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Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya

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Summary. A decline in the density of trees and the deterioration of the habitat of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya, have been accompanied by movement of vervet groups into unfamiliar areas. These home range shifts were documented over a period of 26 months. The largest group moved into the home ranges of neighboring groups and acquired more trees, a resource that had become more limited. The groups whose home ranges were encroached upon did not share their home ranges with the intruders, but instead moved into areas that were unoccupied and had a lower density of trees. The largest group was thus more successful than smaller groups in competition for limited resources. For all but one group, movement into new areas was directly associated with the disappearances of female and immature monkeys. Most of the disappearances were attributable to predation. These results suggest that the cost of predation in unfamiliar areas may contribute to the evolution of philopatry in vervets. However, under unstable conditions, resource competition forces these animals to disperse (in groups) despite the high risk of predation.

Introduction

Many mammalian species are characterized by female philopatry; females remain in their natal home ranges throughout their lives, regardless of whether or not they live in stable social groups (Waser and Jones 1983). In many species, the prevalence of female philopatry is thought to derive ultimately from constraints imposed on female reproduction by nutritional demands. A female's reproductive success depends largely on obtaining sufficient food resources (Trivers 1972; Wrangham 1980), and dispersing may reduce access to foods through lack of knowledge about resources in unfamiliar environments (Waser and Jones 1983) or increased aggression from less familiar individuals (e.g., deermice: Healey 1967; ground squirrels: Dunford 1977).

Males, on the other hand, are seldom philopatric and typically disperse from their natal home ranges around sexual maturity. Although dispersal is thought to be associated with higher mortality among males, only a few studies have been able to document the causes of such mortality (reviewed in Van Vuren 1990). Increased risk of predation appears to be a main cause of dispersal-related mortality. For males, more than for females, the cost of dispersal may be outweighed by increased opportunities to mate with a greater number of non-relatives.

Philopatry and dispersal in most cercopithecine monkey species follow this typical mammalian pattern. Females remain throughout their lives in their natal groups and home ranges, while males emigrate around sexual maturity (Pusey and Packer 1987). Nevertheless, even in those species in which male emigration is the norm, females also occasionally disperse. This dispersal can take three forms. First, females may move from one social group to another whose home range does not overlap with the original group. Second, dispersal may result from the splitting, or fissioning, of an established group (e.g., blue monkeys: Cords and Rowell 1986; redtail monkeys: Struhsaker and Leland 1988; Japanese macaques: Sugiyama 1960; Koyama 1970; rhesus macaques: Chepko-Sade and Sade 1979; long-tailed macaques: van Schaik and van Noordwijk 1988; savannah baboons: Nash 1976). In most cases of group fission, the resulting subgroups initially share the former group's range, but dispersal over time occurs as the smaller of the two groups shifts to a different range (Sugiyama 1960; Furuya 1968; Nash 1976). Finally, an entire social group may expand or shift its range into a new area. During a range shift, one group may supplant another from an already occupied area or it may shift into marginal areas not used by any other group. In this paper, we describe this latter kind of dispersal in six groups of vervet monkeys (*Cercopithecus aethiops*) following the deterioration of their former habitats.

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Groups of vervet monkeys generally occupy relatively small territories which are aggressively defended against incursions by other groups (Cheney 1981; Cheney 1987). In Amboseli National Park, Kenya, the range size of vervet groups between 1977 and 1981 averaged around 23 ha, and each group occupied approximately the same geographical area over that five-year period. However, in a process that began in 1983 and accelerated rapidly after 1985, all vervet groups shifted their ranges substantially. While the largest group moved into the ranges of smaller groups, smaller groups shifted their ranges into marginal and unoccupied areas. These range shifts were apparently the result of habitat deterioration and were facilitated by a decrease in the number of vervet groups.

In this paper we investigate the benefits of range shifts, and describe how such shifts enabled the largest group to acquire more trees relative to both the number it would have had by not shifting and to groups it supplanted. We then examine one cost of dispersal by reporting an association between disappearances of adult female and immature vervets across groups and their use of unfamiliar areas. Although there is no reason why these costs and benefits should not also apply to adult males, we do not consider them here because it difficult to distinguish disappearances of males from emigration to distant groups. The results suggest that greater risk of predation in unfamiliar areas favors range fidelity among females. In unstable environments, however, competition for food resources may cause groups of females to shift into new areas despite the increased risk of predation.

Methods

Study site. Observations were conducted on a population of vervet monkeys in Amboseli National Park, Kenya (2°41′ S, 37°10′ E) from 1977 to 1989 by the authors and their colleagues (see Lee 1981; Andelman 1985; Hauser 1987; Cheney et al. 1988). Amboseli is a semi-arid savannah with little rainfall in January, February, and June through September (Western 1983). The two major tree species in Amboseli are *Acacia xanthophloea* and *A. tortilis*. *Acacia xanthophloea* (or fever tree) is typically found along swamps and watercourses, whereas *A. tortilis* is common in drier habitats. In the ranges of the six main study groups, as in all of Amboseli, there has been a marked and steady decline in the *A. xanthophloea* population over the past 30 years (Western and van Praet 1973). In the study area, an area that was dense woodland in the 1950s, there remained only six scattered fever trees in 1989. This stand dieback has been attributed to a combination of climatic change, stand senescence, and elephant browsing (Western and van Praet 1973; Young and Lindsay 1988; Lindsay, in prep.). In contrast to *A. tortilis* trees, which are still common in Amboseli, fever trees provided vervets in the past with food throughout the year from a variety of plant parts (Struhsaker 1967). The decline in the fever tree population has been correlated with a continuous decline in the vervet monkey population (Struhsakere 1973, 1976; Cheney et al. 1988), supporting the hypothesis that fever trees are important food resources for Amboseli vervets.

Study groups and data collection. Three social groups were studied intensively from 1977 to 1988. Intensive study of three additional groups was begun in 1983 and continued to 1988. Table 1 lists the numbers of males, females, and immatures in each study group as of October 1985 and December 1987, the period dealt with in this paper. The largest group throughout this period of observation was Group B.

All individuals in the six main study groups were individually identified and habituated to observers. As part of the sampling regimen, all births, deaths, wounds and signs of lethargy were recorded whenever each group was sampled. Whenever an animal was not located, the surrounding area was searched for any signs of predation, accident, or death by illness. All eight groups surrounding the main study groups were also censused for possible transfers. In addition, these groups were censused semi-annually every year except 1981.

Group movements and range use were scored on a map divided into quadrats measuring 33 m × 33 m. This map was originally prepared by R. Wrangham in 1978 and was regularly updated to note tree deaths or growth. Home range usage was measured in two ways. From January 1983 until October 1985, it was scored by noting every quadrat entered by a group on a given day. This method provided a measure of range size but not of range use. These data are used here only for describing general range patterns and for determining whether quadrats entered in later years were new.

Beginning in October 1985, a new method for measuring ranging patterns was adopted. During the daily sampling period, the locations of all visible individuals in a given group were scored at 30 minute intervals. This method allowed us to examine more accurately patterns of range use and to calculate rates of new quadrat usage. These rates were calculated for each group (monthly and annually) by dividing the number of new quadrats entered by the number of hours that each group was observed during a given time period. The ranging data from October 1985 to January

Table 1. Group sizes of main study groups in October 1985 and in December 1987

Group	October 1985				December 1987			
	Adult Males	Adult Females	Immatures	Total	Adult Males	Adult Females	Immatures	Total
4	4	2	5	11	0	0	0	0[a]
2	4	5	2	11	0	0	0	0[b]
A	1	5	2	8	0	0	0	0[c]
B	2	7	10	19	4	4	5	13
C	3	4	7	14	2	2	4	8
3	3	5	2	10	1	6	4	11

[a] Remaining members fused with Group 2
[b] Remaining members fused with Group TW3
[c] Remaining members fused with Group TW3

1988 are based on 1627 h of observation, conducted throughout the day but most often between 0630 hours and 1400 hours (see Fig. 1 for sample hours per group). Each group was sampled a maximum of six days every month except in September 1987 when no groups were sampled.

We used quadrats entered between January 1983 and September 1985 as the baseline for each group's home range. Starting in October 1985, we scored as 'new' any quadrat that each vervet group had not previously been observed to enter.

Data on activity budgets were based on 974 focal hours from June 1986 to January 1988. The activity categories included feeding, resting, moving, scanning, grooming, and other behaviors. Point samples of activities (after Altmann 1974) were collected under two regimens. During the first eight months, one animal was sampled every five minutes according to a predetermined random order. If the target animal was not found within two minutes, the next animal in the order was sampled until the target animal was located. After January 1987, information on a larger number of individuals per unit time was collected in scans of the entire group at ten-minute intervals. The group was scanned from left to right to avoid attraction to obvious behaviors such as fighting, and scans were limited to one minute per scan for the entire group. Activity budgets were first calculated for each adult female as percentages of monthly samples in which a particular activity was scored, weighted for unequal sample sizes across hours of the day to control for diurnal variation in activities. Group time budgets were then calculated as monthly means of all individual percentages.

Causes of mortality. Cheney et al. (1988) used the following major categories to classify previous data on vervet mortality: death from *illness* was said to occur when an animal was observed to be listless, weak, or diseased within 24 h of its disappearance. In such cases, the apparent illness was usually evident several days before the disappearance. When unweaned infants disappeared after their mothers died, they were included in the category, *die following mother's death*. This category was separate from *suspected infanticide* which involved deaths of infants following attacks on them by immigrant males. *Predation* consisted of confirmed and suspected predation. Confirmed predation included witnessed kills or observations of predators carrying away monkeys, whereas suspected predation was scored when an animal disappeared within 24 h of having been observed in healthy condition and was not found to have transferred to another group. In many of these cases the remaining group members appeared nervous, and in the morning they were often found alarm-calling or scattered about their range.

In the present analysis, which includes additional data from the years 1984 to 1988, the criteria for determining illness and predation have been changed because animals dying of illness typically showed signs of illness for more than 24 h before they disappeared (median: six days; range: 1–120 days; $n=5$). Here death from illness was scored when an animal was found to be listless, weak, or diseased within 72 h of its disappearance. Suspected predation is redefined as the disappearance of an apparently healthy individual within 72 h of final sighting. One exception occurred when Group B, which was normally easy to find, could not be located for five days despite intensive searches. When the group was found again, one adult female and five juveniles were missing. These disappearances have been included as suspected predation here.

Several animals disappeared while the observer was absent for more than 72 h. In these cases, the probable cause of the disappearances could not be determined and the category was called *observer absent > 72 h.* For this paper we included these deaths as well as deaths to infants following mother's death and predation (suspected and confirmed) under the broad category of *disappearances.* Infants who died before the age of two months while their mothers were still alive were not included in the analysis. Disappearances of adult males were also excluded because males who were not found may have simply transferred to a distant group. It should be noted, therefore, that the estimates of predation and disappearances are conservative estimates because males are, nevertheless, vulnerable to predation. Females were assumed not to transfer when they disappeared because females rarely transfer. Only 11 cases of female transfer have occurred during 11 years of this study and at least seven involved group fusions in which an entire group joined another group (see Hauser et al. 1986; Isbell et al. in prep.).

Statistical analyses. All statistical tests are Wilcoxon matched-pairs, signed-ranks tests, or Spearman rank correlation tests (Siegel 1956). To control for differences among groups caused by habitat differences, the data for each group were analyzed separately. Significance was set at $P=0.05$, and one-tailed tests were used because directions were predicted for the alternative hypotheses.

Results

Benefits of home range shifts

A. Home range use. Yearly rates of movement into new areas between 1985 and 1987 varied among groups (Fig. 1). Some groups moved into new areas at consistent rates over the years (Groups 3 and 4), while the others moved most during one particular year. The high rate of increase for Group A's movement in 1987 was primarily a result of its fusion with Group TW3 (Fig. 2). Following fusion, the remaining members of Group A ceased to use their old range and adopted the range of their new group (see Hauser et al. 1986; Isbell et al. in prep. for a discussion of the causes of fusions). The shifts of Groups B and C appeared to be due primarily to the reduction in suitable habitat. In the past, Group B's territory had the best resources; it included the greatest number of fever trees as well as numerous shrubs and a permanent waterhole (Lee 1981; Cheney and Seyfarth 1987; Hauser 1987). By June 1989, however, only six fever trees remained even in its expanded range.

Among animals in general, a decrease in population density is often correlated with an increase in individual or group home range size (e.g., tree sparrows: Stenger Weedon 1965; great tits: Krebs 1971; rabbits: Myers et al. 1971; sanderlings: Myers et al. 1979). This was

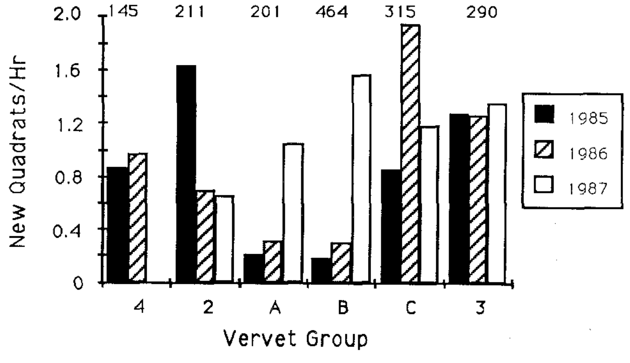

Fig. 1. Hourly rate in which new quadrats were entered between October, 1985 and December, 1987 in six main study groups. New quadrats were those which had not been scored as having been entered since 1983 when systematic records were begun. Numbers above bars represent the number of focal hours spent with each group

Table 2. Home range sizes from June 1986 through January 1988, and total extent of overlap among six vervet groups

Group	Total number of quadrats used	Number of quadrats that overlapped with other groups
4	47 (5.2 ha)	15 (31.9%)
2	142 (15.8)	49 (34.5)
A	121 (13.4)	12 (9.9)
B	115 (12.8)	66 (57.4)
C	224 (24.9)	18 (8.0)
3	150 (16.7)	6 (4.0)

Total amount of overlap for Groups A, C, and 3 underestimated because they overlapped with groups that were not intensively studied

Table 3. Number of newly occupied quadrats that were previously used vs. not used by neighboring main study groups from June 1986 through January 1988

Intruding group	Group intruded upon						
	Number of overlapping quadrats						Non-intrusive quadrats
	4	2	A	B	C	3	
4 ($n=20$)		6 (30)[c]	0	0	0	0	14 (70)
2 ($n=69$)	6 (9)		4 (6)	2 (3)	0	0	57 (83)
A ($n=46$)[a]	0	0		0	0	0	46 (100)
B ($n=87$)	0	27 (31)	8 (9)		1 (1)	0	51 (59)
C ($n=164$)	0	0	0	4 (2)		6 (4)	154 (94)
3 ($n=104$)[b]	0	0	0	0	0		104 (100)

n = Number of new quadrats entered

[a] Some overlap occurred with one group (KITS) that was not a main study group

[b] Overlap occurred with two other groups (KITSW and KITS) that were not main study groups

[c] Numbers in parentheses are percentages

also true in the case of Amboseli vervet monkeys. In 1978, 76 vervets lived in the area incorporated by the three original main study groups and population density was estimated at 96 individuals/km^2. By the end of 1987, only 13 individuals still ranged in the same area and population density had decreased to approximately 13 individuals/km^2 (Cheney and Seyfarth, unpub. data). The ranges of Groups B and C had also increased substantially over this period (Cheney and Seyfarth 1987). Group A, the other original study group, became "extinct" in 1987 when its remaining members abandoned their home range and joined a neighboring group.

B. Exclusive vs. overlapping quadrats, June 1986–January 1988. Vervet monkeys in Amboseli are territorial and normally defend their ranges against incursions by other groups. Perhaps as a result, in no case of range-shifting did a group subsequently share its new range with another group. Instead, vervet groups either supplanted existing groups or moved into unoccupied (and probably marginal) areas.

Total numbers of quadrats that were used by each group between June 1986 and January 1988 are listed in Table 2. The number of quadrats are minimum estimates of range size. Overlap was said to exist when a group used any quadrat between June 1986 and January 1988 that had also been used between 1983 and 1988 by another main study group. Areas of overlap for Groups A, C, and 3 are underestimated because their home ranges overlapped with groups that were not intensively studied. Using this broad time frame, total overlap among groups ranged from 4.0% to 57.4%.

Table 3 shows the extent of overlap among groups as a result of movement into *new* quadrats from June 1986 through January 1988. Of the 87 new quadrats entered by Group B, the largest group, 36 (41%) had been used earlier (between June 1986 and January 1988) by other groups (see also Cheney and Seyfarth 1987). While Group B tended to supplant existing groups, smaller groups shifted their ranges into marginal, unoccupied ranges. This encroachment and the shifting of home ranges are shown in Fig. 2. As recently as 1986, up to three groups (KH3, BTW, and KH4N) had lived in the areas into which Group C moved. However, by the time Group C moved there, these groups were no longer found during censuses, and were presumed to have become extinct.

These range shifts were associated with a substantial decrease in the rate of intergroup encounters. In 1977 and 1978, Groups A, B, and C, the three original study groups, interacted with other groups an average of once every 1.8 days. As late as 1985 and 1986, intergroup interactions still occurred at a rate of once every 1.9 days (Cheney and Seyfarth 1987). By the end of 1987, however, the rate had decreased to once every 6.6 days. Apparently, the decrease in vervet groups not only caused the remaining groups to become more widely dispersed, but also permitted some groups to expand with reduced aggression into vacant areas that had formerly been occupied by groups that now no longer existed.

C. Home range shifts and tree acquisition. Throughout their biogeograpical range, vervets are restricted to areas with trees (Wolfheim 1983), and the Amboseli vervets rely heavily on both *A. xanthophloea* and *A. tortilis* to provide food as well as cover from predators (Struhsaker 1967; Seyfarth and Cheney 1980). When fever trees were more numerous in Amboseli, they provided vervets with a wide range of food items (Struhsaker 1967) which represented about 50% of their diet (Lee 1981; Hauser 1987). Since fever trees have become largely unavailable, the vervets rely more heavily on *A. tortilis* for both food and refuge, although fecundity tends to be higher for groups which have dependable access to *A. xanthophloea* and water (Cheney et al. 1988).

Had Group B stayed in its 1983–1985 home range, by 1989 it would have had access to a total of only 28 living trees. By shifting its home range in 1987, Group

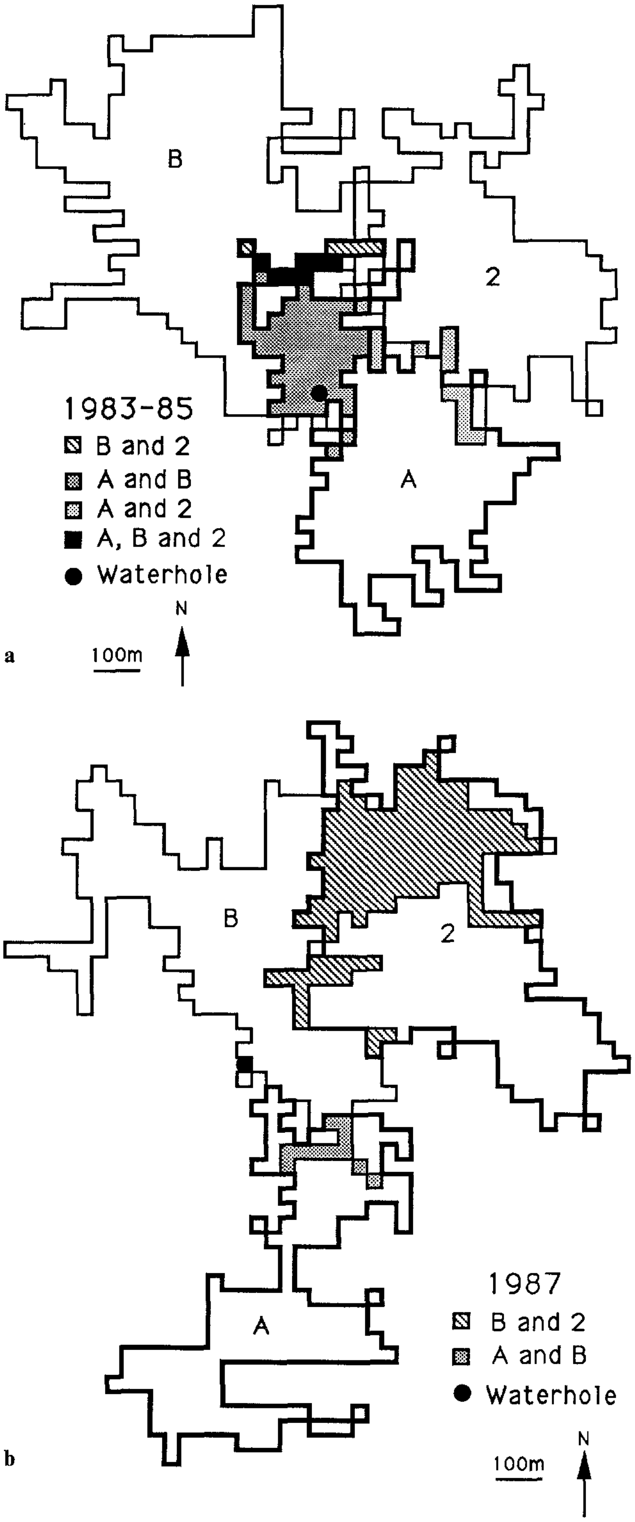

Fig. 2a, b. Comparison of the 1987 home ranges of Groups A, B, and 2 with their home ranges from 1983 through 1985. As Group B shifted its home range south and east into the home ranges of Groups A and 2, Groups A and 2 shifted away. Areas of home range overlap are labeled in the legend

B gained a total of 94 trees within that yearly home range, an increase of 236% (Table 4). In contrast, Groups 2 and A, the groups that were supplanted by Group B, did not gain in total numbers of trees by shifting their home ranges.

Table 4. Total numbers of trees within the home ranges used during 1983–1985 and 1987 for five vervet groups

Group	Numbers of trees		% Change
	1983–85	1987	
2	92	91	−1.0
A	108	93	−14.0
B	28	94	+236.0
C	6	14	+133.0
3	37	103	+179.0

Table 5. Trees acquired as a result of range shifts of vervet groups from June 1986 through January 1988

Group	Number of new quadrats	Number of trees	Density of trees
4	20	14	0.7/quadrat
2	69	45	0.6
A	46	47	1.0
B	87	78	0.9
C	164	34[a]	0.2
3	104	96	0.9

[a] This total included 11 fever trees

Table 5 shows the number and density of trees in newly acquired quadrats. By fusing with Group TW3, Group A gained 1.0 trees/quadrat. Group B gained 0.9 trees/quadrat by expanding into Group 2's home range. Group B's expansion occurred at the expense of Group 2, which added relatively fewer trees (0.6 trees/quadrat). Although Group C expanded its range the most, this group incorporated the fewest trees (0.2 trees/quadrat) because the habitat surrounding its home range included an open plain that had to be crossed to reach more trees (see also Cheney and Seyfarth 1987). Thus, the better habitats (i.e., habitats with a higher density of trees) were already being used by vervet groups, whereas the poorer habitats were unoccupied or left vacant as a result of group extinctions until smaller groups moved into them.

To summarize, when groups shifted into new areas, the largest group supplanted other groups, and the smaller groups acquired areas that were not being used by other extant groups. All groups continued to maintain exclusive access to a large proportion of their new habitats. Movement into such habitats was made easier because group extinctions resulted in more widely dispersed groups and a lower rate of intergroup encounters. While the largest group gained many more trees than it would have acquired by not shifting its home range, supplanted groups were less successful and did not gain more trees. The largest group also gained a higher density of trees in new quadrats than one of the groups it supplanted.

Costs of home range shifts

A. Mortality. Figure 3 shows the proportion of deaths, by group, that were attributed to different causes be-

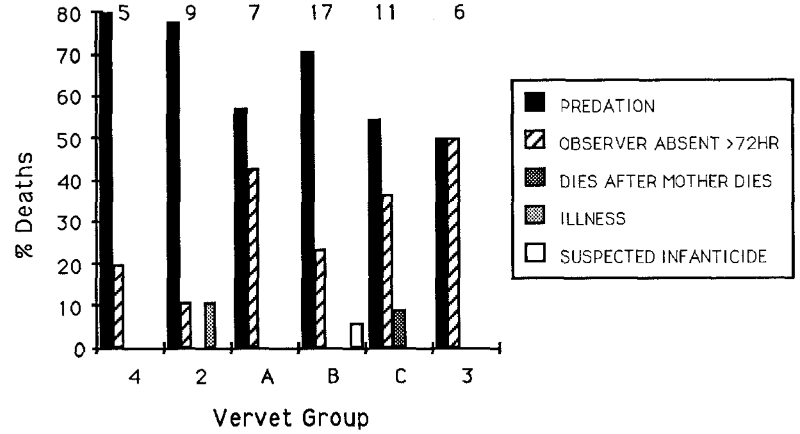

Fig. 3. The proportion of deaths in each group between October, 1985 and December, 1987 that were attributed to (1) predation (confirmed and suspected), (2) illness, (3) suspected infanticide, (4) death of infant of less than one year after its mother has died, and (5) no cause attributable because the observer was absent for more than 72 h. Numbers above bars represent numbers of individuals that disappeared in each group

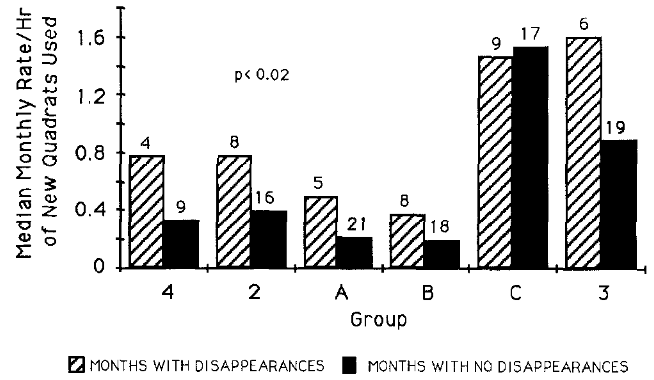

Fig. 4. Median monthly new quadrat usage rate/h, by group, for months when at least one adult female or immature vervet disappeared and for months with no disappearances. Numbers above bars represent numbers of months

tween October 1985 and December 1987. One animal (TH) died after its mother died, one (EE) died of illness, and one (LU) died of suspected infanticide. Thirty-six of 55 (65%) deaths were attributed to probable predation. No animals died after receiving wounds from conspecifics, nor did any animals die after being wounded in a fall. The cause of death for 16 (30%) animals could not be determined because the observer was absent for more than 72 h. However, since it is likely that many of the animals that died during observer absences of more than 72 h also died of predation, the estimated proportion of all deaths due to predation is, at 65%, probably an underestimate. Between October 1985 and December 1987, we sighted leopards (*Panthera pardus*) 20 times, a relatively high rate for a normally secretive and stealthy predator. In 1987, a year of particularly high mortality, disappearances were correlated with leopard alarm calls (Isbell 1990).

B. Home range use and disappearances. To determine whether disappearances were correlated with group movements into new and unfamiliar areas, we compared the median rate of new quadrat use in months when at least one adult female or immature vervet disappeared with the median value for months when none disappeared. Across groups, new quadrat usage rates were significantly higher in months when one or more vervets disappeared than in months when no animals disappeared ($n=6$, $T=1$, $P<0.02$; Fig. 4). This suggests that groups suffered a high cost by moving into unfamiliar areas.

There are several possible explanations for the increased vulnerability of vervets in new or unfamiliar areas. First, individuals may have been preoccupied with exploring their environment rather than with scanning for predators. Second, they may have been more active and thus more conspicuous to predators. This may be the case, for example, for meadow voles (*Microtis pennsylvanicus*) (Ambrose 1972). Third, they may have been less knowledgeable about refuges and escape routes. All these factors have been suggested in the case of white-footed mice (*Peromyscus leucopus*) (Metzgar 1967). Fourth, they may have been unfamiliar with the hunting and ranging behavior of individual predators.

The first possibility can be ruled out for Amboseli vervets because the monkeys did not spend less time scanning as their time increased in new areas (Group 2: $r_s=-0.189$, ns; Group A: $r_s=0.237$, ns; Group B: $r_s=0.002$, ns; Group C: $r_s=-0.138$, ns; Group 3: $r_s=-0.336$, ns). The second possibility, that vervets may have been more active in new areas and more conspicuous, is also not consistently supported. Group 2 spent more time moving as it increased its time in new quadrats ($r_s=0.531$, $P<0.025$), but the other groups did not (Group A: $r_s=-0.247$, ns; Group B: $r_s=-0.157$, ns; Group C: $r_s=-0.044$, ns; Group 3: $r_s=0.059$, ns). The third explanation, that they were less knowledgeable about refuges and escape routes, seems more likely. One of the main predators of vervets is the leopard (Struhsaker 1967; Seyfarth and Cheney 1980; Isbell 1990), which is adept at climbing trees. It is possible that vervets only learn the best escape routes or safest sleeping trees after successful or failed attacks have been made. The fourth explanation, that familiarity with the home range may include knowledge of idiosyncratic hunting patterns of individual predators, is also possible. Over time, vervets may learn where particular individuals are likely to be found. In this case, predation rates would also be expected to increase with the arrival of different individual predators, regardless of how familiar vervets are with their home ranges. Unfortunately, at present we have no way test these possibilities.

Discussion

Over the past three decades, vervets in Amboseli have been faced with a deteriorating environment. This study has shown that a decrease in the number of preferred trees was associated with movements of vervet groups out of familiar areas. However, this movement into unfamiliar areas also apparently increased the animals' risk of mortality. Vervets were more likely to disappear in months when they increased their time in new and unfamiliar areas. Since predation appears to have been involved in the majority of disappearances, a plausible explanation for this mortality pattern is increased vulnerability to predation in unfamiliar areas.

Correlation does not show causality, of course, and it is possible that predation was the cause rather than the consequence of the vervets' movement into new areas. This causal direction is unlikely, however, because predation has been documented as a major cause of mortality since the study began in 1977 (Cheney et al. 1988) and yet the vervets did not begin moving into new areas until recently.

It is possible that, when vervets moved into new areas, they moved into areas that were more dangerous. There are three levels of comparison on which this point can be addressed: (1) differences between two major habitats; (2) differences between occupied and unoccupied areas within the same habitat, and (3) differences among individuals using the same home range. First, because most of the predation in 1987 could be attributed to leopard predation (Isbell 1990), the *A. tortilis* woodlands may have provided leopards with more cover, a requirement for successful hunting (Kruuk 1986). Group C, one of the groups that experienced the fewest losses, moved into areas that included an open plain with very little cover. This was also the only group for which there was no evidence of an association between disappearances and leopard alarm calls in 1987 (Isbell 1990). However, while cover is undoubtedly important in determining suitable habitat for some predators, other characteristics of the habitat are also important. Before range shifts into *A. tortilis* woodlands began, predation was higher in groups that occupied fever tree woodlands where herbaceous cover exists *and* there are waterholes that attract both prey and predators (Cheney et al. 1988). Second, within the same *A. tortilis* woodland, Group B moved into occupied areas while smaller groups moved into unoccupied areas. Because patterns of disappearance were similar for Group B and smaller groups, however, it seems likely that occupied areas were as dangerous as unoccupied areas. Third, data from fusions show that when females and immatures abandoned their home ranges and began using the home ranges of their adopted groups, they were twice as likely to disappear within the first six months of fusion as were members of their adopted groups (Isbell et al., in prep.). Therefore, it is likely that new areas within *A. tortilis* woodlands were more dangerous than familiar areas not because of qualities that were intrinsic to them but because the vervets' lacked knowledge of those areas.

The largest vervet group expanded its range at the expense of smaller groups (see also Cheney and Seyfarth 1987) and smaller groups responded by moving into areas that were unoccupied and poorer in quality. Proximally, smaller groups did not have the option of sharing their home ranges with the intruding group because vervet groups in Amboseli are territorial. Ultimately, however, territoriality results from both the avoidance of certain areas by smaller groups as well as the ability of larger groups to displace such groups from those areas. For smaller groups there may be advantages in obtaining exclusive use of a new area despite the cost of dispersal. First, without exclusive use of their home range, aggression from the larger group might increase because opportunities for aggressive interactions would occur throughout the shared home range rather than be limited to territorial boundaries. Second, because home range size generally increases with additional individuals using resources in the home range after variation in habitat quality is taken into account (Clutton-Brock and Harvey 1977; Isbell in prep.), it is likely that smaller groups would have had to expand their home ranges in any case to accommodate the larger group. Thus, the costs of dispersing into new and unfamiliar areas may have still been incurred whether or not smaller groups shared their home ranges with larger groups.

The savannah environments in which vervets live are particularly dynamic and unstable ecosystems (Norton-Griffiths 1979; Walker and Noy-Meir 1982). Encroachment into home ranges of other groups is likely to increase under two conditions: when numbers of conspecifics increase, resulting in decreasing food resources per individual, and when the absolute amount of resources diminishes, as is currently happening in Amboseli. Under both conditions, larger groups are expected to encroach upon the home ranges of smaller groups, setting in motion a domino effect whereby other groups attempt to shift their home ranges and maintain exclusive use of them. In variable environments such as savannahs, fluctuating resource levels and population sizes are common, and shifts in home ranges are therefore likely to recur despite the higher risk of mortality associated with such movement.

A variety of factors have been hypothesized to favor female philopatry in mammals, including joint defense of resources by relatives, knowledge of food resources, and reduced risk of predation (Wrangham 1980; Waser and Jones 1983). In many species, females are philopatric whether they live solitarily or in groups (Waser and Jones 1983). Reduced risk of predation through familiarity with the habitat is a potential benefit that each female can gain regardless of her social milieu.

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