Behav Ecol Sociobiol (1990) 26:297–300

Behavioral Ecology and Sociobiology

Vigilance and mixed-species association of some East African forest monkeys

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Received May 22, 1989 / Accepted October 11, 1989

Summary. The frequency of looking up was scored as a measure of vigilance behavior in two species of African forest monkeys (genus *Cercopithecus*) that often associate in mixed-species groups. The fact that looking up decreased with increasing foliage density around focal individuals was taken as evidence that looking up is an expression of vigilance for predators. The rate of looking up was higher in single-species groups than in mixed species groups for both species. Association had a more marked effect on the rate of looking up when monkeys fed on plant material as opposed to insects. The adjustment of the rate of looking up with respect to association status does not reflect the presence or absence of other monkeys in the same feeding tree. Although a reduction in vigilance levels probably leads to increased feeding efficiency, it is not a sufficient explanation of mixed-species association in the species under study.

Introduction

Vigilance for predators benefits animals because it reduces the chance of being preyed upon, but it is costly in that it makes time away from or interrupts other important but incompatible activities like feeding. One of the main functional explanations of sociality in animals is that members of groups can decrease the risks of being preyed upon without increasing the cost of being vigilant. Several mechanisms have been proposed, including earlier detection of the predator, interference with its attack through confusion or active defense, hiding behind other victims, and dilution of its effect (reviews in Bertram 1978; Pulliam and Caraco 1984).

Attention has also focussed on how sociality (or increasing group size) can decrease the costs of vigilance without exposing animals to higher predation risks. By sharing the job of being watchful, individuals can devote less time to vigilance or interrupt their other activities less often without sacrificing safety (Pulliam 1973; Parker and Hammerstein 1985). This extra or uninterrupted time then becomes available for other activities, such as feeding. While most studies demonstrating that an increase in group size reduces an individual's vigilance time have been made on single-species groups (e.g., Berger 1978; Lazarus 1978; Abramson 1979; Caraco 1979; Hoogland 1979; Lazarus 1979; Barnard 1980; Bertram 1980; Siegfried 1980; Elgar and Catterall 1981; Lipetz and Bekoff 1982; de Ruiter 1986), the idea has also been applied to mixed-species flocks of birds whose members share common predators and respond to one another's alarm signals (Powell 1974; Barnard and Stephens 1983; Metcalfe 1984; Sullivan 1985).

In mixed-species groups of primates, predation pressure has been singled out as an important, if not the most important, selective force for interspecific sociality (Struhsaker 1981; Gautier-Hion et al. 1983; Cords 1987). Most evidence is circumstantial, however, and consists of plausibility arguments, since predation is very rarely observed. A partial exception to the lack of data are demonstrations that some species increase their use of more open, exposed habitat types when in mixed-species groups (Gautier-Hion et al. 1983; Cords 1987); that they do so because of increased protection against predators remains an untested assumption, though it is known that members of mixed groups share predators and respond to one another's alarm calls (e.g., Gautier-Hion and Tutin 1988). Most discussions of anti-predator benefits in primate mixed-species groups concern reducing the risk of being preyed upon; few have addressed the ways in which association with other species may reduce the costs of vigilance without sacrificing protection, and no relevant data have been published.

The aim of the present study was to examine individual vigilance levels as a function of association with other species in two species of African forest monkeys. Most African forests contain two or more species in the genus *Cercopithecus*. Many sympatric *Cercopithecus* monkeys are known to form mixed-species associations that often are very durable (Gautier-Hion 1988). In East

African rain forests, blue (*Cercopithecus mitis*) and redtail (*D. ascanius*) monkeys are regularly found together in mixed-species groups (Struhsaker 1981; Cords 1987). Association between these two species is sufficiently variable; therefore, it is possible to compare the behavior of the same monkeys when associated with another species and when on their own.

Methods

Observations were made in May and June 1987 and February and March 1989 in the Kakamega Forest, western Kenya (see Cords 1987 for a description of the site). The subjects were members of two habituated groups of blue monkeys (about 20 and 36 members, respectively) and one habituated group of redtails (about 24 members). These same groups had been the focus of an earlier study of mixed-species association between the two species, in which it was found that redtails spend about 75% of daylight hours with blue monkeys while blues spend about 50% of daylight hours with redtails (Cords 1987). (The difference reflects the fact that there is a higher density of blue monkey groups.) Data from the two blue monkey groups were pooled since no between-group differences were found.

Observations were made from paths on the forest floor, usually with the aid of binoculars. Because of poor visibility in the forest, subjects were selected opportunistically as focal animals, but no individual was sampled more than once on a given day. All adults and subadults and some juveniles were individually recognized; the remaining juveniles could be distinguished sufficiently to ensure that no one was sampled more than once per day. Each subject was observed for 1 min while it was feeding, which included ingesting, processing, harvesting, or looking for food. Each sample included at least one instance of ingestion. Sample periods were measured with an electronic audio timer. In most cases, the animal remained in a single feeding tree or liana for the entire sample. If the subject switched from food-related activity to other behavior (such as quick goal-directed movement, self-maintenance, or social interaction), the sample was broken off. The sample was also aborted if the subject's activity became invisible to the observer.

The major predator of these monkeys is a large eagle (*Stephanoetus coronatus*) that swoops down into the group when making an attack (Cords 1987). The monkeys respond by dropping into the cover of dense foliage. Eagles also elicit alarm responses when they fly above the forest canopy over a monkey group and sometimes when they display above the canopy. Vigilance was measured accordingly as the number of times a subject looked up, away from its hands and the substrate that was being searched or from which food was being taken. Look-ups were initially categorized as lasting less than or greater than 2 s (glances and scans, respectively). In the analysis, however, the total frequency of looking up is used as the measure of vigilance since the pattern of differences for scans and for glances was similar. Thus the frequency of looking up should be roughly proportional to the time spent in surveillance. Because adult males spend much time looking out for other adult males, they were excluded from the subject pool. All records were made on adult females and juveniles of both sexes that were at least 8 months old.

Immediately after the sample, the following were noted: whether or not members of the other *Cercopithecus* species were in association, the density of the foliage where the monkey was sitting, the identity of the item being fed upon or searched for, and the species identity of other monkeys in the tree or liana (1989 only). Heterospecific groups were recognized as being in association if a group member, other than an adult male, of one species was 20 m or less from a similar group member of the other species (Cords 1987). In most cases, there was actual intermingling of individuals, and samples from mixed-species groups were always taken from individuals in this zone of intermingling. Foliage density was classified as high, medium, or low. High foliage density characterized many lianas and the crowns of trees like *Teclea, Bosqueia,* and *Bequaertiodendron.* Low foliage density was characteristic of *Celtis africana, Ficus exasperata,* and other species just beginning to put on new leaves. A monkey was very conspicuous in trees with low foliage-density, where most of its body was exposed; in dense foliage, only a part of the animal was typically visible to the observer.

Non-parametric tests were used to evaluate differences in vigilance levels. One-tailed p-values were calculated since research hypotheses predicted the direction of differences. Because five analyses were performed on the same data set, an alpha level of 0.01 was accepted as the criterion for statistical significance.

Results

It was usually impossible to tell exactly where an animal directed its gaze when it looked up, so one cannot be certain that it was looking up only for potential predators. It may also have been looking out for other monkeys, for more distant foraging sites, or for its next travel route. If looking up occurred mainly in these contexts, one would not expect differences in the rate of this behavior corresponding to the foliage density surrounding the focal monkey. Such differences would be expected, however, if monkeys look up for potential predators in a way that takes their own vulnerability into account. Both blue monkeys and redtails increased their rates of looking up as surrounding foliage density decreased (Table 1, Kruskal-Wallis test, $H_{\mathrm{corr}}=10.46$, 2 *df*, $P<0.01$ for blue monkeys; $H_{\mathrm{corr}}=13.25$, 2 *df*, $P<0.01$ for redtails).

Blue monkeys and redtails looked up significantly less often while feeding when they were part of a mixed-species association than when in a group of conspecifics only (Fig. 1; Mann Whitney U Test, $Z=-5.51$ for blues; $Z=-3.77$ for redtails, both $P\ll 0.001$). For blue monkeys, the mean number of look-ups per minute decreased from 4.6 ± 1.5 ($n=67$) when on their own to 3.0 ± 1.3 ($n=59$) while associated. Redtails looked up 4.4 ± 1.4 ($n=59$) times per minute when on their own, and 3.4 ± 1.2 ($n=61$) times per minute when with blue monkeys. The lower rate of looking up in mixed-species groups does not reflect a connection between mixed-

Table 1. Vigilance levels as a function of the surrounding foliage density. Means and ranges are given for the number of look-ups in 1-min samples. The number of samples is given in brackets

	Number of look-ups	Foliage density		
		Low	Medium	High
Blue monkeys	Mean	4.26	3.62	3.00
	Range	1–9	0–7	1–5
	N	(65)	(39)	(22)
Redtails	Mean	4.53	3.77	3.38
	Range	2–7	1–7	1–7
	N	(34)	(52)	(34)

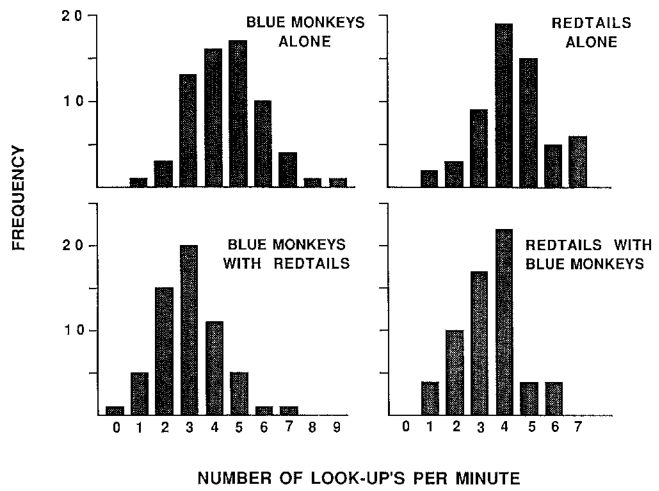

Fig. 1. The frequency of looking up by blue and redtail monkeys while feeding in single and mixed-species groups

species grouping and increased use of areas with high foliage density: blue monkeys do not change their use of areas differing in foliage density as a function of association with redtails, while redtails *decrease* their use of high foliage density areas when associated with blue monkeys (Cords 1987).

The difference in rates of looking up when associated and not associated was re-evaluated as a function of the food items being searched for or consumed. Plant foods (mainly fruit and young leaves) were distinguished from insect foods. Neither species showed a significant difference in looking up rates corresponding to association status when feeding on insects. When feeding on plant items, however, members of both species looked up less frequently in mixed-species groups than in single-species groups (Mann Whitney U Test, $Z=-4.55$, $P \ll 0.001$ for blue monkeys; $Z=-2.70$, $P=0.0035$ for redtails). When looking up rates were compared for insect and plant food, there were no significant differences except for blue monkeys in single-species groups; in this case, looking up rates were lower during insect foraging than during plant foraging (Mann Whitney U Test, $Z=-2.42$, $P=0.0078$).

One cue that a monkey might use in adjusting its rate of looking up as a function of association is the presence of heterospecifics in its own feeding tree or liana. For this analysis, only feeding records made while the subject was part of a mixed-species group were included. A comparison was made between looking up rates when the other species was present in or absent from the subject's tree. Rates of looking up did not differ for either blue monkeys or redtails in these two situations (Mann Whitney U Tests, $T=-1.09$, $P=0.138$ for blues; $Z=-0.74$, $P=0.230$ for redtails). A second comparison was made of looking up rates when the feeding tree contained other monkeys of either species versus no other monkeys. The presence of other monkeys in the tree did not affect rates of looking up for either blue monkeys or redtails (Mann Whitney U Tests, $Z=-0.35$, $P=0.363$ for blues; $Z=-1.06$, $P=0.145$ for redtails).

Discussion

These results suggest that one benefit gained by blue and redtail monkeys in mixed-species groups is that individuals of each species spend less time in surveillance while feeding relative to those in single-species groups. Although feeding efficiency was not measured directly, it is likely that an increase in time for feeding and a decrease in interruptions of this activity would increase efficiency. This relationship has been demonstrated explicity in several other species (Abramson 1979; Lazarus 1979; Sullivan 1984). More efficient feeding may benefit animals in two ways (Bertram 1980). If feeding time is limited, greater efficiency leads to greater food intake. If feeding time is not limited, animals may spend less time engaged in an activity that exposes them to relatively high predation risks. The Kakamega monkeys probably do not have limited feeding time: they spend at least 35% of their day resting, time which might be used for feeding if necessary (Dunbar 1988). Thus the major benefit of reduced individual vigilance for these monkeys is probably the fact that they can spend less time feeding, an activity that is inherently risky because it is incompatible with vigilance and because it occurs relatively frequently in exposed trees. In addition, if vigilance levels for the group as a whole are increased despite the individual decrease, feeding is a safer activity in mixed-species groups than in single-species groups. This effect could not be measured in the study animals, but has been demonstrated in starlings associating with blackbirds (Powell 1974) and in single-species flocks of geese that varied in size (Lazarus 1978).

Association has a more marked effect on vigilance levels when the monkeys are feeding on plant material as opposed to insects. Plant feeding is more likely than insect feeding to occur on exposed branches. Plant feeding accounts for 75–83% of feeding scores annually (Cords 1987). Thus the advantage of feeding with heterospecifics is relevant to most feeding behavior, and especially to that part in which the monkeys are most exposed. The lack of an association effect on looking up rates during insect foraging could be attributed to the fact that insects are often hunted by scanning, so that scanning for prey might mask scanning for predators. This explanation seems unlikely, however, since rates of looking up were not higher during insect foraging than during plant foraging.

Metcalfe (1984) found that adjustment of vigilance levels in mixed-species flocks of shore birds depended on the presence of *visible* neighbors. The Kagamega monkeys, however, apparently do not adjust their vigilance levels according to the presence of other monkeys in the same feeding tree, although these individuals should be the easiest to detect. Other cues indicating the presence of heterospecifics are certainly available, including sighting over longer distances, and hearing vocalizations. In another East African forest, Hauser and Wrangham (1988) have shown changes in scanning rates of blue and redtail monkeys in response to the calls of other primate (and bird) species played back through a speaker.

There is an obvious similarity between the results reported here for rain forest monkeys and those reported for mixed-species flocks of birds in a variety of habitats (Powell 1974; Metcalfe 1984; Sullivan 1985). When members of different species share common predators and recognize one another's alarm signals, association may be an effective way to reduce individual vigilance levels without sacrificing safety, allowing more time for activities incompatible with vigilance such as feeding. The fact that rates of looking up did not differ for the two blue monkey groups, despite an almost two-fold difference in size, suggests that the reduction in vigilance levels in mixed-species groups is not a simple linear effect of numbers of individuals. Rather, mixed-species groups seem to be special, either because of their particularly large size, not achieved in single-species groups, or because of complementarity of the warning systems of the participant species. There is evidence for such complementarity in west African *Cercopithecus*, in which different species seem to specialize in detecting aerial or terrestrial predators (Gautier-Hion et al. 1983).

The advantages of reduced vigilance are not, however, a sufficient explanation for mixed-species grouping in the Kakamega monkeys. Since both blue monkeys and redtails benefit similarly as far as vigilance reduction is concerned, it cannot explain why redtails are primarily responsible for the formation and maintenance of associations with blue monkeys (Cords 1987). It also does not explain month to month variation in the occurrence of mixed-species association. Cords (1987) has argued that other factors, such as differences in male alarm calling thresholds, group size, home range size, and diet, must be invoked for a comprehensive explanation, which includes foraging as well as anti-predator benefits. This leaves open the possibility that reduced vigilance is a beneficial consequence of mixed-species association of these monkeys, rather than a fundamental functional reason for its occurrence.

Acknowledgements. I am grateful to the Goverment of Kenya for permission to work in the Kakamega Forest, to the University of Nairobi for local sponsorship, and to the Kakamega Forest Station staff for practical assistance. The Harry Frank Guggenheim Foundation provided financial support during preparation of the manuscript. I thank the anonymous reviewers and the editor for comments on the manuscript.

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