

## **Mixed-Species Primate Groups in the Kibale Forest: Ecological Constraints on Association**

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*Five species of diurnal primates in the Kibale Forest of western Uganda—red colobus (*Colobus badius*), black-and-white colobus (*Colobus guereza*), redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), mangabeys (*Cercocebus albigena*)—often associate in mixed-species groups that vary in size and composition from day to day. Across this range of species, we found no consistent effect of association on feeding rate. In addition, there is no systematic difference between the species-specific individual feeding rates when animals were in mixed-species groups feeding in a specific tree on one day and when individuals of one of the same species were feeding in the same individual tree on a subsequent day. If associating in a mixed-species group lowers the risk of predation, one might expect that the number of vigilant events would decrease in mixed-species groups. However, the only species to exhibit a consistent decrease in vigilant behavior when in association was the red colobus. Redtail monkeys were more vigilant when in association. We predicted that the density and distribution of food resources would both constrain the frequency of association and the size of mixed-species groups. Based on 22 months of data on food resources and bimonthly censuses, we found no relationship between the frequency of association (except mangabeys) or mean mixed-species group size and the density and distribution of food resources for all species. Finally, we examined the behavior of the monkeys in and out of association before and after the playback of a crowned hawk eagle call (*Spizaetus coronatus*), a known predator. When more species were in association, the amount of time they spent being vigilant following the playback was greater and the response more intense than when fewer species were in association or when the group was alone. The results of this study*

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*illustrate that the nature of the costs and benefits of polyspecific associations for these different monkey species are complex and vary from species to species.*

**KEY WORDS:** polyspecific associations; mixed-species groups; group size; foraging ecology; group living.

## INTRODUCTION

Although evidence is limited, an increase in group size is generally considered to result in increased intragroup feeding competition and, in turn, to constrain group size (Altmann, 1974; Milton and May, 1976; Bradbury and Vehrencamp, 1977; Terborgh and Janson, 1986). This may occur when increased group size leads to increased exploitation competition, requiring the group to travel further to find adequate food resources (Terborgh, 1983; Chapman, 1990a). Thus, for some species group size may be determined by how the addition of new members increases travel costs (Wrangham *et al.*, 1993). The size, density, and distribution of food patches are key variables influencing travel costs. Patch size determines the amount of time that can be spent feeding in the patch by a group of a given size before it is depleted, and the density and distribution of patches determine the travel costs incurred when animals travel between patches.

Fission—fusion societies, such as those found in chimpanzee, spider monkey, and lion societies, are useful systems in which to investigate these concepts (Schaller, 1972; Milton, 1984; Chapman, 1990a,b). In these societies, individuals from a single community are found in small subgroups that change size and composition frequently. Because subgroup size is flexible, subjects can respond to ecological changes that occur on short temporal and spatial scales, and it becomes possible to relate such ecological changes to simultaneous changes in subgroup size (Klein and Klein, 1977; Milton, 1984; Terborgh and Janson, 1986; Chapman, 1990a,b). Because primates are among the most amenable subjects for observational studies in the wild, primate studies have contributed a great deal to our understanding of animal group size (Terborgh, 1983; Terborgh and Janson, 1986). However, studies of primates species with fission—fusion societies [*Pan* (Goodall, 1986; Nishida, 1968); *Ateles* (Klein and Klein, 1977; Chapman, 1990a,b; Chapman and Lefebvre, 1990)] are limited because the individuals are all large-bodied, occur at low densities, and travel long distances, making collection of long-term observations difficult and severely restricting observations on a number of groups. However, mixed-species primate groups—polyspecific associations—represent an analog to such fission—fusion systems. Mixed-species groups occur when groups of different monkey species join and travel together. These associations range in duration from brief encounters in feeding

trees to almost-permanent associations (Waser, 1987). The frequency, duration, and composition of associations may track changes in ecological conditions just as subgroup size tracks changes in fission–fusion societies. Because many species that associate in mixed-species groups have relatively small home ranges, one can quantify how ecological differences between neighboring groups influence the probability that polyspecific associations will be formed.

The density and distribution of food resources may constrain mixed-species groups when the associating species share food resources. If resources are not shared, the concepts may still be applicable if, by being a member of a mixed-species group, one species increases its day range to maintain association. Such models propose a potential foraging cost to polyspecific associations, while more functional explanations have only advocated foraging advantages. Past functional explanations of polyspecific associations fall into broad categories related to foraging and predator avoidance. The predation avoidance hypotheses suggest that polyspecific associations facilitate (1) an increased probability of predator detection (Rodman, 1973; Struhsaker, 1981; Gautier-Hion *et al.*, 1983; Boinski, 1989; Cords, 1990; Terborgh, 1990; Norconk, 1986; 1990a,b), (2) predator confusion (Morse, 1977), (3) a decreased probability of discovery or capture by predators (Hamilton, 1971; Wolf, 1985), and (4) increased predator defense (Struhsaker, 1981; Gautier-Hion and Tutin, 1988). Benefits associated with foraging include (1) access to foods otherwise not available (Struhsaker, 1981; Gautier-Hion *et al.*, 1983; Waser, 1984), (2) efficient use of shared resources (Cody, 1971; Terborgh, 1983; Cords, 1987; Whitesides, 1989; Podolsky, 1990), (3) increased feeding rates when in association (Klein and Klein, 1973; Munn and Terborgh, 1979; Podolsky, 1990), (4) increased resource detection (Gartlan and Struhsaker, 1972; Struhsaker, 1981), and (5) cooperative resource defense (Garber, 1988).

We examined the behavior of five species of primates from the Kibale National Park, western Uganda, in monospecific and polyspecific groups. The major objective was to discern whether ecological constraints on animal group size can explain variation in the size and the frequency of formation of polyspecific associations. We compared the behavior of monkeys in mixed-species and monospecific groups, paying particular attention to feeding rate and vigilance. Scanning the environment for predators is presumed to benefit animals by reducing the chance of being preyed upon. However, scanning is costly because it takes time away from other, incompatible activities, such as feeding (Cords, 1990; Vickery *et al.*, 1991). We predicted that the number of vigilant events would decrease in mixed-species groups, if associating in a mixed-species group lowers the risk of predation. We contrasted feeding rates when monkeys were in polyspecific

groups and when they were alone, to quantify the potential feeding cost associated with being in a member of a mixed-species group. Finally, we examined the behavior of the monkeys in and out of association under an experimental condition in which the group was exposed to a perceived predation threat. We predicted that if mixed-species groups function to reduce predation risk, larger associations would permit a less intense response to a perceived predation threat, e.g., reduced vigilance.

## METHODS

### Study Site

The Kibale National Park, in western Uganda (0°13'–0°41'N and 30°19'–30°32'E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest (Struhsaker, 1975; Skorupa, 1988). Kibale is a unique setting for the study of primate polyspecific associations. The primate fauna has one of the highest recorded biomasses in the world and, with 12 species, is also one of the most diverse. In addition, a number of previous behavioral and ecological studies provide considerable background data (Waser, 1977; Butynski, 1990; Struhsaker and Leland, 1979; Rudran, 1978; Struhsaker, 1975; Oates, 1977). Our behavioral observations focused on the five most common diurnal primate species in the area *Cercocebus albigena* (mangabeys), *Cercopithecus mitis* (blue monkeys), *Cercopithecus ascanius* (redtail monkeys), *Colobus guereza* (black and white colobus), and *Colobus badius* (red colobus).

### Behavioral Sampling

We collected behavioral and ecological data over 22 months (November 1990–August 1992) near the Makerere University Biological Field Station (Kanyawara). We observed feeding and vigilance rates of monkey groups in and out of association over a 3-day period each week (88 weeks). Two or three observers walked through the area, and when a primate group was sighted, we observed them for a 1-hr period. Immediately after finding a group, we searched the vicinity to determine if other species were within 20 or 50 m of the focal group. The 20-m and 50-m criteria have been used in several previous studies to define the distance at which a neighboring group can be considered to be in association (Waser, 1980; Struhsaker, 1981; Whitesides, 1989; Cords, 1990; Oates and Whitesides, 1990). Subsequently, we recorded feeding and vigilance rates of target animals during

a one-minute period. We selected a target animal by rotating through all of the visible adult animals, one after another, then starting the sequence over. Vigilance rate is the number of times the animal looked up, away from the substrate it was on, or away from the food item it was processing during the 1-min period (Cords, 1990). Scans serve to observe conspecifics, track other primate species, or look for predators. Adult males previously have been viewed primarily to scan for conspecifics, and thus Cords (1990) excluded males from her analyses of vigilance. We consider vigilance with males included and excluded. We indexed feeding rate as the number of items that entered the animal's mouth per minute, e.g., the number of whole fruits or the number of leaf bites. After 1 hr of behavioral sampling, we searched for another primate group. We recorded the exact location of the trees in which the group fed.

### Ecological Sampling

We established 26 nonintersecting vegetational transects with their locations selected at random from strata within the existing trail system [logged forest ( $n = 9$ ); valley bottom ( $n = 3$ ); mature forest ( $n = 14$ )]. Each transect is  $200 \times 10$  m, providing a total sampling area of 5.2 ha. We marked each tree  $>10$  cm DBH (diameter at breast height)  $\leq 5$  m of each side of the trail individually with a numbered aluminum tag and measured (DBH;  $n = 2111$  trees). We recorded phenological information once per month. We documented the stage of leaf development—leaf bud, young leaves and mature leaves—via binoculars—and noted the presence or absence of flowers and ripe fruits for all trees. We indexed patch size as DBH (Leighton and Leighton, 1982; Peters *et al.*, 1988). To verify the validity of DBH as an index of patch size, we measured the DBH of a sample of fruiting trees (*Uvariopsis congensis*,  $n = 7$ ; *Tabernaemontana holstii*,  $n = 12$ ; *Myrianthus arboreus*,  $n = 10$ ; *Rothmania urcelliformis*,  $n = 12$ ). Subsequently, we collected and weighed all the fruits on these trees. For each species, DBH is positively correlated with fruit biomass (Chapman *et al.*, 1992). We used the coefficient of dispersion (CD) (Sokal and Rohlf, 1981), based on the number of trees of a species on a transect as the unit, to quantify the pattern of distribution for each tree species. For regressions of the frequency of association with these ecological variables, we indexed food abundance (patch density and patch size) as the sum of the DBHs of the trees providing food in a given month, and we indexed the distribution of food resources as the CD using the transects as a unit.

To obtain a monthly index of the frequency of occurrence of mixed-species groups relative to monospecific groups, we recorded the species

composition of all groups observed on the phenology transects. We conducted this procedure at the beginning of the month when the transects were sampled to determine the phenophase of the trees and in the middle of the month using the same transects. Because of the difficulty of counting animals in dense foliage high in the canopy, we were unable to determine the size of each group encountered. As an index of the size of mixed-species groups we used published accounts of the mean group size for the Kanyawara study area. Thus, we estimated the size of a mixed-species group as the sum of the mean group size of each of the species associating. For each species, we determined the average size of their mixed-species groups for each month and related it to the density and distribution of their food resources.

From the behavioral information, we determined the plant foods eaten during the study (% of the feeding observations devoted to a particular item, e.g., ripe fruit or young leaf, of a particular plant species). In addition, extensive research previously has been conducted on the common primate species in Kibale. We calculated dietary overlap using two sets of data, expressed via the Holmes and Pitelka (1968) index (Struhsaker, 1975; Waser, 1987; Chapman, 1987). First, to determine a measure of dietary overlap that could be applied across the entire census area and related to the monthly estimates of frequency of association, we used the data collected during our observations, as well as published food lists (Waser, 1977; 1987; Struhsaker, 1975; Oates, 1977; Rudran, 1978; Struhsaker and Leland, 1979; Butynski, 1990). We considered a plant part of a particular species to be food if it constituted >2% of a specific diet either in our study or in any previous study. Incorporating these previous studies expands the temporal and spatial scale considered. This was desirable because the bi-monthly censuses to determine frequency of association covered a large area, while our behavioral observations were restricted. Second, to provide a measure of the degree of overlap that would be experienced by a particular group at a specific point in time, we used data collected during our behavioral observations (Table I).

### **Predator Playbacks**

We conducted a playback experiment using crowned hawk eagle (*Spizaetus coronatus*) calls to examine whether the duration or nature of the response to a predator is a function of the number of species in association. Crowned hawk eagles [adult weight, 3.4 to 4.1 kg (Brown *et al.*, 1982)] prey on monkeys in Kibale Forest (Struhsaker, 1975; Struhsaker and Leland, 1979; Skorupa, 1989; Struhsaker and Leakey, 1990). We used an

Table I. Dietary Overlap in a Component of the Primate Community of the Kibale National Park, Uganda<sup>a</sup>

| Species                      | RC   | BW   | MG   | RT   | BL   |
|------------------------------|------|------|------|------|------|
| Red colobus (RC)             | —    | 7.1  | 5.1  | 4.7  | 14.1 |
| Black-and-white colobus (BW) | 52.4 | —    | 13.1 | 13.8 | 14.4 |
| Mangabey (MG)                | 20.8 | 39.8 | —    | 21.2 | 26.2 |
| Redtail (RT)                 | 52.5 | 54.6 | 25.0 | —    | 33.8 |
| Blue monkey (BL)             | 20.2 | 16.0 | 32.0 | 25.2 | —    |

<sup>a</sup>Dietary overlap above the diagonal is based on published data contrasting studies conducted at different times (Waser, 1977, 1987; Struhsaker, 1975; Oates, 1977; Rudran, 1978; Struhsaker and Leland, 1979; Butynski, 1990). Dietary overlap below the diagonal is that calculated directly from our behavioral observations made in this study (Holmes and Pitelka overlap index).

eagle recording obtained in the context of an attack on a red colobus group in the playbacks. The recording was made using a Sony (WC-D6C) cassette recorder and a Sennheiser directional microphone (ME 90).

For each trial we lifted the speaker (Toshiba Model SS-A1W) into the canopy on a series of poles to a height of 11 m. The recording was standardized at an amplitude of 60 dB using a sound level meter (A-weighting, slow response, 60 m from the source). We placed the speaker approximately 20 m from the observer. Experiments commenced 5 min after placement of the speaker. Only one trial was conducted on a particular group on a given day, and intertrial duration averaged 9 days (SD = 5.4 days; range, 2 to 22 days). In each trial, we selected a focal adult male for observation before the playback. We recorded his behavior for 60 sec before the call and for 5 min after the playback. The variables recorded are (1) vigilance rate and duration, (2) the number of alarm calls given by the focal subject, and (3) movement (downward into cover, toward the speaker, upward to the outer branches to an exposed position). Subsequently, we ranked the intensity of the response qualitatively on a scale of 1 to 10, with 1 being the mildest response involving just increased vigilance in the direction of the speaker and 10 being the most dramatic response involving alarm calls and charges.

We examined the distribution of all variables for normality, and when values were not normally distributed, we applied an appropriate transformation (Sokal and Rohlf, 1981). For example, when the percentage of the observations recorded when two species were in association was related to ecological or behavioral variables, it was arcsine<sup>1/2</sup> transformed to normalize

its distribution (Sokal and Rohlf, 1981). We corrected the reverse transformations for bias (Beauchamp and Olson, 1973; Millar, 1984). All probability levels presented are two-tailed.

## RESULTS

### Feeding Rate of Monospecific and Polyspecific Groups

There is no consistent effect of association on the feeding rates across all of the five primate species ( $n = 1983$  feed rates; red colobus  $n = 1124$ ; redtails  $n = 159$ ; black-and-white colobus  $n = 389$ ; mangabeys  $n = 163$ ; blue monkeys  $n = 148$ ). The redtail monkeys had a marginally increased feeding rate when in association, while mangabeys obtained fewer food items per unit time when they were members of a mixed-species group (Table II). The other three species showed no significant change in feeding rate between observations made when they were alone and when they were members of a mixed-species group. We also contrasted the feeding rate of a species when feeding in association in a specific tree to the same species when feeding alone in the same tree on a subsequent day. There is no systematic change in feeding rate that corresponds with being a member of a mixed-species group (paired  $t$ -test = 0.17,  $P = 0.867$ , % change = 2.5,  $n = 9$  trees, mean number of observations of feeding rate per tree = 17). We also contrasted feeding rates on a particular plant species/part when a monkey species was alone and when it was in association. There

**Table II.** The Percentage Change in Feeding Rate When in Association Compared to When That Species Was Feeding Alone [(in Association-Alone)/Alone]<sup>a</sup>

|                         | Mean % change | Probability (P) |
|-------------------------|---------------|-----------------|
| Red colobus             | +2.8          | 0.722           |
| Black-and-white colobus | -5.8          | 0.629           |
| Mangabey                | -41.9         | 0.006           |
| Redtail                 | +37.3         | 0.055           |
| Blue Monkey             | +27.1         | 0.192           |

<sup>a</sup>We define associations as two species  $\leq 20$  m, and a minus means that feeding rate increased when the focal species was alone. The statistical comparison involves  $t$  tests between feeding rates when alone and rates when in association (two-tailed).



were 14 species/part combinations for which these data were available. Again, there is no systematic difference in feeding rates when alone and when in association (paired  $t$ -test =  $-0.47$ ,  $P = 0.649$ , % change =  $-4.3$ , an average of 40 feeding rates contributed to each of 14 plant species/parts).

When we examined the overall feeding rates in pairwise analyses, red-tail monkeys and blue monkeys exhibited increased feeding rates when together (Table III). Black and white colobus had an increased feeding rate when associating with red colobus, but a depressed feeding rate when redtail monkeys were present. Red colobus exhibited an increased feeding rate only when associating with blue monkeys. Mangabeys had a decreased feeding rate only when associating with redtail monkeys.

One might expect that association is favored when feeding rate is positively affected by association and dietary overlap is low. The percentage of the observations recorded when two species were in association is not related to the change in feeding rate ( $r = 0.065$ ,  $P = 0.806$ ) or to the degree of dietary overlap (dietary overlap calculated from the data collected during our observations, as well as published data;  $r = -0.273$ ,  $P = 0.289$ ; Fig. 1). A multiple regression predicting the percentage of time in association from feeding rate and dietary overlap is not significant ( $r^2 = 0.081$ ,  $P = 0.553$ ).

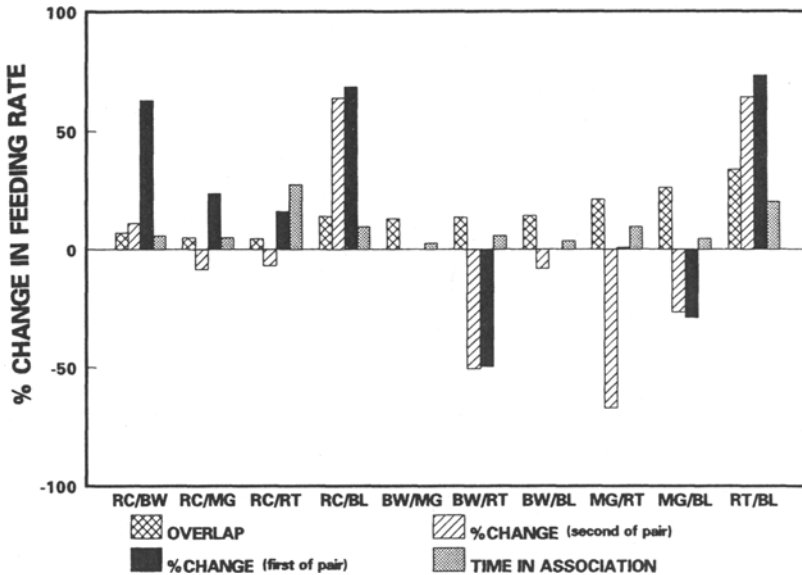
Possibly the effect of association is not to lower the feeding rate of individuals but, instead, to reduce the number of individuals that feed at any given time. Because individuals often are spread throughout a number of different trees, all individuals in a group could not always be located

**Table III.** The Percentage Change in Feeding Rate When in Association with a Specific Monkey Species Compared to When That Species Was Feeding Alone [(in Association-Alone)/Alone]<sup>a</sup>

| Species in association | Focal |        |        |        |        |
|------------------------|-------|--------|--------|--------|--------|
|                        | RC    | BW     | MG     | RT     | BL     |
| Red colobus (RC)       | —     | -62.8* | +23.7  | +16.1  | +68.4* |
| Black-and-white (BW)   | +11.2 | —      | NA     | -49.7  | NA     |
| Mangabey (MG)          | -8.5  | NA     | —      | +0.8   | -28.8  |
| Redtail (RT)           | -6.9  | -50.5* | +67.0* | —      | +73.2  |
| Blue monkey (BL)       | 63.7* | -8.2   | -26.5  | +64.2* | —      |

<sup>a</sup>Associations are two species  $\leq 20$  m of each other. A minus sign means that the feeding rate increased when the focal subject was alone.

\*A  $t$  test between feeding rates when alone and when in association is significantly different ( $P < 0.05$ , two tailed).



**Fig. 1.** The dietary overlap and percentage of time in association (Waser, 1987) and the percentage change in feeding rate associated with being a member of a polyspecific association. Abbreviations for species: RC, red colobus; BW, black-and-white colobus; RT, redbelted; BL, blue monkey; MG, mangabey. Each pairwise species contrast is presented and the percentage change in feeding rate for each of the members of the pair is presented in the order of the pair. For example, for the bars labeled RC/BW, the percentage change in red colobus's feeding rate is represented by the solid bar (first in pair) and the percentage change in black-and-white colobus is represented by the hatched bar (second in pair).

within the time frame of our observations. Thus, we could not directly assess the proportion of each group feeding when alone and in a mixed-species group. However, we used an index of probability of feeding to address this issue. We recorded whether the first animal of each species that we sighted on the census was eating. These data, in combination with data on the composition of each of these groups, allowed us to ask whether feeding or not feeding on first sighting is independent of whether the animal was in a mixed-species group or alone. The probability that the first animal sighted was feeding is not dependent on whether the animal was in a monospecific or polyspecific group (red colobus  $\chi^2 = 0.154$ ,  $P > 0.05$ ,  $n = 142$ ; black-and-white colobus  $\chi^2 = 0.13$ ,  $P > 0.05$ ,  $n = 71$ ; blue monkeys  $\chi^2 = 0.91$ ,  $P > 0.05$ ,  $n = 29$ ; redbelted  $\chi^2 = 1.49$ ,  $P \geq 0.05$ ,  $n = 40$ ; mangabey  $\chi^2 = 0.018$ ,  $P > 0.05$ ,  $n = 32$ ).

### Vigilance in Monospecific and Polyspecific Groups

If associating in a mixed-species group lowers the risk of predation (Struhsaker, 1981; Gautier-Hion *et al.*, 1983; Waser, 1987; Whitesides, 1989), one would expect that the number of vigilant events would decrease in mixed-species groups (Cords, 1990). The only species to exhibit a consistent decrease in vigilant behavior when in association is red colobus (Table IV; total  $n = 3612$ , red colobus  $n = 1811$ , black-and-white colobus  $n = 929$ , redbills  $n = 317$ , blue monkeys  $n = 282$ , mangabeys  $n = 273$ ). This was the case when all age and sex classes were in the analysis and when males were excluded. In contrast, redbill monkeys, the smallest species, showed an increased level of vigilance when in association as compared to when they were alone (including and excluding males).

Certain species may play particularly important roles in predator warning. For example, because black-and-white colobus use the upper canopy more than the other species do [Gebo and Chapman, 1995, % upper canopy use based on 7597 travel and feeding locomotory bouts, black-and-white colobus, 58% of their bouts were in the upper canopy; redbills, 18.5%; blue monkeys, 31.2%; mangabeys, 39.1%; red colobus, 41.1%], they might be more vigilant for crowned-hawk eagles than other species. If this was the

**Table IV.** The Percentage Change in Vigilance When in Association Compared to When That Species Was Alone [(in Association-Alone)/Alone]<sup>a</sup>

|                         | % Change | Probability |
|-------------------------|----------|-------------|
| Red colobus             | -13.6    | 0.003       |
| Excluding males         | -14.7    | 0.063       |
| Black-and-white colobus | -4.6     | 0.412       |
| Excluding males         | -9.4     | 0.263       |
| Mangabey                | -3.2     | 0.754       |
| Excluding males         | -2.2     | 0.190       |
| Redbill                 | +25.44   | 0.005       |
| Excluding males         | +44.8    | 0.008       |
| Blue Monkey             | -3.1     | 0.710       |
| Excluding males         | +4.9     | 0.095       |

<sup>a</sup>Associations are two species  $\leq 20$  m of each other and a minus sign means that attention increased when the focal was alone. The statistical comparison involves *t* tests between vigilance rates when alone and rates when in association (two-tailed).

case, one might find a decrease in vigilance for the focal species only when associating with a species particularly effective at detecting or deterring predators. When the focal troop was in association with blue monkeys, vigilance increased consistently across species (significantly so for red colobus and redbtail monkeys; Table V). Red colobus and redbtails exhibited decreased rates of vigilance when in association with black-and-white colobus relative to when they were alone. When red colobus or redbtail monkeys were with mangabeys, both species were less vigilant in comparison to when they were alone. In contrast, blue monkeys were more vigilant when with mangabeys.

### Density and Distribution of Food Resources and Frequency and Size of Association

We predicted that increased travel costs would limit mixed-species group associations and size during periods of food scarcity. Based on 22 months of data on food resources and bimonthly censuses of the frequency of association ( $n = 314$  groups; 142 red colobus, 71 black-and-white colobus, 40 redbtail, 32 mangabey, 29 blue monkey), the proportion of sightings when a particular species was in a mixed-species group (arcsine/transformed) is not related to the density and distribution of their food resources for any species, except mangabeys (Table VI). For them, the frequency of association is positively associated with the habitatwide levels of food abundance ( $r = 0.778$ ,  $P = 0.002$ ). A multiple regression with the

**Table V.** The Percentage Change in Vigilance When in Association with a Specific Monkey Species Compared to When That Species Was Alone [(in Association-Alone)/Alone]<sup>a</sup>

| Species in association | Focal  |      |       |        |        |
|------------------------|--------|------|-------|--------|--------|
|                        | RC     | BW   | MG    | RT     | BL     |
| Red colobus (RC)       | —      | -6.9 | +2.3  | +15.9  | -26.6* |
| Black-and-white (BW)   | -37.4* | —    | NA    | -83.6* | NA     |
| Mangabey (MG)          | -49.5* | NA   | —     | -59.6* | +69.6* |
| Redtail (RT)           | -2.8   | +2.4 | -27.4 | —      | +18.7  |
| Blue monkey (BL)       | +51.7* | +0.8 | +11.3 | +37.1* | —      |

<sup>a</sup>Associations are two species  $\leq 20$  m of each other. A minus sign means that attention increased when the focal was alone.

\*A  $t$  test between vigilance when alone and vigilance when in association is significantly different ( $P < 0.05$ , two tailed).

**Table VI.** The Relationship (Pearson Correlation) Between the Percentage of the Observations (arcsin $\sqrt{\quad}$  Transformed) When the Target Species Was Found in Association with Other Primate Species and the Density and Distribution of Their Food Resources<sup>a</sup>

|  |                          |  |
|--|--------------------------|--|
| <b>Red colobus</b>                       |                          |  |
| % in association (all) vs food abundance | $r = -0.337, P = 0.171$  |  |
| (All) vs food distribution               | $r = -0.341, P = 0.166$  |  |
| (All) vs abundance+distribution          | $r^2 = 0.118, P = 0.389$ |  |
| <b>Black-and-white colobus</b>           |                          |  |
| in association (all) vs food abundance   | $r = -0.412, P = 0.144$  |  |
| (All) vs food distribution               | $r = -0.249, P = 0.390$  |  |
| (All) vs abundance+distribution          | $r^2 = 0.195, P = 0.302$ |  |
| <b>Redtail Monkeys</b>                   |                          |  |
| % in association (all) vs food abundance | $r = +0.310, P = 0.261$  |  |
| (All) vs food distribution               | $r = +0.272, P = 0.326$  |  |
| (All) vs abundance+distribution          | $r^2 = 0.105, P = 0.515$ |  |
| <b>Blue Monkeys</b>                      |                          |  |
| % in association (all) vs food abundance | $r = +0.050, P = 0.853$  |  |
| (All) vs food distribution               | $r = -0.040, P = 0.879$  |  |
| (All) vs abundance+distribution          | $r^2 = 0.025, P = 0.847$ |  |
| <b>Mangabeys</b>                         |                          |  |
| % in association (all) vs food abundance | $r = +0.778, P = 0.002$  |  |
| (All) vs food distribution               | $r = +0.151, P = 0.623$  |  |
| (All) vs abundance+distribution          | $r^2 = 0.755, P = 0.003$ |  |

<sup>a</sup>The food abundance and distribution variables are log transformed.

density and distribution of mangabey food resources (coefficient of dispersion between transects) as the independent variables explained 76% ( $P = 0.003$ ) of the between-month variance in the frequency of association.

The size of the mean monthly mixed-species groups is not related to the density and distribution of food resources of each species (red colobus  $r^2 = 0.106, P = 0.188$ ; black-and-white colobus  $r^2 = 0.091, P = 0.591$ ; red-tail monkeys  $r^2 = 0.237, P = 0.104$ ; blue monkeys  $r^2 = 0.097, P = 0.515$ ; mangabeys  $r^2 = 0.254, P = 0.232$ ). None of the correlations between mixed-species group size and density or distribution of food resources is significant at the  $P < 0.05$  level.

One might expect that the amount of time one species spent with another would be a function of dietary overlap. For all of the species studied, the percentage of the observations of two species associating is not related to the degree to which their diets overlapped (calculated on a monthly

basis from our behavioral data and published diet lists) in a particular month (in all pairwise comparisons  $P > 0.05$ ).

Predicting the proportion of time each pair of species associated based on the density and distribution of the food of the target species produced only 2 significant relationships of 20 tests (1 significant relationship would be expected of 20 based on chance alone). Black-and-white colobus associated more with blue monkeys when the food resources for the black-and-white colobus were clumped and rare ( $r^2 = 0.438$ ,  $P = 0.042$ ). The proportion of the time that mangabeys associated with blue monkeys increased during periods when the food resources for mangabeys were abundant and uniformly distributed ( $r^2 = 0.474$ ,  $P = 0.042$ ).

### Playback Experiments

We executed 53 experimental playbacks: 27 to groups not in association, 20 to two-species associations, and 6 to associations of three species. We preferentially chose to sample red colobus monkeys, to ensure a large sample of one species. We conducted 37 trials with red colobus as the focal species: 19 alone, 10 with one other monkey species, and 4 with two other species. The remainder of the trials are distributed approximately equally among the other species (range, three to six).

The duration of time spent vigilant increased following the playback [all species, paired  $t$  test = 9.31,  $P < 0.001$ , duration before 2.9 sec (SE = 0.56 sec), duration after 25.7 sec (SE = 2.36 sec); red colobus  $t = 9.58$ ,  $P < 0.001$ , duration before 3.4 sec (SE = 0.63 sec), duration after 20.8 sec (SE = 1.79 sec)]. In all of the trials, the focal animal was vigilant for some time (range, 7 to 76 sec) and looked into the upper canopy as if scanning for an avian predator.

If mixed-species groups function to reduce predation risk, and if relationship is expressed by animals being more "confident" when in a mixed-species group, we would predict the duration that animals were vigilant after the playback to be a function of the number of species they were with. Contrary to what was predicted, the more species that were in association, the greater the amount of time spent being vigilant following a playback (all species  $F = 6.07$ ,  $P = 0.004$ , alone 21.0 sec, with one species 26.5 sec, with two species 46.1 sec; red colobus only  $F = 30.52$ ,  $P < 0.001$ , alone 15.1 sec, with one species 22.2 sec, with two species 43.8 sec).

In trials involving mixed-species groups of three species, the focal male charged in the direction of the speaker during 33% of the trials (all species). In contrast, the focal subject charged the speaker in only 5% of the experiments with two species and only 3.7% of the time when the target

species was alone. Similarly, during 33% of the trials involving three species, the male moved into the top of the canopy to a position that would appear to increase the risk of predation from an aerial predator. This occurred in only 10% of the associations with two species and in only 3.7% of the trials conducted when the focal species was alone. The focal male vocalized in all trials involving mixed-species groups of three species, in 35% of the trials with mixed-species associations of two species, and in only 7.4% of the trials when they were alone. The average qualitative ranking of the intensity of the response (on a 0–10 scale) is 5.2 when three species were in association, 4.0 when two species were together, and 2.7 when the focal species was alone (red colobus: three species = 5.8, two species = 3.9, alone = 2.2).

## DISCUSSION

It is often stated that living in a group (Alexander, 1974; van Schaik, 1983) or a mixed-species association (Struhsaker, 1981; Gautier-Hion *et al.*, 1983; 1988; Boinski, 1989; Oates and Whitesides, 1990; Cords, 1987; 1990; Podolsky, 1990) increases the probability of detecting or deterring predators. Past studies of polyspecific associations show that many of the associating species respond to each others' alarm calls (Struhsaker, 1981; Terborgh, 1983; Gautier-Hion and Tutin, 1988; Oates and Whitesides, 1990; Cords, 1990). However, animals that do not form polyspecific associations will also respond to the alarm calls of other species (Boinski, 1989; Seyfarth and Cheney, 1990).

Some species exhibited higher levels of vigilance when in polyspecific associations, as compared to when alone, while other species exhibited reduced levels of vigilance. The playback experiments of a crowned hawk eagle call, a predator often considered to exert strong selective pressure for mixed-species groups (Struhsaker, 1981; Gautier-Hion *et al.*, 1983; Terborgh, 1990), produced results opposite to what we predicted. The increased rates of vigilance that corresponded to an increase in the number of associating species may reflect a general response to the increased level of activity associated with mixed-species groups. Immediately following the playback, animals may be vigilant to locate the crowned hawk eagle. Subsequently, the animals may be vigilant to branch movements to distinguish between moving primates and possible predators or simply toward other monkeys that are more active following the playback. In contrast, the increased probability of charging into an exposed position or toward the speaker may indicate that the primates are in less danger when in association and are more willing to act aggressively (Gautier-Hion and Tutin,

1988). It has typically been assumed that, by being in association, animals can decrease the amount of time devoted to being vigilant. The results obtained here run counter to this and suggest that animals may have to be more vigilant when in association, which may represent a significant cost.

The density and distribution of food resources were a poor predictor of both the encounter frequency and the size of mixed-species primate groups. This is in contrast to several recent studies that imply that these parameters are good predictors of group size (or subgroup size) in fission-fusion species (Chapman, 1990a,b; Milton, 1984; Chapman *et al.*, 1995). The poor relationship between these ecological variables may be a result of several factors. Some of the model's assumptions may be violated when the model is applied to polyspecific associations. We assumed that by associating with another species, the target species experiences an added travel cost. This may not always be the case. For example, Isbell (1984, 1991) demonstrated that no relationship exists between red colobus group size in Kibale and day range, suggesting that adding additional members to a red colobus group may not create an added travel cost for the group. The ecological constraint model also assumes that it would be advantageous to be in as large a group as possible if there were no ecological constraint. If the advantages of polyspecific associations do not continue to increase with increasing polyspecific group size (at least to the point that the ecological constraints would operate), we would not expect the frequency or size of mixed-species groups to be related to the density and distribution of food resources. Although several possibly advantageous interspecific social interactions have been observed to occur in mixed species groups, e.g., grooming (Struhsaker, 1981; Waser, 1980; Cords, 1987) and play (Struhsaker, 1981; Rudran, 1978; Cords, 1987), many of the social benefits, e.g., increased mating opportunities, that would be derived from increasing the size of a monospecific group may not be realized from associating in a mixed species group. Alternatively, there may be an optimal group size that is less than that which would result if two groups of different species associated (Giraldeau, 1988). Under such conditions, it may be beneficial for two species to associate only under very specific conditions, and thus the association would last only as long as the condition lasted, e.g., while both were feeding in the same fruiting tree. Finally, all or some of the mixed-species associations in Kibale may not be subject to selection. Waser (1982) compared expected with observed rates of encounter for six types of associations in the Kibale Forest that involved mangabeys and concluded that associations may just represent random encounters of groups in all cases except for associations between *Cercocebus albigena* and *Cercopithecus mitis*, *C. ascanius*, and *Pan troglodytes*. Waser (1984) demonstrated that



none of these species maintained association with *C. albigena* as long as expected by the null hypothesis of independent movement.

We found that the percentage change in feeding rate is independent of the proportion of time the species spent together. Some species exhibited an increased feeding rate when in association (versus when alone), while other species showed a decreased rate. Similarly, some species were less vigilant when members of mixed-species groups, while other species were more vigilant. Playback experiments imply that the monkeys were more willing to be aggressive toward a perceived predator but may respond to the general increased level of activity associated with mixed species groups by increasing their level of vigilance. We found little or no relationship between the density and distribution of food resources and the frequency and size of mixed-species groups. This suggests that the costs and benefits of polyspecific associations vary among these monkey species. Some species may be benefiting generally or just at particular times. Other species may be parasitic, themselves benefiting, while inflicting costs to the other members of the association.

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