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Mixed-Species Association of East African Guenons: General Patterns or Specific Examples?

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Sympatric guenons in East Africa associate with one another in mixed-species groups to an intermediate degree. This makes it possible to compare a given group's ecology and behavior when it is part of an association to when it is unaccompanied, and to correlate association tendency with various ecological parameters. Two studies incorporating these approaches have been made of sympatric *Cercopithecus ascanius* and *C. mitis* monkeys in the Kakamega Forest, Kenya, and the Kibale Forest, Uganda. The pattern of and reasons for association in each site are reviewed. Compared to Kakamega, association between *C. ascanius* and *C. mitis* in Kibale occurs less often, and the species appear to benefit relative to one another in different ways. These results suggest that the particular ecological setting greatly influences the nature of the interaction between species, through its effect on population structure, dietary overlap, food distribution, and community composition. The major ecological differences between the two study areas probably reflect post-Pleistocene history and possibly climate, but they have important consequences for the present-day population structure and feeding ecology of each species, and hence affect relations between them as well.

Key words: guenon, mixed-species association, blue monkey, redtail monkey, interspecies relations, East Africa

INTRODUCTION

Unlike the guenons in Gabon which associate in mixed-species groups nearly permanently [Gautier-Hion et al., 1983], and unlike the Diana monkeys in Sierra Leone which spend little time with most other species [Whitesides, 1989], the guenons at two East African sites associate with other species to an intermediate degree. This makes it possible to compare the behavior of monkeys when they are or are not participating in mixed-species groups. The comparison is not confounded by the fact that one is studying different groups or different places: a single group can be observed in both conditions. Furthermore, since participation in mixed-species groups is variable over time, the occurrence of mixed-species association

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TABLE I. A Comparison of the Kakamega and Kibale (Kanyawara) Forests*

	Kakamega		Kibale (Kanyawara)	
Elevation	1,580 m		1,365–1,530 m	
Annual rainfall	222 ± 26 cm (1976–81)		157 ± 20 cm (1977–84)	
Temperature (°C): min/max[1]	11–21/18–29		16.2 ± 0.4/23.3 ± 0.06	
Tree canopy height (non-emergents)	32.5 ± 6.1 m(n = 6)		25–30 m	
Trees/ha	274		268	
Basal cover (m^2/ha)	43		39	
Tree species that are among the 20 most frequent trees in both forests, with their relative percentages in each forest	4.09	*Bosqueia phoberos*	5.0	
	5.83	*Celtis africana*	1.6	
	6.24	*Celtis durandii*	14.0	
	1.64	*Diospyros abyssinica*	14.1	
	1.79	*Ficus exasperata*	1.0	
	11.81	*Funtumia latifolia*	7.8	
	1.53	*Markhamia platycalyx*	15.0	
	3.79	*Olea welwitschii*	1.6	
	2.30	*Teclea nobilis*	3.2	
	2.15	*Trema* spp.	3.6	
Tree species that are among the 20 most frequent trees in only one forest, with their relative percentages in that forest	*Antiaris toxicaria*	7.42	*Aphania senegalensis*	1.3
	Albizia gummifera	4.30	*Chaetacme aristata*	3.5
	Aningeria altissima	2.05	*Chrysophyllum gorungosanum*	1.0
	Cordia abyssinica	3.22	*Dombeya mukole*	2.2
	Croton megalocarpus	7.72	*Millettia dura*	1.4
	Croton sylvaticus	3.79	*Neoboutonia macrocalyx*	1.0
	Fagara macrophylla	2.66	*Parinari excelsa*	1.3
	Ficus mallatocarpa	2.46	*Premna angolensis*	0.9
	Polyscias spp.	1.99	*Strombosia scheffleri*	5.5
	Prunus africana	2.15	*Uvariopsis congensis*	4.9
Percentage of stems included in the 20 most frequent tree species	78.9		90.0	

*Data from Cords [1987] and Butynski (in press). Stem density and basal cover estimates come from a survey of 654 trees with circumference at breast height ≥ 46 cm in three plots totalling 2.4 ha (Kakamega), and from 1,818 trees ≥ 10 m in height from an area of 6.80 ha (Kibale). According to Skorupa and Kasenene [1984], a 9 m tree has a circumference of about 35 cm, so the two samples include comparably large trees. Data on tree species frequencies come from a survey of 1955 trees with diameter at breast height > 20 cm in 22 ha of forest (Kakamega), and from the sample described above for Kibale. Because of the different selection criteria, the Kibale sample includes smaller trees than the Kakamega sample. For this reason, relative rather than absolute densities are given.

[1] Kibale data are averages of daily minima and maxima measured from 1977–83; Kakamega data are ranges of monthly minima and maxima measured from 1976–81.

can be related to various aspects of the participants' ecology, such as feeding and ranging patterns.

These were the approaches taken in studies of mixed-species association of blue monkeys *(Cercopithecus mitis)* and redtail monkeys *(C. ascanius)* in the Kakamega Forest of western Kenya [Cords, 1987] and in the Kibale Forest of western Uganda [Rudran, 1978; Struhsaker, 1981]. These two forests lie only 500 km apart, at nearly the same latitude, and they are broadly similar in terms of climate, physiognomy, and plant species composition (Table I) [Cords, 1987; Struhsaker, 1975; Butynski, in press; personal observation]. They differ notably, however, in the composition of the primate community. The purpose of this paper is to compare associations of blue and redtail monkeys in these two sites, with the goal of identifying factors that determine why, how often, and with whom these guenons form mixed-species associations.

MIXED-SPECIES ASSOCIATION IN THE KAKAMEGA FOREST

In Kakamega, there are four species of diurnal monkeys regularly resident in the study area: beside the two guenons, there are *Papio anubis* and *Colobus guereza.* Baboons are transient, and rarely seen. The guenons react to them by alarm calling and moving away. *Colobus,* on the other hand, are common, and are seen regularly together with one or both guenons. *Cercopithecus* and *Colobus* rarely travel together over longer distances however [see also Marler, 1973], at least partly because the colobus ranges are much smaller than those of the *Cercopithecus* [Cords, unpublished]. The study focussed, therefore, on the relationship between the two guenon species, which spent 50–75% of their time together in mixed-species groups [Cords, 1987].

Null Hypotheses

The association of blue and redtail monkeys does not seem to be a chance phenomenon at Kakamega. Waser's gas models [Waser, 1982, 1984] were used to derive "null" expectations under the hypothesis of independent movement, and it was found that both the encounter rate between heterospecific groups and the duration of encounters were longer than null expectations, the latter by a statistically significant margin [Cords, 1987]. More informally, it seems unlikely that two groups moving independently would by chance take exactly the same path for 4–5 hours (the average encounter length), let alone the 15–30% of associations that lasted 8–12 hours.

Independent movement is a simplistic null hypothesis, however, because it ignores the fact that different species may share resources that serve as points of attraction, even if they are discovered independently. The guenons at Kakamega do share many foods: dietary overlap, measured as the shared percentage of feeding scores on particular plant-species-specific items, ranged from 53 to 74% per month over a 1-year period [Cords, 1987]. If heterospecific groups were simply meeting at shared food sources, one would expect a) greater dietary similarity between species when the heterospecific groups associate than when they are unaccompanied, and b) a correlation between dietary similarity and amount of time spent associated from month to month. Neither relationship was found in Kakamega [Cords, 1987]. Furthermore, heterospecific groups often stayed together during periods when they were not feeding, and when they were not even near major fruit sources.

Benefits of Association

If the monkeys are not moving independently, and are not simply responding to shared resources, it is possible that one or both species benefits from associating, and so seeks the other out. In Kakamega, redtails are responsible for maintaining association with blue monkeys, in that redtails initiated most of the associations, and ended relatively fewer of them [Cords, 1987]. This result suggested that redtails might have especially much to gain from participating in mixed-species groups.

The crowned hawk eagle *(Stephanoetus coronatus)* is the primary predator of monkeys in Kakamega. This bird hunts by stealth, and the monkeys' primary defense is early detection, followed by flight into dense leaves. Neither species seems to be intrinsically more alert than the other: the first alarm is given by a peripheral animal, almost always a female or juvenile, close to the bird's line of flight into the group. Adult males often pick up on these early alarms and produce louder alarm calls specific to their age and sex. Blue adult males are more likely than redtail males to give alarms, and they are more likely to call first [Cords, 1987]. In addition, only blue males have been seen to charge the eagle, though such behavior was observed rarely [Cords, 1987]. The presence of many eyes probably increases the chance that an eagle swooping in will be detected early. In addition, the "rain" of monkeys plummeting into the foliage is probably confusing to a predator trying to single one out, and the chance of any one animal being taken per attack is less if more potential victims are available. Although these anti-predator benefits may affect both blue monkeys and redtails, the effect should be larger for redtails because their groups are smaller in Kakamega [Cords, 1987]. The asymmetry in male alarm calling further biases the benefits toward redtails.

These hypotheses are plausible, but they do not constitute evidence for anti-predator advantages of mixed-species association. Of 21 observed attacks, none was successful. This in itself suggested that the monkeys were pursuing an effective anti-predator strategy, but a difference in the eagle's success rate on prey in single- or mixed-species groups could not be demonstrated [Cords, 1987]. Such a difference may be indicated, however, for guenons in a west African forest, where three of four successful attacks were made on single-species groups [Gautier-Hion et al., 1983]. In sum, the predation data are insufficient to reject or support the idea that mixed-species grouping reduces the chance of being preyed upon, but the idea remains very plausible. The fact that redtails spend more time in more open parts of the forest when with blue monkeys than they do when alone [Cords, 1987] is also consistent with the idea that redtails benefit in terms of avoiding predation.

Mixed-species grouping may allow anti-predator benefits other than reduction of risk. The burden of maintaining a certain level of vigilance can be shared among more animals, so that each can devote more time to feeding, without increasing the risk of being surprised by an eagle. In this case, one might not even expect a difference in predator success rates on single and mixed-species groups. When vigilance levels of feeding monkeys in single- and mixed-species groups were compared, it was found that both blue monkeys and redtails looked up significantly more often per minute when alone than they did when together with the other guenon species (50% increase for blues, 30% for redtails, Cords, 1990).

The anti-predator advantages discussed above may explain a general attraction of heterospecific groups; however, temporal variation in the occurrence of mixed-species groups is not related to the likelihood of an eagle attack, but instead to diet and ranging. Cords [1987] has argued that redtails use blue monkeys as guides to ripe fruit sources not recently fed upon. The benefit here is again asymmetrical in favor of the redtails, because redtails live in smaller groups and occupy larger home ranges than blue monkeys. Thus when a group of redtails comes into an area, there is a good chance that parts of that area were recently used by the "local" group of blue monkeys, which uses the area more intensively than the redtails do (there being more blues on less ground). Blue monkeys usually avoid using parts of their home ranges more than once a day. By teaming up with the "local" group of blues, redtails can ensure that they won't be using a feeding area recently picked over by blues. The degree to which such a benefit is realized depends on exactly what both species are eating. Redtails were especially likely to join blue monkeys in months when the redtails ate rare but preferred plant foods (five species of fruit), all of which were shared with blue monkeys. When preference and diet were considered from the perspective of blue monkeys, however, there was no correlation with the occurrence of mixed-species groups [Cords, 1987].

Again, the redtails seem to be the major organizers of when mixed-species groups occur.

Costs of Association

There are costs as well as benefits to associating in mixed-species groups in Kakamega, and these costs are not the same for the two species. Redtails are at a competitive disadvantage in fruiting trees, from which they are aggressively displaced by blue monkeys. Interspecific dominance is apparently directly related to body size (redtails are about 35% lighter than blue monkeys). Most interspecific social interactions were agonistic, and at least half occurred in feeding trees; the loser usually left the tree, at least temporarily. One way that the redtails lessened this cost was by arriving at fruiting trees slightly ahead of the blues; then they had some uninterrupted feeding time before most of the blues caught up to them.

Blue monkeys in mixed-species groups may have to pay additional travel costs: they move about 16% faster when with redtails than when they are alone [Cords, 1987]. However, one cannot rule out the possibility that redtails join blues only when the latter are moving relatively quickly [Cords, 1987]. The redtails, in any case, do not change their tempo when in mixed-species groups.

MIXED-SPECIES ASSOCIATION IN THE KIBALE FOREST

Although the Kibale Forest is only about 500 km west of Kakamega, it supports a rather different primate community. There are four species of diurnal primates in addition to those found in Kakamega: the grey-cheeked mangabey *(Cercocebus albigena)*, red colobus *(Colobus badius)*, l'hoesti's monkey *(Cercopithecus l'hoesti)*, and chimpanzee *(Pan troglodytes)*. The presence of these species reflects Kibale's greater proximity to the eastern part of Zaire, which was the presumed refugium for East African forest animals during Pleistocene dry periods [Hamilton, 1974, 1988; Livingstone, 1975]. Biotic diversity decreases from west to east across Uganda to western Kenya (Kakamega), and this geographical pattern is believed to correspond to a migration route out of the Zairean refuge at 12,500–12,000 BP, when glaciers receded and forest expanded [Hamilton, 1988].

In the Kanyawara study area of the Kibale Forest (n.b. this discussion will be limited to data from Kanyawara), blue monkeys and redtails are reported to spend 13%–28% of their time together [Rudran, 1978; Struhsaker, 1981]. Operational definitions of mixed-species grouping were similar to those used in Kakamega. Both guenons also spend considerable time with other sympatric primates. Of these, red colobus and mangabeys are more than occasional partners for the guenons in mixed-species groups (Fig. 1). In fact, redtails in Kibale spend somewhat more time with red colobus than they do with blue monkeys. Blue monkeys, on the other hand, spend more time with redtails than with any other species.

Null Hypotheses

Most of these associations can be explained as chance phenomena [Waser, 1986]. In fact, only blue and redtail monkeys may be spending more time together than expected if their movement were independent of one another. Table II shows that Kibale redtails encounter blue monkeys 1.8–3 times more often than predicted, and associations endure almost twice as long as predicted. According to Waser [1984], observed values of duration that exceed predictions by a factor of two have less than a 5% probability of being observed by chance. A statistical evaluation of encounter rates has not yet been developed. The results for blue monkeys are similar: they are together with redtails 1.2–2.2 times more often than predicted.

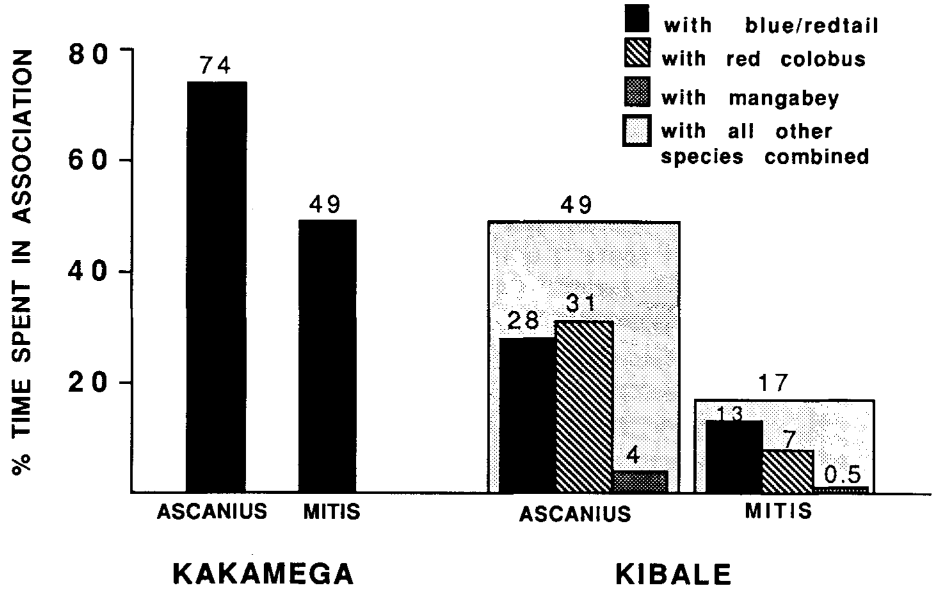

Fig. 1. Percentage of time guenons spend associated with other species in Kakamega and Kibale. Data come from longitudinal study of focal groups by Rudran [1978], Struhsaker [1981] (and unpublished), and Cords [1987]. Except for the Kibale *ascanius*, data represent mean monthly measures (N = 11 months for Kakamega monkeys, N = 13 months for Kibale *mitis*), and associations with *Colobus guereza* are excluded. For Kibale redtails, associations with *C. guereza* are included but account for only 2.6% of observation time [Struhsaker, 1981]; half of this time was spent with *C. guereza* only (Struhsaker, unpublished). Thus exclusion of guerezas would reduce the time spent by Kibale redtails with any partners by about 1.3%.

In evaluating the biological significance of associations between the two guenon species, Struhsaker [1981] proposed two hypotheses. The first is that the two species are converging on common food sources. In Kibale, monthly overlap in the plant diet of blue and redtail monkeys varies from 27 to 55% [Struhsaker, 1981, using 5 months of data referred to in Table IV; overlap measured as in Kakamega]. Dietary overlap is correlated from month to month with the amount of time redtails spend with blue monkeys [Struhsaker, 1981], but not with the amount of time blue monkeys spend with redtails [Rudran, 1978]. Struhsaker noted a close correspondence between the availability of two low-density but popular food sources and associations of redtails with blue monkeys.

Benefits of Association

The latter observation is also consistent with Struhsaker's second hypothesis, namely that blue monkeys use redtails as guides to food sources [see also Rudran, 1978]. The idea is generally similar to that discussed earlier in the context of the Kakamega guenons, except that the roles of the two species are reversed. The reversal reflects a difference in relative group size and home range size between the two study communities. In Kibale, redtails live in larger groups and smaller home ranges than blue monkeys, while in Kakamega the opposite is true (Table III). This means that Kibale redtails use their ranges more intensively than sympatric blue monkeys (Table III), and thus would make the better guides to profitable food sources. In support of this hypothesis, Struhsaker [1981] notes that blue monkeys joined redtails in eight of 13 cases in which it was possible to determine who joined whom, but this is not a statistically significant majority. There are only

TABLE II. A Comparison of Interspecific Encounter Rates, Encounter Durations, and Time Spent Associating in Mixed Groups of Kibale Guenons: Observations Vs. Predictions Under the Null Hypothesis of Independent Movement

		Expected[a]	Observed[b,c]	Sample
Redtails with blue monkeys	Encounter rate (encounters/day)	0.45–0.80	1.41	34 days
	Encounter duration (in hr)	1.07	2.05	54 associations
Redtails with red colobus	Encounter rate	1.71–1.81	1.59	34 days
	Encounter duration	1.77	2.18	59 associations
Blue monkeys with redtails	Encounter rate × duration/12 hr (= % of day mixed with redtails)	6.0–10.9	13.0	13 mo, 1051 hr
Blue monkeys with red colobus	Encounter rate × duration/12 hr (= % of day mixed with red colobus)	18.9–26.7	7.5	13 mo, 1051 hr

[a] Expected encounter rate is given by equation (3) in Waser [1982] expected encounter duration is given by equation (5) in Waser [1984]. Values used in the calculations come from Butynski (in press), Rudran [1978], and Struhsaker [1978, 1981]. For redtails, the range of predicted values reflects variation in group density estimates made by Butynski and Struhsaker. Butynski's estimates, which are based on a longer study period, lead to the higher predicted values. Criterion distance d is 20 m. For blue monkeys, rate and duration measures are multiplied to give an expected percentage of the day in which association occurs, since observed values are not available for rate and duration separately. The range of predicted values reflects variation in group density estimates, and in the criterion distance used by Rudran to define association (5–20 m).

[b] Observed values for redtails come from unpublished records of associations by the TTK group of redtails made by T. Struhsaker on 34 days between March 1973 and June 1974. Mean values are reported. For blue monkeys, observed values come from Rudran [1978], and each value is the mean of 13 monthly scores for Group I.

[c] See text for comments on the statistical comparison of observed and expected values.

TABLE III. Population Structure and Home Range Use by Guenons in the Kakamega and Kibale Forests*

	Kakamega		Kibale	
	C. ascanius	*C. mitis*	*C. ascanius*	*C. mitis*
Population density (ind/km^2)	72	169	140	42
Group density[a] (gps/km^2)	5.17	2.75	4–4.5	1.67–2.94
Group size[b]	22.8 ± 9.0	32.6 ± 8.9	30–35	18.7 ± 8.5
(n groups)	(4)	(5)	(1)	(4)
Annual home range (ha)	36.3 ± 12.7[c]	23 ± 9	24	50.6 ± 14.8
(n ranges)	(4)	(5)	(1)	(4)
Mean % of annual range used in one day[d]	24	34	28	15
Mean % of annual range used in 5 consecutive days[d]	62	70	68	35

*Adapted in part from Table 23 in Cords [1987].

[a] The range of values reflects differences in estimates made by Struhsaker [1978, lower values] and Butynski (in press, higher values).

[b] Means and standard deviations are given except where $n < 4$.

[c] Three measurements come from groups followed less systematically than the focal group, and are probably underestimates; the focal group had a home range of 55 ha.

[d] Calculations based on ranging records for focal groups only.

four cases in which it could be determined who left whom when mixed-species groups disbanded: in three of them, redtails left blue monkeys (Struhsaker, unpublished data). Although the sample sizes are very small, these results suggest that blue monkeys are responsible for the forming and maintaining mixed-species groups in Kibale, and this finding is consistent with the idea that blues use redtails

TABLE IV. Dietary Breadth, Dietary Overlap, and Time Spent in Mixed-species Associations by Guenons in the Kakamega and Kibale Forests*

	Kakamega		Kibale	
	C. ascanius	*C. mitis*	*C. ascanius*	*C. mitis*
Mean % time associated with *Cercopithecus* per month (range)	74 (62–88)	49 (8–72)	18 (0–54)	11 (0–23)
Mean percentage of feeding scores in the top 5 foods per month (range)	56 (45–72)	57 (44–69)	76 (56–100)	76 (44–94)
Mean monthly overlap of plant diets (range)	62% (53–74)		41% (27–55)	
Diet composition (top 4 items)				
% fruits	61.2	54.6	43.7	42.7
% leaves (excluding buds)	6.7	17.1	10.1	16.3
% blossoms and nectar	2.0	3.7	15.3	12.5
% invertebrates	25.1	16.8	21.8	19.8

*Data from Rudran [1978], Struhsaker [1981] (and unpublished), and Cords [1987]. Data for each species at each site come from one focal group. Kakamega data encompass 11 months for each species and all measures. There were 533–1124 feeding scores per month. Kibale *ascanius* data include 10 months of association records, and 7 months of diet records, in which there were 79–187 feeding scores per month. Kibale *mitis* data include 13 months of association records, and 7 months of diet records in which there were 124–254 scores per month. Overlap measures for Kibale are taken from 5 months (Nov. 73–May 74) in which the minimum number of feeding scores per species was 79, and thus do not include all the data given by Struhsaker [1981], Table 8.

as guides. More direct testing of this hypothesis, or predictions derived from it, has not been undertaken.

Anti-predator benefits of mixed-species association are also plausible for the Kibale monkeys [Struhsaker, 1981]. As in Kakamega, the most common predator is the crowned hawk eagle, and early detection, confusion of its attack, and dilution of its effect are all potential benefits of having more animals present. Because blue monkeys live in smaller groups than redtails in Kibale, they should be the greater beneficiaries in this forest. As in Kakamega, however, there are no data on the eagle's successful capture rates on single- vs. mixed-species groups.

Costs

Redtails in Kibale, like those in Kakamega, are recipients of aggression from blue monkeys [Struhsaker, 1981]. Most contests occur in a feeding context, and redtails are usually the losers. Data on travel rates as a function of association are not available for the Kibale monkeys, so this cost cannot be evaluated.

DIFFERENCES BETWEEN THE TWO SITES

Two major differences exist in mixed-species associations of blue and redtail monkeys in Kakamega and Kibale. First, the reasons why each species associates are different in the two communities. In Kakamega, redtails seem to be attracted to blue monkeys per se: both species gain anti-predator benefits, though perhaps the redtails gain more, and redtails use blues as guides to rare but popular food sources. In Kibale, we cannot reject the idea that the monkeys are attracted to common resources, rather than to one another per se. If they are attracted to each other, however, then the benefits to each species are oppositely distributed relative to Kakamega.

The second major difference between the two communities is that the amount of time spent in mixed-species groups is smaller in Kibale than in Kakamega (Fig. 1). Blues in Kibale spend about a fourth as much time with redtails as they do in

Kakamega. Kibale redtails spend about a third as much time with blues as they do in Kakamega. Even when all partners are considered, Kibale blue monkeys spend less than half as much time in mixed-species groups as Kakamega blue monkeys do, while Kibale redtails spend about two-thirds the time in mixed-species groups that Kakamega redtails do. (Note that figures for Kibale blue monkeys may be especially low because of the criteria Rudran [1978] used to recognize mixed-species association: the distance separating members of different species varied from 5 to 20 m, depending on the number of individuals present. Struhsaker [1981] and Cords [1987] used a criterion distance of 20 m regardless of the number of individuals. Rudran's more strigent definition may explain why redtails at Kibale are recorded as spending more time with blue monkeys than blue monkeys spend with redtails: based on relative group densities, one would expect the opposite.)

How can we explain these differences between the two sites? The analyses of mixed-species groups in each site suggest ecological factors are responsible for these differences. Because the ecology of blue and redtail monkeys in the two sites differs in many ways, however, the interpretations presented here are only a subset of those possible. They are offered as hypotheses, rather than as definitive answers. Indeed, since these interpretations have been derived from the Kakamega and Kibale data, these data cannot be used as a test case.

Population Structure and Relative Benefits

Differences in the functional reasons for mixed-species association seem to reflect differences in population structure. Blue monkeys live in larger groups and smaller home ranges than redtails in Kakamega, but the opposite is true in Kibale (Table III). Relative group and home-range sizes have important consequences for mixed-species grouping of the two guenons, because they determine which species gains more pairs of eyes in mixed groups, and which should make the better guide to food sources.

What factors are responsible for the differences in population structure? These differences are related to differences in population density (Table III): blue monkeys are four times more dense and redtails half as dense in Kakamega relative to Kibale. The low blue monkey density in Kibale may reflect the presence of red colobus and mangabeys, and hence may result from post-Pleistocene history [Struhsaker, 1978]. Red colobus and mangabeys are larger than and competitively dominant to blue monkeys, with whom they share many foods [Struhsaker, 1978, 1981]. In a survey of six East African forests, Struhsaker [1978] reports that blue monkeys are less common where these two other species occur, and more common where they are absent.

The lower redtail density in Kakamega may result from the higher density of blues there; as previously discussed, blue monkeys are larger and competitively dominant to redtails, with whom they share many foods. Comparative data from forests other than Kibale are lacking. Alternatively, redtail density may be limited by climate: Kakamega is slightly higher than Kibale, but receives about 65 cm more rain per year (Table I). In general, redtails are limited to lower altitudes than blue monkeys [Wolfheim, 1983], and Kakamega may be very near the upper altitudinal limit.

Differences in population densities are necessary but not sufficient precursors to different group and range sizes. It remains to be explained why the two species show both an increase in group size and a decrease in range size in high-density populations. The determinants of group size in both species are poorly understood. They probably include such factors as the distribution of required resources, the energetics of territorial defense, and within-group competition [Dunbar, 1988].

Group sizes vary by a factor of about 1.5 within populations [Cords, 1986[a]], and group fission in both species has been reported for groups that grew very large [Cords and Rowell, 1986; Struhsaker and Leland, 1988]. Within limits, then, group size may be a somewhat flexible characteristic of the species that can increase with density.

That larger groups occupy smaller home ranges seems to contradict a pattern established for primates as a whole which relates group size (or biomass or metabolic weight) directly to range size [Milton and May, 1976; Clutton-Brock and Harvey, 1977; Harvey and Clutton-Brock, 1981]. This discrepancy may reflect the fact that we are comparing groups from different sites, without correcting for concomitant differences in the distribution of resources. It seems unlikely, however, that this is the entire explanation, since it is a different species in each of the forests that lives in larger groups and smaller ranges; that is, it is not simply that resources, which are similar for both species, are more densely distributed at one of the sites. A more likely explanation for the smaller ranges in higher-density populations is that the habitat is saturated with groups, so that expansion of ranges is impossible [Dunbar, 1988]. After a troop fission among Kakamega blue monkeys forced the smaller splinter group into a small home range [Cords and Rowell, 1986], this group migrated across open scrub during periods when fruit was scarce to feed in very exposed low bush where a plantation had been felled 5 years previously: all neighboring forest habitat was occupied by other groups, so that the range could be expanded only into suboptimal habitat [Cords, unpublished].

Dietary Overlap, Food Distribution, Other Partners, and the Amount of Time Spent in Association

While population structure may affect *how* each species benefits from mixed-species association, other factors can influence the *magnitude* of benefits, and hence how much time is spent in association. Why does association occur less frequently in Kibale than in Kakamega? One critical parameter may be dietary overlap: average monthly dietary overlap between blues and redtails is 1.5 times greater in Kakamega than in Kibale (Table IV). The reason for this is not certain [Cords, 1986[b]], but it may reflect the fact that neither redtails nor blue monkeys in Kakamega concentrate on a few foods as much as they do in Kibale (Table IV). The narrower dietary niches in Kibale may in turn reflect the presence of other species, especially the competitively dominant red colobus and mangabey. The consequence of a lower dietary overlap is clear, however: the fewer foods they share, the less two species will converge on common food sources. Alternatively, if one species acts as a guide, then its usefulness in indicating common food sources will be less the fewer such sources exist. In these ways, the lower dietary similarity between blue monkeys and redtails in Kibale may explain the reduced tendency to associate with one another.

Another potentially important factor in determining how much time is spent in association is the distribution of foods in space and time. Animals that eat rare and patchily distributed foods (such as ripe fruits and flowers) should benefit more than those eating widespread and dispersed foods (such as leaves) in terms of using other species as guides to food sources. Also, the chance of meeting at food sources to which heterospecific groups are independently attracted should be higher when these sources are rare and concentrated. Based on these considerations, one might expect the Kakamega monkeys, who associate more often, to be less folivorous than the Kibale monkeys, but differences are minimal (Table IV).

A more detailed comparison based on the distributions of specific food trees is difficult because of differences in vegetation census methods (see Table I). There is some indication, however, that the species with the larger home ranges in each forest may be harvesting food which is not equally easy to find. Kibale blue monkeys harvest their ten top foods (55% of feeding records) from tree species which comprise 49% of all trees sampled in a vegetation census [Rudran, 1978; Butynski, in press]. Kakamega redtails harvest their top ten foods (50% of feeding records) from trees which comprise only 27% of those samples [Cords, 1987]. In other words, the Kakamega redtails are using relatively rarer trees than the Kibale blue monkeys. For this reason, guides should be more useful in Kakamega than in Kibale.

The presence of other potential partners may also influence the amount of time blues and redtails spend together if these other species can perform equivalent functions. For example, redtails in Kibale spend a considerable amount of time with red colobus, whose diet overlaps little with their own. Red colobus groups are large, however, and contain many alert adult males which may act as effective guards against predation [Struhsaker, 1981]. Redtails have been shown to decrease their scanning rate when red colobus calls are played back to them [Hauser and Wrangham, 1988]. Even if red colobus are only encountered randomly, they may nevertheless lessen the need for redtails to find another group of *guenons.*

SOME GENERAL COMMENTS

In discussing inter-forest differences in mixed-species grouping, I have emphasized foraging benefits of association. This is partly because feeding behavior was important in understanding the temporal patterning of association in both study areas, and partly because comparable data are available. It is also possible, however, that predation pressure differs in the two forests: we simply have no information.

In spite of its preliminary nature, this comparison of *Cercopithecus* association in two forests suggests that the ecological context can have profound effects on mixed-species grouping. Figure 2 summarizes the interrelationships of factors that appear to be relevant to blue and redtail monkeys in East African forests. Its validity must be tested with data from other populations. Regardless of the specific network of factors involved, however, the general point is that the particular nature of the ecological relationship between species is critical. The reason(s) why two species associate in a given community is less directly a product of their identity than of their ecological relation to one another and to other members of their community. For example, Cords [1987] has noted the similarity in explanations for mixed-species association of blue and redtail monkeys in Kakamega, on the one hand, and *Cebus* and *Saimiri* in Manu Park, Peru [Terborgh, 1983], on the other. In both cases, association is frequent and heterospecific groups are attracted to one another. *Cebus* monkeys play a role in their associations with *Saimiri* similar to that played by Kakamega blue monkeys in their association with redtails. *Saimiri* and redtails similarly resemble one another. Overall, the nature of associations, and the roles played by participating species, are equally or more strikingly similar when one compares Kakamega blues and redtails to Peruvian *Cebus* and *Saimiri,* rather than to conspecifics living only 500 km away. This is because even within species, mixed-species association may be explained in different ways, depending on the ecological context.

CONCLUSIONS

1. Blue and redtail monkeys associate in mixed-species groups for different reasons and to different degrees in two East African forests. At Kakamega, redtails

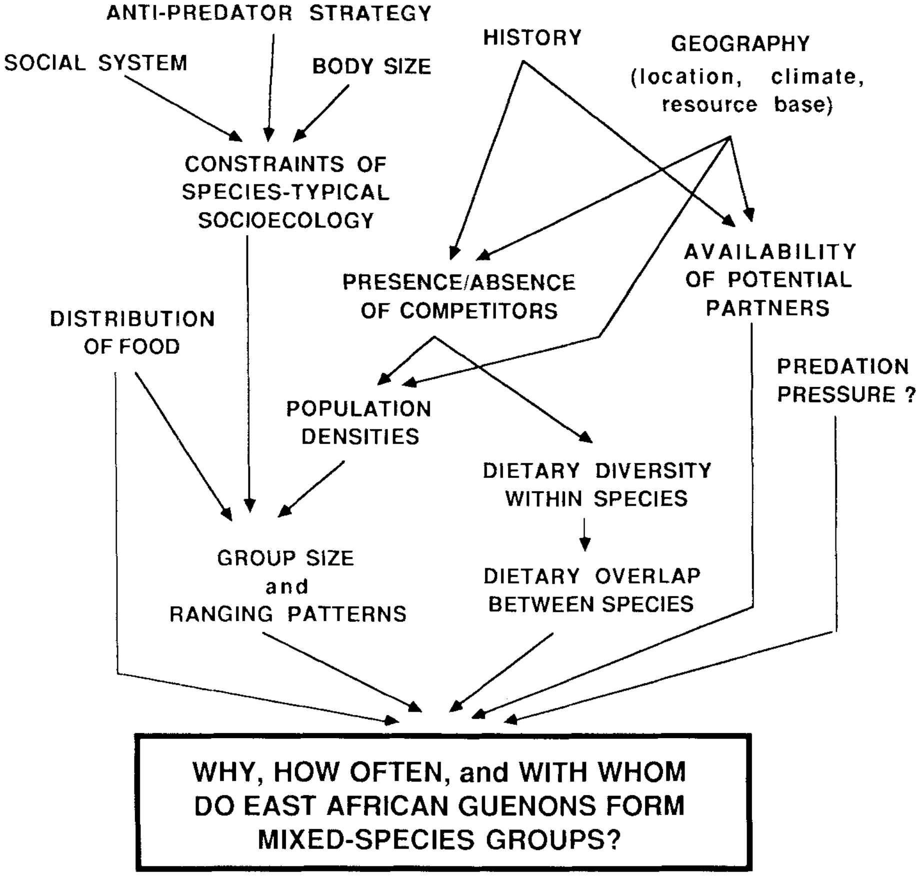

Fig. 2. Summary of factors which influence the mixed-species associations of East African guenons.

are attracted to blue monkeys, and association provides anti-predator and foraging benefits, especially to the redtails. In Kibale, heterospecific groups may simply be meeting at common food sources; alternatively, Kibale blue monkeys may be the primary beneficiaries in terms of finding food or avoiding predation. The two species are together 3–4 times more often in Kakamega than in Kibale.

2. Between-forest differences in the reasons for mixed-species association may reflect differences in population structure (i.e., group size and home-range size). Differences in the amount of time spent associating with other guenons may be related to dietary overlap between species, distribution of resources, and the presence of other primate species.

3. Inter-site differences in population structure, dietary overlap, and community composition can be traced ultimately to historical and geographical differences between the two forests.

4. Within single species, mixed-species association may have different explanations, depending on the ecological context.

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