups were consistently able to exclude lower-ranking animals from food and water (Seyfarth 1980; Wrangham 1981). Such unrestricted access to scarce resources appears to have increased the probability of survival during periods of food scarcity (see below).

B. Reproductive Success and Causes of Mortality

1. Reproductive Success

The unrestricted access of high-ranking females to food and water suggests that such individuals might have had a reproductive advantage over low-ranking females, especially during periods of food scarcity. During the 3.5 year period between March 1977, and September 1980, there were no consistent rank-related differences in birth rates (Table 2). Any variation in reproductive success among females of different ranks should therefore have been correlated with differential offspring survival.

Table 3 considers reproductive success over three birth seasons (1977, 1978, 1979) in terms of both the proportion and the absolute number of a female's infants to survive to 12 months. We consider reproductive success in terms of infant survival for two reasons. First, infant and juvenile mortality was highest during the first 12 months of life (Fig. 1). Second, the inclusion of a female's older offspring (i.e. those

Table 1. The distribution of approach-retreat interactions among adult females in each study group. Individuals are arranged in the rank order that produced the fewest reversals. Data were gathered during 1977 and 1978

Group A		Avoiding							
		LB	DN	BA	MP	AN	LL	VF	OJ
Approaching	LB ^a		29	62	47	67	33	40	11
	DN ^a	39		51	38	37	16	16	13
	BA				70	65	49	55	19
	MP			1		40	44	32	19
	AN						21	21	6
	LL							18	11
	VF								19
	OJ								

Group B		Avoiding						
		SM	BK	AM	FR	DU	PT	MA
Approaching	SM ^b		34	33	49	25	29	23
	BK ^b			46	33	30	27	33
	AM				36	24	25	20
	FR					26	51	37
	DU						34	22
	PT ^b							4
	MA ^b						3	

Group C		Avoiding							
		PR	AP	TD	LH	ML	BB	SZ	LO
Approaching	PR		37	61	48	55	34	38	29
	AP			34	32	40	23	21	20
	TD				21	21	18	15	12
	LH					23	20	26	14
	ML						24	39	22
	BB					1		19	7
	SZ								12
	LO								

^a Switched ranks in 1977

^b Switched ranks in late 1978. Based on focal animal plus sequence sampling

born before 1977) would ignore the possibility that some females might have had infants who died before the start of our study. For purposes of comparison, however, we also indicate the total number of a female's known offspring who survived through 1980 (Tables 2 and 3). As Table 3 indicates, there were no rank-related differences in infant survival in any of the three study groups.

Table 2. The mean rate at which adult females of different dominance ranks gave birth during 1977, 1978, and 1979. The total number of offspring known to have been produced by each female is also shown. Adult females have been assigned the ranks they occupied for the longest period of time. Female rank is expressed in terms of the proportion of individuals whom they dominated in order to permit comparison across groups in which the number of adult females varied

		Adult ♀♀	% of ♀♀ dominated	No. of birth seasons alive (1977-1979)	No. of infs. born	Mean no. infs./year	Total no. of known offspring
Group A	DN	100	3	2	0.67	3	
	LB	86	3	2	0.67	3	
	BA	71	3	2	0.67	3	
	MP	57	1	1	1.00	2	
	AN	43	3	2	0.67	3	
	LL	29	1	1	1.00	3	
	VF	14	1	1	1.00	1	
OJ	0	1	1	1.00	4		
Group B	BK	100	3	0	0	0	
	SM	83	3	2	0.67	2	
	AM	67	3	2	0.67	3	
	FR	50	3	2	0.67	2	
	DU	33	3	2	0.67	2	
	MA	17	3	2	0.67	2	
PT	0	3	3	1.00	3		
Group C	PR	100	3	3	1.00	5	
	AP	86	1	1	1.00	3	
	TD	71	3	0	0	0	
	LH	57	3	3	1.00	5	
	ML	43	3	2	0.67	4	
	BB	29	3	3	1.00	3	
	SZ	14	2	1	0.50	3	
LO	0	3	2	0.67	2		

The results presented in Tables 2 and 3 should be interpreted with caution, since they do not control for female age, a factor which often affects female reproductive success (Altmann 1980; Silk et al. 1981). Although the ages of females in our study population were not known, we were able to identify most females as either multi- or primiparous. Even when female parity was controlled, however, there were no significant differences in infant survival rates among females of high or low rank.

Thus over the short term, two conclusions emerge. First, high-ranking females did not raise more offspring than did low-ranking females. Second, the lack of a positive relation between female rank and reproductive success was not simply an artifact of female age.

2. Causes of Mortality

The lack of a relation between female rank and reproductive success in our study population results in part

Table 3. The proportion and absolute number of infants born in 1977, 1978, and 1979 to adult females of different dominance ranks that survived their first 12 months. The total number of each adult female's known offspring to survive through 1980 is also shown. Spearman correlations r_s illustrate the extent to which ranking by offspring survival is correlated with dominance rank. Females who did not produce offspring have been excluded. See Table 2 for legend and for the total number of offspring born to each female

	Adult ♀♀	% of ♀♀ dominated	% of infs. to survive	No. of infs. to survive	Total no. of surviving offspring
Group A	DN	100	0	0	1
	LB	86	50	1	1
	BA	71	100	2	3
	MP	57	0	0	0
	AN	43	50	1	2
	LL	29	0	0	2
	VF	14	0	0	0
	OJ	0	0	0	1
		$r_s=0.399$	$r_s=0.399$	$r_s=0.148$	
Group B	SM	83	50	1	0
	AM	67	100	2	2
	FR	50	50	1	0
	DU	33	50	1	1
	MA	17	50	1	1
	PT	0	67	2	1
		$r_s=-0.068$	$r_s=-0.207$	$r_s=-0.278$	
Group C	PR	100	33	1	2
	AP	86	0	0	1
	LH	57	33	1	3
	ML	43	50	1	3
	BB	29	0	0	0
	SZ	14	100	1	3
	LO	0	50	1	1
		$r_s=-0.551$	$r_s=-0.158$	$r_s=0.094$	

from the fact that causes of mortality were non-randomly distributed among individuals of different ranks. Table 4 divides causes of mortality into a number of categories.

Confirmed predations occurred when a predation was witnessed, either by ourselves or by scientists conducting research on baboons. Between 1977 and 1980, we confirmed two predations by leopards, five by baboons, one by a martial eagle, two by pythons, and one by an unidentified carnivore.

Animals who disappeared healthy were observed to be in apparent good health within 24 h of their disappearance. In almost all cases when an animal disappeared under such circumstances a predator was observed within 24 h in the range of that individual's group, and the members of the group behaved as if a predation had occurred. The monkeys alarm-called at high rates, were hesitant in descending from

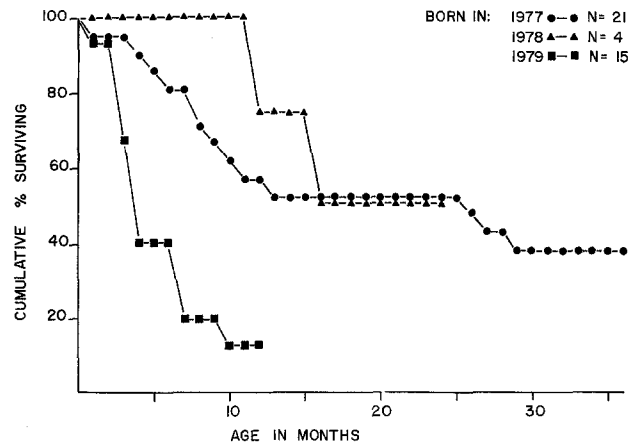


Fig. 1. The cumulative proportion of infants that survived to various ages

Table 4. The causes of mortality among vervets over a 3.5 year period. See text for definitions of each category. The total number of individuals known to have lived in each group during the time period is indicated

	Causes of mortality March 1977–September 1980				
	Predation	Disappear, seen healthy within 24 h	Illness	Die following Mother's death due to	Disappear during observer's absence of 24 h
Group A (36 inds.)	3	2	7	predation: 2 illness: 1 unknown: 1	7
Group B (24 inds.)	1	6	0	0	3
Group C (38 inds.)	6	1	2	predation: 1	6

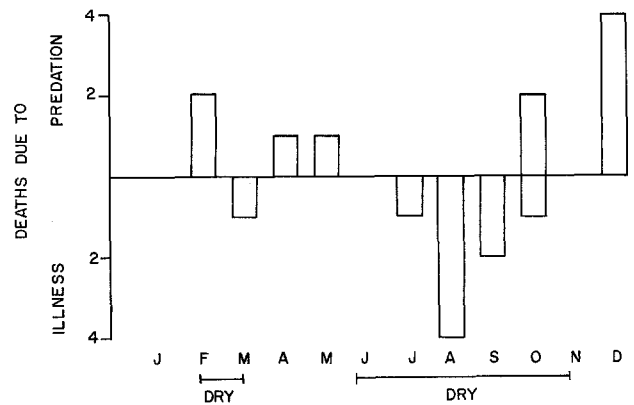


Fig. 2. The seasonal distribution of mortality due to predation and illness. Figures on the y-axis indicate numbers of deaths per month

their sleeping trees, and ran back into the trees at the slightest disturbance. One adult male disappeared in apparent good health, and it was impossible to determine whether he died or emigrated to a distant, non-adjacent group. When adult females or juveniles of either sex disappeared healthy, however, they were presumed to have died. We felt justified in making this assumption because adult and juvenile females have never been observed to emigrate. In the case of juvenile males, all five individuals observed to emigrate were orphans who transferred to adjacent groups in the company of their brothers or peers, and whose movements were therefore easy to document (Cheney and Seyfarth 1981b). At present, we hypothesize that animals who disappeared in apparent good health were preyed upon.

Deaths due to illness were recorded whenever animals manifested unambiguous signs of disease or listlessness within 24 h of their disappearance. In all cases when vervets were observed to die following illness, they showed symptoms of illness for at least 24 h. In seven of nine cases when vervets were said to die of illness, they were afflicted either with a staphylococcal infection of the eye (Else, personal communication) or with a disease in which a male's testicles, which are normally blue, become shrivelled and black. All deaths due to illness occurred during the dry season. Seven of nine such deaths occurred in Group A, which had no surface water during the dry season. In contrast, deaths due to predation were not concentrated in any given month, and did not coincide with those due to illness (Fig. 2).

Five infants, aged between three and eight months, died following their mother's death. The youngest infant to survive its mother's death was aged six months. The next youngest orphan to survive was 16 months of age.

Finally, 16 animals disappeared during a period when the observer was absent for more than 24 h. In such cases, the observer's absence precluded any conclusions regarding the cause of death.

Although the sample of confirmed causes of mortality is small, there is nevertheless evidence that predation and illness affected individuals in a non-random manner. Of nine adult females and juveniles who died of predation, eight were members of families above median rank. In contrast, of seven adult females and juveniles who died following illness, five were members of families below median rank (Two-tailed Fisher exact probability test, $P < 0.10$). The two individuals above median rank who died following illness were members of the fourth-ranking family in a group of eight families.

It is probably not surprising that the members of high-ranking families were at an advantage during

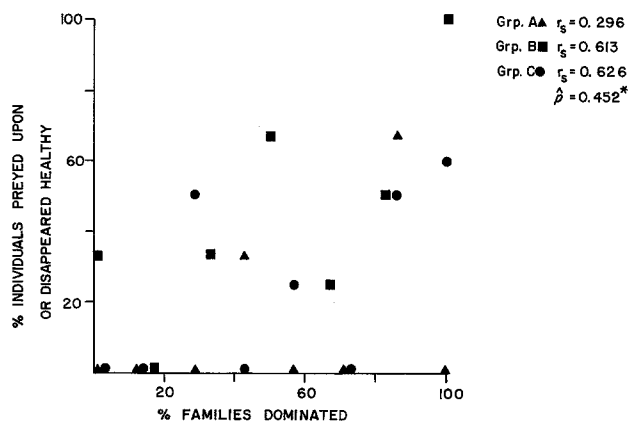


Fig. 3. The relative frequency with which the members of families of different ranks were preyed upon or disappeared healthy between 1977 and 1980. Families are defined as adult females and their offspring, and are arranged on the x-axis according to the proportion of females whom each adult female dominated in approach-retreat interactions. Females have been assigned the ranks they occupied for the longest time period. Analysis excludes animals who disappeared during more than 24 h of the observers' absence. Spearman correlations illustrate the extent to which ranking by dominance was correlated with ranking by mortality. * $P < 0.05$; ** $P < 0.01$.

periods of limited food and water availability, since they were able to exclude others from scarce resources (Wrangham 1981). At least over the short term, however, high-ranking females did not raise more offspring than did low-ranking females, suggesting that access to food and water alone did not determine the probability of survival. Data on confirmed cases of predation suggest that high-ranking females and their offspring were preyed upon more than lower-ranking individuals. In Fig. 3, we consider the correlation between a family's rank and the frequency with which its members were preyed upon or disappeared healthy (probable predation). Overall, the members of high-ranking families were significantly more likely than the members of low-ranking families to die under such circumstances.

C. Correlates of Non-Random Mortality

1. Group Progressions

It is difficult to elucidate the causal factors that contributed to the vulnerability of high-ranking animals to predation. One possibility concerns the manner in which a group moves through its range, and the rank order that animals assume during group progressions. Data gathered in 1978, for example, indicate that the offspring of high-ranking females were significantly more likely than the offspring of low-ranking females to be in the forefront of group progressions (see Cheney and Seyfarth 1981a for a complete descrip-

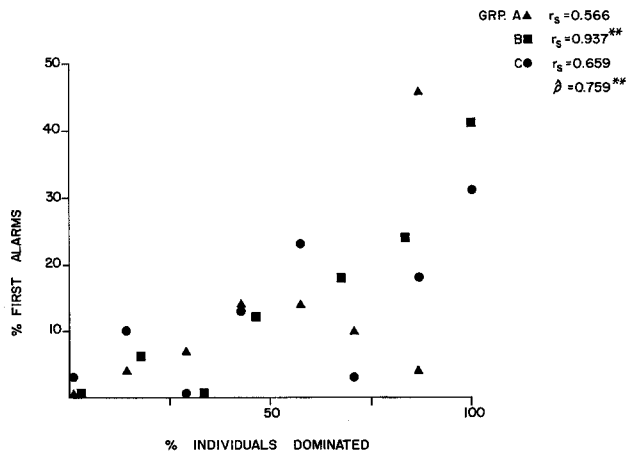


Fig. 4. The relative frequency with which adult females of different dominance ranks were the first to alarm-call at predators. Legend as in Fig. 3. Data based on 28 first alarm calls by females in Group A, 17 in Group B, and 39 in Group C

tion of these results). The offspring of high-ranking females thus preceded other juveniles when the group moved into new areas of its range, a behavior that may have increased their vulnerability to predation. Exactly why high-ranking juveniles preceded their peers is not known. Since such individuals were able to supplant others from food and water, there is no obvious way in which high-ranking juveniles would benefit from leading group progressions. Similarly, there is no evidence that the individuals who led group progressions during 1978 were subsequently more likely than others to be preyed upon or to disappear healthy.

2. Alarm-Calling

Data on causes of mortality suggest that high- and low-ranking animals may have different selective pressures placed upon them, despite living in the same habitat and confronting the same predators and food resources. This raises the possibility that animals of different ranks may respond differently to similar social and environmental variables. For example, results suggest that high-ranking females and their offspring were more vulnerable than other animals to predation. High-ranking females were also more likely than others to be the first to alarm-call when their group encountered predators. Figure 4 illustrates the correlation between dominance rank and the frequency of first alarm calls for adult females. Data are taken from the total number of first alarms given by females in each study group over a 14 month period in 1977 and 1978. Analysis considers only the first alarm call to be given to a predator because such alarms presumably play the greatest role in warning other group

members of danger (for a detailed description of alarm calls to predators, see Cheney and Seyfarth 1981a). As Fig. 4 illustrates, high-ranking females alarm-called more frequently than low-ranking females.

Although we do not know the precise relation between high frequencies of alarm-calling and vulnerability to predation, a number of possible explanations can be ruled out. Because there was no correlation between female rank and reproductive success, it is unlikely that high-ranking females alarm-called most because they had the most relatives, as might be argued by a kin selection hypothesis (see e.g. Sherman 1977). At a more proximate level, films of scanning behavior did not suggest that high-ranking females had a greater probability of spotting predators before others did. Similarly, there was no evidence that alarm-calling increased an individual's vulnerability to predation. All observed cases of predation occurred before any alarm calls had been given, suggesting that predation was most likely to occur before the vervets had become aware of danger (Cheney and Seyfarth 1981a; see also Altmann and Altmann 1970 for a description of vervet interactions with baboons). The frequency with which adult females alarm-called appears to have been primarily a function of both the particular predator involved and some combination of their own and their offsprings' vulnerability. Moreover, the lack of a correlation between alarm-calling and scanning behavior suggests that individuals who had seen predators may have 'chosen' whether to give an alarm call or remain silent (see Cheney and Seyfarth 1981a).

3. Group Defense Against Conspecifics

High-ranking females in the three study groups had a competitive advantage over others, and they appeared to benefit more than others from the resources contained within their group's range. Such differential benefit may have caused high-ranking females to be more aggressive than low-ranking females during intergroup encounters, and to be more active in preventing other vervet groups from utilizing their group's resources.

Vervet groups inhabit largely non-overlapping home ranges. Encounters between groups may involve vocalizations alone, or peaceful mingling and even grooming, playing, and copulation. Frequently, however, intergroup encounters escalate into aggressive chases and physical attacks, in which monkeys of all ages and sex participate (Cheney 1981). Figure 5 illustrates the frequency with which adult females of different ranks were aggressive toward the members of other groups during intergroup en-

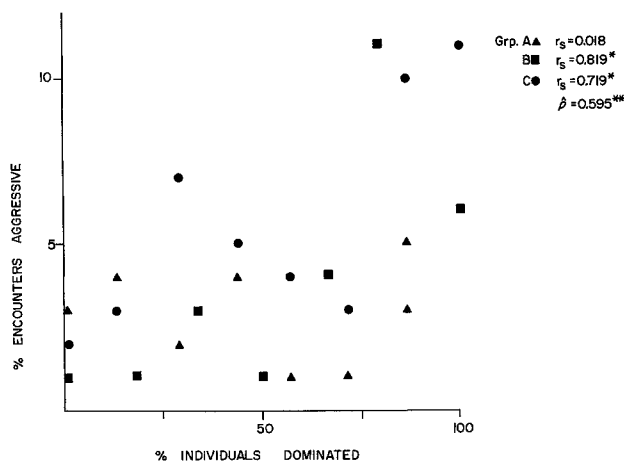


Fig. 5. The relative frequency with which adult females of different dominance ranks were aggressive toward the members of other groups during intergroup encounters. Legend as in Fig. 3. Data based on 96 encounters involving Group A, 139 involving Group B, and 118 involving Group C

Table 5. The proportion of each adult female's interactions with the members of other groups that were friendly. n = total number of friendly and aggressive interactions initiated by Group B females during intergroup encounters in 1977, 1978, and 1980

Adult ♀♀	% of ♀♀ dominated	n	% of friendly interactions
BK	100	85	13
SM	83	42	2
AM	67	28	4
FR	50	36	25
DU	33	24	17
MA	17	65	23
PT	0	45	51

$r_s = -0.786$
 $P < 0.10$

ounters. Such encounters were defined as any vocal or behavioral interactions between the members of different groups (Cheney 1981), and results are based on intergroup encounters observed during 1977 and 1978. Data indicate that high-ranking females in two of the three study groups were significantly more aggressive during intergroup encounters than were low-ranking females.

Friendly interactions between the members of different groups were also non-randomly distributed among adult females of different dominance ranks. Juvenile males and females of all ranks occasionally groomed, played with, touched, or mounted the members of other groups. Among adult females, such friendly interactions were rare. When they did occur, however, they tended to be initiated by low-ranking individuals. In Groups A and C, both of which originally included eight adult females, the only females

over five years of age who were ever observed to initiate friendly interactions with the members of other groups were ranked six and seven. In Group B, all females were observed to initiate such interactions. Rates of friendly interactions, however, were inversely correlated with rank (Table 5). In summary, therefore, while high-ranking females were more aggressive than low-ranking females during intergroup encounters, most friendly interactions were initiated by low-ranking females.

Discussion

Over a 3.5 year period, deaths due to illness and predation operated in a non-random manner on vervet monkeys in Amboseli. Excluding cases in which animals disappeared during the observer's absence, deaths due to illness accounted for 27% of all cases of mortality, and were concentrated among low-ranking animals. Such deaths resulted at least in part from the limited availability of food and water during the dry season (see Wrangham 1981). Predation also seemed to exert strong selective pressures on vervet monkeys. Speaking conservatively, 30% of all deaths in the three study groups were due to predation. If cases in which animals disappeared healthy are included, predation may have been responsible for 58% of all deaths. As with illness, predation affected vervets in a non-random manner: high-ranking animals were more likely than low-ranking animals to be preyed upon. Because illness and predation affected some individuals more than others, they may also have influenced behavior in a non-random manner. In other words, the distribution of causes of mortality suggests that individuals living in the same social group may confront different selective pressures, and may, as a result, respond differently to similar social and environmental variables.

A number of studies have shown a reproductive advantage to females of high rank (see Introduction). In some cases, harassment by high-ranking females may lower the fecundity of low-ranking females (Dunbar 1980; Silk et al. 1981). This did not appear to be the case for the Amboseli vervet monkeys, because there was no relation between dominance rank and birth rate. Instead, the advantage of high rank appeared to be priority of access to food and water, and a lowered probability of mortality during periods of food scarcity. In this respect, data on vervet monkeys resemble those on Toque macaques (Dittus 1977), among whom mortality seems to be socially mediated through intragroup competition for food. Because many of the constraints imposed on low-ranking vervet monkeys also appeared to be social in nature, such individuals may consequently have

adopted social strategies in order to counteract their subordinate status.

Previous studies of baboons, macaques, and vervet monkeys provide a number of illustrations of the manner in which low-ranking females may attempt to improve their competitive abilities. For example, low-ranking females often attempt to interact affinitively with high-ranking females. Such interactions seem adaptive, because they occasionally permit low-ranking females to feed near high-ranking animals, or to gain the support of high-ranking animals in aggressive disputes (Seyfarth 1977, 1980; Chapais and Schulman 1980; Fairbanks 1980). Bonds formed with high-ranking females may therefore permit low-ranking individuals to gain access to resources from which they might otherwise be excluded, even if they do not increment the individuals' ranks. Similarly, low-ranking female vervet monkeys were more likely than high-ranking females to initiate friendly interactions with the members of other groups. Low-ranking females seemed to have the least to gain from the maintenance of the status quo within their groups, and seemed most likely to initiate interactions that might have had the consequence of disrupting group cohesion (see also Chepko-Sade and Sade 1979). In contrast, high-ranking females, who had the most exclusive access to their group's resources, were most active in defending their group's range against incursions by conspecifics, and in segregating their group from intruders.

While high-ranking females in this study had priority of access to food and water, we were unable to document a positive correlation between rank and reproductive success, at least over the short term. This seems due at least in part to the fact that high-ranking animals were more likely than others to die of predation. The precise cause of their vulnerability to predation remains obscure. One behavioral adaptation to such vulnerability, however, seemed to be an increase in the frequency with which high-ranking females gave alarm calls. Such alarm-calling by high-ranking individuals emphasizes that reproductive success may be influenced by many factors. All previous studies documenting a positive correlation between female rank and reproductive success have been conducted either on provisioned groups or in areas where predators are rare. In contrast, results presented here suggest a cost, as well as a benefit, to high rank. This is not to say that such costs necessarily outweigh the benefits. During periods of drought or food scarcity, for example, high-ranking animals are likely to be less vulnerable than others to starvation and disease. The data suggest, however, that patterns of behavior associated with high rank may increase the risk of mortality due to other factors. Individuals

appear to attempt to counteract the liabilities of high rank by changing their response to particular environmental variables.

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