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SHORT COMMUNICATIONS

Human presence reduces predation in a free-ranging vervet monkey population in Kenya

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Predation has been suggested as a major selective force in the evolution of individual and social behavioural patterns, including alarm-calling, polyspecific associations, positioning of group members within groups, group size, and group-living (Hamilton 1971; Sherman 1977; Gautier-Hion et al. 1983; reviewed in Terborgh & Janson 1986). However, predation has been difficult to study in primates (and many other species) because predation and attempts at predation are rarely observed. This is probably due partly to low rates of predation in most primate populations (Cheney & Wrangham 1987). However, predation may not be observed even when it is common. Most primates are diurnal, but some predators, such as leopards, *Panthera pardus*, hunt nocturnally when researchers tend not to be present. For example, although indirect evidence suggests that leopards accounted for at least 50% of all 34 deaths in a population of vervets, *Cercopithecus aethiops*, in just one year, no predation events were ever witnessed (Isbell 1990). In addition, predators are often wary of humans and apparently avoid contact with them (Hamilton 1986a, b). Thus, it is possible that researcher presence may inhibit predators from attacking when prey but not predators are habituated to humans (D. Cheney & R. Seyfarth, personal communication; C. van Schaik, personal communication), and it has even been suggested that differences in predation rates among populations may be caused by differences in researcher presence and behaviour (Wittenberger 1981; Boesch 1991). In support of this, we present evidence here that spatial and temporal variation in human presence was correlated with variation in presumed predation events in a natural vervet monkey population.

This study is based on data collected from June 1986 to November 1987 on six groups of habituated and individually recognized vervets (six to 20 individuals per group) in Amboseli National Park, Kenya. The study area included two habitat types: one dominated by *Acacia xanthophloea*, and the other, *A. tortilis*. The home ranges of two groups included a shared waterhole, while the home ranges of the other four groups had no permanent water (for more complete descriptions of Amboseli and the study area see Cheney & Seyfarth 1990). In addition, a permanent ranger station was located in the corner of the study area at the edge of one group's home range. For determination of home ranges, locations of waterholes and densities of trees see Isbell et al. (1990). Distances from the centre of the home ranges to the ranger station and to the main waterhole were measured from map locations.

The vervet population had a history of high predation (Cheney et al. 1988). None the less, few predation events were ever witnessed, even during a 1-year period of unusually high predation. Indirect evidence suggested that most of the disappearances of females and immatures during this particular year were caused by leopard predation (Isbell 1990; Isbell et al. 1990). Possible explanations for the increase in leopard predation are discussed by Isbell (1990).

All disappearances during 1987, except those suspected to have been caused by illness or infanticide (see also Isbell et al. 1990), were examined in relation to the presence of observers to determine whether leopards might have been inhibited from attacking during periods when researchers were in the field. After returning to the study site after any absence of more than 1 day, a complete census was

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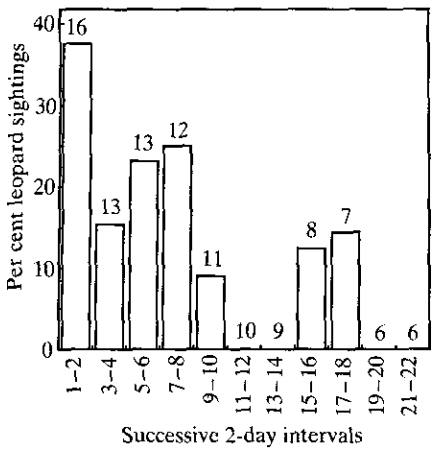

Figure 1. Rate of leopard sightings for successive 2-day periods following the researcher's return for 16 intervals in the field, which varied in length from 2 to 22 days. Sample size above each bar refers to the number of field intervals.

carried out. Animals missing at this time and not later found were assigned as disappearances during the researcher's 'absence'. Animals that disappeared during an active field period were assigned as disappearances during the researcher's 'presence'.

During a 526-day period from June 1986 to November 1987, 25 intervals of researcher presence, varying in length from 1 to 31 days (median: 16 days), alternated with 24 intervals of researcher absence, varying in length from 2 to 37 days (all but one less than 16 days; median: 7 days). This time was divisible into three distinct periods relative to predation. For the first 220 days, the rate of vervet disappearances was relatively constant, averaging one animal every 15 days. Then in January–February 1987, the disappearance rate increased sharply. During this 30-day period, 14 vervets disappeared. Afterwards, the rate of disappearances decreased and remained relatively constant for the last 275 days, averaging one animal every 17 days.

A leopard was seen only once in the period before the peak in rate of disappearances (out of 140 observation days). Thereafter, sightings became relatively common (averaging once every 11 observation days, $N=18$). Beginning with the peak of disappearances, we compared the relative rate of leopard sightings in the first 2 days after returning to the field to the rate of leopard sightings thereafter for each of 16 intervals of researcher presence. Leopards were significantly more likely to be seen in the first 2 days after returning to the field than in the days that followed (19% versus 6%; $\chi^2=4{\cdot}50$, $df=1$, $P<0{\cdot}05$, two-tailed; Fig. 1). This was part of a larger trend towards fewer sightings later in each field session ($r_S=-0{\cdot}80$, $P<0{\cdot}01$; Fig. 1). This is not likely to be an artefact of sampling methodology. No more time was spent and no more area was covered in the field in the first 2 days than in subsequent days. It is more likely that leopards reacted to researcher presence either by leaving the area temporarily or remaining but becoming more secretive.

Because the disappearances were not constant over time, we compared the rates of vervet disappearances in intervals of researcher presence and absence in the periods before, during, and after the burst of disappearances. Before the burst of disappearances, vervets were 3·6 times as likely to disappear during intervals of observer absence as during observer presence (0·036 versus 0·130 per day, $\chi^2=4{\cdot}35$, $P<0{\cdot}05$, two-tailed). Both during and after this burst, however, disappearance rates were not significantly different during intervals of researcher presence and absence. Again, these results are unlikely to be artefacts of methodology because censuses were conducted regularly on the first day after an absence from the field. It suggests instead that leopards initially preyed upon vervets more often during observer absences but that they became habituated to researcher presence over time.

If human presence does inhibit leopard hunting activity, we might expect groups located further from the permanent ranger station to suffer greater losses than groups living closer. We therefore compared rates of disappearances among vervet groups to proximity to the ranger station. However, because such factors as group size, proximity to waterholes, and density of trees might also influence the vulnerability of vervets to predation (Isbell 1990), we also compared rates of disappearances among vervet groups with group size, the density of trees in the home range, habitat type, and distance from the centre of the home range to the main waterhole. Distance from the ranger station was strongly positively correlated with disappearance rate ($r=+0{\cdot}95$, $P<0{\cdot}02$, $N=5$). None of the other characteristics was strongly related to disappearance rate (Table I).

The historic distributions of Old World primates and leopards overlap extensively (Ewer 1973; Wolfheim 1983), and it is likely that leopards have been a major predator of many primate species (Brain 1981; Boesch 1991). These results suggest

Table I. Disappearances per monkey per year from January through to November 1987 for five vervet monkey groups in Amboseli National Park, Kenya, with respect to various environmental factors

Group	Disappearance rate	Distance from		Density of trees	Habitat type
		Ranger station	Waterhole		
3	0·23 (3/13)	0·4 km	1·4 km	8·1/ha	*A. tortilis*
A	0·50 (5/10)	1·3 km	1·2 km	9·0/ha	*A. tortilis*
C	0·54 (7/13)	1·4 km	0·8 km	1·8/ha	*A. tortilis/ A. xanthophloea*
B	0·55 (11/20)	1·6 km	0·4 km	8·1/ha	*A. tortilis/ A. xanthophloea*
2	0·89 (8/9)	2·0 km	0·9 km	5·4/ha	*A. tortilis*
	$r=-0·30$*	$r=+0·95$	$r=-0·48$	$r=-0·35$	
	$r^2=0·09$	$r^2=0·90$	$r^2=0·23$	$r^2=0·12$	
	$P>0·60$	$P<0·02$	$P>0·50$	$P>0·50$	

*Correlation coefficients all have disappearance rate as the dependent variable. The first correlation has group size as the independent variable.

that unless leopards are habituated to human presence, as are most primates prior to study, it will be difficult to study directly the effects of predation on primate behaviour and ecology.

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