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Ecological Partitioning of *Cercopithecus campbelli*, *C. petaurista*, and *C. diana* in the Taï Forest

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*I determined the degree of ecological partitioning among 3 species of guenons (*Cercopithecus campbelli, C. petaurista, and C. diana*) in the Taï Forest, Côte d'Ivoire and used the partitioning data to understand competitive relationships among them. Over a 13-mo period, I measured ecological partitioning in terms of food and canopy stratum use for 2 habituated groups of each guenon species and also collected data on food availability. I found that the study species diverged primarily in food items consumed and vertical strata occupied.* Cercopithecus petaurista *ate much more foliage than the other species did and used mostly the middle strata (5–20 m).* Cercopithecus diana *ate primarily fruit and used mostly the upper strata (>20 m).* Cercopithecus campbelli *ate mostly fruit together with large amounts of animal matter and primarily occupied the ground and low strata (<5 m). Of the specific pairs, the diets of* Cercopithecus campbelli/C. diana *overlapped the most overall and decreased during the season of low fruit availability.* Cercopithecus campbelli *and* C. diana *age/sex classes also overlapped more than the age/sex classes of other species pairs. The results suggest that the potential for competition was more intense for* Cercopithecus campbelli/C.diana *relations than it is for other species pairs. I compare my results from Taï with those from other primate and guenon communities and demonstrate that*

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dietary overlaps and seasonal dietary divergence are lower in Taï than in most other guenon communities.

KEY WORDS: ecological partitioning; *Cercopithecus,* guenons; interspecific competition; Taï forest.

INTRODUCTION

The niche of a species is an *n*-dimensional hypervolume in which the species can maintain a viable population and where each axis of the hypervolume corresponds to a separate biotic or abiotic factor necessary for species survival (Hutchinson, 1978). Based on the principle of competitive exclusion, ecological theory predicts that similar species cannot occupy the same niche, and therefore species are expected to diverge or partition resources in at least some niche dimensions (MacArthur and Levins, 1967; Tokeshi, 1999). Researchers generally consider habitat type, food type, and activity schedule as the major axes along which niches diverge in animal communities (Schoener, 1974; Tokeshi, 1999), and have demonstrated divergence along these axes among primates and between primates and other mammals (Emmons *et al.*, 1983; Gautier-Hion *et al.*, 1980; Struhsaker and Oates, 1975). Here I examine how resources are partitioned among Campbell's guenons (*Cercopithecus campbelli*), lesser spot-nosed guenons (*C. petaurista*), and Diana monkeys (*C. diana*) in an African rain forest and discuss what the partitioning reveals concerning the importance of interspecific competition in them.

The relationship between overlap and competition in resource utilization is one of the most intractable issues in community ecology (Tokeshi, 1999). Extensive overlap indicates either strong or weak competition, and large overlap may exist despite substantial competition between species because shared resources are abundant or because other factors such as predation reduce populations before competition can act (Tokeshi, 1999). It is also possible to explain lack of overlap, by independent evolutionary diversification in niche parameters (e.g., allopatric speciation; Mayr, 1977) or by competition occurring now or having occurred in the evolutionary past (Connell, 1980).

One can study the importance of interspecific competition through experiments, comparative studies, or direct observation. In experiments, one compares treatments where in the species exist together and apart (Lin and Batzli, 2001). Researchers have discussed the caveats to experimental design and interpretation exhaustively (Connell, 1983; Goldberg and Barton, 1992; Roughgarden, 1983; Salt, 1983; Schoener, 1983; Simberloff, 1983; Strong, 1983), and a rise in density, fecundity, or resource utilization of either species when alone compared to when together is strong evidence for the depressing effect of the other species. When subjects are large arboreal animals, however, experimental studies of this type are impractical for ethical, logistical, and conservation-related reasons. Comparative studies look for differences in the morphology (character displacement), density, behavior, or ecology (competitive release and niche shift) of species under sympatric and allopatric conditions (Alatalo *et al.*, 1986; Arlettaz *et al.,* 1997). These comparisons assume that the only difference between sympatric and allopatric situations is the absence of putative competitors in allopatry, which is probably unrealistic. In some cases, as it is here, direct observation of competition and the consequences of such competition is the only practical option. Without experimentation, one can question a causal link between ecological partitioning and competition (Ganzhorn, 1988). Nevertheless, early ecological partitioning studies (Emmons *et al.*, 1983) as well as more recent studies (Ben-David *et al.*, 1995; Fedriani *et a*l., 1999; Ganzhorn, 1988; Kruuk *et al.,* 1993; Vasey, 2000) have provided important data on community organization and species coexistence in several primate and other mammal communities.

Most of the studies on niche partitioning in sympatric forest guenons (Cords, 1987; Galat and Galat-Luong, 1985; Gautier-Hion, 1980; Kaplin and Moermond, 2000; Struhsaker, 1978) have demonstrated extensive (80–90%) overlap in dietary items and forest stratum use. Some studies have suggested the importance of interspecific competition by finer grained analyses of 2 variables: 1) seasonal dietary divergence in food items and 2) comparisons of age/sex classes within and between species (Cords, 1986; Gautier-Hion, 1980).

Greater dietary niche divergence during times of food scarcity is predicted in the hypothesis that interspecific competition drives resource partitioning, whereas broadening of the feeding niche is predicted if interspecific competition is not driving resource partitioning (Smith *et al.*, 1978). Researchers have demonstrated greater niche divergence during times of food scarcity for guenons (Cords, 1987; Gautier-Hion, 1980), squirrels (Emmons, 1980), and birds (Smith *et al.*, 1978).

Comparisons of interspecific vs. intraspecific levels of competition are essential to classic Lotka-Volterra models of competition. Regardless of whether past interspecific competition led to niche divergence, comparing interspecific and intraspecific divergence can show that the potential for continued competition between some species pairs remains as great as or greater than that for competition within species (Gautier-Hion, 1980).

Galat and Galat-Luong (1985) conducted preliminary work at Taï on *Cercopithecus diana*, *C. campbelli*, and *C. petaurista* in the late 1970s-early 1980s and found all 3 species ate primarily fruit (76–78%), mostly in the canopy and emergent trees. Later studies of positional behavior revealed more pronounced vertical stratification with *Cercopithecus campbelli* most often terrestrial and *C. petaurista* most often in the understory (McGraw, 1996, 2000). Wachter *et al.* (1997) and Eckardt and Zuberbühler (2004) confirm the high degree of frugivory by *Cercopithecus diana* but show that animal matter also made up a major part of the diet (27–38%).

Here, I use direct observation of multiple *Cercopithecus campbelli, C. petaurista*, and *C. diana* groups and measurements of food availability to test several hypotheses related to ecological partitioning in forest guenons. I hypothesized that: 1) food item and canopy stratum use are important niche parameters partitioned by the study species; 2) the potential for competition (i.e., dietary overlap) is greater interspecifically than among age/sex classes within the same species; and 3) diets of different species would diverge most during seasons of food scarcity. Further, a heterosexual group of *Cercopithecus campbelli* has not inhabited the largely shared home range of Diana-1 and Petaurista-2 for ≥ 10 yr (Taï Monkey Project [TMP] data). For this reason, I considered *Cercopithecus campbelli* to be the most patchily distributed species at the study site and hypothesized that 4) *Cercopithecus campbelli* suffered most from asymmetric interspecific competition, and predicted that interspecific overlap in dietary items and dietary divergence during food scarcity would be most pronounced for *C. campbelli.*

METHODS

Study Site

I carried out the study in the Taï National Park, Côte d'Ivoire (located between 5°10′ N to 6°20 N and 4°20′ W to 6°50′ W). Taï National Park is one of the last remaining substantial blocks of West African forest and consists of *ca.* 3300 km^2 of forest. The forest is tropical evergreen seasonal lowland forest (Stoorvogel, 1993) with average annual rainfall of 1942 mm falling in 2 wet seasons (September–November, March–May; Korstjens, 2001; this study). Additional information on the site is in McGraw (1996), Korstjens (2001), and Buzzard (2004).

Subjects and Observation Schedule

Two habituated groups each of *Cercopithecus campbelli, C. petaurista,* and *C. diana* ranging in size from 7 to 26 individuals served as study subjects. The groups contained 1 adult male for most of the study, 4–13 adult females,

Table I. Study group compositions

Group	AM	AF	SA	J	Total
Cercopithecus campbelli-1	1	6	0	2 + inf	9
Cercopithecus campbelli-2	1	5	1	2	9
Cercopithecus petaurista-1	1 (2)[a]	8	1	6	16
Cercopithecus petaurista-2	1	4	0	2	7
Cercopithecus diana-1	1	11	2	7	21
Cercopithecus diana-2	1	13	2	10	26

Note. AM, Adult males were fully grown and gave loud calls (Gautier, 1988); AF, adult females were pregnant or had given birth; SA, subadults; J, juveniles were not carried and suckled infrequently. Group compositions are from the end of the study unless noted otherwise.

[a] *Cercopithecus petaurista*-1 frequently contained 2 males from February 2001 to December 2001.

and associated immatures (Table I). Adult females were visibly pregnant or had given birth as determined by pendulous nipples. Subadult males were the same size or slightly smaller than adult males but not giving loud calls. Subadult females were the size of adult females but had not yet given birth. Juveniles were not carried and suckled infrequently, if ever; they ranged in size from larger than infants up to the size just below subadult and adult females. In addition to the study species, red colobus (*Procolobus badius*), black-and-white colobus (*Colobus polykomos*), olive colobus (*Procolobus verus*), sooty mangabeys (*Cercocebus atys*), chimpanzees (*Pan troglodytes*), and putty-nosed guenons (*Cercopithecus nictitans*) are present at the study site. I never observed *Cercopithecus nictitans* in the 1.5-km^2 study grid, but several groups range 2 km of the grid. Potential predators for the guenons are chimpanzees, leopards (*Panthera pardus*), golden cats (*Felis aurata*), crowned hawk-eagles (*Stephanoaetus coronatus*), and human poachers (Boesch and Boesch-Achermann, 2000; Bshary, 2001; Bshary and Noë, 1997).

Group follows occurred from September 2000 through October 2001 except for January 2001. I followed each *Cercopithecus campbelli* and *C. petaurista* group 3 d/mo on average and each *C. diana* group 2 d/mo on average. I followed or attempted to follow individual groups for 2 or 3 consecutive d and again after 2 wk. On most observation days group contact lasted from 0700–0730 h until the guenons stopped moving presumably in sleeping areas (*ca.* 1800 h). Occasionally, group contact lasted from 0700–0730 h until 1230 h or 1200 h until *ca.* 1800 h (Table II).

Table II. Number of observation hours per group per season

	diana-1	*diana-2*	*campbelli-1*	*campbelli-2*	*petaurista-1*	*petaurista-2*
Wet season (1)	44	44.5	71	66	104	93
Dry season	54.5	55	55	55	60	82
Minor wet season	49.5	60	71	87	44	71
Minor dry season	22	44	49	70	38.5	60
Wet season (2)	44	33	43	44	27.5	49.5

Note. Wet season (1): September–November 2000; dry season: December 2000–February 2001; Minor wet season: March–May 2001; Minor dry season: June–August; wet season (2): September–October 2001.

Food Availability

To monitor the production of fruit, foliage, and flowers, I used a fruit trail (Chapman and Wrangham, 1994) running partly through the ranges of all 6 groups. TMP established the fruit trail in 1994 and modified it in 1998 and 2001 to include 5 individuals from each of 54 tree species and 3 liana species. Forty-three (75%) of the plant species on the fruit trail were food species for ≥ 1 of the study species, and they accounted for 80, 62, and 88% ($N = 638, 810, 1071$) of the annual plant feeding records for *Cercopithecus campbelli*, *C. petaurista*, and *C. diana*, respectively (Buzzard, 2004).

I used methods to score resource abundance that TMP has used for 10 yr. Twice a month, I or my assistants, who had 5–10 yr of experience, recorded the presence and abundance of fruit, flowers, or young foliage in a tree or liana on a scale of 0–3: 0 = 0–25% full; 1 = 25–50%; 2 = 50–75%; 3 = 75–100%. The abundance scores a percentages of the maximal value for the plant species under consideration.

To calculate separate indices of fruit and flower availability, I used data from the fruit trail and data on the abundance and size of food species from plant surveys. First, in every month, I averaged the individual phenology scores for fruit/flowers of each food species on the fruit trail. Second, for each species I multiplied the average phenology score by its average DBH (diameter at breast height, cm/ha) from vegetation surveys in all 3 territories because DBH correlates positively with primate food availability and crown size (Chapman *et al.*, 1992; Korstjens, 2001). The vegetation surveys were along 6 transects 25 m wide that varied in length from 500 m to 1 km and had a combined length of 4.7 km. I worked with a local botanist (J. Tahou) to measure and identify all tree and liana species >5 cm DBH. We included every individual of *Cercopithecus caudatum* and *M. barteri* because they frequently fed in trees of these species <5 cm DBH. For plants on the list of food species, I combined my own survey data with similar vegetation surveys of Korstjens (2001, unpub. data) and D. Anderson (unpub.data), which enabled me to increase the total survey area so that it included ≥10% of the home range of each study group. Finally, I added the abundance scores across plant food species to obtain total fruit/flower abundance scores for each month. I considered only mature fruit for the index of fruit availability because individuals ate immature fruits infrequently (2–5% of fruit feeding records $N = 310–745$). I included both flower buds and opened flowers, however, for the index of flower availability because the subjects frequently ate both flower buds and open flowers.

To estimate the abundance of insects, other invertebrates, and other fauna such as tree frogs I established 10 5 m × 5 m quadrants in relatively dense, moderately dense, and relatively open forest throughout the home ranges of all study groups (Buzzard, 2004). I had 4 quadrants in dense forest and 3 each in the other forest types. I had an extra quadrant in dense forest because I had observed that the study species (especially *Cercopithecus campbelli* and *C. petaurista*) frequently used it. On 1 d/mo, I manually and visually searched substrates above the ground within these quadrants for invertebrates and other fauna. To census the actual prey the subjects used (*sensu* Janson and Chapman, 1999), I unrolled old leaves and searched along the bark recording the number of prey items encountered. When possible, we bent down saplings to search substrates up to 5 m. I exhaustively and completely searched the quadrants for 10–15 min and recorded the number and type of every prey item encountered. For analysis, I grouped animal matter into 3 categories: 1) relatively immobile included caterpillars, centipedes, and slugs; 2) mobile included adult insects, spiders, and frogs; and 3) nests included spider nests and insect larvae.

Feeding Data Collection

I collected data on group behavior using 15-min scan samples (Altmann, 1974) at the beginning and midpoint of every hour. Because of visibility constraints and group spread, I required long scans to see enough individuals. I attempted to encounter as many individuals as possible by walking through the group. I observed more *Cercopithecus diana* individuals per scan (mean = 7 ± 1.8 records/scan, $N = 1446$ scans) than *C. campbelli* and *C. petaurista* (mean = 4, 4.4 ± 1.2, 1.4 records/scan, $N = 2340$, 2569 scans, respectively). Individual identification of most or all group members prevented the resampling of individuals within each scan. In addition, movement through the group relative to the group's usual rate of movement made resampling of individuals unlikely.

During group scans, I recorded the activity of each individual and its height in the forest according to a 5-point scale: 0 = ground, 1 = shrub and sapling level up to 5 m; 2 = understory of small trees 5–20 m; 3 = main canopy 20–40 m; 4 = emergents >40 m. Feeding occurred when an individual 1) put food into its mouth; 2) pushed food from its cheek pouches into its mouth; 3) when it was chewing, as long as I had witnessed the ingestion or removal from the cheek pouches in the period immediately preceding the scan; or 4) when subjects prepared items before ingestion, such as rubbing a caterpillar on the bark.

I categorized identifiable food items as follows. Fruit (Fr) could be young or mature distinguished by color. If a fruit-eating individual was in a fruiting tree, I measured the DBH of the tree. Subjects gathered some low fruit from the ground or fallen fruits lying on the ground (FrGr). Foliage (Fo) included leaves, stems, and petioles because individuals often ate stems from lianas and petioles together with leaves and further differentiation was not possible. Animal matter (An) included insects and other invertebrates including nests, as well as frogs. Captures occurred from the air, from rolled up old leaves, or from unrolled leaves that we searched along their length. Flowers (Fl) included both flower buds and mature flowers. The remaining food categories consisted of mushroom (G) and other (O) including bark and moss.

If an individual was chewing on items from its cheek pouches, which could not be identified, I scored it as cheekpouch contents (CP). I added fruit coming out of cheek pouches to the other fruit because the chance of double counting an item—that the subject put into its mouth in 1 scan and pushed from the cheek pouch for chewing in the next scan—was remote (Buzzard, 2004).

I measured dietary overlap between species and age/sex classes by summing the shared percentages of dietary components (Holmes and Pitelka, 1968), a method researchers have used in many earlier studies dealing with dietary overlap in primates (Rudran, 1978).

Statistical Analyses

I used 2-tailed statistical tests for all analyses except the ones related to seasonal patterns. For the latter, hypotheses predicted the direction of the difference enabling 1-tailed tests. I grouped plant feeding records according to months; I combined the feeding data for all species in September and October 2000 and for *C. petaurista* in June and July 2001 because of

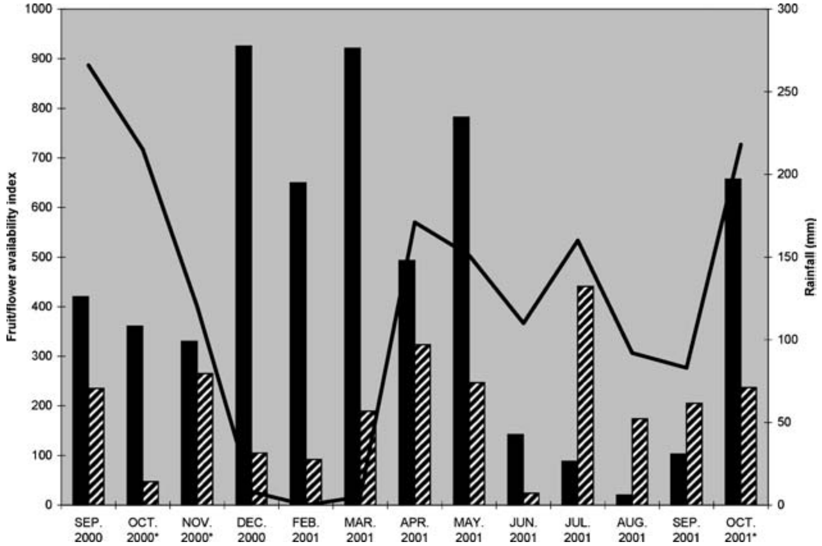


Fig. 1. Indices of fruit (black bars) and flower (striped bars) availability over the study period. I measured the indices by multiplying average phenology scores of fruiting/flowering food species times the cumulative DBH of the food species (cm/ha) and summing the values for each month. The line is monthly rainfall in mm. *Indicates months where the fruit index is anomalously low (see Results).

small sample sizes. To check whether sample sizes were adequate for data analysis in a single month or a 2-mo period, I performed split-half analyses (Buzzard, 2004; Martin and Bateson, 1998). After Wilcoxon matched pair tests on the monthly percentages of different food items demonstrated similarity, I lumped data from 2 groups of the same species. September 2000–October 2001 was the annual period because I combined feeding data from September 2000 and October 2000.

RESULTS

Food Availability

During my study, the rainfall pattern in the Taï Forest consisted of a wet season from September through November, a dry season from December through February, a minor wet season from March through June, and a minor dry season from July through August (Fig. 1). The rainfall amounts are similar to the levels at the site from 1978 to 1981 (Galat and Galat-Luong, 1985) and 1991 to 1999 (Korstjens, 2001).

The index of fruit availability indicated that the lowest availability was from May to August (Fig. 1). The seasonal relationship is even more profound when one considers anomalies and omissions. For example, in October and November 2000 and 2001, most *Memecylon lateriflorum* (Melastomaceae) trees produced large amounts of fruit; however, the *Memecylon lateriflorum* individuals on the fruit trail were an exception, biasing the index downward. Further, *Diospyros mannii* and *D. ivoriensis* (Ebenaceae), 2 of the most common tree species in the forest (Buzzard, 2004), had mast crops in January and February. The species were important foods in January and February but are not represented on the phenology trail. Analysis of prior TMP feeding records and discussion with local botanists indicated a 3-yr interval for such masting events (TMP, unpublished). The aforementioned were the only substantial anomalies in the fruit availability data.

Flowering did not show seasonal variation as extreme as fruiting. The index of flower availability was highest in July and lowest in June (Fig. 1). Leaf availability did not appear to fluctuate throughout the year partly because of the continual fresh growth in and around tree falls and partly because subjects consumed both young and mature leaves from major leaf sources. There was also little seasonal variation in total insect and fauna abundance (Fig. 2). The category of insect nests and spider nests decreased from March to June, but the categories of mobile and relatively immobile prey showed no discernible seasonal pattern.

Diet Items

Annual Comparisons

Unknown items from cheek pouches accounted for 6–9% of dietary items for the study species (Table III), and are not included in further dietary analyses. Fruit from cheek pouches accounted for 8–15% of the annual fruit diets of the study species. Inclusion of fruit from cheek pouches did not greatly alter (1–2%) monthly analyses.

For *Cercopithecus campbelli* and *C. diana,* fruit represented the most common food item during the study but *C. petaurista* consumed foliage most frequently, slightly more than fruit (Table III). Nearly all fruit the 3 species consumed was mature (95–98% of fruit records). Subjects ate both young and mature leaves from all plants that contributed foliage to the diet except *Diospyros* spp.; *Cercopithecus* ate only petioles from

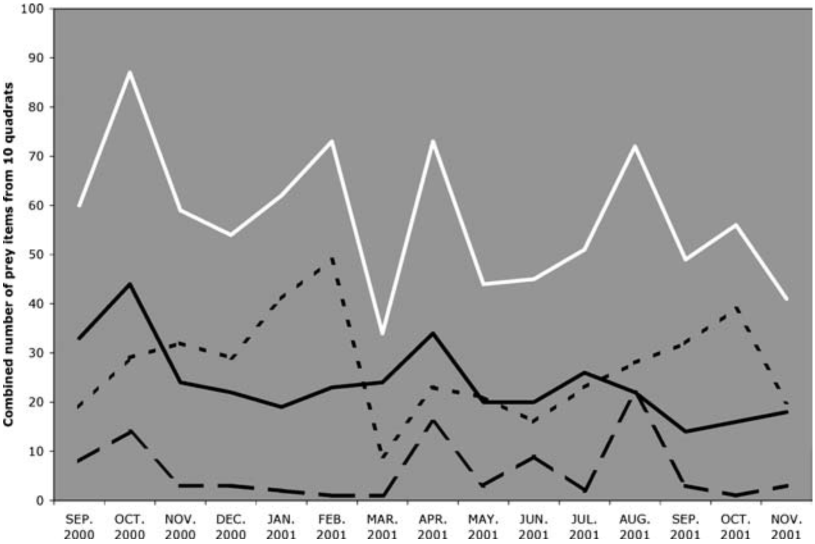


Fig. 2. Phenology of prey items over the study period. Total prey items (white line); ant, spider, and frog nests (short-dashed line); mobile prey (black line); immobile prey such as caterpillars, cocoons, slugs, and insect larvae (long dashed line).

mature leaves of *Diospyros*. Animal matter was also very important for *Cercopithecus campbelli*, and *C. campbelli* fed on animal matter more than twice as much as the other species did (Table III).

Table III. Percentage composition of the diet expressed as food items consumed over a 14-mo period

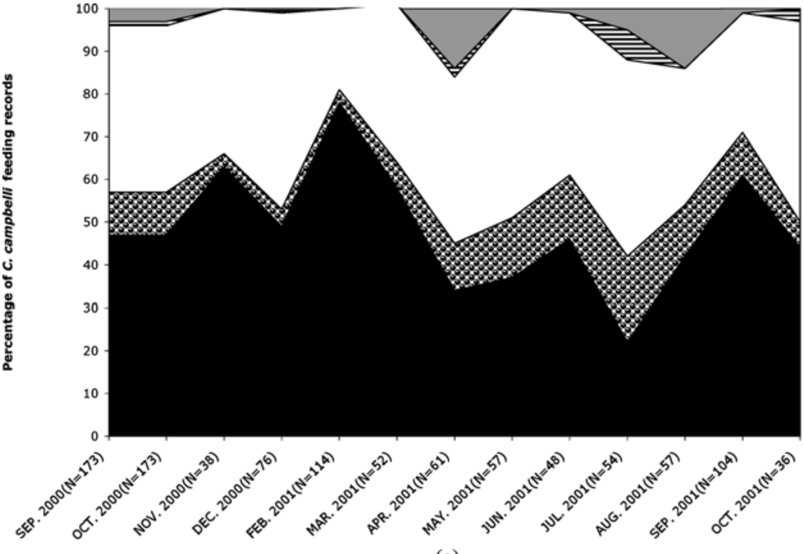
Food item	*Cercopithecus campbelli* (*N* = 953)	*Cercopithecus petaurista* (*N* = 924)	*Cercopithecus diana* (*N* = 1273)
Fruits	46	34	59
Foliage	8	40	16
Prey	33	12	16
Flower	1	6	3
Fungi	2	1	—
Cheek pouch	9	6	6
Other	1	0.1	0.2

Note. Foliage includes leaves, stems, and petioles. Cheek pouch items include only unidentified objects taken from cheek pouch.

Monthly Comparisons

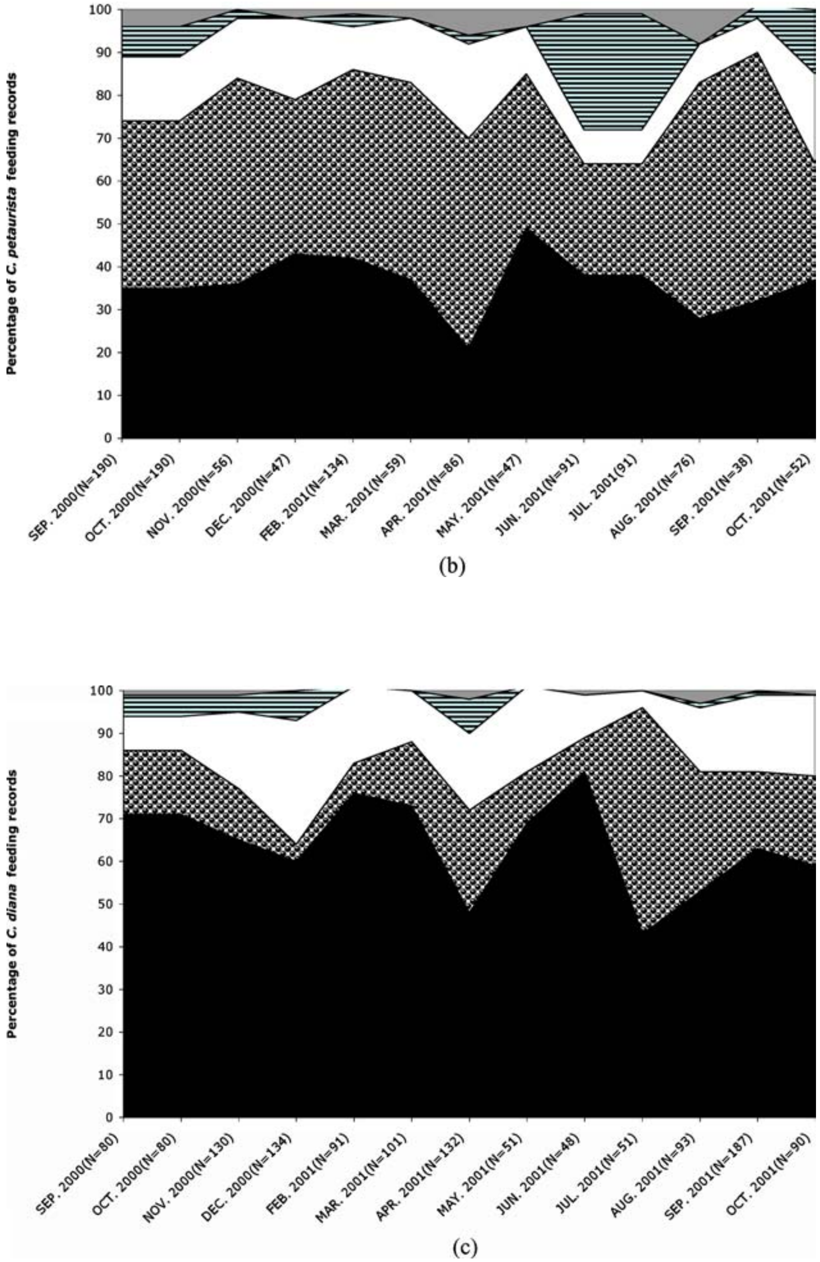
When I examined the diet on a month-by-month basis, the same patterns repeated (Fig. 3). *Cercopithecus diana* consistently ate more fruit than both *C campbelli and C. petaurista* did (Wilcoxon $T_s = 3$, 0, respectively; both $p < 0.05$), and *C. campbelli* consistently ate more fruit than *C. petaurista* did ($T_s = 12$, $p < 0.05$). *Cercopithecus petaurista* consistently ate foliage more than both *C. campbelli* and *C. diana* did ($T_s = 0$, 1, respectively; both $p < 0.05$), and *C. diana* ate more foliage than *C. campbelli* did ($T_s = 6$, $p < 0.05$). *Cercopithecus campbelli* consistently ate more animal matter than *C. diana* and *C. petaurista* did ($T_s = 1$, 0, respectively; both $p <$ 0.05).

The top-ranked monthly food items for *Cercopithecus campbelli, C. petaurista*, and *C. diana* varied somewhat from month to month (Fig. 3). Diets, expressed in terms of major food items, shifted for each species during the minor dry season (July–August), which included the time of lowest fruit availability (May–August). Animal matter, instead of fruit, became the most frequently eaten item for *Cercopithecus campbelli* during July. In



(a)

Fig. 3. The proportion of major food items consumed by (a) *Cercopithecus campbelli*, (b) *C. petaurista*, and (c) *C. diana*. Fruit (black area); foliage (spotted); animal matter (white); flowers (striped). Gray area represents mushrooms and other items such as bark. I combined feeding records of all species in September and October 2000, and feeding records of *Cercopithecus petaurista* in June and July 2001.



(b)

(c)

Fig. 3 (Continued)

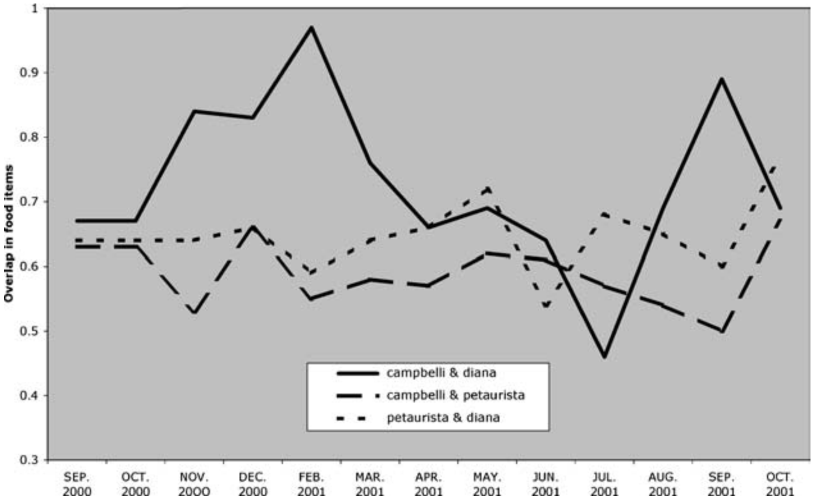


Fig. 4. Overlap in food items (fruit, foliage, prey items, flowers, and mushrooms) between the study species.

June and July, fruit and flowers were the most common food items instead of foliage for *Cercopithecus petaurista*, and foliage replaced fruit as the most common food item for *C. diana* in July.

Overlap in food items among *Cercopithecus campbelli, C. petaurista,* and *C. diana* also varied from month to month (Fig. 4). *Cercopithecus campbelli* and *C. diana* had the highest mean monthly overlap and largest range of overlaps (mean = 73%, 46–97%) compared to both *C. petaurista* with *C. diana* (mean = 65%, 54–77%) and *C. petaurista* with *C. campbelli* (mean = 59%, 50–67%). During the season of lowest fruit availability (May–August) only overlaps between *Cercopithecus campbelli* and *C. diana* are lower than during the rest of the year (Mann-Whitney $U = 25, p < 0.05$, 1-tailed).

There are few correlations between food item overlaps and food item availability. The only positive correlation is between the index of fruit availability and food item overlap for *Cercopithecus campbelli* and *C. diana* ($r_s = 0.67, p < 0.05, N = 13$).

Plant Species and Species-Specific Item Use

Annual Comparisons

The study species at Taï had very diverse diets. *Cercopithecus campbelli, C. petaurista*, and *C. diana* consumed at least 75, 76, and 84 plant species as well as 95, 96, and 105 species-specific items, respectively, when prior TMP feeding records are included with data from the study period (Buzzard, 2004). During the study, patterns of species-specific plant item consumption were very similar to those of plant species use, and the 3 study species consumed many of the same principal plant species and species-specific items. In fact, *Sacoglottis gabonensis* (Humiriaceae)*, Dialium aubrevillei* (Euphorbiaceae), and *Memecylon lateriflorum* (Melastomaceae) were among the top 5 plant species that each species consumed (Buzzard, 2004). The subjects typically ate only 1 item from important plant species, and annual species-specific item overlaps of the species pairs decreased only 0–3% from plant species overlaps, suggesting that the monkeys were not partitioning resources by using different items from the same species (Buzzard, 2004).

The diets of *Cercopithecus campbelli* and *C. diana* shared the most species-specific plant items and plant species. Further, *Cercopithecus campbelli* and *C. diana* also had the highest overlap (47%) in species-specific plant item and plant species use. Liana foliage and fruit were particularly important to *Cercopithecus petaurista,* comprising 28% and 3% of plant food items, respectively. Items from lianas, accounted for only 11% of the diet for the other species. Consequently, *Cercopithecus petaurista* overlapped only from 28–32% in species-specific plant item and plant species use with *C. campbelli* and *C. diana.*

Monthly Comparisons

When *Cercopithecus petaurista* consumed foliage, it was most often from the young leaves and new stems of ≥14 species of lianas (Buzzard, 2004). Unfortunately, *Cercopithecus petaurista* often consumed liana foliage from trees with 2 or more lianas, hampering food item identification. Consequently, 15% of the food items *Cercopithecus petaurista* consumed consisted of unidentified liana foliage, and I included unidentified liana foliage as a plant species in analyses of monthly overlap in species-specific items (Fig. 5). This action increased monthly overlaps only 2–3% on average. Further, the apparent overlap increased only if the subjects consumed different unidentified lianas. All study species ate most of the liana species at least to some degree, however, so that shared consumption of unidentified lianas probably included real overlap of particular liana species.

Monthly overlaps of plant species use and species-specific item use were nearly identical (Buzzard, 2004); therefore, I report only species-specific item use. For all the species, conspecific groups had similar diets,

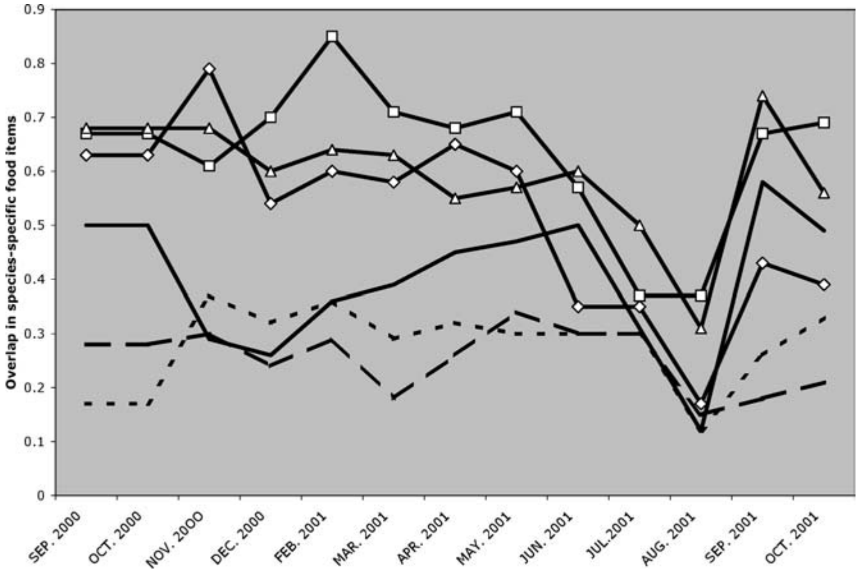


Fig. 5. Overlap in species-specific plant item use between conspecific groups and between the study species over the study period. The lines with squares (*Cercopithecus campbelli*), diamonds (*C. petaurista*), and triangles (*C. diana*) are for conspecific overlap. The black line is for overlap between *Cercopithecus campbelli/C. diana* while the long-dashed line is for overlap between *C. campbelli/C. petaurista* and the short-dashed line is for overlap between *C. petaurista/C.diana*.

and in every month the species-specific overlap between conspecific groups was higher than that involving the species and another species (Fig. 5).

Each month, 1 or 2 items accounted for most interspecific overlap in species-specific item use , and *Cercopithecus campbelli* and *C. diana* had the largest mean monthly overlap and largest range of monthly overlaps in species-specific item use (mean = 39%, range = 12–58%). *Cercopithecus petaurista* with *C. campbelli* and *C. petaurista* with *C. diana* had similar monthly overlaps of species-specific item use (mean = 26%, range = 15–34%) and (mean = 28%, range = 12–37%), respectively.

Species-specific item use by monkeys changed the most during periods of low fruit availability (May–August), when diets for all species were the most diverse (Buzzard, 2004). For all species, the lowest overlaps in species-specific use between conspecific groups were at this time. Further, overlaps between all species pairs dropped off sharply in August (Fig. 5). Over all the months of lowest fruit availability (May–August 2001), however, the average overlap in species-specific consumption was only slightly lower between *Cercopithecus diana* and both *C. campbelli* and *C. petaurista* than the average overlap in the other months (Fig. 5). During months of lowest fruit availability (May–August 2001), the average overlap between *Cercopithecus campbelli* and *C. petaurista* is slightly higher than the average overlap during other months.

For all 3 pairs, neither monthly fruit nor flower availability correlated with dietary overlap in species-specific items; seasonal fruit/flower availability did not correlate with dietary overlaps either. Dietary overlap in species-specific items was associated with dietary item consumption in only 1 case: fruit consumption of *Cercopithecus diana* is positively correlated with species-specific overlap of *C. diana* and *C. campbelli* ($r_s = 0.6, p < 0.05$, $N = 13$ mo). There is no other correlation between diet overlaps and consumption of any species-specific food items from month to month.

Vertical Stratification and Its Effects on Frugivory

Cercopithecus campbelli individuals were on the ground and in the lowest stratum more frequently than the other species were (Table IV). At the other extreme, *Cercopithecus diana* more often used the canopy and emergents than *C. campbelli* and C. *petaurista* did. *Cercopithecus petaurista* more frequently used the understory than the other species did.

I also analyzed the strata used for feeding activity only, with results similar to those for all activity records (Buzzard, 2004). *Cercopithecus campbelli* fed primarily in lower strata. *C. petaurista* fed more than the other species in the middle stratum, and *C. diana* fed more often than the other species in higher strata.

If the analysis was limited to fruit feeding, differences among the 3 monkey species remained. Over the whole study, fruit gathered from the ground and consumed there or in lower forest strata accounted for 27% ($N = 441$) of fruit eating records of *Cercopithecus campbelli* compared to

Table IV. Vertical stratification

	Ground	Low stratum (0–5 m)	Mid-stratum (5–20 m)	Canopy/emergents (>20 m)
Cercopithecus campbelli ($N = 9731$)	8%	50.4	30	11.7
Cercopithecus petaurista ($N = 9944$)	1.2	37.5	42.1	18.8
Cercopithecus diana ($N = 8566$)	1.8	17.8	42.6	37.9

Note. Percentages of all scan records for *Cercopithecus campbelli, C. petaurista,* and *C. diana* in each stratum.

Table V. Percentage of different sized fruit trees used

	Cercopithecus campbelli ($N = 112$)	*Cercopithecus petaurista* ($N = 185$)	*Cercopithecus diana* ($N = 396$)
DBH <10 cm	31	25	12
DBH 10–40 cm	35	43	31
DBH >40 cm	34	32	57

Note. For a fruit tree to be used, subjects had gather and consume the fruit in the tree. Hence *N*'s are fruit feeding records not including fruit gathered on the ground (see Methods). DBH, Diameter at breast height.

19% ($N = 7511$) and 11% ($N = 310$) for *C. diana* and *C. petaurista*, respectively. Furthermore, *Cercopithecus diana* fed on fruit more in larger trees (>40 cm DBH) compared to the other species, while *C. campbelli* used smaller (<10 cm) fruit trees more than the other species did (Table V, $G = 34$, $p < 0.005$).

Age/Sex Differences in Dietary Items

I carried out all analyses of diet and dietary overlap for different age/sex classes only on food items because sample sizes became too small with finer grained analyses. Over the annual period, each age/sex class consumed food items typical of its species (Table VI). Thus, all *Cercopithecus campbelli* age/sex classes ate primarily fruit and also large amounts of animal matter while all *C. petaurista* age/sex classes ate primarily foliage; all *C. diana* age/sex classes ate primarily fruit.

Table VI. Percentages of food items for *C. campbelli*, *C. petaurista*, and *C. diana* age/sex classes over the 13-mo study period

	Fruit	Foliage	Animal Matter
Cercopithecus campbelli			
Adult male ($N = 116$)	67	7	24
Adult female ($N = 515$)	50	11	38
Juvenile ($N = 213$)	42	12	40
Cercopithecus petaurista			
Adult male ($N = 133$)	40	43	7
Adult female ($N = 419$)	35	45	5
Juvenile ($N = 267$)	40	40	12
Cercopithecus diana			
Adult male ($N = 50$)	71	12	12
Adult female ($N = 427$)	63	15	18
Subadult ($N = 183$)	68	15	16
Juvenile ($N = 519$)	61	21	17

Differences among age-sex classes within each species were similar for all 3 *Cercopithecus* species, in all of which adult males ate more fruit but less animal matter and foliage than adult females did. *Cercopithecus campbelli* and *C. diana* adult males also ate more fruit and less animal matter than did juveniles.

For the age/sex classes, I had hypothesized that greater interspecific rather than intraspecific dietary overlap suggests at least the potential for interspecific competition. Dietary overlap in food items was generally greater among the age/sex classes intraspecifically than interspecifically. The only exception was overlap between *Cercopithecus campbelli* and *C. diana,* mirroring earlier results for the 2 species as a whole. For *Cercopithecus campbelli*, intrapecific overlap among age/sex classes is not significantly higher than interspecies overlap with *C. diana* (Table VI, Mann-Whitney $U = 24.5$, $p > 0.05$).

DISCUSSION

Food Partitioning

The 3 species shared most of the principal plant species and species-specific plant foods, but they often ate different amounts of food items (e.g., more foliage than fruit) so diet partitioning was driven primarily by differences in major food items. Based on their work in the 1980s, Galat and Galat-Luong (1985) reported that all Taï guenons ate mostly fruit (76–78% of feeding records), though they identified *Cercopithecus campbelli* as eating a larger proportion of prey than its congeners as in this study. In my study, the guenons were better habituated, however, which enabled better identification of less easily observed dietary items such as prey and liana leaves. The only comparable data for another population of *Cercopithecus campbelli* comes from southeastern Côte d'Ivoire (Bourlière *et al.,* 1970). There, *Cercopithecus campbelli lowei* is largely frugivorous, but Bourlière *et al*. (1970) also describe the guenons taking a large portion of insects often with the same capture techniques (leaf unrolling) as occur at Taï. Like *Cercopithecus petaurista*, several other guenons including *C. ascanius* and *C. lhoesti* eat large amounts of foliage (35% of annual diet, Chapman and Chapman, 2000; Kaplin and Moermond, 2000). Lawes (1991) suggests that increasing foliage in the diet allows *Cercopithecus mitis* to coexist with other guenons because leaves are a relatively abundant resource. *Cercopithecus petaurista*, however, ate an even higher percentage of foliage over the study (40%) than *C. lhoesti* and most populations of *C. ascanius* and *C. mitis* did (Chapman *et al*., 2002).

My study confirmed the high fruit consumption by *Cercopithecus diana* documented elsewhere (Curtin, 2002; Eckardt and Zuberbühler, 2004; Oates and Whitesides, 1990; Wachter *et al.,* 1997; Whitesides, 1991). Unlike earlier studies, however, I found that animal matter contributed less to the diet of *Cercopithecus diana* (15.9% of annual diet in this study vs. 27–38% at Taï, Eckardt and Zuberbühler, 2004; Wachter *et al*., 1997; 25–31% at Tiwai, Oates and Whitesides, 1990; 25% at Bia, Ghana, Curtin, 2002).

Stratum Partitioning

The 3 species used the same forest strata but to different degrees. I confirmed a preference in *Cercopithecus campbelli* for lower forest strata as McGraw (1996, 2000) noted previously. All Taï guenons ate substantial portions of fruit from the ground (11–27% of fruit records) but *Cercopithecus campbelli* consumed fruit primarily from the ground or from small-diameter fruit trees (<10 cm DBH); the relative preference for low strata was an important factor in niche partitioning.

Cercopithecus diana, like *C. campbelli,* ate primarily fruit, but *C. diana* were most often in the forest canopy and ate fruit mainly from trees with medium and large DBH. The relative preference for medium to large trees by *Cercopithecus diana* agrees with earlier findings that *C. diana* is limited to old secondary and primary forest (Booth, 1956; Oates, 1988). At times, *Cercopithecus diana* used aggressive interference competition to drive the other species (especially *C. campbelli*) from large trees; during August and September 2001, only *Cercopithecus diana* preferred *Oldfieldia africana* (Euphorbiaceae), 1 of the larger trees in the forest (Buzzard, 2004). Aggressive interference competition also maintains a disparity in feeding tree size between *Varecia variegata rubra* and *Eulemur fulvus albifrons* (Vasey, 2000).

Vertical stratification contributed less to ecological partitioning than differences in food items in *Cercopithecus petaurista*. *Cercopithecus petaurista* primarily used strata intermediate between *C. campbelli* and *C. diana*, though activity of *Cercopithecus petaurista* in the canopy and large DBH trees was likely underestimated because of their cryptic nature. *Cercopithecus petaurista* spent much of their time hidden in dense liana growth as reflected by high consumption of liana food items.

Waser (1987) identifies patch size as the niche dimension most universally differentiating sympatric frugivorous primates, but other researchers have not noted such partitioning via size of feeding trees and fruit collection from the ground in other arboreal forest guenons. Terrestrial food collection by semiterrestrial forest guenons, e.g., *Cercopithecus lhoesti, C. neglectus*, is not surprising. Gathua (2000) reported terrestrial collection of cotyledons of *Bosqueia phoberos* (Moraceae) by arboreal *Cercopithecus ascanius*, but they account for <1% of the annual diet. Substantial terrestrial food collection by mainly arboreal guenons such as *Cercopithecus campbelli, C. petaurista*, and *C. diana* is unexpected, and may be critical not only for understanding niche partitioning among the species but also for appreciating the amount of competition with other community frugivores such as duikers (*Cephalophus* spp.) and squirrels (e.g., *Epixerus* spp., Emmons *et al*., 1983; Gautier-Hion *et al*., 1980).

Comparisons Among Other Primate Communities

Comparing diets and dietary overlaps from 3 guenon species at Taï with other communities could be problematical because of interannual differences among studies and because different studies have used different methods to assess dietary composition, especially in the case of indirect methods (stomach contents) that Gautier-Hion (1980) used. However, I agree with Chapman *et al.* (2002) that differences among communities are too large to be explained by interannual and methodological differences. Thus, though I am comparing different methodologies over different times, the overlap comparisons among communities are still instructive.

A great deal of variation exists among primate communities in resource overlap and species relationships. Two extreme cases involve 2 lemur species at Ranomafana (*Eulemur rubriventer* and *E. fulvus rufus*, Overdorff, 1993) and 3 colobines at Taï (*Procolobus verus, P. badius*, and *Colobus polykomos*, Bergmann, 1998). The lemurs exhibit many dietary similarities with no significant difference in overall dietary composition or plant species preferred. Evidence for interspecific competition is evident in that inter specific dietary overlaps range from >50% during times of fruit abundance to 6% during fruit scarcity. Further, the *Eulemur fulvus rufus* migrate from the study area when fruit is scarce and return thereafter. Much less dietary overlap exists in the Taï colobine community than between the lemurs at Ranomafana (Bergmann, 1998). For example, monthly species-specific diet overlaps averaged only 1.4–12.4% among colobine species at Taï. Such low overlaps indicate clear niche separation and little potential for interspecific competition at present.

The guenons at Taï showed intermediate patterns. Their diets were more different in terms of food items than reported for most other guenon communities. At most other sites annual and monthly food item overlaps between guenon species were considerably higher (83–95%) than at Taï (57–71%, Table VII). The only exceptions are *Cercopithecus mitis* and *C. lhoesti* in Nyungwe Forest, Rwanda, where the semiterrestrial

Table VII. Annual and monthly overlap in major food items such as fruit, foliage, and insects as well as species-specific plant food items from various guenon communities

Study site	*Cercopithecus* species pair	Annual food item overlap	Annual species-specific overlap	Monthly food item mean (range)	Monthly species-specific mean (range)	Reference
Taï, Cote d'Ivoire	*C. campbelli/C. diana*	71	51%	73 (46–97)	39 (12–58)	1
	C. campbelli/C. petaurista	57	34%	59 (50–67)	26 (15–36)	1
	C. petaurista/C. diana	71	37%	65 (54–77)	28 (11–37)	1
Kakamega, Kenya	*C. mitis/C. ascanius*	84	70%	77 (67–93)	62 (53–74)	2
Kibale, Uganda	*C. mitis/C. ascanius*	85	34, 39	—-	34 (5–55)	3,4,5
Makokou, Gabon	*C. pogonias/C. nictitans*	84	—	—	—	6
	C. pogonias/C. cephus	95	—	—	—	6
	C. cephus/C. nictitans	89	—	—	—	6
Dja, Cameroon	*C. pogonias/C. nictitans*	84	—	—	—	7
	C. pogonias/C. cephus	95	—	—	—	7
	C. cephus/C. nictitans	83	—	—	—	7
Nyungwe, Rwanda	*C. mitis/C. lhoesti*	47%	—	—	25% (17–38)	8

Note. References: 1, this study; 2, Cords (1986); 3, Struhsaker (1978); 4, Struhsaker (1981); 5, Lambert (2002); 6, Gautier-Hion (1980), 7, Poulsen *et al.* (2002), 8, Kaplin and Moermond (2000). Gautier-Hion (1980) used Pianka's (1973) index to measure overlap and Poulsen *et al.* (2002) used Schoener's (1974) index. All other references measured overlaps by summing shared percentages of resource use (Holmes and Pitelka 1968).

The methods used to gather feeding data varied considerably between studies. For example, Struhsaker (1978) collected feeding data for multiple individuals every 30 min while Lambert (2002) collected continuous feeding data for individuals over 30-min periods. Species-specific overlaps from this study include items from unidentified lianas.

C. lhoesti differs substantially in the items it consumes compared to arboreal *C. mitis* (47% annual food item overlap).

Annual plant diet overlap values based on plant species were reduced by 20–34% relative to values based on items, suggesting that the Taï guenons increased ecological segregation by taking shared items from different plant sources. The drop-off in monthly overlaps was greatest for *Cercopithecus petaurista* and *C. diana* (34%) and for *C. campbelli* and *C. petaurista* (23%), suggesting that they showed the greatest dietary segregation by using different plant sources. Unlike some guenon communities, the Taï guenons showed very little divergence in the items they ate from shared plant species. Monthly species-specific item overlaps were practically identical to plant species overlaps for the species-pairs at Taï. *Cercopithecus campbelli* and *C. diana* had the highest average monthly species-specific overlap of Taï guenons (39%), which most resembled the overlap of *C. mitis* and *C. ascanius* at Kibale (34%). *Cercopithecus campbelli* and *C. petaurista* had the lowest overlap at Taï, which resembled the guenons at Nyungwe, and none of the species-specific plant food overlaps at Taï were as high as the overlap between *C. mitis* and *C. ascanius* at Kakamega (Table VII).

One reason why overlaps in species-specific items may have been lower at Taï than in other communities is that the potential for interspecific competition is less intense for the guenons at Taï than for guenons at other forests. Support of this contention, however, requires more long-term studies, using similar methods, on ecological partitioning and resource at Taï and other communities. To more convincingly demonstrate differences in the potential for interspecific competition, such studies would have to show consistent interspecific differences in overlap values during different levels of resource availability.

As in previously studied guenon communities (Kakamega, Makokou, and Dja, Cameroon), at Taï there was much overlap in strata use, but different species concentrated their activities in higher or lower strata to different degrees. At Kakamega, *Cercopithecus mitis* and *C. ascanius* overlap in 92% of height records, but *C. mitis* have 5% more records >20 m while *C. ascanius* have 8.4% more observations than *C. mitis* in the middle stratum, 7–20 m (Cords, 1987). At Makokou, *Cercopithecus cephus* have average stratum heights 3–9 m lower than those of *C. nictitans* and *C. pogonias* (Gautier-Hion *et al.,* 1983). Similarly, at Dja, there is no significant difference in *Cercopithecus nictitans* and *C. pogonias* feeding heights and both species overlap in 80% of feeding height records with *C. cephus* (Poulsen *et al.*, 2002). Among the 3 Taï species, there was more distinct vertical stratification than in the other studies and even more distinct stratification occurred at Nyungwe, where semiterrestrial *Cercopithecus lhoesti* use the ground much more than sympatric *C. mitis* did (38% vs. 2.4% of observations, Kaplin and Moermond, 2000). Vertical stratification is also important in the niche partitioning of Sumatran anthropoids (*Hylobates lar, Macaca fascicularis, Pongo pygmaeus*, and *Presbytis thomasi*: Ungar, 1996) as well as the niche partitioning of tamarins (*Saguinas fuscicollis*) and marmosets (*Callithrix emiliae*, Lopes and Ferrari, 1994).

Seasonal Variation in Food Availability and Diet

Abundance of fruit, flowers, and insects at Taï showed qualitatively similar patterns to forest from nearby southeastern Liberia (Gatter, 1997): abundance of fruits varied bimodally and was more variable than the abundance of flowers, while insects were available throughout the year.

Researchers have used seasonal divergence in diet during times of food scarcity to demonstrate interspecific competition in various taxa (birds: Smith *et al.,* 1978; mammals: Emmons, 1980; Gautier-Hion, 1980). An examination of seasonal variation in dietary overlaps between the study species suggested the effects of interspecific competition among Taï guenons, especially *Cercopithecus campbelli* and *C. diana*. The diets of *Cercopithecus campbelli, C. petaurista*, and *C. diana* diverged most noticeably and dietary diversity indices increased during the season of low fruit availability (May–August, this study; Buzzard, 2004). In addition, dietary overlap, whether measured as items or species-specific plant items, declined for all 3 guenon pairs during low fruit availability. The seasonal diet divergence is greatest between *Cercopithecus campbelli* and *C. diana*, and consequently, they had the lowest food item overlap during the season of low fruit availability. Further, *Cercopithecus campbelli* and *C. diana* are also the only species pair with a positive correlation between food item overlap and fruit availability.

At Makokou, Gabon, overlaps in food items also decline in certain months for the *Cercopithecus nictitans*/*C. cephus* and *C. nictitans/C. pogonias* pairs; the average seasonal overlap of 92% and 88% decline to monthly overlaps of 60% and 53%, respectively (Gautier-Hion, 1980, 1988). Thus, dietary overlaps for the *Cercopithecus nictitans*/*C. cephus* and *C. nictitans/C. pogonias* pairs reduce their overlap by 32–35% during the season of low fruit availability. Similarly, the difference between the average food item monthly overlaps and the lowest monthly overlap is 27% for *Cercopithecus diana* with *C. campbelli* at Taï. Gautier-Hion (1980) offered such divergence at Makokou as evidence of interspecific competition. Food item overlaps are much higher over the year in Makokou; therefore, the divergence may be more important. Among the 3 species at Taï, different food item preferences reduced food item and species-specific item overlap throughout the year so the amount of seasonal divergence was minimized. Dietary divergence in food items is not as great at Kakamega, where the average monthly overlap of food item overlap (78%) drops to a low of only 68% (Cords, 1986, 1990), and the average monthly species specific item overlap of 62% drops to only 53% (Cords, 1990).

The diet of *Cercopithecus petaurista* did not diverge from the diets of *C. diana* and *C. campbelli*, during the season of low fruit availability as much as the latter 2 species diverged from each other. The monthly species specific overlaps for *Cercopithecus petaurista/C. diana* (11–37%, mean = 28%) and *C. petaurista/C. campbelli* (15–36%, mean = 26%) closely resembled the monthly range for *C. lhoesti* and *C. mitis* (17–38%, mean = 25%; Kaplin and Moermond, 2000). The community of *Cercopithecus lhoesti* and *C. mitis* is characterized by the high amounts of terrestrial herbs *C. lhoesti* consume in secondary forest. Similarly, high consumption of liana foliage by *Cercopithecus petaurista* is responsible for the low overlaps with other species.

Age/Sex Class Differences

In intraspecific comparisons, social and physiological reasons exist for greater fruit consumption in adult males and greater prey consumption in adult females and juveniles (Cords, 1986; Gautier-Hion, 1980). Some age/sex differences in consumption of different food items in my study were common to the study species and resembled age/sex differences in other forest guenon communities (Cords, 1986; Gautier-Hion, 1980). At Taï, as in other guenon communities, adult males of all species ate more fruit than conspecific adult females did. Males spend much of their time vigilant for other males and potential predators, and the rapid harvesting of fruit, especially when combined with cheek pouch use, facilitates vigilance. Adult females and juveniles of all species consumed more prey items than conspecific adult males did, as others have found (Cords, 1986; Gautier-Hion, 1980; Vasey, 2002). Females may need to eat more prey to support the protein demands of pregnancy and lactation (Vasey, 2002). Increased prey consumption by juveniles may also represent an increased protein demand in response to faster growth or energetic requirements (Gaulin, 1979).

Dietary overlap between the age/sex classes of different species at Makokou is an important aspect of interspecific relationships (Gautier-Hion, 1980). For example, adult male *Cercopithecus cephus* overlap more with adult *C. nictitans* while female *C. cephus* overlapped more with adult *C. pogonias*. In addition, during the dry season, male *Cercopithecus nictitans* overlap more in food item use with adults of other species than with female *C. nictitans*. Interspecific age/sex differences were not as important in Taï. Variation in interspecific age/sex overlap, however, provided further evidence for the greater importance of interspecific competition between *Cercopithecus campbelli*/*C. diana* compared to other species pairs. Specifically, age/sex classes of *Cercopithecus campbelli* and *C. diana* overlapped much more with each other than either overlapped with *C. petaurista*. In the case of *Cercopithecus petaurista*, intraspecific overlap was considerably higher than interspecific overlap, suggesting that the potential for intraspecific competition was higher than interspecific competition for *C. petaurista*. Caution is required, because of low sample sizes.

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