

## Sudden Short-Term Increase in Mortality of Vervet Monkeys (*Cercopithecus aethiops*) Due to Leopard Predation in Amboseli National Park, Kenya

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A substantial increase in mortality, due mainly to predation, occurred during 1987 in a population of vervet monkeys (*Cercopithecus aethiops*) studied from 1977 to 1989 in Amboseli National Park, Kenya. It has been shown that vervets moving into new and unfamiliar habitats are more at risk from predation. However, this does not entirely explain the increase in predation in 1987 because predation decreased after 1987 while movement into new areas continued. An increase in leopard alarm calls relative to previous years in four of five groups, and an association between disappearances and leopard alarm calls given by vervets in the same four groups, suggest that leopards, a main predator of vervets, accounted for the increase in mortality. The vervets' increased vulnerability to leopard predation in 1987 did not appear to be related either directly or indirectly to continued habitat deterioration because 1) mortality rates after 1987 decreased to pre-1987 levels and 2) the vervets' behavior did not appear to change to make them more vulnerable than in previous years. The increased vulnerability appeared to be due in part to an increase in the presence of leopards. However, it is unclear why predator presence temporarily increased.

**Key words:** African green monkey, predation risk, population decline

### INTRODUCTION

Investigations of predation on primates have typically been limited to responses of individuals to the threat of predation, i.e., detection distances [van Schaik et al., 1983], alarm calls [Cheney & Seyfarth, 1981], group cohesion [Altmann & Altmann, 1970], and group size [van Schaik & van Hooft, 1983; Terborgh, 1983; Terborgh & Janson, 1986]. However, accurate measurements of predation risk also depend on some ability to monitor the behavior of predators; measuring only the responses of prey to the threat of predation is unlikely to provide the kind of information needed to resolve questions concerning the influence of predation on primate behavior. Below, I illustrate the difficulty of estimating predation rates and risk based only on observations of prey by describing a sudden increase in the

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rate of mortality in a population of vervet monkeys (*Cercopithecus aethiops*) living in Amboseli National Park, Kenya. Although this increase in mortality was apparently the result of an increase in predation rate, the monkeys' increased vulnerability did not appear to be due primarily to changes in their *own* behavior. Instead, the increase in predation rate appears to have been due at least in part to a change in the behavior of their *predators*.

The three main predators of vervets in Amboseli are pythons (*Python sebae*), martial eagles (*Polemaetus bellicosus*), and leopards (*Panthera pardus*) [Seyfarth & Cheney, 1980]. Each has a different hunting style and each elicits a different response from vervets. Pythons are constrictors and hunt by remaining hidden and motionless in bushes until the victim approaches sufficiently close that the python can strike and suffocate its prey. When vervets detect pythons, they usually approach, watch it, and give low amplitude alarm calls [Seyfarth et al., 1980].

Martial eagles are diurnal hunters, adept at striking quickly from the air. They have slender legs and feet, and generally kill animals that weigh no more than they weigh [Brown, 1977]. Because they have long wings and relatively short tails, martial eagles have poor maneuverability in thick vegetation [Brown, 1977]. Young vervets are thus more vulnerable to martial eagles than adult vervets, and all are more vulnerable when they are in open areas with few trees or bushes into which they can escape [Cheney & Seyfarth, 1981].

Leopards typically hunt between dusk and dawn and readily climb trees, as well as hide in bushes, to catch their prey [Turnbull-Kemp, 1967; Eisenberg and Lockhart, 1972; Busse, 1980]. When vervets detect leopards, they run high into trees and orient toward the leopard while giving loud alarm calls [Seyfarth & Cheney, 1980; Cheney & Seyfarth, 1981]. Leopards are very secretive and tend to avoid human contact [Turnbull-Kemp, 1967; Schaller, 1972].

During 1987, a number of vervet groups in Amboseli experienced a marked increase in mortality. While vervet mortality since at least 1985 appears to have been related at least partially to the movement of some groups into new and unfamiliar areas [Isbell et al., in press], movement into new areas cannot account for the relatively sudden increase in predation in 1987 because predation decreased in subsequent years while movement into new areas continued. It is not my intent here to clarify the role of predation on primate social behavior and social organization, but merely to document this short-term increase in mortality associated with predation and examine potential causes of the increased predation. The results suggest that the increase in predation may have been due an increase in predator presence, but it is not clear why predator presence increased in 1987.

## METHODS

### Study Site and Subjects

Amboseli National Park is part of a semi-arid savannah located in southern Kenya (2° 41'S, 37° 10' E). Since the mid-1950s the swamps in Amboseli have spread, and large stands of fever trees (*Acacia xanthophloea*) have died [Western, 1983]. This die-off has been attributed to a combination of stand senescence, short-term climatic change, and elephant browsing, which may interact in complex ways [Western & van Praet, 1973; Young & Lindsay, 1988; Lindsay, in preparation].

Fever trees are important as food and refuge sites for vervet monkeys. In the mid-1960s when fever trees were still found in dense groves, vervets slept and fed in fever trees year-round [Struhsaker, 1967]. Currently, however, there are very few fever trees left in the main study area, and vervets now rely heavily on *A. tortilis* for food and refuge, although they feed in *A. tortilis* less often than they fed in fever trees and take fewer plant parts from them [Wrangham & Waterman,

1981; Cheney & Seyfarth, 1987; Cheney et al., 1988]. The vervet population has declined along with the fever tree population [Struhsaker, 1973, 1976; Cheney et al., 1988], suggesting that its decline is a result of reduced food resources. This on-going population decline has been gradual in comparison with the sudden increase in mortality during 1987.

Vervets live in small, multi-male, multi-female groups that occupy home ranges that are defended by both sexes against incursions from neighboring groups [Cheney, 1981; Cheney & Seyfarth, 1987]. Females form the stable core of vervet groups and remain in their natal groups for life, while males emigrate to neighboring groups around sexual maturity and may transfer between groups repeatedly throughout their lives [Cheney & Seyfarth, 1983].

### Data Collection

The long-term study began in 1977 with intensive monitoring of three groups and semi-annual censuses of up to eight neighboring groups. In 1983, three more groups were added to the intensive monitoring effort. Demographic data were collected regularly from each of the main study groups from 1977 to 1988 by D. Cheney and R. Seyfarth and their colleagues [Lee, 1981; Andelman, 1985; Hauser, 1987; Cheney et al., 1988; Isbell, 1990]. All monkeys were individually identified and monitored for injuries, illnesses, births, deaths, disappearances, immigrations, and emigrations. Following disappearances by adult and subadult males, all groups surrounding the main study groups were checked for possible transfers.

Causes of vervet mortality were analyzed previously by Cheney et al. [1988] using the following categories: when an animal was observed to be listless, weak, or diseased within 24 hours of its disappearance, death from *illness* was said to occur. In such cases, the apparent illness was usually noticeable 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 males. *Predation* consisted of confirmed and suspected predation. Confirmed predation involved observed kills or sightings of predators with monkeys. Suspected predation included the disappearance of an animal within 24 hours of having been observed in healthy condition and not found to have transferred to another group.

The present analysis includes additional data from the years 1984 to 1988, and the criteria for determining illness and predation have been changed because signs of illness were typically apparent for longer than 24 hours (median: 6 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 hours of its disappearance. Suspected predation is redefined as the disappearance of an apparently healthy individual within 72 hours of final sighting. One exception occurred when Group B, which was normally easy to find, could not be located for 5 days despite intensive searches. When the group was found again with one adult female and five immatures missing, these deaths were scored as suspected predation.

Several animals disappeared while the observer was absent for more than 72 hours. In such cases, the category was called *observer absent > 72 hr* because the causes of the disappearances could not be determined. For this paper I also included these deaths, as well as deaths following mother's death and predation, under the category of *disappearances*. This category therefore includes all categories of mortality except illness and suspected infanticide. Infants who died before the age of 2 months were considered neonatal deaths and were not included in the

analysis. Adult males were also excluded, because males who disappeared and were not found may have simply transferred to a distant group. The estimates of predation and disappearances are therefore probably underestimates, because males are also vulnerable to predation. Females were assumed not to transfer when they disappeared because females rarely transfer. Only 11 cases of female transfer have been recorded during 11 years of study and at least 7 of these clearly involved group fusions in which an entire group joined another group [Hauser et al., 1986; Isbell et al., in preparation).

During 1986–1988, I recorded all alarm calls given by vervet monkeys during periods of observation. When an alarm was given, I noted the type of alarm call [following Seyfarth et al., 1980], as well as the date, time, individual(s) giving the call, their locations, and, when possible, the species of animal that elicited the alarm. Alarm call bouts were defined as calls given with a discrete beginning and end, separated by other alarm bouts from the same group by at least 60 minutes. The date, time, and location of predator sightings in the absence of alarm calls were also noted. Alarm calls given in 1987 are here compared with those given by the same groups in 1982 [S.J. Andelman, unpublished data], January through July 1983 [D.L. Cheney and R.M. Seyfarth, unpublished data], January through June, 1985 [Cheney and Seyfarth, unpublished data], July through December 1986 [L. A. Isbell, unpublished data], and January, May, and June, 1988 [Isbell, unpublished data].

Locations of individuals (on the ground, in bushes, or in trees) and their activities (feeding, resting, moving, grooming) were scored in scan samples [after Altmann, 1974] taken every 10 minutes during 474 hours of systematic sampling of focal groups in 1987. All individuals within groups were scored from left to right to avoid a possible bias toward obvious or easily observed behaviors, and all scans were terminated at the end of one minute regardless of the number of individuals located. Percentages of time spent on the ground represent the proportion of total monthly scores in which members of each group were observed on the ground.

Maps of the study site, divided into  $33 \times 33$  m quadrats and showing the locations of all trees, were drawn originally by R. Wrangham in 1978 and updated regularly by subsequent observers as trees died and groups expanded their ranges. During 1987, the quadrat location of each individual in a particular group was recorded directly onto the map every 30 minutes. To measure female group spreads, I calculated the distance between the centers of the two most separated quadrats occupied by females at each point sample, and then obtained an average female group spread for each month. Only the samples in which all adult females were located were used in these calculations.

### Statistical Analyses

For a comparison of mortality and predation rates per 100 individuals per year, the mortality data from all groups were pooled and normalized with square root transformations, and values for 1987 were compared with means from the previous 10 years using an outlier test [Sokal and Rohlf, 1981]. Otherwise, the data from different groups were separated to control for possible differences in habitat quality. This was important because in the past, differences in habitats were associated with differences in predation rates [Cheney et al., 1988]. Tests were also conducted among groups to detect trends. I have given probability values in all tests whether or not  $P < 0.05$  to provide the reader with more information with which to interpret the results. The probabilities were obtained from Conover [1980] and Siegel [1956]. Potential seasonal variation was controlled by restricting comparisons to similar months across years within each group. All nonparametric

tests were one-tailed because directions were predicted for alternative hypotheses [Siegel, 1956].

## RESULTS

### Mortality Rates, 1977–1987

In 1987, the percentage of females and immatures that died ranged from 23% in Group 3 to 89% in Group 2 (Table I). The mortality rate in 1987 was 65% ( $n = 34$  deaths), while the estimated predation rate for that year was at least 45% ( $n = 23$  deaths; Fig. 1). Suspected predation accounted for the majority of deaths (70%) in 1987. This frequency represents a conservative estimate, since it is likely that a significant proportion of the deaths that occurred during the observer's absence from the group was also due to predation. Despite this apparently high predation rate, no actual predation events were observed and the parts of only one body were ever retrieved—the jaws and fur of adult female TY (Group B), who had been seen alive the day before, were found under a bush below the tree in which her group had slept the night before. Leopard tracks and scats were found near the remains. The failure to discover any remains following a predation event is not surprising, given the small size of vervets (adult females weigh between 3 and 4 kg) and the prevalence of predators and scavengers in Amboseli. Between 1977 and 1986, vervet remains were recovered only twice following predation by leopards, even in those cases when the location and time of the capture were known [Cheney & Seyfarth, unpublished data].

Both overall mortality and suspected predation rates were significantly higher in 1987 than the mean for the previous 10 years (overall mortality, 1977–1986: 22% per yr; 1987: 65%,  $P < 0.05$ ; predation, 1977–1986: at least 11% per yr; 1987: at least 45%,  $P < 0.05$ ). This increase in mortality affected both group size and the overall number of groups. In January, 1987, the numbers of females and immatures per group ranged from 6 to 17. By December, the largest group had decreased to nine. In that time, two main study groups (Groups 2 and A) also became extinct after their remaining members joined other neighboring groups following the reduction of their groups to single adults and accompanying juveniles [Isbell et al., in preparation]. The decline in vervet numbers was not limited to the main study groups. With 14 females and immatures in January, 1987, census group KH4 was one of the larger groups in the study population. Within 10 months, however, it had been reduced to one adult male, one adult female, and four immatures. By May, 1988, this group, reduced further to one female and four immatures, fused with one of the main study groups (Group C). Although the exact cause of these losses can never be precisely known, the dramatic increase in disappearances for this group during the same year indicates that high mortality extended beyond the main study groups.

### Causes of Predation

**Predator presence.** I saw one python and heard three alarm calls given to snakes in 1987. Martial eagles were seen on seven occasions and alarm calls to avian predators were heard 12 times. Although leopards are generally secretive and rarely observed, 19 sightings were made of a minimum of four leopards in the study area (one adult male, one adult female, and two presumed offspring). Alarm calls to terrestrial carnivores were heard on 32 occasions during 1987.

Because leopards were sighted more than twice as frequently as other predators despite their stealthy behavior, it was my impression that the increase in predation may have been due in part to leopard predation. To test whether leopard presence might have been associated with disappearances, I compared median

**TABLE I. Adult Female and Immature Vervets Who Disappeared From the Study Population in Amboseli National Park, Kenya, and Were Presumed Dead During 1987**

Group	Total in group	Adult females	Immatures
2	9	JR	NS
		LI	EC
		BE	BB
		BT	PR
A	10	ES	ST
		BA	PG
		SV	
B	20	NT	TU
		TY	SS
		WM	UN
		AM	TC
			BM
C	13	AC	NO
		LO	BK
			CO
			AO
			CZ
3	13		MI
			PF
			OZ
			DA
			RK
Totals		13	21

leopard alarm call bout rates in months in which at least one female or immature vervet disappeared with months in which none disappeared. Although cheetahs (*Acinonyx jubatus*) and servals (*Leptailurus serval*), which resemble leopards, also elicit leopard calls from vervets, they were seen so rarely (cheetahs:  $n = 2$ ; servals:  $n = 0$ ) that most alarm calls were presumed to have been directed at leopards. Alarm call rates were found to be higher in months when vervets disappeared among four of the five groups (Table II). Group C, the only group for which the rates were not different, had recently moved into a relatively open area [Cheney & Seyfarth, 1987; Isbell et al., in press] with fewer of the shrubs that provide leopards with cover for successful hunting [Kruuk, 1986].

The association between leopard alarm calls and disappearances among four of the five groups suggests that leopards may have been responsible for a majority of the disappearances in 1987, but it does not explain why leopards killed vervets substantially more often than in previous years. The greater frequency of sightings in 1987 (1.6 sightings/month) relative to previous years (e.g., January–July, 1983: 0.2/month; 1986: 0.08/month) suggested that leopard presence in the study area increased in that year. I examined this further by comparing the number of months in which leopard alarm call rates were higher or lower in 1987 with similar months in 1982, 1983, 1986, and 1988. Since all of the yearly comparisons were consistent within groups, the data were pooled within groups to increase the sample size. The results suggest that vervets in four of five groups gave more alarm calls and detected leopards more often in 1987 than in other years (Table III). This presum-

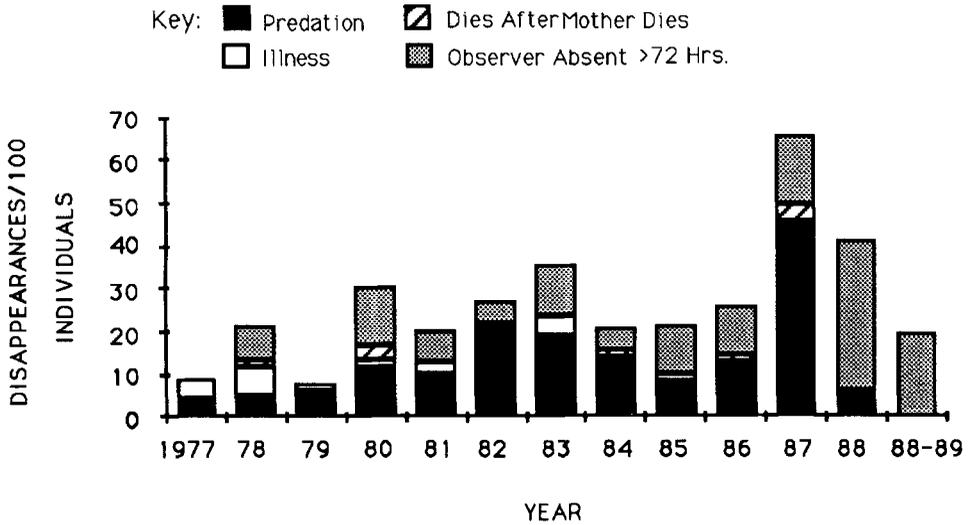


Fig. 1. Mortality rates of adult female and immature vervets from 1977 to 1989. Rates of mortality and predation in 1987 are significantly higher than the average for all previous years ( $P < 0.05$ ). Mean annual mortality was estimated from January through July, 1988 for bar labeled 1988, and from August, 1988 through June, 1989 for bar labeled 1988–1989. See text for definitions of categories.

**TABLE II. Median Monthly Alarm Call Rates/100 hr for Months When at Least One Adult Female or Immature Vervet Disappeared and for Months With no Disappearances in 1987\***

Group	In months with at least one disappearance (no. of months)	In months with no disappearances (no. of months)
2	3.79 (6)	0 (3)
A	15.38 (3)	0 (8)
B	8.53 (4)	7.14 (7)
C	0 (4)	0 (7)
3	8.77 (3)	0 (8)

\*Within groups, Mann-Whitney U tests: Group 2:  $U = 8, P = 0.39$ ; Group A:  $U = 9.5, P = 0.29$ ; Group B:  $U = 12.5, P = 0.39$ ; Group C:  $U = 12, P = 0.22$ ; Group 3:  $U = 9, P = 0.24$ . Trend among groups, sign test:  $x = 0, P = 0.06$

ably reflects a real increase in leopard presence rather than an improvement in the ability of vervets to detect leopards. An increase in my own sightings of leopards, independent of alarm calls (e.g., 1986:  $n = 0$ ; 1987:  $n = 9$ ), supports this explanation. In Group C, leopard alarm call rates in 1987 were not different from other years (Table III). Group C was also the only group for which monthly leopard alarm call rates and disappearances were not associated.

Taken together, the relationship between leopard alarm calls and disappearances, the increase in leopard sightings and alarm calls in 1987, and the consistent pattern of these associations among the study groups, provide strong indirect evidence that more vervets were preyed upon in 1987 because leopards were present more often in that year than in other years.

**TABLE III. Sign Test Comparisons of Leopard Alarm Call Rates in 1987 With 1982, 1983, 1986, and 1988 (Between Similar Months Across Years To Control for Possible Seasonal Differences in Predator Activity).**

Group	Number of times that months with higher call rates occurred in 1987	Number of times that months with lower call rates occurred in 1987	<i>P</i> value
2	6	1	0.06
A	16	6	0.03
B	19	4	0.001
C	3	7	0.17
3	7	1	0.04

**Habitat deterioration.** Because of the loss of trees as refuges, it might be expected that continued deterioration of the habitat contributed to the vervets' vulnerability to leopard predation. Fewer trees once grew in groves within the area encompassed by the home ranges of the main study groups, but only 12 scattered fever trees were surviving as of July, 1988 [see Isbell et al., in press]. If vervet mortality and vulnerability to predation had somehow been linked to habitat deterioration, the mortality rate might be expected to have remained high in 1988. However, in the first 7 months of 1988, mortality decreased to 41%. Although the population was no longer observed regularly after July 1988, a census was taken in June, 1989. The mean annual mortality rate from August, 1988 to June, 1989 was 20% (Fig. 1). These estimates are comparable to levels before 1987 and suggest that the vervets' vulnerability did not increase as an obvious consequence of their changing environment.

It is also possible that habitat deterioration might have been indirectly responsible for the increase in predation by effecting a change in the behavior of the vervets. For example, with fewer trees in their habitat, vervets may have increased their vulnerability to leopards by spending more time on the ground [Stanford, 1989]. Time spent on the ground was not related to increased predation, however (Group 2:  $U = 7$ ,  $P = 0.36$ ; Group A:  $U = 7.5$ ,  $P = 0.18$ ; Group B:  $U = 7$ ,  $P = 0.12$ ; Group C:  $U = 7$ ,  $P = 0.32$ ; Group 3:  $U = 4$ ,  $P = 0.07$ ; trends among groups: sign test,  $x = 2$ ,  $P = 0.50$ ). Instead, it was more closely related to the wet seasons when vervets fed on grasses that were only available with the onset of the rains (Group 2:  $U = 1$ ,  $P = 0.02$ ; Group A:  $U = 8$ ,  $P = 0.12$ ; Group B:  $U = 6$ ,  $P = 0.06$ ; Group C:  $U = 12$ ,  $P = 0.33$ ; Group 3:  $U = 6$ ,  $P = 0.06$ ; trends among groups: sign test,  $x = 0$ ,  $P = 0.03$ ). In contrast, predation occurred mainly during the dry seasons during 1987 (17 of 23 individuals).

Alternatively, the reduction in trees may have caused group members to become more separated from other members of their groups when they fed in different trees. This may have increased their vulnerability to predation because there were fewer others nearby either to help detect predators [e.g., Hoogland, 1979; Robinson, 1981; van Schaik & van Noordwijk, 1986] or to be preyed upon when an attack was made [Hamilton, 1971; van Schaik, 1983]. Although group spreads during predation events are unknown, female group spreads in months with and without disappearances were not different (Group 2:  $U = 5.5$ ,  $P = 0.18$ ; Group A:  $U = 7$ ,  $P = 0.26$ ; Group B:  $U = 4$ ,  $P = 0.04$ ; Group C:  $U = 12$ ,  $P = 0.40$ ; Group 3:  $U = 4$ ,  $P = 0.43$ ; trends among groups: sign test,  $x = 2$ ,  $P = 0.50$ ).

Finally, with the deterioration of the vervets' habitat, group size decreased an

average of 50% from 1977 to 1986 [Cheney & Seyfarth, 1987]. It has been suggested that larger groups are more likely than smaller groups to detect predators or to detect them earlier [van Schaik, 1983; van Schaik et al., 1983]. It is possible that during 1987 vervet groups became so small that they were ineffective in detecting predators. Monthly alarm call rates were not significantly correlated with monthly group sizes in any of the five groups during 1987, however (Group 2:  $r_s = 0.435$ ,  $P > 0.10$ ; Group A:  $r_s = -0.174$ ,  $P > 0.10$ ; Group B:  $r_s = -0.120$ ,  $P > 0.10$ ; Group C:  $r_s = 0.272$ ,  $P > 0.10$ ; Group 3:  $r_s = 0.055$ ,  $P > 0.10$ ; all tests:  $n = 11$  except Group 2:  $n = 9$ ). Moreover, alarm call rates in 1987 were higher than in 1988 despite the continued decrease in group sizes. Group size appears to have had no influence on the vervets' ability to detect predators.

## DISCUSSION

As a result of a long-term study on the vervet population in Amboseli, it was possible to document an unusually high, short-term increase in predation and to suggest that at least part of the cause of the vervets' increased vulnerability to predation was due to increased leopard presence. On the other hand, because the vervets' predators were not also studied and no predation events witnessed in 1987, it is not clear whether the increased presence of leopards was due to a change in the predators' behavior alone or to a change in the way that vervets and leopards interacted during predation events.

Several possible explanations might account for the increase in leopard predation during 1987:

1. Leopard presence might have increased simply as a consequence of greater leopard density.
2. The same number of leopards may have increased their time in the study area independent of the behavior of the vervets.
3. The same number of leopards may have spent more time in the area because the vervets presented consistently easy targets since fewer trees were no longer available for nighttime refuge. This seems an unlikely explanation, however, because mortality decreased in 1988 and 1989 while nighttime use of *A. tortilis* trees did not.
4. Individual leopards may have idiosyncratic patterns of hunting that must be learned by vervets over time, and if a leopard immigrated into the study area in 1987, greater vulnerability might be expected until its habits could be learned.
5. Individual leopards may have a preference for hunting vervets. Felids, especially leopards, are reported to have individual preferences for particular prey species [Kruuk, 1986], perhaps as a result of early experience with that prey [Caro, 1980]. Related to this is the possible reduction of predation to normal levels after 1987 as a result of a reduction in hunting pressure when vervet densities decreased.
6. One of the leopards may have become habituated to people and was thus less frequently frightened away by workers. My increasingly longer opportunities to observe the adult male leopard supports this possibility.
7. The behavior of vervets under attack may be different from their behavior at other times and it may have changed for some reason in 1987. For example, the success of an attack may depend on how widely group members are spread at the moment of attack, which may or may not be measured by average monthly group spreads. Similarly, while alarm calls may indicate the presence of a predator, they may not be given when an attack actually occurs. When vervets detect leopards, alarm calls are typically given once the alarmist has climbed into a tree (personal observation) and is presumably out of danger. It is not known whether vervets give

alarm calls to leopards at the time of attack as well. Discrimination among these non-mutually exclusive possibilities requires knowledge of the behavior of predators or interactions between predator and prey at the time of attack, neither of which is available.

This study highlights two problems for research on predation of primates. One is that when the predator is a nocturnal, secretive felid that consumes most, or all, of its primate prey, direct observation of predation is virtually unobtainable *even when predation rates are high*. Second, predation risk cannot be accurately assessed without a better understanding of the interactions between primates and their particular predators. Estimates of vulnerability based only on numbers of predator species [e.g., van Schaik, 1983; Terborgh & Janson, 1986; Robinson, 1988] or the responses of primates to our perceptions of the threat of predation, such as detection distances [e.g., van Schaik et al., 1983], are clearly inferior to direct estimates of predation risk. This study shows that predation risk is complicated by the behavior of predators and will therefore be difficult to measure. Joint studies of the behavior of predators and primates are necessary to evaluate predation risk accurately particularly as it relates to primate social behavior, even though the relative rarity of predation events may offer small sample sizes for the effort expended.

## CONCLUSIONS

1. Mortality in a population of vervet monkeys during 1987 was estimated at 65%, a substantial increase from the previous 10 years. Suspected predation accounted for 70% of the deaths in 1987.
2. The vervets' increased vulnerability to predation did not appear to be due to changes in their behavior alone. Instead, the increase in predation rate appears to have been due in part to an increase in the presence of leopards.
3. Since leopards were not studied, it is unclear why leopard presence increased in 1987.
4. This study demonstrates the difficulty of obtaining accurate estimates of predation risk when only the prey are studied, and questions the value of such estimates in investigations of the influence of predation on behavior.

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