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Niche Separation of Black-and-White Colobus Monkeys (*Colobus angolensis* and *C. gureza*) in the Ituri Forest

by

Carolyn M. Bocian

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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ABSTRACT

Niche Separation of Black-and-White Colobus Monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri Forest

by

Carolyn M. Bocian

Co-advisors: Professors John Oates and Carol Simon

I studied the ecology and social organization of sympatric *Colobus angolensis* and *C. guereza* to test the hypothesis that basic species differences may explain their niche separation. Field work was conducted in the Okapi Wildlife Reserve, Central Ituri Forest, from late 1992 to early 1994. Systematic observation of study groups over a 12-month period examined food selection, habitat use, and ranging patterns. Census work was conducted in three forest types to determine patterns of local abundance. Analyses of food chemistry examined the relationship between food selection and specific chemical measures.

In most months, *Colobus guereza* was primarily folivorous; *C. angolensis* was less specialized. In contrast to *C. angolensis*, seed-eating by *C. guereza* seemed to be a compensatory response to young leaf scarcity. Leaf selection by *C. angolensis* was negatively correlated with fiber content; for *C. guereza*, no such correlation was found. Interspecific diet overlap was highest for two categories of foods: young leaves of rare deciduous trees, and seeds of common leguminous trees.

The species differed in their social organization and in patterns of range use. *C. angolensis* occurred in large, multi-male bisexual groups, and frequently formed temporary associations with other conspecific groups. The study group used a large home range which overlapped extensively with those of other groups. *C. guereza* formed smaller, bisexual groups, with one or two adult males. The study group used a much smaller range, within which one area was used intensively; range overlap with conspecific groups was low. *C. angolensis* ranging patterns were associated with food availability, while those of *C. guereza* were associated with the proximity of conspecific groups.

The study groups differed in habitat use. *C. angolensis* used closed-canopy forest much more than did *C. guereza*; *guereza* seemed to prefer open-canopy areas. Census results suggest that *C. guereza* may be twice as abundant in secondary forest than it is in mature mixed forest; the species is apparently rare in *Gilbertiodendron*-dominant forest. *C. angolensis* occur at similar densities in secondary and in mature mixed forest, but at lower densities in *Gilbertiodendron* forest.

Evidence from this study suggests that:

1. *C. guereza* shows a strong tendency toward folivory; this tendency may reflect a specialized ability to process leaf fiber;
2. Species differences in social organization may partially explain their differences in ranging patterns; such differences may lead to very different patterns of resource exploitation;
3. In sympatry, species differences in habitat use may reflect preferences for different forest types;
4. Basic species differences may be stronger determinants of *Colobus* niche separation than are interspecific interactions.

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May this work benefit the animals.

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Chapter 1. INTRODUCTION

I. Community Ecology

A. Historical Development of Resource Partitioning Theory

Resource partitioning, or the manner in which nutrients and habitat are utilized by co-occurring, closely-related species, is generally manifested by differences in nutrient consumption, habitat use, and/or time of activity. In the classical sense, the main reason resource partitioning is studied is to "analyze the limits interspecific competition places on the number of species that can stably coexist" (Schoener, 1974). This rationale built on the theoretical work of Volterra (1926) and Lotka (1932), experimental work by Gause (1934), and the theoretical contributions of MacArthur and Levins (1967), and came to dominate niche separation studies. The result was that interspecific competition was considered a primary determinant of resource partitioning among coexisting species, and, in a broader sense, of community composition and structure. Because dissatisfaction with competition-based coexistence models led to consideration of alternative processes, the assumptions of the most influential of these models will be considered.

Based on the principle of competitive exclusion, the MacArthur and Levins model (1967) described limits to the similarity of coexisting species, or the minimum amount of separation in resource use necessary for coexistence. The model was based on the Lotka-Volterra competition equations, which assume that, in a two-species system, equilibrium conditions are determined by each species' carrying capacity and by the intensity of interspecific competition, but not on their intrinsic rates of increase. The approach developed by MacArthur and Levins sought to describe the niche of each species, within a three-species system, as a resource utilization curve. They assumed that 1) resource use along the niche axis was normally distributed; 2) curves for different species were at different positions on the axis; and 3) the two peripheral species had similar carrying capacities. The models generated a range of carrying capacity ratios (or "favorable habitat"), and of niche overlaps, which allow three species to coexist at equilibrium.

Some criticisms of this approach focused on assumptions about resource use; e.g., that resource utilization curves of different coexisting species often have different shapes and are not normal distributions, and that, in many cases, it is not realistic to consider resource use in only one dimension (Abrams, 1983). Other criticisms were directed specifically at the use of equilibrium models, which cannot simulate community dynamics under nonequilibrium conditions. For example, Rotenberry (1980) has argued that under conditions of environmental variability, autecological factors are likely to have much more impact on community structure than is interspecific competition; he suggests that competitive relationships may be less likely to develop under such conditions.

Consideration of alternative processes gained momentum with Connell's (1983) review of field experiments studying interspecific competition. Most of these studies were not designed to separate the effects of interspecific and intraspecific interactions; however, in those that were, and in which competition was demonstrated, intraspecific competition was as strong or stronger than interspecific in three-fourths of the studies. Other field and experimental evidence suggests that predation and parasitism (Strong, 1982), intraspecific competition (Rosewell *et al.*, 1990), and environmental variability (Rotenberry, 1980) can be of primary influence in some communities. Finally, Bourlière (1985) discusses the influence of competition among taxonomic groups, spatial heterogeneity of the vegetation, and history and paleoecology in contributing to differences in structure among communities.

Community modelling has proliferated since the 1960s, and it is not the intent of this thesis to discuss the relative merits of theoretical vs. empirical studies. However, disagreements which arose between the two lines of enquiry, have, perhaps, underlined the necessity of asking appropriate questions in examining species coexistence. Increasingly, for example, field ecologists have begun to consider whether the ecology of individual species, the influence of species at different trophic levels, and environmental variability may be more influential than competition with closely-related species in determining observed patterns of resource utilization (Strong, 1983).

B. Studies of Resource Partitioning in Mammals

To underline some of the difficulties in interpreting observed patterns of coexistence, the present section will discuss selected studies of resource partitioning in mammals. These studies encompass several orders of mammals (Carnivora, Rodentia, Artiodactyla, and Primates) and a variety of ecosystems.

Trombulak (1985) carried out an experimental field study of two sympatric chipmunks, *Eutamius townsendii* and *E. amoenus*, in the Cascade Mountains (Washington State). His intent was to discern the effect on home range size of competitive interactions that do not result in habitat separation. The two species did not partition habitat nor microhabitat, and had similar home range sizes. Between-species diet overlap was high, and both were active at the same time of day. After removal of the behaviorally dominant (and larger) species, *E. townsendii*, home range expansion was observed in individual *E. amoenus* that had smaller ranges in the presence of *E. townsendii*. Furthermore, juvenile recruitment (and population density) of *E. amoenus* increased after removal of the other species. Trombulak seems to have demonstrated the density-dependent effects of interspecific competition, at least of *E. townsendii* on *E. amoenus*. More importantly, for this two-species system, interspecific competition did not result in resource partitioning; rather, competition led to strong interference interactions and depressed population growth in one species.

Johnson and Franklin (1994) compared the feeding ecology of sympatric gray and culpeo foxes in southern Chile, to determine whether seasonal and species differences in prey utilization were related to prey availability, or if differences reflected prey selection by each species. Their results indicated that 1) both foxes preyed on the same categories of vertebrates, but in different proportions; 2) home ranges of gray and culpeo foxes did not overlap, and each used a different habitat type; and 3) prey availability was different in the ranges of each species, suggesting that differences in feeding habits between species reflected habitat differences. Johnson and Franklin concluded that gray and culpeo foxes had similar optimal diets, and that the larger culpeo foxes excluded gray foxes from habitat with optimal prey. Further, they hypothesized that the two species minimized competition by "adjusting body size", and therefore daily energy intake, such that each species could occupy a different habitat.

These authors point out that size differences between gray and culpeo foxes increase with latitude, and that both are found from northern Chile south to Tierra del Fuego. However, it is not clear from their report whether these species always co-occur. If allopatric populations exist, a comparison of morphological and ecological characteristics with sympatric populations might clarify the significance of their findings. They seem to assume that resource partitioning would be the effect of interspecific competition in writing "...ecological theory predicts that, for these two closely related carnivores to coexist, they will reduce interspecific competition by partitioning resources (Rosenzweig, 1966)." However, Trombulak's work on chipmunks has demonstrated that interspecific competition does not always lead to resource partitioning.

Some sympatric herbivores also show evidence of habitat partitioning. Dunbar (1978) studied niche separation in a community of seven herbivores occurring in high altitude heath and moorland (Simien Mountains National Park, Ethiopia). The community consisted of gelada baboons and six artiodactyls - ibex, klipspringer, bushbuck, bush duiker, and recently-introduced horses and cattle. The seven species could be roughly divided into two dietary categories, graminivores and true herbivores. Diet overlap between two graminivores, or two herbivores, was apparently minimized by habitat partitioning. With the exception of gelada, each species showed a distinct preference for a specific habitat type, i.e., escarpment, ridge top, or gorge, although all species except horses used all three of these areas. Seasonal changes in the amount of diet overlap were observed; e.g., during the wet season, when fresh graze was abundant, the diet of horses and gelada was almost entirely grass blades. During the dry season, gelada switched to grass rhizomes and roots, while horses continued searching for grass blades. In general, Dunbar observed that where overlap was high between two species, diets diverged markedly when non-renewable foods were scarce.

Dunbar points to an additional factor which may reduce interference, and the likelihood of competition, among species: their social systems are different, such that their spatial distribution within the study area differed. He does not, however, address the question of what may lead to their habitat separation.

Emmons' (1980) study of resource partitioning among nine species of African rain forest squirrels sought to evaluate the primary influences on their species richness in African forests compared to Nearctic forests. Two species were restricted to certain habitats, while the other seven showed vertical stratification in vegetation use; species occupying a given habitat and foraging level differed in body size, and the four largest species had short activity periods. No interspecific aggression was observed. Emmons found, as did Dunbar (above), that different species' diets were most divergent during the major dry season, with each species concentrating more on its "specialty", and that diets were more similar during the season of greatest food abundance.

Emmons concludes, after finding no evidence to the contrary, that interspecific food competition has been the primary selective factor determining the observed pattern of resource partitioning. Emmons further suggests that the high taxonomic diversity of this community may "implement" ecological diversity among the nine species. She discusses her conclusions as consistent with MacArthur and Levins' (1967) predictions concerning species packing and environmental predictability, and suggests that increased food productivity and environmental certainty may contribute to increased species packing. Her assumptions, and those of MacArthur and Levins, concerning mechanisms promoting species richness, as well as predictions concerning the importance of interspecific interactions, are completely different than those of Connell (1980) and others (e.g., Strong, 1982). Connell suggests that high species diversity is often associated with changing species composition resulting from environmental disturbance. In his view, high species diversity reduces the likelihood of consistent co-occurrence of a species pair, such that divergence due to competition is less likely. This rationale might lead one to suspect that inherent species differences could be at least as significant as interspecific competition in determining patterns of resource partitioning.

A finer-grained level of dietary separation was discernible in Murray and Brown's (1993) experimental test of niche separation in Serengeti ungulates. Thirty ungulate species occur in the Serengeti-Mara ecosystem (northern Tanzania and southwestern Kenya), twelve of which subsist on a diet almost entirely composed of grass. Two wildebeest, two topi, and one hartebeest were captured and used in experimental trials estimating food intake (bite rate and bite weight) and the degree of selection for both green (young to intermediate growth) and late growth leaf. The authors found that foraging behavior was strongly influenced by the growth stage of grass, and suggest that each species has specialized on a different growth stage: wildebeest, on early growth; topi, on green growth at an intermediate or mature stage; and hartebeest, on late growth which is dry and senescent. Furthermore, the nature of a species' ranging patterns may be related to the growth stage on which it specializes - wildebeest and topi (early and intermediate growth feeders) are migratory species, while hartebeest (late growth feeders) are residential. In the Serengeti, green growth is localized and ephemeral, appearing after rainstorms and fire, but this growth soon dries without recurring rainfall.

Murray and Brown suggest that growth stage is a primary determinant of niche separation, but suggest factors that may be additional components of niche space: the mobility of ungulate species, the distance between pastures of different growth stage, and the duration of a given growth stage.

C. Studies of Resource Partitioning in Nonhuman Primates

1. Special Considerations.

A fundamental challenge in studying resource partitioning in primate communities is the necessity of conducting observational rather than experimental field studies, since experimental studies are, in most cases, not feasible for ethical and logistical reasons. Removal experiments have been carried out with ants and rodents (e.g., Brown & Davidson, 1977; Trombulak, 1985) and other taxa. Such manipulations would be difficult to carry out with primates because 1) many populations are classified as vulnerable, if not endangered; experimental manipulation of such populations would, in most cases, be difficult to justify; 2) the psychological impact on the animals of such manipulations would compromise interpretation of results; and 3) even if animals were removed from experimental plots, others of the same species could move into these areas, as there would be no means of excluding them.

An additional consideration is the following: it is not known whether interspecific competition in primates is more likely to occur by interference, by exploitation, or both. Ecologists working with other taxa offer varying opinions on the relative importance of exploitation vs. interference. Tilman (1987) argues that interspecific aggression is rarely the proximate cause of competition; Strong (1983), that competition often takes the form of interference rather than exploitation; Roughgarden (1983), that exploitation should cause the evolution of interference mechanisms. Waser (1987) raises a related issue, which concerns the frequency and effects of interspecies aggression in primates: how often do such interactions occur, and how effective are they in excluding potential competitors? Waser's observation that many authors describe mixed-species feeding associations in which aggression does not occur raises additional questions: if two species do not interact aggressively, is there no potential for interference? Or could interference be manifested as displacement, without aggression?

Without experimental manipulation, one cannot be certain if the availability of a shared food results in competition by exploitation. In fact, some would argue that many niche overlap studies are meaningless (e.g., Case, 1984). Measuring the effects of other processes that may influence a species' habitat and food choice, such as predation, disease, intraspecific competition, and environmental disturbance or variability, is probably no less difficult than measuring the effects of interspecific interactions or diet overlap. Thus, those who study resource partitioning in primates (and other taxa) can offer evidence in support of an hypothesis, but cannot rule out most alternatives. This does not mean that such studies should be dismissed; primates constitute a significant proportion of total mammalian biomass in some ecosystems (Struhsaker, 1975), are sources of food for large felids and raptors (Cheney & Wrangham, 1987), and play a role in seed dispersal (e.g., Howe, 1982). Thus, an understanding of proximate factors contributing to primate species coexistence, and speculation about the origins of species differences, may contribute to a better understanding of community dynamics.

2. Patterns of Niche Separation and Proximate Influences.

With the exception of the Neotropical owl monkey (*Aotus trivirgatus*), anthropoid primates are diurnal. Thus, general time of activity (i.e., day vs. night) is not a factor in niche separation among anthropoids (but may be in prosimian communities; Ganzhorn, 1989), although coexisting species may differ somewhat in the hour at which foraging progressions or rest periods begin (e.g., Curtin, 1980). MacKinnon and MacKinnon (1980) pointed to the possibility that different peaks of activity may reduce the potential for conflict at shared food sources. Most studies suggest that species differences in habitat use, in ranging patterns, and/or in diet composition are the primary means by which niche separation occurs in primate communities.

Proximate influences on niche separation are not explicitly considered by some of the authors whom I cite below. As used in the niche separation literature, "proximate influences" may refer either to proximate mechanisms (the physiological causes of behavior or behavioral mechanisms; e.g., Steklis, 1993) or to environmental cues.

a. Differences in habitat use. Habitat differentiation may occur at several levels. Sympatric populations may locally segregate into different habitat types (allotopy), or use the same type of habitat (syntopy). Rodman (1991) describes almost complete habitat separation between *Macaca nemestrina* and *M. fascicularis* in Indonesia; *M. nemestrina* occurs on dry, hilly terrain, while the latter uses wetter, riverine terrain (for other examples of allotopic habitat use, see Gartlan & Struhsaker, 1972; Kinzey & Gentry, 1979). MacKinnon and MacKinnon (1980) report similar habitat differentiation between the two species in Malaysia. Rodman (1991) proposes that structural differences in vegetation (such as the thickness of ground vegetation, ground slope, the number of saplings and vines, the number and size of canopy gaps, and canopy density) are proximate indicators of habitat boundaries to *M. nemestrina* and *M. fascicularis*, and that recognition of these cues is a behavioral mechanism maintaining their habitat separation.

Although syntopic populations show overlap in habitat use, such that members of different species may be seen in proximity, one or more species within the community may exhibit habitat preferences. For example, Curtin (1980) reports differences in habitat preferences between Malaysian populations of *Presbytis melalophos* and *P. obscura*; *P. melalophos* was often observed in riverine areas, while *P. obscura* preferred mature forest. Dunbar and Dunbar (1974) and Moreno-Black and Maples (1977) also report differences in habitat preferences among essentially syntopic species. A third level of differential habitat use may occur through vertical stratification, or differential use of vegetation levels (Booth, 1956; Gautier-Hion & Gautier, 1979; Galat & Galat-Luong, 1985). For example, Gautier-Hion and Gautier observed intensive use of mature forest by *Cercopithecus cephus*, *C. pogonias*, and *C. nictitans* in northeastern Gabon, although *C. cephus* was found more often at lower heights (5 to 15 m) than *C. pogonias* and *C. nictitans* (10 to 25 m). In Ghanaian forests, Booth observed differential use of vegetation levels among species eating the same general food types.

Ganzhorn (1989) reported an additional form of habitat differentiation, by microhabitat use, among seven lemur species in eastern Madagascar. *Indri indri*, for example, used mature forest with an unrestricted layer of vertical supports; *Avahi laniger*, uniform stands of relatively young trees; *Microcebus rufus*, the "fine-branch-niche".

b. Differences in ranging patterns. Co-occurring species may differ in the average distance a group travels each day, in the proportion of the home range visited on a daily basis, in the distribution of time spent in different parts of the range (utilization diversity), and in annual home range size. Some workers have implicated food density, food dispersion, and food renewal rates as the proximate factors underlying interspecific differences in primate ranging patterns (e.g., Gautier-Hion and Gautier, 1979; Struhsaker, 1980).

In the Kibale Forest (Uganda), for example, *Cercopithecus ascanius* feeds primarily on fruit and arthropods, while *Procolobus badius* is primarily folivorous. Struhsaker's *C. ascanius* study group travelled about 2.23 times farther and used about 2.25 more quarter-hectare quadrats per day than did his *P. badius* study group; utilization diversity was higher for the *P. badius* group; the annual home range of the *P. badius* group was about twice that of the *C. ascanius* group (Struhsaker, 1980). Struhsaker suggests that species differences in ranging patterns are related to differences in density, dispersion, and renewal rates of fruits and arthropods as compared to leaf material; leaves occur at higher density but have a slower renewal rate than fruits and arthropods. MacKinnon and MacKinnon (1980) relate differences in body size between *Hylobates syndactylus* and *H. lar* to differences in foraging and ranging patterns. *H. syndactylus* is twice as large as *H. lar*. In the Krau Game Reserve (Malaysia), *H. syndactylus* day ranges were one-third the length of *H. lar*'s; the former species revisited favored food trees, while the latter used twice as many, more widely-dispersed food sources.

c. Differences in diet composition. Within a primate community, different species vary in overall levels of folivory, frugivory, and insectivory. Any one species may show great temporal variation in consumption of general food categories, such that in one month it may be primarily folivorous, and in other months either frugivorous or insectivorous (e.g., Chapman, 1987). The degree to which co-occurring species share the same foods is expressed as diet overlap (Holmes & Pitelka, 1968) or similarity (e.g., Pianka's (1973) index); most studies of niche separation in primates report the Holmes and Pitelka measure.

Whether overlap in use of a particular food item is likely to have serious consequences for the two (or more) species involved depends upon two related factors: the item's abundance during the time of overlap, and whether an inability to obtain sufficient quantities of it will limit an individual's potential for survival and reproduction. The first factor can be estimated; in most cases, the second factor is difficult to evaluate during short-term studies of long-lived animals such as primates.

For example, the mean monthly diet overlap between *Colobus guereza* and *Procolobus badius* in the Kibale Forest was 7.1% (range 2.0-15.7% over twelve months) for all food items; in the three months when overlap was highest, most of this overlap (ranging from 7.2% to 10.0%) was accounted for by the young leaves, leaf buds, and/or fruits of *Celtis durandii*, one of the most common trees in the forest (Struhsaker & Oates, 1975). The authors conclude that *C. durandii* is probably not a limiting resource for either colobine, and that the small amount of interspecific diet overlap does not constitute food competition. In the same forest, Struhsaker (1980) estimated diet overlap between *P. badius* and *Cercopithecus ascanius*; over a thirteen-month period, diet overlap ranged from 0.0-20.6%, with a mean value of 4.7%. Struhsaker observed that overlap was greatest in months when both *P. badius* and *C. ascanius* fed on super-abundant food items; these items were considered super-abundant because, in spite of heavy feeding by monkeys, a high proportion of them were not consumed. Struhsaker suggests that interspecific competition probably does not occur as the diets of the two species are sufficiently different.

Chapman's (1987) study of three sympatric primates in the Santa Rosa National Park (Costa Rica) reports a wider range of diet overlap. From 1984 through mid 1985, values are presented for 12 months. Mean overlap between *Alouatta palliata* and *Ateles geoffroyi* was 22.9% (range 0.0-83.7%); between *Cebus capucinus* and *A. geoffroyi*, 23.6% (range 0.0-43.0%); and between *C. capucinus* and *A. palliata*, 5.0% (range 0.0-30.1%). In this study, tree species for which diet overlap was high varied from being common to rare. Chapman concludes, for these primates in Santa Rosa, that diet overlap probably acts only intermittently as a selective force determining diet choice, because diets, diet overlap, and the plants for which overlap occurs are all highly variable.

Milton (1984) has pointed to the potential role of gut morphology and digestive processes, such as food passage rate, as proximate mechanisms in niche separation. Ganzhorn (1988) has suggested that plant chemistry may proximately influence differences in food choice, specifically among sympatric lemurs, reflecting species differences in abilities to obtain protein, to detoxify plant allelochemicals, and to perceive tastes.

3. General Trends.

Comparison among different studies is somewhat problematic, because duration of study periods are different, sampling protocols differ, and levels of detail in data analysis differ. However, some general trends seem to emerge from these studies:

a) When two species coexist allotopically, little to no overlap may occur in resource use, with each species eating foods found in their respective habitats. This appears to be the case with *Callicebus moloch* and *C. torquatus* in Peru (Kinzey & Gentry, 1979): although the species overlap in terms of geographical distribution, they may only rarely come into contact with each other because they use different habitats.

b) In two communities outside of the tropical moist forest zone (the Bole Valley, Ethiopia and the Diani Beach, Kenya coastal forest), both of which are low in primate species richness (5-6 species), clear species differences in habitat and food utilization are evident. The authors (Dunbar & Dunbar, 1974; Moreno-Black & Maples, 1977) suggest that competition is uncommon or minimal in these communities. However, the Bole Valley study involved 3 species of different genera, and the Diani study, 4 species of 3 genera; species of different genera may be expected to show greater differences in resource use than congeners.

c) In lowland or medium-altitude rain forest (M'passa, Gabon; Tai Forest, Côte d'Ivoire; Kibale Forest, Uganda; and Kuala Lompat, Malaysia), where primate species richness is higher, overlap is higher between congeners in habitat and food utilization. Gautier-Hion & Gautier (1979) and Galat and Galat-Luong (1985) observed that diets were most similar when food was readily available, but diverged when food availability decreased. Similarly, Struhsaker & Oates (1975) and Curtin (1980) noted that overlap was highest for common food items. Terborgh's (1986) study in Cocha Cashu, Peru, reported a high divergence in foods consumed by capuchins (*Cebus* spp.), squirrel monkeys (*Saimiri sciureus*), and tamarins (*Saguinus* spp.) when soft fruit was not available; in this case, the divergence was among rather than within genera.

Chapman (1987), however, points to an important consideration: one species' diet, and interspecific diet overlap, may vary considerably from one year to the next (see also Struhsaker, 1975; Waser, 1977). For example, *Quercus oleoides* acorns were abundant at Santa Rosa in both 1984 and 1985; Chapman's *Cebus* study group fed heavily on acorns in 1984, but were not observed eating them in 1985.

4. Potential Underlying Processes.

Rodman (1991) seems to suggest that niche separation in *Macaca nemestrina* and *M. fascicularis* is the result of interspecific competition and character displacement. In a related manner, Ganzhorn (1988, 1989) is less direct in implicating competition as a causal mechanism, but nevertheless bases his arguments on competition theory to the exclusion of alternatives (although, admittedly, divergence in sympatry is a more plausible explanation for species whose distributions are restricted to an island than for species with wide geographical distributions), and considers species differences in resource utilization as a major factor facilitating coexistence. While few would doubt that species differences in food and habitat use may enhance their ability to coexist, such lines of reasoning are less useful in explaining situations where niche overlap is high, or where overlap is highly variable from one year to the next.

For example, several coexisting species may derive mutual benefits by virtue of their coexistence, particularly in the case of mixed-species associations. Such associations could facilitate location of food sources, offer protection from predators (Oates & Whitesides, 1990), or both (Gautier-Hion & Gautier, 1979; Galat & Galat-Luong, 1985).

Chapman's (1987) conclusions raise important issues. Following Wiens (1977) and Strong (1983), he suggests that diet overlap may act only intermittently as a selective force favoring diet divergence. The specific conditions favoring diet divergence may be site-dependent, because diets may differ in different regions among which gene flow is possible. Potential causes of such variability are well worth considering. With respect to tropical forests, Terborgh (1986) and others suggest that fruit and flower production will be more unpredictable and irregular in more uniform climates. While such unpredictability would have a greater impact on frugivorous primates, it could also be expected to influence food choice in those populations of folivores that, in some months, become primarily granivorous (e.g., Maisels *et al.*, 1994).

Species differences evolved in allopatric populations, or autecological factors, could be major determinants of niche separation and coexistence (Gartlan & Struhsaker, 1972; Struhsaker & Oates, 1975; Kinzey & Gentry, 1979; Curtin, 1980; MacKinnon & MacKinnon, 1980). For example, differences in food preferences between sympatric species may be the result of differences in phylogenetically stable characteristics, such as gut morphology or dentition (MacKinnon & MacKinnon, 1980; Terborgh, 1986); differences in foraging patterns may reflect differences in limb structure and locomotor behavior (Curtin, 1980).

In fact, several mechanisms may be responsible for resource partitioning in a given community, but the influence of any one factor may vary over time, perhaps depending to some extent on how each species responds to variability in its environment. The most coherent approach to studying niche separation in primates, and other taxa, is to consider a number of alternative processes that could produce an observed pattern. Although one may not be able to rule out the influence of any potential causal factors, careful observation, and consideration of the available data on allopatric populations, can at least broaden our understanding of species coexistence.

II. Ecology and Social Organization of Black-and-White Colobus Monkeys

A. Species Distributions and Field Studies

Following Oates *et al.* (1994), the African colobines (Cercopithecidae, subfamily Colobinae) comprise two genera, the olive and the red colobus (genus *Procolobus*) and the black-and-white colobus (genus *Colobus*). The black-and-white group includes five species (*C. satanas*, *C. angolensis*, *C. polykomos*, *C. vellerosus*, and *C. guereza*; Oates & Trocco, 1983) which are, for the most part, distributed allopatrically from Sierra Leone and Liberia east to the Indian Ocean coasts of Kenya and Tanzania. Hybridization between *C. polykomos* and *C. vellerosus* may have occurred in southwestern Côte d'Ivoire (Oates & Trocco, 1983; Groves *et* *al.*, 1993). Two areas of *Colobus* sympatry are known; *C. guereza* and *C. satanas* were sympatric in southeastern Cameroon to northern Congo, although recent information indicates that human activities may have eliminated *C. satanas* from this overlap zone (Mitani, 1990). *C. guereza* and *C. angolensis* are still sympatric in the Ituri Forest region of northeastern Zaire (Hart *et al.*, 1986).

Although the majority of *Colobus* populations occur in moist lowland forest, some populations are found in montane forest, savannah woodland and deciduous forest, and dry coastal forest.

Information from studies of a year or more in duration is available for three species: *Colobus guereza* in Uganda (Oates, 1977a & b), *Colobus satanas* in Cameroon and Gabon (McKey, 1978a; McKey & Waterman, 1982; Harrison, 1986; Harrison & Hladik, 1986), and *Colobus polykomos* in Côte d'Ivoire (Galat-Luong, 1983) and Sierra Leone (Dasilva, 1989). *Colobus vellerosus* was the subject of an intensive study, but only limited published information (Olson, 1986) is available from this work.

B. Ecology of Black-and-White Colobus Monkeys

Most populations of black-and-white colobus that have been studied are folivore/frugivores; *C. guereza* in the Kibale Forest appears to be an exception in its high degree of folivory (leaves accounted for 81% of its annual diet; Oates, 1977a). Colobine frugivory sometimes includes consumption of fleshy fruit, such as fruit of the Sapotaceae family (Maisels *et al.*, 1994), or *Ficus* spp. (Dunbar & Dunbar, 1974). Most colobine frugivory, however, involves seed consumption, especially of the Leguminosae (Dasilva, 1994; Maisels *et al.*, 1994), whose seeds are encased in dry pods.

A characteristic of the Colobinae is the development of a chambered stomach; most genera, including *Colobus*, possess three chambers, while *Procolobus* and several Asian genera have a fourth chamber. Plant cell wall material is retained in the acidic forestomach, where cellulose is broken down by microbial fermentation (Bauchop, 1978), and, possibly, qualitative plant defense compounds such as alkaloids may be detoxified (Oates *et al.*, 1977). Most workers (e.g., Hladik, 1978) consider this anatomical and physiological specialization to function primarily as a mechanism allowing high degrees of folivory. Chivers (1994) suggests that, alternatively, the large forestomach of colobines may primarily represent a seed-eating adaptation.

Field studies since 1978 (e.g., McKey, 1978a; Curtin, 1980; Dasilva, 1989) show that seeds are a major component of some colobine diets; seeds may be more concentrated sources of toxins than are leaves (Waterman & Kool, 1994). McKey (1978b) proposed that forestomach fermentation may have evolved to allow detoxification of plant secondary compounds. However, Cork and Foley (1991) argue that the evidence linking forestomach microbes to deactivation of plant toxins is equivocal. As Kay and Davies (1994) point out, the influence of plant toxins on colobine digestion has not been systematically studied.

Comparison of food selection data over a 12-month period from three comparable studies (Oates, 1977a; McKey *et al.*, 1981; Dasilva, 1994) illustrates differences in young leaf, mature leaf, and fruit or seed consumption among *Colobus* populations. *C. guereza*'s annual diet in the Kibale Forest comprised 65.2% young leaves, 13.1% mature leaves, and 14.5% fruit. *C. satanas* at Douala-Edéa was more granivorous than folivorous; seeds accounted for 53.2% of its diet, young leaves, 18.1%, and mature leaves, 20.5%. The diet of *C. polykomos* at Tiwai was roughly intermediate between *C. guereza* at Kibale and *C. satanas* at Douala-Edéa; young leaves comprised 29.7% of the diet, mature leaves, 26.4%, seeds, 31.7%, and other fruit, 2.9%.

Home range sizes vary among different black-and-white colobus species, presumably reflecting differences among sites in tree species composition and diversity, and in *Colobus* diets. Comparable size estimates range from 24 ha and 28 ha for *C. polykomos* (Dasilva, 1989) and *C. guereza* (Oates, 1977a) respectively, to 84 ha for *C. satanas* (Harrison, 1986). Some populations show use of distinct core areas, such as *C. satanas* in Douala-Edéa (McKey & Waterman, 1982) and *C. guereza* in Kibale, while others do not (e.g., *C. polykomos* at Tiwai).

C. Summary of Black-and-White Colobus Social Organization

Four of five *Colobus* species exhibit a multimale, bisexual social system (although detailed information is lacking for *C. vellerosus*); *Colobus guereza* is the exception with its unimale group structure. The studies discussed in Sections II.A. and B. report mean group sizes ranging from 6.0 (Oates, 1977b) to 15.5 (Olson, 1986) animals. Social groups typically contain from 1 to 4 adult males, from 2 to 7 adult females, and immature animals. Oates (1977b) suggests that, in *C. guereza*, maturing males are more likely to emigrate than females from their natal group; Dasilva (1989) suggests that both male and female *C. polykomos* may emigrate. No comparable information is available for *C. satanas*, *C. angolensis*, or *C. vellerosus*.

III. The Ituri Forest Study

I conducted a study of niche separation in *Colobus angolensis* and *C. guereza* from late 1992 through early 1994 in the Ituri Forest (northeastern Zaire), the only known region where populations of different black-and-white colobus species are still sympatric. The Ituri, located within the eastern Congo Basin, is a portion of the lowland tropical forest belt stretching across equatorial Africa, and is contiguous with forest to the south and west.

The greater part of the geographical range of *C. angolensis* is in Zairian forests, thus the Ituri Forest may be considered representative *C. angolensis* habitat. Most *C. guereza* populations, however, occur in savannah woodland or in riverine, medium-altitude, or montane forest north and east of the tropical moist forest zone. While the behavior and ecology of *C. guereza* has been the subject of numerous studies (albeit in varying levels of detail and study duration), the species has not been previously studied in the moist evergreen forests of central Africa. Little comparable information is available for *C. angolensis*, which has been the subject of only two published studies. Moreno-Black studied habitat utilization in four primate species, one of which was *C. angolensis*, for six months at Diani Beach, Kenya (Moreno-Black & Maples, 1977; Moreno-Black & Bent, 1982). Maisels *et al.* (1994) studied food selection in sympatric *Procolobus badius* and *C. angolensis* in the western Congo Basin (Salonga National Park, Zaire), but their data for *angolensis*, covering an eight-month period, were not obtained from habituated animals.

My study of sympatric *Colobus* in the Ituri Forest sought to accomplish five goals:

1. To describe interspecific differences and similarities in resource use through analyses of food selection, food chemistry, ranging behavior, and habitat utilization.
2. To determine whether patterns of range use are associated with food choice and/or food availability, and whether *C. angolensis* and *C. guereza* ranging patterns are influenced by similar factors.
3. To determine whether preferences for different forest types may be a factor in niche separation, and if one species is locally more abundant than the other, by examining estimates of population density in three different forest types.
4. To describe the social organization of each population, and consider how social differences may contribute to niche separation.
5. To determine whether these data would allow me to discriminate between two hypotheses concerning the nature of *Colobus* coexistence.

Hypothesis I. *C. angolensis* and *C. guereza* coexist as competitors with little or no niche separation. To test this hypothesis, I predicted the following:

(a) extensive overlap in diet and habitat use will be observed in all months of the year;

(b) neither *C. angolensis* nor *C. guereza* will change their ranging patterns when a preferred, shared food item is scarce;

(c) during these periods of scarcity, both species will use the same alternative food sources;

(d) patches of preferred food sources in short supply will be defended against heterospecific groups;

(e) one species will displace the other from preferred feeding sites.

Hypothesis II. Niche separation occurs, and is primarily the effect of species differences evolved in allopatry. To test this hypothesis, I predicted the following:

(a) where one *Colobus* species occurs in either mature or secondary forest, the other will be rare or absent;

(b) if both species use the same forest type (e.g., mature or secondary forest), there will be little or no dietary overlap in all months of the year; each species will specialize in using different components of the habitat mosaic;

(c) foods consumed by one species will require different mechanical and/or chemical processing than foods consumed by the other;

(d) patterns of habitat and food utilization in each species in sympatry will be similar to patterns observed in allopatric populations.

At least two other hypotheses could be proposed to explain present-day niche separation in *Colobus*: the patterns are the effect of predation, or of competition in the past. Neither of these hypotheses is testable. It is not possible to predict how predation might affect *Colobus* feeding and ranging patterns. If competition had occurred in the past, I might expect to observe the following: (a) when a preferred, shared food item is scarce, one or both species will shift to different items that require similar mechanical and/or chemical processing (e.g., seeds of different plant species); and (b) in allopatric populations, patterns of habitat and food utilization in one or both species will converge on that of the other. If "prediction" (a) were upheld, this might suggest diet divergence in sympatry; if both "predictions" (a) and (b) were upheld, this might suggest that, in sympatry, one species had excluded the other from portions of its fundamental niche. However, it is not possible to rule out alternative explanations for these scenarios, should they occur.

Chapter 2. STUDY SITE, STUDY ANIMALS, AND METHODS

I. The Ituri Forest

The Ituri Forest covers approximately 70,000 km^2 northeast of the Zaire River's southward bend, bounded to the north by savanna, to the east by the highlands of the Western Rift Valley, and by contiguous forest to the south and west. The region is drained by the Ituri River and its tributaries; altitude ranges from 600 m in the western Ituri to 1200 m in the east. Mean annual precipitation for the years 1986-1995, measured at three sites in the central Ituri, ranged from 1674 mm to 1783 mm (Hart & Carrick, 1996); there is a dry season from mid-December through February.

Two types of mature forest occur in the Ituri region, both of which are dominated by the Caesalpinioideae (Leguminosae) (Hart & Hart, 1986). In the first type, *Gilbertiodendron dewevrei* accounts for over 90% of the canopy; these monodominant stands may cover hundreds of square kilometers. *Gilbertiodendron*-dominant forest is considered to be the climax forest type in eastern Zaire (Hart *et al.*, 1989). The second type of mature forest is more mixed in composition; in mixed forest, one species may comprise up to 40% of the canopy. Dominant species in mixed forest are either *Julbernardia seretii* or *Cynometra alexandri.*

Species of larger mammals occurring in the Ituri include leopard, forest elephant, forest buffalo, and seven species of duiker. The okapi (*Okapia johnstoni*), the aquatic civet (*Osbornictis piscivora*), the giant genet (*Genetta victoriae*), the owl-faced monkey (*Cercopithecus hamlyni*), and Dent's monkey (*Cercopithecus wolfi denti*) are endemic to the Ituri and regions east and south. Primate species richness is high in the Ituri (thirteen anthropoid and two to four prosimian species; Table 2.1).

Previous research in the Ituri has focused on the culture of the Mbuti pygmies (Turnbull, 1965), the ecology of single-species-dominant and mixed forests (T. Hart, 1985; Hart *et al.*, 1989), the ecology of frugivorous forest ungulates (J. Hart, 1985), and the role of forest food resources in Mbuti hunter-gatherer society (Hart & Hart, 1986). A census of primate populations in the northern and central Ituri was conducted by Thomas (1991).

A portion of the central Ituri was gazetted as the Okapi Wildlife Reserve in 1993.

II. The Basakwe Study Site

A. General Description

My study was conducted in the Okapi Wildlife Reserve, approximately 100 km west of the forest's eastern boundary. The study site, Basakwe, is about 30 km northwest of the nearest village, Epulu (1°32'N, 28°32'E); the site was, therefore, relatively undisturbed. The study area encompassed approximately 900 ha (9 km^2), at an elevation of 790 m.

Two-thirds of the site had been used 10 years previously by J. and T. Hart, and the skeleton of a trail system was still in place in those areas. Trails had never been cut in the eastern third of Basakwe. To facilitate study group follows, old trails were cleared and new trails established at north-south and east-west intervals of 250 m over most of the site (see Figure 2.1); however, one of the study groups sometimes ranged east, northeast, and southeast of the trail system. Two hundred seventy-five hectares of forest surrounding and east of Basakwe camp were further subdivided into trails at 125 m intervals. This finer subdivision allowed more accurate mapping of study group movements in an area that was used by both groups; however, it was impossible to cut trails at such close intervals over the entire 900 ha.

B. Floristic Composition and Habitat Types

The Basakwe site was established within an area of mature mixed forest, where *Cynometra alexandri* is the dominant tree species (43% of all trees $\geq$ 30 cm diameter at breast height). *Julbernardia seretii* and *Gilbertiodendron dewevrei* are virtually absent at the Basakwe site, although *J. seretii* is common in forest only 5 km northwest of the Basakwe area. Table 2.2 lists species comprising 1% or more of all trees $\geq$ 30 cm dbh at Basakwe. Ninety-three species were identified in the study area; an additional 17 were not identified.

The forest canopy reaches a height of 30-40 m, with emergents extending above 40 m. In order to describe the characteristics of forest used by *Colobus*, four habitat classes within mature mixed forest were distinguished, based on the nature of the canopy and the presence/absence of swamps and small rivers. Two intergrading types of upland forest habitat were distinguished. In type 1, a high density of mature, broad- and full-crowned caesalpiniaceous (especially *Cynometra alexandri* but also *Erythrophleum suaveolens* and *Cassia mannii*) resulted in a relatively closed canopy. In other areas where the canopy was more open (type 2), tree species characteristic of old secondary forest, such as *Celtis prantlii*, *Alstonia boonei*, *Strombosia pustulata*, *Strombosiopsis tetrandra*, and *Albizia* spp. were interspersed with caesalpiniaceous trees.

Swamp forest (habitat type 3) supported smaller-stature trees, especially *Hallea stipulosa*, *Macaranga schweinfurthii*, *Cola lateritia*, and *Anthocleista schweinfurthii*. These areas were also characterized by the presence of tall grasses or thick undergrowth. Although swamp forest was never inundated during heavy rains, the soil was water-logged until the beginning of the dry season. Type 4 habitat ("mixed-type") was a mosaic of upland, swamp, and/or riverine forest.

The method used to sample habitats is described below (see VI.A.3.). Areas characterized as predominantly closed canopy *Cynometra* forest (type 1) comprised 34.4% of the Basakwe site, while areas covered predominantly by the more open canopy type 2 forest accounted for 16.2% of the site. Areas primarily covered by swamp forest (type 3) represented 13.4% of the site; areas of mixed-type (type 4) cover, 36.0%.

C. Primate Fauna and Their Predators

All anthropoid species found in the Ituri Forest occur at the Basakwe site. Three of these species, although present, were apparently uncommon to rare and seem to prefer other types of forest (Hart *et al.*, 1986). These include *Cercopithecus neglectus*, which, in the Ituri, is associated with riverine habitat; *Cercopithecus hamlyni*, which is more common in or near *Gilbertiodendron* forest; and *Papio anubis*, which is more common in young secondary forest. Two prosimian species, presumably *Perodicticus potto* and *Galagoides demidoff*, were heard periodically by field assistants.

Predators of Ituri primates include large raptors and leopards. The crowned hawk-eagle (*Stephanoaetus coronatus*) is a major predator of primates in other African forests (e.g., the Kibale Forest: Struhsaker & Leakey, 1990), and is also present in the Ituri. Predation was viewed directly only once by field assistants during the course of the study; in this case, an eagle (species unknown) was in the process of killing an adult *Cercopithecus ascanius* on the ground.

Chimpanzees are predators of monkeys, especially colobus, in other forests (e.g., Gombe National Park; Stanford, 1995). However, chimpanzees do not occur in high densities in the Ituri as they do at Gombe, and, while they may hunt Ituri monkeys, they are probably not major predators. Hunting by humans occurs in other parts of the Ituri, but Mbuti living in the vicinity of Epulu are primarily net-hunters in search of duikers.

III. Project Timetable

The Ituri Forest *Colobus* study entailed 21 months of field work (Sept. 1992 to May 1994). From September through November 1992, the project was based at one of J. and T. Hart's study sites. During this time, work focused on building a team of Mbuti field assistants, gaining experience in finding and following groups of black-and-white colobus, and locating a suitable area in which to establish a project camp and study area. By late November 1992, I had chosen the Basakwe area as my permanent study site, and the focus of work shifted to finding potential study groups in that area. Construction of camp buildings and trail clearing was initiated in December.

Although potential study groups had been identified by late November, it was difficult to maintain consistent contact with groups until late December, when the project team began to occupy the new camp. From late November 1992 through mid-February 1993, several groups of both *Colobus angolensis* and *C. guereza* were followed, and eventually one group of each species was chosen as a study group (see below, Sec. IV). The process of habituating these groups entailed approximately two months of consistent, daily dawn-to-dusk contact, and was carried out by me and my Mbuti assistants. By mid-February 1993, the study groups were judged sufficiently calm to allow close observation, and systematic data collection was initiated.

With some exceptions (i.e., changes of study groups and loss of contact with study groups; see Sec. IV), daily dawn-to-dusk contact was maintained with these groups through March 1994. This was deemed necessary primarily because the *C. angolensis* group was difficult to relocate when contact was lost: the group consistently visited new areas of its extensive home range from one month to the next, showed no apparent preference for any one part of the study area, and sometimes ranged beyond the trail system into "unmarked" forest. In order to maintain consistency in the degree of human contact experienced by the *C. angolensis* versus the *C. guereza* group, both groups were followed daily by field assistants. Therefore, the project team was large, consisting of 8 Mbuti trackers, a project assistant, and myself.

Other work related to the project was carried out at the Basakwe site: phenological sampling, collection of primate census data, enumeration of tree species, habitat characterization, and collection of plant specimens for identification and chemical analysis.

Work was completed at Basakwe in late March 1994. In April, primate census data were collected in *Gilbertiodendron* forest at the Lenda study site (see below, Sec. V.). Also in that month, a trail system was measured and cut in an area of disturbed secondary forest (Eboyo; Sec. V) for the collection of primate census data. Most of the Eboyo data were collected in May by the project assistant and Mbuti project members (because I left Zaire in early May 1994).

IV. Study Animals

A. The *Colobus guereza* Study Group

From late November 1992 to mid-January 1993, three *C. guereza* groups were contacted in the forest near Basakwe camp. Each was named according to the geographical relationship of their range with respect to camp. Each was followed for varying periods of time in attempts to habituate them. If contact with one group was lost, and if the group could not be easily relocated, another group was located and followed. During the seven weeks, however, contact was made more often with two of these groups (the Southwest and the Southeast groups) than with the third (the North Central group). After 19 Jan. 1993, consistent contact was maintained with the Southwest group.

The Southwest group was composed of 5 animals - 1 adult male, 2 adult females, 1 subadult male, and 1 infant male. The animals were well-habituated by mid-February, and one 5-day follow with systematic data collection was completed with this group from 28 Feb. to 4 March 1993. On 13 March, one of the group's adult females was found dead (apparently killed by an eagle), and her infant had disappeared. Although contact was maintained with the remaining three animals for several subsequent days, the "group" had become incohesive and difficult to follow, and the decision was made to discontinue contact.

The North Central group was relocated in late March 1993. This group was composed of 8 animals - 1 adult male, 2 adult females, 1 adult of unknown sex, 1 young subadult of unknown sex, 1 juvenile male, 1 juvenile female, and 1 infant. A 5-day follow of the North Central group was carried out from 1-5 April. During this period, it was never possible to clearly view the adult of unknown sex, although its tendency to rest and feed away from other group members suggests that it may have been a subordinate adult male or large subadult male. The North Central group had not had sufficient previous human contact to become habituated; in addition, the group was found to range too far northwest of camp, and contact with the group was discontinued by mid-April.

The Southeast group was relocated, and habituation re-initiated, on 28 April 1993. When the group was first contacted the previous December, it was composed of 8 animals, including 2 adult males, 3 adult females, 1 subadult female, and 2 juvenile females. An infant male had been born in the intervening months, and all other group members were still present. Daily contact was maintained with this group, and systematic data collection began on 23 May. Thereafter, continuous contact was maintained with this group, which became the *C. guereza* study group, through late March 1994. Group size grew to 10 animals with the birth of another infant in July 1993; the group maintained this composition until the last day of contact (late March 1994). The group was lost only twice, for a period of 1 or 2 days, during these 11 months.

B. The *Colobus angolensis* Study Group

I did not begin to understand the social organization of *C. angolensis* until after several months of systematic data collection (see Chap. 6, Social Organization). Hence, in late 1992 and early 1993, it was not clear how many groups used the area near Basakwe camp, nor how many inhabited the study area. In contrast, by December 1992, at least five *C. guereza* groups were distinguishable at or near the Basakwe site. During December 1992 and January 1993 several different *C. angolensis* groups were contacted and followed while attempting to habituate a potential study group. Maintaining consistent contact with a specific *C. angolensis* group was difficult, because 1) groups ranged much farther and were less cohesive than *C. guereza* groups; 2) groups did not appear to use core areas, and adult males rarely emitted loud calls (roars), such that a group could not be relocated by listening for vocalizations in a specific part of the forest; and 3) sexual size dimorphism was less apparent in *C. angolensis* than in *C. guereza*, making it more difficult to accurately assess the age/sex class composition of a *C. angolensis* group.

A group designated as Mike's group (the name given to a marker, or recognizable, individual - an adult male with a deformed mouth), was followed with some consistency, and habituated by mid-February 1993; the first 5-day follow of this group was conducted from 15-19 February. At this time, Mike's group consisted of 17 animals: 11 adults (2 adult males, 6 adult females, and 3 adults of undetermined sex), 2 subadults (one male and one female), 3 juveniles, and 1 infant. Contact with the group was maintained into March, and a second 5-day follow initiated on 21 March. On the fourth day of this follow (24 March), Mike's group encountered another *C. angolensis* group. Although I did not know at this stage of the study that such encounters sometimes extended into overnight associations, apparently the two groups slept in proximity. On the following morning, an *angolensis* group began to leave the sleeping trees at 06:55; I followed this group, not knowing at the time that I had left Mike's group behind.

Thus the second group, later named the Mondiale group (named for a trail at the edge of the study area, the "Mondiale", which the group sometimes crossed), became the new study group. The group composition [in late March 1993, 19 animals: 13 adults (2 adult males, 4 adult females, 7 adults of undetermined sex), 1 subadult (of undetermined sex), and 5 juveniles] was roughly similar to Mike's group, and the animals were habituated. However, the absence of Mike, and the young infant in his group, made it clear that a different group was being followed. Only two possible scenarios can explain this switch between two habituated groups. Habituated animals could have transferred from Mike's group into the Mondiale group during the period when the groups were associated. This seems unlikely, however, as Mike's group was relocated briefly 3 months later, and the group composition was unchanged. A second possibility seems more likely: from late November 1992 into January 1993, several different *C. angolensis* groups were followed in attempts to habituate animals. The Mondiale group could have been one of these groups.

During the 5-day follow of the Mondiale group conducted in April 1993, the sex of 3 adult animals was still unknown. In early June, the group of 19 animals was composed of 5 adult males, 8 adult females, 1 subadult male, and 5 juveniles. This composition remained unchanged through March 1994, although group size grew to 20 animals with the birth of an infant in February 1994.

From late March 1993 through late March 1994, contact with the Mondiale group was lost approximately six times. In most cases, the group was relocated within one to three days. On two occasions, however, the group was more difficult to find; in one case, it took a week; in another case, three weeks.

V. Other Study Areas

Two additional study areas near Epulu village, known as Lenda and Eboyo, were utilized for the collection of primate census data. Three weeks of work was carried out at each site.

Lenda was established by J. and T. Hart in an area of *Gilbertiodendron* forest. Although forest at this site is primarily *G. dewevrei*-dominant stands, smaller areas of old secondary forest and swamp forest occur as well. Where *G. dewevrei* is dominant at Lenda, the species accounts for approximately 66% to 90% of all canopy trees in continuous stands of hundreds of hectares.

The Eboyo site was established on a 300-hectare mosaic of old and young secondary forest, including 2 tracts of land (of about 3-5 ha each) which had recently been cleared for cultivation. The area was, therefore, not free of human disturbance, as were the Lenda and Basakwe sites.

VI. Methods

A. Observation of Study Groups

1. Temporal Distribution of Follows and Description of Sampling Protocol.

Systematic observations of study groups were made during dawn to dusk, consecutive 5-day follows that occurred at approximately monthly intervals. The change in *C. guereza* study groups, and the occasional loss of the *C. angolensis* group, disrupted the intended schedule of collecting monthly data from each group. For example, two follows for each group were carried out with only two weeks between the previous and subsequent follows. For all other follows, the intervening period was approximately four weeks. During each follow, the investigator was accompanied by an Mbuti assistant - in most cases, the same individual from one follow to the next. In addition to tracking the animals' movements, this assistant aided in identifying plants on which *Colobus* fed.

Thirteen *C. angolensis* and twelve *C. guereza* follows were completed between Feb. 1993 and March 1994; for this thesis, data analysis is restricted to the last eleven follows for each study group (April 1993 through March 1994). Data presented for *C. angolensis* were collected from one group - the Mondiale group. Ten of eleven follows for which data are presented for *C. guereza* were collected from the Southeast group, and data from one follow of the North Central group are used.

During follows, the group's daily movements were traced on prepared maps of the study area, from the site of first contact (between 05:15 and 05:45) until the animals settled in their sleeping trees (between 18:15 and 18:45). Observations of individual animals were made at 15-minute intervals from 06:00 to 18:15 by scan sampling (Altmann, 1974), for a total of 50 sample periods per day. In scans, all animals that were clearly visible were sampled. In order to avoid bias in sampling conspicuous activities, only those activities sustained for more than 3 sec were recorded. Information noted for each sampled individual included the following:

- age/sex class (described below);
- activity (described as one of five mutually exclusive categories: rest, feed, locomote, social interaction, or other);
- behavior (described below);
- height (distance from the ground to the animal's position in a tree crown);
- number of group members within 2.5 m;
- study area cell occupied (see below); and
- presence of other primate species within 50 m.

Observational methods used in this study generally follow those of Oates (1977a, 1977b) and Struhsaker (1975) in their studies of colobus monkeys.

2. Descriptions of Specific Data Categories.

a. Determination of age/sex classes. *Colobus guereza* were sexed according to the criteria described by Oates (1977b). These criteria did not apply to *C. angolensis*, because the physical appearance of the perineal region differs between species. Male *guereza* have fused, gray-colored ischial callosities encircled by an unbroken ring of white hair; in females, the callosities (also gray) are separate, and the encircling ring of white hair is broken ventrally. This ring of white hair is absent in *C. angolensis*; males have fused, pink ischial callosities with a raised ridge along the fusion line. In female *angolensis*, the callosities (also pink) are separate. Estrous females show a slight perineal swelling along the inner edges of each callosity; this swelling resembles the appearance of the raised, fusion-line ridge in male animals. Perineal swelling is absent in *C. guereza*.

In distinguishing age classes, I classified animals as infants, juveniles, subadults, or adults. I based my determination of an animal's age class on previous personal experience with captive *C. guereza* of known age and sex, i.e., on differences in size, pelage, and behavior. I assumed that wild *guereza* females, like captive females, were fully-grown by the age of five or six; males, by about age seven. I further assumed that *C. angolensis* develop at the same rate as *C. guereza*.

In both species, newborn infants are completely white. The pelage changes color gradually, so that by the age of three and a half to four months, infants have acquired the black-and-white pattern characteristic of adult pelage. Animals estimated (or known) to be one year old or less were classified as infants. Young vs. older infants were discerned by their coat color pattern, by their behavior, and by the behavior of other group members toward them. For example, young infants often received intense attention from the group's adult females, subadult females (if present), and juveniles. Infants up to at least six months of age were always carried by adult or subadult females during group progressions, whereas older infants began to move independently during progressions. In addition, older infants actively participated in playing bouts with juvenile and subadult animals. Such differences in the behavior of young and older infants, and in the nature of other group members' behavior toward them, were especially important clues in distinguishing quickly among different *C. angolensis* groups when conspecific group encounters occurred.

Animals classified as juveniles were less than half the size of adult females; their pelage still had the fluffy appearance of younger animals. During rest periods, juveniles stayed close to adult animals. Both juveniles and young subadults frequently engaged in play. Subadult animals were more than half the size of adult females. Large subadult males were approximately the size of adult females.

Adult *guereza* have a distinctive, double-humped crown, which is most developed in adult males. The crown of the head is not humped in *C. angolensis*.

b. Behavior. I recorded additional information on the sampled activity:

i. Food choice. If an animal was feeding, the relative age and type of plant part, and the species of plant, were noted whenever viewing conditions were clear. If the plant species could not be identified, but the plant part was clearly seen, the activity and behavior were recorded as, for example, "feed, young leaf, species unknown". If the animal was eating but the food item could not be seen clearly, the observation was recorded as "feed, unknown item".

Additional methods of describing food selection (including determination of monthly diets, annual diets, and estimating diet diversity), and of describing diet overlap between *Colobus* species, are given in Chapter 4 (Food Selection and Diet Overlap).

ii. Rest, locomote, social interaction, other. Each of these activities was further described under the category "Behavior", but the information is not presented in this thesis.

c. Study area cell occupied. Use of a trail system allowed demarcation of the study area into cells of approximately 1.56 ha, or the area enclosed by intersecting north-south and east-west trails cut at 125 m intervals. Some cells were greater than or less than 1.56 ha if trail lines deviated from cardinal directions. This occurred where trails had to circumvent barriers, such as large fallen trees or small rivers.

In the eastern third of the study area (see Figure 2.1), trails were cut at intervals of only 250 m or 500 m. In this part of the forest - used by the *C. angolensis* study group but not by the *C. guereza* group - Atoka (my assistant) estimated cell position, which I later checked when we reached trail markings during a follow. I periodically checked Atoka's estimates of distance and direction travelled. His sense of direction was always correct, and his distance estimates highly accurate: when the animals were within areas demarcated by 250 m or 500 m trails, his distance estimates usually fell within plus or minus 15 m of trail positions later checked. Even when the *C. angolensis* group ranged beyond the trail system, Atoka had a good sense of how far the animals were from marked trails. For this reason, I consider his position estimates in unmarked forest sufficiently accurate.

3. Description of Range Use Patterns.

a. Day range length. I used a mapping wheel to measure day range lengths (daily travel distances) from a group's mapped movements for each day of follows: 55 days for *C. guereza*, and 52 days for *C. angolensis*.

b. Habitat utilization. I calculated the percentage of all observations, on both monthly and annual bases, in which a cell was occupied. Cells were coded as one of four habitat types, and the proportional use of each type was determined by summing over all cells of the same type.

I walked 22.5 km of north-south trails, spaced at 250 m intervals, to sample cells for habitat type. Assuming visibility of 50-60 m into cells, whose boundaries lay at 125 m intervals, approximately half of each cell's area was sampled. I assigned a habitat code to a cell after its length had been traversed. I sampled and coded 358 cells in this manner.

c. Other descriptors of range use patterns. Further methods of describing ranging patterns, including measures of cell use diversity, core area use, and annual home range size are given in Chapter 5 (Range Use).

B. Phenology

1. Description of Phenology Transect and Sampling Period.

I established a phenology transect along 7.5 km of contiguous trails, most of which were located within the ranges of both *Colobus* study groups. I sampled phenology every 4 to 5 weeks, coinciding as closely as possible with both study group follows, from February 1993 through March 1994 (13 samples total); I did not collect phenology data in September 1993.

In choosing individuals for the transect, young trees were avoided, as well as trees whose crowns could not be clearly viewed. When established in February 1993, the transect consisted of 77 individual trees representing 21 species. By the third sample (late April 1993), 7 species had been added for a total of 28 tree species, with 99 individuals on the transect. No new species were added after this date, but new individuals were added of species already represented. By early November 1993 (sample number 9), the transect consisted of 177 individuals. No new trees were added after this date. Most species chosen for phenological sampling were *Colobus* food plants; sample sizes for 20 species ranged from 4 to 12 individuals per species, with most falling in the range of 5 to 10 individuals. Of the remaining 8 species, 5 were eaten only rarely by *Colobus*, and 3 were never observed to be eaten; these 8 species were represented by only 1 to 3 individuals.

Two important *Colobus* food species, *Angylocalyx pinnaertii* and an unidentified species (vernacular name "Dikpolo"), were not included on the phenology transect, because their importance as food items did not become apparent until late in the study. Lianas, on which *Colobus* occasionally fed, were also not included on the transect, primarily because I did not have time to attempt their identification.

The species identification of most individuals on the transect was verified by T. Hart; those not verified by her were of relatively common species that were well-known to project workers.

2. Scoring Method.

In assigning phenological scores to individual trees, I scanned the tree crown with binoculars to estimate the relative abundance of distinct plant structures. Scores were assigned for young leaves (including leaf buds), mature leaves, flowers (including floral buds), and fruit. Scores estimated the percent of the crown, to the nearest 5%, bearing young and mature leaves; for flowers and fruit, scores estimated the percent present of the maximum possible. Flower and fruit abundance was estimated differently than leaf abundance because flowers and fruit are not necessarily evenly distributed within a given tree crown. The method of phenological scoring used in this study is modified from Oates (1977a).

Prior to data analysis, I converted scores to a 5-point scale as follows: a score of 0% was converted to a score of "0"; scores of 1-25% were converted to a score of "1"; 26-50%, to "2"; 51-75%, to "3"; and 76-100%, to "4". This conversion was made primarily for practical reasons (I found that analyzing data based on increments of 5%, or even 10%, would have been extremely time-consuming; furthermore, such a fine-grained level of analysis would have made the interpretation and presentation of results more complex than necessary). Data converted to a 5-point scale still serves the purpose of describing the seasonal availability of *Colobus* food items; 5-point scales have been used by other workers (e.g., McKey *et al.*, 1981) to describe phenological patterns and food availability. The method by which phenology scores were combined with relative estimates of plant species dominance (Sec. VI.C., below) to obtain food availability indices is described in Chapter 4 (Food Selection and Diet Overlap).

C. Enumeration of Tree Species

Using a 5-m strip width, trees greater than or equal to 30 cm diameter at breast height (dbh) were counted and identified along 10 km of north-south and 10 km of east-west study area trails (20 km total). The total area sampled for trees of this size class was 10 ha. Subsamples of small trees (greater than or equal to 10 cm dbh and less than 30 cm dbh) were counted and identified at 100 m intervals, 10 m on either side of each 100-m marker, for a total subsample length of 4 km and subsample area of 2 ha. Trees whose identities were unknown at the specific or generic level could, in most cases, be assigned a family-level name. Lianas were not enumerated, because none had been identified (except by vernacular names) during the course of the study.

The relative dominance of each species was calculated as a proportion, or the number of individuals of a species divided by the total number of trees counted.

The method of tree enumeration used at Basakwe was modified from T. Hart (unpublished methods), McKey *et al.* (1981), and Struhsaker (1975).

D. Plant Chemistry

I collected leaf, seed, fruit, and flower samples at Basakwe and near Epulu village. Most samples were dried in a small "drying room" (at Epulu or Basakwe), in which samples were placed on racks approximately 4 ft. above a smoldering fire; drying time ranged from 24 to 48 hours. Less often, samples were sun-dried; this method of drying usually took at least 48 hours. I stored the samples in paper bags or envelopes in Epulu, transferred them to sealable plastic bags for transport, and re-transferred them to paper envelopes for storage in New York.

I analyzed leaves of 21 tree species - 15 *Colobus* food species and 6 nonfood species; for all but 2 of these 21 species, both young and mature leaves were analyzed. The fruit or seeds of 15 food species (13 tree, 2 liana species), and the flowers of 3 tree species (2 food, 1 nonfood species) were also analyzed.

In each procedure, I analyzed samples in duplicate. All of the above samples were analyzed for nitrogen content using the Kjeldahl method (Maynard & Loosli, 1969); the percent dry weight of recovered nitrogen (N) was converted to an estimate of crude protein (N X 6.25). All samples were also analyzed for total phenolics content by the Folin-Denis method (Coley, 1983), using a tannic acid standard, and for condensed tannins content by the acid butanol method (Swain, 1979), using a quebracho standard. Young and mature leaf samples were analyzed for neutral and acid detergent fiber content by the method of Goering and Van Soest (1970).

E. *Colobus* Population Densities

I used three census methods to obtain density estimates for primates at the Basakwe, Lenda, and Eboyo sites: single-observer line transect sampling, multiple-observer sweep sampling, and auditory (vocalization) sampling. I describe here my use of the latter two methods in obtaining density estimates for *C. guereza* and *C. angolensis*; single-observer sampling methods are described in Chapter 3 (Patterns of Local Abundance in Different Forest Types).

1. Auditory Sampling: *C. guereza*.

C. guereza were rarely seen during single- or multiple-observer transect sampling; they were behaviorally more cryptic when encountered by humans than were other arboreal primates. For this reason, auditory sampling of early morning loud calls (roars) was employed to obtain additional density estimates for this species.

Auditory sampling is a method of estimating the number of social groups within a given listening radius. The method has been used by others (e.g., Brockelman & Ali, 1987) for censusing primates living in small social groups within defined ranges, and that reliably emit loud calls at a particular time of day. At Basakwe, adult male guereza roared on most mornings (except when it was raining heavily) between 04:00 and 07:00; this roaring was "contagious", in that the roaring of one male seemed to elicit roaring responses from males in other groups.

Marler (1972) estimated that *C. guereza* roaring in the Budongo Forest (Uganda) could be heard up to a distance of approximately one mile (1.6 km). *C. guereza* roaring at the Ituri study sites, where the terrain is level to gently undulating, was estimated to be detectable up to distances of approximately 1 km. This distance was based on opportunistic assessments made at Basakwe when the location of roaring individuals was known in relation to the person hearing them.

We conducted auditory sampling on seven mornings at Basakwe in February and March 1994; on 6 mornings at Lenda in April 1994; and on 6 mornings at Eboyo in May 1994. Four or five predesignated listening posts were each assigned to a pair of field assistants. Listening posts were spaced at distances of 1 to 1.5 km to achieve a balance between sampling as much of the study area as possible and providing some degree of overlap in adjacent teams' listening areas. These 2-man teams remained at their locations from 04:00 until 07:30; for all occurrences of *C. guereza* roaring (as well as *C. angolensis* roaring and the "moaning" vocalization of *Cercopithecus hamlyni*), the following information was recorded: the time the vocalization was heard, the species, the approximate location of the vocalizing animal(s), the number of vocalizing individuals at each location, and the number of roaring bouts heard from each location.

At Basakwe, the approximate area sampled varied from 310 to 390 ha, depending upon the number of teams involved in censusing on a given day; at Eboyo, the area sampled varied from 240 to 310 ha; at Lenda, sample area was always 310 ha. For each day of sampling, the location of roaring animals was plotted on a map to determine the number of *C.*

guereza groups present within the listening area. The method by which I estimated density from these data is described in Chapter 3 (Sec.II.C.2.).

2. Multiple-observer Sweep Sampling: *C. angolensis*.

Unlike *C. guereza*, *C. angolensis* rarely roared during early morning hours; therefore, a different method was employed to estimate *angolensis* population density. Multiple-observer sweep sampling (hereafter, "sweeps"), specifically for *C. angolensis* groups, was conducted at Basakwe for 3 or more consecutive days per month from May through October 1993 for 3 purposes: 1) to determine average group size, group compositions, and the number of groups utilizing the study area; 2) to obtain information on the organizational dynamics of the population; and 3) to locate the study group if contact had been lost. Additional sweep sampling for all primate species was carried out at Basakwe in February and March 1994, at Lenda in April 1994, and at Eboyo in May 1994 (6 samples per site).

C. angolensis sweeps were conducted during the animals' major peaks of daily travel, either in the early morning (beginning at approximately 06:30) or in mid to late afternoon (beginning at about 14:30). Depending on the number of available trackers/observers, ranging from 5 to 10 people walking singly or in pairs, transects were spaced at parallel intervals of 125 m or 250 m. Transect length ranged from 2 to 3 km. When a *C. angolensis* group was encountered, an Mbuti tracker attempted to follow the group for as long as possible (usually several hours) in order to assess group composition. During each series of 3-day sweeps, contact was maintained with several groups simultaneously for periods ranging from several hours to several days, so that I could follow and observe different groups. A different part of the study area was surveyed on consecutive days of a sweep, such that after 3 days, a large proportion of the study area had been surveyed.

This method of sweep-sampling deviates substantially from that used by other workers (e.g., Whitesides *et al.*, 1988) in that 1) it does not utilize a perpendicular distance model to estimate densities, and 2) observers left the transect to observe and follow the animals. The modified technique was used to ascertain the total number of groups using the Basakwe site. The modifications were introduced to circumvent a major complicating factor: *C. angolensis* groups sometimes form temporary associations with other conspecific groups, such that the number of groups present, as well as the size and composition of groups, could not be accurately assessed by a cursory observation.

F. Data Processing and Analysis

I processed and analyzed data on an IBM mainframe system at the City University of New York. I used SAS statistical software (versions 5.18 and 6.08) for data processing and most analyses, including Wilcoxon 2-sample tests and Spearman rank-order correlations. I used BMDP (IBM/OS version 1990) program 4F to analyze two-way and multiway frequency tables. My use of Wilcoxon tests follows Siegel and Castellan (1988); correlation analyses follow Sokal and Rohlf (1981); chi-square analyses follow Everitt (1992).

Table 2.1. The Ituri Forest primate community: 15-17 species.

- Family Lorisidae
  - Subfamily Lorisinae
    - *Perodicticus potto*
  - Subfamily Galaginae
    - *Galagoides demidoff*
    - *Galagoides thomasi?*
    - *Galago matschiei?*

- Family Cercopithecidae
  - Subfamily Cercopithecinae
    - *Papio anubis*
    - *Lophocebus albigena*
    - *Cercocebus galeritus*
    - *Cercopithecus ascanius*
    - *Cercopithecus hamlyni*
    - *Cercopithecus lhoesti*
    - *Cercopithecus mitis*
    - *Cercopithecus neglectus*
    - *Cercopithecus wolfi*
  - Subfamily Colobinae
    - *Procolobus badius*
    - *Colobus angolensis*
    - *Colobus guereza*

- Family Pongidae
  - *Pan troglodytes*

Table 2.2. Species comprising 1% or more of all large trees on the Basakwe study area. Large trees: ≥ 30 cm dbh; small trees: 10 cm ≤ dbh < 30 cm. Rel. dom. = relative dominance, or proportion of total trees sampled in each size class; density = number per hectare. Sample area = 10 ha for large trees, 2 ha for small trees.

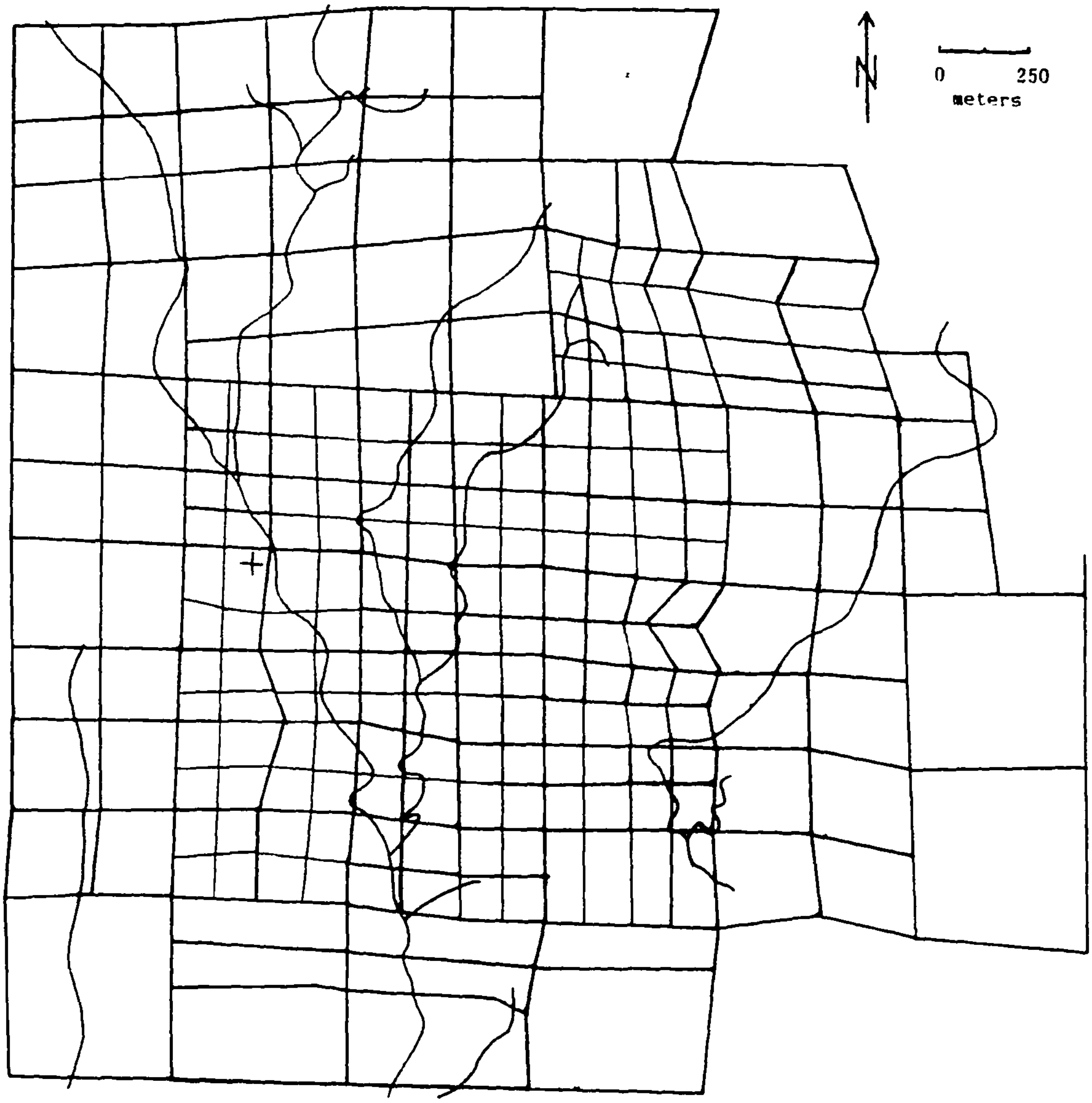
		Large trees		Small trees	
Family[a]	Species	Rel. dom.	Density	Rel. dom.	Density
Caesal	*Cynometra alexandri*	0.428	58.8	0.146	79.5
Euphor	*Cleistanthus michelsonii*	0.066	9.0	0.052	28.0
Rubiac	*Hallea stipulosa*	0.060	8.3	0.024	13.0
Caesal	*Erythrophleum suaveolens*	0.031	4.3	0.007	4.0
Euphor	*Macaranga schweinfurthii*	0.025	3.5	0.013	7.0
Ulmace	*Celtis prantlii*	0.023	3.1	0.001	0.5
Rhizop	*Commiphyton gabonense*	0.023	3.1	0.006	3.5
Apocyn	*Alstonia boonei*	0.019	2.6	0.002	1.0
Euphor	*Drypetes* spp.[b] (Roko)	0.017	2.4	0.004	2.0
Stercu	*Cola lateritia*	0.015	2.1	0.011	6.0
Sapota	Unidentified sp.	0.015	2.0	0.010	5.5
Annona	*Annonidium mannii*	0.015	2.0	0.000	0.0
Olacac	*Strombosia pustulata*	0.013	1.8	0.012	6.5
Tiliac	*Desplatsia dewevrei*	0.011	1.5	0.047	25.5
Morace	*Ficus* spp.[c]	0.011	1.5	0.000	0.0
Olacac	*Strombosiopsis tetrandra*	0.010	1.4	0.000	0.0
Caesal	*Cassia mannii*	0.010	1.4	0.003	1.5
Myrtac	*Syzygium* sp.	0.010	1.4	0.006	3.5
		0.802			

[a] Family abbreviations: Caesal - Caesalpiniaceae; Euphor - Euphorbiaceae; Rubiac - Rubiaceae; Ulmace - Ulmaceae; Rhizop - Rhizophoraceae; Apocyn - Apocynaceae; Stercu - Sterculiaceae; Sapota - Sapotaceae; Annona - Annonaceae; Olacac - Olacaceae; Tiliac - Tiliaceae; Morace - Moraceae; Myrtac - Myrtaceae.

[b] At least two species, one identified as *D. ituriensis*.

[c] Two or more species; none identified to species level.

Figure 2.1. The Basakwe study site, Okapi Wildlife Reserve. Map indicates position of small rivers, marked trails, and Basakwe camp (+).



Chapter 3. PATTERNS OF LOCAL ABUNDANCE IN DIFFERENT FOREST TYPES

I. Introduction

Much of the geographical range of *Colobus angolensis* is in lowland evergreen or semideciduous forest in Zaire; other populations are largely restricted to mountainous regions of Uganda, Rwanda, and Tanzania. Most *C. guereza* populations occur in gallery forest, savannah woodland, or montane forest north and east of the range of *C. angolensis*. Less commonly, populations of each species are found in other types of forest; e.g., *C. angolensis* inhabits patches of coastal forest in Kenya; *C. guereza* occurs in lowland evergreen forest in Zaire (see Wolfheim 1983 for descriptions of the species' distributions).

Population density estimates for *C. guereza* at different sites suggest that the species is successful in marginal habitats, such as gallery forest in the Bole Valley, Ethiopia or at Limuru, Kenya (Table 3.1). Other black-and-white colobus species, particularly *C. satanas* and *C. angolensis*, may be less likely to survive in marginal or fragmented areas. In southeastern Cameroon and northern Congo, for example, Mitani (1990) did not observe *C. satanas* in secondary forest near human settlements. *C. angolensis* density is low in the Magombera Forest (Tanzania), a forest fragment of less than 12 km^2 from which commercial timber has been removed (Decker, 1994). Both *C. polykomos* and *C. guereza* seem to occur at higher densities in forest subjected to low levels of disturbance (and where hunting is absent; Oates, 1996). Onderdonk and Chapman (1996) ascribe the success of *C. guereza* in small forest fragments to the species' flexibility. Johns and Skorupa (1987) have suggested that *C. guereza* may be a "light-loving" species, a tendency perhaps related to the maintenance of body temperature while subsisting on a low-quality (i.e., high-fiber) diet (Oates, 1977a; Watkins *et al.*, 1985).

Where *C. guereza* is sympatric with *C. angolensis*, niche differences might be reflected locally in their patterns of abundance in different forest types. Based on his census results in the

Ituri, Thomas (1991) has concluded that "...the two species show strongly complementary habitat distributions, *C. guereza* being found in roadside secondary forest and *C. angolensis* mainly in primary mixed forest..."; he further suggests that these differences are a "potential example of competitive niche displacement". To further examine this possibility, I estimated black-and-white colobus densities from census data collected at three study sites. Each site represented one of three forest types near Epulu: mature mixed forest (Basakwe study site); monodominant *Gilbertiodendron dewevrei* forest (Lenda study site); and secondary forest (Eboyo study site). On the bases of known distribution patterns for other populations of each species, and anecdotal reports of local distributions, I expected that 1) *C. angolensis* would be more abundant than *C. guereza* in mature mixed forest; 2) *C. guereza* would be more abundant than *C. angolensis* in secondary forest; 3) *C. angolensis* density would be higher in mature mixed forest than in either *Gilbertiodendron* or secondary forest; and 4) *C. guereza* density would be higher in secondary forest than in either mature mixed or *Gilbertiodendron* forest.

I compare my results with those obtained by Thomas, and briefly discuss the implications of my findings. Further discussion of *Colobus* habitat distribution patterns in relation to their coexistence appears in Chapter 7.

II. Study Areas and Methods

A. Study Areas

The Basakwe site is reached by travelling 9 km west of Epulu village, then walking 24 km into the forest; the Lenda site, 6 km east of Epulu, is reached by walking 8 km into the forest. The Eboyo site is near the Lenda study area, located approximately 1.5 km from the nearest road. The forest at Basakwe and Lenda is virtually undisturbed by human activity. Such is not the case at Eboyo; during the period of census data collection, two small settlements (estimated to contain less than 30 people each) were located on the edge of the study area.

The floristic composition of each study area is quite different, although one feature they share is the inclusion of areas of swamp forest. Of three caesalpinioid trees which occur as dominant or co-dominant species in the Ituri - *Cynometra alexandri*, *Gilbertiodendron dewevrei*, and *Julbernardia seretii* (previously classified as *Brachestygia laurentii*, Hart & Hart, 1986) - two are dominant, respectively, at each of the mature forest sites. On the 900-ha Basakwe site, *C. alexandri* is dominant, comprising 43% of all large trees; *J. seretii* and *G. dewevrei* are virtually absent. At Lenda, the degree of *G. dewevrei* dominance varies over the 750-ha site. Of the area used for primate censuses, 75% is dominated by *G. dewevrei*, ranging from approximately one-third to greater than 90% of all large trees (Hart *et al.*, 1989, and pers. obs.); 25% of the census area is covered by species characteristic of old secondary forest, where *G. dewevrei*, *C. alexandri*, and *J. seretii* are present but individuals are dispersed. *G. dewevrei* is common at the 300-ha Eboyo site, *J. seretii* is less common, and *C. alexandri* is rare. Pioneer species, such as *Musanga cecropioides* and *Macaranga* sp., are common at Eboyo. The area also contained two recently-cultivated fields (covering a combined area of about 10 ha), and two stands of domestic palms.

B. Sampling Methods

I used two line-transect sampling methods, one with a single observer and one with multiple observers, to count *C. angolensis* and *C. guereza* groups. A third method, auditory sampling of loud calls by multiple listeners, was also used to count *C. guereza* groups, because adult males of the species emit early-morning loud calls. The method was not appropriate for counting *C. angolensis*, since males of this species rarely produce early-morning calls. Conversely, *C. guereza* were rarely observed during sampling of single- or multiple-observer transects at Basakwe and Lenda; therefore, auditory sampling was the best means by which *C. guereza* groups could be counted at these sites.

I followed the method of Whitesides *et al.* (1988) for single-observer line transect sampling. At each study site, I walked a U-shaped transect of 5 km, reversing my direction of travel between successive samples. I began walking the transect between 06:15 and 06:30.

The method used for multiple-observer line transect sampling was modified from the sweep quadrat technique described by Whitesides *et al.* For auditory sampling, I followed the method of Brockelman and Ali (1987). Descriptions of these sampling methods and of modifications used in this study are given in Chapter 2 (Sec. VI.E.).

C. Analytical Methods

1. Transect Samples.

a. Number and length of samples.

Multiple-observer sampling was conducted for 6 days at each of the 3 study sites. The number of single-observer sample days varied among sites; at Basakwe, 24 samples were collected, but only 23 are used in calculating densities (heavy rain occurred during one census; this sample was discarded). At Lenda, I sampled the transect on 8 days, and an assistant sampled it on 4 additional days, for a total of 12 samples. I sampled the Eboyo transect on only 1 day; although densities could not be estimated from one single-observer sample, sighting distances of 2 *C. guereza* groups observed during that sample are used in the calculation of the species-specific sample width (see below).

In multiple-observer sampling, each observer (or pair of observers) walked a total of either 2 or 3 km; in single-observer sampling, the transect length was always 5 km. The total sample length used to calculate sample area at each site, by each method, is the length of all samples combined. Total sample lengths are given in Table 3.2.

b. Estimating species-specific total sample width.

I used the histogram-inspection method described by Whitesides *et al.* (1988) to calculate estimates of total sample width. Estimates are based on sightings from the single-observer samples, and are subsequently used in calculating densities for both the single- and multiple-observer samples. For each *Colobus* species, the method involved 4 steps:

i) determining the mean group spread, or the approximate diameter of a circle enclosing all group members (obtained from estimates made during study group follows);

ii) determining a fall-off census sighting distance, by producing a histogram of sighting frequency vs. the perpendicular distance from the transect to the first individual seen (Fig. 3.1). The fall-off distance was the lower bound of the distance interval at which the number of groups seen dropped to one-half or less of the immediately preceding interval. Because *Colobus* groups were encountered infrequently, sightings of each species from the single-observer samples were combined for all 3 study sites to produce the histograms. The number of combined sightings of *C. angolensis* groups was 13, and of *C. guereza*, only 4;

iii) estimating an effective distance, or the distance at which the number of groups detected at greater distances equals the number of groups undetected at smaller distances, calculated as:

$$\text{effective distance} = (N_t/N_f)(\text{fall-off distance})$$

where N_t = total number of group sightings and N_f = number of group sightings at distances less than the fall-off distance;

iv) estimating the total sample width, defined as twice the width sampled on one side of the transect, by the following formula:

$$\text{total width} = 2(1/2 \text{ mean group spread} + \text{effective distance}).$$

Fall-off distances given in Table 3.3 show that both species were difficult to detect, although *C. angolensis* groups were detected at slightly greater distances (15 m) than were *C. guereza* groups (10 m). Differences between species in detectability and in mean group spread (32 m for *C. angolensis*; 15 m for *C. guereza*) result in a larger estimate of total sample width for *C. angolensis* than for *C. guereza* (64 m vs. 41 m).

c. Estimating sample area. I estimated the total areas sampled (Table 3.4) for *C. angolensis* and *C. guereza*, by both single- and multiple-observer sampling, by multiplying the species-specific total sample width by the total length sampled.

d. Estimating densities. Density estimates (Table 3.4) are expressed as the number of groups per km^2, and as the number of individuals per km^2. To obtain the latter value, I multiplied the number of groups per km^2 by mean group size. Mean group sizes were estimated from the best available data for each site: for Basakwe, from all distinguishable groups found in the study area during intensive surveys; for Lenda, from groups observed opportunistically and during single- and multiple-observer sampling; for Eboyo, from groups observed during multiple-observer sampling. Sample sizes on which mean group size estimates are based are given in Table 3.4. Although some workers (e.g., Thomas, 1991) include sightings of solitary animals in their density estimates, I do not, because only one solitary black-and-white colobus was observed during census work - an adult male *C. guereza* in secondary forest at Eboyo.

2. Auditory Samples.

a. Number of samples. Auditory sampling by multiple pairs of "listeners" was conducted for 7 mornings at Basakwe, 6 mornings at Lenda, and 6 mornings at Eboyo.

b. Estimating the listening radius. During more than a year of previous work at the Basakwe site (before beginning auditory sampling), I determined that roaring *C. guereza* could be heard at distances up to 1 km by estimating distances between roaring animals, whose locations were known, and the persons who had heard them. However, since the maximum detectable distance is often much greater than the average detectable distance, I used the median of distance estimates between listeners and roaring animals (500 m, Fig. 3.2) as the listening radius (the radius of a circle surrounding each team of listeners within which roaring animals could be heard). This value was the median of 28 estimates obtained during auditory sampling at Basakwe, and was also used as the listening radius for Lenda and Eboyo.

c. Estimating the sample area. For each day of auditory sampling, I mapped the positions of all pairs of listeners, then drew a circle of 500-m radius around each listening post. I estimated the area of overlap among listening posts and the area of non-overlap, and added these 2 values to obtain an estimate of total sample area. At Basakwe, sample areas among days ranged from 3.1-3.9 km^2; at Eboyo, from 2.4-3.1 km^2. The sample area was always 3.1 km^2 at Lenda.

d. Estimating densities. For each day of auditory sampling, I mapped the locations of all roaring animals. The total number of animals mapping within the sample area produced a crude estimate of the number of groups present. Animals mapping outside of the sample area were not included in this total. I assumed that only one adult male in a *C. guereza* social group roared, and that a roaring animal was part of a group, because solitary males are not known to roar. These assumptions are based on previous observations by other workers (e.g., Marler, 1972; Oates, 1977b), and on my own observations in the Ituri.

Brockelman and Ali (1987) suggest two methods for estimating group density from auditory census data, based on their work with gibbons (*Hylobates*). Their preferred method equates the total number of groups present to the cumulative number of groups that sing (in the case of gibbons) over a sample period of *x* days. This method, however, requires that groups are individually identifiable acoustically, such that the proportion of groups expected to sing over a given sample period can be estimated. A human listener cannot distinguish acoustically among *C. guereza* males. Furthermore, with the exception of the *C. guereza* study group at Basakwe, whose location was always known, I could not individually identify different groups on the basis of their call location. The second method used by Brockelman and Ali sets the number of groups present equal to the highest number of males roaring on any one day. However, since the number of groups present in a given area will vary from day to day as a result of group movements, I calculated a mean value over all sample days at each site.

Density estimates thus obtained for *C. guereza* are given in Table 3.4, in terms of groups per km^2, and individuals per km^2. I calculated the latter value by multiplying the number of groups present by mean group size, using the same group size values that were used to estimate densities from transect data.

3. Estimating density from home range size and overlap.

I calculated an additional density estimate for *C. guereza* at Basakwe, based on the study group's home range size and range overlap with conspecific groups. Following Whitesides *et al.* (1988), and assuming that *C. guereza* uses all available and appropriate habitat,

$$\text{group density} = 1/(E+(A/2)+(B/3)+\ldots)$$

where E = area of a group's exclusive range; A = mean area of overlapping use with one other conspecific group; and B = mean area of overlapping use with two other conspecific groups.

The method cannot be applied to *C. angolensis*. This study group probably experienced complete range overlap with conspecific groups, and it is impossible to determine how much of its range overlapped with one other group, with two other groups, up to an observed total of seven other groups using its home range.

III. Results

A. Detection of Groups

Strip width estimations for *C. angolensis* and *C. guereza* are based on small sample sizes, because the total numbers of group sightings are low for single-observer sampling. The low number of group detections by either single or multiple observers is reflected in the large standard errors for density estimates (for two estimates, the standard error value is almost equal to the statistic on which it is based). The 95% confidence limits given below for single-observer values point to the imprecision in these estimates, as the ranges of values thus generated are broad.

Such difficulties in detecting groups of black-and-white colobus are probably the result of at least two factors: poor visibility in the Ituri, where the terrain is relatively flat; and the behavior of *Colobus* groups when they detect human observers. Animals either fled upon detection; maintained their position, but remained motionless and silent; or emitted an alarm vocalization (the "snort" described by Marler and Oates for *C. guereza*; *C. angolensis* produce a similar vocalization). These responses are similar to those observed in other primate species, but *Colobus* alarm snorts are generally lower in amplitude than the alarm calls of other arboreal primates. In addition, Ituri Forest *Colobus* were rarely observed in mixed-species associations, a behavioral characteristic which could render them less detectable than arboreal *Cercopithecus*, *Lophocebus*, *Cercocebus*, and *Procolobus*.

B. Comparisons of Density Estimates

1. *Colobus angolensis*.

Basakwe: mature mixed forest.

My density estimate from multiple-observer sampling (0.9 group/km^2 or 12.5 individuals/km^2; n = 6 days) is 75% of the single-observer estimate (1.2 groups/km^2 or 16.7 individuals/km^2; n = 23 days); each estimate is within one standard error of the other. The 95% confidence limits for the mean number of groups detected per single-observer census (mean = 0.39, L_1 = 0.14, L_2 = 0.64, n = 23) yield a lower limit of 0.43 group/km^2 or 5.98 individuals/km^2, and an upper limit of 1.99 groups/km^2 or 27.66 individuals/km^2.

Lenda: *Gilbertiodendron*-dominant forest.

My density estimate from multiple-observer sampling (0.2 group/km^2 or 1.3 individuals/km^2; n = 6 days) is one-fifth of the single-observer estimate (1.1 groups/km^2 or 7.0 individuals/km^2; n = 12 days); the two estimates are more than one standard error different from each other. The multiple-observer estimate falls within the 95% confidence limits calculated for the mean number of groups detected per single-observer census (mean = 0.33, L_1 = 0.02, L_2 = 0.64, n = 12), yielding a lower limit of 0.05 group/km^2 or 0.35 individual/km^2, and an upper limit of 2.03 groups/km^2 or 12.99 individuals/km^2.

All four sightings of *C. angolensis* groups during single-observer samples were in old secondary forest, as were sightings of two other groups immediately beyond the end of the transect route (6 total sightings of what appeared to be 4 different groups). The single group detection during multiple-observer samples occurred in an area where approximately 50% of all large trees were *Gilbertiodendron dewevrei*. Twenty percent of the single-observer transect route was covered by old secondary forest, while the remaining 80% was in forest dominated (to varying degrees) by *G. dewevrei*. The census route sampled by multiple observers was composed of a similar ratio of old secondary forest (30%) to *G. dewevrei* forest (70%). The large difference in density estimates obtained by the two sampling methods is, therefore, not related to a difference between transects in forest composition. The discrepancy between single- and multiple-observer estimates is considered further in Section IV.B. (below).

Well before beginning census work at Lenda, I expected that *C. angolensis* (and *C. guereza*) density would be low. I therefore asked field personnel working at the site to record opportunistic sightings of both species, which they did for 7 weeks during mid-1993. Of 8 total *C. angolensis* sightings, only 1 was in an area of forest dominated by *G. dewevrei*; 7 sightings were in old secondary forest.

Eboyo: secondary forest.

I completed only one single-observer census at the Eboyo site, during which no *C. angolensis* groups were observed. My density estimate for multiple-observer sampling at Eboyo is 0.7 group/km^2 or 13.5 individuals/km^2 (n = 6 days). Three *C. angolensis* groups, of 12, 16, and 30 animals, were observed during multiple-observer sampling. Groups of more than 20 animals observed at Basakwe were, in most cases, known to be associations of at least 2 distinct groups.

The group of 30 seen at Eboyo may have been more than one group - which would change the group density and mean group size estimates, but not the estimate of number of individuals per km^2.

2. *Colobus guereza*.

Basakwe: mature mixed forest.

My *C. guereza* density estimate calculated from multiple-observer sampling (0.3 group/km^2 or 2.4 individuals/km^2, $n = 6$ days) is 75% of the single-observer estimate (0.4 group/km^2 or 3.2 individuals/km^2; $n = 23$ days); each estimate is within one standard error of the other. Both estimates are less than the value calculated from auditory sampling (0.6 group/km^2 or 5.1 individuals/km^2; $n = 7$ days). Values of 2.4 and 5.1 individuals/km^2 fall within the 95% confidence limits for mean number of groups seen per single-observer census (mean = 0.087, $L_1 = -0.038$, $L_2 = 0.212$, $n = 23$), yielding a lower limit of essentially zero and an upper limit of 1.04 groups or 8.32 individuals/km^2.

Estimating density by home range size and overlap produces the highest density value. The *C. guereza* study group used a home range of 100 ha. Assuming that other groups used the study group's range only to the extent that I observed, the area of exclusive range use = 0.78 km^2, the mean area of overlapping use with one other conspecific group = 0.11 km^2; an area of overlapping use with two other conspecific groups does not exist. The density thus obtained is 1.2 groups/km^2, or 9.6 individuals/km^2.

Lenda: *Gilbertiodendron*-dominant forest.

C. guereza groups were not detected by any of the three sampling methods. I saw only one *C. guereza* group at Lenda, in old secondary forest that was not on the transect route.

During the same seven-week period for which *C. angolensis* group sightings were reported opportunistically by field personnel (above), 8 *C. guereza* groups were seen in the study area. Two of these sightings were in *Gilbertiodendron*-dominant forest; the remaining 6, in old secondary forest.

Eboyo: secondary forest.

My density estimate from multiple-observer sampling (1.8 groups/km^2 or 17.6 individuals/km^2; n = 6 days) is slightly higher than the estimate calculated from auditory sampling (1.4 groups/km^2 or 14.0 individuals/km^2; n = 6 days), although the latter estimate has a lower standard error.

IV. Discussion

A. Probable Sources of Error in Density Estimation

Error in transect width estimation is the most likely source of error in calculating density. Some of this error may be due to the values used for fall-off distances; however, I found it difficult to observe the study groups when they were more than 15-20 m from me. Therefore, fall-off distances of 15 m and 10 m (for *C. angolensis* and *C. guereza* respectively) for unhabituated groups seem to be reasonable estimates of detectability. A more likely source of error is in the use of estimates of mean group spread based on one group - the study group - of each species. I would expect this error to be more pronounced for *C. angolensis* than for *C. guereza*. Large *C. angolensis* groups, such as the study group, appeared to be less cohesive than smaller groups; large groups are therefore likely to have larger group spreads. Although estimates of group spread for unknown groups were noted during censuses, these figures were not used in calculating transect width, because I could not be certain if I was observing an entire group or a group fragment.

B. Within-Site Variation in Density Estimates

1. Estimating Densities From Multiple- vs. Single-observer Transect Samples.

Estimates derived from multiple-observer transect samples are lower than corresponding estimates from single-observer samples. These differences are not great for Basakwe: the multiple-observer estimates for *C. angolensis* and *C. guereza* are 75% of the single-observer estimates. But for *C. angolensis* at Lenda, the multiple-observer density estimate is one-fifth the value of the single-observer estimate. This result is difficult to interpret. Four sightings of groups during single-observer sampling, as well as 2 additional sightings just beyond the transect route, were localized in two distinct areas - one a span of 125 m, the other a span of about 60 m. These 6 sightings occurred over a period of 24 days, in an ecotone area between *Gilbertiodendron* and old secondary forest; 3 of these sightings appeared to be repeat encounters of the same group. Such an observation raises the possibility that *C. angolensis* ranging patterns in or near *Gilbertiodendron* forest may differ in comparison to mixed forest; i.e., in the former forest type, groups may intensively use certain areas before moving on to another. In the absence of ranging data from the Lenda site, however, I cannot evaluate the significance of this observation. Unknown factors related to the animals' behavior, or to the sampling methods, may have caused the large differences in density estimates at Lenda.

Although my multiple-observer sampling method is not directly comparable to the sweep sampling method employed by Whitesides *et al.* (1988), they report a similar discrepancy in estimates derived from multiple vs. single observers for *Colobus polykomos* and *Procolobus verus* - animals that are "relatively silent and cryptic...typically in small groups (often less than ten)". *C. angolensis* are also relatively silent and cryptic, and at Lenda, the mean group size was only 6.4 animals (*n* = 5 groups). Difficulty in detecting groups, in addition to those factors discussed above, may partially explain the low density estimate obtained from multiple-observer sampling. However, given the broad range of the 95% confidence interval for the single-observer estimate, within which the multiple-observer estimate falls, I cannot discount the value as "too small".

2. Estimating Densities From Transect vs. Auditory Samples.

For *C. guereza*, the Basakwe density estimates derived from transect sampling are lower than those derived from auditory sampling (the multiple-observer estimate is half the value of the auditory estimate). Apart from dawn calling by adult males, I found *C. guereza* to be even more quiet and cryptic than *C. angolensis*; in fact, Thomas (1991) did not see *C. guereza* on his transects in mature forest. Of the 3 census-based estimates for Basakwe, I suggest that the best estimate is that based on auditory sampling, primarily because the animals are difficult to detect visually in mature forest.

For Eboyo, estimates calculated from multiple-observer transect sampling and from auditory sampling are not very different. The only additional evidence concerning *C. guereza*'s relative abundance at Eboyo derives from one single-observer census conducted there, during which I encountered 2 *C. guereza* groups - the same total number of groups that I encountered during 23 censuses at Basakwe

3. Estimating Densities From Transect Samples vs. Home Range Size.

The *C. guereza* density estimate based on home range size may be an overestimate, because I cannot be sure that other conspecific groups did not use the study group's range more extensively than I observed. This estimate is considerably higher than the three census-based estimates, and is given here primarily to suggest an upper limit to *C. guereza* density at the Basakwe site.

C. Inter-Habitat Comparisons

In the introduction to this chapter, I made four predictions concerning patterns of black-and-white colobus abundance in different forest types. To evaluate these predictions, I have summarized density estimates for both species in Table 3.5.

1. Is *C. angolensis* more abundant than *C. guereza* in mature mixed forest?

Assuming that the auditory sampling estimate is the most reliable estimate of *C. guereza* density at Basakwe (5.1±1.11 individuals/km^2), the species occurs at half or less than half the density of *C. angolensis* (12.5-16.7 individuals/km^2) in mature mixed forest. *C. angolensis* is roughly twice as abundant as *C. guereza* at this site; this result is in line with the predicted pattern.

2. Is *C. guereza* more abundant than *C. angolensis* in secondary forest?

Both estimates for *C. guereza* at Eboyo (14.0-17.6 individuals/km^2) are only slightly higher than the estimate for *C. angolensis* (13.5 individuals/km^2). At this site, *C. guereza* may be only slightly more abundant than *C. angolensis*; I expected to find a larger difference between the species' densities.

3. Is *C. angolensis* density higher in mature mixed forest than in either *Gilbertiodendron* or secondary forest?

C. angolensis density at Lenda, taken as the range between multiple- and single-observer transect estimates, is 10%-42% of the species' density at Basakwe. The Lenda census data and opportunistic observations at the site suggest that *C. angolensis* rarely utilize areas of the forest where *G. dewevrei* accounts for more than half of all large trees; instead, they use ecotone areas where the tree species composition is more varied. It is possible that the animals feed on *G. dewevrei* during years of mast fruiting, but the species was not in fruit when I worked in the Lenda forest. Even if *C. angolensis* range into *G. dewevrei* forest to feed on seeds of that species, they would presumably soon be obliged to leave monodominant areas in search of other food sources.

As expected, *C. angolensis* are more than twice as abundant in mature mixed forest (12.5-16.7 individuals/km^2) than they are in or near *Gilbertiodendron*-dominant forest (1.3-7.0 individuals/km^2). Density in mature mixed forest is similar to - but perhaps slightly higher than -

density in secondary forest (13.5 individuals/km^2); I expected to find a larger intersite difference in density.

4. Is *C. guereza* density higher in secondary forest than in either mature mixed or *Gilbertiodendron* forest?

Because *C. guereza* was neither seen nor heard during census work at Lenda, it is impossible to estimate the species' density in or near *Gilbertiodendron* forest. They are apparently rare, although not completely absent from this forest type, as groups were sometimes encountered in the study area. *C. guereza* are apparently much more abundant in secondary forest (14.0-17.6 individuals/km^2) than they are in or near *Gilbertiodendron* forest. The species is roughly two to three times more abundant in secondary forest than it is in mature mixed forest (5.1 individuals/km^2). Both results are in line with the predicted pattern.

D. Comparison with Previous Work in the Ituri

Thomas (1991) reports group density estimates for *C. angolensis* and *C. guereza* in different forest types within the Ituri. I compare his estimates with mine for secondary forest and mature mixed forest (Tables 3.6 and 3.5). He distinguishes among three types of secondary forest; I list only his estimates for *Musanga*-dominated secondary forest. Although the Eboyo site was not dominated by *Musanga cecropioides*, the species was common at the site, and the other two types of secondary forest that he censused are not comparable to the forest at Eboyo. In addition, he distinguishes among mature mixed forest near, and remote from, secondary forest. I list only his estimates for mixed forest remote from secondary forest, as this type is more comparable to the Basakwe forest. Thomas did not encounter black-and-white colobus in a continuous stand of *Gilbertiodendron dewevrei* (> 100 ha) that he sampled, although he observed primates in and near smaller stands of *G. dewevrei*; it is not clear whether those observations include sightings of *C. angolensis* and/or *C. guereza*.

Two locations sampled by Thomas are based on a small total sample length (Table 3.6): 13.2 km in secondary forest near Adey, and 9.7 km in mature mixed forest near Andingbey. Use of short sample lengths may greatly over- or underestimate densities. For example, had I presented estimates based on one census walk at Eboyo, where my sample length was equal to 5 km, I would have estimated the density of *C. gureza* at 10.0 groups/km^2, and *C. angolensis* at 0.0 group/km^2. I therefore compare my Eboyo estimates only with Thomas' estimates for Ngodingodi, and my Basakwe estimates only with his for Epulu.

My *C. angolensis* density estimate for secondary forest is twice that of Thomas' (0.7 vs. 0.32 group/km^2), although his estimate falls within the range of my standard error. His estimate for *C. guereza* in secondary forest (1.25 groups/km^2) is only slightly lower than mine (1.4-1.8 groups/km^2); his estimate falls within the range of my standard error. The difference in *angolensis* density estimates, if real, may to some extent be attributable to local variation between sites: Thomas' census area at Ngodingodi is in the northern Ituri Forest; my Eboyo site is in the central Ituri. Our two mature mixed forest sites were, however, in the same general area. In mixed forest near Epulu, Thomas estimates *C. angolensis* density at 1.36 groups/km^2; this is only slightly higher than my single-observer estimate for the species at Basakwe (1.2 groups/km^2), and falls within the range of my confidence limits. His density estimate for *C. guereza* at the Epulu site is 0.0 group/km^2 (the lower boundary of my confidence limits for single-observer sampling); my best estimate for the Basakwe site is 0.6±0.14 group/km^2 (obtained by auditory sampling).

Thomas' conclusion that, in the Ituri, the two species show "strongly complementary habitat distributions" seems unwarranted by these data. *C. guereza* does occur in mature mixed forest, but is difficult to detect by methods other than auditory sampling. My data indicate a distribution pattern of an assymetrical, rather than a complementary, nature: *C. angolensis* occurs at similar densities in mature mixed and in secondary forest, while *C. guereza* is at least twice as abundant in secondary than in mature mixed forest. Other *guereza* populations are successful in marginal habitats (see above, Sec. I); in the Ituri, the higher abundance of the species in secondary forest may be related not only to a higher density of deciduous food plants (see Chapter 4), but also to sunlight accessibility. Although competition between *C. angolensis* and *C. guereza* could have resulted in some degree of "niche displacement", as Thomas suggests, it seems just as likely that *C. guereza*'s distribution pattern in the Ituri may reflect habitat preference.

V. Summary

1. *Colobus angolensis* occurs at similar densities in mature mixed forest and in secondary forest. The species also occurs in transitional forest near areas where *Gilbertiodendron dewevrei* dominance is high, at approximately half the density observed in mixed and secondary forest.

2. In secondary forest, *Colobus guereza* may reach two to three times the density at which it occurs in mature mixed forest. Although *C. guereza* was observed in transitional forest near areas of *G. dewevrei* dominance, no sightings occurred along the transect route, and adult male roaring was not heard during auditory censuses. *C. guereza* is apparently rare in this forest type.

3. In mature mixed forest, *C. angolensis* is roughly twice as abundant as *C. guereza.* In secondary forest, *C. guereza* density may be slightly higher (by several individuals per km^2) than that of *C. angolensis*. *C. angolensis* occurs at higher densities than *C. guereza* near *Gilbertiodendron*-dominant forest, but the magnitude of the difference cannot be determined.

4. In closed forest, auditory sampling may be a more reliable method of counting *C. guereza* groups than is line-transect sampling.

Table 3.1. Density estimates for other populations of black-and-white colobus monkeys. Forest types abbreviated as E (evergreen), S (semievergreen or semideciduous), F (forest fragment), G (gallery forest); ? indicates information was not provided by the author. Values in parentheses under individuals/ha are included to allow comparison of magnitudes among estimates from different sites.

location	forest type	species	groups/km^2	ind/km^2	ind/ha	reference
Douala-Edéa, Cameroon	E	*C. satanas*	2.23-2.78[a]			McKey 1978a
Lopé, Gabon	S	*C. satanas*	0.6-2.2[a]	12.7-16.4	(0.13-0.16)	White 1992
Magombera Forest, Tanzania	?,F	*C. angolensis*	1.5[b]	9.0	(0.09)	Decker 1994
Tiwai, Sierra Leone	S	*C. polykomos*	5.0-6.1[c]			Oates *et al.* 1990
Tai Forest, Côte d'Ivoire	S	*C. polykomos*		23.5[d]	(0.24)	Galat & Galat-Luong 1985
Kibale Forest, Uganda	S	*C. guereza*		100[a]	(1.0)	Oates 1974
Budongo Forest, Uganda	S	*C. guereza*		48.6[e]	(0.49)	Suzuki 1979
Bole Valley, Ethiopia	S,G	*C. guereza*			0.5-1.4[e], 3.7[d]	Dunbar & Dunbar 1974
Kakamega Forest, Kenya	S?	*C. guereza*			2.5[d]	von Hippel 1996
Limuru, Kenya	S,G	*C. guereza*			5[d,f]	Schenkel & Schenkel-Hulliger 1967

[a] derived from transect-width estimation

[b] count of all groups at site

[c] range derived from transect-width estimation and home range size

[d] estimate derived by dividing number of animals by area occupied

[e] method of obtaining estimate not reported

[f] estimate reported by Dunbar and Dunbar (1974) based on Schenkel and Schenkel-Hulliger's map of group ranges

Table 3.2. Total transect lengths sampled by single and multiple observers at each study site. N = number of samples per method at each site.

study site	sampling method	*n*	total sample length (km)
Basakwe	single-observer	23	115.0
Basakwe	multiple-observer	6	83.5
Lenda	single-observer	12	60.0
Lenda	multiple-observer	6	82.0
Eboyo	single-observer	1	5.0
Eboyo	multiple-observer	6	69.0

Table 3.3. Values used to calculate species-specific total sample width. Estimates of mean group spread are based on observations of study groups. Fall-off and effective distances are based on total number of group sightings during single-observer samples, pooled over 3 study sites; for *C. angolensis*, n = 13; for *C. guereza*, n = 4. See text for formulas used to calculate effective distances and total sample widths.

	mean group spread (m)	fall-off distance (m)	effective distance (m)	total sample width (m)
C. angolensis	32	15	16	64
C. guereza	15	10	13	41

Table 3.4. Density estimates obtained by different sampling methods at each study site. Basakwe = mature mixed forest; Lenda = *Gilbertiodendron*-dominant forest; Eboyo = secondary forest. For sampling method abbreviations, s-o = single-observer transect, m-o = multiple-observer transect, aud = auditory. Number of groups refers to the total number of groups seen by transect sampling, or to the total number of adult males heard during auditory sampling. Mean ± S.E. indicates mean number of groups detected per census.

A. *C. angolensis*

study site	sampling method	*n*	number of groups	mean ± S.E.	sample area (km^2)	density ± 1 S.E. grp/km^2	mean group size[a]	density ± 1 S.E. ind/km^2
Basakwe	s-o	23	9	0.39±0.122	7.4	1.2±0.38	13.9	16.7±5.28
Basakwe	m-o	6	5	0.8±0.31	5.3	0.9±0.36	13.9	12.5±4.94
Lenda	s-o	12	4	0.33+0.142	3.8	1.1±0.45	6.4	7.0±2.88
Lenda	m-o	6	1	0.17±0.167	5.2	0.2±0.19	6.4	1.3±1.24
Eboyo	s-o	1	0	---	0.3	---	---	---
Eboyo	m-o	6	3	0.50±0.224	4.4	0.7±0.31	19.3	13.5±5.89

[a] Basakwe: *n* = 8; Lenda: *n* = 5; Eboyo: *n* = 3.

(Table 3.4, continued)

B. *C. guereza*

study site	sampling method	*n*	number of groups	mean ± S.E.	sample area (km^2)	density ± 1S.E. grp/km^2	mean group size[a]	density ± 1 S.E. ind/km^2
Basakwe	s-o	23	2	0.09±0.060	4.7	0.4±0.29	8.0	3.2±2.32
Basakwe	m-o	6	1	0.17±0.167	3.4	0.3±0.29	8.0	2.4±2.34
Basakwe	aud	7	15	2.1±0.55	22.7	0.6±0.14	8.0	5.1±1.11
Basakwe[a]	---	--	--	---	--	1.2	8.0	9.6[b]
Lenda	s-o	12	0	---	3.8	---	---	---
Lenda	m-o	6	0	---	5.2	---	---	---
Lenda	aud	6	0	---	18.8	---	---	---
Eboyo	s-o	1	2	---	0.2	---	---	---
Eboyo	m-o	6	5	0.8±0.40	2.8	1.8±0.86	9.8	17.6±8.40
Eboyo	aud	6	23	3.8±0.70	15.7	1.43±0.216	9.8	14.0±2.15

[a] Basakwe: *n* = 5; Eboyo: *n* = 5.

[b] estimate based on home range size; see Sec. II.C.3. for derivation.

Table 3.5. Summary of black-and-white colobus density estimates from Table 3.4. For Basakwe and Lenda, values in parentheses are confidence limits of single-observer estimates; for Eboyo, values in parentheses are the standard error range of multiple-observer estimates.

forest type and location	Density Range			
	C. angolensis		*C. guereza*	
	grp/km^2	ind/km^2	grp/km^2	ind/km^2
mature mixed (Basakwe)	0.9-1.2 (0.4-2.0)	12.5-16.7 (6.0-27.7)	0.3-1.2[a] (0.0-1.0)	2.4-9.6[a] (0.0-8.3)
Gilbertiodendron and surrounding forest (Lenda)	0.2-1.1 (0.05-2.0)	1.3-7.0 (0.4-13.0)	density unknown	
secondary (Eboyo)	0.7 (0.4-1.0)	13.5 (7.6-19.4)	1.4[b]-1.8 (0.9-2.7)	14.0[b]-17.6 (9.2-26.0)

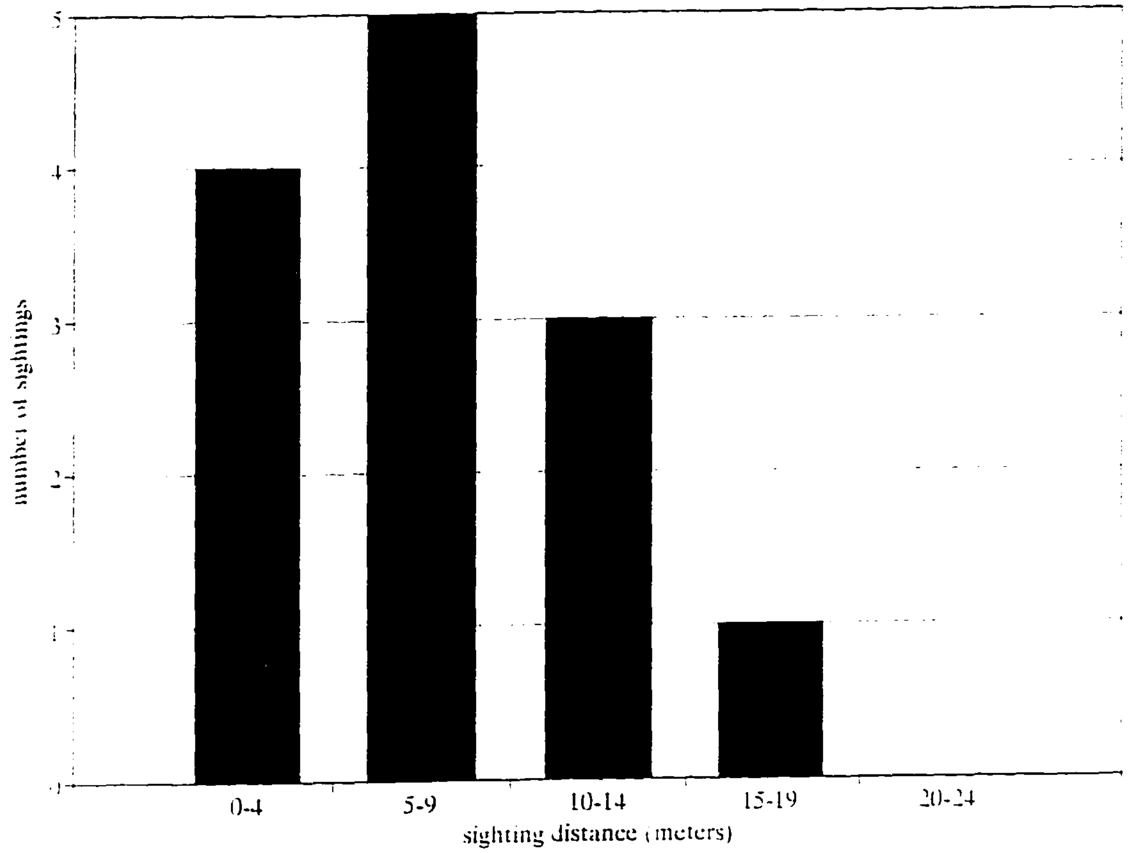
[a] 1.2 grp/km^2 and 9.6 ind/km^2 are home range estimates.
[b] auditory estimate.

Table 3.6. Group density estimates for black-and-white colobus from Thomas (1991), derived from hazard-rate analysis of line transect data. Estimates are from two transects in mature mixed forest remote from secondary forest, and from two transects in *Musanga*-dominated secondary forest. Total sample lengths are given for comparison with Table 3.2. Standard errors and confidence limits for these estimates are not available, nor are estimates for individuals/km^2.

forest type and location	total sample length (km)	Density	
		C. angolensis grp/km^2	*C. guereza* grp/km^2
mature mixed (Andingbey)	9.7	1.34	0.0
mature mixed (Epulu)	86.0	1.36	0.0
secondary (Ngodingodi)	120.7	0.32	1.25
secondary (Adey)	13.2	0.99	2.55

Figure 3.1. Perpendicular (transect to animal) sighting distances. Sighting records are combined for all three study areas.

a. *C. angolensis* (*n* = 13 sighting distances)



(Figure 3.1. continued)

b. *C. guereza* (*n* = 4 sighting distances)

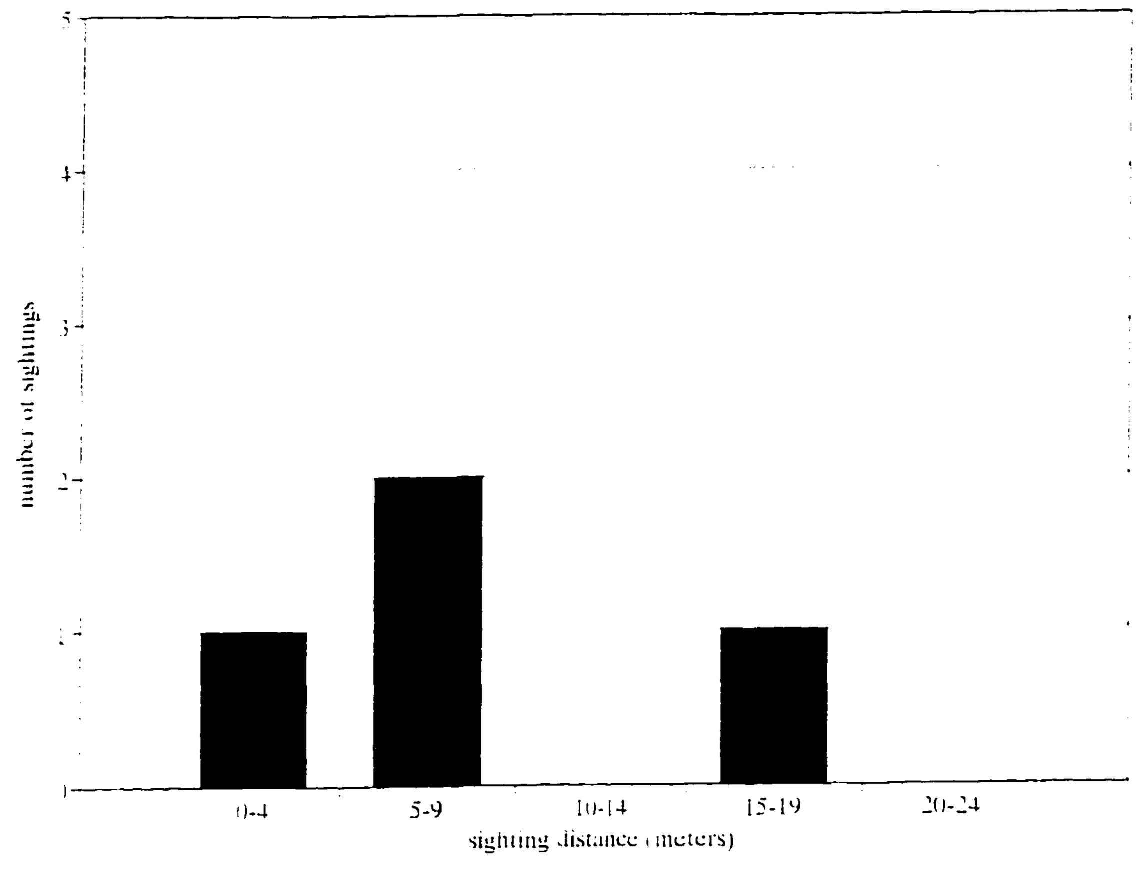
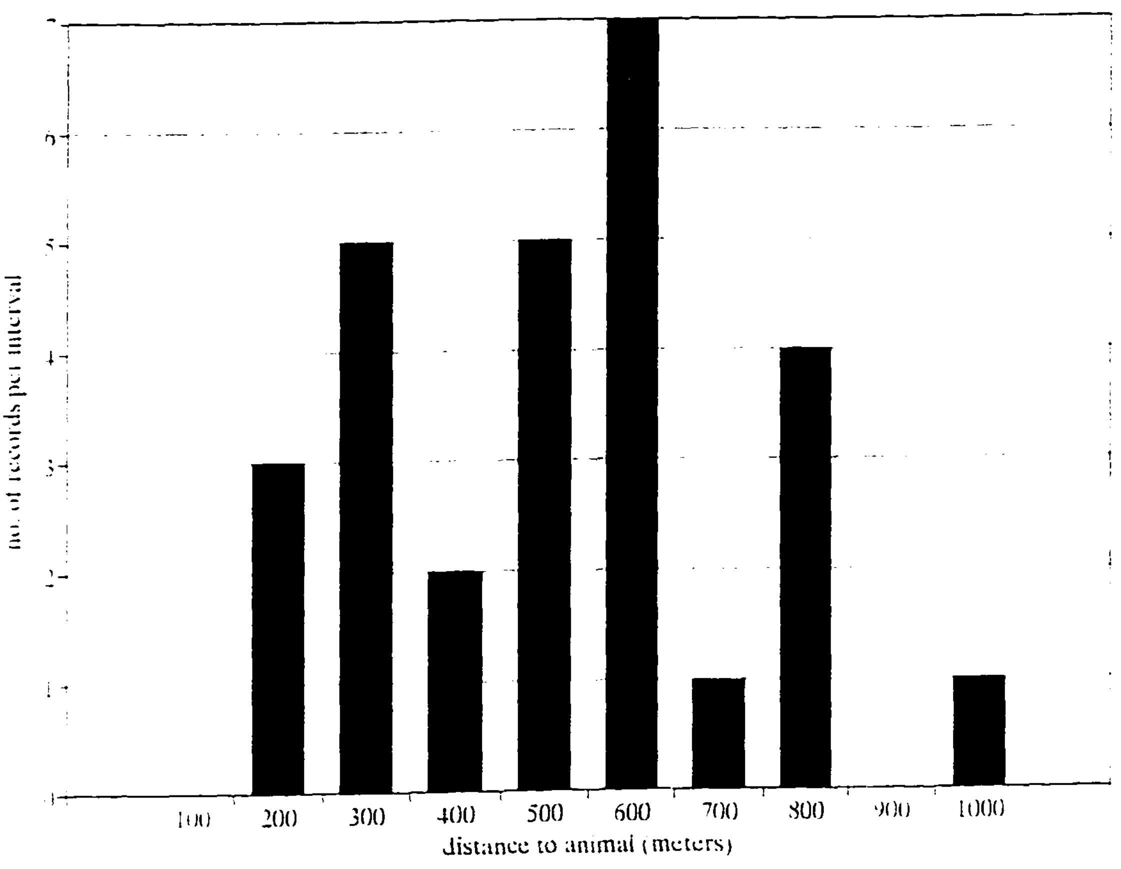


Figure 3.2. Estimates of listener to animal distance made during auditory sampling for *C. guereza* at Basakwe (*n* = 28 estimates). X-axis values are in intervals of 100 m (e.g., "200" = 101-200 m).



Chapter 4. FOOD SELECTION AND DIET OVERLAP

I. Introduction

Coexisting, closely-related species may show dietary convergence during periods of food abundance, and divergence during periods of food scarcity. Such seasonal variation in diet overlap has been amply demonstrated in mammals - for example, among prosimians, among cercopithecine monkeys, and among tree squirrels in the Makokou region of Gabon (Charles-Dominique, 1971; Gautier-Hion & Gautier, 1979; Emmons, 1980); and among callitrichid and cebid monkeys at Cocha Cashu, Peru (Terborgh, 1983). In these studies, dietary divergence was associated with periods during which animals became more specialized in their feeding habits. Observation of such divergence has been viewed as evidence that food competition determines resource partitioning patterns (Emmons, 1980); this view implies that competition is an important selective pressure in the evolution of species differences in abilities to harvest or process certain foods. Chapman (1987) has questioned this view, suggesting that diet overlap may influence feeding habits only intermittently; thus, food competition is not likely to be an important determinant of diet divergence.

Different populations of black-and-white colobus monkeys differ in the degree to which they consume leaves and fruit. Some populations are primarily folivorous, and choose young leaves preferentially over other food types (e.g., *Colobus guereza* in Uganda: Oates, 1977a). Other populations include substantial quantities of seeds in their diets, and are more accurately described as folivore-granivores (*C. satanas* in Cameroon and Gabon: McKey *et al.*, 1981; Harrison & Hladik, 1986; *C. polykomos* in Sierra Leone: Dasilva, 1989; *C. angolensis* in central Zaire: Maisels *et al.*, 1994). What is not clear is whether such differences merely reflect inter-habitat differences in available food plants, or whether they reflect differences in dietary specialization or preference. For example, Dasilva (1994) has suggested that the pattern of seed eating shown by *Colobus polykomos* is an indication of preference, rather than of a compensatory response to a lack of high-quality foliage.

The biochemical correlates of seed selection by colobines are not well understood (reviewed by Waterman and Kool, 1994). Leaf selection seems to follow a pattern which maximizes nitrogen intake while minimizing intake of digestion inhibitors - either plant fiber and phenolic compounds (McKey *et al.*, 1981), or plant fiber alone (Oates *et al.*, 1980; Mowry *et al.*, 1996). A study of captive *C. guereza* provides some evidence that the species has the ability to process foods with an especially high fiber content (Watkins *et al.*, 1985); similar data are not available for other colobines.

If dietary separation between *C. angolensis* and *C. guereza* in the Ituri Forest can be explained by species differences in food preference and food processing ability, and if such characteristics are evident in allopatric populations, then the potential link between food competition and diet divergence is weakened. If dietary separation is primarily due to species differences, then *C. angolensis* and *C. guereza* should (1) show different preferences for different plant parts, and (2) select items that require different food processing abilities.

In the following analysis of black-and-white colobus diets at Basakwe, I first discuss patterns of food preference, and examine whether these patterns are associated with specific phytochemical measures. Subsequently, I examine (a) how diet overlap changes with fluctuations in young leaf and seed abundance; (b) the manner in which each species compensates for the scarcity of preferred foods; and (c) whether particular foods or food types are likely to be limiting resources for one or both species.

II. Methods

A. Diet Composition and Interspecific Comparisons

1. Data Collection and Identification of *Colobus* Foods.

I report observations of study groups made during eleven 5-day follows per group, from April 1993 through March 1994. I collected activity data by scan sampling at 15-min intervals from 06:00 to 18:00; feeding was one of five activities scored. My sampling protocol is described in Chapter 2 (Sec. VI.A.1).

Plant species and plant parts eaten were identified to the extent possible during data collection - i.e., when visibility was adequate and when I could identify the species. If animals were feeding on a known species but the part ingested was not visible, the animals were scored as feeding on that species, but the plant part was scored as "unknown". If animals were feeding but neither the plant species nor the plant part could be identified, I scored their activity as "feed", and the species/part ingested as "unknown". Samples of unknown species eaten on more than a few occasions were collected for later identification; most of these unknowns were identified by T. Hart and her colleagues.

Colobus ate leaves, fruit, and flowers. During data collection, I recorded leaf-eating as either ingestion of leaf blades or of petioles; I recorded fruit-eating as either ingestion of fruit pulp or of seeds; any flower structure ingested was simply recorded as "flower". I attempted to discern the relative growth stage of ingested leaves and fruit. Young leaves were distinguished from mature by their color and turgidity; leaf size was a less reliable characteristic, except for leaf buds and newly-expanded leaves. In general, it was more difficult to discern the degree of maturity of whole fruits and seeds, because fruits of different plant families varied widely in shape, size, and color. When possible, I examined fallen, partially-consumed fruits as the animals were eating. I did not distinguish between immature and mature flowers; for some species producing small flowers, I could not consistently discriminate between buds just beginning to open and fully-expanded flowers.

In sum, I recorded plant parts as follows: young leaf blade, mature leaf blade, or leaf blade of undetermined age; leaf petiole; unripe fruit, ripe fruit, or fruit of undetermined age; unripe seed, ripe seed, or seed of undetermined age; and flower. For the sake of brevity, I hereafter refer to leaf blades as "leaves"; petiole feeding comprised a very small percentage of observations.

2. Description of Annual and Monthly Diets.

I report annual diet composition, by plant part, plant species, and plant item (species by plant part) as the percentage of total feeding observations: for *C. angolensis*, $n = 2457$, collected over 52 days in 11 months; for *C. guereza*, $n = 1336$, collected over 55 days in 11 months.

To compare levels of food species diversity in the diet of each study group, I calculated indices of diet diversity using Shannon's formula (Begon *et al.*, 1990):

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where s = the number of food species consumed, and p = the proportional representation of each food species in the diet. Diet diversity indices were calculated for the entire sample (annual diversity) and for each 5-day follow (monthly diversity).

I calculated selection ratios (SR) for food species using Clutton-Brock's (1975) formula, where

$$SR = \frac{\text{\% of total feeding observations made on a species}}{\text{\% of trees in enumeration sample accounted for by a species}} \times 10.$$

Selection ratios for food items were calculated by changing the numerator in the above equation to "percentage of total feeding observations made on an item".

I sometimes found it difficult to distinguish young from mature leaves of several important food species. Such difficulty was most pronounced with *Celtis mildbraedii*, whose young leaves emerge within a whorl of mature leaves, and, to a lesser extent, with *Celtis zenkeri*. I therefore present annual diet summaries (Sec. III.A) in terms of both (a) young and mature leaf consumption and (b) total leaf consumption. I discuss monthly diets and diet overlap (Sec. III.B) in terms of total leaf consumption, but include data on overlapping use of young leaves whenever possible. If I had expressed overlap in leaf consumption based only on records in which age classes were clearly distinguished, I believe that I would have greatly underestimated diet overlap.

3. Evaluation of Diet Overlap.

I compared nine months of paired data sets to analyze interspecific diet overlap. I evaluated overlap by calculating the shared percentage of an item common to the diet of both *Colobus*. For example, if an item comprised 20% of *C. guereza*'s diet and 30% of *C. angolensis*' diet, overlap for that item was 20%. This method of expressing diet overlap (Holmes & Pitelka, 1968) has been used in other comparative studies of sympatric primate diets (e.g., Struhsaker and Oates, 1975; Maisels *et al.*, 1994).

Although it would have been preferable to compare twelve months of feeding data, this was not possible because the timing of several study group follows was disrupted. I was not able to collect data in July 93 for *C. angolensis*, nor in September 93 for *C. guereza*. In addition, group follows in January 94 were separated by 3 weeks; diet overlap comparisons with January data may not be temporally appropriate, so I do not compare them.

B. Evaluation of Food Availability

1. Phenology and Tree Enumeration.

I have described the composition of my phenology sample and the scoring method, as well as my method for enumerating tree species, in Chapter 2 (Sections VI.B. and VI.C, respectively). I sampled phenology once a month from February 93 through March 94 (with the exception of September 93, for which I have no phenology data).

In Sec. III.A.2 (below), I give coefficients of dispersion (CD) for 7 tree species. These coefficients, which derive from my enumeration data, are ratios of sample variance to sample mean. For a given species, the CD was calculated by dividing the variance in frequency of occurrence of individual large trees (among eighty 250-m subsamples) by the mean number of individuals per subsample. A coefficient near 1 or equal to 1 indicates a random distribution; values greater than 1 indicate a clumped distribution; values less than 1 indicate repulsion (Sokal & Rohlf, 1981).

2. Availability Indices.

Estimates of plant part abundance, or food availability, were calculated from phenology and enumeration data. In phenology sampling, scores for individual trees estimated the percent of the crown, to the nearest 5%, bearing young and mature leaves, or, in the case of flowers and fruit, scores estimated the percent present of the maximum possible. A mean abundance score was calculated for each plant structure, as the average phenological score over all sample trees of a given species. For example, if 5 of 10 sample trees had a score of 25% for young leaves, and the other 5 had a score of 75%, the mean abundance score was 50% for young leaves. I multiplied mean abundance scores by the species' relative abundance in the study area (or the percentage of all large trees greater than or equal to 30 cm dbh accounted for by that species), to yield an availability index for a given plant structure. Availability indices estimate the proportion of the forest canopy bearing a particular plant item, e.g., *Cynometra alexandri* young leaves, at a particular point in time.

Other workers (e.g., Oates *et al.*, 1980; Marsh, 1981; Dasilva, 1989) have incorporated estimates of crown volume in calculating availability indices. The index I use was calculated by a simpler method, modified from that of T. Hart (unpublished methods); this method allows me to make relative comparisons of the abundance of 5 plant items in evaluating diet overlap between *Colobus* species.

C. Plant Chemistry

I analyzed leaf, seed, fruit, and flower items for crude protein, acid detergent fiber, total phenolics, and condensed tannins content. Sample sizes and methods used for chemical analysis are given in Chapter 2 (Sec. VI.D).

D. Data Analysis

I used chi-square analyses to test for interspecific differences in the percentage of observation time animals fed on (a) different plant parts and (b) different plant types (trees or lianas). I used Spearman correlation and partial correlation analyses to test for associations between selection ratios and 5 measures of young leaf chemistry: crude protein, acid detergent fiber, total phenolics, and condensed tannins content; and the ratio of protein to fiber. I used Wilcoxon 2-sample tests to (a) test for differences in young leaf chemistry between the most frequently-consumed food plants and common nonfood plants, for each *Colobus* species, and (b) test for interspecific differences in diet diversity indices.

III. Results

A. Annual Diets.

1. Plant Parts.

Table 4.1 summarizes the plant part composition of study group diets from April 93 through March 94. Leaves comprised slightly more than half the diet of both *C. angolensis* (51.1%) and *C. guereza* (57.9%); fruit, roughly one-fourth (27.5% and 24.6%, respectively); the remainder was composed of flowers (7.2% and 2.9%, respectively), rare items, and undetermined items. I tested for species differences in diet composition with two chi-square analyses. In the first analysis, I used total leaf, total fruit, and flower as plant part categories; in the second, I used young leaf plus leaf bud, mature leaf, seed, and flower. Both analyses produced significant chi-square values at $p < 0.001$. I then partitioned the degrees of freedom for the former contingency table, testing for independence between *Colobus* species and levels of total leaf or total fruit consumption; this partitioned chi-square is not significant. When total leaf and total fruit are collapsed into one category and compared with flower consumption, the chi-square is significant (at $p < 0.001$). *C. angolensis* and *C. guereza* differ only in the proportion of flowers in their diets.

Because I had difficulty distinguishing fully-formed young leaves from mature leaves of several important food plants, my values for both young and mature leaf consumption are minimum estimates. Therefore, I did not partition the contingency table which tested for differences in young leaf, mature leaf, seed, and flower consumption. In a first analysis of this table, however, differences in flower consumption account for most of the magnitude of the chi-square value (29.07 of 38.25), followed by differences in mature leaf consumption (5.29 of 38.25).

2. Plant Species.

The total number of food plant species identified or distinguished (Table 4.2) for *C. angolensis* was higher than for *C. guereza* (37 species - 34 tree and 3 liana vs. 31 species - 26 tree and 5 liana, respectively). For *C. guereza*, however, the percentage of feeding observations in which undistinguishable trees and lianas were taken (10.2%) was higher than for *C. angolensis* (6.7%); therefore, the two species probably include similar numbers of plant species in their diets. For both *Colobus*, leguminous trees accounted for about 30% of all feeding observations, followed by trees of the Ulmaceae family.

If only "good" observations are considered (i.e., those in which I could clearly distinguish tree from liana feeding), the study groups differed significantly in the proportion of total feeding observations in which trees or lianas were consumed ($X^2 = 60.28$, 1 d.f., $p < 0.001$). For *C. angolensis*, feeding on trees accounted for 91.0% of observations; lianas, 5.7%. *C. guereza* fed on trees during 79.8% of observations; on lianas, 12.5%. I interpret this apparent species difference with some caution: for *guereza*, I could not determine the type of plant taken (tree vs. liana) for 7.3% of observations; the comparable value is lower for *angolensis* (2.7%).

Table 4.3 ranks the top 20 food plants, by percent of total feeding observations, for each *Colobus* species. *C. guereza*'s annual diet was slightly more diverse (*H* = 3.17) than that of *C. angolensis* (*H* = 2.99). For example, the top 50% of *angolensis* observations consisted of feeding on 5 plant species; for *guereza*, 7 species plus unknown lianas. Most strikingly, *Colobus* differed in their use of *Cynometra alexandri*, the dominant tree species in the study area. *C. alexandri*, an evergreen species, was the top-ranking food plant for *angolensis* (15.1% of observations), but accounted for only 3.7% of *guereza* feeding observations. *Celtis mildbraedii*, the second-ranking species for *angolensis*, is deciduous. For *C. guereza*, the 2 most frequently consumed plants were *Erythrophleum suaveolens* and *Albizia gummifera*; these are deciduous trees.

Most food trees listed in Table 4.3 are middle to upper canopy species, with the exception of *Desplatsia dewevrei*, *Drypetes* spp. (Sungba), and *Rauvolfia vomitoria*. *Colobus* consistently fed in small (less than 30 cm dbh) individuals of these species; their densities are therefore given in terms of small trees to reflect their availability to *Colobus*. Most food plants occur at densities of less than 10 trees per hectare, except for *C. alexandri*, *D. dewevrei*, and *Drypetes* spp. (Sungba).

To distinguish frequently-consumed foods from preferred foods, I calculated selection ratios for the plant species appearing in Table 4.3. A particular food may be "selected", i.e., consumed more often than would be expected from the species' density if (a) it is available for a long period of time, (b) it occurs at high density on an individual tree, or (c) the animal prefers it to other foods (Clutton-Brock, 1975). The selection ratios in Table 4.3 are a relative comparison, among food species, of consumption with respect to species density. For example, the low selection ratios for the top food species in each table - for *C. angolensis*, *Cynometra alexandri*;

for *C. guereza*, *Erythrophleum suaveolens* - indicate that these species were probably not preferred foods, but were frequently consumed because they are common, suitable food sources. Other common species (e.g., *Cleistanthus michelsonii* and *Hallea stipulosa*) were not eaten during the study period, which suggests that they were not suitable food sources. Rare plants with the highest selection ratios, *Amphimas pterocarpoides* for *C. angolensis* and *Albizia gummifera* for *C. guereza*, were major food sources for each species, respectively, for 2 months - the time period during which *Amphimas* flowers and *Albizia* young leaves were available. The high selection ratios for these species suggest a preference for the food items they provided.

I calculated coefficients of dispersion (CD, Table 4.3) for 7 food species: those 5 with the highest selection ratios, and the 2 most frequently consumed species. *E. suaveolens*, *A. gummifera*, *A. pterocarpoides*, and *C. zenkeri* show a random dispersion pattern (CD approximately equal to 1). *C. alexandri* and Dikpolo show a clumped pattern (CD greater than 1), as does *C. mildbraedii*, but to a lesser extent. Of the 7 species, those with high selection ratios are either (a) rare and randomly dispersed - *A. gummifera*, *A. pterocarpoides*, and *C. zenkeri*, or (b) rare and clumped - Dikpolo and *C. mildbraedii*. The two "non-selected" species are either common and clumped (*C. alexandri*) or relatively common and randomly dispersed (*E. suaveolens*).

3. Plant Items.

a. Characteristics of principal food items and preferred items. Table 4.4 summarizes the 20 most frequently consumed food items for each *Colobus* species. The two lists combined include a total of 28 different food items; of these 28, 12 are included in both lists (but account for different percentages of each species' diet). Eight of *guereza*'s top 20 items are not included in the *angolensis* top 20, and vice versa. If, instead, diets are compared by rank order of the 20 highest selection ratios (Table 4.5), some of the food items in Table 4.4 drop out. Three do so because enumeration frequencies are not available (Ngoto, Njambal, and *S. golungensis*), and, therefore, selection ratios could not be calculated; two others (*C. alexandri* leaves and seeds for *guereza*) drop out because they are replaced by items with slightly higher selection ratios.

Species differences in preference for certain food types are not apparent from Table 4.4. For example, the top 50% of *angolensis* records are comprised of 8 items: 1 flower, 3 seed, and 4 leaf; of these leaf items, 3 are from deciduous trees, and 1 is from an evergreen. Eleven items comprise the top 50% of *guereza* records - 3 seed and 8 leaf; of these leaf items, 6 are from deciduous trees, 1 from an evergreen, and 1 from a species thought to be evergreen. If the focus is shifted to selection ratios (Table 4.5), differences in preference are clear. For *angolensis*, selection ratios for items 1-5 form a cluster - the ratio for item 6 is less than half that of item 5; items 6-20 were weakly selected compared to the first five. These 5 items include 3 different plant parts - 1 flower, 1 seed, and 3 leaf. All 3 leaf items are from deciduous trees; selection ratios for these leaf items are similar in magnitude. For *guereza*, items 1-4 form a cluster distinct from lower-ranking items. These first 4 items, all leaves, are of deciduous trees. The selection ratio for *A. gummifera* is 4 times the ratio for *C. mildbraedii*. Seeds, other fruit parts, and flowers were weakly selected by *guereza*.

b. Item chemistry and selection. To determine whether *angolensis* and *guereza* prefer leaves of similar nutritional quality, I used correlation analyses to test for association between selection ratios and relevant chemical measures for young leaves: crude protein (CP) content, acid detergent fiber (ADF) content, and the ratio of crude protein to fiber (protein/ADF). I also tested for association between selection ratios and young leaf total phenolics and condensed tannins content. Although selection ratios for each plant species are based on leaves of all age classes, I assume that when leaf age could not be determined, in most cases the animals were probably eating young leaves. I make this assumption for two reasons. First, all observations of leaf-eating for certain food plants occurred during periods of young leaf flush; this is especially pronounced for *Celtis zenkeri* and *C. mildbraedii* (Fig. 4.1), *Albizia gummifera*, and Dikpolo.

For *Cynometra alexandri*, the relationship is less clear, although this species produced young leaves in most months (Fig. 4.1). Second, for all leaf items except *Ficus* spp. in Table 4.4, the percentage of young leaves eaten is much higher than that of mature leaves. I therefore compared selection ratios for total leaf consumption for a particular species with chemical measures for young leaves of that species.

Leaf item selection ratios are positively correlated with protein/ADF values for young leaves (*C. angolensis*: $r_s = 0.736$, $p = 0.024$; *C. guereza*: $r_s = 0.761$, $p = 0.006$; see Table 4.6). For leaf items selected by both *C. angolensis* and *C. guereza*, protein/ADF values fall into two clusters. The four plant species with the highest selection ratios for *C. angolensis* (ranks 2, 3, 4, and 6) have the highest protein/ADF values (1.12-2.44). Five plant species with lower selection ratios (ranks 10, 15, and 17-19) have much lower protein/ADF values (0.45-0.60). *C. guereza* shows a similar pattern of selectivity. Six plant species with the highest selection ratios (ranks 1-6) have the highest protein/ADF values (0.83-2.44). Five species with lower selection ratios (ranks 8, 13, 16, 18, and 20) have lower protein/ADF values (0.25-0.55).

When crude protein and fiber are examined individually with respect to selection ratios, the pattern of association is somewhat different between *Colobus* (Table 4.6). While both species select positively for crude protein content, the correlation is significant for *C. guereza* ($r_s = 0.827$, $p = 0.002$) but not for *C. angolensis* ($r_s = 0.550$, $p = 0.125$). This pattern is maintained when variability in fiber content is held constant: the correlation between selection ratio and protein content is significant for *C. guereza* (partial $r_s = 0.725$, $p = 0.018$), but not for *C. angolensis* (partial $r_s = 0.525$, $p = 0.182$). For both species, there is a significant negative correlation between selection ratio and fiber content (*C. angolensis*: $r_s = -0.733$, $p = 0.025$; *C. guereza*: $r_s = -0.664$, $p = 0.026$). When variability in protein content is then held constant, the negative correlation between selection ratio and fiber content is still significant for *C. angolensis* (partial $r_s = -0.721, p = 0.044$), but is much lower in magnitude and not significant for *C. guereza* (partial $r_s = -0.399, p = 0.253$).

For *C. guereza*, the association between selection and leaf fiber content is influenced by leaf protein content - i.e., *guereza* are not strongly selecting against fiber, but rather selecting for protein. For *C. angolensis*, the association between selection and leaf fiber content is not influenced by leaf protein content - *angolensis* strongly select against fiber, and select only weakly for protein.

Young leaf condensed tannins content (expressed as percent dry weight quebracho tannin equivalents) is not correlated with *angolensis* or *guereza* selection ratios (*angolensis*: $r_s = -0.268$, $p = 0.520$; *guereza*: $r_s = 0.281$, $p = 0.431$). Young leaf total phenolics content (expressed as percent dry weight tannic acid equivalents) is positively correlated, although weakly, with *guereza* selection ratios ($r_s = 0.612, p = 0.060$); total phenolics are not correlated with *angolensis* selection ratios ($r_s = 0.310, p = 0.456$).

I did not test for associations between seed, fruit, or flower selection ratios with item chemistry because (a) the pattern of age preference for seeds or fruit was not clear; (b) I could not consistently collect both ripe and unripe seeds or fruit of a particular species; and (c) each *Colobus* species consumed only 2 flower items. Two points, however, bear mentioning here. The crude protein content of *A. pterocarpoides* flowers (25.0%) is much higher than that of *A. boonei* flowers (15.9%); *C. angolensis* strongly selected the former item, while the latter was only weakly selected. *L. cupanioides* seeds were also strongly selected by *angolensis*, but they are low in crude protein (9.1% for ripe seeds).

c. Young leaf chemistry of food and nonfood species. For this comparison, I used the five leaf foods most frequently consumed by each *Colobus* species, and four nonfood leaf items. Two food species were high-ranking for both *Colobus* (*Celtis mildbraedii* and *C. zenkeri*) and were used as food items for both species. Three food species were different; for *C. angolensis*, other species used were *Cynometra alexandri*, *Alstonia boonei*, and *Angylocalyx pinnaertii*; for *C. guereza*, these were *Albizia gummifera*, *Ficus* spp., and *Desplatsia dewevrei*. The same four nonfood species were used for both comparisons (*Hallea stipulosa*, *Erythrophleum suaveolens*, *Strombosia pustulata*, and *Cassia mannii*). *H. stipulosa* is the third most common tree species in the Basakwe study area (relative dominance = 6.1% for large trees); *E. suaveolens* is the fourth most common species (3.2%); *S. pustulata* and *C. mannii* are less common (1.3% and 1.0%, respectively). Combined frequencies for these four species is 12.2%.

I used Wilcoxon 2-sample tests to test for differences in crude protein, acid detergent fiber, total phenolics, and condensed tannins content between food and nonfood species. For each *Colobus* species, only one comparison approached significance (*C. angolensis* young leaf ADF content, $p = 0.0662$; *C. guereza* young leaf CP content, $p = 0.0662$).

B. Monthly Diets

1. Plant Parts.

I have summarized the monthly composition of *Colobus* diets by plant part in Table 4.7. *C. guereza* was primarily folivorous from April through June 93, and again from November 93 through March 94; in these months, leaf-eating accounted for more than 60% of feeding observations. In the intervening months (July, August, and October), seeds and other fruit parts accounted for more than half of their diet and leaf consumption decreased. Flowers were never major food items. Taking into account the high percentage of unknown plant parts consumed in the first four months does not change this overall pattern - that is, even if all unknown plant parts were either all leaves or all fruit/seeds, adding these percentages to total leaf or total fruit values would not change the type of plant part dominating the diet.

The *angolensis* data show a different pattern. Although they also fed most heavily on fruit or seeds from August through October, in 2 additional months (April and February) these items comprised a third of their diet. Flowers never dominated their diet, but were important food items in 2 months, when they accounted for one-fourth to one-third of feeding observations (December and January). In all months, leaves were important foods, but only in 2 months (November and March) did they comprise more than 60% of feeding observations.

C. guereza and *C. angolensis* differ, therefore, in their degree of specialization for different plant parts (Figure 4.2). During 9 months, roughly two-thirds or more of the *guereza* diet was composed of one plant part - in 8 months, leaves; in 1 month, seeds. In only 3 months did one plant part comprise more than two-thirds of the *angolensis* diet - in 2 months, this was leaves; in 1 month, seeds.

2. Diet Diversity.

C. angolensis and *C. guereza* do not differ in mean monthly food species diversity (Table 4.8; Wilcoxon $Z = -0.328$, $n = 11$, $p = 0.743$). Diets were least diverse when *Erythrophleum suaveolens* seeds accounted for the majority of feeding observations (in September for *C. angolensis*; in October for *C. guereza*). I could not discern a specific factor related to higher diversity in other months; increasing diversity may simply be associated with decreasing availability of *Erythrophleum* and *Cynometra* seeds.

3. Interspecific Diet Overlap.

a. Mean monthly overlap. Monthly diet overlap for all food items ranged from 14.0% to 38.7%, averaging 28.5% for the nine months used in interspecific comparisons (Fig. 4.3). In any one month, the maximum amount of overlap accounted for by one food item ranged from 4.0% to 27.8%, with a mean of 15.7%.

b. Major overlap items, and months of highest overlap. In Table 4.9 I have summarized, for each month, the primary food item consumed by each *Colobus* species, and the food item for which overlap was highest. In presenting values for item overlap, I consider only those items which fall within the top 50% of feeding observations; overlap for minor items often occurred, but such minor overlap is not likely to have serious consequences for either species.

Five food items comprised the highest sources of diet overlap over the nine months considered here. In seven months, *C. angolensis* and *C. guereza* overlapped in their use of one major food item. In five of these seven months, the primary overlap item was deciduous tree leaves (*Celtis zenkeri* in April and May (Fig. 4.1.a); *C. mildbraedii* in June (Fig. 4.1.b); and Dikpolo in February and March). I assume that overlap for *C. zenkeri*, Dikpolo, and *C. mildbraedii* involved overlapping use of young leaves, because these species peaked in young leaf production during the period of shared use by *Colobus*. In the two remaining months (August and October), seeds of leguminous trees (*Cynometra alexandri* and *Erythrophleum suaveolens*; Fig. 4.4) were the primary overlap items.

Diet overlap peaked, therefore, during two different phenological stages. High overlap was synchronized with maximum young leaf production of *C. zenkeri* and *C. mildbraedii* (and presumably of Dikpolo; see below). Overlap for *C. alexandri* seeds occurred when fruit production was maximal, but for *E. suaveolens*, there was a time lag of two to three months between maximum fruit production and high overlap for seeds.

Diet overlap was lowest in November, when only one of these five items was available - *C. mildbraedii* young leaves. This item comprised almost half of *C. angolensis* feeding observations in November. *C. guereza* shifted to feeding on liana leaves, *Margaritaria discoidea* seeds, and *Alstonia boonei* young leaves; these three items combined accounted for almost half of November feeding observations.

c. Relative availability of particular foods. Table 4.10 compares availability indices (AI) of five food items - *Celtis zenkeri*, *C. mildbraedii*, and *Cynometra alexandri* young leaves, and *C. alexandri* and *E. suaveolens* seeds - with their frequency of consumption by *Colobus*. I present leaf consumption as both (a) the percentage of observations in which young leaves were clearly distinguished and (b) the percentage of observations which includes leaves of all age classes. I describe *C. alexandri* young leaf availability because this item was an important food for

Colobus angolensis, and because the species is abundant in the study area. I did not sample Dikpolo phenology, since the species was not used as a food plant until the end of the study; it is a deciduous tree, so I assume that young leaf production was minimal in months when *Colobus* did not eat its leaves.

In April 93, almost all *C. zenkeri* leaves eaten by *guereza* were distinguished as young leaves (36.1% compared to 38.9% for leaves of all age classes); for *angolensis*, slightly more than half (13.8% young leaves compared to 24.2% for leaves of all age classes). In May and June, young leaves were less often distinguished from mature leaves. In September and October, most records of *C. mildbraedii* leaf consumption by *angolensis* were accounted for by feeding on young leaves. In other months, young leaves were less often distinguished, as was always the case for *C. guereza*. In all months when *C. alexandri* leaves were eaten, by either *angolensis* or *guereza*, young leaves accounted for one-third to two-thirds of all leaf consumption records. Thus, I assume that young leaves of these three species were consumed more frequently than mature leaves.

In months when young leaves were most abundant - April for *C. zenkeri* (AI = 0.14), May for *C. alexandri* (AI = 4.63), and June for *C. mildbraedii* (AI = 0.15), availability indices for *C. zenkeri* and *C. mildbraedii* were 3.0-3.2% the value for *C. alexandri*; indices for the two *Celtis* species were almost equal. Peak availability for Dikpolo young leaves should be similar in magnitude to that of *C. mildbraedii*; the former species occurs at two-thirds the density of the latter, but seemed to produce a larger young leaf crop.

Colobus stopped feeding on *C. zenkeri* after June; young leaves were no longer available. *C. mildbraedii* produced young leaves again in October and November; *angolensis* continued to feed on this species, as did *guereza*, but much less frequently than *angolensis*. In most months, *C. alexandri* produced young leaves, which were consumed by *angolensis* but rarely by *guereza*.

C. alexandri and *E. suaveolens* fruit production peaked in July. In this month, the abundance of *E. suaveolens* seeds (AI = 0.48) was 4% that of *C. alexandri* seeds (AI = 12.0). The increase in consumption of *C. alexandri* seeds from June to August by *C. angolensis* suggests that *angolensis* probably included this food in their diet during July. Similarly, *C. guereza* probably ate *E. suaveolens* seeds in September, as consumption of this item increased from August to October. After October, very little fruit of either species was available.

IV. DISCUSSION

Monthly diet overlap between *C. angolensis* and *C. guereza* at Basakwe is comparable in degree to that reported for *Procolobus badius* and *C. angolensis* in the Salonga (mean overlap 21%, range 7-35%; Maisels *et al.*, 1994), and for *Alouatta palliata* and *Ateles geoffroyi* (mean 22.9%, range 0.0-83.7%) and *Cebus capucinus* and *A. geoffroyi* (mean 23.6%, range 0.0-43.0%) at Santa Rosa, Costa Rica (Chapman, 1987). Diet overlap was considerably higher than that reported for *P. badius* and *C. guereza* in the Kibale Forest (mean 7.1%, range 2.0-15.7%; Struhsaker & Oates, 1975). The significance of different degrees of diet overlap is not clear, since the impact of overlap on a species pair will depend on several factors, including the degree of similarity in their food preferences, and the types and quantity of foods available.

How similar are the food preferences of *C. angolensis* and *C. guereza*? During the year of study, they showed no difference in their total consumption of leaves and fruit. Their monthly patterns of plant part consumption, however, were quite different. *C. guereza* was primarily folivorous in 8 of 11 months; *C. angolensis*, in only 2 of 11 months. Both species were primarily granivorous in 1 month (or possibly 2 months, taking into account the 1 month for which data were not collected).

At this site, then, *guereza* appears to be a specialist folivore. It shows a strong preference for leaves of deciduous trees, particularly those which are high in crude protein;

furthermore, leaf fiber content does not seem to be a major factor influencing leaf selection. *Angolensis* is more generalized in its feeding patterns; items for which it shows strong preference include leaves of deciduous trees, as well as flowers and seeds. The *angolensis* pattern of leaf selection seems to minimize fiber ingestion, rather than maximize protein.

The specific conditions which describe food scarcity for *C. guereza*, therefore, may be different than for *C. angolensis*. When young leaves of deciduous trees are not available, *guereza* consumes young leaves of evergreens, seeds of leguminous trees and lianas, or liana leaves. The *guereza* pattern of seed consumption suggests that seeds are eaten because they are seasonally abundant, i.e., to compensate for young leaf scarcity. *Angolensis* also eat seeds that are seasonally abundant, yet other seed and flower items are preferred foods even when young leaves are available. *Angolensis* may experience periods of food shortage less frequently than *guereza*. Young leaves of evergreen trees are available throughout much of the year - leaves of one evergreen, *Cynometra alexandri*, were frequently consumed by *angolensis*.

During the year of study, five food items were the primary sources of diet overlap in different months. Two of these items, *Cynometra alexandri* seeds and *Erythrophleum suaveolens* seeds, were relatively abundant during the period of overlapping use. Three items were rare: young leaves of *Celtis zenkeri*, *C. mildbraedii*, and Dikpolo; these species all occur at densities of less than 1 large tree per hectare. During 4 months (April to June, and February) one of these rare items was the primary food for one or both *Colobus* species.

The degree of diet overlap, and the items for which overlap occurs, may change from one year to the next. If, however, overlap occurs for rare items - specifically young leaves of some deciduous species - *C. guereza* is more likely to be adversely affected by overlapping use than *C. angolensis*. The *guereza* population may be limited by the availability of deciduous leaves. Although this factor may also influence *angolensis* abundance, the species seems to be more flexible in using alternative food sources.

C. guereza in the Ituri is less folivorous than it is in the Kibale Forest, where, over a 12-month period, leaf-eating accounted for 77% of feeding records (Oates, 1977a). This difference is most likely due to intersite differences in availability of suitable leaf foods - at Kibale, *C. guereza*'s primary food was a common deciduous species, *Celtis durandii*. *C. angolensis* in the Salonga were primarily granivorous (seeds comprised 50% of feeding records) over an 8-month study period (Maisels *et al.*, 1994); this proportional representation of seeds may have been lower had the animals been studied over a full year. During a 6-month study of *angolensis* in Kenya, leaves comprised 57% of the diet; seeds and other fruit parts, 32%; flowers, 11% (Moreno-Black & Maples, 1977). These data, considered together with data from the Basakwe site, suggest a greater tendency toward folivory in *C. guereza*, and a tendency toward a less specialized diet in *C. angolensis*.

How would such dietary differences manifest morphologically? Chivers (1994) points to an increase in stomach size with increasing folivory among colobine species. His analysis includes data for *C. guereza*, but none are available for *C. angolensis*. Thus, I can only speculate that the species may differ in this aspect of gut morphology. Fiber is digested slowly, requiring a longer retention time in the forestomach than other food components; retention time is affected by the size of the forestomach (Kay & Davies, 1994). *C. guereza* at Basakwe did not avoid eating fibrous leaves, in contrast to *C. angolensis*; *guereza* may, therefore, be more capable of digesting fiber than *angolensis*. Furthermore, *guereza* spend more time inactive than *angolensis* (see Chapter 5, Sec. III.A) - which may be directly related to differences in their diets.

I cannot, therefore, reject the hypothesis that dietary separation in sympatric *Colobus* is primarily due to species differences; there is no reason to implicate food competition as a major determinant of their dietary separation.

V. SUMMARY

1. In terms of plant parts eaten, the annual diets of *C. angolensis* and *C. guereza* differed only in the proportional representation of flowers; leaf and seed proportions in the diet were not different between species.

2. *C. guereza* consumed lianas more frequently than *C. angolensis*. For both *Colobus*, the most frequently consumed family of plants was the Leguminosae (30% of feeding observations), followed by the family Ulmaceae.

3. The two most frequently consumed food items differed between *Colobus*. For *C. angolensis*, these were *Celtis mildbraedii* leaves and *Cynometra alexandri* leaves; for *C. guereza*, these were *Erythrophleum suaveolens* seeds and *Albizia gummifera* leaves.

4. Analysis of annual diets suggests that *C. angolensis* has broader food preferences; highly-preferred foods included 1 flower, 1 seed, and 3 leaf items; *C. guereza*'s most highly preferred foods consisted only of leaf items. Analysis of monthly diets indicates similar trends: *C. guereza* is primarily folivorous in most months, while *C. angolensis* is more general in its feeding habits.

5. In contrast to *C. angolensis*, seed-eating by *C. guereza* did not seem to indicate seed preference; rather, seeds were consumed primarily when preferred foods - young leaves of deciduous trees - were not available.

6. *C. guereza* leaf selection shows a strong positive correlation with young leaf protein content; the negative association between leaf fiber content and leaf selection is weak and nonsignificant. Conversely, *C. angolensis* leaf selection shows a strong negative correlation with young leaf fiber content; the positive association between leaf protein content and leaf selection is weaker and nonsignificant. Comparison of food and nonfood leaf items suggests similar trends: for *C. guereza*, young leaf crude protein content differs between food and nonfood species; for *C. angolensis*, young leaf acid detergent fiber content differs between food and nonfood species.

7. *C. angolensis* and *C. guereza* overlapped in their consumption of five main food items. Three of these were the leaves of rare species; overlap for these items occurred when young leaf availability was highest. Two items were commonly-available seeds; overlap for one of these foods coincided with the period of highest availability; for the other, overlap occurred when availability started to decline.

8. Although the food items preferred by both *Colobus* are rare, *C. angolensis* may be less affected by food scarcity than *C. guereza*, because in most months, *angolensis* also fed on the leaves of a common species (*Cynometra alexandri*). The availability of leaves of deciduous trees may limit the *guereza* population in this forest.

9. Species differences in food preferences and food processing ability may explain dietary separation in sympatric populations.

Table 4.1. Plant part composition of *Colobus* annual diets[a]. Values represent percent of total feeding observations (*C. angolensis*: $n = 2457$; *C. guereza*: $n = 1336$).

Plant part	*C. angolensis*	*C. guereza*
leaf bud	2.4	3.5
young leaf	23.5	26.2
mature leaf	2.4	3.8
leaf, undetermined age	22.0	24.2
petiole	0.8	0.2
total leaf	51.1	57.9
unripe seed	5.5	6.7
ripe seed	1.3	3.8
seed, undetermined age	15.3	11.5
total seed	22.1	22.0
fruit pulp	5.4	2.6
total fruit	27.5	24.6
flower	7.2	2.9
lichen	0.4	0.2
other items (soil, wood)	0.0	0.5
undetermined items	13.6	13.8
	100.0	100.0

[a] Two analyses of *Colobus* species by plant part yield significant chi-square values: (a) plant parts = total leaf, total fruit, flower: $X^2 = 25.85$, 2 d.f., $p < 0.001$; (b) plant parts = young leaf (including leaf bud), mature leaf, seed, flower: $X^2 = 38.25$, 3 d.f., $p < 0.001$.

Table 4.2. Plant species consumed by colobus study groups from April 1993 through March 1994. Values represent percent of total feeding observations (*C. angolensis*: *n* = 2457; *C. guereza*: *n* = 1336).

A. *C. angolensis*[a]

family	species	species total	family total
Leguminosae			
Caesalpinioideae	*Cynometra alexandri*	15.14	
	Erythrophleum suaveolens	6.19	
	Amphimas pterocarpoides	2.28	
Mimosoideae	*Piptadeniastrum africanum*	1.22	
	Albizia sp.	0.04	
Papilionoideae	*Angylocalyx pinnaertii*	5.70	30.57
Ulmaceae	*Celtis mildbraedii*	13.26	
	Celtis zenkeri	4.23	
	Celtis prantlii	0.90	
	Celtis adolfi-friederici	0.08	18.47
Apocynaceae	*Alstonia boonei*	8.30	8.30
Euphorbiaceae	*Drypetes* spp. (Roko[b] group)	2.47	
	Discoglypremna caloneura	1.14	
	Drypetes spp. (Sungba[b] group)	0.94	4.55
Moraceae	*Milicia excelsa*	2.89	
	Antiaris africana	0.81	
	Ficus spp.	0.28	3.98
Sapindaceae	*Lecaniodiscus cupanioides*	3.66	3.66
Olaceaceae	*Strombosia pustulata*	2.36	
	Strombosiopsis tetrandra	0.73	
	Strombosia grandifolia	0.04	3.13
Tiliaceae	*Desplatsia dewevrei*	1.95	1.95
Annonaceae	*Xylopia aethiopica*	1.42	
	Monodora myristica	0.37	1.79
Rutaceae	*Zanthoxylum macrophyllum*	1.47	
	Zanthoxylum lemairei	0.24	1.71
Dilleniaceae	*Tetracera* sp.?	1.59	1.59

(Table 4.2.A., continued)

family	species	species total	family total
Sapotaceae	*Gambeya* sp.?	0.53	
	Omphalocarpum sp.?	0.37	
	Manilkara sp.	0.16	1.06
Loganiaceae	*Anthocleista schweinfurthii*	0.28	0.28
Connaraceae	*Agelaea* sp.?	0.20	0.20
Bignoniaceae	*Spathodea campanulata*	0.16	0.16
Combretaceae	*Pteleopsis hylodendron*	0.16	0.16
Sterculiaceae	*Cola lateritia*	0.04	0.04
Unknown	Dikpolo[b] (unid. tree)	8.30	
Unknown	Njambal[b] (unid. liana)	0.08	
Unknown	other lianas	3.83	
	other trees	2.85	
	lichen	0.41	
	epiphytes	0.16	
Unknown items		2.69	
		100.00	81.60

[a] Total number of tree and liana species in diet:

- 31 tree species identified or distinguished
- 3 tree groups, identified to generic level; each group includes 2 or more species [*Drypetes* spp. (Roko group) includes *D. ituriensis*; *Drypetes* spp. (Sungba group) includes *D. bipindensis*; *Ficus* spp.]
- 3 liana species, unidentified but distinguishable

[b] Vernacular name

(Table 4.2, continued)

B. *C. guereza*[c]

family	species	species total	family total
Leguminosae			
Caesalpinioideae	*Erythrophleum suaveolens*	9.81	
	Cynometra alexandri	3.74	
	Cassia mannii	2.62	
Mimosoideae	*Albizia gummifera*	9.36	
Papilionoideae	*Angylocalyx pinnaertii*	4.12	29.65
Ulmaceae	*Celtis mildbraedii*	5.09	
	Celtis zenkeri	3.52	
	Celtis prantlii	2.47	11.08
Euphorbiaceae	*Drypetes* spp. (Sungba[d] group)	3.00	
	Margaritaria discoidea	2.25	
	Drypetes spp. (Roko[d] group)	2.01	
	Discoglypremna caloneura	1.50	8.76
Apocynaceae	*Alstonia boonei*	5.31	
	Rauvolfia vomitoria	1.20	6.51
Moraceae	*Ficus* spp.	4.72	
	Milicia excelsa	1.12	5.84
Tiliaceae	*Desplatsia dewevrei*	4.12	4.12
Oleaceae	*Schrebera golungensis*	2.62	2.62
Dilleniaceae	*Tetracera* sp.?	1.27	1.27
Loganiaceae	*Anthocleista schweinfurthii*	1.12	1.12
Combretaceae	*Pteleopsis hylodendron*	1.12	1.12
Rhizophoraceae	*Commiphyton gabonense*	1.05	1.05
Rutaceae	*Zanthoxylum macrophyllum*	0.90	
	Zanthoxylum lemairei	0.07	0.97
Olacaceae	*Strombosia pustulata*	0.37	
	Strombosiopsis tetrandra	0.07	0.44
Connaraceae	*Agelaea* sp.?	0.07	0.07

(Table 4.2.B., continued)

family	species	species total	family total
Unknown	Dikpolo[d] (unid. tree)	4.42	
Unknown	Njamba1[d] (unid. liana)	2.92	
	Njamba2[d] (unid. liana)	0.07	
	Teka[d] (unid. liana)	0.07	
Unknown	other lianas	8.08	
	other trees	2.10	
	lichen	0.22	
Other items	wood	0.15	
	soil	0.07	
Unknown items		7.26	
		100.00	74.62

[c] Total number of tree and liana species in diet:
- 23 tree species identified or distinguished
- 3 tree groups, identified to generic level; each group includes 2 or more species [*Ficus* spp.; *Drypetes* spp. (Sungba group) includes *D. bipindensis*; *Drypetes* spp. (Roko group) includes *D. ituriensis*]
- 5 liana species, unidentified but distinguishable

[d] Vernacular name

Table 4.3. Characteristics of the top twenty food species and their selection by *Colobus*. Density (#/ha) values are for trees $\geq$ 30 cm dbh (except for *D. dewevrei*, Sungba, and *R. vomitoria*; see below). CD = coefficient of dispersion, SR = selection ratio (see text for explanation); sp.tot = species total, percent of feeding observations (*C. angolensis*: *n* = 2457; *C. guereza*: *n* = 1336); cum % = cumulative percent.

A. *C. angolensis*

species	growth form[a]	#/ha	CD	SR	SR rank	sp.tot., % obs.	cum. %
Cynometra alexandri	L,E	58.8	1.80	4	16	15.14	15.14
Celtis mildbraedii	M-L,D	0.6	1.28	302	2	13.26	28.40
Alstonia boonei	M-L,D	2.6		44	9	8.30	36.70
Dikpolo (unid. tree)	M,D	0.4	1.47	286	3	8.30	45.00
Erythrophleum suaveolens	L,D	4.3	0.94	20	13	6.19	51.19
Angylocalyx pinnaertii	M-L,E	0.4		197	6	5.70	56.89
Celtis zenkeri	L,D	0.2	0.99	280	4	4.23	61.12
Unknown lianas						3.83	64.95
Lecaniodiscus cupanioides	M,D	0.2		247	5	3.66	68.61
Milicia excelsa	L,D	0.4		100	7	2.89	71.50
Unknown trees						2.85	74.35
Drypetes spp. (Roko)	L,E?	2.4		14	15	2.47	76.82
Strombosia pustulata	L,E	1.8		18	14	2.36	79.18
Amphimas pterocarpoides	L,D?	0.1	1.00	329	1	2.28	81.46
Desplatsia dewevrei[b]	S,E	25.5		4	16	1.95	83.41
Ngoto (unid. liana)[c]						1.59	85.00
Zanthoxylum macrophyllum	L,D	0.7		29	10	1.47	86.47
Xylopia aethiopica	M,E	0.8		24	12	1.42	87.89
Piptadeniastrum africanum	L,D	0.2		80	8	1.22	89.11
Discoglypremna caloneura	M-L,D	0.6		25	11	1.14	90.25
Drypetes spp. (Sungba)[b]	S,E?	59.0		1	17	0.94	91.19
Celtis prantlii	M-L,D	3.1		4	16	0.90	92.09

[a] Relative size of mature trees: S - small tree; M - medium-sized tree; L - large tree. D - deciduous; E - evergreen.

[b] For *D. dewevrei*, *Drypetes* spp. (Sungba), and *R. vomitoria*, densities are given for small (10 cm $\leq$ dbh < 30 cm) rather than large trees. Selection ratios for these species are based on their proportional contribution to the total number of small trees (rather than large trees) in the enumeration sample.

[c] Density of lianas not assessed.

(Table 4.3, continued)

B. *C. guereza*

species	growth form[a]	#/ha	CD	SR	SR rank	sp.tot., % obs.	cum. %
Erythrophleum suaveolens	L,D	4.3	0.94	31	9	9.81	9.81
Albizia gummifera	L,D	0.3	0.98	427	1	9.36	19.17
Unknown lianas						8.08	27.25
Alstonia boonei	M-L,D	2.6		28	10	5.31	32.56
Celtis mildbraedii	M-L,D	0.6	1.28	116	5	5.09	37.65
Ficus spp.	L,D	1.5		43	6	4.72	42.37
Dikpolo (unid. tree)	M,D	0.4	1.47	152	3	4.42	46.79
Angylocalyx pinnaertii	M-L,E	0.4		141	4	4.12	50.91
Desplatsia dewevrei[b]	S,E	25.5		9	14	4.12	55.03
Cynometra alexandri	L,E	58.8	1.80	1	16	3.74	58.77
Celtis zenkeri	L,D	0.2	0.99	233	2	3.52	62.29
Drypetes spp. (Sungba)[b]	S,E?	59.0		3	15	3.00	65.29
Njamba1 (unid. liana)[c]						2.92	68.21
Cassia mannii	L,D	1.4		25	11	2.62	70.83
Schrebera golungensis[d]	L,D	?				2.62	73.45
Celtis prantlii	M-L,D	3.1		11	13	2.47	75.92
Margaritaria discoidea	M,D	0.8		38	7	2.25	78.17
Unknown trees						2.10	80.27
Drypetes spp. (Roko)	L,E?	2.4		11	13	2.01	82.28
Discoglypremna caloneura	M-L,D	0.6		34	8	1.50	83.78
Ngoto (unid. liana)[c]						1.27	85.05
Rauvolfia vomitoria[b]	S,D	3.0		22	12	1.20	86.25

[a,b,c] See footnotes to Table 4.3.A.

[d] Did not appear on enumeration transect.

Table 4.4. Principal *Colobus* food items, ranked from 1 through 20, by percent of total feeding observations. Imm: immature; mat: mature; undet: undetermined age; item: total for all age classes.

A. *Colobus angolensis*

rank	item	% imm	% mat	% undet	% item	cum %
1	*Celtis mildbraedii* leaves	3.01	0.20	10.05	13.26	13.26
2	*Cynometra alexandri* leaves	4.55	0.08	4.35	8.98	22.24
3	Dikpolo (unid. tree) leaves	6.39	0.65	1.26	8.30	30.54
4	*Erythrophleum suaveolens* seeds	3.30	0.04	2.85	6.19	36.73
5	*Celtis zenkeri* leaves	1.79	0.12	2.32	4.23	40.96
6	*Cynometra alexandri* seeds	0.20	0.45	3.30	3.95	44.91
7	*Lecaniodiscus cupanioides* seeds			3.66	3.66	48.57
8	*Alstonia boonei* flowers			3.22	3.22	51.79
9	*Alstonia boonei* leaves[a]	1.34	0.08	0.69	2.68	54.47
10	*Angylocalyx pinnaertii* leaves	2.52	0.08	0.04	2.64	57.11
11	*Amphimas pterocarpoides* flowers			2.28	2.28	59.39
12	*Strombosia pustulata* seeds	0.00	0.73	1.47	2.20	61.59
13	*Drypetes* spp. (Roko) seeds	0.65	0.00	1.38	2.03	63.62
14	*Milicia excelsa* fruit			1.71	1.71	65.33
15	*Desplatsia dewevrei* leaves	1.30	0.08	0.28	1.66	66.99
16	Ngoto (unid. liana) seeds			1.59	1.59	68.58
17	*Xylopia aethiopica* fruit			1.42	1.42	70.00
18	*Piptadeniastrum africanum* seeds	1.10	0.00	0.04	1.14	71.14
19	*Discoglypremna caloneura* leaves	0.61	0.00	0.53	1.14	72.28
20	*Milicia excelsa* leaves	0.94	0.04	0.98	0.98	73.26

[a] Item total includes feeding on petioles.

(Table 4.4, continued)

B. *Colobus guereza*

rank	item	% imm	% mat	% undet	% item	cum %
1	*Erythrophleum suaveolens* seeds	4.42	0.00	4.94	9.36	9.36
2	*Albizia gummifera* leaves	8.61	0.07	0.67	9.35	18.71
3	*Celtis mildbraedii* leaves	0.67	0.00	4.42	5.09	23.80
4	Dikpolo (unid. tree) leaves	1.87	0.30	2.25	4.42	28.22
5	*Ficus* spp. leaves	0.37	0.67	3.14	4.18	32.40
6	*Desplatsia dewevrei* leaves	2.62	0.00	1.42	4.04	36.44
7	*Celtis zenkeri* leaves	1.95	0.07	1.50	3.52	39.96
8	*Drypetes* spp. (Sungba) leaves	1.80	0.00	1.20	3.00	42.96
9	*Alstonia boonei* leaves	2.17	0.15	0.60	2.92	45.88
10	Njambal (unid. liana) seeds	0.97	0.00	1.95	2.92	48.80
11	*Cassia mannii* seeds	0.15	2.25	0.22	2.62	51.42
12	*Celtis prantlii* leaves	1.05	0.07	1.35	2.47	53.89
13	*Margaritaria discoidea* seeds	0.00	0.90	1.35	2.25	56.14
14	*Cynometra alexandri* leaves	0.75	0.00	1.20	1.95	58.09
15	*Schrebera golungensis* leaves	1.20	0.00	0.75	1.95	60.04
16	*Angylocalyx pinnaertii* leaves[a]	1.57	0.00	0.00	1.72	61.76
17	*Alstonia boonei* flowers			1.65	1.65	63.41
18	*Cynometra alexandri* seeds	0.00	0.22	1.35	1.57	64.98
19	Ngoto (unid. liana) seeds			1.27	1.27	66.25
20	*Discoglypremna caloneura* leaves	0.45	0.00	0.75	1.20	67.45

[a] Item total includes feeding on petioles.

Table 4.5. Principal *Colobus* food items ranked by item selection ratio (SR), and item chemistry. Items indicated as fl (flower), lf (leaf), yl (young leaf), ml (mature leaf), sd (seed), fr (fruit), ufr (unripe fruit), rfr (ripe fruit), us (unripe seed), rs (ripe seed). Phytochemical measures indicated as CP (crude protein), ADF (acid detergent fiber), TP (total phenolics), CT (condensed tannins). CP and ADF expressed as percent dry weight; Prot/ADF = CP/ADF; TP expressed as percent dry weight tannic acid equivalents; CT expressed as percent dry weight quebracho tannin equivalents.

A. *C. angolensis*

SR rank	species	item	SR	item ana-lyzed	CP	ADF	Prot/ ADF	TP	CT
1	*A. pterocarpoides*	fl	329	fl	25.0	—	—	3.2	0.6
2	*C. mildbraedii*	lf	302	yl	32.8	21.0	1.56	1.0	0.0
				ml	15.6	26.9	0.58	2.6	0.0
3	Dikpolo	lf	286	yl	23.2	9.5	2.44	5.8	0.7
4	*C. zenkeri*	lf	280	yl	25.0	22.4	1.12	3.2	0.0
				ml	18.4	25.0	0.74	3.8	0.0
5	*L. cupanioides*	sd	247	rs	9.1	—	—	6.4	6.1
6	*A. pinnaertii*	lf	91	yl	24.2	12.8	1.91	2.3	57.6
				ml	17.3	38.7	0.45	1.7	30.6
7	*P. africanum*	sd	80	us	20.9	—	—	0.1	2.9
8	*M. excelsa*	fr	59	ufr	16.9	—	—	6.5	27.8
				rfr	20.9	—	—	0.3	1.5
9	*M. excelsa*	lf	34	—	—	—	—	—	—
10	*D. caloneura*	lf	25	yl	17.5	38.6	0.45	—	—
				ml	14.6	37.5	0.39	4.7	28.2
11	*X. aethiopica*	sd	24	—	—	—	—	—	—
12	*E. suaveolens*	sd	20	us	13.4	—	—	1.7	11.0
13	*S. pustulata*	sd	18	rs	18.8	—	—	0.4	1.2
14	*A. boonei*	fl	17	fl	15.9	—	—	2.5	18.1

(Table 4.5.A., continued)

SR rank	species	item	SR	item ana-lyzed	CP	ADF	Prot/ ADF	TP	CT
15	*A.. boonei*	lf	14	yl	22.2	40.1	0.55	2.7	2.8
				ml	17.5	20.7	0.85	2.3	2.1
16	*Drypetes* sp.[a]	sd	12	us	23.8	—	—	—	—
				rs	11.2	—	—	0.5	1.5
17	*D. dewevrei*	lf	4	yl	20.6	44.6	0.46	0.0	0.0
				ml	16.8	46.9	0.36	0.0	0.0
18	*C. alexandri*	lf	2	yl	25.9	43.2	0.60	5.6	11.4
				ml	18.8	40.4	0.47	8.0	21.6
19	*Drypetes* sp.[b]	lf	1	yl	16.6	36.7	0.45	0.9	0.6
				ml	11.2	42.6	0.26	2.6	0.0
20	*C. alexandri*	sd	1	us	22.8	—	—	0.9	2.2

B. *C. guereza*

SR rank	species	item	SR	item ana-lyzed	CP	ADF	Prot/ ADF	TP	CT
1	*A. gummifera*	lf	427	yl	31.9	38.3	0.83	7.0	29.3
				ml	19.1	44.4	0.43	4.2	21.8
2	*C. zenkeri*	lf	233	yl	25.0	22.4	1.12	3.2	0.0
				ml	18.4	25.0	0.74	3.8	0.0
3	Dikpolo	lf	152	yl	23.2	9.5	2.44	5.8	0.7
4	*C. mildbraedii*	lf	116	yl	32.8	21.0	1.56	1.0	0.0
				ml	15.6	26.9	0.58	2.6	0.0
5	*A. pinnaertii*	lf	59	yl	24.4	12.8	1.91	2.3	57.6
				ml	17.3	38.7	0.45	1.7	30.6
6	*Ficus* sp.	lf	38	yl	30.0	31.5	0.95	1.4	2.1
				ml	20.3	29.7	0.68	0.4	0.7
7	*M. discoidea*	sd	38	rs	4.2	—	—	0.4	0.0

(Table 4.5.B., continued)

SR rank	species	item	SR	item ana-lyzed	CP	ADF	Prot/ ADF	TP	CT
8	*D. caloneura*	lf	34	yl	17.5	38.6	0.45	—	—
				ml	14.6	37.5	0.39	4.7	28.2
9	*A. pinnaertii*	sd	31	us	20.0	—	—	2.2	7.3
10	*E. suaveolens*	sd	30	us	13.4	—	—	1.7	11.0
11	*C. mannii*	sd	25	us	14.4	—	—	1.1	11.7
				rs	15.0	—	—	—	—
12	*R. vomitoria*	sd	22	rs	9.1	—	—	1.3	1.5
13	*A. boonei*	lf	15	yl	22.2	40.1	0.55	2.7	2.8
				ml	17.5	20.7	0.85	2.3	2.1
14	*C. prantlii*	lf	11	ml	10.9	27.8	0.39	1.2	0.0
15	*A. boonei*	fl	9	fl	15.9	—	—	2.5	18.1
16	*D. dewevrei*	lf	9	yl	20.6	44.6	0.46	0.0	0.0
				ml	16.8	46.9	0.36	0.0	0.0
17	*Drypetes* sp.[a]	sd	3	us	23.8	—	—	—	—
				rs	11.2	—	—	0.5	1.5
18	*Drypetes* sp.[b]	lf	3	yl	16.6	36.7	0.45	0.9	0.6
				ml	11.2	42.6	0.26	2.6	0.0
19	*Drypetes* sp.[a]	fl	1	—	—	—	—	—	—
20	*Drypetes* sp.[a]	lf	1	yl	13.1	52.5	0.25	2.9	0.0
				ml	12.5	44.8	0.28	1.8	0.0

[a] "Roko" group; *D. ituriensis*?

[b] "Sungba" group; *D. bipindensis*?

Table 4.6. Spearman correlation and partial correlation coefficients between leaf item selection ratios and young leaf chemical measures (from Table 4.5). Variables abbreviated as SR (selection ratio), Prot/ADF (protein/fiber), CP (crude protein), ADF (acid detergent fiber), TP (total phenolics), and CT (condensed tannins).

A. SR with Prot/ADF, CP, ADF

variables	*C. angolensis* (*n* = 9)	*C. guereza* (*n* = 11)
SR, Prot/ADF	+0.736**	+0.761***
SR, CP	+0.550	+0.827***
SR, ADF	-0.733**	-0.664**
SR,CP (partial variable: ADF)	+0.525	+0.725**
SR, ADF (partial variable: CP)	-0.721**	-0.399

B. SR with TP,CT

variables	*C. angolensis* (*n* = 8)	*C. guereza* (*n* = 10)
SR,TP	+0.310	+0.612*
SR, CT	-0.268	+0.281

* $p < 0.1$; ** $p < 0.05$; *** $p < 0.01$.

Table 4.7. Monthly composition of *Colobus* diets by plant part. Values represent percent of feeding observations during 5-day follows: yl+lb = young leaves and leaf buds, ml = mature leaves, totlf = total leaf (young + mature + leaves of undetermined age + petioles), totfr = total fruit (seeds and other fruit parts), unknown = undetermined items; consumption of other items (lichen, soil, wood) not included.

A. *C. angolensis*

month	yl+lb	ml	totlf	seed	totfr	flower	unknown
4/93	29.2	0.4	42.7	35.4	36.9	5.0	15.4
5/93	18.1	4.6	56.9	1.8	21.4	0.0	21.7
6/93	11.6	0.0	59.3	18.1	23.2	0.0	17.6
7/93	—	—	—	—	—	—	—
8/93	4.2	2.8	23.2	56.5	57.9	1.4	17.6
9/93	16.1	1.1	25.2	63.2	70.1	0.0	4.6
10/93	15.5	1.8	35.7	43.3	44.0	1.4	15.2
11/93	25.6	1.0	81.9	7.0	7.5	0.0	10.6
12/93	32.0	8.3	55.2	0.5	0.5	34.3	10.2
1/94	32.8	1.4	45.6	14.4	17.5	23.4	13.4
2/94	46.9	1.8	59.2	24.5	33.1	1.8	5.9
3/94	51.8	3.1	73.3	0.0	11.8	6.2	8.7

B. *C. guereza*

month	yl+lb	ml	totlf	seed	totfr	flower	unknown
4/93	52.8	2.8	75.1	0.0	2.8	0.0	22.2
5/93	39.2	0.0	74.5	0.0	0.0	0.0	25.5
6/93	6.4	3.8	62.8	0.0	10.3	2.6	24.4
7/93	2.7	1.4	10.9	41.1	52.1	0.0	31.5
8/93	0.0	2.9	14.3	52.8	54.2	11.4	17.1
9/93	—	—	—	—	—	—	—
10/93	6.0	1.2	8.4	83.8	85.6	0.6	5.4
11/93	29.3	8.0	63.3	23.9	23.9	0.0	12.7
12/93	47.0	4.7	80.1	8.6	8.6	0.0	11.4
1/94	55.4	3.2	74.7	5.4	5.4	10.2	7.5
2/94	41.1	3.3	79.5	7.9	9.2	0.0	11.3
3/94	20.2	5.5	64.4	6.8	14.2	5.5	16.0

Table 4.8. Food species diversity (*H*, Shannon's index) for 5-day pooled samples.

month	*C. angolensis*	*C. guereza*
4/93	1.89	1.61
5/93	2.34	1.73
6/93	1.99	1.96
7/93	—	1.84
8/93	1.54	1.78
9/93	1.06	—
10/93	1.92	1.07
11/93	1.65	2.31
12/93	2.20	2.40
1/94	1.91	1.86
2/94	1.77	2.02
3/94	1.90	2.29
mean, 11 months:	1.83	1.90

Table 4.9. Monthly summary of primary *Colobus* food items, primary overlapping items, and total diet overlap (all items). Values for primary food item are percentage of monthly feeding observations. Primary overlap item includes only those falling within the top 50% of each species' monthly diet. Values for primary overlap item and total diet overlap are percentages; see text for calculation. NA indicates that diet overlap was not calculated.

month	primary food item		primary overlap item	total diet overlap
	C. angolensis	*C. guereza*		
4/93	*L. cupanioides* seeds, 34.6	*C. zenkeri* leaves, 38.9	*C. zenkeri* leaves, 24.2	30.0
5/93	*C. mildbraedii* leaves, 17.8	*C. zenkeri* leaves, 25.5	*C. zenkeri* leaves, 12.5	29.0
6/93	*C. mildbraedii* leaves, 38.0	*C. mildbraedii* leaves, 20.5	*C. mildbraedii* leaves, 20.5	24.7
7/93	—	Njambal seeds, 23.3	NA	NA
8/93	*C. alexandri* seeds, 39.8	Njambal seeds, 31.4	*C. alexandri* seeds, 11.4	37.0
9/93	*E. suaveolens* seeds, 63.2	—	NA	NA
10/93	*E. suaveolens* seeds, 27.8	*E. suaveolens* seeds, 73.1	*E. suaveolens* seeds, 27.8	29.8
11/93	*C. mildbraedii* leaves, 45.2	Unknown lianas leaves, 19.3	none	14.0
12/93	*A. pterocarpoides* flowers, 25.9	*A. gummifera* leaves, 20.9	none	18.6
1/94	*A. boonei* flowers, 23.4	*A. gummifera* leaves, 43.0	NA	NA
2/94	Dikpolo leaves, 43.2	Dikpolo leaves, 23.2	Dikpolo leaves, 23.2	38.7
3/94	*C. alexandri* leaves, 30.3	*Ficus* spp. leaves, 15.3	Dikpolo leaves, 12.9	34.5

Table 4.10. Monthly comparison of food item availability and item consumption by *C. angolensis* and *C. guereza*. AI = availability index. Values in columns "ang" and "gue" are percent of study groups' monthly feeding observations accounted for by the indicated plant part.

A. Young leaf availability and young leaf consumption.

	C. zenkeri			*C. mildbraedii*			*C. alexandri*		
month	AI	ang	gue	AI	ang	gue	AI	ang	gue
2/93	0.01	—	—	0.00	—	—	0.00	—	—
3/93	0.11	—	—	0.00	—	—	1.86	—	—
4/93	0.14	13.8	36.1	0.02	0.0	0.0	1.56	0.0	5.6
5/93	0.10	2.8	15.7	0.07	3.6	2.0	4.63	3.6	7.8
6/93	0.07	0.0	2.6	0.15	4.2	3.8	0.00	0.5	0.0
7/93	0.05	—	0.0	0.04	—	0.0	0.00	—	0.0
8/93	0.07	0.0	0.0	0.02	2.8	0.0	0.61	0.0	0.0
9/93	—	0.0	—	—	11.5	—	—	4.6	—
10/93	0.02	0.0	0.0	0.12	13.7	0.0	0.26	4.0	0.0
11/93	0.02	0.0	2.0	0.11	5.5	0.0	3.59	5.5	2.0
12/93	0.02	0.0	0.0	0.06	1.8	2.4	3.81	0.5	0.5
1/94	0.01	0.0	0.0	0.05	0.0	0.0	0.35	10.3	0.0
2/94	0.05	0.0	0.0	0.04	0.4	0.0	1.08	0.0	0.0
3/94	0.00	0.0	0.0	0.04	2.6	0.0	1.57	22.6	0.0

B. Young leaf availability and total leaf consumption.

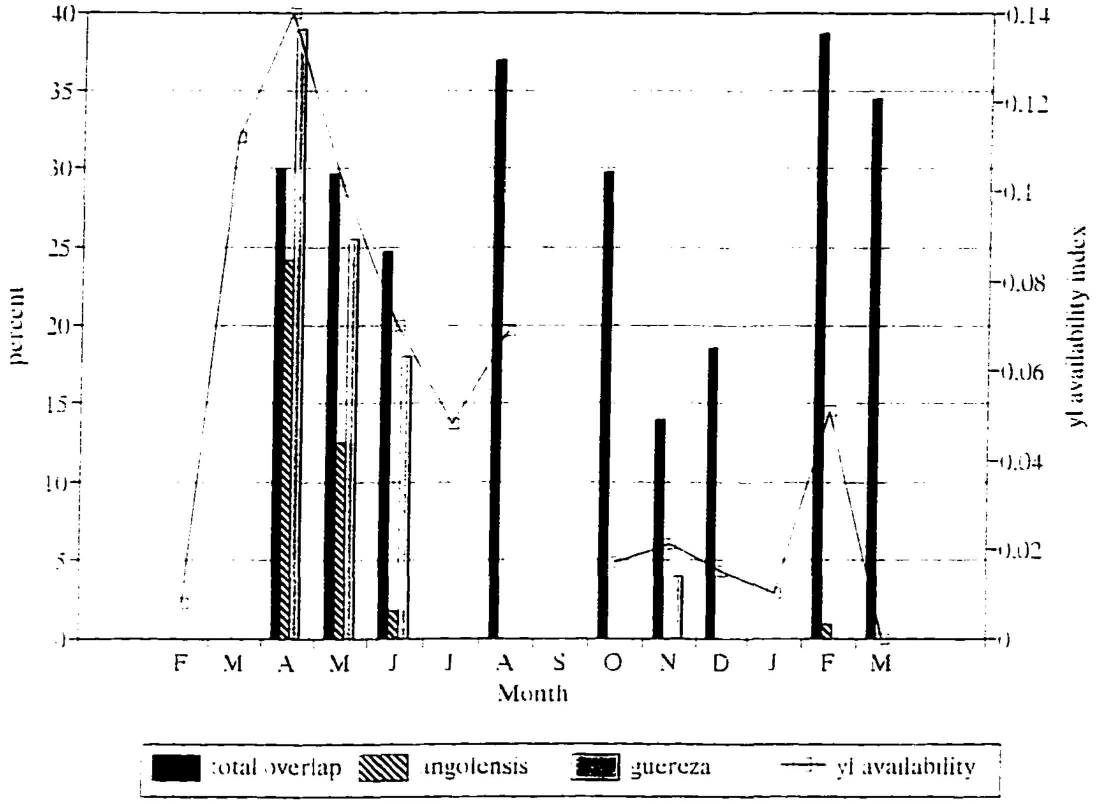
	C. zenkeri			*C. mildbraedii*			*C. alexandri*		
month	AI	ang	gue	AI	ang	gue	AI	ang	gue
2/93	0.01	—	—	0.00	—	—	0.00	—	—
3/93	0.11	—	—	0.00	—	—	1.86	—	—
4/93	0.14	24.2	38.9	0.02	0.0	0.0	1.56	0.0	11.1
5/93	0.10	12.5	25.5	0.07	17.8	5.9	4.63	6.4	19.6
6/93	0.07	1.8	18.0	0.15	38.0	20.5	0.00	3.7	0.0
7/93	0.05	—	0.0	0.04	—	0.0	0.00	—	1.4
8/93	0.07	0.0	0.0	0.02	18.5	10.0	0.61	0.0	0.0
9/93	—	0.0	—	—	12.6	—	—	12.6	—
10/93	0.02	0.0	0.0	0.12	13.7	0.0	0.26	15.2	0.0
11/93	0.02	0.0	4.0	0.11	45.2	4.0	3.59	12.1	4.0
12/93	0.02	0.0	0.0	0.06	3.2	14.2	3.81	3.7	2.4
1/94	0.01	0.0	0.0	0.05	0.0	3.2	0.35	17.6	0.0
2/94	0.05	0.9	0.0	0.04	0.9	0.0	1.08	0.0	0.0
3/94	0.00	0.0	0.0	0.04	3.1	0.0	1.57	30.2	0.0

C. Seed availability and seed consumption.

	C. alexandri			*E. suaveolens*		
month	AI	ang	gue	AI	ang	gue
2/93	0.00	—	—	0.04	—	—
3/93	0.00	—	—	0.04	—	—
4/93	4.63	0.0	0.0	0.00	0.0	0.0
5/93	4.63	0.0	0.0	0.28	0.0	0.0
6/93	6.19	5.1	0.0	0.35	0.0	0.0
7/93	12.04	—	17.8	0.48	—	0.0
8/93	6.67	39.8	11.4	0.31	8.8	4.3
9/93	—	0.0	—	—	63.2	—
10/93	0.26	0.0	0.0	0.27	27.8	73.0
11/93	0.00	0.0	0.0	0.00	0.5	0.0
12/93	0.00	0.0	0.0	0.00	0.0	0.0
1/94	0.00	0.0	0.0	0.00	0.0	0.0
2/94	0.00	0.0	0.0	0.00	0.0	0.0
3/94	0.00	0.0	0.0	0.00	0.0	0.0

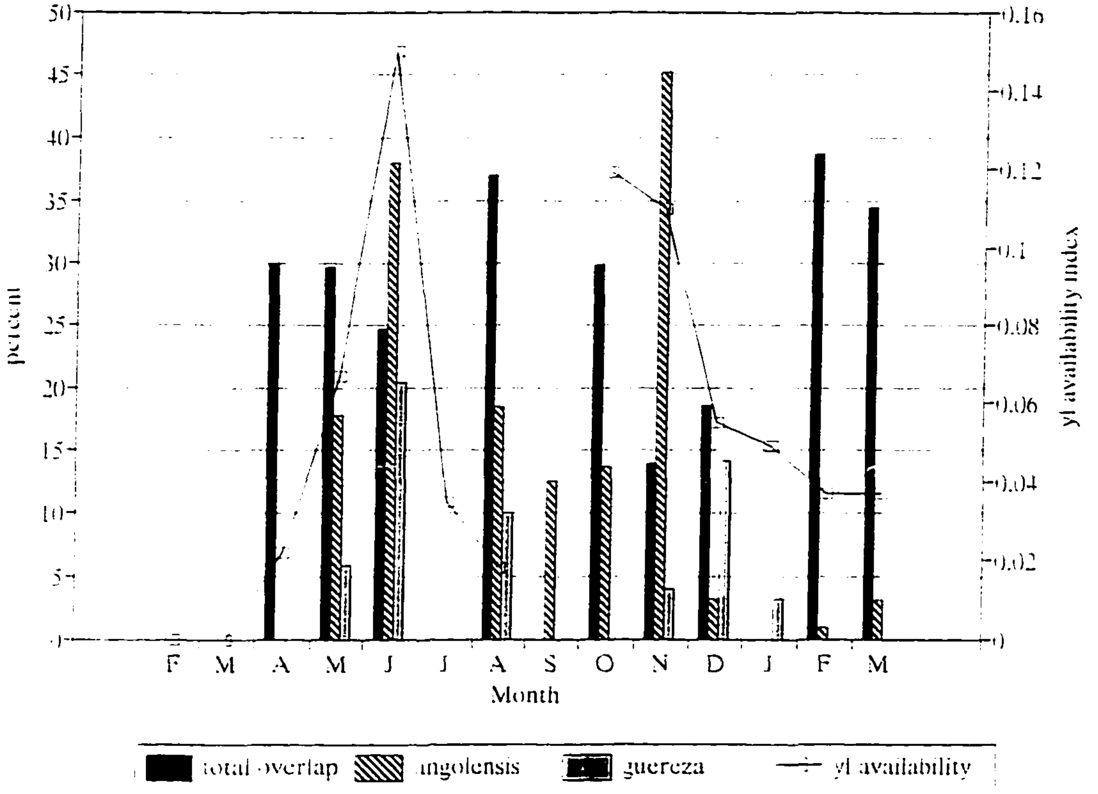
Figure 4.1. Monthly comparison of total diet overlap (all items), leaf consumption by *Colobus*, and young leaf availability of three major food plants. Diet overlap and leaf consumption are reported for April 93 to March 94; young leaf availability, for February 93 to March 94. Values for *angolensis* and *guereza* represent the percent of feeding observations accounted for by leaves of all age classes of the indicated plant species.

a. *Celtis zenkeri*



(Figure 4.1, continued)

b. *Celtis mildbraedii*



(Figure 4.1, continued)

c. *Cynometra alexandri*

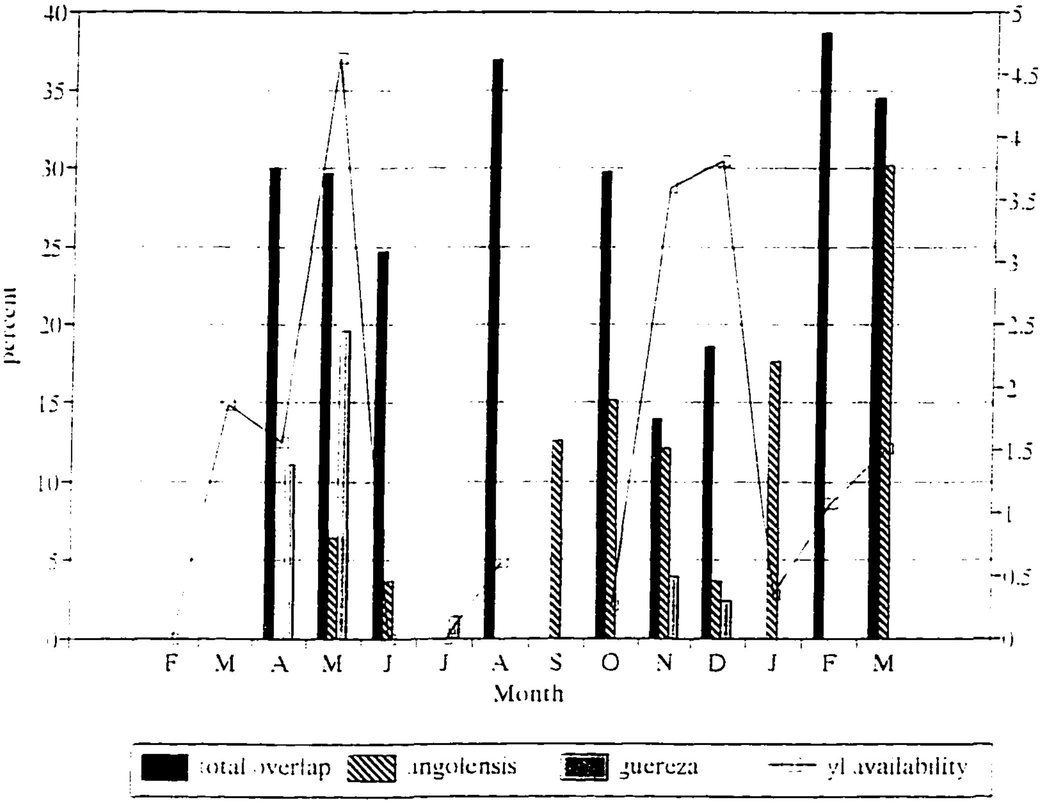
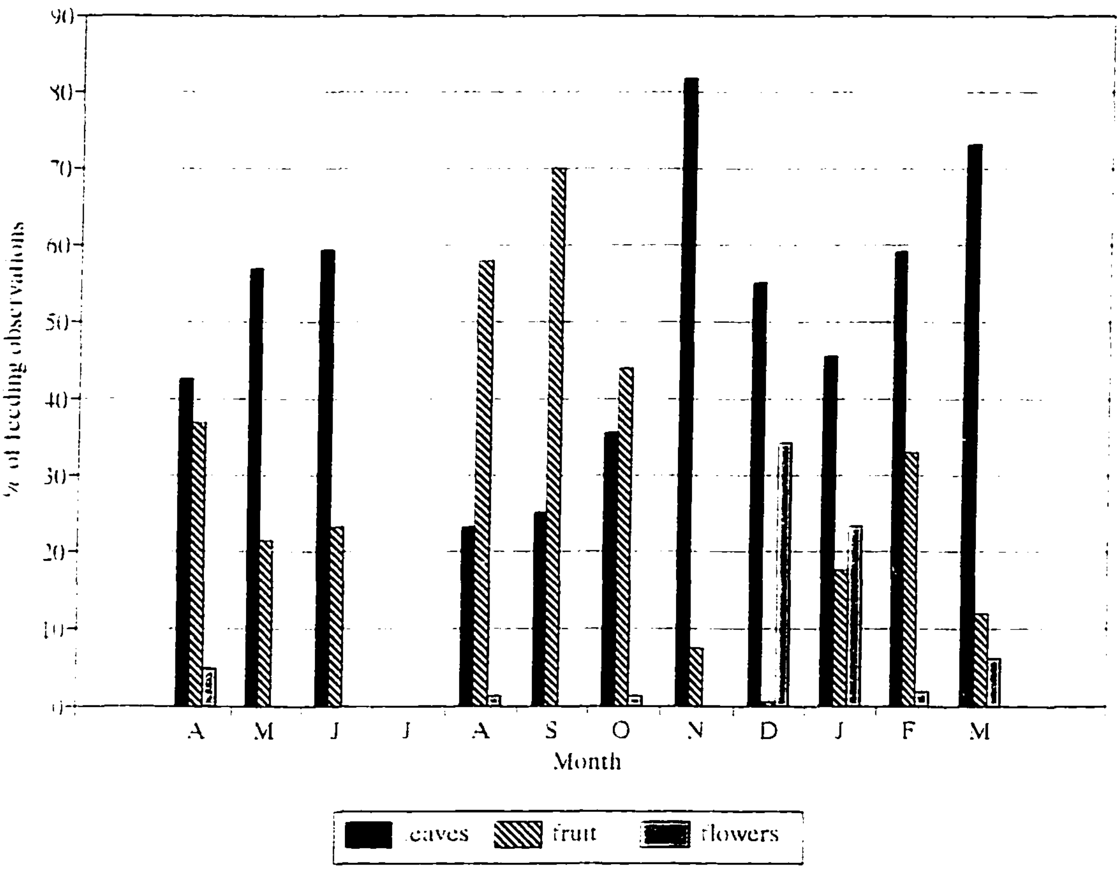


Figure 4.2. Plant part composition of *Colobus* diets from April 93 to March 94.

a. *C. angolensis*



(Figure 4.2, continued)

b. *C. guereza*

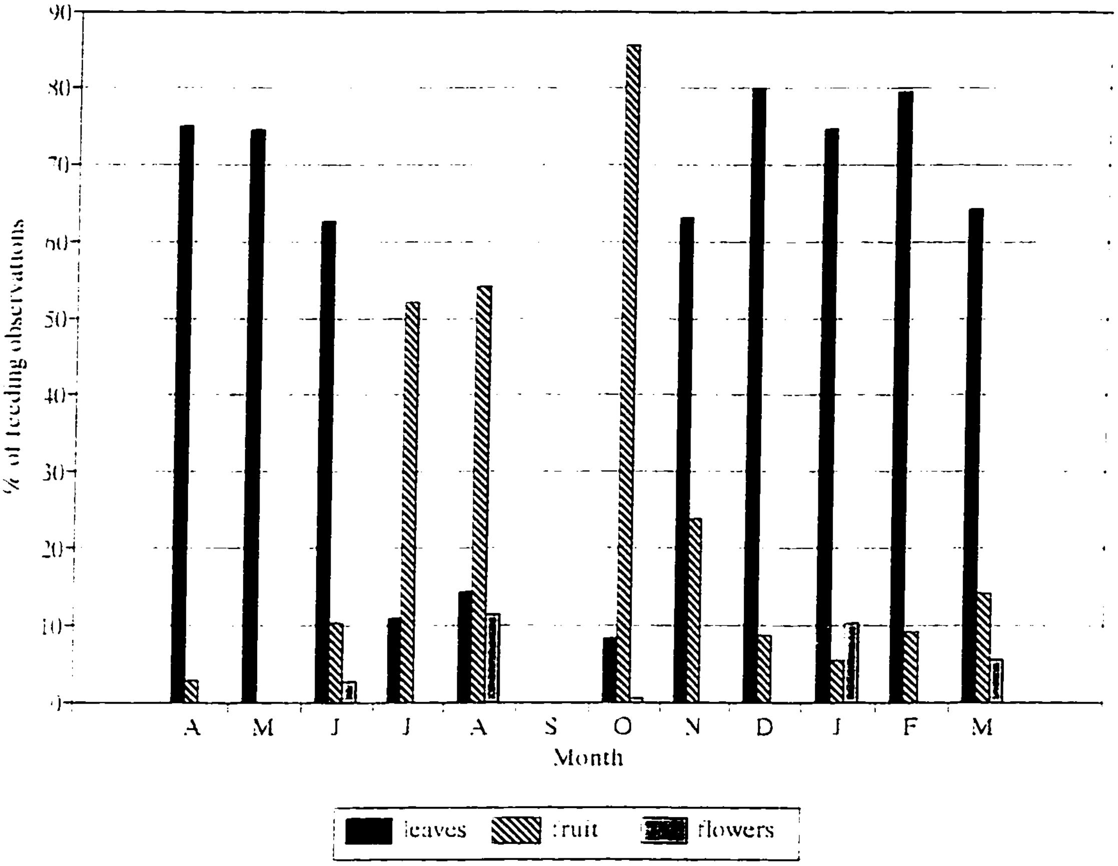


Figure 4.3. Monthly diet overlap between *C. angolensis* and *C. guereza*, from April 93 to March 94. Vertical bars represent percent overlap for all food items, and for the primary shared food item.

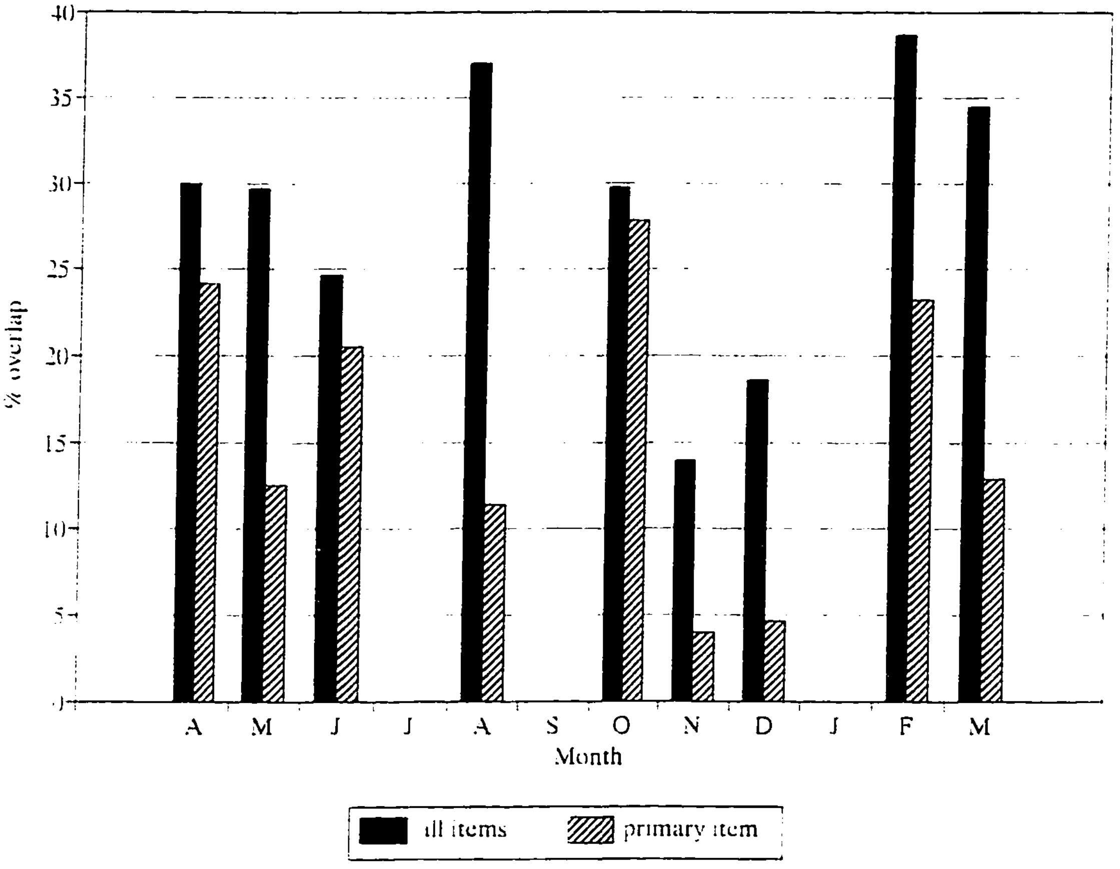
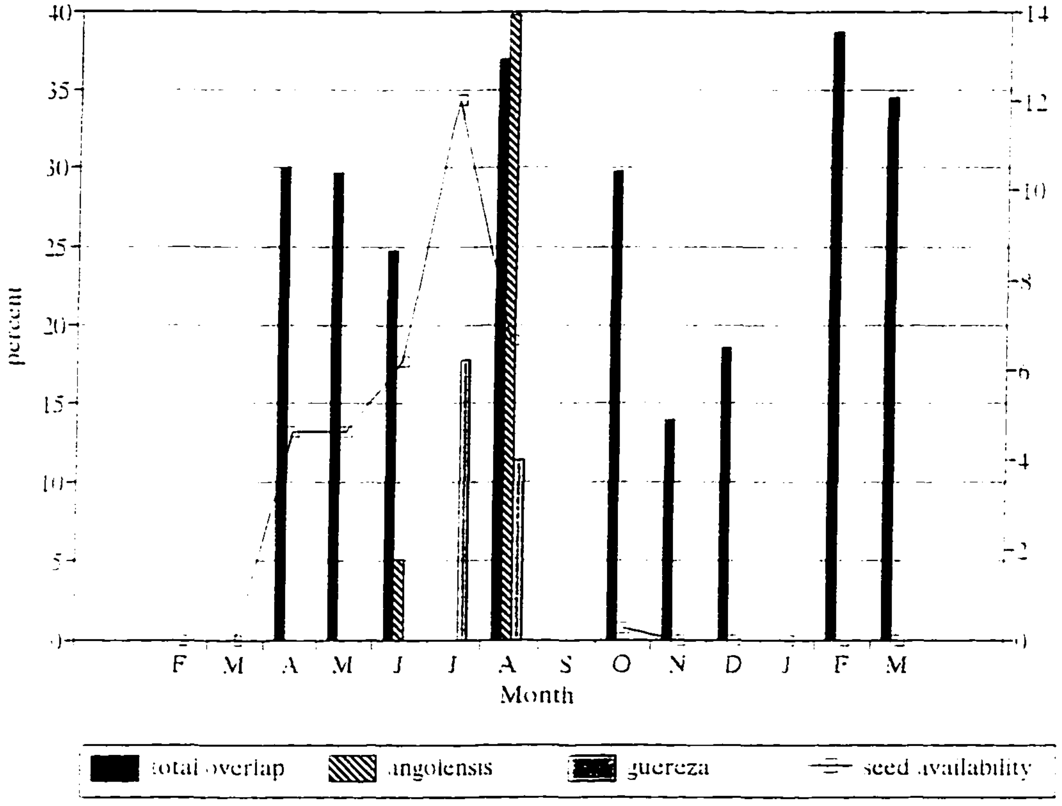


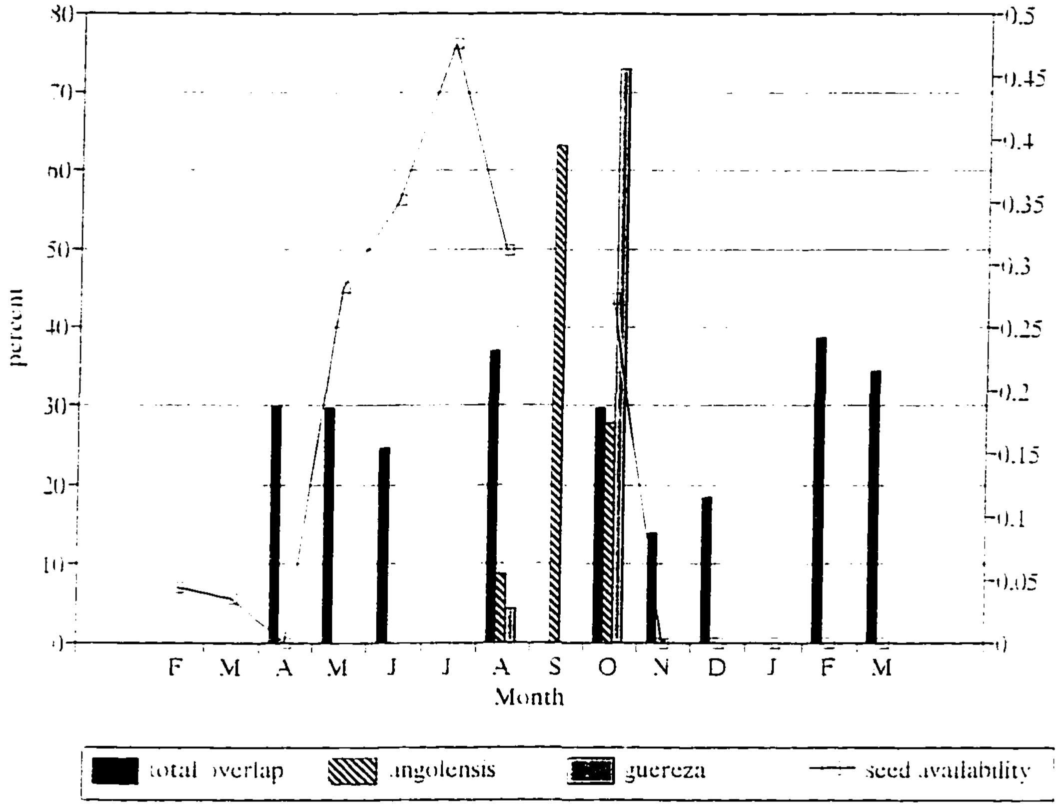
Figure 4.4. Monthly comparison of total diet overlap (all items), seed consumption by *Colobus*, and seed availability of two major food plants. Diet overlap and seed consumption are reported for April 93 to March 94; seed availability, for February 93 to March 94. Values for *angolensis* and *guereza* represent the percent of feeding observations accounted for by seeds of the indicated plant species.

a. *Cynometra alexandri*



(Figure 4.4, continued)

b. *Erythrophleum suaveolens*



Chapter 5. RANGE USE

I. Introduction

Many studies of primate ranging patterns have focused on determining whether the use of space by a single species is associated with specific environmental or behavioral factors. Such work has sought to develop a framework within which interpopulation and interspecific differences in ranging patterns may be explained. Stanford (1991a), for example, has suggested that granivory in colobine monkeys is strongly correlated with large home range sizes. The expectation that primate ranging patterns should be related to the density and dispersion of food plants, or to the availability of important food items, is difficult to test. As Struhsaker (1975) has pointed out, similar ranging patterns could result from different patterns of food plant distribution (e.g., a rare species with a clumped distribution vs. a common but dispersed species) if the density of food in an individual tree is high.

Nonetheless, some studies suggest an association between temporal variability in ranging patterns and variation in a specific environmental or behavioral factor. For example, *Presbytis melalophos* had longer day ranges when either fruit or flowers were major diet components (Bennett, 1986); *Colobus satanas* travelled farther and used a larger range area when mature leaf consumption increased, while a decrease in day range was associated with an increase in rainfall (McKey & Waterman, 1982). In two different populations of *Procolobus badius*, changes in ranging patterns were associated with different factors: either the availability of young plant growth (Marsh, 1981b), or the proximity of conspecific groups (Struhsaker, 1975). Other studies have demonstrated that different conspecific groups may influence each other's movement patterns even when groups are spatially separated (*Lophocebus albigena*: Waser, 1976; *Cercocebus galeritus*: Kinnaird, 1992).

Proximate factors that influence the movements of primate groups may play a role in the ecological separation of sympatric species, yet the subject has rarely been addressed. An exception to this is the work of Rodman (1991), who has suggested that differences in vegetation structure provide cues to sympatric *Macaca fascicularis* and *M. nemestrina*; recognition of these cues may be a mechanism by which these species maintain habitat separation. Ganzhorn (1989) raises the possibility that differing energetic needs may underlie the species separation of lemurs into structurally and phenologically distinct microhabitats.

In the Ituri Forest, *Colobus angolensis* and *C. guereza* show syntopic habitat use, overlap in their use of several important food plants (Chapter 4), and exhibit different types of social organization (Chapter 6). Do their patterns of activity and range use contribute to ecological separation, and are their ranging patterns associated with the same proximate factors? To address these questions, I examined activity and ranging patterns of both species at the Basakwe site. My analysis first compares 1) activity budgets, day range lengths, and daily activity patterns; 2) use of vertical space and habitat use; and 3) home ranges, including range area, diversity of range use, range composition, and spatial overlap with conspecific groups. Subsequently, I examine associations between specific components of range use and variables describing weather, diet composition, food plant density and availability, and the proximity of conspecific groups.

II. Methods

I describe ranging and activity patterns from observations made during 11 monthly 5-day follows of each study group (April 93 through March 94). I collected data by scan sampling at 15-min intervals from 06:00 to 18:00. During scans, the activity of individual animals was scored as one of five mutually exclusive categories: feed, locomote, rest (inactive), social interaction, or other. I estimated, to the nearest meter, the vertical distance from the ground to a sampled individual's position in a tree crown; estimated heights were later pooled into 10-meter increments to facilitate analysis of height by activity (feed, rest, and travel). In addition, I recorded the study area cell occupied by each sampled individual. Cells were coded according to habitat type (see below); I express habitat use as the percentage of monthly, and total, sample periods during which study groups occupied each of four habitat types.

During follows, I traced daily group movements on a 1:15,625 study area map. I estimated day range lengths (or "daily travel distances") by measuring these tracings with a mapping wheel.

To describe the habitat composition of the study area, I sampled 358 cells measuring approximately 125 m^2 (558 ha total), coding each cell according to its predominant (>50% of sampled area) habitat type: closed-canopy mature forest, broken-canopy old secondary forest, swamp forest, and mixed-type forest (see Chapter 2, Sec. II.B). I describe home range compositions by expressing the number of cells of each habitat type entered as a percentage of the total number of cells entered.

I estimated home range size by multiplying the total number of study area cells occupied during sample periods by the area of each cell (approximately 1.56 ha). For *C. angolensis*, this represents the area used by the study group from April 93 through March 94. For *C. guereza*, data for April 93 are excluded in estimating home range size, because a different *guereza* group was followed in that month; home range size is given as the area used by the study group from May 93 through March 94.

I used Shannon's formula (Begon *et al.*, 1990) to calculate monthly indices of range use diversity:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where s = the number of cells entered during a 5-day sample, and p = the proportion of scan samples during which cell i was occupied.

I used chi-square analyses to test for species differences in 1) activity budgets, or the percentage of total observations in which animals engaged in each of five activities; 2) vertical distribution of activities; and 3) habitat use. I used the Wilcoxon 2-sample test to test for species differences in day range lengths and cell use diversity. I used Spearman correlation analyses to test for association 1) between indices of cell use and diet diversity and 2) among 17 variables describing weather, range use patterns, diet composition, food plant density and availability, and the proximity of conspecific groups.

I compare my results describing *C. guereza* ranging behavior with those of Oates (1977a, 1977b; Kibale Forest, Uganda) because the methods and duration of his study were most similar to mine; I also include comparisons with other studies of shorter duration. *C. angolensis* range use has not previously been studied by other workers.

III. Activity and Ranging Patterns

A. Activity Budgets, Day Range Lengths, and Daily Activity Patterns

1. Activity Budgets.

Figure 5.1 illustrates the percentage of total activity samples (*C. angolensis*: $n = 9298$; *C. guereza*: $n = 6839$) in which animals engaged in each of five activities: feed, locomote (within or between trees), rest (inactive), social interaction, or other. To test for species differences in activity, I used the likelihood ratio criterion to compare observed frequencies for each activity with expected values. The species differed significantly in their activity budgets ($X^2_L = 171.77$, 4 d.f., $p < 0.001$). *C. guereza* spent more time inactive and less time feeding than did *C. angolensis*.

2. Day Range Lengths.

The species differ significantly in day range length ($Z = 5.053$, $n = 107$, $p < 0.001$). *C. angolensis* day ranges were longer than those of *C. guereza* (Table 5.1); values for *angolensis* range from 312 m to 1914 m (mean 983 m, $n = 52$); for *guereza*, from 268 m to 1112 m (mean 609 m, $n = 55$). When data from 5-day samples are pooled, *C. angolensis* mean monthly values range from 825 m to 1154 m ($n = 11$); *C. guereza*, from 479 m to 797 m ($n = 11$). Similarly, *C. angolensis* used almost twice as many cells (mean 35.2, $n = 11$) during a 5-day follow than did *C. guereza* (mean 19.8, $n = 11$).

Mean day range length was only slightly higher for *C. guereza* at Basakwe (609 m) than at the Kanyawara study site in the Kibale Forest (535 m, range 288-1004 m; Oates, 1977a).

3. Daily Activity Patterns.

For each study group, I summarized the percentage of hourly observations in which individuals were feeding, moving about (including any type of locomotion within or between trees), inactive, or engaging in social interactions; these summaries are given in Figure 5.2.a-d.

C. guereza. Guerezas usually remained in or near the previous night's sleeping tree(s) for one to three hours after sunrise. From mid-morning until about noon, the animals travelled between successive feeding sites. Foraging was followed by an early afternoon rest period; by mid-afternoon, the animals initiated another series of feeding progressions. Foraging usually continued until 17:30-18:00, and by sunset, the group settled in one or two trees for the night.

Group movements were usually initiated by an adult female, although this animal did not necessarily stay at the head of the progression. The group was cohesive, in that all members generally followed the same arboreal pathway, and no more than 10 minutes passed between the movement of the first animal and that of the last.

C. angolensis. In contrast to the *guereza* pattern, *angolensis* often left their sleeping trees at sunrise or shortly thereafter. The group alternately travelled, foraged, or rested briefly until mid to late morning. By late morning the group generally stopped moving, and rested for several hours. A second series of feeding progressions began in mid afternoon; *angolensis* usually continued moving and feeding until 17:30-18:30. By sunset, the group settled in two or three trees for the night.

Although adult *angolensis* of both sexes were observed leading group progressions, males seemed to lead more often than females. Different "subgroups" followed different arboreal pathways, with the entire group reassembling at the end of a group movement. The time between movement of the first animal and that of the last was highly variable, ranging from 15 to 45 minutes. In comparison with *C. guereza*, *C. angolensis* group movements were not cohesive.

Interspecies comparisons. The main difference between *C. guereza* and *C. angolensis* activity patterns was in the time of day at which groups initiated their first movement. Both species stopped travelling during heavy rain, and early morning rain delayed progression from the sleeping trees (although this was more pronounced in *guereza* than in *angolensis*). In both species, social interactions among group members were infrequent (5.3% of observations) compared to other activities.

B. Use of Vertical Space and Habitat Use

1. Vertical Distribution of Activities.

Heights at which *C. angolensis* and *C. guereza* rested, fed, and travelled are summarized over 11 months, and presented in Table 5.2. Chi-square analysis of species by height by activity indicates that the species differ ($p < 0.001$) in their distribution of each activity among vertical strata.

Both species tended to rest at heights of 21-30 m; however, *angolensis* rested at 11-20 m more often than did *guereza*, while *guereza* rested at 31-40 m more often than did *angolensis*. The most frequently used vertical layer for feeding was 21-30 m for both species, although *angolensis* used this layer more often than did *guereza*, and *guereza* used the understorey (0-10 m) when feeding much more than did *angolensis*. During group travel, both species primarily used the middle and lower canopy. *Angolensis* used the middle canopy (21-30 m) for travel twice as much as the lower canopy (11-20 m), while *guereza* travelled in the middle canopy only slightly more than in the lower canopy.

Overall, *C. guereza* tended to rest somewhat higher, and fed and travelled somewhat lower, than did *C. angolensis*.

2. Habitat Use.

Habitat use over 11 months is summarized in Table 5.3. The species differ significantly in their frequency of occurrence in different habitat types. *C. angolensis* tends to occur most often in closed canopy forest (38.5% of sample periods) and mixed-type forest (33.2%), and uses swamp forest infrequently (8.5%). In contrast, *C. guereza* tends to occur most often in mixed-type forest (42.0% of sample periods), followed by swamp forest (30.7%), while closed-canopy forest is used much less frequently (11.9%). Both species use areas that are predominately broken-canopy old secondary forest to about the same extent (*angolensis*, 19.8%; *guereza*, 15.4%).

Monthly habitat use by each species is summarized in Table 5.4. In most months, *C. angolensis* primarily used closed-canopy and mixed-type forest, followed by broken-canopy old secondary forest. In contrast, *C. guereza* primarily used swamp and mixed-type forest in most months, followed by broken-canopy old secondary growth.

It is not surprising that *C. angolensis* tended to frequent closed-canopy and mixed-type forest, since its primary food species during the period of study [*Cynometra alexandri*, *Celtis mildbraedii*, *Alstonia boonei*, an unidentified tree ("Dikpolo"), and *Erythrophleum suaveolens*] occur in these habitat types. During the period of study, *C. guereza* fed on one unidentified liana species ("Njamba 1") common in swamp forest, but did not feed on large trees common in this forest type (such as *Hallea stipulosa* and *Macaranga schweinfurthii*). When *guereza* fed in swamp forest, however, it was not always possible to clearly see what they were eating, as they tended to feed at heights under 15 m in trees choked with lianas. Therefore, they were probably feeding on small trees, shrubs, or lianas growing in swamp forest. The primary plant species consumed by *C. guereza* were *E. suaveolens*, *Albizia gummifera*, unidentified lianas (other than "Njamba 1"), *A. boonei*, and *C. mildbraedii*. *E. suaveolens* is more prevalent in closed-canopy than in other forest types; *A. gummifera*, *A. boonei*, and *C. mildbraedii* occur in old secondary growth or mixed-type forest, while lianas are common in all forest types.

C. Home Ranges

1. Home range areas.

During the period of study, the *C. guereza* group (the Southeast group of 9-10 animals) entered 64 study area cells; the *C. angolensis* group (the Mondiale group of 19-20 animals) entered 238 cells. These totals yield home range estimates of 100 ha for *C. guereza*, and 371 ha for *C. angolensis* (Fig. 5.3). Seventy-two percent of the *guereza* group's range was also used by the *angolensis* group.

Figure 5.4 shows the cumulative number of new 1.56 ha cells entered by each group with each successive month. The curve for *C. guereza* begins to level off at follow 6 (Oct. 93), increasing only slightly thereafter; this suggests that the area used by the group from May 93 through March 94 probably represents its entire home range. In contrast, the curve for *C. angolensis* never reaches an asymptote. The group continued to enter "new" regions of the study area, even during the last month of study (March 94), indicating that the *angolensis* group's home range is probably larger than the area they used during the course of the study. Records from daily follows of the study groups by field assistants support these observations: the *C. guereza* group used only four additional cells (or 6.2 ha) beyond the total of 64 cells used during systematic 5-day follows, while the *C. angolensis* group entered at least 16 additional cells (or 25.0 ha) beyond the total of 238 cells used during systematic follows.

Estimating home range size by multiplying cell area by the number of cells entered is generally considered to over-estimate range area, because the estimate includes areas (lacunae) within cells that are not used by the animals. Other studies of African colobines (e.g., Struhsaker, 1975; Oates, 1977a; McKey & Waterman, 1982; Harrison, 1986; Olson, 1986; Dasilva, 1989) report estimates of home range areas based on the grid method, i.e., overlaying a grid system of 50 m X 50 m (0.25 ha) cells on a composite map of the animals' movements. I used the simpler method of multiplying cell area by number of cells for two reasons: 1) for both species, encircling the total area over which the animals ranged shows that, by virtue of their travel paths, they actually entered more cells than are accounted for during sampling periods (and that are included in home range estimates); and 2) use of the grid method would still not exclude small lacunae, for example, areas of about 5m^2.

Therefore, even if a value of 100 ha over-estimates home range area for the *guereza* group, it probably does so only slightly. Since the *angolensis* group did not appear to use its entire home range during the course of the study, a value of 371 ha is likely an underestimate. Nevertheless, these estimates indicate that 1) in mature forest, *C. angolensis* groups use home ranges that are substantially larger than those used by *C. guereza* groups; and 2) in comparison to previously-studied black-and-white colobus populations, those at Basakwe use larger home ranges. In the Kibale Forest, *C. guereza* home range size was estimated at 29-31 ha (Oates, 1977a); in the Budongo Forest (Uganda), at 14 ha (Suzuki, 1979); and in the Bole Valley (Ethiopia), at 2.1 ha (Dunbar, 1987). Home range area for the Basakwe *angolensis* study group exceeds that of *C. satanas* at Lopé, Gabon, whose home range of 84-184 ha (Harrison, 1986) is the highest previously-reported value for *Colobus*.

2. Core area utilization.

C. guereza. The area used most intensively by the Southeast group, during 40% of all observations, is a contiguous block of 14 ha (or 14% of the group's home range area; Fig. 5.5). The Kanyawara study group in the Kibale Forest also showed intensive use of a particular area; this group occupied a contiguous block of forest for 44% of sample periods, in an area which accounted for 8.6% of the group's total range (Oates, 1977a).

Other *guereza* groups were neither observed nor heard within the Southeast group's core area while the group was in residence; however, in an area of 14 ha, other groups could have been present without being detected. On 3 occasions, 2 other groups were observed in this core area, which was, therefore, not an area of exclusive use. Given the low population density of *C. guereza* at Basakwe, however, incursions by other groups into the Southeast group's core area may have been infrequent.

C. angolensis. The area used most intensively by the Mondiale group, accounting for 40% of all observations, was not a contiguous block of forest; rather, these 42 ha were scattered throughout the group's range (Fig. 5.5). Furthermore, the 3 most heavily-used cells (occupied for a total of 10.0% of sample periods) were in different parts of the study area. The straight-line distance between the first and second cell was 1400 m; between the first and third, 781 m; and between the second and third, 1094 m.

3. Habitat composition of home ranges.

All 64 cells used by the *C. guereza* study group were sampled for habitat composition; 194 of the 238 cells (81.5%) used by the *C. angolensis* group were sampled. The habitat composition of each study group's home range in relation to the composition of the study area is shown in Figure 5.6.

The habitat composition of the *angolensis* group's range is almost identical to that of the study area: primarily closed-canopy and mixed-type forest. The *gueteza* group used closed-canopy, swamp, and, to a lesser extent, mixed-type forest disproportionately with respect to the representation of each habitat type in the study area; they seem to avoid closed-canopy forest, selecting instead swamp forest and mixed-type habitats. This avoidance of closed-canopy and selection of swamp forest is even more pronounced within the group's core area (Figure 5.7).

4. Ranging Diversity.

Cell use diversity (Table 5.5) for 5-day pooled samples is significantly different between *C. angolensis* and *C. guereza* [Wilcoxon 2-sample test (n = 11 for both species), $Z = 3.284$, $p = 0.001$]. *C. angolensis* show a more diverse pattern of cell use, with a mean H of 3.063 (range 2.459 to 3.413); for *C. guereza*, mean $H = 2.508$ (range 2.153 to 2.830). The association between cell use diversity and food species diversity is considered below (Sec. IV.A).

5. Spatial Overlap With Conspecific Groups.

C. guereza. In addition to the Southeast group, four other *C. guereza* groups were identified using the Basakwe site. Two of these groups were observed on several occasions within the home range of the Southeast group, occupying 14 cells (21.9%) of the latter group's range (6 of which were in their core area). The remaining two groups used forest at the boundaries of the Southeast group's range, and may have also used parts of that group's range. It is probable, therefore, that much more of the Southeast group's range overlaps with other groups. My density estimates for *C. guereza* at the Basakwe site range from 2.4-9.6 individuals/km^2. In a home range area of 100 ha (1 km^2), the Southeast group probably encounters other groups only rarely. In fact, during systematic follows of the group, encounters (in which groups were within 50 m of each other) occurred on only 2 of 50 observation days, spanning a period of 10 months.

Although the spatial distribution pattern of *C. guereza* groups at Basakwe is qualitatively similar to that observed at Oates's Kanyawara study area, between-site differences in population density, home range size, and home range overlap result in major differences in the frequency of intergroup encounters. At Kanyawara, the population density of *C. guereza* was estimated at 100 individuals/km^2; 74.2% of the primary study group's range was used by other groups on one or more occasions, and other groups were seen within 50 m of the study group on most days of systematic observation (Oates, 1977b).

C. angolensis. The Mondiale group probably experienced 100% range overlap with other groups; other groups were observed using most of the study group's range, and group encounters were common. Eight groups (including the Mondiale) were identified in the study area, where *C. angolensis* density is estimated at 12.5-16.7 individuals/km^2. Observations made on other groups suggest that they all have similar ranging patterns, i.e., large home ranges in which intergroup encounters are common.

IV. Correlates of Ranging Behavior

I used 17 variables in a correlation analysis based on data pooled over 5 days, from 11 monthly samples. These variables describe:

1) weather (2 variables):
    - percentage of observations raining,
    - mean daily temperature (degrees Celsius);

2) range use (3 variables):
    - mean day range length (m),
    - number of 1.56 ha cells entered (5-day total),
    - percentage of observations occurring in the three most frequently-used cells;

3) diet composition (8 variables):
    - number of species in the diet,
    - number of items in the diet,

- percentage of feeding observations accounted for by young leaves, mature leaves, leaves of all age classes, seeds, fruit (including seeds), flowers;

4) food plant density and availability (3 variables):

- density (number/ha of trees $\geq$ 30 cm dbh) of the primary food species,
- mean abundance score of the primary food item (average phenological score over all sampled individuals of a species),
- availability index of the primary food item (mean abundance score multiplied by the relative dominance of the plant species),

5) proximity of conspecific groups (1 variable):

- the percentage of observations in which conspecific groups were near (within 50 m of) the study group.

For three of the eleven *C. guereza* monthly samples, density estimates were not available for the primary food species (the unidentified liana species "Njamba 1" and *Ficus* spp.). For these months, density, abundance, and availability values for the second-ranking food species/food item were used. Correlation analyses were then performed on two *C. guereza* data sets: one set for which sample size = 11 (using the substituted values just described), and one set for which sample size = 8 (deleting the 3 monthly samples for which values were unavailable for the primary food item); this was done to determine whether substituted values altered the pattern of correlations. Reference is made to this truncated data set as needed; otherwise, results refer to values where sample size = 11.

Correlation analyses, calculating Spearman rank-order coefficients, were performed in three sequential steps. Results are presented first for zero order correlations, followed by second order partial correlations controlling for the effects of weather, and finally for first order partial correlations between selected pairs of variables.

A. Zero Order Correlations

Table 5.6 presents the 17-variable correlation matrix for *C. angolensis*. Mean day range length is significantly correlated with the number of cells entered ($r_s = +0.644, p < 0.05$), density of the primary food species ($r_s = -0.705, p < 0.05$), and availability index of the primary food item ($r_s = -0.891, p < 0.001$). The number of cells entered is significantly correlated with the percentage of observations in the top three cells ($r_s = -0.612, p < 0.05$), the number of food species and the number of food items ($r_s = +0.712, p < 0.05$; $r_s = +0.814, p < 0.01$), and with availability index ($r_s = -0.621, p < 0.05$). The percentage of observations in the top 3 cells is significantly correlated with mean daily temperature ($r_s = -0.692, p < 0.05$).

The correlation matrix for *C. guereza* is given in Table 5.7. Mean day range length is significantly correlated with the number of cells entered and the percentage observations in the top 3 cells ($r_s = +0.604, p < 0.05$; $r_s = -0.691, p < 0.05$), and with flower consumption ($r_s = +0.644, p < 0.05$). The number of cells entered and the percentage of observations in the top 3 cells are not significantly correlated with any other variables (except for mean day range length). In the truncated data set (where $n = 8$), mean day range length is significantly correlated with the number of cells entered ($r_s = +0.771, p < 0.05$), and with seed consumption ($r_s = -0.781, p < 0.05$); although a weak correlation is still found with flower consumption ($r_s = 0.436$), the value is not significant ($p = 0.280$).

Interspecific differences in the factors with which range use is associated are, therefore, indicated in a first analysis. For *C. angolensis*, the strongest correlation is between mean day range length and availability index of the primary food item; the second strongest correlation is between number of cells entered and the number of food items in the diet. For *C. guereza*, the only significant correlation (other than those between range use variables) is between mean day range length and flower consumption (when $n = 11$) or seed consumption (when $n = 8$).

B. Controlling for the Effects of Weather

In the next stage of the analysis, the effects of rainfall and temperature were held constant in calculating the partial correlation matrix for the remaining 15 variables. Significant zero order and second order correlations are given in tables 5.8 and 5.9 for *C. angolensis* and *C. guereza*, respectively. For both species, the overall pattern of correlation is not greatly altered when the effects of weather are removed. These patterns are summarized as follows:

C. angolensis.

1. Mean day range length is negatively correlated with both the density of the primary food species and availability of the primary food item; the strongest correlation is with the latter.
2. The number of cells entered is positively correlated with the number of food species and the number of food items in the diet, and negatively correlated with the primary food item's availability. The negative correlation between the number of cells entered and the density of the primary food species becomes significant when the effects of weather are controlled. For this range use variable, the strongest correlation is with the number of food species.
3. The positive association between the percentage of observations in the top 3 cells and young leaf consumption becomes significant when the effects of weather are controlled. No other correlations are significant.

C. guereza.

1. Mean day range length is positively correlated with flower consumption when sample size = 11; when sample size is reduced to 8, day range length is negatively correlated with seed consumption ($r_s = -0.796$), but not significantly ($p = 0.058$). No other correlations are significant (except with other range use variables).
2. The number of cells entered is correlated only with mean day range length.
3. The negative correlation between the percentage of observations in the top three cells and the percentage of observations proximal to conspecific groups reaches significance when the effects

of weather are controlled (and when $n = 11$). When $n = 8$, this correlation is higher in magnitude ($r_s = -0.744$), but is not significant ($p = 0.090$).

C. Distinguishing Among Common Correlates

The analyses described above suggest that, of the three range use variables used, mean day range length is the most informative in detecting interspecific differences in ranging correlates. The strongest correlates of day range length in *C. angolensis* are availability of the primary food item and density (of the same plant species). Because these correlates of range use are, in turn, correlated with each other, further analysis was needed to determine whether one variable's effect was independent of the other's. In the case of *C. guereza*, further analysis was needed to discern whether any other variable affected the correlation between day range length and flower consumption. Therefore, a third series of correlation analyses was performed with 14 of the original 17 variables. Three variables were excluded because they were correlated with other variables within their subset: the number of cells entered and the percentage of observations in the top 3 cells (both are correlates of mean day range length); and the number of food species (a correlate of the number of food items).

For *C. angolensis*, partial correlations were calculated for two variable pairs - day range length with food plant density, and day range length with the availability index; for *C. guereza*, partials were calculated for one variable pair - day range length with flower consumption. First order correlations were obtained for these 3 variable pairs with each of the 12 remaining variables (for a total of 36 correlations). The analysis indicates that:

1. Eleven partial correlations between *C. angolensis* day range length and density of the primary food species range from -0.675 ($p = 0.032$) to -0.816 ($p = .004$); the zero order correlation between day range length and density is -0.705 ($p = 0.015$). Only the twelfth variable, food item availability, significantly effects the correlation between *C. angolensis* day range length and

density of the primary food species: the correlation disappears when item availability is held constant (partial $r_s = +0.066, p = 0.856$).

2. Eleven partial correlations between *C. angolensis* day range length and food item availability range from -0.877 ($p = 0.0009$) to -0.910 ($p = 0.0003$); the zero order correlation between day range length and availability is -0.891 ($p = 0.0002$). Controlling for the effect of the twelfth variable, plant density, gives a partial correlation of -0.769 ($p = 0.0093$). Therefore, inclusion of plant density in a zero order analysis contributes slightly to the correlation between day range length and availability, but the latter two variables are still significantly correlated when the effects of density are held constant. Recall that the availability index is defined as the mean abundance score of a plant item multiplied by the relative dominance of the plant species; this definition thereby incorporates a measure of the plant species' abundance.

3. Nine of the twelve partial correlations produced between *C. guereza* day range length and flower consumption are significant, ranging from +0.648 ($p = 0.0428$) to +0.823 ($p = 0.0034$). The zero order correlation between these variables is +0.644 ($p = 0.0323$). When the effects of 3 variables are held constant, the correlation becomes slightly lower and nonsignificant: with young leaf consumption, partial $r_s = +0.631$ ($p = 0.0506$); with total leaf consumption, partial $r_s = +0.628$ ($p = 0.0517$); and with the percentage of observations proximal to conspecific groups, partial $r_s = +0.581$ ($p = 0.0779$). Inclusion of these variables in a zero order analysis contributes slightly to the association between *C. guereza* day range length and flower consumption, but their effects appear to be minor.

D. Additional Analyses

In order to keep the number of variables at a manageable level, I did not include indices of cell use diversity or food species diversity in the preceding analyses, although I did examine their correlation with each other. Cell use diversity in *C. angolensis* is positively correlated with diversity in their use of food plant species ($r_s = 0.645$, $p = 0.032$, $n = 11$; Table 5.5). For *C. guereza*, the two diversity indices are only weakly associated ($r_s = 0.273$, $p = 0.416$, $n = 11$).

V. Discussion

Colobus angolensis and *C. guereza* are quite different in their patterns of range use. Within mature forest, *C. guereza* prefer areas where the canopy is open and lower in stature - swamp and mosaic-type habitats. While *C. angolensis* also uses open-canopy areas, they are just as likely to use high, closed-canopy forest. Species differences in the vertical distribution of activities, especially feeding and movement between feeding sites, are likely the result of these habitat differences. That such differences may be related to behavioral preferences, i.e., to a particular type of vegetation structure, can not be ruled out; they may also be related to differences in diet. These differences suggest some degree of ecological separation, similar to that observed by Curtin (1980) in sympatric *Presbytis melalophos* and *P. obscura*: the former species preferred riverine habitat, while the latter preferred mature forest.

Compared to other populations of *Colobus*, those in the Ituri Forest - particularly *C. angolensis* - use much larger home ranges. One possible explanation for this is the low availability of suitable food plants, some of which are shared by *C. angolensis*, *C. guereza*, and possibly *P. badius*. In the Kibale Forest, where *C. guereza* and *P. badius* co-occur in the absence of *C. angolensis*, *C. guereza* density was much higher (at the time of Oates' study) than what I observed in the Ituri. Major foods of the Kibale population, however, were common species.

Why do *angolensis* at Basakwe use a home range that is four times the area used by *guereza*? Two measures of range use are associated with diet composition: *angolensis* stay in one location longer when their consumption of young leaves increases; *guereza* range farther when their consumption of flowers increases. There is no obvious reason why these correlational differences should be related to differences in range size: during the year of study, *C. angolensis* and *C. guereza* differed little in their overall consumption of leaves and fruit, and flowers were a minor component of both species' diets.

C. angolensis travel farther when the availability of their primary food item decreases; *C. guereza* movements were not associated with measures of food density or availability. Similarly, *angolensis* show a more diverse pattern of cell use with an increase in food species diversity; no such association was found for *guereza*. Instead, *guereza* movements were associated with the proximity of other conspecific groups - the study group spent less time in one location when other groups were nearby. *Guereza* intergroup encounters were infrequent, yet the values for the percent of observations in the top three cells is lowest in the two months when group encounters occurred.

To infer that *guereza* movements are associated with avoiding conspecific groups, but *angolensis* movements are not, is not warranted by these data. Similarly, it seems unreasonable to conclude that *guereza* range use is completely unrelated to patterns of food availability, yet the association is strong for *angolensis*. Species differences in home range sizes may be primarily due to differences in their social organization.

Certainly, other factors that were not included in my analysis may be affecting the animals' ranging patterns. The data do suggest, however, that ranging behavior in each species is most strongly associated with different factors.

VI. Summary

1. *C. angolensis* and *C. guereza* differed in their activity budgets; *guereza* spent more time inactive and less time feeding than did *angolensis* .

2. The species differed significantly in their distribution of activities among vertical strata; *C. guereza* rested higher, and fed and travelled lower, than *C. angolensis*. They also differed in

habitat use: *angolensis* used closed-canopy forest more often than *guereza*, while *guereza* used swamp forest more often than *angolensis*.

3. *C. angolensis* used a home range almost four times the area used by *C. guereza*. *Guereza* intensively used a smaller, contiguous block of forest within their range, while *angolensis* did not. Similarly, the *guereza* pattern of cell use was less diverse than that of *angolensis*. *Angolensis* home ranges overlapped extensively, perhaps completely, and group encounters were common. *Guereza* home ranges showed some degree of spatial separation; a minimum of 22% of the study group's range was used by other groups. *Guereza* group encounters were infrequent.

4. *C. angolensis* day range length was inversely correlated with availability of their primary food item. *C. guereza* day range length was positively correlated with flower consumption. The percentage of observations in the top 3 cells was positively correlated with young leaf consumption for *angolensis*, and negatively correlated with the proximity of conspecific groups for *guereza*.

5. Species differences in ranging behavior result in some degree of ecological separation. Ranging patterns of each species are proximally associated with different factors.

Table 5.1. Mean day range lengths (in meters) and number of 1.56 ha cells entered by each study group during systematic follows (5-day pooled samples). For *C. angolensis*, *n* = 52; for *C. guereza*, *n* = 55.

	C. angolensis			*C. guereza*		
month	mean	range	# of cells	mean	range	# of cells
4/93	1040	525-1500	38	710	450-1100	26
5/93	1154	805-1649	45	610	383-844	23
6/93	1024	633-1879	41	682	498-1112	21
7/93	—	—	–	537	268-805	13
8/93	926	594-1313	35	797	498-1035	21
9/93[a]	977	684-1270	13	—	—	–
10/93	920	479-1380	32	575	268-901	24
11/93	1031	594-1572	35	479	345-729	14
12/93	1079	383-1914	51	499	307-767	14
1/94	825	430-1650	23	637	479-748	23
2/94	932	703-1649	36	522	288-863	16
3/94	902	312-1406	38	648	460-901	23
mean±SE		983±56.1			609±28.4	
mean			35.2			19.8

[a] mean value based on only 2 days (*C. angolensis*)

Table 5.2. Vertical distribution of activities, summarized for 11 months (April 93 - March 94). A = *C. angolensis*, G = *C. guereza*, % = percent of observations within each activity category. For *C. angolensis*, *n* = 7575; for *C. guereza*, *n* = 5285. Chi-square values are based on observation frequencies.

	understorey (0-10m)		lower canopy (11-20m)		mid canopy (21-30m)		upper canopy (31-40m)	
	A	G	A	G	A	G	A	G
Rest[a] %	1.4	2.2	26.5	21.9	64.9	63.0	7.2	12.9
Feed[b] %	2.8	10.0	29.2	28.6	58.8	51.1	9.2	10.3
Travel[c] %	2.3	5.2	30.4	42.2	64.6	51.6	2.7	1.0

[a] $X^2_L = 82.54$, 3 d.f., $p < 0.001$.

[b] $X^2_L = 85.84$, 3 d.f., $p < 0.001$.

[c] $X^2_L = 43.11$, 3 d.f., $p < 0.001$.

Table 5.3. Habitat use, summarized for 11 months (April 93 - March 94). Values indicate the percent of total sample periods during which study groups occupied each habitat type (*C. angolensis*: $n = 2351$; *C. guereza*: $n = 2534$; chi-square value[a] based on observation frequencies).

habitat	*C. angolensis*	*C. guereza*
closed canopy (type 1)	38.5	11.9
old secondary (type 2)	19.8	15.4
swamp (type 3)	8.5	30.7
mixed-type (type 4)	33.2	42.0

[a] $X^2 = 687.8$, 3 d.f., $p < 0.001$.

Table 5.4. Monthly habitat use, based on 5-day pooled samples. Values represent percent of observations in which each habitat type was occupied by study groups. A: *C. angolensis*; G: *C. guereza*.

	type 1 (closed canopy)		type 2 (broken canopy)		type 3 (swamp)		type 4 (mixed)	
month	A	G	A	G	A	G	A	G
4/93	62.0	16.2	9.4	19.5	2.3	19.5	26.2	44.9
5/93	36.0	21.3	9.6	27.7	6.4	6.8	48.0	44.2
6/93	39.0	8.0	22.5	24.4	6.5	18.9	32.1	48.7
7/93	–	18.4	–	2.8	–	54.0	–	24.8
8/93	7.9	0.8	40.8	10.8	7.2	68.0	43.7	20.4
9/93[a]	54.9	–	0.0	–	23.9	–	21.2	–
10/93	17.2	41.9	7.4	4.0	18.4	11.2	57.1	43.0
11/93	57.2	18.9	0.5	15.0	7.8	27.6	33.7	38.6
12/93	18.9	0.0	36.7	4.2	0.4	34.2	43.9	61.6
1/94	39.9	5.5	35.2	27.6	18.0	18.0	6.9	48.8
2/94	48.8	0.0	20.7	30.2	6.2	32.3	24.3	37.5
3/94	57.7	4.7	29.7	19.8	0.0	35.0	24.1	52.6

[a] sample based on only 2 days (*C. angolensis*)

Table 5.5. Monthly diversity indices (Shannon's index, *H*) for cell use and diet (food species). Monthly values are based on 5-day pooled samples.

	C. angolensis		*C. guereza*	
month	cell use	food spp.	cell use	food spp.
4/93	2.926	1.893	2.830	1.606
5/93	3.413	2.343	2.640	1.726
6/93	3.400	1.987	2.590	1.962
7/93	—	—	2.153	1.835
8/93	3.134	1.539	2.804	1.781
9/93[a]	2.459	1.061	—	—
10/93	3.046	1.923	2.404	1.068
11/93	2.914	1.653	2.469	2.310
12/93	3.324	2.201	2.164	2.405
1/94	2.679	1.910	2.649	1.856
2/94	3.171	1.769	2.161	2.015
3/94	3.232	1.898	2.721	2.294
mean	3.063	1.834	2.508	1.896
minimum	2.459	1.061	2.153	1.068
maximum	3.413	2.343	2.830	2.405

[a] value based on only 2 days (*C. angolensis*)

Table 5.6. *C. angolensis* correlation matrix: weather, range use, diet composition, food plant density and availability, and proximity to conspecific groups. See text for description of variables.

	variable	1	2	3	4	5	6	7	8	9
1	% obs. raining		-0.012	+0.201	+0.466	-0.368	+0.081	+0.166	+0.312	-0.397
2	mean temp.			0.000	+0.556	-0.692*	+0.203	+0.414	+0.064	+0.543
3	day range length				+0.644*	-0.091	+0.508	+0.420	-0.164	+0.036
4	# cells entered					-0.612*	+0.712*	+0.814**	+0.160	+0.352
5	% obs. top 3 cells						-0.466	-0.580	+0.255	-0.278
6	# food species							+0.939***	-0.210	+0.374
7	# food items								-0.041	+0.506
8	% young leaves									+0.260
9	% mature leaves									

	variable	10	11	12	13	14	15	16	17
1	% obs. raining	+0.574	-0.312	-0.201	-0.043	-0.314	+0.112	-0.247	-0.108
2	mean temp.	+0.369	-0.474	-0.351	+0.112	+0.104	-0.228	-0.059	+0.133
3	day range length	+0.164	-0.173	-0.209	-0.303	-0.705*	+0.327	-0.891***	+0.068
4	# cells entered	+0.447	-0.584	-0.516	+0.159	-0.560	+0.342	-0.621*	+0.041
5	% obs. top 3 cells	-0.282	+0.218	+0.055	+0.196	-0.143	+0.209	+0.064	+0.311
6	# food species	-0.061	-0.261	-0.284	+0.170	-0.374	+0.452	-0.415	-0.274
7	# food items	+0.055	-0.397	-0.356	+0.286	-0.278	+0.370	-0.292	-0.161
8	% young leaves	+0.473	-0.609*	-0.573	+0.667*	-0.281	+0.236	-0.036	+0.571
9	% mature leaves	-0.068	-0.374	-0.292	+0.395	+0.104	-0.073	-0.023	+0.231
10	% leaves		-0.791**	-0.745**	-0.070	-0.277	0.000	-0.382	+0.580
11	% seeds			+0.964***	-0.350	+0.263	-0.064	+0.373	-0.534
12	% fruit				-0.378	+0.383	-0.227	+0.436	-0.580
13	% flowers					-0.192	+0.443	+0.201	+0.101
14	density						-0.783**	+0.811**	-0.199
15	mean abun. score							-0.345	+0.155
16	avail. index								-0.160
17	% obs. proximity								

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 5.7. *C. guereza* correlation matrix: weather, range use, diet composition, food plant density and availability, and proximity to conspecific groups. See text for description of variables.

	variable	1	2	3	4	5	6	7	8	9
1	% obs. raining		-0.273	-0.200	+0.124	+0.036	-0.183	-0.055	-0.009	+0.027
2	mean temp.			-0.100	+0.139	-0.068	+0.631*	+0.597	+0.264	+0.364
3	day range length				+0.604*	-0.691*	-0.430	-0.340	-0.173	-0.264
4	# cells entered					-0.203	-0.234	-0.184	+0.249	-0.401
5	% obs. top 3 cells						+0.124	-0.005	+0.200	-0.300
6	# food species							+0.944***	+0.316	+0.705*
7	# food items								+0.152	+0.772**
8	% young leaves									+0.173
9	% mature leaves									

	variable	10	11	12	13	14	15	16	17
1	% obs. raining	-0.073	0.000	+0.055	-0.555	-0.064	+0.515	+0.218	0.000
2	mean temp.	+0.232	-0.354	-0.228	-0.164	-0.333	-0.146	-0.610*	+0.598
3	day range length	-0.191	-0.339	-0.064	+0.644*	-0.060	+0.005	-0.036	+0.373
4	# cells entered	+0.014	-0.367	-0.267	+0.322	-0.447	+0.132	-0.369	+0.113
5	% obs. top 3 cells	+0.155	+0.385	+0.036	-0.481	+0.009	-0.100	+0.018	-0.596
6	# food species	+0.238	+0.129	+0.073	+0.175	-0.025	-0.353	-0.348	+0.225
7	# food items	+0.097	+0.153	+0.207	+0.286	+0.084	-0.281	-0.202	+0.415
8	% young leaves	+0.873***	-0.596	-0.836**	-0.297	-0.867***	+0.451	-0.809**	-0.224
9	% mature leaves	+0.309	-0.037	+0.064	+0.094	+0.032	+0.096	-0.100	+0.447
10	% leaves		-0.532	-0.800**	-0.357	-0.807**	+0.497	-0.755**	-0.149
11	% seeds			+0.853***	+0.110	+0.792**	-0.676*	+0.651*	-0.376
12	% fruit				+0.332	+0.950***	-0.606*	+0.818**	+0.075
13	% flowers					+0.298	-0.519	+0.055	+0.406
14	density						-0.559	+0.895***	+0.038
15	mean abun. score							-0.182	+0.112
16	avail. index								-0.075
17	% obs. proximity								

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 5.8. *C. angolensis* range use: comparison of significant zero order correlations and partial correlations, controlling for the effects of weather (percentage of observations raining and mean daily temperature). Availability index refers to the primary food item.

range use variable	correlated variable	r_s	partial r_s
mean day range length	no. cells entered	+0.644*	+0.820**
	density primary food sp.	-0.705*	-0.695*
	availability index	-0.891***	-0.888**
no. cells entered	% obs., top 3 cells	-0.612*	-0.116[a]
	no. of food sp.	+0.712*	+0.839**
	no. of food items	+0.814**	+0.823**
	density primary food sp.	-0.560[b]	-0.728*
	availability index	-0.621*	-0.712*
% obs., top 3 cells	mean daily temperature	-0.692*	–
	young leaves, % obs.	+0.255[c]	+0.715*

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.
[a] $p = 0.766$.
[b] $p = 0.073$.
[c] $p = 0.450$.

Table 5.9. *C. guereza* range use: comparison of significant zero order correlations and partial correlations, controlling for the effects of weather (percentage of observations raining and mean daily temperature). Percentage of observations in proximity refers to the presence of conspecific groups within 50 m.

range use variable	correlated variable	r_s	partial r_s
mean day range length	no. cells entered	+0.604*	+0.697*
	% obs., top 3 cells	-0.691*	-0.719*
	flowers, % obs.	+0.644*	+0.666[a]
no. cells entered	–	–	–
% obs., top 3 cells	% obs. proximity	-0.596[b]	-0.715*

*$p < 0.05$.
[a] $p = 0.050$.
[b] $p = 0.053$.

Figure 5.1. *Colobus* activity budgets, by percent of total activity samples (*C. angolensis*, *n* = 9298; *C. guereza*, *n* = 6839). Activities designated as F (feed), L (locomote), R (rest or inactive), S (social interaction), or O (other).

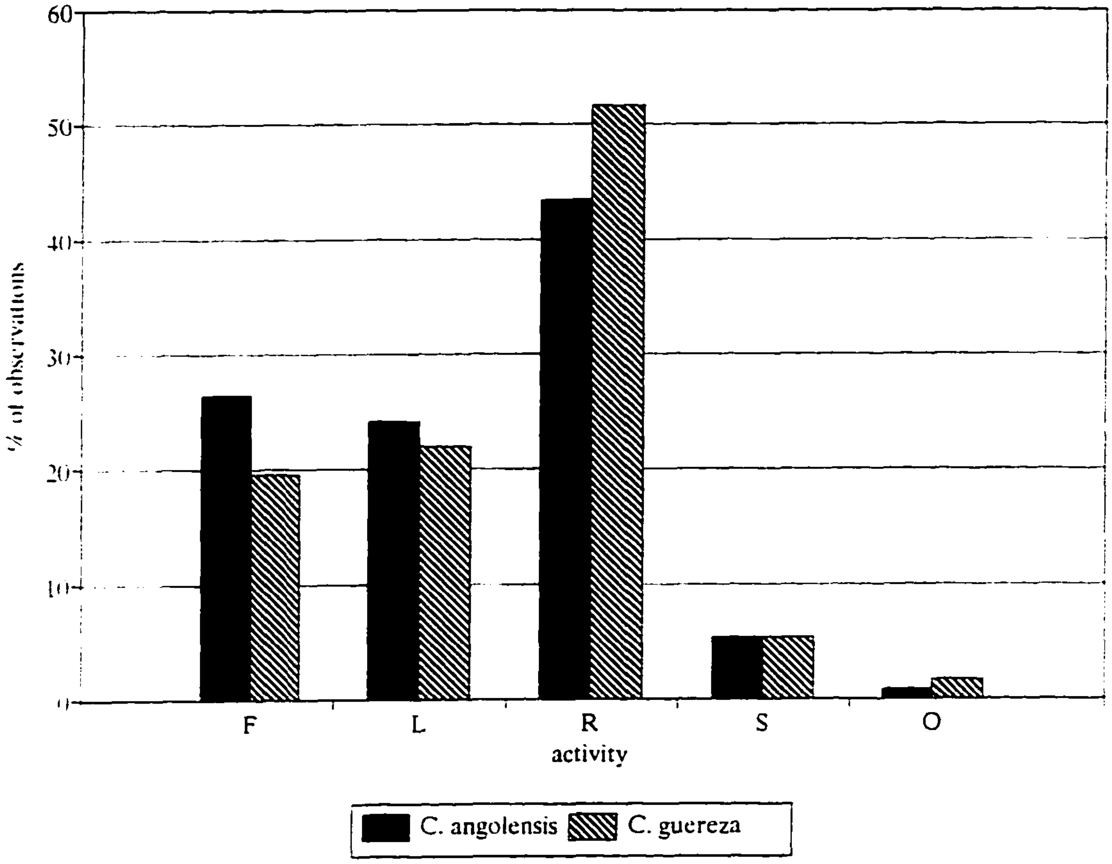
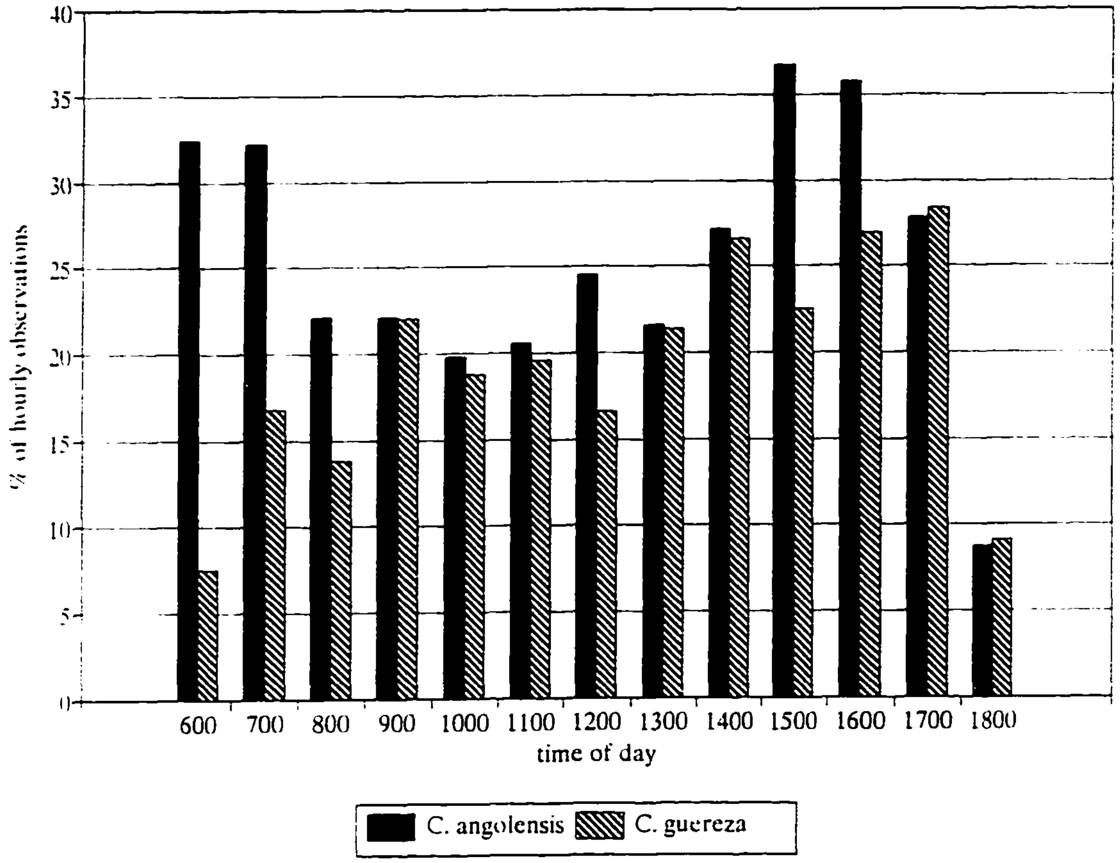


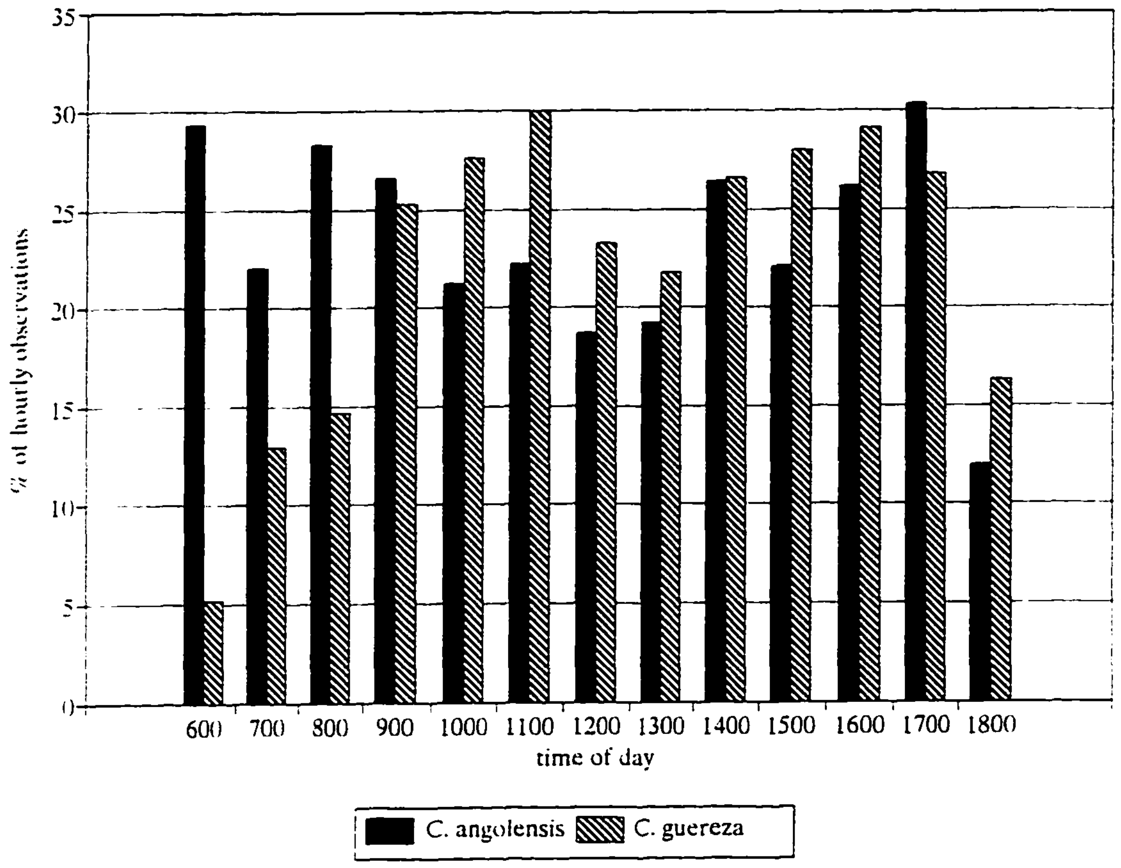
Figure 5.2. Daily activity patterns, as percent of hourly samples. X-axis indicates hourly periods; e.g., 600 = 06:00-06:59.

a. Feed



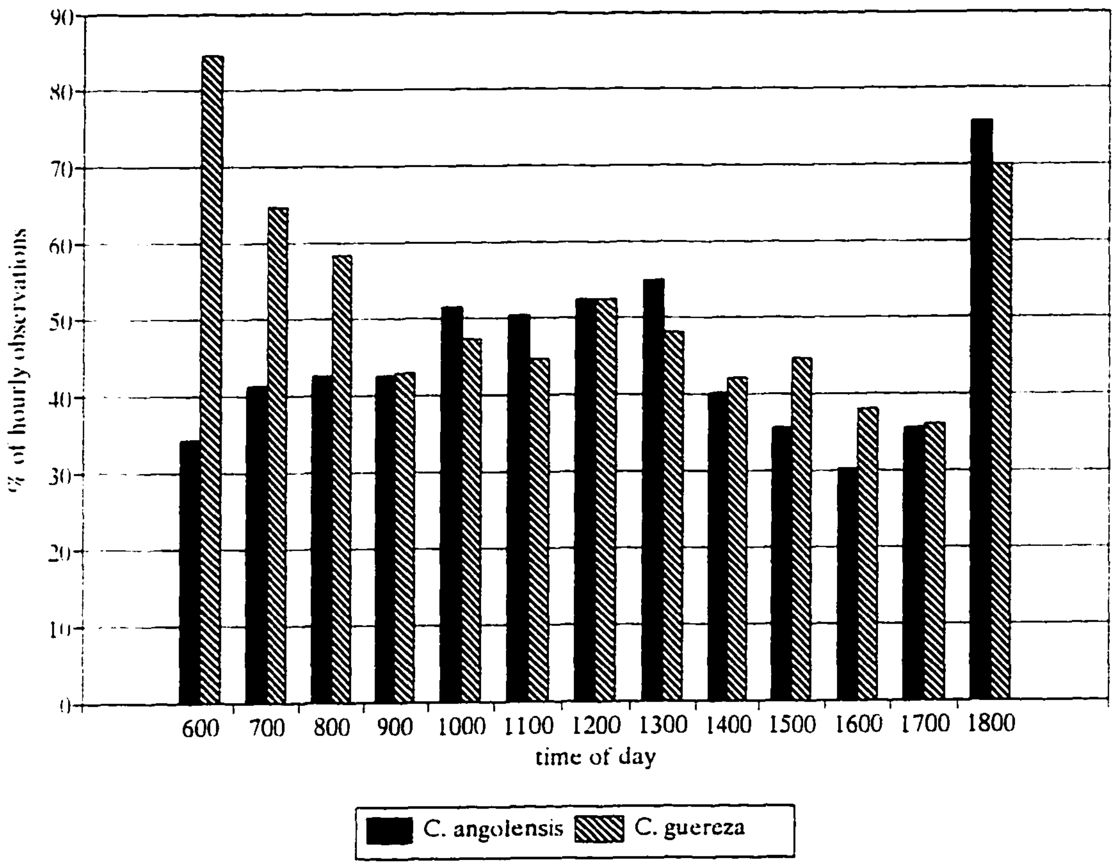
(Figure 5.2, continued)

b. Locomote



(Figure 5.2, continued)

c. Rest (inactive)



(Figure 5.2, continued)

d. Social interaction

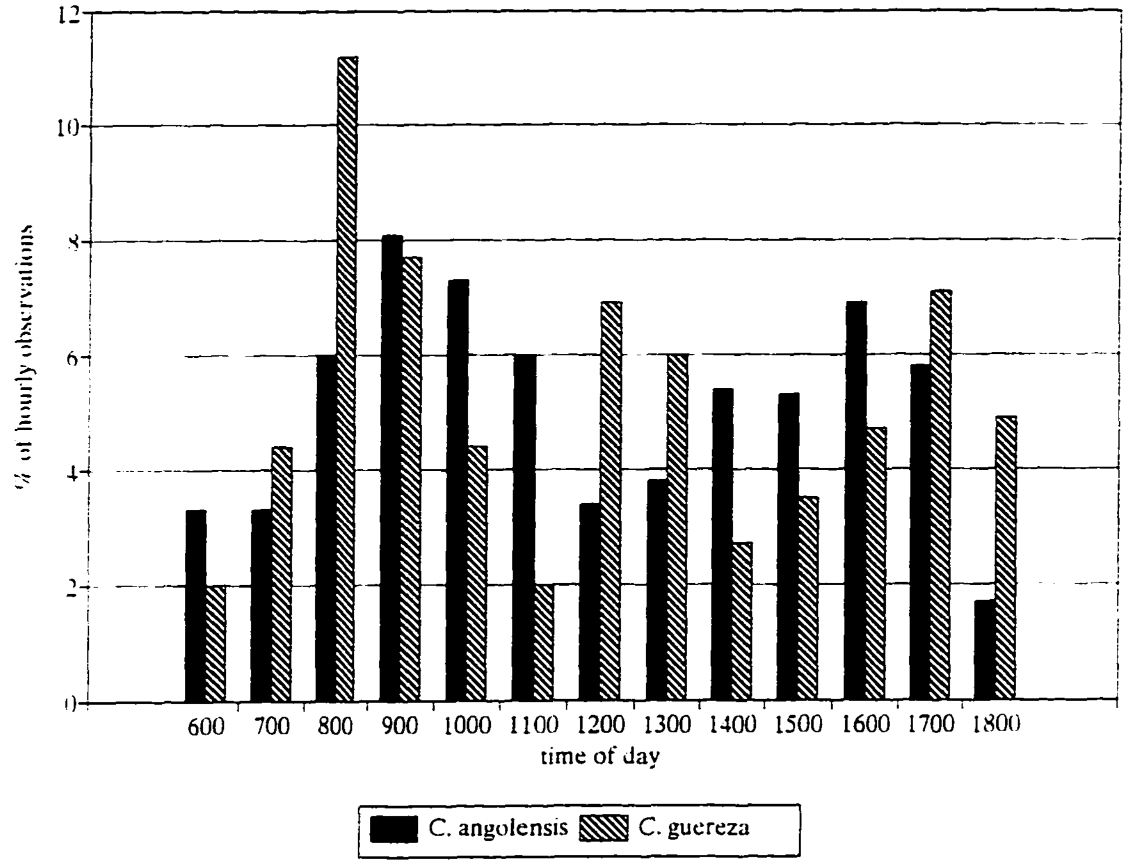


Figure 5.3. Home ranges of the Basakwe study groups. Areas used by both groups are indicated by black diagonal lines. Areas used only by the *C. guereza* (Southeast) group include the black cells contained within the area used by both groups, plus the 5 black cells indicated by arrows. All other black cells are areas used only by the *C. angolensis* (Mondiale) group.

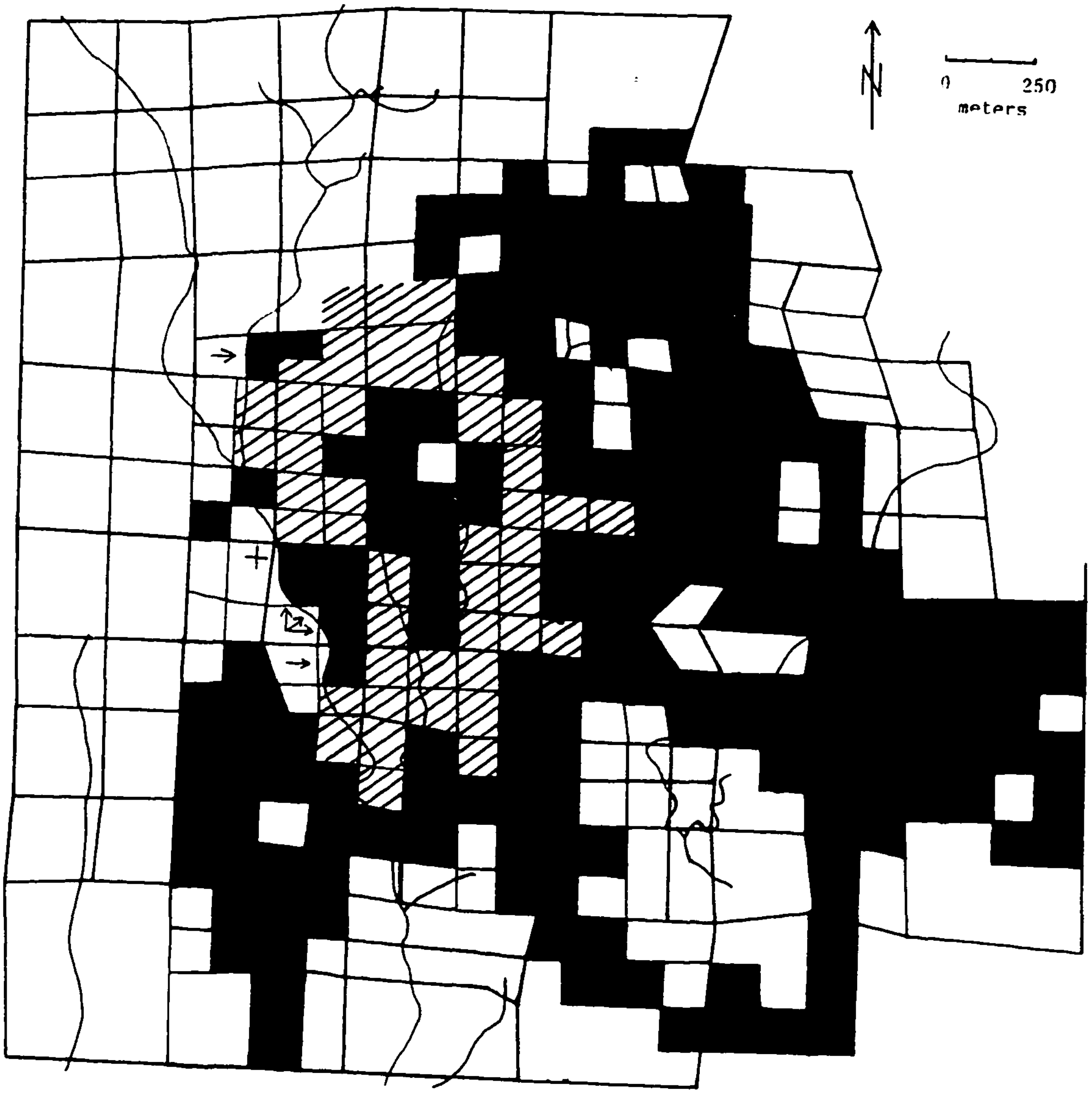


Figure 5.4. Cumulative number of new 1.56 ha cells entered by each study group, from April 1993 (follow 1) through March 1994 (follow 11).

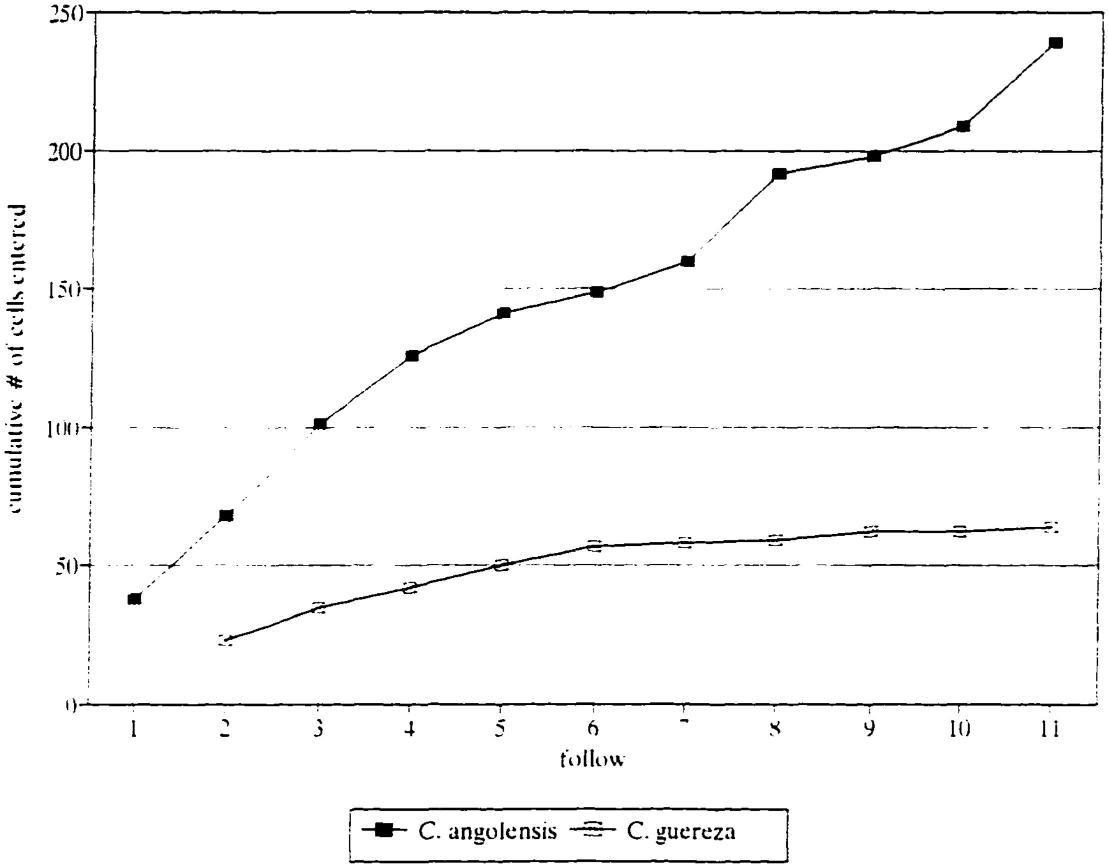


Figure 5.5. Areas of intensive use, accounting for 40% of all observations for each group. The Southeast group's core area comprised 9 cells: the black cells indicated by arrows, plus the cell indicated by black diagonal lines. The areas used most heavily by the Mondiale group include all other black cells, plus the cell indicated by black diagonals.

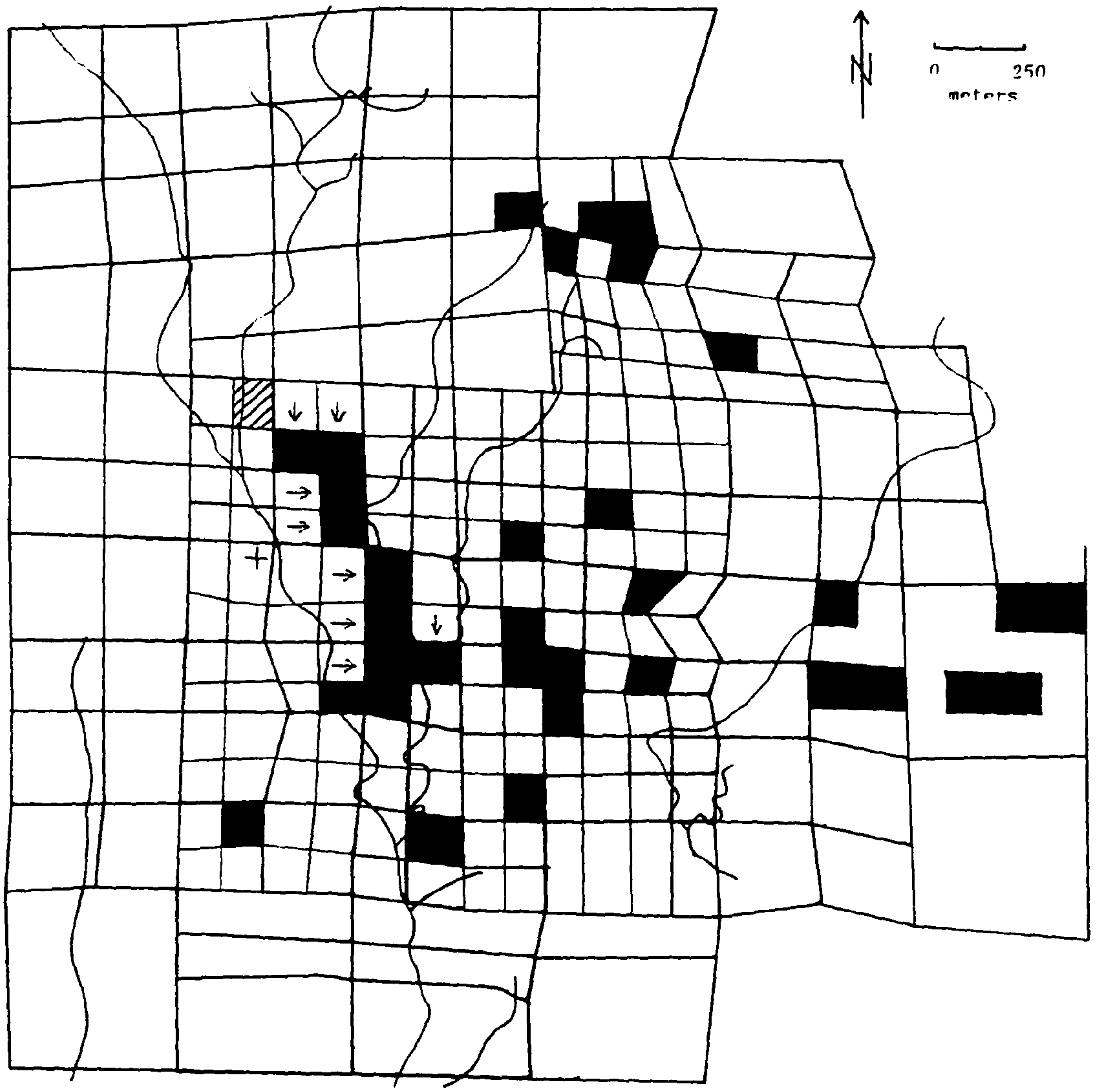


Figure 5.6. Habitat composition of study area and of study group home ranges. Type 1 = closed canopy, mature forest; type 2 = broken canopy, old secondary forest; type 3 = swamp forest; type 4 = mixed-type forest.

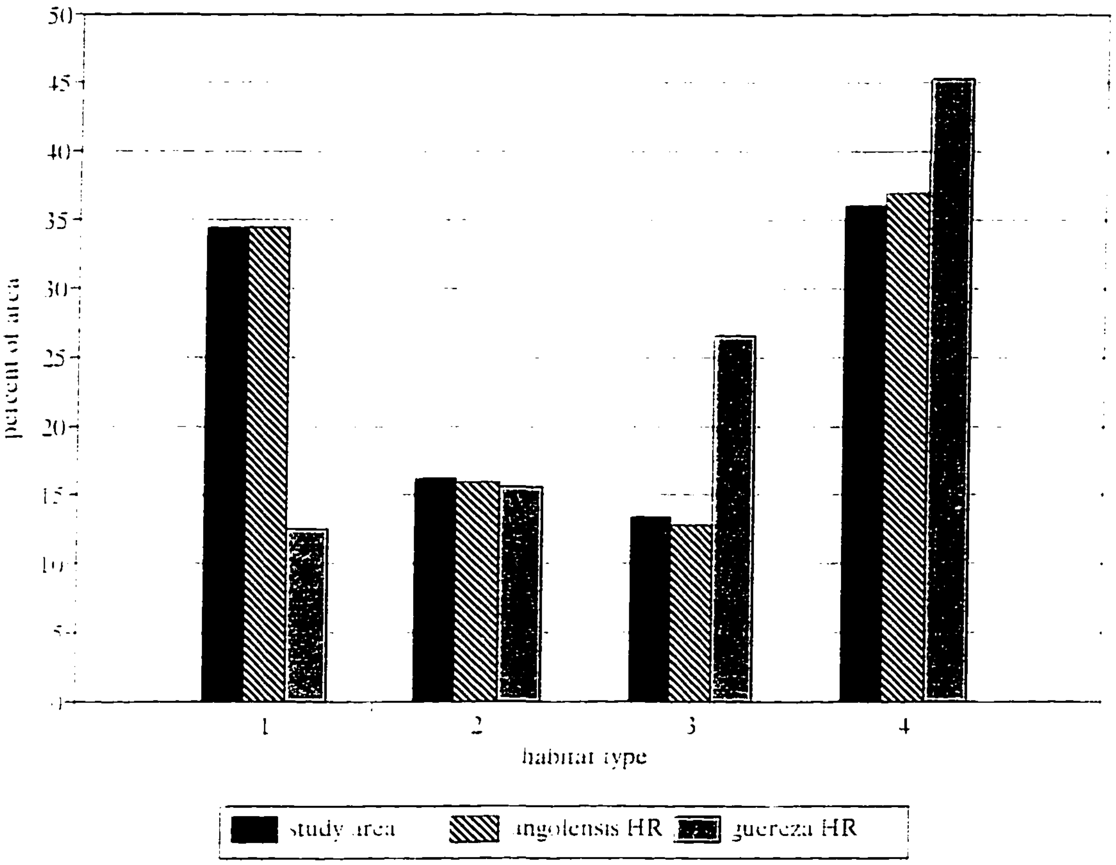
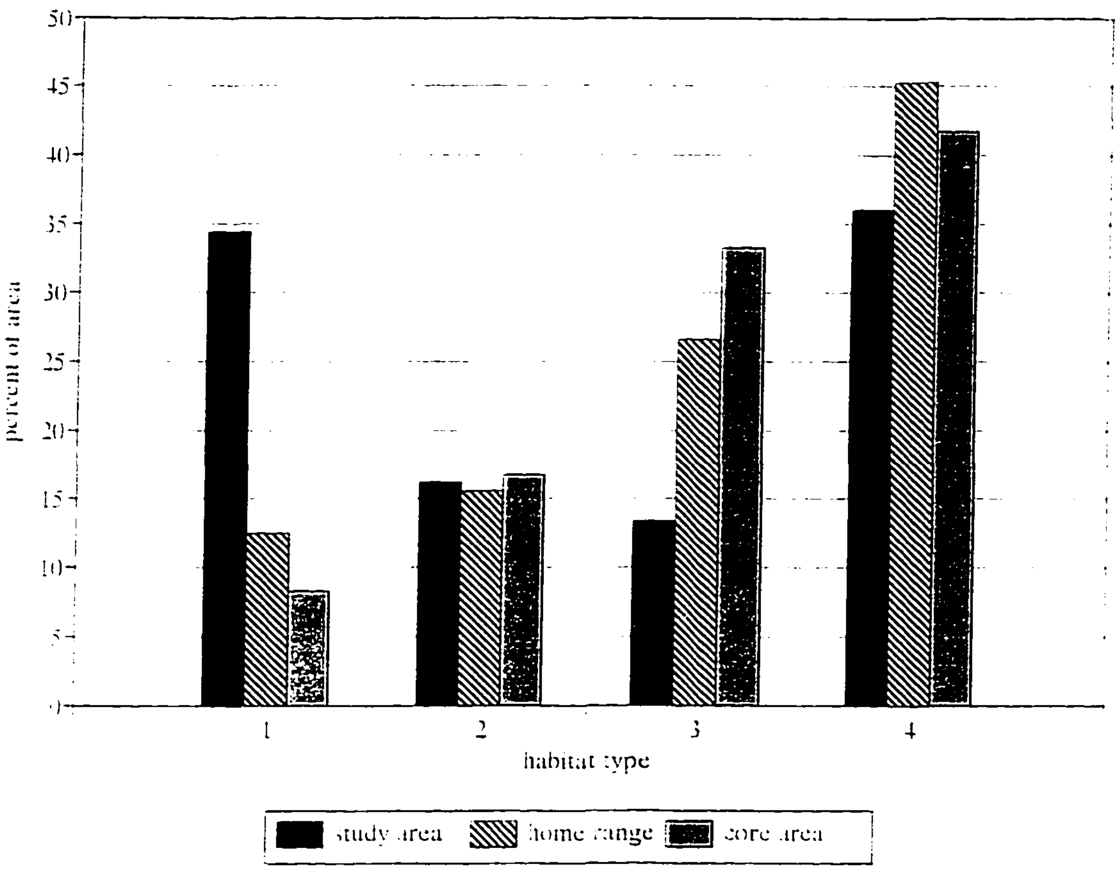


Figure 5.7. Comparison of C. *guereza* core area habitat composition with that of the group's home range, and with the study area. Habitat types as in Figure 5.6.



Chapter 6. SOCIAL ORGANIZATION

I. Introduction

Recently, workers in the field of primate socioecology have argued that intraspecific variability in social systems is common, particularly in New World primates (Kinzey & Cunningham, 1994). Others question whether social systems even exist (e.g., Rowell, 1993). Rowell suggests that a social system may be perceived by the observer, but not by the animals, and doubts that these perceived systems are emergent properties of social relationships. Steklis (1993) offers an alternative view, that genotypic and ontogenetic constraints determine which behavioral phenotypes will occur in a population; these behavioral phenotypes then define a range of possible social structures.

Strier (1994) has argued that an understanding of primate social systems, and the diversity seen in such systems, must take into account the interaction of phylogenetic, ontogenetic, demographic, and physiological factors. Yet the occurrence of similar patterns of behavior and social organization in different populations of the same species, for which ecological and demographic factors would differ, would suggest some degree of genotypic influence on social organization. In this chapter, I describe the behavior and social organization of sympatric *Colobus guereza* and *C. angolensis*. I then consider whether patterns observed in the Ituri Forest are similar to those observed in other populations of each species. In my concluding chapter (Chap. 7), I return to the topic of interspecific differences in social behavior, and consider whether these differences contribute to *Colobus* niche separation and coexistence in the Ituri.

II. Methods

A. Terminology

I follow Richard's (1985) definitions of the terms "social structure" and "social organization". Social structure refers to the content and quality of relationships among all members of a social group. Social organization refers to a set of spacing and social behaviors that characterize a population of animals. Attributes of social organization include group composition, social structure, the spatial distribution of groups, and interactions among groups.

B. Determination of Group Compositions

Most of the data which I present in this chapter are based on observations at the Basakwe study area, although I also include data based on short-term observations at the Lenda site. Group compositions for Basakwe are based only on my own observations. For Lenda, compositions of three groups are based on my observations; the remaining two groups were observed by a reliable field assistant.

1. Basakwe.

C. angolensis group compositions at Basakwe are based on observations made during surveys; the survey method is given in Chapter 2 (Sec. VI.E.2.). The duration of contact time with each group was variable, ranging from approximately one hour to more than one day. I attempted to remain with each group long enough to determine, to the extent possible, its age and sex class composition. I maintained contact with larger groups for longer time periods to ensure that I was observing one group, rather than two groups in association.

C. guereza groups were much more difficult to locate, and to observe, in mature forest. Three of the five groups whose compositions are given here were habituated to varying degrees; I followed the least habituated of these three for 5 consecutive days, and had made previous intermittent contact with them. Two additional unknown groups were observed only briefly, and their age-sex class composition could not be accurately determined.

2. Lenda.

At this site, two *C. angolensis* groups were encountered during single-observer censusing, one group during multiple-observer censusing, and two groups opportunistically. Duration of contact with groups ranged from 18 to 90 min. I encountered only one *C. guereza* group at this site, which I observed only briefly.

C. Description of Roaring Behavior

During systematic follows of study groups from March 1993 through March 1994 (118 days total), I recorded all occurrences of roaring by group males. Contact with a group began at 05:30 and was maintained until 18:30; these times sometimes varied by plus or minus 15 minutes depending on a group's location in the study area, and time of sunrise and sunset.

I follow the terminology used by Oates and Trocco (1983) in describing the elements of a colobus roar, i.e., phrases, sequences, and bouts, although in this chapter, I discuss roaring only in terms of bouts. Oates and Trocco defined a bout as a series of roaring sequences separated from other bouts by a nonroaring period of at least one minute. I used, instead, a one-hour criterion in counting bouts, because in cases of extended roaring (15 to 20 min by the same animal, during which several nonroaring periods occurred) the animal may still have been responding to the original stimulus.

For each occurrence of roaring, I recorded time of day, the number of males roaring, and whether any sound was heard prior to the onset of roaring (e.g., a falling tree, or the vocalizations of other animals) that may have been a stimulus.

III. Social Organization of Study Populations

A. Group Composition

Basakwe. The average size of *guereza* groups at Basakwe (7.8 animals, $n = 5$; Table 6.1.A) is smaller than that of *angolensis* groups (13.9 animals, $n = 8$; Table 6.2.A). The species also differ in the number of adult males per group. The adult of unknown sex in *guereza* group III was peripheral to the group, suggesting that it may have been a second adult male; *guereza* groups I, II, and III contained only one or two adult males. Six of eight *angolensis* groups, for which some or most adults were sexed, contained from two to five adult males.

Lenda. In forest near *Gilbertiodendron*-dominant stands, *angolensis* groups may be smaller (mean size = 6.4 animals, $n = 5$; Table 6.2.B) than those in mature mixed forest, and groups may contain one or several adult males. Lenda group I had only one adult male. Group III was most likely a one-male group - with a composition of 4 young animals, a subadult, and 3 adults, the adult of unknown sex must have been an adult female. Group IV contained 2 adult males. Groups II and V probably contained at least 2 adult males, as there was only one infant (and no juveniles) in group II, while group V contained neither juveniles nor infants.

I could not determine the composition of the sole *guereza* group encountered at Lenda (Table 6.1.B). No *guereza* groups were heard during auditory censuses in *Gilbertiodendron* forest (see Chapter 3, Sec. III.B.2). Therefore, I include additional information from opportunistic encounters of *C. guereza*, as well as *C. angolensis*, on or near the study area (Table 6.3). These data, collected by New York Zoological Society personnel, give no further information on group compositions. They do, however, provide some indication of the range of group sizes present at Lenda, as well as the habitat types in which groups were encountered.

B. Social Structure

In both *C. guereza* and *C. angolensis*, adult females and young animals form the social core of a group. Young animals - infants three months of age or older, juveniles, and small subadults - interact most with other animals, by either playing with each other, or by seeking the company of adult females. Adult females seem to have strong social bonds; reciprocal grooming among them is common, and they tend to rest near each other in a cluster with young animals.

The species differ primarily in the social role of adult males, in terms of (a) the manner in which other group members interact with them, and (b) how they interact with each other. In the *C. guereza* study group (SE group, Table 6.1.A), one male was clearly dominant to the other. The subordinate male occasionally interacted, by playing, with young animals (as did the dominant male), but tended to rest and feed away from the core of the group. This did not seem to be by choice: his attempts to approach were discouraged by threats from other adult animals, especially by the dominant male. Most interactions between the two males, although infrequent, were of an aggressive nature. I never heard the subordinate male roar, a behavior which, in this species, seems to function partially as a mechanism to maintain intergroup spacing (Sec. III.D., below). Towards the end of the study, this animal was frequently chased by adult females (or the dominant male), and he became increasingly peripheral to the group.

In the *C. angolensis* study group (Mondiale group, Table 6.2.A), two adult males seemed to share a position of dominance. I could not discern differences in rank level among the three other males. Although subordinate adult male *angolensis* sometimes rested at a distance from other group members, they were not chased away; in fact, aggressive acts toward subordinate males were infrequent. Adult male *angolensis*, like *guereza*, occasionally interacted with young animals, but they also interacted with each other. It was not uncommon to see adult males grooming each other, or resting in proximity. Furthermore, two examples of adult male behavior suggest some degree of cooperation. First, at least four of the five group males participated in jumping-roaring displays, which, in this species, sometimes occur when animals seem aroused or alarmed (Sec. III.D., below). Second, during aggressive encounters with other *angolensis* groups, two males worked together by chasing away extra-group males, or by positioning themselves between other group members and the encountered group.

C. Spatial Distribution of Groups and Interactions Between Groups

1. C. guereza.

Different *guereza* groups maintained some degree of spatial separation. I discussed range overlap in Chapter 5 (Sec. III.C.5), and estimated that two groups used a minimum of 22% of the SE group's home range. The true amount of overlap is probably higher - in a range area of 100 ha, other groups could easily have used parts of the study group's range without being detected. However, *guereza* density is low at Basakwe (2.4-9.6 individuals/km^2), and intergroup encounters, in which groups were within 50 m of each other, were infrequent.

During 60 days of systematic follows of *guereza* groups, encounters with other groups occurred on only 2 occasions. In both cases, groups met at the periphery of the SE group's range. On the morning of the first encounter, three adult males - including the SE group male - roared at 06:20 within a 500 m radius of the SE group. A total of five additional roaring bouts from the three adult males were heard from 07:20-11:30; at 11:30, the roaring male was judged to be about 150 m away from the SE group. The SE group did not leave the area where they were feeding and resting. By 11:45, the second group had approached the SE group to a distance of 25-50 m. The two groups maintained their respective positions until 12:45, when the second group (of at least 6 animals) entered an *Alstonia boonei* occupied by the SE group. At this point, animals from what appeared to be both groups were running about in the *Alstonia*, and young animals were heard squealing, but the adult males did not vocalize. The SE group promptly left the tree, then gradually moved away from the vicinity of the second group.

The second encounter involved what I suspect were the "remnants" of the first study group - the SW group. Before dawn on the morning of the encounter, several exchanges of roaring were heard from the SE group male and a male about 250 m away from the study group. By 06:30 the SE group had moved about 30 m from their sleeping tree, and had settled in a *Pteleopsis hylodendron*, where they continued to rest. At 08:00, I saw 2 animals leave the vicinity of the *Pteleopsis* - an adult male and a small subadult (hereafter referred to as the SW group) - who moved only 15 m away. The two groups maintained these positions, inactive, until 09:00. At this time, the SW group adult male, followed by the small subadult, ran toward and entered the SE group's *Pteleopsis*. As in the first encounter described above, only the infants and juveniles vocalized. Animals in the SE group ran back and forth between the *Pteleopsis* and a nearby tree, while the SW group animals ran off to the south. The SE group ran in the opposite direction, settling down again after a progression of about 15 min.

During each of these encounters, the role of the SE group adult males was not clear. In both cases, the entire group - including the subordinate male - was in one tree. In the first encounter, no members of the SE group "stood their ground" when the second group entered their tree; rather, the group was chased away. In the second encounter, the leaping back and forth between trees by the SE group - particularly adult animals - may have had the effect of intimidating the second group, as the SW group retreated first. This second encounter was clearly initiated by the SW group adult male, although this group was unusual in that it was composed of only 2 animals. During the first encounter, it was not clear which animal of the unknown group first entered the SE group's tree.

2. C. angolensis.

Most or all of the Mondiale group's range was used by other conspecific groups. I can not estimate the amount of range overlap the group experienced for two reasons: (a) they continued to enter new areas with each successive month of study, and (b) due to time constraints, I could not follow other *angolensis* groups long enough to get even a rough idea of their range size. However, one other habituated group (Mike's group, Table 6.2.A) was consistently recognizable by a marker individual. I followed this group in January, February, March, and May 1993 for several days each month. Mike's group was observed in the northern and southern areas of the Mondiale group's range, suggesting that other large groups have ranges similar in size to that of the Mondiale group, and that range overlap is extensive between groups.

To distinguish between brief encounters and longer associations involving 2 *angolensis* groups, I arbitrarily defined an encounter as proximity between 2 groups lasting less than one hour, and an association as proximity lasting an hour or longer. I defined proximity as a separation between groups of 50 m or less, primarily because this distance was my limit for visual detection of another group.

The study group associated with or encountered other groups on 25 of 62 days, or 40% of the days on which I collected systematic data from them; I observed these associations and/or encounters during 11 of 13 five-day follows (Feb. 93 - March 94). It is likely, however, that they occurred more often than I was able to detect, especially during the early months of the study. In addition, groups sometimes approached and maintained a loose "association" with the study group at distances greater than 50 m. While such occurrences were not counted as encounters or associations, they may still have influenced the study group's behavior.

During some encounters/associations, members of the two groups simply rested, fed, or travelled in proximity. Animals of one group periodically watched those of the other, and groups sometimes mixed together in the same feeding tree. The travel movements of groups in association were generally more diffuse than those of a single group. I never observed members of different groups interacting in an obviously affiliative manner (such as by grooming); interactions seemed to be either neutral or aggressive in nature.

Aggression during encounters was generally initiated by the approach of one to several animals - either one or two adult males, who were sometimes followed by several adult females. The intensity of aggression increased when one or two extra-group adult males infiltrated a cluster of study group animals. When this occurred, the extra-group animals were chased away - either by several adult males, or by a "team" of adult males and females. Persistent attempts by extra-group males usually resulted in a confrontation with one of the study group males; these confrontations involved snarling, grappling, and sometimes biting. During several such events, animals fell to the ground while fighting.

To illustrate the nature of *angolensis* group encounters and associations, I describe below those which occurred during five consecutive days (29 Dec. 93 to 2 Jan. 94):

Day 1. Two group encounters:

11:45. The Mondiale group is resting; another *angolensis* group is travelling about 25 m east of them, but they do not approach, and appear to be moving away from the study group.

13:45. Again, the study group is resting. Another *angolensis* group approaches the study group to within 15-20 m. I then see one adult male chasing another, while a third adult male assumes a vigilant posture and is scanning the immediate area. I suspect that an animal from the other group approached the study group, and was the animal being chased, because there was no apparent tension among study group members until the second group encountered them. After this altercation, the second group appears to have left the area.

Day 2. Association, beginning at 10:40 and apparently continuing until dark:

10:30. The study group is leaving an area where they have been feeding. They stop travelling at 10:40, about 30 m from another *angolensis* group. Animals from the 2 groups are looking in each other's direction. An adult female from the study group had been ahead of her group, but she returned to their location after seeing the second group. There are at least 7 animals in the other group - 6 adults and a large infant/small juvenile.

10:40-12:30. Both groups maintain their positions; animals are resting.

12:30. The study group moves a short distance, passing the other group with no apparent interaction. By 12:45 they are feeding in an *Amphimas pterocarpoides* (eating flowers). At 13:30, I still have not seen the other *angolensis* group.

15:30. There are more than 19 *angolensis* in the *Amphimas*, and some of them are a bit frightened of me. The second group apparently followed the study group to this tree.

16:15. The study group moves to another tree ("Dikpolo", an unidentified species) 10-15 m away and begins feeding; the other group remains in the *Amphimas*. I can see 6 animals in the other group: an adult male, an adult female with a black-and-white infant, and 3 other adults.

17:15. The study group begins another short progression, stopping to feed in an *Alstonia boonei*, then leaving this tree for a *Cynometra alexandri* and an unidentified tree. They settle here for the night. The other group is still within 50 m of the study group.

Day 3. Continuation of previous day's association, until 08:30:

06:00. The study group begins feeding in the same *Alstonia*. I hear grunting vocalizations from the other *angolensis* group.

06:45. The study group returns to and begins feeding in the *Amphimas* of yesterday. The second group is only 10-15 m away, in the "Dikpolo". Some of the study group remains in the *Amphimas*, resting or engaged in grooming. Others are resting in a contiguous *Cynometra*, as are several members of the other group. Animals from the 2 groups are occasionally looking at each other.

08:30. The groups are separating, each moving in a different direction. No subsequent encounters occurred today.

Day 4. Association, 09:15-13:55.

06:00-09:00. Animals are travelling between feeding sites.

09:00-09:15. The group is in a progression; they stop about 20 m from another *angolensis* group. Animals in the second group are resting.

09:15-11:00. Both groups maintain their positions, apparently resting.

11:00. Members of both groups are feeding in the same tree (a *Drypetes* sp.).

11:30. The study group begins to leave the area; the second group moves in a parallel progression about 20 m away.

12:15. Both groups have stopped moving. Most of the study group is resting in one *Cynometra.*

13:00. One study group adult male is apparently alone in another, contiguous *Cynometra* - between his group and the other group. Six animals from the other group - 2 adult males, 2 adult females (one carrying an infant), a subadult, and a juvenile - enter his tree; he leaves, joining his group in the other *Cynometra.* One of the 2 adult males from the other group retreats. The remaining adult male, with the 2 adult females, are sitting together, looking at the study group. They maintain their position for about 5 min, until they see me - then retreat from the *Cynometra,* as do the subadult and juvenile. The study group maintains its position, resting; the other group is no more than 25 m away.

13:55. The study group begins to leave the area. I count 19 animals moving; apparently no animals from the second group are following. No other groups are encountered for the rest of the day.

Day 5. No group encounters.

D. Adult Male Loud Calls

1. Frequency of occurrence.

I separate frequencies of occurrence for *Colobus* roaring into two categories: roaring heard from any *Colobus* group throughout the day (including the study group), and roaring heard from study group males only. Total number of roars in each category are further divided into those produced predawn (00:01-06:00) and after dawn (06:01-24:00).

a. Roaring by any *Colobus* group. I heard 303 bouts of *Colobus* roaring: 231 (76.2%) were *C. guereza* males; 67 (22.1%) were *C. angolensis* males; and 5 (1.7%) were undetermined. Of 92 predawn roars, 87 (94.5%) were *C. guereza* males; 2 (2.2%) were *C. angolensis* males; and 3

(3.3%) were undetermined. Of 211 after dawn roars, 144 (68.2%) were *C. gureza* males; 65 (30.8%) were *C. angolensis* males; and 2 (1.0%) were undetermined.

b. Roaring by study group males. During 60 days of *C.guereza* follows, I heard 60 roaring bouts from the dominant male. Of these 60 bouts, 17 were predawn and 43 were after dawn roars. During 58 days of *C. angolensis* follows, I heard 9 roaring bouts; 8 of these roars were after dawn, while only 1 was a predawn roar.

2. Contexts in which roaring occurs.

Most predawn roaring by *C. guereza* involved choruses of individual adult males calling from several different locations. Roaring during the day was often heard after treefalls, duiker screams, or the vocalizations of other primate species, and seemed to be associated with a heightened state of arousal or alarm. When I was with the study group, I never heard the subordinate male roar, nor did I see him participate in jumping-roaring displays.

In *C. angolensis*, jumping-roaring displays involved at least 4 adult males, and were observed only when the animals seemed aroused or alarmed - e.g., as with *C. guereza*, after treefalls, duiker screams, or the vocalizations of other primate species (including *C. guereza*). In contrast, abbreviated roars by individual males were heard during low-intensity agonistic encounters between adult males within the same social group, or during aggressive interactions between adult males and extra-group males travelling with the study group. Spatially separated individual males sometimes engaged in countercalling, also by abbreviated roars.

E. Mating Systems and Societies

1. *C. guereza*.

The subordinate male in the SE group clearly had social bonds with the young animals, suggesting that he had been a group member for at least several years. I can not be certain that this male never copulated with adult females, but I never observed him even attempting to do so. In spite of the increasing level of aggression directed toward him from other adults, he seemed to be attempting to maintain contact with the group. These observations, taken together, suggest that the subordinate male was still in his natal group - and would probably soon emigrate.

During follows of the NC group, I observed only one adult male roaring. If the adult of unknown sex (Table 6.1.A) - who seemed to be peripheral to the group - was a male, he did not roar. The SW group of 5 animals contained only one adult male.

Assuming that the study groups are typical of the population, *C. guereza* in the Ituri Forest exhibit a harem-based, polygynous mating system. Occasionally, I observed adult females soliciting copulations, although this was not always the case. Females showed no physical signs of estrus. Their society appears to be matrilineal - the social bonds among adult females suggest that they are related, while males probably emigrate at maturity. These observations are consistent with reports from other populations (Sec. IV.A., below).

Female emigration may occur when group composition is disrupted. In March 1993, the SW group was reduced from 5 (1 adult male, 2 adult females, 1 subadult male, 1 infant male) to 3 animals (1 adult male, 1 adult female, 1 subadult male) by the attack of a predator. I attempted to follow the remaining 3 animals for 2 days after this attack, but the group had become incohesive. On 1 July 1993, I saw a lone adult female *guereza* with the *angolensis* study group for 7 hours; on that day, the *angolensis* group was in the previous range of the SW group. Furthermore, the encounter between the SE group and an adult male-subadult pair, in March 1994, occurred in the previous range of the SW group. The lone female may have been a former member of the SW group; if so, she emigrated at some point after the other adult female was killed.

2. C. angolensis.

Angolensis seem to exhibit a promiscuous mating system, although my study was not long enough to provide an accurate assessment. In the study group, at least 2 adult males copulated with adult females. I suspect that more than 2 did so, however, because I observed two different types of copulatory behavior. Some copulations occurred within the main cluster of animals - in the presence of another adult male - while others occurred between a consorting pair at some distance from other animals. These observations, while anecdotal, suggest that the 2 high-ranking males tolerated each other's sexual behavior, while subordinate males attempted to conceal their copulations from dominant animals. In addition, extra-group males may have attempted to copulate with group females (Sec. IV.B., below), but I can not substantiate this possibility.

I never observed *angolensis* females soliciting copulations; in many cases, adult males grabbed females and copulated forcibly. In estrous females, the clitoris is more visible, and the perineum swells slightly. Harrison (cited in Oates, 1994) observed similar signs of estrus in *C. satanas*. Estrus is not synchronized among all group females; during any one month, I observed from 2 to 5 adult females (of 8 total) with perineal swelling.

The amount of available information does not allow description of *Colobus angolensis* society as either matrilineal or patrilineal. Newton and Dunbar (1994, p. 345), for example, have most recently proposed a classification scheme for colobine societies based on a number of reproductive, social, and ecological attributes. Following their heuristic framework, *C. angolensis* show characteristics of both patrilineal (sexual swellings, rare female mating solicitation, and common male-male grooming) and matrilineal (distinct natal pelage, infant handling, and common female-female grooming) societies. If patrilineality and matrilineality are considered as 2 ends of a continuous societal spectrum, *angolensis* is probably closer to the matrilineal end. I consider this topic further in Sec. IV.B. (below).

IV. Inter-Population Comparisons

I discuss *C. angolensis* in considerably more detail than *C. guereza*, because information concerning social behavior and organization in the former species has not previously been published.

A. *Colobus guereza*

Different populations of *C. guereza* exhibit similar patterns of social organization, i.e., spatially separated one-male groups with a system of male transfer (Marler, 1969; Groves, 1973; Dunbar & Dunbar, 1974; Clutton-Brock, 1975; Oates, 1977b; Suzuki, 1979). Multi-male group structures have been reported; e.g., in the Bole Valley, Ethiopia, Dunbar and Dunbar (1976) found that 3 of 18 groups were multi-male at the time of their study. One of these multi-male groups later divided into 2 groups, with one adult male accompanying each of the newly-formed groups. Multi-male structures are presumed to be temporary, resulting from the maturation of males in their natal group, or from the immigration of extra-group males (Oates, 1977b; Dunbar, 1987).

Von Hippel (1996) argues that one-male groups are not typical for *C. guereza*, largely based on his observations of multi-male groups in the Kakamega Forest, Kenya. His interpretation, however, is confounded by at least two factors: (a) he did not distinguish subadult animals as a distinct age class - an important distinction when labelling a group "one-male" or "multi-male", and (b) his study was short, spanning a 2-month period - not long enough to distinguish a difference in social status among adult males in the same group, especially considering that observation time was divided among seven groups. For example, my primary guereza study group contained two adult males, from the time I first observed the group in December 1992 until the end of the study in March 1994. The difference in social status between these two males was striking; by early 1994, the subordinate male was clearly being "encouraged" to emigrate.

B. *Colobus angolensis*

Both multi-male and one-male groups have been reported in *C. angolensis*. Multi-male groups occur in the Diani Beach forest (Kenya; Moreno-Black & Maples, 1977; Moreno-Black & Bent, 1982), in the Sango Bay forests (Uganda; Oates, 1974), in the Nyungwe Forest Reserve

(Rwanda; A. Vedder, pers. comm.), and in the Ituri Forest (this study). Groves (1973) observed mostly one-male groups in Northeastern Tanzania.

Associations of two or more groups (referred to as "super-troops" in the literature) have been observed at Diani Beach, Sango Bay, Nyungwe, and the Ituri. A group of about 30 *C. angolensis* seen in the Mahale Mountains, Tanzania by Nishida *et al.* (1982) may have also been a super-troop formation. The study group at Diani Beach associated with another group during approximately one-third of observation days, comparable to my observed value of 40% in the Ituri.

Of the six populations I have mentioned, the Northeastern Tanzanian population is exceptional in its one-male group structure. Reported group sizes in this region were small (mean = 4.9 animals, *n* = 37). Maisels *et al.* (1994) also reported small group sizes, of 3-7 animals, in the Salonga National Park, Zaire (group compositions are not given). In some cases, the number of males in a group may be related to group size; I observed one, possibly two, one-male groups at the Lenda study area, where mean group size was 6.4 animals (Table 6.2.B). At Basakwe, however, I also observed a group of 6 adult animals, containing at least 3 adult males (Table 6.2.A). Considering all populations for which information is available, it seems reasonable to conclude that *C. angolensis* shows a strong tendency to form multi-male groups, and to associate with other conspecific groups.

At Diani Beach, *C. angolensis* rarely roared; Moreno-Black and Bent associated this "...apparent lack of intertroop spacing behaviour..." with super-troop formation, and with the generally pacific nature of these formations. These observations are consistent with my own in the Ituri.

Closer examination of events occurring during group associations, and of variability in group compositions, may be the first step in answering basic questions about *angolensis* society - e.g., what is their mating system and dispersal pattern? The fluid nature of their society, particularly with respect to super-troop formation, suggests that both males and females may leave their natal group - depending on the circumstances.

For example, on 27 Sept. 93, my study group encountered other groups three times, with no apparent co-mingling of groups - except for the approaches of one or two extra-group animals. The first encounter occurred at 08:45, the second at 11:30. At 14:20, 4 adult animals - at least 2 of which were adult males - were involved in a chase; it seemed as though the 2 adult males were chasing the other 2 adults. At 16:15, a third encounter occurred; I could not assess whether all 3 encounters involved the same *angolensis* group. At 17:30, an adult male from the study group chased another adult male to a distance of 50 m; one adult male returned to the group. On the following morning, at 05:55, several animals were heard snarling and seen chasing each other; 10 min later, 2 adult males fell to the ground fighting - to the extent that one male bit the other's neck. During this altercation, both males emitted abbreviated roars. By this time, it was clear that an unknown adult male had been maintaining contact with the study group - and he was still with them during a progression at 08:00, in which all animals were clearly seen. I do not know how long this unknown male stayed with the study group, because they encountered yet another group at 08:30, after which we lost contact with them for over a week. By that time, the extra animal was gone.

Aggressive interactions between members of 2 groups did not occur during every encounter or association, but they were not uncommon. Nor was it uncommon to find an extra animal or two temporarily travelling with the study group. It appears that adult males periodically try to maintain contact with other groups - similar to the "haunting" behavior or actual group "permeation" described by Hrdy (1977) for adult male *Presbytis entellus*. In *C. angolensis*, the motivations for such behavior may be several. Adult males may be attempting to transfer, either singly or in pairs, to other groups. Alternatively, these males may be trying to "steal" copulations (although this was impossible to verify) or to coerce females to leave their group. I have only indirect evidence for this second possibility. Some groups, such as Basakwe groups V, VI, and VII, and Lenda group V, lack infants and juveniles, or contain only one (Tables 6.2). Such compositions suggest that these groups were relatively new - perhaps formed by cohorts of adult males stealing females from other groups. This manner of group formation has been reported in at least one other colobine, *Trachypithecus pileatus* (Stanford, 1990).

Based on these observations, I suspect that male emigration is more common than female emigration. Adult females in the study group were clearly bonded. The close relationship between the two co-dominant males in this group suggests that they may have left their natal group together. While lower-ranking males were not peripheralized, as in *C. guereza* groups, the comparatively greater group spread in *C. angolensis* groups may facilitate the coexistence of several adult males. Observations of adult males presenting to other males, and the relatively low level of within-group male-male aggression, suggest that a dominance hierarchy was maintained.

Multi-level societies have been reported in several Asian colobines, including *Rhinopithecus brelichi* (Bleisch *et al.*, 1993), *R. bieti* (Kirkpatrick, 1996), and *Nasalis larvatus* (Yeager, 1990, 1991). In these species, however, one-male units coalesce to form larger bands. In *C. angolensis*, multi-male groups form temporary associations, in which the identity of associating groups is variable. Structurally and behaviorally, *angolensis* group associations may be more similar to those observed in the Tana River crested mangabey, *Cercocebus galeritus* (Kinnaird, 1992), rather than those of Asian colobines.

C. angolensis group associations seem to be more than a simple meeting of groups at abundant food sources - because groups may travel together for several hours or more than one day. Hrdy (1977) suggested four possible functions of group encounters in *Presbytis entellus*, in which one or several males approach a bisexual group: extra-group males may 1) obtain information about females' reproductive states; 2) obtain information concerning the physical condition of adult males; 3) steal copulations; or 4) take over the group. These are all potential explanations for the functional significance of group associations in *C. angolensis*, especially since adult males can not rely on loud calls to locate other groups. Given that some of these associations are relatively peaceful, however, I would suggest a fifth possibility - that these animals may just be curious about other groups, or "updating their information" about the composition of different groups - in which they may well have relatives.

V. Summary

1. In the Ituri Forest, *C. guereza* occur in one-male bisexual groups in which adult females exhibit strong social bonds. Adult males are generally intolerant of each other. Spatial overlap among conspecific groups is small, and group encounters are infrequent.

2. *C. angolensis* in the Ituri occur in multi-male bisexual groups in which adult females exhibit strong social bonds. A dominance hierarchy is evident among adult males. Group ranges are completely overlapped by other conspecific groups. Group encounters are common, and sometimes lead to the formation of temporary associations.

3. Socially, the species differ primarily in the degree of tolerance among adult males within the same social group, and in the nature of intergroup relations. *C. guereza* loud calls seem to maintain spatial separation among conspecific groups. *C. angolensis* rarely roar; in this species, loud calls do not seem to function as a group spacing mechanism.

4. Different populations of each species exhibit the same respective patterns of social organization, suggesting that social organization in *C. guereza* and *C. angolensis* is, to some extent, phylogenetically constrained.

Table 6.1. Composition of *C. guereza* groups. AM, AF, AU = adult male, adult female, or adult of undetermined sex; SAM, SAF, SAU = subadult male, subadult female, or subadult of undetermined sex; J = juvenile; I = infant (black-and-white and white infants combined); U = animal of undetermined age-sex class.

A. Mature mixed forest (Basakwe study area)

group	AM	AF	AU	SAM	SAF	SAU	J	I	U	total
SE	2	3			1		2	2		10
SW	1	2		1				1		5
NC	1	2	1			1	2	1		8
IV			3				3		5	11
V			4			1				5

5 groups: mean group size = 7.8

B. Mixed forest near *Gilbertiodendron*-dominant forest (Lenda study area)

group	AM	AF	AU+SAU	J	I	total
I	1	1	5	2	1	10

Table 6.2. Composition of *C. angolensis* groups; abbreviations as in Table 6.1.

A. Mature mixed forest (Basakwe study area)

group	AM	AF	AU	SAM	SAF	SAU	J	I	U	total
Mondiale	5	8		1			5			19
Mike's	2	6			1	1	2	1	4	17
III	2		9				2	2		15
IV	3	2	8			2	2	1	2	20
V			11					1		12
VI	3		3							6
VII			7							7
VIII	5	4	1			1	2	2		15

8 groups: mean group size = 13.9

(Table 6.2, continued)

B. Mixed forest near *Gilbertiodendron*-dominant forest (Lenda study area)

group	AM	AF	AU	SAM	SAF	SAU	J	I	U	total
I	1	1				1		1		4
II[a]	1	3	2					1		7
III	1	1	1			1	3	1		8
IV	2	2			1		1	1		7
V[a,b]			4			2				6

5 groups: mean group size = 6.4

[a] composition based on field assistant's report.
[b] sighting occurred 250 m from an area where *Gilbertiodendron* accounted for more than 50% of all large trees.

Table 6.3. Opportunistic sightings of *Colobus* groups on or near Lenda study area, 3 May - 22 June 93, by NYZS field personnel.

A. *C. guereza*

forest type	number of animals
old secondary	12
old secondary	1, with > 8 *angolensis*
old secondary	6
old sec./*Gilbertiodendron* ecotone	8
Gilbertiodendron	2
young secondary	5
old secondary	> 9
old secondary	7, with 4 *angolensis*

B. *C. angolensis*

forest type	number of animals
old secondary	> 8
old secondary	> 10
old secondary	> 8, with 1 *guereza*
old secondary	> 5
old secondary	> 8
old secondary	> 5
old secondary	8
old sec./*Gilbertiodendron* ecotone	9
old secondary	4, with 7 *guereza*

Chapter 7. DISCUSSION

Is interspecific competition a major determinant of *Colobus* niche separation? Or are *C. angolensis* and *C. guereza* sufficiently different in habitat use and food selection that competition is unlikely? I designed this study to distinguish between two hypotheses: (1) *C. angolensis* and *C. guereza* coexist as competitors with little or no niche separation, and (2) niche separation occurs, and is primarily the effect of species differences evolved in allopatry. To evaluate these hypotheses, I review *C. angolensis* and *C. guereza's* habitat use, food selection, and ranging patterns, and consider the potential influence of proximate factors (either proximate mechanisms or environmental cues) on *Colobus* niche separation. Subsequently, I assess predictions generated from my hypotheses in considering how *Colobus* niche separation may have come about.

I. Habitat Use and Vertical Distribution of Activities

The species differ in their relative abundance in three forest types near Epulu - mature mixed forest, *Gilbertiodendron*-dominant forest, and secondary forest. Both occur at low density, estimated at less than 20 individuals/km^2, in all forest types (see Table 3.4). *C. angolensis*, however, is at least twice as abundant as *C. guereza* in mature mixed forest. *C. angolensis* also occurs near *Gilbertiodendron*-dominant forest, but *guereza* was neither observed nor heard during census work there; I assume, then, that *angolensis* is more abundant than *guereza* in this forest type. In secondary forest, the two species occur at roughly similar densities: for *guereza*, this density is about twice that in mature mixed forest; *angolensis* density is approximately equal in both forest types.

Differential habitat use is further reflected in the study groups' use of habitats within mature forest: *C. guereza* shows a preference for open-canopy areas, particularly swamp forest; *C. angolensis* uses different habitats, including closed-canopy forest, in proportion to their representation in the study area. The species also differ in the vertical distribution of their activities: *C. guereza* feed and travel lower, and rest higher, than *C. angolensis*.

Are *angolensis* and *guereza* responding to different environmental cues in their choice of habitat? It seems likely that they may recognize differences in vegetation structure, as Rodman (1991) has proposed for sympatric *Macaca fascicularis* and *M. nemestrina*. Studies of *C. guereza* in Uganda (Oates, 1977a) and Ethiopia (Dunbar & Dunbar, 1974) have noted that *guereza* spend most of their time inactive, waiting for several hours after sunrise to move away from their sleeping area; activity patterns in these populations are similar to those of Ituri Forest *guereza* (Figure 5.2). Oates (1977a) noted that *guereza* often begin their day with sunbathing on exposed branches, and has suggested that *guereza* use sunlight, during the coolest part of the day, to maintain body temperature when the stomach is empty. In contrast, *C. angolensis* generally leave their sleeping trees at sunrise and start searching for food (Figure 5.2). These observations suggest that *angolensis* and *guereza* satisfy their energetic requirements in different ways; these differences may be related to their choice of habitat in the Ituri, and to their distribution of activities in different vertical strata.

Waser (1987) has suggested that comparison of primate densities in undisturbed and adjacent disturbed forest may indicate whether certain factors limit population density. Because sympatric *angolensis* and *guereza* occur at similar densities in disturbed forest, yet *angolensis* is considerably more abundant than *guereza* in mature forest, I suggest that availability of suitable habitat is more likely to limit *guereza* population density than is competition with *angolensis*. Within mature forest, *guereza* may be limited by the availability of open-canopy areas where sunlight is more accessible, such as swamp and mosaic-type habitats.

In his model of speciation in black-and-white colobus, Grubb (1978, 1982) proposed that *C. angolensis* differentiated from *C. satanas* in the East- and South-Central forest regions and that, after subsequent periods of dispersal and isolation, *C. guereza* diverged from its ancestor in forest galleries. The current distribution of *angolensis* and *guereza* suggests that each species is most successful in different forest types: *angolensis* in mature forest, specifically in Zaire; *guereza* in younger forest or forest islands, north of the tropical forest zone and into East Africa.

II. Food Selection

The dominant plant species in the study area (*Cynometra alexandri*) was the most frequently consumed food of *C. angolensis*; this plant was not a major component of *C. guereza's* diet. With the exception of *C. alexandri* and *Erythrophleum suaveolens*, important food plants for both *Colobus* were uncommon to rare in the study area. However, aggressive interspecific interactions at shared feeding sites were never observed. Over 107 days of group follows, displacement from a common food source of one species by the other was observed on only two occasions.

On an annual basis, neither species was more folivorous nor granivorous than the other. Seed-eating by *C. guereza*, however, was concentrated in a 3-month period, while *C. angolensis* consumed seeds throughout the year. Monthly patterns of food choice, then, indicate that *C. guereza* was primarily folivorous in most months, while *C. angolensis* was more general in its feeding habits. Young leaves of deciduous trees were preferred foods of both species, although *C. angolensis* also selected strongly for specific flower and seed items. *C. guereza's* pattern of leaf selection seemed to maximize crude protein intake, but was not strongly associated with leaf fiber content. Conversely, *C. angolensis* leaf selection minimized fiber intake, but was not strongly associated with leaf protein content.

Food selection in some colobines has been positively associated with protein content (*Colobus satanas*: McKey *et al*., 1981; *C. polykomos*: Dasilva, 1994; *Presbytis rubicunda* and *P. melalophos*: Davies *et al*., 1988); in other colobines, food selection seems to minimize fiber intake, rather than maximize protein intake (*Presbytis johnii*: Oates *et al*., 1980; *Trachypithecus* *auratus*: Kool, 1992). Both Oftedal (1991) and Kool (1992) have suggested that, where protein levels in vegetation are high relative to dietary requirements, there may be little or no advantage in selecting foods high in protein. The biological significance of the correlation between *guereza* leaf selection and protein is, therefore, difficult to assess; they may be selecting for another nutrient which tends to be correlated with protein. Furthermore, the Kjeldahl procedure for nitrogen determination will overestimate protein content (calculated as percent nitrogen X 6.25) if the analyzed material contains other sources of nitrogen, such as nonprotein amino acids and alkaloids; the correlation of *guereza* leaf selection with protein may be confounded by the presence of nonprotein nitrogen.

The differences in *guereza* and *angolensis* leaf selection with respect to fiber (ADF) content may be biologically significant. For example, Milton (1984) pointed to the potential role of gut morphology and digestive processes, such as food passage rate, as proximate mechanisms in niche separation. Chivers and Hladik (1980) related morphological variation in the gastro-intestinal tract to different gross categories of diet among primates; Chivers (1994) further documented an increase in stomach size with increasing folivory among different colobine species. Fiber is digested slowly, requiring a longer passage rate, than other components of food (see, e.g., Kay & Davies, 1994). *C. angolensis* and *C. guereza* may differ in food passage rate, in stomach size, and/or in some other factor related to food processing; however, this possibility can not be further evaluated without comparative data on gut anatomy and digestive processes.

III. Ranging Patterns

C. angolensis showed a more diverse pattern of range use, travelled farther each day, and used a much larger home range than *C. guereza*. *C. guereza* intensively used a smaller, contiguous block of forest within their home range; *C. angolensis* did not use one specific area of their range intensively. The home ranges of *C. angolensis* groups overlapped completely with those of other conspecific groups; group encounters were common. The home ranges of *C. guereza* groups showed some degree of spatial separation; group encounters were infrequent.

How might these differences in ranging patterns lead to niche separation? *C. angolensis* ranging patterns were proximately associated with food availability, and with dietetic diversity; *C. guereza* ranging patterns were not associated with either of these factors. Species differences in ranging patterns may be related to different patterns of resource exploitation. In terms of general food categories, *C. angolensis* exhibits a broader food niche in most months than does *C. guereza*. Because *angolensis* use such a large range, it is less likely that they will know the location of specific food trees; the increase in their day range with decreasing food availability suggests that they may be searching for particular foods. In contrast, *guereza* may know the location of specific trees, especially in their area of intensive use. I cannot explain the association between *guereza* movements and the degree to which they consume flowers. However, the correlation between *guereza* ranging patterns and the proximity of conspecific groups may point to a behavioral influence on their movements.

C. angolensis occur in large, multimale, bisexual groups; *C. guereza* occur in smaller bisexual groups, with one or two adult males. Within the genus *Colobus*, there appears to be a relationship between the degree of male-male tolerance and the contexts in which loud calls are produced; *C. angolensis* and *C. guereza* represent two ends of a behavioral continuum. Adult male *angolensis* in the same social group are generally tolerant of each other, but this is not true for adult male *guereza* in the same social group. *C. angolensis* groups often form temporary associations with other conspecific groups; *C. guereza* groups rarely come into contact with each other. Marler (1969, 1972) suggested that *guereza* loud calls may play a role in maintaining intergroup spacing; *angolensis* loud calls do not appear to serve this function.

The behavior of adult females may have an equal, if not greater, influence on group ranging patterns, but species differences in female behavior are not obvious. For example, Bennett and Sebastian (1988) noted that in primate species in which females transfer between groups, home ranges tend to overlap considerably. While it is tempting to suggest that male-male tolerance in *angolensis* is related to extensive home range overlap and formation of group associations, evidence from other studies indicates that tolerance between males is not necessary for the development of these behaviors. Other species in which groups temporarily associate, and in which home ranges overlap extensively, occur in one-male groups (*Nasalis larvatus*: Bennett & Sebastian, 1988; Yeager, 1991; *Trachypithecus pileatus*: Stanford, 1991b).

Thus, differences in social organization between *C. angolensis* and *C. guereza* may only partially explain their differences in ranging patterns. Proximately, the primary influence on ranging patterns seems to differ between species, with *angolensis* using environmental cues; *guereza*, behavioral mechanisms.

IV. Evaluation of Hypotheses and Conclusions

A. Evaluation of Hypotheses

The data used to test the following predictions have been presented and discussed in preceding chapters.

Hypothesis 1. To test hypothesis 1 (*C. angolensis* and *C. guereza* coexist as competitors with little or no niche separation), I made 5 predictions:

(a) extensive overlap in diet and habitat use will be observed in all months of the year;

(b) neither *C. angolensis* nor *C. guereza* will change their ranging patterns when a preferred, shared food item is scarce;

(c) during these periods of scarcity, both species will use the same alternative food sources;

(d) patches of preferred food sources in short supply will be defended against heterospecific groups; and

(e) one species will displace the other from preferred feeding sites.

Predictions (a), (b), (d), and (e) were not upheld. Prediction (c) was essentially not upheld, with one qualification: in one month when food items preferred by both species were scarce (October 93), the primary food of both species was *Erythrophleum suaveolens* seeds. This tree was common in the study area; shared consumption of its seeds is not likely to have resulted in competition.

Hypothesis 2. To test hypothesis 2 (niche separation occurs, and is primarily the effect of species differences evolved in allopatry), I made 4 predictions:

(a) where one *Colobus* species occurs in either mature or secondary forest, the other will be rare or absent;

(b) if both species use the same forest type (e.g., mature or secondary forest), there will be little or no dietary overlap in all months of the year; each species will specialize in using different components of the habitat mosaic;

(c) foods consumed by one species will require different mechanical and/or chemical processing than foods consumed by the other;

(d) patterns of habitat and food utilization in each species in sympatry will be similar to patterns observed in allopatric populations.

Predictions (a), (b), and (c) were upheld. Prediction (d) was essentially upheld, if habitat use is considered in terms of broad categories (i.e., mature vs. younger forest), and food use in terms of food preferences.

B. Conclusions

The influence of other processes on *Colobus* niche separation can not be ruled out; such processes may include predation, competition with other taxonomic groups, parasitism, disease, disturbance, and environmental variability (reviewed by Strong, 1983). Abiotic factors may also influence community structure (see, e.g., Dunson & Travis, 1991). However, the primary intent of my study was to determine whether species differences in resource use was more likely due to their separate evolutionary histories, or to their interactions in sympatry. My results are equivocal, primarily because the absence of exploitation competition cannot be ruled out by an observational study. *C. angolensis* and *C. guereza* do not compete by direct interference. They do not coexist with extensive niche overlap. Their patterns of resource use can be explained by species differences, characteristics which are evident in other populations of each species. I suggest that these species differences may be stronger determinants of their niche separation than are interspecific interactions.

APPENDIX

Appendix 1.1. Annual diets (April 93 - March 94); values represent percent of total feeding observations (*C. angolensis*: *n* = 2457; *C. guereza*: *n* = 1336). Plant parts abbreviated as follows: yl+lb = young leaves and leaf buds; ml = mature leaves; totlf = total, leaves of all age classes (including petioles); totfr = total, seeds and other fruit parts; fl = flower; ui = undetermined item.

A. *C. angolensis*[a]

species or food type	yl+lb	ml	totlf	seed	totfr	fl	ui	total
Cynometra alexandri	4.55	0.08	8.98	3.95	3.95	0.00	2.20	15.14
Celtis mildbraedii	3.01	0.20	13.26	0.00	0.00	0.00	0.00	13.26
Alstonia boonei	1.34	0.08	2.68	0.00	0.45	3.22	1.95	8.30
Dikpolo (unid. tree)	6.39	0.65	8.30	0.00	0.00	0.00	0.00	8.30
Erythrophleum suaveolens	0.00	0.00	0.00	6.19	6.19	0.00	0.00	6.19
Angylocalyx pinnaertii	2.52	0.08	2.64	0.00	0.65	0.00	2.40	5.70
Celtis zenkeri	1.79	0.12	4.23	0.00	0.00	0.00	0.00	4.23
Unknown lianas	0.73	0.41	1.75	0.20	0.44	0.08	1.55	3.83
Lecaniodiscus cupanioides	0.00	0.00	0.00	3.66	3.66	0.00	0.00	3.66
Milicia excelsa	0.94	0.04	0.98	0.00	1.71	0.00	0.20	2.89
Unknown trees	0.33	0.12	0.61	0.16	0.53	0.41	1.30	2.85
Drypetes spp. (Roko)	0.24	0.00	0.24	2.03	2.03	0.00	0.20	2.47
Strombosia pustulata	0.00	0.00	0.00	2.20	2.20	0.00	0.16	2.36
Amphimas pterocarpoides	0.00	0.00	0.00	0.00	0.00	2.28	0.00	2.28
Desplatsia dewevrei	1.30	0.08	1.66	0.00	0.00	0.04	0.24	1.95
Ngoto (unid. liana)	0.00	0.00	0.00	1.59	1.59	0.00	0.00	1.59
Zanthoxylum macrophyllum	0.33	0.00	0.61	0.00	0.12	0.20	0.53	1.47
Xylopia aethiopica	0.00	0.00	0.00	0.00	1.42	0.00	0.00	1.42
Piptadeniastrum africanum	0.00	0.04	0.08	1.14	1.14	0.00	0.00	1.22
Discoglypremna caloneura	0.61	0.00	1.14	0.00	0.00	0.00	0.00	1.14
Drypetes spp. (Sungba)	0.49	0.04	0.90	0.00	0.00	0.00	0.04	0.94
Celtis prantlii	0.28	0.00	0.81	0.00	0.00	0.00	0.08	0.90
Antiaris africana	0.28	0.00	0.44	0.00	0.00	0.00	0.37	0.81
Strombosiopsis tetrandra	0.00	0.00	0.00	0.73	0.73	0.00	0.00	0.73
Sapotaceae sp. (Amelinda)	0.00	0.00	0.00	0.00	0.53	0.00	0.00	0.53
lichen								0.41
Apambuka (unid. tree)	0.00	0.00	0.00	0.04	0.37	0.00	0.00	0.37
Monodora myristica	0.00	0.00	0.00	0.00	0.00	0.33	0.04	0.37
Anthocleista schweinfurthii	0.00	0.28	0.28	0.00	0.00	0.00	0.00	0.28
Ficus spp.	0.16	0.04	0.24	0.00	0.00	0.00	0.04	0.28
Zanthoxylum lemairei	0.12	0.00	0.20	0.00	0.00	0.00	0.04	0.24
Amanjenje (unid. liana)	0.00	0.00	0.04	0.00	0.16	0.00	0.00	0.20
Manilkara sp.	0.00	0.00	0.04	0.00	0.04	0.00	0.08	0.16
Spathodea campanulata	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.16
Pteleopsis hylodendron	0.12	0.00	0.16	0.00	0.00	0.00	0.00	0.16

(Appendix 1.1.A., continued)

species or food type	yl+lb	ml	totlf	seed	totfr	fl	ui	total
Unknown epiphytes	0.00	0.00	0.04	0.00	0.00	0.08	0.04	0.16
Njamba1 (unid. liana)	0.00	0.04	0.04	0.08	0.08	0.00	0.00	0.08
Celtis adolfi-friederici	0.04	0.00	0.04	0.00	0.00	0.00	0.04	0.08
Albizia sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04
Cola lateritia	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04
Strombosia grandifolia	0.00	0.00	0.00	0.04	0.04	0.00	0.00	0.04
Unknown	0.33	0.12	0.69	0.08	0.12	0.00	1.87	2.69
								100.00

[a]Total number of tree and liana species in diet:

- 31 tree species identified or distinguished
- 3 tree groups, identified to generic level, which include 2 or more species [*Drypetes* spp. (Roko) includes *D. ituriensis*; *Drypetes* spp. (Sungba) includes *D. bipindensis*; *Ficus* spp.]
- 3 liana species, unidentified but distinguishable

B. *C. guereza*[b]

species or food type	yl+lb	ml	totlf	seed	totfr	fl	ui	total
Erythrophleum suaveolens	0.30	0.00	0.45	9.36	9.36	0.00	0.00	9.81
Albizia gummifera	8.61	0.07	9.35	0.00	0.00	0.00	0.00	9.36
Unknown lianas	1.94	1.50	5.54	0.00	0.67	0.22	1.65	8.08
Alstonia boonei	2.17	0.15	2.92	0.00	0.00	1.65	0.75	5.31
Celtis mildbraedii	0.67	0.00	5.09	0.00	0.00	0.00	0.00	5.09
Ficus spp.	0.37	0.67	4.18	0.00	0.22	0.00	0.30	4.72
Dikpolo (unid. tree)	1.87	0.30	4.42	0.00	0.00	0.00	0.00	4.42
Angylocalyx pinnaertii	1.57	0.00	1.72	0.00	0.89	0.00	1.50	4.12
Desplatsia dewevrei	2.62	0.00	4.04	0.00	0.00	0.00	0.07	4.12
Cynometra alexandri	0.75	0.00	1.95	1.57	1.57	0.00	0.22	3.74
Celtis zenkeri	1.95	0.07	3.52	0.00	0.00	0.00	0.00	3.52
Drypetes spp. (Sungba)	1.80	0.00	3.00	0.00	0.00	0.00	0.00	3.00
Njamba1 (unid. liana)	0.00	0.00	0.00	2.92	2.92	0.00	0.00	2.92
Cassia mannii	0.00	0.00	0.00	2.62	2.62	0.00	0.00	2.62
Schrebera golungensis	1.20	0.00	1.95	0.00	0.00	0.07	0.60	2.62
Celtis prantlii	1.05	0.07	2.47	0.00	0.00	0.00	0.00	2.47
Margaritaria discoidea	0.00	0.00	0.00	2.25	2.25	0.00	0.00	2.25
Unknown trees	0.59	0.00	1.26	0.07	0.29	0.15	0.37	2.10
Drypetes spp. (Roko)	0.07	0.07	0.14	0.45	0.45	0.15	1.27	2.01
Discoglypremna caloneura	0.45	0.00	1.20	0.00	0.22	0.00	0.07	1.50

(Appendix 1.1.B., continued)

species or food type	yl+lb	ml	totlf	seed	totfr	fl	ui	total
Ngoto (unid. liana)	0.00	0.00	0.00	1.27	1.27	0.00	0.00	1.27
Rauvolfia vomitoria	0.00	0.07	0.14	0.00	0.60	0.00	0.45	1.20
Anthocleista schweinfurthii	0.00	0.82	1.12	0.00	0.00	0.00	0.00	1.12
Milicia excelsa	0.00	0.00	0.00	0.00	0.97	0.00	0.15	1.12
Pteleopsis hylodendron	0.82	0.00	1.12	0.00	0.00	0.00	0.00	1.12
Commiphyton gabonense	0.15	0.00	0.45	0.00	0.00	0.22	0.37	1.05
Zanthoxylum macrophyllum	0.52	0.00	0.59	0.00	0.00	0.00	0.30	0.90
Strombosia pustulata	0.00	0.00	0.00	0.37	0.37	0.00	0.00	0.37
lichen								0.22
wood								0.15
Amanjenje (unid. liana)	0.07	0.00	0.07	0.00	0.00	0.00	0.00	0.07
Njamba2 (unid. liana)	0.00	0.00	0.00	0.07	0.07	0.00	0.00	0.07
Strombosiopsis tetrandra	0.00	0.00	0.00	0.07	0.07	0.00	0.00	0.07
soil								0.07
Teka (unid. liana)	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.07
Zanthoxylum lemairei	0.07	0.00	0.07	0.00	0.00	0.00	0.00	0.07
Unknown	0.07	0.00	1.04	0.07	0.14	0.07	5.99	7.26
								100.00

[b] Total number of tree and liana species in diet:

- 23 tree species identified or distinguished
- 3 tree groups, identified to generic level, which include 2 or more species [*Ficus* spp.; *Drypetes* spp. (Sungba) includes *D. bipindensis*; *Drypetes* spp. (Roko) includes *D. ituriensis*]
- 5 liana species, unidentified but distinguishable

Appendix 1.2. Chemical analysis of plant parts from tree and liana species in the Central Ituri Forest[a].

Family/species	Item	CP	ADF	TP	CT
Caesalpinioideae[b]					
Cynometra alexandri	yl	25.9	43.2	5.6	11.4
	ml	18.8	40.4	8.0	21.6
	us	22.8	--	0.9	2.2
Erythrophleum suaveolens	yl	27.5	50.0	1.8	8.8
	ml	13.4	33.2	10.5	36.3
	us	13.4	--	1.7	11.0
Gilbertiodendron dewevrei	yl	20.3	38.6	9.8	64.9
	ml	13.1	63.1	5.2	28.7
Cassia mannii	yl	17.5	26.7	11.4	61.7
	ml	11.2	29.5	7.5	40.0
	us	14.4	--	1.1	11.7
	rs	15.0	--	--	--
	fl	--	--	6.6	32.2
Amphimas pterocarpoides	fl	25.0	--	3.2	0.6
Mimosoideae[b]					
Albizia gummifera	yl	31.9	38.3	7.0	29.3
	ml	19.1	44.4	4.2	21.8
	us	42.2	--	0.3	3.7
Piptadeniastrum africanum	us	20.9	--	0.1	2.9
Papilionoideae[b]					
Angylocalyx pinnaertii	yl	24.4	12.8	2.3	57.6
	ml	17.2	38.7	1.7	30.6
	us	20.0	--	2.2	7.3
Ulmaceae					
Celtis mildbraedii	yl	32.8	21.0	1.0	0.0
	ml	15.6	26.9	2.6	0.0
Celtis zenkeri	yl	25.0	22.4	3.2	0.0
	ml	18.4	25.0	3.8	0.0
Celtis prantlii	ml	10.9	27.8	1.2	0.0
Euphorbiaceae					
Drypetes sp. (Sungba group)	yl	16.6	36.7	0.9	0.6
	ml	11.2	42.6	2.6	0.0

(Appendix 1.2, continued)

Family/species	Item	CP	ADF	TP	CT
Drypetes sp. (Roko group)	yl	13.1	52.5	2.9	0.0
	ml	12.5	44.8	1.8	0.0
	us	23.8	–	–	–
	rs	11.2	–	0.5	1.5
Margaritaria discoidea	rs	4.2	–	0.4	0.0
Discoglypremna caloneura	yl	17.5	38.6	–	–
	ml	14.6	37.5	4.7	28.2
Apocynaceae					
Alstonia boonei	yl	22.2	40.1	2.7	2.8
	ml	17.5	20.7	2.3	2.1
	fl	15.9	–	2.5	18.1
Rauvolfia vomitoria	rs	9.1	–	1.3	1.5
Moraceae					
Ficus sp.	yl	30.0	31.5	1.4	2.1
	ml	20.3	29.7	0.4	0.7
Milicia excelsa	ufr	16.9	–	6.5	27.8
	rfr	20.9	–	0.3	1.5
Tiliaceae					
Desplatsia dewevrei	yl	20.6	44.6	0.0	0.0
	ml	16.8	46.9	0.0	0.0
Olacaceae					
Strombosia pustulata	yl	18.1	54.3	0.0	2.1
	ml	15.3	53.8	2.7	2.1
	rs	18.8	–	0.4	1.2
Strombosiopsis tetrandra	rs	10.3	–	2.3	29.4
Sapindaceae					
Lecaniodiscus cupanioides	rs	9.1	–	6.4	6.1
Rutaceae					
Zanthoxylum macrophyllum	yl	19.7	19.8	3.8	2.9
	ml	22.2	22.2	1.4	10.4
Loganiaceae					
Anthocleista schweinfurthii	yl	22.8	29.3	2.5	1.4
	ml	14.4	42.3	0.6	0.0

(Appendix 1.2, continued)

Family/species	Item	CP	ADF	TP	CT
Irvingiaceae					
Klainedoxa gabonensis	yl	9.7	7.4	38.4	0.0
	ml	7.2	32.6	10.0	0.0
Rubiaceae					
Hallea stipulosa	yl	16.0	47.1	4.0	63.4
	ml	10.3	44.2	3.3	80.5
Dilleniaceae					
Tetracera sp.?	rs	9.1	--	2.5	60.0
Unknown					
Dikpolo (unid. tree)	yl	23.2	9.5	5.8	0.7
Njamba2 (unid. liana)	us	21.2	--	2.3	58.8
	rs	19.0	--	2.8	69.9

[a] Plant parts analyzed include young leaves (yl), mature leaves (ml), unripe seeds (us), ripe seeds (rs), unripe fruit (ufr), ripe fruit (rfr), and flowers (fl). Values represent percent dry weight for crude protein (CP), percent dry weight for acid detergent fiber (ADF), percent tannic acid equivalents for total phenolics (TP), and percent quebracho tannin equivalents for condensed tannins (CT).

[b] Caesalpinioideae, Mimosoideae, and Papilionoideae are subfamilies of the Leguminosae family.

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