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The Journal of Animal Ecology, Vol. 55, No. 3 (Oct., 1986), 811-827.

Journal of Animal Ecology (1986), **55**, 811–827

INTERSPECIFIC AND INTRASPECIFIC VARIATION IN DIET OF TWO FOREST GUENONS, *CERCOPITHECUS ASCANIUS* AND *C. MITIS*

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SUMMARY

(1) A log-linear model of variance in the consumption of fruit, leaves, insects and other plant foods by sympatric Kenyan guenons showed that species identity, age–sex class, time of year, and all two-way interactions of these factors were significant sources of dietary variation.

(2) Blue monkeys were more folivorous and less frugivorous and insectivorous than redtails. The two species used different plant species and substrates as sources of insect prey. Redtails used capture methods more appropriate for mobile prey more often than blue monkeys. Both species showed a bimodal annual seasonality in their consumption of fruit, leaves and insects, but differed in how the proportions of these items in the diet inter-relate.

(3) In both species, adult males were highly frugivorous, whereas adult females were more insectivorous and/or folivorous. Juvenile size was directly related to the proportions of leaves and of insects in the diet, but inversely related to the proportion of fruit. The largest juveniles were more folivorous and insectivorous than adults. Some age–sex differences were found in the plant species and substrates used for insect capture, and in capture methods.

(4) The diets of some heterospecific age–sex classes were more similar than those of some conspecific age–sex classes in degree of frugivory and insectivory, and in how the monthly proportions of the three major dietary components covaried. Dietary similarity of conspecifics tended to exceed that of heterospecifics, however, when plant species-specific items and the number of individuals in each species–age–sex class were taken into consideration.

(5) These results and comparisons with other *Cercopithecus* communities suggest that dietary variation between species and between species–age–sex classes is related to body size, the physiological demands of reproduction and growth, social constraints, and competition, especially for fruit.

INTRODUCTION

Theoretical studies of community structure and organization usually take the species, or more precisely the population, as the fundamental ecological unit. From an evolutionary perspective, this view is justified because of the reproductive integrity of individual species. From an ecological perspective, however, such a view may oversimplify relations between individuals comprising the community, since differences *within* a population—the

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'between-' and 'within-phenotype' components of population niche width—are not distinguished (Roughgarden 1974; Fox & Morrow 1981). As Roughgarden points out, one reason for making this distinction is that different selection pressures act on the two components of niche width. If one considers a species' dietary niche axis, for example, variance between phenotypes may depend on environmental productivity and the number of sympatric competing species (Roughgarden 1974), whereas within-phenotypic variance reflects individual foraging strategies which are themselves functions of resource distribution, body size, and physiological and social constraints (e.g. Pyke 1984). Thus, factors influencing a population's ecological relations with other members of its community may act in different ways which are not apparent without considering variation within the population itself.

There have been few ecological studies of interspecific relations among primates, though sympatry is common among primate species. Even where two or more species have been studied in detail at one site (Struhsaker & Oates 1975; Struhsaker 1978, 1980, 1981; Chivers 1980; Gautier-Hion 1980; Terborgh 1983), interspecific comparisons are often problematical because the different species were studied at different times, in different habitat types, or by different investigators using different methods (but see Hladik 1977). Furthermore, interspecific differences are seldom examined along with within-species variation. When such an analysis was made of the dietary niches of sympatric guenons in Gabon, however, it was found that sex differences in the consumption of fruit, leaves and insects within one species could be greater than differences between sex classes of different species, so that mean species-characteristic feeding patterns were of limited use in understanding the ecological relationships among the three species studied (Gautier-Hion 1980).

In this paper, between- and within-species variation in the diets of two guenons, *C. ascanius schmidti* (Matschie) and *C. mitis stuhlmanni* (Matschie), living sympatrically in a Kenyan forest are examined in order to evaluate the roles of such factors as competition, body size, and physiological and social constraints in determining the ecological relations between these two species in this study area. Comparisons with two other studies of the same or closely related species (Gautier-Hion 1980; Rudran 1978; Struhsaker 1978, 1981) allow one to consider the generality of these conclusions.

METHODS

Study area and animals

Members of the genus *Cercopithecus* are found in most equatorial African forests. Sympatry of two or three species (and as many as five, Gartlan & Struhsaker 1972) is typical. Sympatric guenons frequently form mixed-species groups, in which the activity patterns and forest strata used by different species coincide (Gautier-Hion & Gautier 1974; Struhsaker 1981; Cords 1984b).

My study was conducted in the Kakamega Forest in western Kenya (0° 14′N, 34° 52′ E, 1580 m) for 11 months between March 1980 and February 1981 (July excluded). Kakamega is a moist semi-deciduous forest most similar to the Congo Basin forests farther west (see Cords 1984b for a complete description). There are three species of diurnal monkeys (the two guenons and *Colobus guereza*) permanently resident in the study area of 1·5 km^2. Observations were made on one group of redtails (*C. ascanius*, averaging two adult males, nine adult females, one large juvenile, five medium-sized juveniles, and five small juveniles) and one group of blue monkeys (*C. mitis*, averaging one adult male, sixteen adult females, two large juveniles, eleven medium-sized juveniles, and thirteen small juveniles). The defining characteristics of these age–sex classes are detailed in Cords (1984b): 'large juveniles' in this study are 75–100% the size of adult females, but are not fully developed sexually. Adult male redtails are 1·4 and adult male blues 1·7 times heavier than conspecific adult females (A. J. Haddow, unpublished). Redtails of a given age–sex class are smaller than their blue monkey counterparts, and appear to match the next smallest blue monkey class in size (Cords 1984b). Both groups were well habituated from 8 months of prior observation and individuals were recognized from natural markings.

Data collection and analysis

Each month, first the redtail and then the blue monkey group was followed from dawn to dusk for 5–6 days; then another 2–3 days were spent on each group, beginning with the redtails. The home range of the redtails (60 ha) completely circumscribed that of the blue monkeys (38 ha). Therefore, sampling of the two groups coincided closely in time and space, and differences in the foods available to them were minimal.

Feeding was scored using the method of Rudran (1978), which measures the frequency of feeding rather than dietary composition *per se*. A feeding score consists of a particular monkey ingesting a particular item from a particular plant species. For plant foods, a new feeding score was recorded for the same combination of monkey, item and plant only if 30 minutes had elapsed, or if the identity of at least one of the three parameters changed. For insect foods, the substrate from which prey were taken and the method of capture were also considered. (The actual prey ingested was seldom identified.) Suckling by small juveniles was not scored. In the analyses, species differences were evaluated using all records from each species, even where age–sex class could not be identified. In comparisons between age–sex classes, records in which age–sex class was not known were omitted. Observation conditions prevented gathering data on time spent feeding.

The influences of monkey species identity, age–sex class and month on consumption of different items in the diet were analysed using log-linear models with weighted least squares estimation (Feinberg 1977; SAS Institute 1982). Only feeding records in which the actor was identified to age–sex class were included in the models. These analyses are valid only if the sample of feeding observations reflects group membership, so that no individuals are scored disproportionately. The 30-minute rule helps to ensure that one individual is not scored repeatedly. Also, I made a deliberate effort to circulate frequently throughout the group (which was typically spread over 50–100 m), rather than to wait beneath large fruiting trees or in other limited places where visibility was good.

The extent to which observations were representative can be assessed quantitatively by comparing the frequency with which recognized individuals were scored with that expected if all individuals were sampled at an equal rate. Not all monkeys were individually known throughout the study; nor could the specific identity of each individual be ascertained on each feeding record, usually because a face-on view was often required for positive identification. Considering only those scores in which individuals were identified, which are taken to be a random sample of all scores, and correcting for the amount of time particular individuals had not yet been recognized, a comparison of the observed and expected number of scores was made for adult females of both species (there were not enough individually recognized juveniles).

Thirteen of the sixteen adult female blue monkeys and six of ten adult female redtails were scored as frequently as expected (*G* test, 2-tailed $P > 0{\cdot}05$). Of those females who deviated from the number of records expected, two blue monkeys and three redtails had more scores than expected, while one of each species was under-represented. For four of these females, the deviation from expected values can probably be explained by considering the unusual ease or difficulty with which they could be identified: for example, one redtail female had a large lump on her back which made her, unlike other females, recognizeable from the backside. On the other hand, the two under-represented females had to be seen from just the right angle for positive identification. The remaining three females are over-represented for unknown reasons; deviation from the expected number of observations for these females is between 18 and 28%.

Several aspects of the plant diet are considered. Dietary overlap is measured using the index of Holmes & Pitelka (1968), in which shared percentages of dietary components are summed. Dietary diversity is calculated using the Shannon–Wiener equation for entropy, $H = -\sum p_i \ln p_i$, where p_i is the proportion of the ith plant species, or species-specific item in the diet (Pielou 1966). Diversity is affected both by the number of categories in the diet, and the evenness with which feeding records are cast into those categories. Evenness in use of dietary components, calculated as $J = H/H_{max} = H/\ln N$ (where N is the number of categories used), reflects only the degree to which records are evenly divided among the categories. Diversity and evenness are calculated on the basis of consumption of plant species and species-specific item omitting records in which plant species was unidentified, and for species-specific items, omitting records when the item was unidentified.

All statistical tests are two-tailed unless otherwise noted. G test statistics are adjusted with Williams' correction (Sokal & Rohlf 1981).

RESULTS

The log-linear model

The log-linear model incorporated species identity, age–sex class and month in explaining variation in the consumption of four classes of food: fruit, leaves (including leaf buds and petioles), insect prey and other (e.g. seeds, blossoms, gum). All three variables and all possible two-way interactions had a significant influence on the consumption of these items (Table 1). To check for systematic variation not explained by the model, the residuals were plotted against month, but there were no patterns.

A final check on the validity of log-linear modelling of these data involved applying the same techniques to a subset of data, in which each feeding record was identified to individual monkey, and using only those individuals who were recognized for most of the 11-month period (to avoid empty cells). The objective was to see whether the influence of individual identity would change the significance of any of the main or interaction effects given in Table 1. All effects remained significant, except for age–sex class and the

TABLE 1. Log-linear model of the consumption of major food items (fruit, leaves, insects, and other) by blue and redtail monkeys

Source	d.f.	Chi-square	Probability
Intercept	3	3444·89	0·0001
Species	3	323·45	0·0001
Age–sex class	12	173·88	0·0001
Month	30	382·93	0·0001
Species * Age–sex class	12	57·43	0·0001
Species * Month	30	203·10	0·0001
Age–sex class * Month	120	149·34	0·0359
Residual	120	130·36	0·2441

interaction of age–sex class with species; this result was not unexpected, since most of the individuals in the sample were adult females, and other age–sex classes were represented by only 1–2 individuals per species (and there were no small or medium juveniles). Individual identity also significantly influenced diet composition ($P = 0{\cdot}0001$), but will not be discussed further in this paper.

Differences between species

Annual patterns

In the eleven observation months combined, redtails ate more fruit, more insects and more gum than blue monkeys; blue monkeys ate more leaves, both young and mature, more seeds and more blossoms than redtails (Table 2). Overlap of the plant diet was 77·0% for plant species (seventy-five were eaten by both monkeys), but less (70·4%) for species-specific items, since the monkeys may eat different items from the same plant. Over the year, blue monkeys appear to have used slightly more ($n = 104$ identified) plant species for plant food than redtails ($n = 98$ identified), but this difference may be due to the greater number of feeding records for the blues. Evenness of use of plant species and species-specific items was very similar for the two species [plant species, $J = 0{\cdot}758$ (blues), $J = 0{\cdot}759$ (redtails); species-specific items, $J = 0{\cdot}716$ (blues), $J = 0{\cdot}707$ (redtails)].

There were minor differences between blues and redtails in the plant species used as sources of insect prey (Cords 1984b). Both species captured about 35% of their prey from about 6% of the plant species used for prey capture. While the degree of specialization on source species is not different, only three plant species were in the top five source species of both blues and redtails (Cords 1984b).

Both species capture most of their insect prey from the surfaces of mature leaves, which are used frequently in all months (Table 3). However, blues caught prey from moss- and epiphyte-covered surfaces and from dead wood more often than redtails, while the latter used lichen-covered and bare surfaces and stems, twigs, and leaf axils more often than blues. Differences between the species were not large, but the overall substrate profiles differed significantly.

The two species also differed in the motor patterns used for prey capture (Table 4), although all patterns were used by both. Blues ingested more prey directly from the

TABLE 2. Annual diets of blue and redtail monkeys expressed as percentages of total feeding observations

Item	Blue ($n = 10167$)	Redtail ($n = 9009$)
Fruit	54·6	61·3
Insects	16·8	25·1
Leaves: young*	16·6	6·8
mature	2·3	0·4
Blossoms, nectar*	3·7	2·0
Seeds	2·5	0·4
Gum	1·9	2·8
Stems and shoots	1·1	0·7
Other, unidentified	0·5	0·5

$G_{\text{adj}} = 967{\cdot}46$, 8 d.f., $P < 0{\cdot}001$

* Includes buds.

TABLE 3. Substrates from which insect prey are taken

	Blues		Redtails	
Substrate	% use over 11 months	C.V. of monthly % use	% use over 11 months	C.V. of monthly % use
Mature leaf	61·9	11·9	60·1	14·1
Young leaf	2·2	85·5	2·5	71·5
Dead leaf	6·7	36·7	5·2	46·9
Trunk or branch with moss and/or epiphytes	9·1	69·4	6·8	76·1
Trunk or branch with lichen or bare	10·1	38·5	13·2	43·9
Spider web	1·8	32·8	2·6	115·3
Stem, twig, axil	5·5	27·3	8·6	42·6
Dead wood*	2·5	53·4	0·5	119·7
Other	0·4	—	0·4	—
n	1502		1836	

$G_{adj} = 55{\cdot}2$, 8 d.f., $P < 0{\cdot}001$

* Dead wood includes under bark, barkless branches, and soft rotton wood.

TABLE 4. Methods of insect prey capture, 11 months combined

Capture method*	Blue % of captures ($n = 1254$)	Redtail % of captures ($n = 1378$)
Slow hold direct	9·7	7·5
Slow no hold direct	4·4	6·0
Slow pick	5·7	7·0
Medium uncurl leaves	4·0	2·0
Medium hold direct	42·4	29·1
Medium no hold direct	4·0	6·5
Medium pick	21·1	28·1
Medium pounce, swipe	1·4	2·8
Fast direct	1·0	0·9
Fast pick, swipe	3·6	6·2
Fast pounce	2·7	3·9

$G_{adj} = 89{\cdot}3$, 10 d.f., $P < 0{\cdot}001$

* Slow, medium, fast: speed of motor pattern.
Direct: ingested from substrate without handling.
Hold: substrate held or braced with 1 or 2 hands.
No hold: substrate not held or braced.
Pick: taken from substrate to mouth with 1 or 2 hands.

substrate (i.e. without manipulation) than redtails. Redtails used more fast action patterns including picks, swipes and pounces. These patterns suggest differences (particularly in mobility) in the kinds of prey captured. The preponderance of immobile cocoons and sapsuckers in the identified prey of blue monkeys (29/41), and its relative absence for redtails (9/27), provides preliminary direct evidence corroborating this conclusion.

Seasonal changes

Figure 1 indicates an annual bimodal seasonality in the consumption of major food items by both species, with fruit intake highest in the middle of the rainy and dry seasons. The proportions of insects in the total diets of the two species were positively correlated ($r_s = 0{\cdot}739$, $P = 0{\cdot}010$, $n = 11$ months), but the proportions of leaves (young, mature and

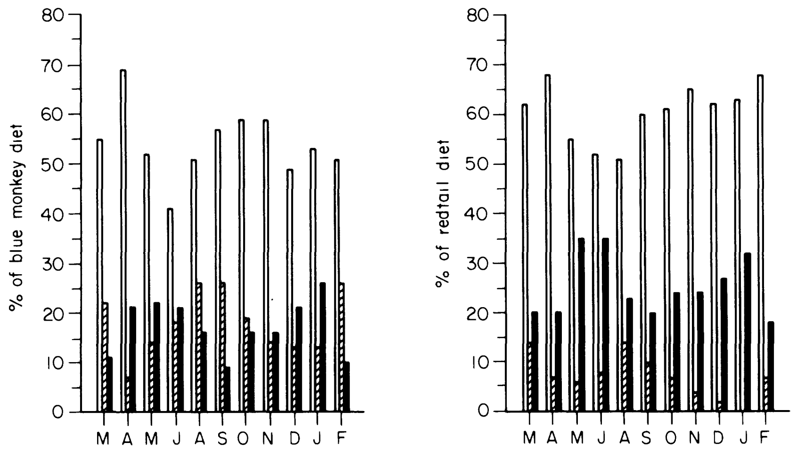

FIG. 1. Seasonal variation in the consumption (% feeding scores) of three major dietary constituents by blue monkeys and redtails: fruit (□) leaves (▨); insects (■).

total) and fruit were not. If only the plant diet is considered, however, the fraction of fruits ($r_s = 0\cdot628$, $P = 0\cdot038$) and of total leaves ($r_s = 0\cdot724$, $P = 0\cdot010$) in the diets of the two species were positively correlated.

Blues and redtails differed in the way their diets changed in months when fruit intake is low. Blue monkeys increased their intake of leaves ($r_s = -0\cdot773$, $P = 0\cdot005$), particularly mature leaves ($r_s = -0\cdot797$, $P = 0\cdot003$); fruit consumption was not correlated with the proportion of young leaves. The fraction of insects was uncorrelated with either fruit or total leaf consumption, but instead correlated negatively with other protein sources such as seeds ($r_s = -0\cdot663$, $P = 0\cdot037$) and young leaves and buds ($r_s = -0\cdot948$, $P < 0\cdot001$). For redtails, an increase in insect and leaf intake combined accompanied lower fruit consumption (not surprising since these three items comprised most of the diet). The proportion of insects was not related to the amount of other protein-rich items in the redtail diet.

Both blues and redtails concentrate on a few species and species-specific items each month for plant food (Cords 1984b). The two species did not differ in monthly measures of diversity or evenness of use of plant species or species-specific items (Wilcoxon Matched Pairs Signed Ranks Test, $P > 0\cdot05$). For both species, about 57% of plant feeding observations were accounted for by the five most frequently used species-specific items each month. Monthly overlap in use of species-specific items ranged from 53·1 to 73·8% (median = 59·6%). This overlap was positively related to the monthly proportion of fruit in the plant diet of both blues ($r_s = 0\cdot727$, $P = 0\cdot011$) and redtails ($r_s = 0\cdot747$, $P = 0\cdot008$) and was negatively related to the proportions of leaves ($r_s = -0\cdot700$, $P = 0\cdot016$ for redtails; $r_s = -0\cdot579$, $P = 0\cdot062$ for blues).

Differences between age–sex classes

Annual patterns

Figure 2 shows differences between age–sex classes in the proportions of major components of the diet over the 11 sample months combined. Among the blues, the adult male stands out because of his relatively high consumption of fruit and low consumption of

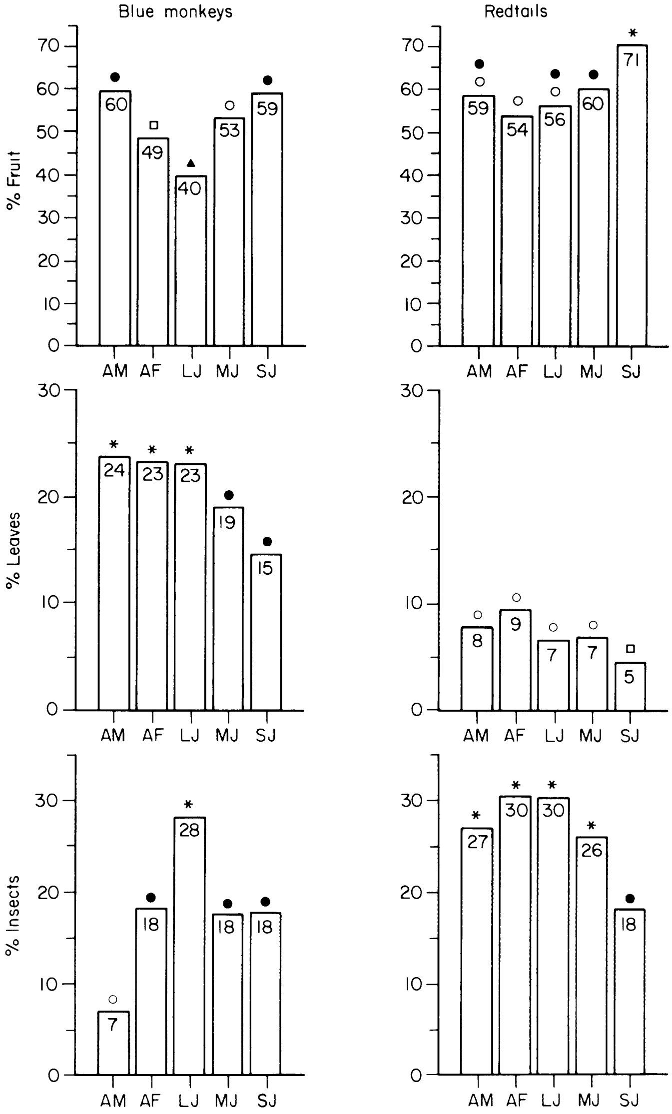

FIG. 2. Age–sex variation in consumption (% feeding scores) of three major food items for the 11 months combined. Unplanned tests for the homogeneity of replicates tested for goodness-of-fit (Sokal & Rohlf 1981) were used to test for differences between all possible sets of age–sex classes of both species in each dietary category. The experimental error rate alpha = 0·05 (i.e. for each type). Symbols are used to group statistically indistinguishable species–age–sex classes for each food type. Sample sizes are: for blues, AM (adult male) 334, AF (adult female) 3092, LJ (large juvenile) 665, MJ (medium juvenile 3102, SJ (small juvenile) 2041; for redtails, AM 661, AF 3196, LJ 411, MJ 2427, SJ 1588.

insects; leaf intake was similar to that of other large monkeys, namely adult females and large juveniles. Adult females were intermediate in their intake of fruit and insects, relative to adult males and large juveniles. Among the juveniles, body size was negatively related to fruit intake, and positively related to the proportions of leaves and insects.

Among the redtails, adult females stand out because of their lower fruit and higher leaf consumption relative to all other age–sex classes. Like blue monkey males, redtail males were among the most frugivorous age–sex classes, but unlike his blue monkey counterpart, the redtail male was also among the most insectivorous. Body size among the juveniles was negatively related to the proportion of fruit, but positively related to the proportion of insects. Small juveniles were the least folivorous redtails.

The effect of pregnancy and lactation on the diets of adult females could not be fairly evaluated using data pooled from the entire year: since there were more pregnant and lactating females at certain times of year (especially November–July), the effect of seasonal changes would confound comparisons between females who were and were not pregnant or lactating. Therefore, comparisons were made for each month separately between females known to be pregnant (<5 months before birth, Rowell 1970) or lactating (<5 months after birth, when infants begin to eat solid food regularly, though they still suckle) and all other adult females. Among blue monkeys, significant differences occurred in only three (November, December, January) of the 11 months. There were no pregnant or lactating redtail females in the first 3 months of the study, but in the remaining 8 months, their diet differed significantly from that of other females in October and December. When significant differences occurred, pregnant and lactating females (of both species) ate relatively less fruit and more insects than other females. The proportion of fruit in the diet of pregnant and lactating females varied from 63% to 83% of that for other females, while the proportion of insects was 1·2–3 times higher. Relative leaf intake for the two groups of females was variable from month to month.

In fruit and insect consumption, differences between age–sex classes of one species sometimes exceeded differences between age–sex classes of the two species. For example, the second most frugivorous set of animals includes both blue ($n = 2$) and redtail ($n = 3$) age–sex classes, and was distinct from one blue and three redtail age–sex classes comprising another *less* frugivorous set of animals. Only the degree of folivory of the different age–sex classes segregated clearly along species lines, with blue monkeys forming the two most folivorous sets, and redtails forming the two least folivorous sets.

In analysing age–sex differences in insect feeding, blue adult males have been excluded since there were too few records with detailed information on substrate and capture method. Most plant species that were sources of insect prey were used by all age–sex classes of each species. There were small differences in the identity of those species used most often: in every pairwise comparison between the four blue age–sex classes, 1–5 of the top 5 species were shared ($\bar{x} = 3{\cdot}5$). In pairwise comparisons of the 5 redtail age–sex classes, 3–4 of the top 5 species were shared ($\bar{x} = 3{\cdot}3$). One species was among the top 5 insect sources for all blue monkey age–sex classes, whereas 3 species were shared in the top 5 sources by all redtail age–sex classes.

In both species there were significant differences between age–sex classes in the profiles of substrates used for catching insects (G tests, $P < 0{\cdot}05$). Juveniles concentrated more on stems, twigs or leaf axils than adults. Among the redtails, the adult males and juveniles used bare or lichen-covered surfaces more and moss- and epiphyte-covered surfaces less than adult females. Among the blues, however, this trend was reversed for adult females and juveniles.

In both species there was also a tendency for the smallest juveniles to use a greater proportion of slow motor patterns in capturing prey, while larger animals relied relatively more on methods of intermediate speed. Juveniles also used slightly more fast picks, swipes and pounces than conspecific adults. Differences in capture speed were significant at the alpha = 0·05 level only among the blue monkey age-sex classes ($G = 14{\cdot}60$, 6 d.f., $P < 0{\cdot}05$ for blues, $G = 15{\cdot}23$, 8 d.f., $P < 0{\cdot}10$ for redtails).

Seasonal changes

Monthly fluctuations in the proportions of fruit, leaves and insects consumed by different age-sex classes are shown in Fig. 3. The bimodal seasonality in consumption of these major dietary constituents for each age–sex class was similar to that seen for each species as a whole, although the exact locations of peaks and valleys for different classes often varied by a month or two. There were no obvious differences in the shapes of the dietary trajectories of each age–sex class which would indicate two or more distinct patterns of variation as reported by Gautier-Hion (1980) for *Cercopithecus* in Gabon. Coefficients of variation for each species–age–sex class of the percentage contribution of the different items to the diet were similar for each category of food with two exceptions. First, for all types of food and for both species, the relative intake by adult males was more variable from month to month than that for other classes. Second, all redtails were more variable in their leaf intake than all blue monkey age–sex classes.

Certain age–sex classes were consistently more frugivorous, insectivorous, or folivorous than others, in spite of fluctuations over time (Fig. 3). Friedman analysis of variance confirmed the pattern of statistically indistinguishable groupings of age–sex classes described above for the year as a whole.

Age–sex classes of both species differed in the way the proportions of the three main dietary components covaried from month to month (Spearman rank correlations, 1-tailed tests, alpha = 0·05). For all blue monkey classes, fruit and insect consumption were uncorrelated, as they were for the species as a whole. Fruit and leaf consumption were uncorrelated for all but the adult male, a pattern that contrasts with that for all age–sex classes combined. Also unanticipated are the negative correlations between leaf and insect consumption for all blues except small juveniles. For redtails, fruit and insect consumption were negatively related for three of the five age–sex classes (adult males, large and medium-sized juveniles) but not for the species as a whole. Fruit intake was negatively correlated with insect or leaf intake only for adult females.

These results indicate four patterns of relationships in the monthly consumption of fruit, insects and leaves by different age–sex classes. For redtail adult males and large and medium juveniles, fruit and insect consumption were inversely correlated over time. For blue adult females and large and medium juveniles, the proportions of insects and leaves were inversely related. For blue adult males and redtail adult females, leaf consumption were inversely related to both fruit and insect consumptions. For small juveniles of both species, there were no correlations between any pair of the three major dietary constituents.

Examination of plant-species-specific items allows a finer discrimination of dietary differences between age–sex classes. Monthly overlap of species-specific items in the plant diet was computed for every paired combination of species–age–sex classes: there were twenty-five pairwise measures between species and ten within each species. The median and range of monthly overlaps for each pair is given in Table 5. Again, similarities between age–sex classes of different species sometimes exceeded similarities between different age–sex classes of conspecifics. Within-species overlaps, however, were larger than between-species overlaps in 7 of the 11 months for blue monkeys (all but March, June, Ocrober and January) and in 9 of 11 months for redtails (all but August and October; Mann–Whitney *U*-tests, $P < 0{\cdot}05$). In all but one of the months when differences are not statistically significant, the tendency for intraspecific overlaps to exceed interspecific overlaps is still apparent.

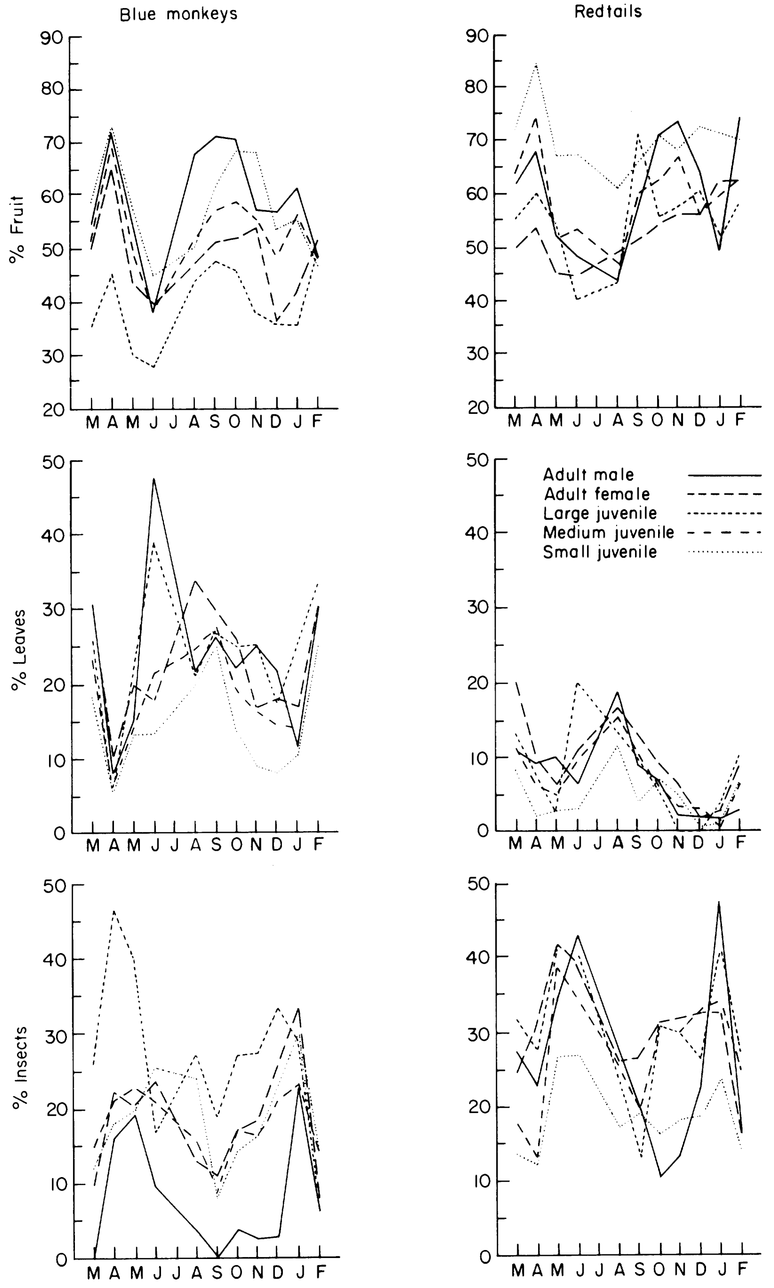

FIG. 3. Seasonal variation in the consumption (% feeding scores) of three major dietary constituents by different species–age–sex classes.

To assess monthly fluctuations in within- and between-species overlaps relative to one another, the median of the ten within-species overlap measures for each species in each month was compared to overall monthly between-species overlap (calculated without regard to age–sex class). For blue monkeys, the median of the within-species overlap was

TABLE 5. Medians and ranges of 11 monthly overlaps of species-specific items in the plant diets of different species–age–sex classes of blue and redtail monkeys. The overlap measure is the sum of the shared percentages of dietary components (see Methods)

(a) Between-species overlaps

Blue Redtail	Adult male	Adult female	Large juvenile	Medium juvenile	Small juvenile
Adult male	46 (28–61)	50 (40–58)	44 (31–66)	49 (37–64)	53 (40–63)
Adult female	49 (28–62)	58 (45–66)	49 (39·60)	59 (47–73)	58 (49–71)
Large juvenile	35 (21–62)	44 (24–62)	38 (11–54)	46 (27–62)	46 (33–60)
Medium juvenile	46 (25–62)	50 (41–60)	44 (35–63)	54 (46–69)	56 (49–76)
Small juvenile	44 (23–61)	47 (40–60)	43 (23–62)	52 (46–68)	57 (31–73)

(b) Overlap within blue monkeys

	Adult female	Large juvenile	Medium juvenile	Small juvenile
Adult male	54 (27–72)	46 (28–60)	58 (35–67)	55 (29–66)
Adult female		61 (22·73)	73 (61–78)	64 (52–73)
Large juvenile			57 (33–77)	56 (32–77)
Medium juvenile				72 (57–80)

(c) Overlap within redtails

	Adult female	Large juvenile	Medium juvenile	Small juvenile
Adult male	62 (58–72)	57 (37–69)	64 (48–75)	61 (47–65)
Adult female		61 (40–72)	74 (68–79)	71 (61–79)
Large juvenile			42 (26–72)	59 (50–70)
Medium juvenile				77 (67–86)

positively correlated with between-species overlap over the 11 months ($r_s = 0{\cdot}72$, $P < 0{\cdot}010$), but for redtails, the correlation was not significant ($r_s = 0{\cdot}38$). The median of within-species overlaps in each species is also correlated with the proportion of fruit in its plant diet (blues, $r_s = 0{\cdot}65$, redtails, $r_s = 0{\cdot}67$, $P < 0{\cdot}040$, $n = 11$ months), as was seen earlier for interspecific overlap.

DISCUSSION

Sympatric guenons in the Kakamega Forest show both inter- and intra-specific differences in the plant species and items eaten, in the substrates and methods used for catching insect prey, and in the patterns of temporal variation in consumption of major dietary components. Theoretical and empirical studies (e.g. Clutton-Brock 1977; Pyke 1984) suggest that the variation observed may be explained by the different requirements of animals of different sizes and with different physiological and social constraints, as well as by the availability of those foods that are required. The role of these factors is considered here in conjunction with a comparison of the Kakamega monkeys with conspecifics or closely related species in two other African forests.

Interspecific differences

Smaller animals are expected to include a smaller fraction of leaves and a bigger fraction of insects in their diet than larger ones; this is because smaller animals require proportionately more energy, because the capacity to process food increases with body size more slowly than energetic requirements do, and because food value is generally inversely related to availability (at least at the gross level of food items; review in Gaulin 1979). In the Kibale Forest, Uganda, as in Kakamega, blue monkeys are more folivorous than the smaller redtails (Struhsaker 1978, 1981). Kakamega blues also eat fewer insects and less fruit than redtails as predicted, but such differences are not significant in Kibale.

Although the kinds of plant items eaten by the two species in Kibale are more similar than in Kakamega, annual dietary overlap of species-specific items in Kibale is less than half (33·8%) of its value in Kakamega (70·4%), indicating that the two monkey species in Kibale do not use the same plant species. Greater species-specific overlap in Kakamega probably occurs on a monthly time scale as well, since all monthly overlap measures in Kakamega exceed even the annual overlap for Kibale (monthly overlaps are not published for Kibale). Much dietary overlap in both study areas results from the common use of fruits. The greater overlap in Kakamega probably reflects the higher proportion of fruit in the diets of both species there.

The degree of specialization on particular foods can influence dietary similarity between species. Annual evenness (J) of plant species use is nearly identical in the two study areas (Cords 1984b). In a single month, however, Kibale blues seem to concentrate considerably more on a few species-specific items than their Kakamega counterparts: the top five foods account for 63–94% ($\bar{x} = 76\%$, $n = 7$ months; Rudran 1978) of the Kibale blue monkey diet, but only for 44–69% ($\bar{x} = 57\%$, $n = 11$ months) of the diet of Kakamega blues. (Similar data are not available for Kibale redtails.) Thus the dietary niche, at least of blue monkeys, appears to be broader in Kakamega than in Kibale, increasing, in principle, the number of foods which could be shared between species.

Another difference between the two study populations concerns specialization in insect foraging. In Kibale, redtails catch more prey from foliage, from fewer plant species, and from fewer species-specific substrates than blue monkeys do (Struhsaker 1978). These differences do not occur in Kakamega, where both species concentrate equally on different plant species and on leaves as sources of insects. Also, both of the Kakamega monkey species are more diverse in their choice of plant species as insect sources; the degree to which they concentrate on particular substrates is similar to that of the Kibale redtails. In both study populations, redtails use capture methods appropriate for mobile prey more often than blue monkeys.

In sum, the data show that the diets of blue and redtail monkeys diverge less in Kakamega, and (at least) blue monkeys there also have a broader plant diet than in Kibale. Also, both species in Kakamega are less specialized on particular plant species as insect sources, but concentration on certain substrates is as high as it is for Kibale redtails. Several hypotheses, which are not mutually exclusive, may explain these overall differences. (i) Kakamega blue monkeys may have undergone a competitive release in the absence of *Colobus badius* and *Cercocebus albigena*, two larger primates with precedence at feeding sites shared with blue monkeys (Struhsaker 1978). The higher population density of blues in Kakamega relative to Kibale (169 vs. 42 per km^2; Cords, 1986) is consistent with this hypothesis. (ii) Differences between Kakamega and Kibale may reflect the fact that the Kakamega forest is poorer in plant species than Kibale (Hamilton 1974). Kakamega blues (and possibly redtails) may have to sample more widely in order to satisfy dietary requirements. (iii) Ecological segregation could be more limited in Kakamega because of the lower plant-species richness. The fact that Kakamega monkeys used more plant species and plant-specific items than their Kibale counterparts, however, speaks against this hypothesis. (iv) Finally, the sampling schedules of the two studies may influence the results. There are several times more feeding records for each species in Kakamega, where visibility is less limited due to a more open middle canopy layer. Furthermore, the Kibale monkeys were sampled on about 38% fewer days per month than those in Kakamega. If the number of plant species seen to be used increases with observation time (Rudran 1978), and day-to-day variation in diet also occurs (Cords 1984b), the number of observation days per month could well affect apparent dietary breadth, and consequently measures of dietary overlap.

Intraspecific differences

In Kakamega, adult males are more frugivorous and less insectivorous than conspecific adult females, though differences are not significant for redtails. The same pattern was observed in Kibale blue monkeys (Rudran 1978) and in *C. nictitans* and *C. cephus*, close relatives of blues and redtails respectively, in Gabon (Gautier-Hion 1980). There were no sex differences among adults in the proportion of leaves eaten in Kakamega, Kibale blue monkeys, or *C. cephus* in Gabon; in *C. nictitans* however, females were more folivorous than males. Furthermore, pregnant and lactating females in Kakamega ate relatively more insects than other females in months when differences occurred. In Gabon, pregnant and lactating females, who were identified only by the time of year, increased their consumption of insects and young leaves.

The above patterns would not be expected on the basis of body size alone. Gautier-Hion (1980) attributed sex differences in the diet of adult guenons in Gabon to social and physiological constraints acting on adult males and females respectively. Adult male blues and redtails, like their west African congeners, spend much time being vigilant. Vigilance is directed primarily toward other adult males, who are active competitors for mates (Cords 1986). Vigilant scanning of the surroundings is incompatible with insect foraging, and the inclusion of a large fraction of fruit in the diet would allow males, who usually have precedence at feeding sites within fruiting trees, to ingest required calories quickly (Rudran 1978). Females, on the other hand, not only spend noticeably less time scanning but also may need more protein than males because of pregnancy and lactation (Sadlier 1969). The conservatively delimited lactation period of 4 months used in the previous analyses should not obscure the fact that most females are probably pregnant or lactating at any given time.

The question remains why sex differences among adults are so much less marked in the Kakamega redtails than in the blues. During the period of observation, only the redtail group underwent a 6-month multi-male influx when male–male agonistic interactions were frequent (Cords 1984a). If anything, vigilance *vis-à-vis* other males during this time increased, and so one would expect exaggeration of sex differences. Perhaps, however, redtail males are more efficient insect foragers than blue monkey males relative to conspecific females: this could be a consequence of absolute body size and/or sexual size dimorphism, both of which are smaller in redtails.

Differences between the immature size classes are less obviously related to social or physiological demands. In Kakamega, smaller juveniles are more frugivorous and less folivorous than larger ones. While these relationships are as predicted by arguments based on body size, it is unexpected that smaller animals are less insectivorous. Smaller juveniles, however, may be less skilled in finding or catching insects (Kinzey 1977), as suggested by their greater concentration on slow motor patterns for prey capture. They may also adopt a time-minimizing feeding strategy allowing more time for social play (Rudran 1978) and may still obtain a significant amount of protein from their mothers' milk. Finally, larger juveniles going through puberty are growing faster than smaller juveniles (Gautier-Hion & Gautier 1976), who therefore may require relatively less protein.

The diets of immature blue monkeys in Kakamega differ in their relationship to adult diets from those reported for Kibale, where all juveniles (and 'sub-adults') are less frugivorous and more insectivorous than adults (Rudran 1978). This pattern is replicated only for large juveniles in Kakamega: smaller juveniles there are among the most frugivorous age–sex classes, and are equally insectivorous as adult females. This difference in the two study populations may reflect the intensity of interference in fruiting trees by the larger *Colobus badius* and *Cercocebus*, which should affect the smallest guenons most; thus small and medium juveniles in Kakamega, where these competitors are absent, would be excluded from fruiting trees less often than their Kibale counterparts.

Intra- and interspecific differences

In Kakamega, dietary similarity of heterospecific age–sex classes is often higher than that of conspecifics. This pattern is evident in the degree of frugivory and insectivory (but not of folivory), in diet overlap of plant species-specific items, and in the way that monthly intakes of fruit, leaves and insects inter-relate. The identity of species–age–sex classes that are grouped together as similar depends on what aspect of the diet one considers.

In another *Cercopithecus* community, Gautier-Hion (1980) similarly found that adult conspecifics could differ more from one another in their annual and seasonally varying consumption of fruit, fibre and prey than sex classes of different species. Gautier-Hion's data come from stomach content analyses of monkeys collected over a period of 10 years and a radius of 50 km. Apparent sex, species and seasonal differences could be due to variation in foods available during this extended period and over this large area. Some similar patterns were found in Kakamega, however, where sampling was more closely matched for time and location.

The two populations differ in patterns of seasonal variation. In Kakamega, all species–age–sex classes show bimodal distributions of fruit, leaf and insect consumption over the year; none consume these items at a rate as constant as *C. pogonias* and *C. cephus* females in Gabon. It is unlikely that seasonal changes in production are stronger in Kakamega than in the Makokou Forest in Gabon: Kakamega's driest months are characterized by 75–100 mm more rain (on average) than those in Makokou (where average rainfall drops to near zero annually), and the number of fruiting species available does not drop to under half its maximal value as in Makokou (Gautier-Hion 1980; Cords 1984b). The difference in variability between the two populations may reflect the phenology of certain important plant species, differences in insect abundance, or the large methodological differences between the two studies.

The above analyses ignore the identity of the plant species used and the representation of different age–sex classes in a monkey group. If one considers plant species-specific items in the diet, there is an overall tendency for plant diet overlap between paired conspecific age–sex classes to exceed overlap between heterospecifics in most months in Kakamega. The trend is even more marked if overlaps between species–age–sex classes are weighted according to the number of individuals in each class.

Temporal variation in measures of dietary overlap suggests that competition influences dietary variation of blue and redtail monkeys at Kakamega. Overlap should be highest when food is abundant and competition is reduced. Production was not directly assessed, but inter- and intra-specific overlaps of species-specific items were high in months when the monkeys' plant diets contained a lot of fruit, most of which came from trees or vines that were common or that produced large crops (Cords 1984b). The same pattern was observed for between-species overlap in Kibale (Struhsaker 1978). In Gabon, similarities in fruit, insect and leaf intake between *and* within species also were high when fruit constituted a particularly large part of the diet. These periods corresponded to times of high fruit production, which was measured directly (Gautier-Hion 1980). These results suggest that the magnitude of inter- and intra-specific dietary differences in Kakamega is affected by food abundance, and specifically that divergence of diets is greatest when fruit is least plentiful. The frequent occurrence of aggressive interference between and within species indicates one mechanism by which competition can act.

ACKNOWLEDGMENTS

I thank the Government of Kenya for permission to study in the Kakamega Forest, and the Forest Station staff for practical and essential assistance and hospitality. The financial support of the National Science Foundation, University of California Research Expeditions Program, Sigma Xi and the U.C. Zoology Department is also gratefully acknowledged. For comments on earlier versions of the manuscript, I thank K. Milton, B. Mithchell, and T. E. Rowell.

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(*Received 26 July 1985*)