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Ecology and Behavior of the Niger Delta Red Colobus
(*Procolobus Badius Epieni*)

BY

JAN LODEWIJK R. WERRE

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

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ABSTRACT

Ecology and Behavior of the Niger Delta Red Colobus (*Procolobus badius epieni*)

by

Jan Lodewijk R. Werre

Adviser: Professor John F. Oates

I studied the ecology and social organization of a group of red colobus in the Niger Delta, Nigeria. This population was new to science, being discovered in 1993. I conducted a survey that attempted to determine the red colobus distribution area, the condition of the forest, and socio-economic activities conducted in the distribution area. I found that the local population had already been exploiting the timber resources in the area for sale on the national market over more than two decades. As a result few sections of the forest remained in relatively undisturbed condition.

After selection of a study area a grid system a grid system was completed and a vegetation enumeration and two phenology samples, one for the swamp and one for the dry-land area, were established. Around the same time habituation of a red colobus group was started and the first of 12 monthly follows took place in September 1996.

Because the survey indicated that the red colobus distribution was restricted to only a small section of the delta I wanted to determine what, if any, ecological variables could be responsible for this. To achieve this I also established a vegetation enumeration and phenology sample in a section of forest near Ukubie, about 10 km from Gbanraun, where the red colobus did not occur. A comparison of these two forest blocks would assist in the identification of ecological variables that determine habitat availability in the Niger Delta.

A comparison of the two vegetation enumerations and phenology samples indicated that the forests were similar in terms of species composition and phenology, but that they differed in a number of spatial aspects. The forest in Ukubie showed lower densities for the top 10 species and less clumping. The forest in Gbanraun showed very high densities for the top three tree species, but lower densities for the remaining species. The most common large tree in both Gbanraun and Ukubie was not only more common, but also showed a more clumped distribution at Gbanraun. As a result the forest at Gbanraun contained a larger number of *Ctenolophon* (a tree which young leaves provided around 40% of the study group's diet) food patches.

The data collected on the behavior and ecology of the study group indicated that they were similar in behavior and ecology to other populations inhabiting rain forest. The greatest deviation this population showed from the observed red colobus patterns was that this group traveled significantly longer distances during each month.

A number of patterns in feeding behavior and range use were detected which all indicated that *Ctenolophon* food patches played a central role in the study group's ecology. This confirmed that Ukubie was unavailable for the red colobus because it lacked these patches, or patches of other species that could have performed the same role.

It is suggested, therefore, that the presence of food patches is a requirement for red colobus habitat availability, and that this explains the gaps, which lack these food patches, in the red colobus distribution.

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: DISTRIBUTION SURVEY

CHAPTER 3: DESCRIPTION OF STUDY SITES

CHAPTER 4: METHODS

CHAPTER 5: VEGETATION OF THE STUDY SITES

CHAPTER 6: FEEDING BEHAVIOR

CHAPTER 7: RANGE USE

CHAPTER 8: SOCIAL BEHAVIOR

CHAPTER 9: DISCUSSION

APPENDIX

LIST OF TABLES

LIST OF FIGURES

LIST OF MAPS

CHAPTER 1

INTRODUCTION

1.1. Introduction

The population of red colobus monkeys (*Procolobus badius epieni*) in the Niger Delta was not discovered by science until 1993 (Powell, 1993). As a result two tasks had to be completed before the actual study of the behavior and ecology of, as well as a conservation effort for, this monkey could be initiated. The first task was to survey and establish the distribution area and status of the Niger Delta red colobus population. The second task was the selection of a suitable study site.

The proposal drafted for this study placed a strong emphasis on conservation because initial observations indicated that the population was already under heavy pressure. It was, therefore, planned to investigate not only the status of the Niger Delta red colobus, but also to pay close attention to sources of human pressure on the population. These data would then be used to identify suitable conservation areas for the Niger Delta red colobus, or *epieni* in the local Ijaw language, and its associated ecosystem. During the survey it soon became clear, however, that the forest in the central Niger Delta had been degraded to such an extent that there were very few relatively undisturbed areas remaining where a conservation effort might be possible.

My initial survey also indicated that the Niger Delta red colobus has an unusual distribution. This monkey occupies only the delta's central sector, and is absent in other sections of the delta that appear to be ecologically similar. These observations made me aim this study to an investigation of a number of ecological variables hypothesized to be responsible for the discrete distribution boundaries.

The earliest field studies of primates indicated the important role ecology played in the development and maintenance of social systems. Crook and Gartlan (1966) made the first attempt to understand differences in primate social organization in terms of their ecology, an effort continued by others (Crook, 1970; Eisenberg *et al.*, 1972; Altmann, 1974). It soon became clear, however, that there was no simple link between variation in social systems and differences in environment (Struhsaker, 1969; Rodman & Cant, 1984). It was evident, though, that ecology, and specifically the distribution of food in time and space, influenced social organization, although this relationship was complex (Clutton-Brock & Harvey, 1977; Oates 1987).

Red colobus populations clearly illustrate the complexities associated with explaining the relationship between ecology and behavior. These monkeys occur in a great variety of habitat types and show considerable variation in group and home range size. Most populations live in relatively species-rich and aseasonal environments, where they generally have large group sizes (averaging around 40 to 50 members). A number of other populations inhabit species-poor and strongly seasonal environments and they have generally smaller group sizes (averaging around 15 to 25 members). All groups, however, despite inhabiting different habitats, show varying degrees of overlap for group size and other aspects of their behavior and ecology (Struhsaker, 1975; Marsh, 1978, 1979*b*; Starin 1991; Oates, 1994*b*).

Past efforts to develop a better understanding of how environmental variables determine red colobus behavior have included a number of studies that compared sympatric colobine species (Struhsaker & Oates, 1975; Clutton-Brock, 1975*a*; Maisels *et al.*, 1994; Davies *et al.*, 1998.). Despite the longstanding recognition that studies comparing the diet of the same species at more than one location (how can observed dietary variation be explained in terms of available of potential foods) few have been conducted for colobines (Oates, 1977; Marsh, 1981*a,b*). Of the few available studies the majority make a comparison between either widely separated sites (McKey *et al.*, 1981; Oates *et al.*, 1990; Kay *et al.*, 1997), or within the same site but comparing disturbed and undisturbed environments (Mitchell, 1994; Struhsaker, 1997; Siex & Struhsaker, 1999). A recent study of red colobus in six areas in or near Kibale National Park, Uganda is the first available study to compare variation in the diet of the same species at more than one location (Chapman & Chapman, 1999). Chapman & Chapman's (1999) small-scale comparison indicated large differences in diet and behavior of the red colobus between the different sites. Though this type of study is useful in determining the degree of variation possible in a species' activity budget, it is less likely to identify those environmental variables likely to determine the presence or absence of a species that determine habitat availability. The identification of these variables is best achieved through a comparison of sites, within the same forest block, where the study species does and does not occur.

1.2. Specific Aims

The focus of my research was to determine the habitat requirements of the Niger Delta red colobus.

The specific aims of the study were as follows:

- To collect data on the social organization of a group of Niger Delta red colobus.
- To describe the ecology of a group of Niger Delta red colobus, with an emphasis on diet and ranging behavior.
- To describe the research area's flora, and compare it with respect to species composition, structure, and phenology with a forest located just outside the boundary of the red colobus distribution area.
- To identify, using the ecological differences observed between the two forests, those variables that might be responsible for the red colobus' present distribution.
- To compare the obtained results with observations for other populations in order to discern generalities in habitat requirements for red colobus.

1.3. Discovery of the Niger Delta Red Colobus

In 1993 a previously unknown population of red colobus monkeys (*Procolobus badius*) was discovered in the Niger Delta during a survey of the distribution of larger mammals conducted for the Nigerian Natural Resources Conservation Council (NARESCON) (Powell, 1993). This survey uncovered a number of species new to the delta or even Nigeria, and most surprisingly a population of red colobus, now considered to be a new subspecies, *Procolobus badius epieni* (Grubb & Powell, 1999). The first locality where specimens were collected was the village of Gbanraun (4° 47' N, 5° 35' E) in Southern Ijaw Local Government Area (SILGA) in what was then Rivers State. In 1997 the Federal Government created a number of new states and the section where the red colobus is found became Bayelsa State.

At the beginning of 1994 a group of primatologists made the first observations of these red colobus during a visit to Gbanraun, where they observed three different groups (Oates, 1994). In July 1994 I visited the Niger Delta in order to determine the Niger Delta red colobus' distribution and status, and to investigate the possibility of conducting a long-term study of their behavior and ecology. I returned at the end of 1995 to complete the survey, after which a study site was located where a group was studied from September 1996 through August 1997.

1.4. Background on Red Colobus Monkeys

1.4.1. *Taxonomy and distribution*

The African colobines can be separated into two genera: *Colobus*, which are the different forms of black-and-white colobus monkeys, and *Procolobus* containing both the red colobus group and the olive colobus. A number of authors (Hill & Booth, 1957; Kuhn, 1967; Brandon-Jones, 1984; Strasser & Delson, 1987; Groves, 1989; Oates *et al*., 1994*b*) have suggested that the olive colobus is sufficiently distinct from the red colobus group to warrant the separation of *Procolobus* into two subgenera: *Piliocolobus* for the red colobus and *Procolobus* for the olive colobus.

Most taxonomists recognize 14 -17 different forms in the red colobus group: *badius*, *temminckii*, *pennantii*, *kirkii*, *rufomitratus*, *tholloni*, *bouvieri*, *foai*, *gordonorum*, *preussi*, *oustaleti*, *tephrosceles*, *ellioti*, and *waldroni* (Rahm, 1970; Oates *et al*., 1994*b*). Further work on the red colobus of the Congo Basin by Colyn (1991) suggests that a number of subspecies there have been overlooked. The *ellioti* subspecies can be separated into the *langi* and *semlikiensis* subspecies, while the *foai* subspecies also contains *lulindicus*. However, red colobus taxonomy is far from being resolved. Apart from differences of opinion on the number of forms present, there is presently also no consensus on the number of species encompassed by the red colobus group. Some taxonomists recognize only one species (Rahm, 1970) while others recognize up to five species (Dandelot, 1971; Oates, 1986). Though the red colobus group shows more diversity than can be contained within a single species concept, the present lack of consensus on the most appropriate classification favors a continued use of Rahm's (1970) classification (Oates *et al.*, 1994*b*).

The red colobus group's diversity is reflected in their distribution. They occur from the Senegambia through the Guinean forest belt into the Congo Basin and via forest islands in East Africa into Zanzibar (**Map 1.1**, p. 19). Their distribution over this large area is, however, patchy. The largest gaps occur between western Cameroon and the Central African Republic (Congo Republic), and between western Ghana and the Niger Delta. Though the red colobus occurs in the East African region its distribution here is extremely patchy.

1.4.2. *Red colobus field studies*

For only six of the 14-17 different forms of red colobus have field studies of a duration of one year or more been conducted: *P. b. tephrosceles* in Kibale, Uganda (Struhsaker, 1974, 1975, 1978, 1981; Struhsaker & Leland, 1985; Struhsaker & Pope, 1991; Isbell, 1984; Chapman & Chapman, 1999), and Gombe, Tanzania (Cluton-Brock, 1972, 1974, 1975*a*, 1975*b*; Stanford, 1995, 1998); *P. b. rufomitratus* on the Tana River, Kenya (Marsh, 1978, 1979*a*, 1979*b*, 1981*a*, 1981*b*, 1981*c*; Decker, 1989, 1994); *P. b. badius* at Tiwai, Sierra Leone (Oates, 1994*b*; Davies *et al.*, 1998); *P. b. temminckii* at Fathala, Senegal (Gatinot, 1975, 1977), and Abuko, Gambia (Starin, 1981, 1991); *P. b. kirkii* at Jozani, Zanzibar (Mturi, 1991, 1993; Siex, 1995; Struhsaker *et al.*, 1997; Siex & Struhsaker, 1999*a,b*); and *P. b. tholloni* at Salonga, Democratic Republic of the Congo (Maisels *et al.*, 1994). These different study locations reflect the large variety in red colobus habitat; Kibale, Tiwai, and Salonga have moist forest (more than 1500 mm precipitation with a short dry season) with which the monkeys are traditionally associated. The other locations though, all show more seasonality, varying from riverine forest at Tana, riverine forest and Sudanese savanna at Fathala and Abuko, to a mixture of coral rag, flood forest, and mangrove on Zanzibar.

1.4.3. *Social organization*

All studies, as well as more casual observations, confirm that red colobus generally live in large groups. Group size can range from 12 on the Tana River (Marsh, 1979*a*) to more than 80 animals in Kibale (Struhsaker, 1975), but typically consists of between 24 and 40 monkeys. The larger group numbers appear to be associated with moister habitat (Struhsaker, 1975).

Groups nearly always contain more than one male and many females, which commonly outnumber the males 2:1. The exception is on the Tana River in Kenya, where single-male groups were encountered (Marsh, 1979*a*). Both adult and juvenile red colobus females change groups more freely than males who appear to be the more stable elements of the group (Marsh, 1979*a,b*; Struhsaker & Leland, 1979). An exception to this pattern was observed by Starin (1991) who observed that the majority of both males and females left their natal group. Adult females groom one another relatively little, while adult males groom each other more often. The relatively high level of social interaction between males could indicate that the males in one group are related, which is also reflected by the cooperation that they show each other during aggressive encounters (Struhsaker, 1975; Struhsaker & Leland, 1979). Again the group studied by Starin (1991) deviated significantly from the general pattern. Not only did adult males hardly groom each other, but they also showed less pronounced cooperation during intergroup encounters.

1.4.4. *Ecology*

Early studies of red colobus indicate that leaves, especially young leaves, form the most important component of their diet (Clutton-Brock, 1972; Struhsaker, 1975). The red colobus' possession of a chambered stomach, which allows for the breakdown of cellulose by microbial fermentation (Bauchop & Martucci, 1968), and possibly the detoxification of plant defense compounds allows for this high degree of folivory (Freeland and Janzen, 1974; Waterman & Kool, 1994). Subsequent studies have indicated, however, that though young leaves are usually the single most important food item, other items such as unripe seeds and fruits, and flowers and floral buds can also form a significant portion of the yearly diet (Maisels *et al.*, 1994; Davies *et al.*, 1998) Diversity of the number of plant species in the diet can vary considerable, ranging from 22 (Marsh, 1981*b*) to 89 (Starin, 1991). This variation may be the result of differences in species composition between sites and associated differences in food item availability.

Though the activity budget of red colobus varies from site to site, most studies show some similarity. The highest proportion of the monkey's time is spent either resting (31-61%) or feeding (25-47%), while moving (4-13%) and other activities, including social interactions and play (3-12%) take up the remainder of their time. The differences in the activity budgets may be the result of differences in habitat but could also be the result of significant differences in the group members' behavior (Oates, 1994*b*).

Groups are generally tolerant of one another but there appears to be a dominance hierarchy among groups with overlapping home ranges, that can supplant one another based on the number of males in the group (Struhsaker & Leland, 1979). Other studies, however, indicated little home range overlap and avoidance of intergroup encounters (Gatinot, 1975; Marsh, 1979*b*; Stanford, 1998). The lack of an adult male red colobus loud call may be an indication of the general peaceful coexistence of neighboring groups.

Red colobus home ranges can show considerable variation in size. On the Tana River one group had a mean home range size of 9 ha while a group in Kibale had a mean range size of 65 ha (Struhsaker, 1975). The large variety in habitat, as well as the varying degrees of group overlap, makes it difficult to discern a particular pattern in range use, but the distribution of food items in space and time is likely to play an important role.

Red colobus have a graded vocal communication system reflecting the importance of intragroup communication in their large groups (Marler, 1970).

Female red colobus can display a pronounced swelling of the perineal region, but a large degree of variation between populations has been observed. The size of the swelling can range from very small as for *P. b. tephrosceles* to huge as for *P. b. preussi* where the swelling can be larger than 25% of the total body volume (Struhsaker, 1975;

Oates, 1994*b*). Though the swelling is periodic it has been difficult to determine if it is correlated with sexual receptivity. Two studies (Struhsaker, 1975; Starin, 1991) suggest, however, that this is the case. Dominant adult males appear to perform most of the copulations which may be the result of male-male competition and/or female choice (Struhsaker, 1975; Starin, 1991). Females of *temminckii*, *badius*, and *preussi* produce quaver calls during copulation but in Kibale *tephrosceles* males only give quaver calls when harassing other pairs copulating (Struhsaker, 1975; Starin, 1991; Oates, 1994*b*). In seasonal environments there appears to be a birth pattern with the majority of births occurring at the beginning of the dry season (Starin, 1991). In areas with a less seasonal environment the occurrence of birth peaks becomes less distinct (Struhsaker & Leland, 1987).

The newborn infants have different coat coloration from adults, but the pattern varies from one subspecies to another (Struhsaker, 1975). Mothers rarely, if ever, allow other females to handle or carry their young infants.

1.5. Ecology of the Niger Delta

1.5.1. *General description*

The Niger Delta extends south from Aboh (5°33'N, 6°31'E) to the Benin River (5°44'N, 5°04'E) on the west, and the Imo River (4°27'N, 7°35'E) in the east. The total area of approximately 25,000 km^2 is contained within three states, Rivers, Bayelsa, and Delta, of the Nigerian Federation (**Map 1.2**, p. 20).

The depression through which the Niger River runs developed during the middle to upper Cretaceous as the result of subsidence of a part of the African shield. Although the contemporary Niger River system was not established until some time during the Quaternary, the Niger Delta is the product of both fluviatile and marine sediment build-up since the upper Cretaceous. The delta shows some relief that is responsible for the meandering and frequent shifting of the Niger and its branches. Over time the decreasing slope gradient of the Niger River bed and associated lower stream velocities has resulted in an increase of tidal activity in the exits of the numerous Niger branches, resulting in the formation of the coastal barrier islands (NEDECO, 1961, 1966).

The climate in the Niger Delta is characterized by a long rainy season from March-April through October. Precipitation levels increase when moving from the most northern part of the delta (1000-2500mm) to the coastal area, where the study site is located, which has a mean annual precipitation fluctuating between 1600-4000 mm, making it one of the wettest areas in Africa. At the study site the wet season peaks in July, at a monthly mean of about 700 mm, after which a month long, relatively dry spell follows, with monthly mean rainfall of about 250 mm. The only real dry months are January and February but even during this period an average monthly mean of 150 mm is recorded in the delta's wettest parts. Unfortunately no measurements at the study site were taken because it proved to be impossible to monitor a rain gauge accurately for the whole period of the study. [This was because I had no assistant available to monitor the gauge accurately during my absence, and the heavy rainfall often exceeded the capacity of the available rain gauge after two to three days.] Relative humidity in this part of the delta rarely dips below 60% and fluctuates between 90% and 100% for most of the year.

During most of the rainy season cloud cover is nearly continuous resulting in 1500 mean annual sunshine hours and an average annual temperature of approximately 28° C (Ojo, 1977; Barbour *et al.*, 1982).

Presently there is little information available on the delta's ecology. Most of the data relate to fish, with little or nothing on the remainder of the flora and fauna. Happold's (1987) *The Mammals of Nigeria* is the standard work available for the mammals of Nigeria, but it includes only a few records actually obtained in the Niger Delta.

Surveys for wildlife in the delta were not conducted until the late 1980's, and focussed mainly on primates in the Taylor Creek and Oguta areas (Anadu & Oates, 1988; Oates, 1989; Werre, 1991; Oates *et al.*, 1992). During these surveys the presence of five diurnal primate species (*Cercopithecus mona*, *C. nictitans*, *C. erythrogaster*, *Cercocebus torquatus*, and *Procolobus verus*) was confirmed. The first survey for all larger mammals and all sections of the Niger Delta was conducted by Powell (1993, 1995). The discovery of a number of new species for the delta, and even Nigeria, during both Oates' (1989) and Powell's (1997) limited surveys is a good indicator of the paucity of biological data for the delta. Currently some patterns are emerging but much work is still required to provide a clearer picture, especially on the population status of different species.

The most important determinant of biological variation in the delta is its hydrology. In addition to precipitation, the major determinants of variation in the hydrological regimen are the Atlantic Ocean's tidal movements and the associated salt/brackish water zone, and the Niger flood. This flood begins toward the end of the rainy season in August, peaks in October, and tapers off in December. Some fluctuation is determined by the yearly variation in rainfall, but after the completion of the Kainji dam in the Niger at Bussa in 1968 the timing and level of flooding is also determined by the opening and closing of the dam's sluices. Though the level of flooding decreases going downstream into the delta, the water level still rises approximately 3 m in the area where the study was conducted.

Based mostly on variations in the presence/absence of tidal movement and/or the Niger flood, three major ecological zones can be recognized; the coastal barrier islands, mangrove, and freshwater swamp forest. Of these three zones, the freshwater forest can be further subdivided into three regions (**Map 1.3**, p. 21) (Powell, 1995). Preliminary *ad lib*. observations of the delta's forest vegetation suggest that a number of tree species can be found over most of the delta but, depending on the area's hydrology, at different densities. **Table 1.1** (p. 18) lists a number of species observed at most locations visited, but further systematic studies of the vegetation need to be conducted for a more accurate description.

1.5.2. *Coastal barrier islands*

The coastal barrier islands are large sand banks along the Atlantic Ocean's coast covered with freshwater forest. The perimeter generally consists of a narrow band of mangroves, but the interior consists of swamps, which are only fed by rainwater, supporting freshwater forest. During the survey the largest coastal barrier island was crossed and many of the same tree species observed in the other freshwater swamp forest zones were observed (*Sacoglottis gabonensis, Hallea ledermannii, Symphonia globulifera*), but at different densities.

Powell (1995) indicates that the fauna of the different coastal barrier islands varies considerably, which might also be the case for the flora. It appears, however, that the faunal and floral assemblages on these islands are poorer than those of the inland freshwater swamp forest. The islands definitely warrant further investigation, not only because some harbor relic populations of elephant, hippopotamus, and possibly chimpanzees, but also because the forest on some islands appears to be less affected by human activities then in the rest of the delta.

1.5.3. *Mangrove zone*

The vegetation of the mangrove zone consists mainly of a few Rhizophoraceae species (*Rhizophora racemosa, R. harrisonii, R. mangle*) and is generally species poor. Mangrove areas are often considered to show little variation. In the delta, however, a large number of freshwater swamp forest islands dot this zone, and even in the mangrove area itself distinct variation in regeneration rates and associated fauna make it less homogeneous than is often assumed (Powell 1993, 1995). *Cercopithecus mona* appears to be the only monkey inhabiting this, apparently the best preserved ecological zone of the Niger Delta.

1.5.4. *Freshwater swamp forest zone*

This zone can be subdivided into a number of sub-zones based on hydrological variation. Each zone appears to be characterized by its own particular floral and faunal assemblage, but faunal and floral zones do not always overlap. These divisions are based on Powell's (1995) work (which provides the only available information) but, due to the lack of systematically collected data, they should be considered tentative. As work progresses and more information on the delta's ecosystem is collected, boundaries are likely to shift, and new sub-zones to be identified.

- Flood Forest Zone: This zone shows strong seasonal variation. During the dry season the soil is dry save for the seasonal flood channels, a few permanent creeks, and some lakes. During the rainy season water levels slowly rise, eventually leading to complete inundation during the Niger River flood, which lasts generally from October through December. Some of the more common tree species here are *Sacoglottis gabonensis*, *Uapaca* spp., *Irvingia gabonensis*, *Klainedoxa gabonensis*, *Treculia africana*, and *Ficus vogeliana*.

  This zone was the habitat of Niger Delta pygmy hippopotamus, and in the Taylor Creek area there are still a few members of a once large elephant herd (Werre, 1991). The pygmy hippopotamus is probably now extinct though some rumors of its continued presence persist.

- Eastern Flank: A thorough investigation of the delta's hydrology indicated that the more westerly situated waterways have been growing in size at the expense of those in the east (NEDECO, 1961). As a result the Orashi, the most easterly situated river in the Niger drainage, decreased steadily in size and started to silt up. Presently the Orashi River receives very little of the Niger flood and continues to decrease in size.

  The eastern flank is thought to have been flood forest when the Orashi River was still a major distributary of the Niger, but started to change in composition as the river's importance in the Niger's drainage system decreased (Powell, 1995). However, no work in the area has been conducted to confirm this, and the present assumptions are based on reports of faunal similarities with both the flood forest zone (reports of the Niger Delta pygmy hippopotamus presence) and the presence of what Powell (1995) considers lowland forest non-swamp species (Ogilby's duiker and Sclater's guenon).

- Marsh Forest Zone: This zone is where the red colobus as well as another new mammalian record for Nigeria, the black-fronted duiker, occur. The zone can again be subdivided into a section that is not influenced by the Niger River's flooding where the red colobus occurs, and a section that is influenced by the flood where they are absent. Though this zone does show variation in tree species composition, *Uapaca* spp., *Hallea ledermannii*, *Klaineanthus gaboniae*, and *Xylopia* spp. are in most places the most important contributors to the canopy. Closer to the mangrove zone *Ctenolophon englerianus* becomes the most common large tree. The understory is dominated by *Raphia* spp. that, mostly in the western half of this zone, can form large single-dominant forests.

This study was conducted in the marsh forest zone, and a vegetation enumeration was conducted for both sub-divisions. A detailed description is presented in **Chapter 6**.

1.6. Summary

Even though available information on the Niger Delta's ecology is still far from complete some patterns are emerging. The Upper Guinea and Lower Guinea flora and fauna, which were once considered to be separated by the Dahomey gap, overlap in the delta. It contains outlier populations of some species from each of these floras and faunas, and the presence of the Niger Delta red colobus confirms Grubb's (1990) suggestion that the delta is a small center of endemism. The traditional view that the Niger is a significant zoogeographical barrier is incorrect, and the situation in reality is far more complex since the delta definitely allows species to move from one side to the other (Happold, 1987; Powell 1995).

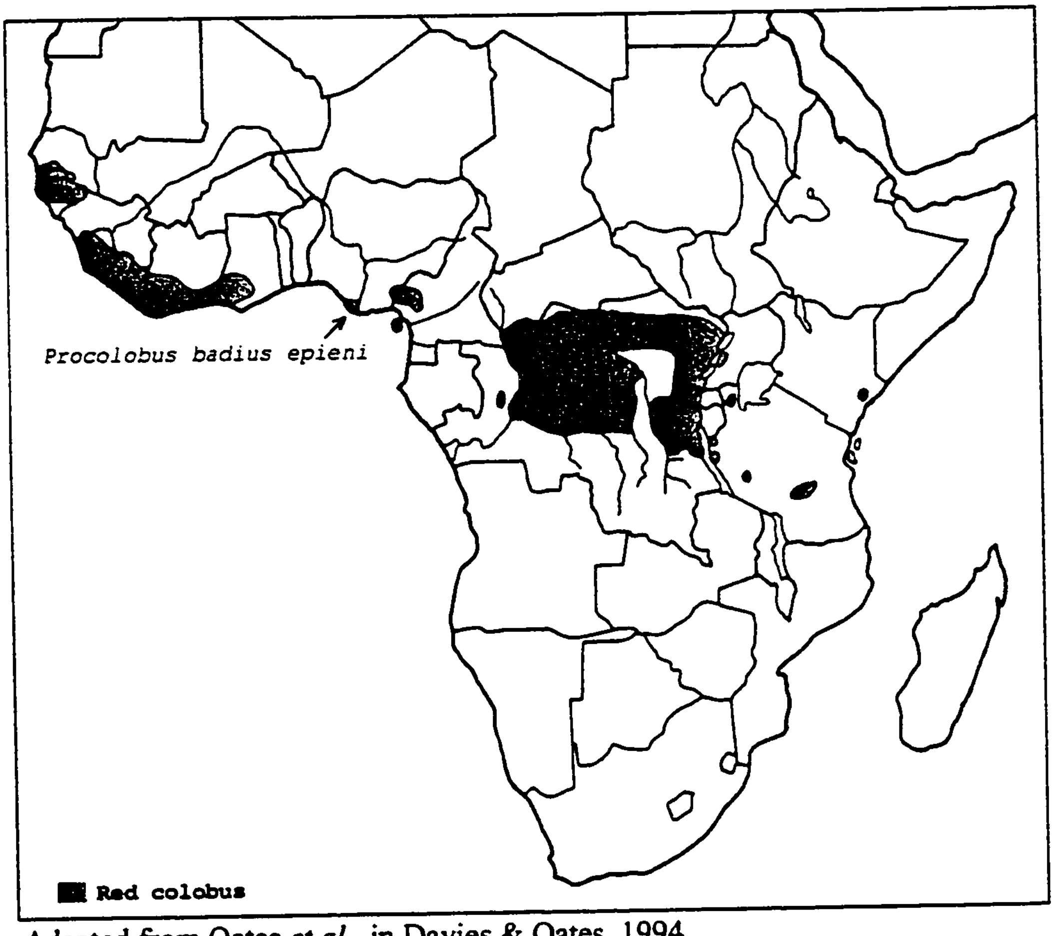
Though some patterns, mainly based on known hydrological variation, indicate that the delta can be divided into a number of different ecological zones, much work to confirms this remains to be done. The flora of the delta definitely requires further investigation before less tentative divisions can be made. Even though most of the tree species found in the delta occur in the upper and lower Guinean rain forest the delta's floral assemblages appear to be unique.

Table 1.1: *Tree species common throughout the delta's freshwater swamp forests.*

SPECIES	FAMILY
Cleistopholis patens	Annonaceae
Xylopia spp.	Annonaceae
Pycnanthus spp.	Myristicaceae
Symphonia globulifera	Guttiferae
Pentadesma butyracea	Guttiferae
Ceiba pentandra	Bombaceae
Sacoglottis gabonensis	Humeriaceae
Anthostema aubreyanum	Euphorbiaceae
Uapaca heudelotii	Euphorbiaceae
Erythrophleum ivorense	Ceasalpinioideae
Klainedoxa gabonensis	Irvingiaceae
Irvingia gabonensis	Irvingiaceae
Elaeis guineensis	Palmae
Raphia hookeri	Palmae
Raphia vinifera	Palmae

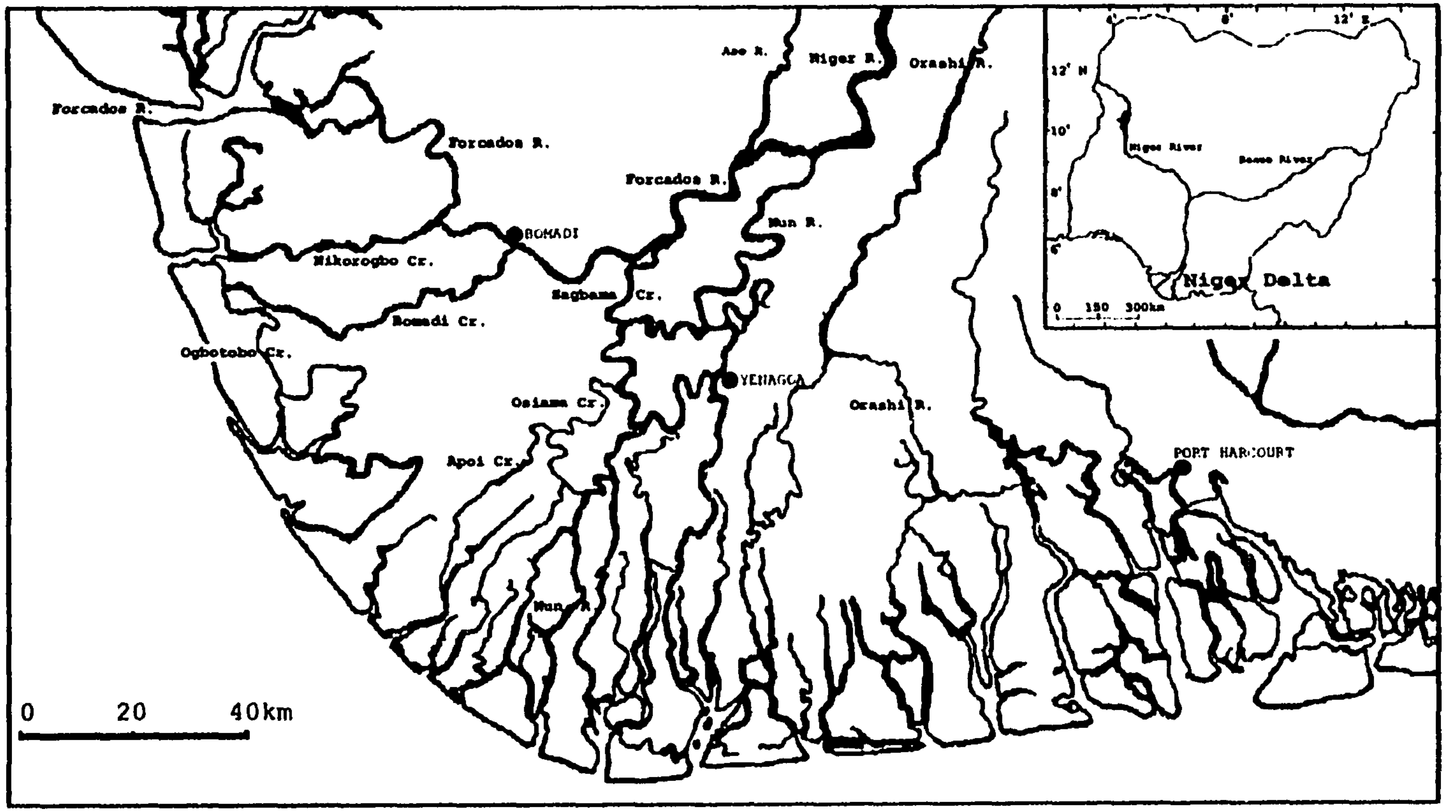
This table is based on *ad lib.* observations. Once vegetation enumerations in other sub-zones of the delta have been conducted significant changes are to be expected.

Map 1.1: *General Distribution Map of Red Colobus*



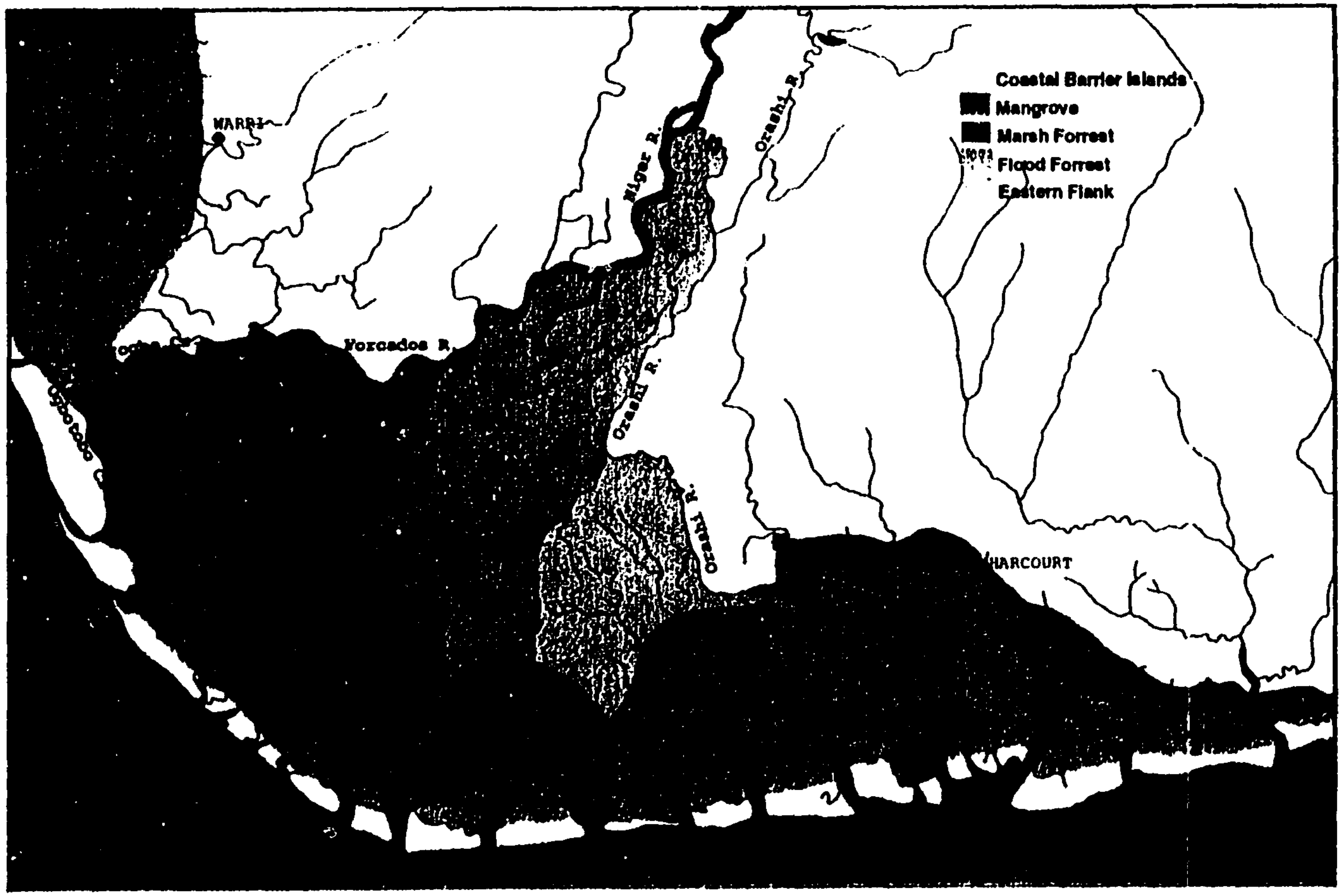
Adapted from Oates *et al.*, in Davies & Oates, 1994.

Map 1.2: *Nigeria and the Niger Delta*



Adapted from NEDECO, 1961 & Happold, 1985.

Map 1.3: *Ecological Zones of the Niger Delta*



Adapted from Powell, 1993.

CHAPTER 2

DISTRIBUTION SURVEY

2.1. Introduction

A list of plant and animal names in the different Ijaw dialects of the Niger Delta compiled by K. Williamson (in Powell, 1993) listed a number of names for monkeys not yet matched to a species. Though some of these names reflect dialectical differences and referred to a known species, one name stood out, *epieni*. During the NARESCON (1993) survey C.B. Powell received a skin from a freshly killed primate that was identified by the hunter who shot it as *epieni*. Powell (1993) identified the skin as belonging to a red colobus monkey, a species for which, up to this point, not a single record of its presence in the Niger Delta existed. Soon after the discovery of red colobus at Gbanraun further reports were received of their presence in other parts of the delta, indicating that their distribution was most likely restricted to the central delta. So far point only skins were collected and none of the NARESCON staff had actually observed the monkeys. In 1993 C. B. Powell contacted J. F. Oates in New York informing him of his discovery. As a result a small expedition to Gbanraun was organized where the red colobus was finally observed (Oates, 1994*a*).

Now it was confirmed that red colobus indeed occurred in the delta, I could initiate a study project, but would have to take a number of steps before an intensive study of the ecology of the Niger Delta red colobus could commence. First a survey was conducted to establish red colobus distribution boundaries, investigate the condition of the forest, and assess the human activities affecting the red colobus population. This chapter describes the information collected during the survey.

2.2. Methods

C. B. Powell, who had been collecting information on locations where the red colobus were present, was consulted in Port Harcourt, Nigeria. Maps were obtained of the area where the red colobus monkeys had been reported. I was also allowed to, briefly, examine satellite imagery for the identification of large, undisturbed, forest blocks. Using this information two different categories of locations were identified: a) locations that were reported to harbor a red colobus population and/or relatively undisturbed forest, and b) locations that appeared to be located on the boundaries of the red colobus distribution area. During a preliminary survey of July 1994, and an extensive survey from December 1995 through February 1996, 19 locations were visited (**Map 2.1**, p. 51, see also **Table 2.1**, p. 47).

Travelling in the Niger Delta is both complicated and expensive. The road system stops at the edge of the delta and further travelling must be done by boat. Due to the high costs associated with this mode of transport I could not afford to hire my own boat and was forced to join the regular passenger boats, which often resulted in long delays. Moreover, some of the locations visited were so remote that boat changes in the interior of the delta would be required which often resulted in delays of a number of days.

Once I arrived in a village, community leaders would be informed of the reason for my visit. I then asked them to identify the most competent hunters for interviews, and I asked for permission to enter their forest for a survey. During the interviews information was obtained on the presence and distribution of larger mammals. The primates of the Taylor Creek area, which I had surveyed in 1989 and 1990 (Werre, 1991), were confirmed by Powell's (1993) survey to be widely distributed in the delta, but I sought to more precisely determine their distribution. Hunters were asked to provide animal names in their own language (a number of different dialects of Ijaw) that were then checked against a list of native animal names compiled by K. Williamson (in Powell, 1993). If the hunter did not speak English (they nearly always did) an interpreter was used. Apart from providing the animal names, hunters were also asked to describe both the appearance (size, coat color patterns) and characteristic behavior of the primates they indicated as present. Next I showed illustrations in field guides (Dorst & Dandelot, 1970; Haltenorth & Diller, 1980) to see if they could identify the animals they had mentioned. At the locations that were thought to be on the boundary of the red colobus distribution area an extra effort was made to determine the exact locations where the monkeys occurred, and whether this had always been the case. For this purpose I also attempted to interview the community's oldest inhabitants in an effort to determine if the present distribution boundaries were a relatively new phenomenon. During the second part of the interview I attempted to identify which human activities were undertaken in the forest.

At the end of the interview the hunter who appeared most competent was asked to show me the least disturbed part of the forest where it would be possible to observe primates, especially red colobus. The forest was then surveyed on foot and/or by canoe. On most of the surveys only one hunter was used, and on no occasion were they allowed to bring any hunting equipment. During the surveys on foot existing trails were used, while the surveys by canoe generally followed the great many canals that loggers had dug into the forest to evacuate cut trees. When primates were located they were observed with 10x40 binoculars and notes were made of the species identity, number seen, and behavior. Sightings and tracks of other mammals were also recorded, as well as the condition of the forest for the whole length of the survey (see **Appendix 1** for all mammals recorded in the Niger Delta). *Ad lib.* observations on forest composition were also collected. Any sign of human activity in the forest was recorded, the type of activity identified, the relative importance of, and the apparent impact on the forest, determined.

The observations made during my forest surveys led me to conclude that the information provided by the hunters during interviews was generally reliable. However, minor inaccuracies no doubt arose from the fact that many hunters did not have a great deal of experience.

2.3. Survey Findings

My survey indicated that the forests of the Niger Delta are under heavy human pressure. Most communities had already exhausted all valuable timber species on their lands. The only large, undisturbed, section of forest encountered was the beach ridge island behind Ogbotobo, but this is situated outside the red colobus distribution area.

The delta's inhabitants fish mostly to sustain themselves, and sell or barter their surplus for cassava, yams and other agricultural products which can not be grown in the delta. Due to the delta's rapidly increasing population demand is outstripping the fish population's productivity, with the result that fish are now imported from other areas in some sections of the delta. Until recently hunting pressure in the delta has been low, and mammal populations had probably been affected more by habitat disturbance than by hunting. Recently this situation has begun to change (see p. 48).

Table 2.1 (p. 47) lists the localities and the dates they were visited. The number of each village corresponds with the numbers on **Map 2.1** (p. 51). **Table 2.2** (p. 48) lists all diurnal primate species identified by interviewed hunters at each location. All areas surveyed fell within the red colobus distribution area unless otherwise indicated. What follows is a more detailed description of my observations at each location.

2.3.1. *Sampou*

This small town is located approximately 5 km from the Apoi Creek and can only be reached by a 1.5 hour trip on foot or by dug-out canoe during the rainy season. The town itself consists of no more than about 30 houses and is without any amenities.

Two separate surveys of the forest were undertaken here. The first, on foot, examined the dryer parts of the forest, while the second survey, by canoe, covered the large swamp surrounding most of the village. The survey on foot passed first through about 0.5 km of small farms after which the forest was reached. Once there it soon became clear that extensive logging was taking place. My guide attempted to create the impression that the forest was in good condition by making a circle in a small section of unlogged forest. Outside this section, however, the remainder of the forest had been logged extensively. No primates were seen, but a group of *Cercopithecus mona* was heard. No large mammals were seen, but some tracks of unidentified duiker(s) and red-river hog (*Potamochoerus porcus*) were observed. Upon return to the town further inquiries indicated that all forest on community land had been logged, and that the only opportunity to observe red colobus would be in the swamp. The following day the swamp was entered by canoe, using the numerous logging canals. These canals were filled with hundreds of logs waiting to be transported to the main creek. After about 2 hours during which an estimated distance of 2 km was covered a group red colobus was encountered. The group was very wary and only five individuals were observed, but the motions in the trees indicated that the group must have contained at least 30 monkeys. Unfortunately few vocalizations were heard, and the group fled rapidly. No other primate species were encountered.

Apart from some farming on the few drier spots around the town, human activities here are restricted to fishing and logging.

2.3.2. *Azama*

Azama has a school but no other amenities. The forests around this village had been logged even more extensively than the forest in the vicinity of Sampou. A short trip into the forest indicated that the swamp where red colobus could be encountered was the same swamp that had already been surveyed from the Sampou side. Though hunters interviewed claimed that red colobus were still present, they said they occurred only in very small numbers far from the town. Because this community is situated on the Apoi Creek, which was identified as a possible distribution boundary, an extra effort was made to determine the red colobus' distribution in this area. Every report, including those of older residents, confirmed that the red colobus had always occurred on the west (town) side of Apoi Creek.

The investigation into the presence of other large mammals resulted in a hunter giving me part of a duiker's cranium that included the horns and forehead. Upon return to Port Harcourt the duiker was identified as *Cephalophus nigrifrons*, the black-fronted duiker, which previously was known only from southern Cameroon eastward (Ansell, 1971; Dorst & Dandelot, 1970).

The main human activities in this community are fishing, logging, and some farming. Logging is presently decreasing in importance due to exhaustion of the surrounding forest's commercial species.

2.3.3. *Ogboinbiri*

Ogboinbiri's location next to an oil company's installation makes it a popular village with the surrounding population. This is, with Ukubie, the largest community on the Apoi Creek, with the result that the surrounding forest has been seriously damaged. All commercial tree species have been logged and the forest in the drier areas has been felled for farms.

Hunters indicated that red colobus are present, but that they were now only found at a few locations far from town. A survey by canoe was conducted which followed an approximately 2 km long slot, dredged by an oil company to reach a well point. At the end of the slot a short trip through the forest on foot indicated that the forest here had already been severely degraded because the slot allowed for easy evacuation of logs. Though it is possible that red colobus still occur here none were encountered. Only traces of the activity of brush-tailed porcupine (*Atherurus africanus*) and the tracks of a few unidentified duikers were observed. Inquiries about the distribution of red colobus in the area also indicated that the red colobus here also only occurs on the west (town) side of the Apoi Creek.

The village inhabitants' most important economic activity is fishing. Farming and working for the many oil-industry related projects on community land also provide some income. There are a number of dug-out canoe makers active in town but commercial logging has decreased substantially in importance with the exhaustion of commercially important species in the surrounding forests.

2.3.4. *Keme-Ebiama*

Keme-Ebiama is located approximately 4 km downstream from Ogboinbiri on the Apoi Creek. It is a medium sized-town without amenities other than a largely unused housing estate build by Rivers State government in the 1980's. The forest is in a similar condition as at Ogboinbiri, with most of the commercial species exhausted.

Though the red colobus was familiar to all hunters they had now become rare, and were reported to be seen only occasionally. The survey of the forest indicated that extensive logging was taking place in all of the community's forest, and during the survey no monkeys were encountered. The tracks of unidentified duikers, as well as sitatunga (*Tragelaphus spekei*) and red-river hog were observed. Hunters, as well as the town elders here, also confirmed that the red colobus had always been found on the west (town) side of the Apoi Creek.

Fishing is the most important human activity followed by logging and farming. This was also the only town encountered in the area where palm oil was produced on a small scale.

2.3.5. *Gbanraun*

This village is located on the headwaters of the Pennington River and can now be reached via a canal, dredged by the State Government, from the Apoi Creek. It is a small village with most of the population distributed over the many fishing camps surrounding the main town. Though logging is of importance, some sections of the forest are still in good condition (but never totally unlogged), probably because community lands are extensive.

Surveys on foot were conducted at three different locations around the town, which all required travelling to a disembarkation point by canoe. The section of forest visited in 1994 was being logged and no red colobus were observed. Upon my return in 1995 the same section of forest was visited again and three red colobus were observed. It soon became clear, however, that these were the only remaining red colobus in that section, and that logging continued at a steady pace. I decided, therefore, to survey the much more swampy forest across the Pennington River from the village. Here, generally intact forest was observed which showed relatively minor signs of recent logging. Red colobus were encountered at all locations visited, and at one their numbers were impressive. *Cercopithicus nictitans*, *C. mona*, and *Cercocebus torquates* were also seen and/or heard at each of the locations visited, and it was much easier to observe the monkeys here than at any other location visited. During the surveys a large number of tracks from unidentified duikers, water chevrotain (*Hyemoschus aquaticus*), sitatunga, and red-river hog were encountered.

Fishing and logging are the most important human activities in Gbanraun. Farming, apart from a few plantain farms located on the few dry spots in the forest, plays little or no role in the local economy.

2.3.6. *Kokologbene*

Kokologbene is located approximately 1.5 km downstream from the canal to Gbanraun along the Apoi Creek. It is a small town of recently arrived immigrants with the result that they can only lay claim to a small parcel of land.

The hunters interviewed indicated that all six expected primate species were present, and that the red colobus was well known here and often observed, but only known from the west-side of Apoi creek. During the survey of the forest on foot no monkeys were seen but the vocalizations of *C. mona*, *C. nictitans*, and *Ce. torquatus* were heard. In the forest tracks of unidentified duikers, sitatunga, and red-river hog were quite common.

Fishing and logging are the most important human activities, and there are also a number of large plantain farms around the village.

2.3.7. *Ukubie*

This is the last community along the Apoi Creek before you enter the mangroves. Though the place has a large number of inhabitants they spend most of the year in fishing camps located in the mangrove zone. Most of the forest has been logged, but red colobus is reported to be relatively common. Interviews with the hunters indicated that red colobus here are always found in mixed-species groups. The groups are generally smaller than at Gbanraun, which one informant had visited. Moreover, he was certain that this had been the case for a long time because his father had made this same observation, about forty years ago. It also became clear that the red colobus here only occurs on the west (town) side of the Apoi Creek.

A survey on foot indicated that most of the forest had been logged. No red colobus were seen and only the vocalizations of *C. mona* and *C. nictitans* were heard. An abundance of sitatunga and red-river hog tracks were encountered.

Fishing is the most important human activity here, followed by logging. There is very little dry land around Ukubie, and farming is restricted to a few plantain farms on river levees.

2.3.8. *Ogbotobo*

Ogbotobo is located on a coastal beach ridge island. Though there are a few dry areas, most of the interior consists of continuous swamp making the island's interior practically inaccessible. As a result logging is restricted to the island's perimeter.

Ogbotobo is the only location were the marsh forest zone is not separated from the beach ridge islands by mangroves which, according to all informants interviewed, the red colobus never enter, and it could, therefore, be the only section of this zone inhabited by red colobus. Interviews with hunters indicated that they know all expected primate species (including chimpanzees), except olive colobus. Though hunters' reports on the presence of chimpanzees sounded convincing, no evidence was found in the forest. Red colobus is likely to inhabit the marsh forest across from the Ogbotobo Creek since it is continuous with sections of forest where the monkeys are known to occur. Ogbotobo hunters also claimed that red colobus is present on the island itself, and I decided that the survey, which was conducted on foot, should focus on determining this. The first survey brought me to a number of places where a hunter claimed to have shot red colobus. None were observed, and remarks made by this hunter led me to believe that he shot monkeys there, but not necessarily red colobus. This survey was followed by a second during which the width of the island, approximately 10 km, was crossed on foot. During this trip the only extensive area of undisturbed forest in the delta was encountered. It was not hard to understand why this was the case, since the whole interior consisted of swamps which are extremely difficult to negotiate. No primates were encountered, and no evidence of the presence of other mammals was recorded.

The most important human activities at Ogbotobo are fishing and logging.

2.3.9. *Orobiri*

The beach ridge island on which Ogbotobo is located was crossed on foot and Orobiri, which is located on the Atlantic Ocean, visited. Here the inhabitants spend most of their time fishing in the ocean and, therefore, know little of the forest. The hunters interviewed had no knowledge of the red colobus and were not even familiar with its Ijaw name, *epieni*. Only three diurnal primate species are known, *Cercopithecus mona*, *C. nictitans*, and *Cercocebus torquatus*, corroborating the assumption that the beach ridge island's fauna is poorer than that of the other zones of the Niger Delta.

2.3.10. *Bomadi*

Bomadi is a small town, situated on the bifurcation of the Forcados River and Bomadi Creek. It is one of the few towns that can be reached by a road ending at the Forcados River at Bomadi Overside. A hunter was located and interviewed, and he identified all six primate species including the chimpanzee. Initially I was given the impression that red colobus was also on the west (town) side of the Bomadi Creek and decided to survey this area. Farming is of some importance in Bomadi, and farms extended at least for 2 km around the village after which a swamp was entered. In the swamp we heard a group of *C. nictitans*, and when we arrived at the hunter's camp he showed me the skin of a sitatunga he had recently shot. In the camp I continued to interview the hunter and came to the conclusion that red colobus only occurs east of the Bomadi Creek. This hunter was also familiar with chimpanzees, but he indicated that these days they only occur west of the Forcados River.

Most of the dry land here has been farmed and all the forest has been logged, with some sections having been converted into rubber plantations. Apart from farming, fishing, and logging the distillation of palm wine into 'native gin' and the collection of rubber also provide an income.

2.3.11. *Olota*

This town is located downstream from Bomadi on the west bank of the Forcados River. The village inhabitants are Urhobo, and not Ijaw as in the other towns visited.

Farming is more important here and the inhabitants, who have immigrated into traditional Ijaw land, are not allowed to fish extensively.

The red colobus is not known here and none of the hunters interviewed was familiar with them. During the survey of the forest, which is different in composition than the marsh forest, signs of heavy logging were observed everywhere. Upon return to the town I was invited to a hunter's house, where I was shown a fresh skin of a juvenile chimpanzee he had shot behind the town, corroborating the information of the Bomadi hunter. Little to no evidence of other large mammals was observed except for some tracks of red-river hogs.

2.3.12. *Egbemo-Angalabiri*

Informants in Port Harcourt reported that the forest behind this community contained a large population of red colobus. Hunters interviewed here confirmed that this was the case, but said that their numbers had been decreased significantly due to extensive logging. During the survey of the forest my guide informed me that the inhabitants of this community had started logging as far back as the late 1950s, and that it would be extremely unlikely that we would encounter a group of red colobus. The forest was indeed heavily logged with few trees taller than 15 m. No primates were encountered but tracks of sitatunga, unidentified duikers, and red river hog were seen everywhere.

Fishing, logging, and gin distillation in the raphia swamps are the most important human activities in this area.

2.3.13. *Norgbene*

The swamps behind Norgbene contained, in the past, a large number of abura (*Hallea ledermannii*, previously known as *Mitragyna ciliata*), the Niger Delta's most valuable timber species. This tree is, according to the hunters interviewed, the most important food-species for the red colobus here, and they reported, therefore, that the monkeys had become very scarce as a result of extensive logging. One survey on foot, and one by canoe were conducted. During the survey on foot no red colobus were observed but two different groups of *C. nictitans* were seen. At a distance of about 2 km from the town a section of unlogged forest on a dry ridge was encountered. Evacuation canals had already been dug but all logging had been stopped because this part of the forest was regarded as belonging to a deity, and was therefore not supposed to be disturbed. For the second survey we set of by canoe, and after three hours during which approximately 3 km were covered we encountered one wary group of approximately 30 red colobus. The monkeys fled immediately after contact, and no vocalizations were heard.

For their income, people here depend, like the inhabitants of Egbemo-Angalabiri, on fishing, logging, and gin distillation from palm wine.

2.3.14. *Lalagbene*

In a north north-easterly direction from Lalagbene the forest becomes drier. The hunters here indicated that they know red colobus, but that these monkeys were never found in great numbers because they are restricted to the few swampy areas. The interview also confirmed that red colobus are only found on the east side of the Bomadi Creek.

During the survey of the forest no primates were encountered. The forest here is different in composition from other sections of the marsh forest zone, possibly warranting another subdivision after further investigation. Though sections of the forest have hardly been logged, most has been converted to farmland, which is the most important human activity here.

2.3.15. *Adi-Egbe*

The interviews of hunters at Adi-Egbe indicated similar conditions to those of Lalagbene, except that the hunters here are familiar with *P. verus* which they claim to be common. Red colobus is also known from the few swamps in the area but hardly ever encountered. The forest was not surveyed at this location.

2.3.16. *Adagbabiri*

Adagbabiri is a farming community, with some seasonal fishing in the surrounding small creeks. The hunter interviewed knew of red colobus but had never observed them. This confirms that though red colobus occurs in the area the monkeys are restricted to the few swampy areas, and are never very common. The hunter here was familiar with olive colobus, which he also claimed to be common in the area. A short survey of the surrounding forest indicated that basically all forest had been converted to farmland.

2.3.17. *Eriama*

The situation here was similar to that in the previous two towns. Red colobus are known but restricted to the few swampy areas. Community lands contain a sacred lake, which is said to harbor a population of Nile crocodiles, and a large area of sacred bush. Unfortunately I was not allowed to visit these sites.

During the survey of the forest no primates were heard or seen, and only the tracks of duikers encountered. The forest I was shown appeared to be in good condition and had only been selectively logged. Farming is also the main occupation here.

2.3.18. *Toru-Ebeni*

This town is situated on the Sagbama Creek, and is considerably larger than its neighbors. The hunter interviewed here said he had heard of the red colobus but indicated that it is no longer present. Of the other primates expected to be present in the area, only olive colobus was not known. A short survey of the town's surroundings indicated extensive farming, and the little forest remaining has been logged heavily leaving little suitable habitat for wildlife.

Farming is the most important human activity, followed by fishing in the Sagbama Creek.

2.3.19. *Bolou-Orua*

This is a small town also located on the Sagbama Creek. The forest on the west (town) side had been extensively logged, and though hunters knew red colobus it was said to be no longer present in significant numbers. The forest on the opposite side of the Sagbama Creek was also visited, but all hunters indicated that no red colobus was ever observed on this side of the creek.

Farming, fishing, and logging are the most important human activities.

2.4. Results

2.4.1. *Red Colobus Distribution*

The data collected during the survey, supplemented with information from Powell (1993, 1995), clearly indicate that the distribution of the red colobus is limited to only a small section of approximately 2000 km^2 of the Niger Delta (**Map 2.1**, p. 50). The boundaries in the west are defined by the Forcados River and the Bomadi Creek, and in the east by the Sagbama, Osiama, and Apoi Creeks. This triangle is closed by the mangrove zone and the Ogbotobo beach ridge island that he monkeys apparently do not use. These boundaries appear to be natural, and not caused by hunting pressure and/or other human activities. Though some of the boundary creeks of the red colobus distribution area are among the largest in the delta, most of the delta's primates occur on both sides, suggesting that these waterways do not function as natural barriers. None of my informants indicated that there were any differences in hunting pressure or human food preferences on either side of the boundary creeks, and I did not observe any difference in the frequency of hunting signs (*e.g.*, spent carbide). This suggests that the red colobus' unusual distribution is best explained by differences between the ecology of the distribution area and that of the surrounding areas.

The hypothesis that ecological differences are responsible for the red colobus' distribution is further supported by the observation that the hydrology of the forests on both sides of the Apoi Creek is different. Sections of forest on either side of the creek were visited, and a number of significant differences were observed. The forest sections outside the red colobus distribution area were, including the depressions, drier for most of the year. Only during the approximately three months of the Niger flood was the forest inundated, and to a much higher degree than on the creek's other side, creating a more pronounced seasonal environment. Within the red colobus distribution area the narrow elevated ridges running through the forest stayed dry while the remainder was swamp. Though large sections of these swamps would dry partially out during the dry season (December/January) the variation in water levels was not as pronounced. That these hydrological differences caused differences in the forest habitat was even supported by the limited data collected during the survey on forest composition. Though the forest on both sides of the creek shared a large number of tree species, *ad lib.* observations suggested strongly that both structure and species composition was different. An added point of interest was that it became clear during the survey that the red colobus preferred swamp habitat, and would only venture out to drier section during part of the year. Outside the distribution area the swamps would dry out for much longer periods of the year making it likely that the vegetation in these swamps was significantly different, rendering them unsuitable to red colobus.

2.4.2. *Human Activity*

The delta's most important human activity is fishing, which is practiced in many different forms. Fishing activity reaches its peak after the Niger flood in October/November. This is the only major human activity that appears not to affect the forest in any adverse way. During the survey it became clear, however, that fish catches are declining. This may be because the fish population is decreasing and/or because the number of people depending on these resources is increasing. Despite this decrease, communities will still allow outsiders to fish their waters in return for a yearly fee. People fishing in Gbanraun come from as far as Ogoni (east of the delta), suggesting that the delta's edges and surrounding areas are already overexploited. This increases the pressure on the delta's fish population even more, and will possibly result in serious fish shortages in the near future.

Though farming is only of importance in the few areas where there is a significant amount of dry land, in most parts of the delta it is restricted to the seasonally exposed river and creek levees. The main crops grown are cassava and plantain, some sugar cane and maize, as well as a number of different vegetables. In the delta's wettest parts the few drier spots available are converted into plantain farms. Most of the delta has never supplied sufficient agricultural products to feed its inhabitants. However, people always caught enough fish so that the surplus could be traded for agricultural products with upland communities. In its present form it is unlikely that farming will become a threat to the delta's forests.

Logging has taken place since at least the 1950s but has only gained in importance as an important cash earner during the last decade. In the beginning, only a few species such as abura (*Hallea ledermannii*), alstonia (*Alstonia boonei*), white akumi (*Coelocaryon preussii*), red akumi (*Pycnanthus marchalianus*), lugbo (*Anthostema aubreyanum*), and paa (*Cleistopholis patens*) were extracted in the marsh forest zone (**Table 2.3**, p. 49). These species deliver a good quality of wood and their logs also float. The most commonly used extraction method employs narrow canals, approximately the width of a large tree log, which are dug into the forest from the nearest creek. With the use of hand-winches the logs are pulled into and through these logging canals. Upon reaching the creek the logs are then tied together into rafts that are attached to one another. The long trains of rafts thus formed can contain up to two thousand 6 m long logs at a time, and are pulled to their final destination (most often Lagos) by tugboats. Though sometimes non-floating species are tied into a raft of floating species, they are generally left for the community's own use (*e.g.*, for dug-out canoes, building material).

Now the great majority of valuable floating species has been exhausted in the marsh forest zone, where they once formed a large part of the canopy. Therefore, a new trend appears to be developing in the delta, and a second group of species, consisting mainly of *Uapaca* spp. and *Xylopia* spp., is about to be exploited. With logging being the only major cash earner, apart from fishing, every effort is being made to exploit as many tree species as possible. Also, out of sheer need, logging in remote locations, which was previously deemed uneconomical, is now increasing. Though the new forms of exploitation are not yet practiced on a large scale there are indications that this soon may be the case. An added problem is that the large number of logging canals dug by the loggers function as drains, with the result that large sections of the forest now stay drier for a much longer period.

Because the delta produces approximately 3% of the world's oil a large number of multinational oil companies are operating in the area, and it is often assumed that their activities pose the greatest threat to the environment. The red colobus distribution area contains a number of oil fields and is crossed by pipelines, and during the survey a special effort was made to identify possible environmental problems caused by activities of the oil industry. No new spills and little evidence of past spills were observed, even though large areas were surveyed. This does not mean that spills are not occurring and that no damage is done. It does, however, indicate that these activities do not cause damage to such a level that the ecosystem is permanently altered. It appears that the damage is restricted to a few localized spots, which as of yet do not affect the overall integrity of the delta's ecosystem.

The only permanent negative effects of oil-industry related activities observed were the changes caused in hydrology through the dredging of slots and canals. Canals sometimes connect waterways with a different ecology, causing profound changes, not only to the water regime but also the composition of the forest around these locations. Affected areas either get waterlogged or dry out, and the vegetation starts to die. Most often, however, the local inhabitants look favorably on these projects since they often shorten their travel time, and/or provide new access to areas previously considered too remote for exploitation.

2.4.3. *Hunting pressure*

The native (Ijaw) inhabitants of the delta are mainly fishermen. In nearly every town visited the number of hunters was limited, and they were often not very experienced. Interviews indicated that most villagers looked upon the forest as a dangerous place and hunting as an activity not worth pursuing since the creeks are full of fish. Every village had, however, a couple of individuals who enjoyed hunting and the dietary variation it brought.

Informants indicated that in the past people only hunted for red-river hog and sitatunga, and that monkeys were considered to be too small. Even nowadays most hunters concentrate on terrestrial mammals, and hunt mostly at night with a carbide lamp. Moreover, most informants indicated that if they encountered red colobus they would leave them alone because of their poor taste.

Unfortunately this situation has recently changed for two different reasons. The first reason is that fish catches are decreasing in the delta and therefore other protein sources have gained in importance. As a result hunters are now also interested in smaller mammals such as primates, and spend more time hunting. The second problem is an increase of outsiders into the central delta who come to either fish or log. The number of experienced hunters among them appears to be much higher, and they also shoot all animals encountered. During interviews with them I was told that indeed red colobus tasted bad but after smoking the meat it could be sold in markets outside the delta where nobody was familiar with this unpalatable monkey.

Though hunting in the delta has not yet reached alarming proportions, present developments indicate that pressure is increasing and will continue to do so. This, in combination with the high level of logging, paints a bleak future for the delta's wildlife.

2.5. Summary

The survey indicated that the Niger Delta red colobus is restricted to a relatively small section of the central delta, and that the pressure on natural resources within this area is increasing rapidly. There are presently no functioning forest reserves in the area and no government institution is monitoring human activities in the delta. As a result there is no effort from the Rivers, Bayelsa, or Delta State Forestry Departments to guide the increasing logging activities within the delta. As a result exploitation of the forests is taking place in a totally unorganized way, and nowhere are any measures applied which could create some form of sustainability. The combination of uncontrolled logging without any replanting and a rapid increase in population, partially through population growth but also through immigration, has resulted in a continuous increase of the forest's degradation.

An additional problem is that, as a result of oil company activities and a number of federal and state development projects, large sections of the delta, which were previously too remote for human activities, have been opened up. Now roads, canals, and slots provide access to these places resulting in an increase in population density and exploitation. As a result it has become extremely difficult to find even a small section of forest that has not been negatively affected by human activities. If exploitation continues at the rate observed during the survey it is not unreasonable to estimate that all of the Niger Delta's forests will be severely degraded over the next 20 years.

The forests within the red colobus distribution area are no exception, and have all been degraded to various degrees by human exploitation. During the survey no intact forest, apart from a few small sections on dry ridges, was encountered. None of the surveyed swamps, which appear to be the red colobus' preferred habitat, had remained unlogged. In most places all the most valuable timber species were gone, and in quite a few locations large-scale exploitation of less valuable species had started. Given our lack of biological information on the delta's ecosystem this is a very alarming development, because soon whole sections will disappear before they have been investigated.

The alarming rate of deforestation in the delta has also affected the red colobus population. At none of the visited locations, apart from Gbanraun, were red colobus observed in large numbers. At most locations the monkeys were well known but had become rare, and even in Gbanraun a medium-sized group, which had been observed in 1994, was reduced to three animals by the beginning of 1996. Most of the swamps in the freshwater forest zone contain large numbers of abura, the most valuable floating timber species in the delta, which is usually extracted first. There are strong indications that abura is an important food species for the red colobus with the result that even during the early stages of the logging process the swamps become uninhabitable for them (Werre & Powell, 1997).

Table 2.1: *Locations surveyed (numbered in correspondence with* **Map 2.1**).

#	LOCATION	DATE
1	Sampou	29 July – 1 August 1994
2	Azama	1 August – 2 August 1994
3	Gbanraun	5 – 8 August 1994, 31 March – 15 April 1996
4	Bomadi	9 – 12 August 1994
5	Olota	13 August 1994
6	Norgbene	17 – 21 August 1994, 20 – 23 December 1995
7	Ogboinbiri	25 – 29 August 1994, 28 – 30 November 1995, April 1996
8	Keme-Ebiama	8 December 1995
9	Kokologbene	9 December 1995
10	Ukubie	10 – 14 December 1995
11	Egbemo-Angalabiri	4 – 6 January 1995
12	Ogbotobo	8 - 10 January 1996
13	Orobiri	11 – 12 January 1996
14	Lalagbene	14 January 1996
15	Adi-Egbe	15 January 1996
16	Adagbabiri	16 January 1996
17	Eriama	17 - 19 January 1996
18	Toru-Ebeni	20 January 1996
19	Bolou-Orua	11 February 1996

Table 2.2: *Diurnal primate species reported at each surveyed location. Underlined italics indicate visual or auditory contact by me, all other records come from hunters' reports.*

#	LOCATION	SPECIES
1	Sampou	*CMO*, CNI, CER, CTO, ***PBE***, PVE
2	Azama	CMO, CNI, CER, CTO, **PBE**, PVE
3	Gbanraun	*CMO*, *CNI*, CER, *CTO*, ***PBE***, PVE
4	Bomadi	CMO, *CNI*, CER, CTO
5	*Olota	CMO, CNI, CER, CTO, PVE, PAN
6	Norgbene	CMO, *CNI*, CER, CTO, ***PBE***
7	Ogboinbiri	CMO, CNI, CER, CTO, **PBE**, PVE
8	Keme-Ebiama	CMO, CNI, CER, CTO, **PBE**, PVE
9	Kokologbene	*CMO*, *CNI*, CER, *CTO*, **PBE**, PVE
10	Ukubie	*CMO*, *CNI*, CER, CTO, **PBE**, PVE
11	Egbemo-Angalabiri	CMO, CNI, CER, CTO, **PBE**, PVE
12	*Ogbotobo	CMO, CNI, CER, CTO, **PBE**, PAN?
13	*Orobiri	CMO, CNI, CTO
14	Lalagbene	CMO, CNI, CER, CTO, **PBE**
15	Adi-Egbe	CMO, CNI, CER, CTO, **PBE**, PVE
16	Adagbabiri	CMO, CNI, CER, CTO, **PBE**, PVE
17	Eriama	CMO, CNI, CER, CTO, **PBE**, PVE
18	Toru-Ebeni	CMO, CNI, CER, CTO, **PBE**
19	Bolou-Orua	CMO, CNI, CER, CTO, **PBE**, PVE

CMO: *Cercopithecus mona*, CNI: *C. nictitans*, CER: *C. erythrogaster*, CTO.: *Cercocebus torquatus*, **PBE**: ***Procolobus badius epieni***, PVE: *Procolobus verus*, PAN: *Pan troglodytes*.

* Locations outside the red colobus distribution area.

Table 2.3: *Tree species' native names and use*

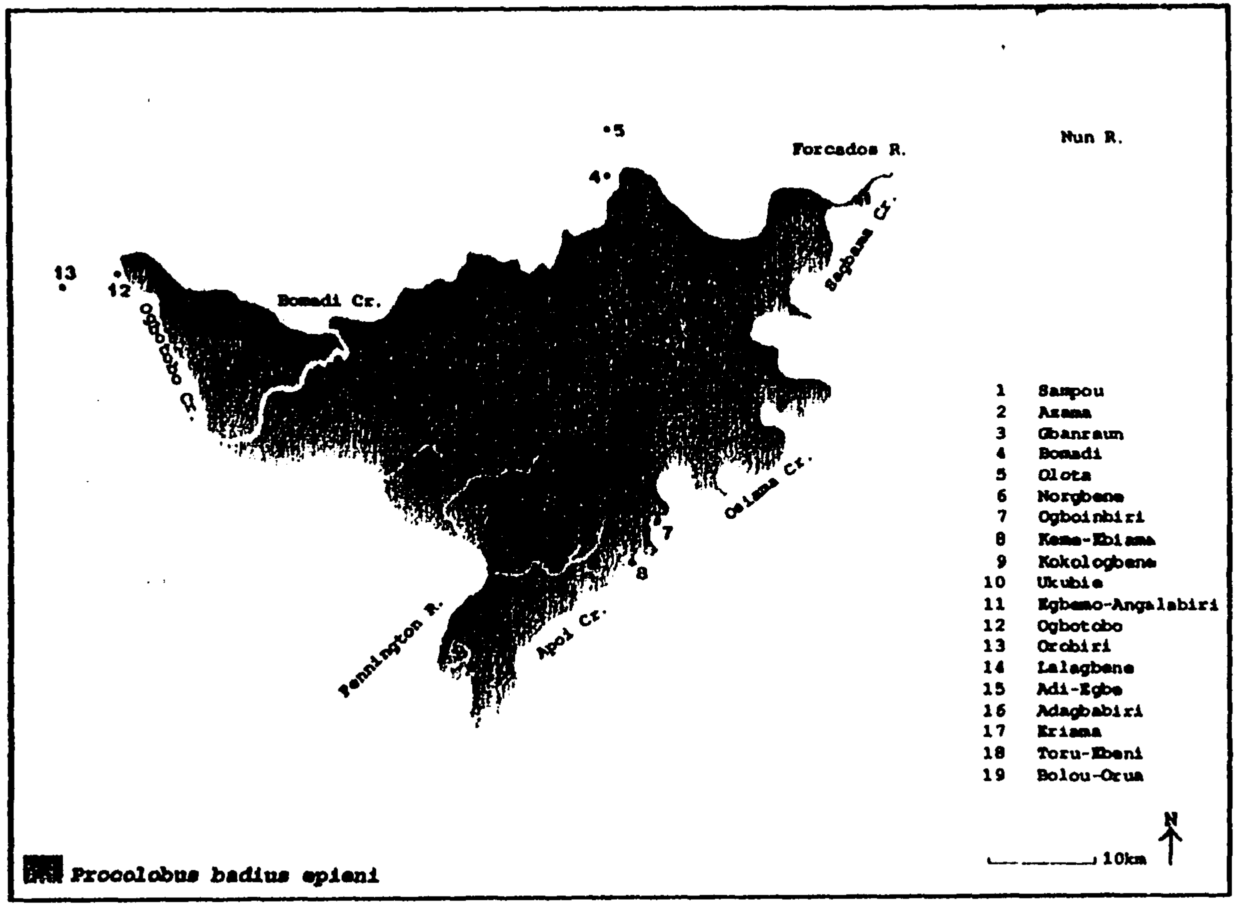
#	SPECIES	NATIVE NAME	NATIVE USE
1	*Cleistopholis patens*	Paa	Timber 2
2	*Xylopia staudtii*	Ifou	Timber 4, seeds help pregnancy
3	*Xylopia aethiopica*	Ngetero	Timber 2, seeds are spice
4	*Hexalobus crispiflorus*	Itawein	Timber4, fruit edible
5	*Monodora myristica*	Kokolo	Seeds are spice, bark clears the stomach
6	*Beilschmiedia* sp.	Bolui	
7	*Pycnanthus marchalianus*	Iyoro aboh	Timber2 (red akumi)
8	*Staudtia stipitata*	Ongoh iyonwie	
9	*Coelocaryon preussii*	Owei aboh	Timber 1 (white akumi), carve canoe
10	*Scottelia mimfiensis*	ewono	
11	*Ourateae calantha*	Keme ungbo	Timber 4
12	*Lophira alata*	Kuru	Timber 4, carve canoe
13	*Syzygium guineense*	Epemu	Timber 4, carve canoe, chewing stick
14	*Spathandra blakeoides*	Bilayaimo	Timber 4, carve canoe
15	*Cassipouria barteri*	Owei biakaki	
16	*Anopyxis klaineana*	Aki	Timber 4, best firewood
17	*Symphonia globulifera*	Okilolo	Timber 4
18	*Pentadesma butyraceae*	Obobi	Timber 4, fruit is laxative
19	*Mammea africana*	Bolo	Timber 3, 4, carve canoe
20	*Garcinia smeathmannii*	Iyoro biakaki	
21	*Garcinia kola*	Ikain	Timber 4, bitter kola
22	*Sterculia tragacantha*	Poro	
23	*Cola nitida*	Dabio	
24	*Ceiba pentandra*	Afalafase	Timber 3
25	*Sacoglottis gabonensis*	Tala	Timber 3, edible fruit, bark flavors palm wine
26	*Ctenolophon englerianus*	Zjoweintin	Timber 3, 4, carve paddle
27	*Anthostema aubreyanum*	Lugbo	Timber 2
28	*Macaranga* spp.	Igbaragba	Timber 4, boiled leaves, bark heals wound
29	*Uapaca staudtii*	Okruba Ile	Timber 3, 4, carve canoe, edible fruit
30	*Uapaca heudelotii*	Ijo Ile	Timber 3, 4, carve canoe, edible fruit
31	*Discoglyprimna caloneura*	Omeh	
32	*Spondianthus preussii*	Okpolota	Timber 4, boiled young leaves make poison
33	*Kleineanthus gaboniae*	Buofaha	Firewood
34	*Oxystigma mannii*	Entophia	Timber 2
35	*Erythrophleum ivorense*	Ire	Carve canoe, Timber 3
36	*Piptadeniastrum africanum*	eshan	Timber 3
37	*Treculia africana*		Seeds edible (native rice/beans)
38	*Musanga cecropioides*	Akpowei	
39	*Klainedoxa gabonensis*	Ako	Timber 4, carve canoe
40	*Irvingia gabonensis*	Ogboin	Edible seed (ogbono)
41	*Dacryodus edulis*		Edible fruit (pear)
42	*Carapa procera*	Ofau	Timber 3, 4
43	*Lovoa trichilioides*	Apupo	Timber 1 (walnut)
44	*Guarea cedrata*	Cedar	Timber 1 (ceder)
45	*Diospyros preussii*	Olumba	
46	*Anthocleista* spp.	Osuowei	Root is laxative, fruit aides during childbirth
47	*Alstonia boonei*	Kugbo	Timber 2
48	*Funtumia africana*	Ugpaskara	Used to carve kitchen utensils
49	*Rothmannia megalostigma*	Mbrumu	Firewood, Timber 4

Table 2.3: *Continued*

#	SPECIES	NATIVE NAME	NATIVE USE
50	*Nauclea diderrichii*	Owoso	Timber 1
51	*Nauclea vanderguchtii*	Lalawei	Timber 1, bark in kaikai helps against malaria
52	*Hallea ledermannii*	Baa	Timber 1 (abura)
53	*Massularia acuminata*	Ewa	Chewing sticks
54	*Vitex grandifolia*	Boron	Used to carve idols
55	*Raphia vinifera*	Bea	Midribs leaves and leaflets timber 4
56	*Raphia hookeri*	Koro	Palm wine
57	*Elaeis guineensis*	Loh	Palm nuts (oil palm)

Native names are in Ijaw (Apoi Clan dialect). Timber categories: 1, Commercially most valuable; 2, Commercially valuable; 3, Sold commercially on occasion, most often as pre-sawed planks; 4, Used locally for house or furniture construction. Native use information comes from local informants.

Map 2.1: *Locations Surveyed and Distribution of Procolobus badius epieni*



CHAPTER 3

DESCRIPTION OF STUDY SITES

3.1. Introduction

Information on the availability of resources is essential for the understanding of an animal's ecology, *i.e.*, the interactions with its surroundings (Ricklefs, 1979; Mitchell, 1994). The study of an organism's habitat is, therefore, not only essential for an understanding of its primary requirements but for all aspects of its behavior.

The primary focus of this research project was to determine what factors were responsible for the differential use of the Niger Delta's forests by the red colobus. It was observed that only a small section of the central delta was occupied by the monkeys, and that, apparently, even within their distribution area only swamps were used on a year-round basis. In order to provide an explanation of the monkey's distribution, one of the objectives of this study was to assess forest composition, structure, and phenological patterns, both within and outside the distribution area.

Based on the findings of the survey, Gbanraun was selected as the most appropriate location on which to focus an ecological study on the Niger Delta red colobus, for the following reasons:

- Gbanraun was the only location where red colobus were encountered in large numbers.
- Some sections of the forest in Gbanraun still maintained their integrity, despite logging activities.

- Gbanraun was the location where the first red colobus was discovered in 1993. From that time the inhabitants had become interested in the establishment of a research center and had banned hunting of all monkeys.

It was, therefore, not very difficult to obtain permission from the community to use an area of approximately 140 ha, where any form of human activity would be forbidden, for a study site. An added advantage was that the study site was close (approximately 3 km) to the Apoi Creek, the eastern boundary of the red colobus' distribution area. This facilitated the establishment of another study site at Ukubie, which was located across the Apoi Creek, just outside the red colobus distribution area (**Map 3.1**).

3.2. General Description of the Gbanraun Study Site

A number of surveys of the forests in the vicinity of Gbanraun helped to determine the most suitable location for the establishment of a study site. Unfortunately, due to the high level of human activity in the area only the wettest and most remote areas were found to be suitable, and these had been logged to various degrees. The section of forest I finally selected was located approximately 4.5 km south-west from Gbanraun town between the Pennington River and Apoi Creek (**Map 3.1**, p. 62). Despite the relatively short distance from Gbanraun it took between two to three hours, depending on the time of year, to reach the site from the town. The first leg of the trip, which took approximately 45 minutes, was by dug-out canoe down the Pennington River. The second leg continued for 1 to 1.5 hours via a small creek and eventually logging canals into the forest, followed by a 20 minute walk over relatively dry terrain to the camp. During the dry season canoes could not get as far into the forest and a 45 minute walk over swampy ground was required. The forest here is dissected by transects which were cut by the Western Geophysical Company during 1994 for 3-dimensional seismic prospecting on behalf of the Nigerian Agip Oil Company. These existing transects were used as reference lines for the establishment of the study site over a total area of 126 ha.

The terrain in the study site consists of a mosaic of seasonal swamps, of which the wettest parts may persist through the whole year, and drier ridges (old river levees) that only get inundated during heavy rains. The Niger flood does not affect the forest in this section. The levees' soils consist of alternating layers of coarse-textured and medium-textured sediments that, to a depth of approximately 1 m, overly moderately fine or fine textured sediments. These alternate layers can consist of fine sand, loamy sand, loam or silt-loam cover silty clay, but most often silty clay loam. In the swamps fine textured soils are peat covered. Soils here have very high silt and organic content (NEDECO, 1966).

Hallea ledermannii (= *Mitragyna ciliata*) was probably once a common tree at this site, but it is now very scarce, since this was the main species logged in this area during the 1980s. Interviews with one of the loggers indicated that about 100 *H. ledermannii* were extracted over an area of about 100 ha, together with smaller numbers of *Alstonia boonei*, *Cleistopholis patens*, *Coelocaryon preussii*, and *Pycnanthus marchalianus*. Other than logging, human activities at the study site were restricted to fishing in the many logging canals, trapping of snails (achatinid land snails.), the collection of chewing sticks (*Massularia acuminata*), and some hunting, mainly for red-river hog (*Potamochoerus porcus*), sitatunga (*Tragelaphus spekei*), and duikers (*Cephalophus* spp.).

3.2.1. *The Primates at Gbanraun*

Hunters interviewed in Gbanraun indicated that they were familiar with the following primate species: a dwarf galago (probably a *Galagoides* sp.), Bosman's potto (*Perodicticus potto*), red-capped mangabey (*Cercocebus torquatus*), putty-nosed guenon (*Cercopithecus nictitans*), mona monkey (*C. mona*), white-throated guenon (*C. erythrogaster*), red colobus (*Procolobus badius epieni*), and olive colobus (*P. verus*). The golden potto, *Arctocebus calabarensis*, and an unidentified monkey have also been reported to be in the area (Powell, 1995), but I could not confirm the presence of these two primates. At the study site the calls of a dwarf galago (*Galagoides* sp.) were heard at irregular intervals around the camp and the animals were twice seen from a great distance. The call was recorded and compared with calls of other dwarf galagos recorded by S. K. Bearder (1992); it appeared to be different from other populations.

Initially it was planned to estimate primate densities from samples taken along transects. It soon became clear, however, that this was impossible because the swamps were too difficult to negotiate to cover transects of significant length (5 km or more). Instead the location of encounters with all primate groups were recorded during the five day follows of the red colobus and this, augmented with spot sightings made outside the follows, was used to arrive at a rough estimate of their density within the study site (**Table 3.1**, p. 61).

C. nictitans was the most common guenon at the study site, often occurring in mixed species groups with *P. badius*, or *Ce. torquatus* and/or *C. mona*. The study site was used fully or partially by six different groups of *C. nictitans*, each of approximately 15 monkeys. One group, which spent a relatively large amount of time in the vicinity of the red colobus study group, became fully habituated to my presence.

The study site overlapped only partly with the home range of a group of mona monkeys. This group never entered the swamps and consisted of approximately 15 animals. Apart from this group a solitary male accompanying a group of red-capped mangabeys was encountered.

Ce. torquatus was mainly found in the drier sections of the research area, where it was common. Four different groups, all of about 15 animals, occupied sections of the research area. Though the mangabeys formed mixed species groups with both *C. nictitans* and/or *C. mona* they were never observed together with *P. badius*. During my study I got the impression that the red colobus avoided the mangabeys by moving in opposite directions when loud calls were heard in the vicinity.

The red colobus was abundant at the study site and constituted by far the largest part of the primate biomass. These monkeys occupied all sections of the study site and formed large groups. In total four different groups had home ranges that fell partially or fully within the research area. The smallest group was estimated to contain approximately 30 individuals, two groups 60 individuals, and the largest group up to 80 individuals.

Though hunters reported *P. verus* and *C. erythrogaster* as present in the area, these species were not observed at the study site. It appears that the great number of creeks and rivers in the red colobus distribution area form at least short-term boundaries, resulting in a patchy distribution of the primate species present.

3.2.2. *Predation*

Chimpanzees (*Pan troglodytes*) and crowned hawk-eagles (*Stephanoaetus coronatus*) appear to be the two most common predators, other than man, of red colobus (Struhsaker & Leakey, 1990; Boesch, 1994). Chimpanzee hunting pressure has even been hypothesized to be a possible factor in the evolution of red colobus social organization (Busse, 1977; Noë & Bshary, 1997; Stanford, 1998; Treves, 1999).

Chimpanzees did not occur in the study area, and were never recorded as present in the red colobus distribution area during this and other surveys (Powell, 1993, 1995). There are, however, a number of reliable reports from surrounding area, and a population of chimpanzees has actually been observed in an area with a much denser human population, Nembe, to the east (Bocian, 1999). I also observed the fresh skin and a skull in a town, Olota, which is approximately 10 km north of the Bomadi Creek that forms the western boundary of the Niger Delta red colobus distribution area. This suggests that chimpanzees have not inhabited the most central part of the delta recently, since it is least disturbed by humans.

Crowned hawk-eagles were observed in the study area, and a continuation of the surveys conducted by C. B. Powell (1993, 1995) suggests that they are relatively common within the central Niger Delta (C. B. Powel, 1997, pers. com.).

Before I started to follow the study group I had observed a large bird of prey at a great distance, and identified it as possibly being a crowned hawk-eagle. I interviewed my assistants who confirmed the presence of a bird with “mighty feet” that would kill monkeys. I never saw the bird again until the third follow in December 1996, when it was observed swooping through the forest canopy close to the group. The group reacted with very loud and lengthy vocalizations. After this, two attacks on the study group and one attack on a *Cercopithecus nictitans* were observed, all of which were unsuccessful. The two attacks on the study group were both executed in the same manner. The bird must have sat in a tree from which the group could be observed and launched itself from there with great speed attempting to grab/stab an exposed monkey. In both cases the first attack was followed by a second half-hearted attack that did not lead to the same intense reaction of loud vocalizations from the group.

In January 1997 I found the nest of a breeding pair of crowned hawk-eagles with young located, approximately, in the center of the study group’s home range. Because the tree that held the nest was standing in water (which prevented termites and most other possible consumers from removing bones that had fallen out of the nest) I was able to collect several skulls, two of which were definitely colobine skulls, indicating that attacks were successful at times. In May 1997 a young eagle first observed in the vicinity of the group, and continued to be present during the remaining follows. Crowned hawk-eagles continue to care for their young up to a year after they have left the nest (Fry *et al.*, 1988). During this period the young eagle still continued food-calling (a loud wee-wee-wee sound) which made it easy to detect the birds’ presence. The young bird was on a number of occasions observed to attack a member of the group, but was always unsuccessful and would immediately be challenged by the adult males, as described by Struhsaker & Leakey (1990). The other monkeys, though not vocalizing loudly or stopping their activities, became more careful and avoided the locations from where the bird was calling.

There were also reports of very large pythons (*Python sebea*) at the study site, and one 3 m long specimen was observed. Attacks by pythons on primates have been recorded in savanna habitat (Cheney and Seyfarth, 1990) and even on red colobus in the riverine forest of Abuko (Starin, 1991). Some records of predation on primates in rain forest habitat are available from South America (Chapman, 1986; Heyman, 1987) but no similar reports have come from the African rain forest (Treves, 1999).

3.3. General Description of the Ukubie Study Site

Ukubie (4°40' N, 5°50' E) is situated on the west bank of the Apoi Creek, the eastern boundary of the red colobus distribution area. Interviews with local hunters and surveys of the surrounding forest confirmed the creek's status as a red colobus distribution boundary, with no red colobus occurring on the eastern side of the creek. Across from the village, on the eastern side of Apoi Creek, is a sacred forest where no one is allowed without special permission and all categories of human activity, other than prayer, are forbidden. Around this sacred forest was the only section of unlogged forest that I could locate along the creek, and permission from the community was obtained to start a vegetation enumeration here. An area of 100 ha was selected as a study site where a vegetation enumeration was conducted, and a phenology sample also established.

This study site, which is approximately 10 km south of the Gbanraun study site, is located across from the town of Ukubie approximately 200 m behind the Apoi Creek's levee (**Map 3.1**, p. 62). The forest here is affected by the Niger River flood with the result that the water table stays high throughout the year, and is only around 10 cm below the surface during the dry season. The study site consisted of swamp, with no dry ridges. The soils are river basin soils, produced by frequent flooding of the Apoi Creek. The floodwater is deprived of the coarser-textured sediments resulting in the deposition of fine-textured clay-rich soils. Either peat and/or layers of muck cover these soils. The deeper strata often contain the fibers of the former mangrove vegetation (NEDECO, 1966).

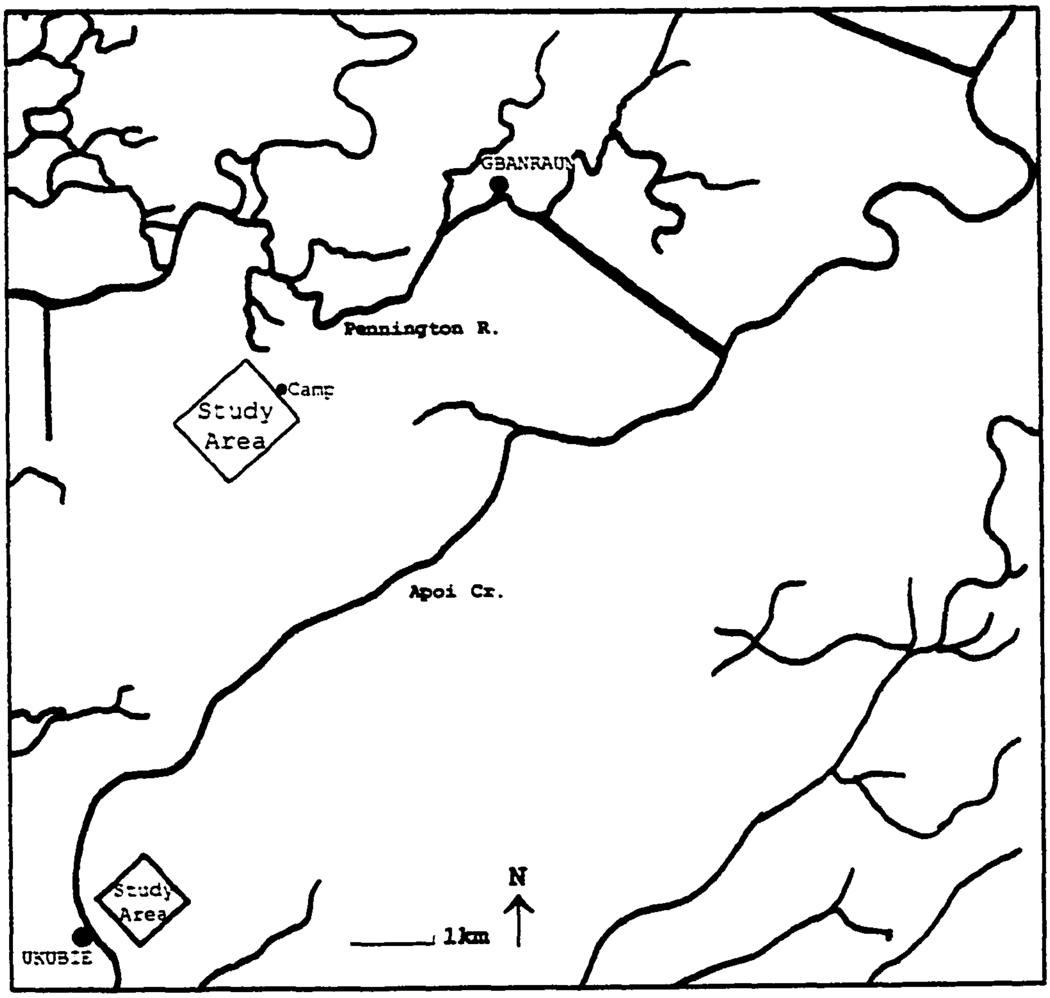
3.3.1. *The primates at Ukubie*

Interviews with hunters suggested that 5 species of diurnal primate, *Cercocebus torquatus*, *Cercopithecus nictitans*, *C. mona*, *C. erythrogaster* and *P. verus* occurred within the study. Only *C. nictitans* and *C. mona* were observed and *Ce. Torquatus'* vocalizations were heard. I did not obtain any evidence of the presence of the other species. No systematic efforts were made to establish primate densities but *ad lib.* observations suggested that these were considerably lower than at the Gbanraun study site.

Table 3.1: *Estimated diurnal primate densities at the Gbanraun study area (126 ha) based on spot sightings.*

species	# groups	Total # indiv.	Total # indiv. in study area	Indiv./ha
Cercopithecus mona	1	16	10	0.08
Cercopithecus nictitans	6	90	60	0.48
Cercocebus torquatus	4	60	45	0.36
Procolobus badius	4	205	150	1.20

Map 3.1: *Location of the Gbanraun and Ukubie Study Sites*



CHAPTER 4

METHODS

4.1. Establishment of Research Area

Undertaking behavioral research on a group of Niger Delta red colobus monkeys presented a number of problems. The survey had indicated that the red colobus are mainly found in swamps, and Gbanraun was no exception. Because of the difficulties in establishing a base camp in the swamp, I selected a dry ridge on the edge of a large swamp. This had as a disadvantage that an average a distance of 1 km had to be covered to reach potential study groups. The swampy conditions also made it impossible to survey the area efficiently in order to establish the number of groups present, and determine the boundaries of their home ranges. Therefore, I decided to start by establishing a grid system that was thought to overlap with the home ranges of at least two groups. As the number of trails increased, more efficient surveys of the area allowed for more accurate estimates of group home ranges, information that in turn directed the expansion of the grid system. By this procedure, I was able to identify a study group and establish a grid system that encompassed its range.

At first I cut trails every 100 m, but it soon became clear that my movements through the swamp were too slow to keep contact with the group at these intervals, and I therefore decided to cut trails at 50 m intervals within the home range of the study group. It took six men about five months to complete the grid system over an area of approximately 110 ha, which indicates how difficult work is in the delta's swamps. The completed grid is shown in **Map 7.1** (p. 167). Over the 12-month period of the red colobus study the group left the grid system on two occasions and it was, therefore, eventually enlarged to cover a total area of 126 ha.

4.2. Problems Encountered During Follows

Working in a swamp poses a number of problems not encountered in most primate studies, but the biggest problem was movement. During the wet months, floodwater covered the area to a depth of about 50 cm and even in the dry months the many roots, branches, and mud made movement not only slow (approximately 1.5 km/hour when moving fast) but also extremely tiring. Given these conditions it also proved to be impossible to move during darkness, and as a result I was never able to contact the group exactly at dawn or was able to leave at dusk. Though contact times varied, depending on the distance of the study group from the camp, the animals were generally already active upon my arrival but still at the same location were they had been left the night before. At the end of the day the group was generally left about 45 minutes before dusk.

Due to the group's large size it was relatively easy to keep contact and observe a number of monkeys during most scans. It proved very difficult, however, to shift position regularly, and I was often forced to make my observations from one spot over long periods of time.

4.3. Study Animals

4.3.1. *The study group*

During the establishment of the grid system the main selection criterion for the study group was its proximity to the camp. Given the fact that it took about 1 hour to cover a distance of 1 km in the swamp, following a group located too far from the camp would have resulted in too much travelling time. It soon became clear that at least three groups made use of sections of the selected area near the camp. Fortunately all groups were suitable as study groups with similar size and age-sex composition.

From May through July 1996 the three groups were followed, initially by an assistant and me, but eventually as the size of the grid system increased, only by me. On each occasion I attempted to follow the group for as long as possible while collecting *ad lib.* data on behavior, diet and, most importantly, range use and group composition. Extra emphasis was placed on the identification of animals that were easy to recognize, allowing for accurate identification of each group. Eventually by the end of July 1996 I was able to select what appeared to be the most appropriate group, a decision mostly based on the location of their home range, and obtained enough information on their range use to complete the grid system.

It took until January 1997 to obtain a relatively accurate estimation of the study group's size and composition. At no time did I obtain a count that I felt was fully accurate, but the results of a number of separate counts in the course of the study suggested an average size of 60 monkeys, including 7 adult males, 26 adult females, 17 subadult males and/or females, 6 juveniles, and 4 infants.

4.4. Temporal Distribution of Follows and Sampling Protocol

Systematic observations of the study group were made from dawn to dusk. An effort was made to complete each follow over a period of five consecutive days at one-month intervals, beginning in September 1996. Twelve follows were completed for which data are included in this thesis. In one month the group could only be followed for four days, and I was able to obtain five consecutive sample days in only eight months. The samples were rarely at exact monthly intervals (**Table 4.1**, p. 74). This variation was caused by the difficult logistics of working in the area. On two occasions I lost the group, and on other occasions malaria and the heavy precipitation lasting for days made it impossible to either find or follow the group.

The day before each follow was started an assistant was asked to find the study group. Once the study group had been located he would stay until dusk, and report the coordinates where he had left the group. The next morning I would locate the group alone, and continue to complete the follow by myself.

During follows the group's daily movements were plotted on a small map of the study area, from the location of first contact until departure. Observations of individual monkeys were made by scan sampling at 15 minute intervals (Altmann, 1974). I recorded the activities of no more than eight individuals, in order to avoid over representing the most visible activities in my sampling, during each sample. Information recorded for each sampled individual included the following:

Age/sex class: monkeys were sexed according to the criteria of Struhsaker (1975). I distinguished between the following age classes; infants, juveniles, subadults, and adults.

Activity: Recorded as one of the following five mutually exclusive categories: inactive, feed, travel, move, or social interaction. For each of these categories the following additional information was collected:

- Inactive; if an animal was inactive a distinction would be made, when possible, as to whether the animal was sleeping or awake.
- Feed: when a monkey was feeding the relative age and type of plant part, as well as species was recorded. If a feeding record was scored, but any of the additional information unclear, a question mark was added. Additional information on the method used to describe food selection will be provided in **Chapter 6**.
- Travel: all locomotion outside movement between feeding patches and resting places.
- Move: all movement within a resting place or feeding patch.
- Social interaction: for this category the following activities were recorded; groom, play, agonistic behavior, and sexual behavior.

General impression of the total group's activity: I estimated, for the activity states inactive, feed, and travel, which of these activities 50% or more of the group was engaged in during each scan sample.

Height: Distance from the ground estimated in 5 m increments for each animal sampled.

Study-area cell occupied: The transects prepared in the group's home range divided it into 0.25 ha cells. Transects running East-West were numbered, and transects running North-South lettered. Each cell occupied by the monkeys included in the scan sample as well as the cells occupied by the group during movement were recorded by using the letter and number of the two trails which crossed at the cells South-East corner (H5). The cells occupied were then recorded on a prepared map of the study site for each day of each follow.

Description of range use patterns:

- Day range length in meters was measured with a mapping wheel from prepared maps of the study area. Because the group was so large it occupied more than one cell at any given time, and would often spread out over a large area with sections of the group travelling via slightly different routes that could not be simultaneously observed. In those cases the distance covered by what appeared to be the center of the group was selected.
- Habitat selection was determined by calculating the percentage of observations (both on a monthly and yearly basis) in which a cell was occupied. During the establishment of the grid system cells were categorized as swamp, transition zone or dry land.

Further methods of describing ranging patterns, monthly and annual home range use, core area use, and home range overlap are provided in **Chapter 7**.

4.5. Vegetation Studies

Since the forest in the red colobus distribution area is a mosaic of habitat types, which are used differentially by the monkeys, it was important to determine how these habitat types differed. A vegetation enumeration, which included a sample of trees DBH ≥ 30 cm and a smaller subsample of trees with a DBH ≥ 10 cm < 30 cm, was conducted in the research area at Gbanraun. The sections sampled in the enumeration were then subdivided into three different subsamples (swamp, transition zone, and dry land) that were compared to one another in terms of composition and structure. Variation in the temporal patterns of food item production was monitored through two different phenology samples; one for the forest's dry-land section, and one for the swamp. The study site at Ukubie included only one habitat type, swamp, making it unnecessary to establish subsamples and conduct more than one phenology sample.

Because I had ample time to observe the red colobus before the establishment of the phenology transects I was able to include their most important food species in the phenology sample. An assistant identified all tree species first by their native name, after which I identified the scientific name with the help of *Trees of Nigeria* (Keay, 1989), and the *Flora of West Tropical Africa* (Hutchinson & Dalziel, 1954 – 1972). Those trees that remained unidentified at the start of the phenology sample were included under the native name (when available). Further into the study I obtained the assistance of a Nigerian botanist, J. Ariwaodo, who helped with the remaining identification. In a number of cases Ariwaodo used the herbarium of the University of Ibadan, Ibadan, Nigeria to identify plant samples from the field.

4.5.1. *Phenology samples at Gbanraun and Ukubie*

Gbanraun: Two separate phenology transects were established at Gbanraun. The first transect was located in the dry-land section of the study area, and had a total length of 1500 m. The second transect was located in the swamp, and had a total length of 2800 m.

The phenology samples were not established until October 1996 in the dry-land section and November 1996 in the swamp section. Both samples included not only the red colobus' most important food species, but also the forest's most common species.

The individuals selected for the phenology samples were mature trees, whose crowns could be observed with 10x40 binoculars from the ground. The dry-land sample contained 74 trees representing 10 species, and the swamp sample contained 93 trees representing 10 species (**Table 4.2**, p. 74). No new trees were added during the study period, but two trees in the swamp sample broke and were then excluded. Fifteen samples in the dry area were collected from October 1996 through January 1997, with no data collected during October 1997. Fourteen samples for the swamp were taken from November 1996 through January 1997, also with no data for October 1997.

Ukubie: It took until January 1997 to find a suitable section of forest outside the red colobus distribution area because all forest areas surveyed had been logged to too great an extent for a representative enumeration. Negotiations with Ukubie for permission to conduct a vegetation enumeration in their forest, and the enumeration itself, were time consuming, and not completed until the end of February, after which the phenology sample was established. Since I was scheduled to depart in August after the completion of the 12 month study of the red colobus, J. Ariwaodo, was trained to continue sampling.

The Ukubie sample contained 94 trees representing 10 different species (**Table 4.2**, p. 74). Selection criteria were the same as for Gbanraun. The tree species selected, with one exception, where the same as those sampled at Gbanraun, thus aiding direct comparison.

The phenology samples at Ukubie were taken over a period of 12 months, from February 1996 through September 1996, and from November 1996 through January 1997. Unfortunately, due to logistical problems, Ariwaodo was not able to visit the study sites during October 1997.

4.5.2. *Scoring method*

The same methods were used at both Gbanraun and Ukubie. Individual tree crowns were scanned with binoculars for estimation of the relative abundance of distinct plant structures. Scores were assigned for young leaves (including leaf buds), mature leaves, old leaves, flowers and flower buds, and unripe and ripe fruit. Both leaf age and fruit ripeness were determined by color and/or size. For all leaves, flowers, and fruits their percentage of the total possible was estimated according to 10% increments. Initially it was my intention to convert the scores to a five point scale with a score of 0% converted to a score of "0", scores of more than 0% through 20% to a score of "1", etc. following Struhsaker's method (1975). I decided, however, against this conversion for the following reasons: fruits and flowers for a number of species in the sample were so hard to detect that it was extremely difficult to accurately estimate their abundance; therefore. they were treated in my comparative analysis of Gbanraun and Ukubie_as present or not present. I was, however, able to collect accurate data for those flowers and seeds that formed the largest contribution to the study group's diet: *Uapaca* spp. flowers and seeds, and *Klaineanthus gaboniae* seeds, and I present these data in Chapter 6. Scores for young leaves were considered to be accurate (at 10% increments) but conversion to a five point scale would have obscured some subtle monthly variations across the same species in the three different phenology samples.

4.6. Tree Species Enumeration

4.6.1. *Gbanraun emmeration*

The method of tree enumeration used for this study was adapted from McKey *et al.* (1981) and Struhsaker (1975).

The enumeration in Gbanraun was restricted to the study site. Initially it was planned that the enumeration would extend beyond the study area. This plan had to be abandoned, because of the problems associated with covering long distances in the swamp.

Using a 10 m strip width, all trees with a diameter at breast height (DBH) of ≥ 30 cm within the grid system were sampled along 20.9 km of transect, for a total area of 20.9 ha. To assess patterns across the sample, the sample strip was divided into 100 m long plots.

For each tree the following data categories were collected; height in meters, crown diameter, crown shape, and location in the sample plot. In the DBH ≥ 30 cm enumeration all trees sampled were tagged with a numbered aluminum tag. DBH was recorded with the use of a special DBH tape measure, height in meters was calculated with the use of a clinometer, and crown diameter and location were measured with a surveyor's rope laid out along the transect. Crown shape was categorized by its closest resemblance to a shape for which a volume can be calculated (*e.g.*, elliptic, obovate). Along the 20.9 km of transect from the DBH ≥ 30 cm sample, another 418 sample plots of 0.01 ha for trees with a DBH ≥ 10 cm < 30 cm were established for a total area of 4.18 ha. For this category only information on species, height, and location was collected. Lianas were not enumerated because the task of identifying them would be too time consuming.

4.6.2. *Ukubie enumeration*

The same methods were used at Ukubie. The transects here had a total length of 10 km for a total area of 10 ha. No subsample for trees with a DBH < 30 cm was established at this site.

Table 4.1: *Temporal distribution of red colobus follows.*

1996				1997							
Sep	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**
21	18	15	11	17	12	3	17	4	15	6	2
22	19	16	12	18	13	4	18	12	16	8	3
23	20	17	13	19	14	5	19	28	17	9	4
24	21	18	14	20	15	6	20	29	18	28	5
	22	25	15	21	16	7	21	30	19	29	6
		26									

Table 4.2: *Species and total number of trees included in the phenology samples.*

SPECIES	GBANRAUN		UKUBIE
	dry	swamp	
Uapaca staudtii	–	10	–
Uapaca heudelotii	10	10	10
Ctenolophon englerianus	9	10	10
Klaineanthus gaboniae	10	–	10
Xylopia staudtii	–	9	10
Rothmannia megalostigma	2	8	–
Symphonia globulifera	10	10	10
Funtumia africana	10	10	10
Pentadesma butyraceae	10	9	10
Coelocaryon preussii	5	5	4
Pycnanthus marchalianus	5	5	–
Hallea ledermannii	3	7	10
Anthostema aubrevanum	–	–	10
TOTAL	**74**	**93**	**94**

CHAPTER 5

VEGETATION DESCRIPTION OF THE STUDY SITES

7.1. Introduction

Taken together, this research confirmed the conclusion that primate ranging behavior is strongly influenced by the way resources are distributed in time and space (Milton, 1980; Sigg & Stolba, 1981; Stanford, 1991), and by features of the primates themselves. Body weight, for example, has been shown to be an important influence on ranging behavior (Milton & May, 1976; Clutton-Brock & Harvey, 1977; Temerin *et al.*, 1984).

Early investigations of primate ranging behavior focused mainly on species living in savanna, or other open habitats, and led to the conclusions about the interaction between social structure and ecology (*e.g.*, DeVore, 1963; Altmann & Altmann, 1970; Struhsaker & Gartlan, 1970). These studies were soon supplemented by research on rain-forest species (*e.g.*, Struhsaker, 1975; Oates, 1977; Waser, 1977; Wrangham 1977).

Beyond these generalizations, field studies have attempted to identify the finer details of the factors responsible for observed variation in ranging patterns (Struhsaker, 1975; Oates, 1977; Marsh, 1981a; Stanford, 1998). Food distribution and abundance, habitat structure, group size, movements on previous days, weather patterns, and inter- and intragroup social interactions have all been suggested as potential determinants of variation in ranging. However, few studies of red colobus have identified significant correlations between one or more of these variables and ranging patterns (Isbell, 1984).

characteristic of, and adapted to, waterlogged soils (Richards, 1939). This scenario fits the Niger Delta well, apart from the mangrove zone, which generally precedes raphia swamp here, but which can also evolve directly into freshwater swamp forest. Richards' (1939, 1996) description of Akilla and Nikrowa broadly agrees with Schnell's description of a typical Upper Guinean freshwater swamp forest (1976). At Akilla, *Hallea ledermannii* is also the most common larger tree, but some other species such as *Alstonia congensis*, *Anthostema aubryanum*, and a *Spondianthus* sp. are also common.

5.2. Species Composition and Diversity of the Study Sites

5.2.1. *Gbanraun*

The forest at Gbanraun can best be described as follows: The forest floor is covered, especially in areas where the canopy opens, with members of the Marantaceae and Zingiberaceae. Small palms, *Eremospatha* and *Podococcus* spp., are also common. The shrub and/or small tree layer is dominated by *Diospyros preussii* augmented with *Ouratea* spp. *Massularia acuminata*, *Monodora myristica*, *Homalium* spp., and *Alchornea cordifolia*. The mid-story of the forest is dominated by two *Raphia* spp., *R. hookeri* and *R. vinifera*, and the following tree species: *Klaineanthus gaboniae*, *Cassipourea barteri*, *Uapaca paludosa*, *Rothmannia megalostigma*, *Spondianthus preussii*, *Funtumia africana*, a *Beilschmiedia* sp., *Sterculia tragacantha*, and *Macaranga* spp. *Uapaca staudtii* and *U. heudelotii* are by far the most common species, and form the largest part of the canopy. *Ctenolophon englerianus* is the most common emergent, and together with the two *Uapaca* species it dominates the appearance of the forest, especially in the swamp. *Xylopia staudtii*, *Pentadesma buteracea*, *Symphonia globulifera*, *Hexalobus crispiflorus*, *Coelocaryon preussii*, *Pycnanthus marchalianus*, and *Alstonia boonei* are also important contributors to the canopy (**Table 5.1 & 5.2**, pp. 99 & 100).

The forest shows a considerable amount of intra-habitat variation determined by drainage. The largest part of the study area was swamp, the next largest section of the study site was dry land, and these two areas were separated by a smaller transition zone. What follows are descriptions of these three zones.

In the drier areas the forest is relatively open and easy to walk through. These dry-land areas are situated on the remnants of river levees that run as long, narrow bands through the forest. The tree sample from the dry area at Gbanraun (5 ha of a total sample of 20.9 ha) showed relatively high diversity and density (**Table 5.6**, p.104). There were 34 species among 471 trees, with an overall density of 94.2 trees/ha. Some trees reached heights of about 45 m, but the upper canopy is generally around 20 m. The largest species here are *Klainedoxa gabonensis*, *Erythrophleum ivorense*, and *Sacoglottis gabonensis* which can, as in the case of one enormous hollow *S. gabonensis*, attain a DBH of 2.5 m. Lianas and epiphytes, mostly ferns and *Begonia* spp., are abundant. Of the shrubs and small tree species that fell mostly outside the enumeration (< 10 cm DBH) *Diospyros preussii* occurs at the highest density. Other common small trees and shrubs include *Massularia acuminata*, *Monodora myristica*, *Ouratea* spp., *Homalium* spp., and *Alchornea cordifolia*. Within the DBH ≥ 10 cm < 30 cm enumeration *Klaineanthus gaboniae* was by far the most common mid-story tree species with a density of 43.17 trees/ha (**Table 5.2**, p. 100). Due to the difficulty of identifying the different *Uapaca* spp. when small, only a combined density estimate of 39.5 trees/ha for the three species present was obtained. Of the three *Uapaca* spp. recorded in this sample only *U. paludosa* was not included in the DBH ≥ 30 cm enumeration (**Table 5.1**, p. 99). Palms also formed an important component of the forest's mid-story. *Elaeis guineensis* and *Raphia hookeri* are common over the whole dry-land subsample while *R. vinifera* occurs more sporadically. Apart from palms, *Klaineanthus gaboniae*, *Rothmannia megalostigma*, *Pentadesma buteracea*, and *Symphonia globulifera* form the largest component of the mid-story. Within the DBH ≥ 30 cm size class, as elsewhere, the two *Uapaca* spp. combined reach the highest density. This is, however, the only part of the study site where *U. heudelotii* is more common than *U. staudtii* indicating its preference for the forest's drier sections. Other common large tree species are *Ctenolophon englerianus*, and *Irvingia gabonensis*. Apart from these species a large number of other species such as a *Dacryodes* sp., *Nauclea diderichii*, and *Lovoa trichilioides* were only recorded in the dry subsample. A further 24 tree species were recorded from this area, but fell outside the increasing the area's actual species richness considerably (**Appendix 2**).

The swamp at Gbanraun dries up only partially during the dry season. Trees here rarely reach heights of more than 30 m and the upper canopy is generally around 20 m. Though overall tree species density is low, 80.8 trees/ha, the vegetation is dense, and the forest "floor" is also covered with members of the Marantaceae and Zingiberaceae. The smaller trees and shrubs here are dominated by *Diospyros preussii*. *Elaeis guineensis* has largely disappeared but *Raphia hookeri* and *R. vinifera* occur at high densities. *Calamus deerratus* is also present, but at low densities. The swamp's most common mid-story tree species are *Cassipourea barteri*, *Uapaca paludosa*, and *Macaranga* spp., with *Klaineanthus gaboniae* being far less common (**Table 5.4**, p. 102). The number of species in the DBH ≥ 30 cm enumeration recorded here, 26, was considerably less than in the dry-land area, especially considering that no other species outside the enumeration were observed.

Though all species but one, *Oxystigma mannii*, were also found in the dry-land section their densities show a number of significant differences. In the swamp *U. staudtii* has the highest density (25.6 trees/ha) and *U. heudelotii* is considerably less common, with a density of 12 trees/ha, and the forest here is also dominated by *Ctenolophon englerianus* (with *Alstonia boonei* the swamp's largest tree), reaching a density of 16.2 trees/ha making it the forest's second most common species. Other common species are *Xylopia staudtii*, *Funtumia africana*, *Hexalobus crispiflorus*, and *Symphonia globulifera*. *Oxystigma mannii* occurred exclusively in two different sections of the swamp where they formed single-dominant stands: however, the largest specimens had been logged. Another tree species underrepresented is *Hallea ledermannii*, which also had been logged in the swamp. An estimated 100 individual *Hallea* trees had been extracted from the study site together with a much smaller number of *Alstonia boonei*, *Cleistopholis patens*, *Coelocaryon preussii*, and *Pycnanthus marchalianus*. It is, therefore, likely that *H. ledermannii*'s density was approximately 2 to 3 trees/ha before logging, a lower density than observed in most other sections of the delta's freshwater swamp forest.

The section of forest between the dry-land area and swamp, the transition zone subsample, was the first to dry out during the dry season. In species composition it resembled the swamp most, with a number of species found characteristic of the dry subsample only in the drier sections (**Table 5.5**, p. 103). Though **Table 5.5** indicates that species richness, 21, is lower than in the swamp, approximately 10 extra species outside the enumeration were identified for this section.

5.2.2. *Ukubie*

At the Ukubie study site a section of swamp was enumerated for trees with a DBH ≥ 30 cm (**Table 5.6**, p. 104). The dry-land forest at Ukubie had been extensively logged, rendering it unsuitable for an enumeration that would include many of the tree species originally present. However, a single day survey of some dry sections near Ogboinbiri, approximately 20 km north-east from Ukubie, indicated that the drier sections here, as in Gbanraun, have a more open forest floor and larger emergents. *Diospyros preussii*, the same *Beilschmiedia* sp., a different *Rothmannia* sp., *Spondianthus preussii*, *Cassipourea barteri*, and *Sterculia tragacantha* were some of the more common smaller trees. Some of the larger trees were of the same species as observed in Gbanraun: *Uapaca heudelotii*, *Xylopia* spp., *Alstonia boonei*, *Klainedoxa gabonensis*, *Pentadesma buteracea*, and *Symphonia globulifera*. *Ctenolophon englerianus* was missing but *Lophira alata*, *Pycnanthus angolensis*, and *Ficus vogeliana*, tree species absent or extremely uncommon in Gbanraun were common here.

The swamp enumerated in Ukubie never got flooded to the same degree as Gbanraun, but the area was more tidal. During high tide the forest floor became soggy, preventing the forest from drying out during the dry season. The only time of year that the forest became flooded to a significant degree was during the Niger flood, but for the rest of the year it was possible to avoid wet feet in most places.

The forest is more open than at Gbanraun and though Marantaceae and Zingiberaceae species are common they were generally restricted to the more open areas. *Diospyros preussii* is also the most common small tree with *Monodora myristica* and *Ouratea* spp. also being present. The mid-story consisted of *Klaineanthus gaboniae*, *Sterculia tragacantha*, *Funtumia africana*, *Cassipourea barteri*, *Macaranga* spp., and *Spondianthus preussii*. As in Gbanraun *Uapaca staudtii* and *U. heudelotii* form a large component of the canopy. However, *Klaineanthus gaboniae*, *Ctenolophon englerianus*, *Pentadesma buteracea*, and *Anthostema aubreyanum* occurred at similar densities, giving the forest a more heterogeneous appearance. The number of species (29) is relatively low, as is the density, only 64.9 trees/ha.

5.3. Comparison of Gbanraun and Ukubie

5.3.1. *Diversity*

Studies of red colobus populations have indicated that these monkeys concentrate their feeding in some of the largest tree species in their habitat, and that these food trees are often clumped in their distribution. This, and their preference for young growth, which results in a high degree of temporal variation for different food items, results in red colobus exploitation of patches that are clumped both spatially and temporally, and often widely dispersed (Oates, 1994*b*). These observations suggest that a forest's diversity, as well as phenology which will be discussed in **Section 5.8**, plays an important role in determining habitat availability for these monkeys.

"Diversity can be measured by recording the number of species, by describing their relative abundances or by using a measure which combines the two components" (Magurran, 1988). A comparison in tree species diversity for the forest of the two study sites should, therefore, may indicate how they spatially differ, which in its turn could confirm the present observations for red colobus habitat requirements, and, possibly, indicate requirement(s) not yet identified.

5.3.2. *Tree species diversity*

Based on the species composition of both sites there appears to be little difference between the two forests. Eight of the top 10 species occurring in Gbanraun are also in Ukubie's top 10. *Rothmannia megalostigma* is the only species common in Gbanraun that was not included in the Ukubie enumeration, although the tree was observed outside the sample plots. *Anthostema aubreyanum*, common in Ukubie, was not included in the Gbanraun enumeration but also observed in very small numbers outside the sample plots. At the family level (**Tables 5.7 & 5.8**, pp. 105 & 106) there is also little difference between the two sites where the top 5 for family rank shows a strong correlation ($r_s = 0.9$, $p=0.1$, $df = 5$).

In order to come to a more accurate measure of both heterogeneity and diversity for the two sites two different indices were calculated: Shannon-Wiener's index H'

$$H' = -\Sigma\, p_i \ln p_i$$

where p_i = the proportion of individuals in the *i*th species, and Simpson's index D

$$D = \Sigma(n_i(n_i-1) / (N(N-1))$$

where n_i = the number of individuals in the *i*th species and N = the total number of individuals (Greig-Smith, 1967; Magurran, 1988). Although Shannon's index takes the evenness in abundance of a species into account a seperate measure of evenness was calculated as follows,

$$E = H' / \ln S$$

where S = species richness (Peet, 1974). Evenness, E, occurs when species are equal, or virtually equal in distribution (Magurran, 1988). Values for E are constrained between 0 and 1.0, which represents equal abundance for all species. An effort was also made to establish differences in diversity between Ukubie and the different subsamples from Gbanraun.

The results are presented in **Table 5.9** (p. 107), and results of additional calculations of H' variance and a t–test show significant differences between the samples (**Table 5.10**, p. 107). Ukubie has not only the highest degree of diversity but is also significantly different, not only from the total Gbanraun enumeration, but also all subsamples. Within Gbanraun the dry-land subsample has, as expected, the highest diversity, but only the transition subsample is significantly different in diversity from the swamp and dry-land section.

Ukubie shows the highest degree of evenness (0.8302) and the total Gbanraun sample the lowest (0.6513). Comparison of the different Gbanraun subsamples indicates little variation not only between them but also with the total enumeration.

Because Shannon's index is biased toward the number of species in the sample without taking their abundance into account, it is useful to also calculate Simpson's index. This index belongs to a second group of diversity indices, also referred to as dominance measures, because they are weighted towards the abundances of the commonest species rather than providing a measure of species richness (Magurran, 1988). As D increases, diversity increases and Simpson's index is, therefore, usually expressed as 1/D. Simpson's index also shows the highest degree of diversity for Ukubie, but to a far greater extend than Shannon's index illustrating how species abundance can affect these indices.

The distribution of species abundance in Ukubie is more even, with the top 9 species occurring at relative densities not dropping below 4%, while only the top 5 species at Gbanraun have relative densities above 4%. Moreover, the top 3 species at Gbanraun account for 65% of the sample but at Ukubie only 39%. The difference in diversity between Gbanraun and Ukubie, therefore, reflects the dominance of a few abundant tree species interspersed with a relatively large number of rare species with low densities at Gbanraun, and the even distribution of Ukubie's top 5 species and lack of rare species with low densities.

Species diversity is often illustrated by means of a species area curve (Reitsma, 1988) (**Figure 5.1**, p. 111). The curve for Ukubie climbs faster and becomes saturated before an area of 1 ha has been sampled. The Gbanraun curve climbs more slowly and remains unsaturated after an area of one hectare has been sampled. This also supports the conclusion reached above that the forest in Gbanraun contains a small number of very common species interspersed with a large number of very rare species. In Ukubie on the other hand the most common species occur at more or less equal densities, giving the forest a more heterogeneous appearance, but there are fewer rare species at low densities.

The lack of correlation for the density ranking of the top five species also corroborates this.

The diversity measures discussed so far all measure intrahabitat diversity (α diversity). The other category of diversity, interhabitat diversity (β diversity), describes change in species composition between sites (Greig-Smith, 1983; Magurran, 1988). Two similarity measures were used to determine the degree of similarity between Gbanraun and Ukubie, as well as that of the three subsamples and Ukubie. Sorenson's index, modified by Bray and Curtis (1957) (also referred to as Czekanowski's index [Curtis, 1959; Greig-Smith, 1983]) is calculated as follows;

$$C_N = 2_{jN} / (aN + bN)$$

where aN = the total number of individuals in site A, bN = the total number of individuals in site B, and jN = the sum of the lower of the two abundances recorded for species found in both sites. The second index applied is the Morisita-Horn index modified by Wolda (1983);

$$CmH = 2\Sigma(an_i bn_i) / (da + db)\, aN \times bN$$

where aN = the total number of individuals at site A, and an_i = the number of individuals in the *i*th species in A. Sorenson's index is strongly influenced by species richness and sample size while the Morisita-Horn index is sensitive to the abundance of the most common species (Wolda, 1981, 1983; Magurran, 1988). In cases of complete similarity both indices are 1 while 0 indicates complete dissimilarity. Sorenson's index (**Table 5.11**, p. 108) indicates that the greatest degree of dissimilarity is found between Ukubie and Gbanraun as a whole (0.88) with the subsamples showing little or no dissimilarity. The Morisita-Horn index (**Table 5.12**, p. 108) also indicates dissimilarity between Gbanraun and Ukubie (0.79), but detects the largest degree of dissimilarity between the dry land, transition, and swamp subsamples. The greatest degree of dissimilarity observed by this index, however, is between Ukubie and the transitory subsample (0.65).

Both indices identify Ukubie as being most dissimilar from Gbanraun as a whole. Sorenson's index, however fails to pick-up on the differences between the subsamples. This is undoubtedly the case because though species diversity is broadly similar, the respective density distributions of these species show considerable differences. This is confirmed by the Morisita-Horn index which, being more sensitive to the variation in density of the most common species, indicates a slightly higher degree of dissimilarity between the swamp and transition zone subsample on the one hand and the dry-land subsample on the other hand.

5.4. Forest Structure

5.4.1. *DBH distribution and Basal Area*

The average DBH measures for the ≥ 30 cm DBH enumerations in Gbanraun and Ukubie are respectively 49.0 cm and 47.5 cm. A one-way analysis of variance indicated no significant difference in the distribution of DBH between the two sites. When comparing the subsamples with one another and with Ukubie some significant differences are observed between the swamp and the dry-land subsamples ($F = 9.72$, $p = 0.005$, $df = 883$), the transition and dry-land subsamples ($F = 7.15$, $p = 0.01$, $df = 914$), and a barely significant difference between Ukubie and the swamp subsample ($F = 3.92$, $p = 0.05$, $df = 1073$). (**Figure 5.2**, p. 112).

Graphically the distribution of basal area per DBH class in a standard forest is roughly asymmetrically bell-shaped with a broad peak between 10 and 50 cm DBH and a long tail for large diameters (Reitsma, 1988). Irregularities in the higher DBH classes can, however, cause significant change as a few trees can more than double the basal area in a size class. In my enumeration this phenomenon is shown by *Ctenolophon englerianus* which, due to a small number of very large trees has the largest basal area in both the Gbanraun and Ukubie DBH ≥ 30 cm enumeration. The only sample where *Ctenolophon englerianus* does not have the largest basal area is the dry-land subsample where *Uapaca heudelotii* has both the highest density and largest basal area (**Table 5.6**, p. 104).

Because there is a direct relationship between basal area and DBH, the analyses of variance among Gbanraun, Ukubie and the subplots are identical to those found for DBH.

5.4.2. *Tree height*

About 50 % of all trees in the DBH ≥ 30 cm enumeration for Gbanraun and Ukubie fell within the 20-25 m height category but the frequency distribution for tree height was different (**Figure 5.3**, p. 113). Average tree height in Gbanraun was 21.6 m and in Ukubie 23.7 m for the DBH ≥ 30 cm enumeration. The respective average heights for the swamp, transition, and dry-land subsamples were 21.9 m, 22.0 m, and 20.5 m. One-way analyses of variance indicated a significant difference between Gbanraun and Ukubie (F = 108.7, p = 0.001, df = 2298), the swamp and dry-land subsamples (F = 21.3, p = 0.001, df = 873), transition and dry-land subsamples (F = 25.7, p = 0.001, df = 908), and the total DBH ≥ 30 cm enumeration for Gbanraun and the dry-land subsample (F = 19.5, p = 0.001, df = 2128).

The DBH/height relation of an individual species reflects its adaptive strategy (Reitsma, 1988). Species that reach intermediate height and DBH are generally understory species that require moderate amounts of light. Trees that may grow to emergents are light demanding and need large gaps to establish themselves. As a result individuals in the smaller diameter classes of this category are rare in undisturbed mature forest, a phenomenon also observed by Richards (1939) in western Nigerian forests. This absence is reflected by the difference in relative dominance of the most common emergent in Gbanraun, *Ctenolophon englerianus*, and the most common understory species, *Klaineanthus gaboniae*. *C. englerianus* has a relative dominance of 33.80% and *K. gaboniae* of 3.84% in the DBH ≥ 30 cm enumeration (33.80), but in the DBH ≥ 10 cm < 30 cm enumeration their relative dominance are respectively 4.73% and 18.42%. This phenomenon could also explain the near absence of *Hallea ledermannii* and relatively small number of other large tree species in the DBH ≥ 10 cm < 30 cm enumeration.

5.4.3. *Crown dimensions*

Average crown diameter in Gbanraun was 8.9 m, and 62.5% of all trees had a crown diameter between 5 and 10 m. Crown diameter in Ukubie was significantly smaller (F = 269.7, p = 0.001, df = 2297) at 6.0 m, but the crown diameter of the majority of trees here also fell between 5 and 10 m. The main difference between the two sites is that 27.3% of all crown diameters fell between 0 and 5 m in Ukubie with only 7.2% between 15 and 20 m while the reverse is the case in Gbanraun with only 4.7% of all trees having a crown diameter of 0 to 5 m and 26.5% falling in the 15 to 20 m group (**Figure 5.4**, p. 114).

5.5. Spatial Distribution of Trees

There are two distribution patterns that depart from randomness: clumping of individuals, or a uniform spacing of individuals. In the tropical rain forest clumped patterns predominate, while regular patterns are seldom found (Greig-Smith, 1983).

Coefficients of dispersion (variance/mean) were calculated for all tree species included in the phenology samples of Gbanraun and Ukubie. In Gbanraun the sample was further subdivided to compare the coefficients of dispersion for these tree species between the three identified zones, swamp, transition, and dry land (**Table 5.13**, p. 109). A t-test was used to determine if each coefficient of dispersion showed significant difference between the observed ratio and unity.

Before interpreting the results it is important to consider the following: Pielou (1969) indicates that it is unreasonable to postulate that a pattern is random when it does not show significant clumping, because there is no ground to favor randomness over any other imaginable pattern. As used in this study the coefficient of dispersion is simply an estimate of a population parameter. Therefore, if a coefficient of dispersion is found to be close to 1 this should not lead to the immediate conclusion that the pattern is indeed random. That conclusion is valid only if observations from the field support this.

The coefficients of dispersion in Ukubie show no significant deviation from a random pattern. Only *Uapaca heudelotii* shows some, but no significant, clumping which probably reflects its preference for drier spots. In Gbanraun only 4 out of 11 species show a significant degree of clumping, which was supported by observations from the field, indicate that here also the distribution of most species is also random. The swamp subsample shows a clumped distribution for 2 species, the transition subsample for 4, and the dry-land subsample for 5. Since the transition subsample most resembles the total sample in composition (a mosaic of dry and wet sections) it is not surprising it also resembles the total sample in terms of spatial distribution.

The swamp has the lowest degree of spatial diversity. *Uapaca heudelotii* shows the highest degree of clumping, which is probably related to its occupation of the drier spots. The second tree species here showing significant clumping is *Ctenolophon englerianus* that also has the highest relative density in the swamp (20.05).

The transitory sample shows significant clumping for four different species. The *Uapaca* spp. reflect their respective preference for the drier and wetter areas, and clumping presumably occurs as the result of the wet/dry mosaic of this area. *Xylopia staudtii* has a preference for wet areas, also resulting in its absence in the drier areas and, therefore, a clumped distribution.

In the dry-land subsample the same three species as in the transition subsample show a clumped dispersal pattern, probably for the same reasons. *Klaineanthus gaboniae*, a species that clearly prefers dry areas, also shows a clumped pattern. *Symphonia globulifera*'s clumped distribution reflects its preference for wetter areas.

In order to determine whether there were significant differences in spatial distribution between the sites indices of clumping were calculated as follows:

$$\frac{\text{Observed variance}}{\text{Observed mean}} - 1$$

This allows for a test of significance of the difference between values obtained from the different samples, and takes the form of calculating:

$$\omega = -0.5 \ln v_1\lambda_2 / \lambda_1 v_2$$

where λ_1 and λ_2 are the observed means and v_1, v_2 are the observed variances of the two sets of data (Greig-Smith, 1983). When ω lies outside the range $\pm 2.5 / \sqrt{(N - 1)}$, where N is the number of samples in each set, a significant difference for the coefficient of dispersal is indicated. For this procedure equal sample sizes are a requirement. As a result only the Gbanraun subsamples could be compared with each other, and with a subsample of equal size from Ukubie (**Table 5.14**, p. 110). Though repeated comparisons affect the level of significance to some degree, the number of comparisons in this case is too small to affect the results significantly. Only one significant difference in distribution was found within the Gbanraun study site. *Uapaca staudtii*'s distribution was significantly different in the dry subsample, reflecting this species' preference for the wet pockets in this area. More differences were found between Ukubie and the three subsamples. *U. heudelotii*, *Symphonia globulifera*, and *Coelocaryon preusii*'s distribution in Ukubie is significantly different than their distribution in the three subsamples. *U. staudtii* only shows a significant difference when Ukubie is compared to the dry subsample.

5.6. Tree Morphology

Morphological data can be used to establish an accurate typology of rain forest vegetation (Reitsma, 1988; Richards, 1996). Though it is outside the scope of this study to pay attention to all morphological characteristics, some attention was paid to root systems that often characterize trees in freshwater forest (Richards, 1996). In southern

Nigeria 7.3% of all trees ≥ 10 cm DBH in a section of freshwater forest had stilt roots (Richards, 1939). In Gbanraun this number is considerably higher with 40% of all trees ≥ 10 cm DBH, and in Ukubie 36% of all trees ≥ 30 cm DBH having stilt roots. Apart from this adaptation a large number of tree species have pneumorhizae: aerating or "breathing" roots (Richards, 1996). They often have the appearance of loops or knees and meander for long distances over the forest floor. In Gbanraun *Hallea ledermannii*, *Symphonia globulifera* and *Pycnanthus marchalianus* have such roots. *Xylopia staudtii* shows another variety by sending down branches which form lateral, stilt-like roots (Jenik, 1978). Nearly all trees of the swamp, 56%, showed either the adaptations mentioned above or they showed another adaptation. *Alstonia boonei*, for example, produced large lenticels on its exposed roots that also appear to function as pneumorhizae (Jenik, 1967).

The structure of a root system plays an important role in the determination of a tree's survivability. In the rain forest heavy winds and failure of the root system under stress of gravity are probably the most common cause of death (Richards, 1996). Growing to a large size on soft, wet soil must pose some specific structural problems. Though no systematic data were collected, Gbanraun showed ample evidence of this in the number of trees that fell over along transects each month. In most cases there was no visible damage to the tree, suggesting that a healthy tree had been uprooted. Apart from stilt roots, buttresses are the other most common structural support found in rain forest trees. In the Gbanraun swamps there was only one common tree species, *Alstonia boonei*, with buttresses. It may be, therefore, that a stilt-root system is the best available structural adaptation for growing on swampy soils.

5.7. Summary of Forest Composition and Structure

In terms of diversity, the forest at Ukubie shows a significantly higher degree of diversity than that at Gbanraun (Table 5.11). This difference in diversity is caused by the dominance at Gbanraun of three tree species (65%) interspersed with a relatively large number of rare species, while in Ukubie the top 10 species account for 82% and fewer total species were recorded in the sample.

The distribution of DBH and basal area, which have a direct relationship, show no significant difference between Gbanraun and Ukubie. There is a significant difference in average tree height between Gbanraun (21.6 m) and Ukubie (23.7 m), but average crown diameter is considerably larger in Gbanraun (8.9 m) than Ukubie (6.0 m). Though the *Uapaca* spp. in both Gbanraun and Ukubie have the highest relative density (50.70% and 24.96%), in terms of relative dominance *Ctenolophon englerianus* is by far the most important species (33.80% and 26.62%).

Coefficients of dispersion for Ukubie show no significant deviation from a random pattern. Only *Uapaca heudelotii* shows some, but no significant, clumping which probably reflects its preference for drier spots. In Gbanraun only 4 out of 11 species show a significant degree of clumping indicating that here also the distribution of most species is relatively uniform. *Uapaca heudelotii* shows the highest degree of clumping confirming that this tree species is restricted to the drier spots. The second tree species here showing significant clumping is *Ctenolophon englerianus*, which also has the highest relative density in the swamp (20.05%). This suggests that *C. englerianus* is not only more common in the swamp, but that it occurs here in aggregations.

Significant differences in dispersion patterns were found between Ukubie and the three Gbanraun subsamples. The distributions of *Uapaca heudelotii*, *Symphonia globulifera*, and *Coelocaryon preusii*'s at Ukubie are significantly different from their distributions in the Gbanraun subsamples. Overall tree species dispersion in Gbanaraun cannot, however, be considered significantly different from Ukubie.

5.8. Phenology

5.8.1. *Young leaf production*

Young leaf production saw some seasonal variation at Gbanraun. In terms of the percentage of trees with young leaves, peaks of leaf production were registered in both the wet and the dry forest samples (**Figure 5.5**, p. 115). The first peak occurred during December 1996 when approximately 80% of the trees had young leaves, which was followed by a similar peak during May 1997. The third peak occurred during September 1997 when all trees in the swamp sample, and more than 80% in the dry sample had young leaves. During the December peak of 1997 nearly all trees in both samples carried small quantities of young leaves, and this phenomenon extended into January 1998. Ukubie showed a similar pattern, with peaks during September 1997 and December 1997/January 1998. The minimum percent of trees with young leaves in the Gbanraun dry sample was 25.3% during March 1997. In the wet sample the minimum was 34.3% in February 1997. The phenology sample in Ukubie was not monitored during some of these months, but the August 1997 showed a minimum of 57.2%. The average percentage of trees with young leaves over the whole phenological sample in the Gbanraun dry-land area was 58.7% (s.d. = 24.7), in Gbanraun swamp forest 69.1% (s.d. = 21.6), and in Ukubie 76.94% (s.d. = 17.0). A t-tests for those months with shared samples indicated no significant differences in the percentage of trees with young leaves between the three sites.

The total quantity of young leaf production showed a somewhat different picture. Some of the tree species included in the phenology samples produced young leaves for most of the year but often at low quantities. Therefore, when the quantity of young leaves produced in each month was calculated, only one peak during December 1996 was observed, when 32.8% of all leaves in the dry-land area and 28.9 % in the swamp sample were young (**Figure 5.8**, p. 118). This pattern did not repeat itself exactly during December of 1997 but the phenology sample for January 1998 indicates an increase in young leaf production. This may have been the result of the late arrival of the rainy season that year. Unfortunately no data are available for Ukubie during February 1997, but the data collected for the other months indicate a similar pattern. A t-test for those months that the samples shared also indicated no significant differences between the sites in the percentage of young leaves present each month.

A comparison of the forests of Gbanraun and Ukubie with that of the Douala-Edea Reserve in Cameroon (the forest closest to the delta for which data could be found) shows a similar pattern. Douala-Edea also has high rainfall (3000-4000 mm) and relatively dry months from December through January. Young leaf production takes place throughout the year at Douala-Edea with, as in Gbanraun and Ukubie, a peak at the beginning and end of the dry season (Gartlan in Richards, 1996). However, despite these similarities no red colobus are present. Though no data from other red colobus study sites indicated similar high levels of young leaf production, data for Kibale also suggests a relatively even distribution of young growth (Struhsaker, 1975, 1997). Even though Kibale sees much less precipitation than Gbanraun it typically falls in every month, and despite substantial variation in phenological patterns over the long period that Kibale Forest's phenology has been monitored, young growth is produced during every month of the year. Tiwai Island, Sierra Leone however, shows a much higher degree of seasonality (Dasilva, 1989, 1994; Davies *et al.*, 1998). Plant part production followed a highly seasonal pattern with a serious food-supply bottleneck during two months of the year when only mature leaf parts were abundant.

5.8.2. *Flower and fruit production*

Flower production showed a less obvious pattern than young leaves and fruit for most of the year (**Figure 5.6**, p. 116). The only peak was observed in January 1998 when 52.6% of the trees in the Gbanraun swamp sample and 67.3% of all trees in the Ukubie sample flowered. Though the Gbanraun "dry" forest sample also saw an increase over the two previous months flower production peaked here in April. The average percentage of trees with flowers over the whole phenological sample in Gbanraun dry-land area was 31.8% (s.d. = 10.7), 35.4% (s.d. = 8.9) in the Gbanraun swamp, and 39.3% (s.d. = 12.7) in Ukubie. Paired sample t-tests for those months that the samples shared indicated there were also no significant differences in the percentage of trees with flowers between the three sites.

Fruit production also showed two peaks of production during the phenology sampling (**Figure 5.7**, p. 117). The first occurred during February 1997 when 36.4% of all trees in the dry and 54.3% of all trees in the swamp sample carried fruits. The second peak was in September 1997 when 69.4% of all trees in the dry-land area and 83.8% of all trees in the swamp sample carried fruits. Ukubie showed the same pattern, also peaking in September 1997 at 79.2%. The average percentage of trees with fruit over the phenological sample in Gbanraun dry land was 33.1% (s.d. = 19.4), 58.9% (s.d. = 111.9) in Gbanraun swamp, and 40.77% (s.d. = 19.9) in Ukubie. Paired sample t-tests for those months that the samples shared indicated no significant differences in the percentage of trees with fruit between the three sites.

Both fruit and flower production are high at the two sites. Of the 14 species sampled six (43%) carried flowers and/or fruits in small numbers for most of the year The lack of significant differences in phenology between the two sites also indicates that all trees in the phenology samples were producing young leaves, flowers and fruits at approximately the same time. Given the problems of establishing a measure of actual quantities of these plant parts produced I could not determine if any significant differences existed there. My phenology records, however, suggest that this was not the case.

5.8.3. *Summary phenology*

All phenology samples recorded high levels of new plant growth for much of the year. The average percentage of trees with young leaves was over 60%, a high productivity rate indicative of a forest without a dry season. A comparison with young leaf production in a forest in Borneo (Mitchell, 1994), which is also considered to be strongly aseasonal, indicates that the average percentage of trees with young leaves was considerable lower (20%). This suggests that the sampled section of the Niger Delta forest in this study is highly productive.

Comparisons in productivity and temporal variation for the same species in the three different samples indicated a lack of significant differences both between the subsamples, and between Gbanraun and Ukubie. This indicates that though there are significant structural and spatial differences between the two sites, temporal variation is lacking.

Table 5.1: *Vegetation enumeration Gbanraun study Area; DBH ≥ 30 cm.*

SPECIES	FAMILY	N	DENSITY	R. DENS.	BASAL AREA	R. DOM.
Uapaca staudtii *	Euphorbiaceae	521	26.05	31.52	4.18	20.02
Uapaca heudelotii *	Euphorbiaceae	317	15.85	19.18	2.45	11.74
Ctenolophon englerianus *	Ctenolophonaceae	238	11.90	14.40	7.06	33.80
Klaineanthus gaboniae	Euphorbiaceae	95	4.75	5.75	0.80	3.84
Xylopia staudtii *	Annonaceae	68	3.40	4.11	0.58	2.77
Rothmannia megalostigma	Rubiaceae	44	2.20	2.66	0.30	1.42
Symphonia globulifera *	Guttiferae	42	2.10	2.54	0.25	1.22
Funtumia africana	Apocynaceae	41	2.05	2.48	0.28	1.35
Pentadesma butyraceae *	Guttiferae	36	1.80	2.18	0.25	1.18
Hexalobus crispiflorus *	Annonaceae	32	1.60	1.94	0.29	1.40
Alstonia boonei *	Apocynaceae	28	1.40	1.69	1.96	9.40
Macaranga spp.	Euphorbiaceae	27	1.35	1.63	0.20	0.95
Irvingia gabonensis *	Irvingiaceae	20	1.00	1.21	0.34	1.61
Coelocaryon preussii *	Myristicaceae	18	0.90	1.09	0.19	0.93
Pycnanthus marchalianus *	Myristicaceae	17	0.85	1.03	0.14	0.69
Syzygium owariense	Myrtaceae	15	0.75	0.91	0.20	0.96
Erythrophleum ivorense *	Ceasalpinioideae	11	0.55	0.67	0.16	0.74
Spondianthus preussii	Euphorbiaceae	10	0.50	0.60	0.09	0.41
Musanga cecropioides	Moraceae	9	0.45	0.54	0.04	0.21
Hallea ledermannii *	Rubiaceae	9	0.45	0.54	0.16	0.78
Oxystigma mannii *	Ceasalpinioideae	8	0.40	0.48	0.08	0.37
Cassipouria barteri	Rhizophoraceae	8	0.40	0.48	0.07	0.35
Spathandra blakeoides *	Melastomataceae	4	0.20	0.24	0.05	0.25
Dacryodes sp. *	Burseraceae	4	0.20	0.24	0.04	0.18
Cleistopholis patens *	Annonaceae	4	0.20	0.24	0.05	0.22
Anthocleista sp.	Loganiaceae	3	0.15	0.18	0.04	0.20
Sacoglottis gabonensis *	Humiriaceae	3	0.15	0.18	0.29	1.39
Klainedoxa gabonensis *	Irvingiaceae	2	0.10	0.12	0.13	0.65
Discoglypremna caloneura	Euphorbiaceae	2	0.10	0.12	0.02	0.08
Sterculia tragacantha	Sterculiaceae	2	0.10	0.12	0.01	0.05
Xylopia sp. *	Annonaceae	2	0.10	0.12	0.02	0.10
Mammea africana *	Guttiferea	2	0.10	0.12	0.08	0.37
Lovoa trichilioides *	Miliaceae	1	0.05	0.06	—	0.03
Guarea cedrata *	Miliaceae	1	0.05	0.06	—	0.03
Nauclea diderichii *	Rubiaceae	1	0.05	0.06	—	0.03
Unidentified (4 spp.)		8	0.40	0.48	0.06	0.28
TOTAL		**653**	**82.65**	**100**	**20.86**	**100**

Total area sampled is 20 ha.

Density = relative density species A / total density of all species × 100.

Relative density (R. DENS) = # species A / total individuals all species × 100.

Basal area = $m^2.ha^{-1}$.

Relative dominance (R. DOM) = basal area species / total basal area × 100.

* = Canopy species.

Table 5.2: *Vegetation enumeration at Gbanraun study area: DBH ≥ 10 cm < 30cm.*

SPECIES	FAMILY	N	DENSITY	R. DENS.	BASAL AREA	R. DOM.
Klaineanthus gaboniae	Euphorbiaceae	177	43.17	19.60	0.86	18.42
Uapaca spp.	Euphorbiaceae	162	39.51	17.94	0.91	19.65
Xylopia staudtii	Annonaceae	78	19.02	8.64	0.34	7.36
Macaranga spp.	Euphorbiaceae	57	13.90	6.31	0.28	6.02
Rothmannia megalostigma	Rubiaceae	45	10.98	4.98	0.26	5.56
Ctenolophon englerianus	Ctenolophonaceae	42	10.24	4.65	0.22	4.73
Hexalobus crispiflorus	Annonaceae	41	10.00	4.54	0.21	4.48
Funtumia africana	Apocynaceae	38	9.27	4.21	0.27	5.81
Cassipouria barteri	Rhizophoraceae	33	8.05	3.65	0.17	3.60
Spondianthus preussii	Euphorbiaceae	31	7.56	3.43	0.16	3.34
Symphonia globulifera	Guttiferae	21	5.12	2.33	0.14	2.98
Oxystigma mannii	Ceasalpinioideae	21	5.12	2.33	0.10	2.06
Pycnanthus marchalianus	Myristicaceae	17	4.16	1.88	0.07	1.59
Beilschmiedia sp.	Laureceae	16	3.90	1.77	0.06	1.39
Pentadesma butyraceae	Guttiferae	15	3.66	1.66	0.08	1.65
Sterculia tragacantha	Sterculiaceae	13	3.17	1.44	0.05	1.13
Coelocaryon preussii	Myristicaceae	9	2.20	1.00	0.06	1.39
Musanga cecropioides	Moraceae	8	1.95	0.89	0.06	1.29
Ouratea sp.	Ochnaceae	6	1.46	0.66	0.01	0.31
Irvingia gabonensis	Irvingiaceae	5	1.22	0.55	0.03	0.62
Garcinia smeathmannii	Guttiferea	5	1.22	0.55	0.02	0.41
Monodora myristica	Annonaceae	4	0.98	0.44	0.02	0.46
Syzygium owariense	Myrtaceae	3	0.73	0.33	0.04	0.82
Xylopia sp.	Annonaceae	3	0.73	0.33	0.02	0.46
Cleistopholis patens	Annonaceae	3	0.73	0.33	0.01	0.31
Cola nitida	Sterculiaceae	2	0.49	0.22	—	0.21
Dacryodes sp.	Burseraceae	2	0.49	0.22	0.02	0.46
Vitex grandifolia	Verbenaceae	2	0.49	0.22	—	0.15
Hallea ledermannii	Rubiaceae	2	0.49	0.22	—	0.10
Zanthoxylum gilletii	Rutaceae	2	0.49	0.22	—	0.10
Treculia africana	Moraceae	2	0.49	0.22	—	0.10
Staudtia stipitata	Myristicaceae	1	0.24	0.11	—	0.05
Spathandra blakeoides	Melastomataceae	1	0.24	0.11	—	0.05
Mammea africana	Guttiferea	1	0.24	0.11	—	0.15
Sacoglottis gabonensis	Humiriaceae	1	0.24	0.11	—	0.05
Anthostema aubreyanum	Euphorbiaceae	1	0.24	0.11	—	0.05
Erythrophleum ivorense	Ceasalpinioideae	1	0.24	0.11	—	0.10
Hannoa kleineana	Simaroubaceae	1	0.24	0.11	0.01	0.31
Klainedoxa gabonensis	Irvingiaceae	1	0.24	0.11	—	0.05
Guarea cedrata	Miliaceae	1	0.24	0.11	—	0.10
Diospyros preussii	Ebenaceae	1	0.24	0.11	—	0.05
Anthocleista sp.	Loganiaceae	1	0.24	0.11	—	0.15
Unidentified (4 spp.)		4	0.98	0.44	0.02	0.46
TOTAL		**903**	**220.24**	**100**	**4.50**	**100**

Total area sampled is 4.18 ha.

Density = relative density species A / total density of all species × 100.

Relative density (R. DENS) = # species A / total individuals all species × 100.

Basal area = $m^2.ha^{-1}$.

Relative dominance (R. DOM.) = basal area species / total basal area × 100.

Table 5.3: *Vegetation enumeration Ukubie study area: DBH ≥ 30 cm.*

SPECIES	FAMILY	N	DENSITY	R. DENS.	BASAL AREA	R. DOM.
Uapaca staudtii *	Euphorbiaceae	95	9.50	14.64	1.32	9.12
Klaineanthus gaboniae	Euphorbiaceae	84	8.40	12.94	0.88	6.12
Ctenolophon englerianus *	Ctenolophonaceae	73	7.30	11.25	3.84	26.62
Uapaca heudelotii *	Euphorbiaceae	67	6.70	10.32	0.90	6.23
Pentadesma buteraceae *	Guttiferae	55	5.50	8.47	0.93	6.43
Anthostema aubreyanum *	Euphorbiaceae	41	4.10	6.32	0.96	6.66
Xylopia staudtii *	Annonaceae	37	3.70	5.70	0.53	3.67
Coelocaryon preusii *	Myristicaceae	32	3.20	4.93	0.53	3.70
Hexalobus crispiflorus *	Annonaceae	30	3.00	4.62	0.45	3.11
Pycnanthus marchalianus *	Myristicaceae	17	1.70	2.62	0.29	2.02
Alstonia boonei *	Apocynaceae	15	1.50	2.31	2.39	16.59
Sterculia tragacantha	Sterculiaceae	14	1.40	2.16	0.23	1.61
Funtumia africana	Apocynaceae	13	1.30	2.00	0.17	1.16
Musanga cecropioides	Moraceae	12	1.20	1.85	0.13	0.87
Cassipouria barteri	Rizophoraceae	12	1.20	1.85	0.13	0.92
Macaranga spp.	Euphorbiaceae	11	1.10	1.69	0.13	0.90
Symphonia globulifera *	Guttiferae	10	1.00	1.54	0.09	0.64
Hallea ledermannii *	Rubiaceae	6	0.60	0.92	0.08	0.55
Lovoa trichilioides *	Miliaceae	5	0.50	0.77	0.06	0.40
Spondianthus preussii	Euphorbiaceae	4	0.40	0.62	0.04	0.29
Chrysophyllum pruniforme *	Sapotaceae	3	0.30	0.46	0.07	0.45
Ficus vogeliana	Moraceae	2	0.20	0.31	0.09	0.64
Cleistopholis patens *	Annonaceae	2	0.20	0.31	0.04	0.31
Xylopia sp. *	Annonaceae	2	0.20	0.31	0.01	0.07
Monodora myristica	Annonaceae	1	0.10	0.15	0.01	0.06
Kleinedoxa gabonensis *	Irvingiaceae	1	0.10	0.15	0.02	0.13
Unidentified (3 spp.)		5	0.50	0.77	0.10	0.71
TOTAL		**649**	**64.90**	**100**	**14.42**	**100**

Total area sampled is 10 ha.

Density = relative density species A / total density of all species × 100.

Relative density (R. DENS.) = # species A / total individuals all species × 100.

Basal area = $m^2.ha^{-1}$

Relative dominance (R. DOM.)= basal area species / total basal area × 100.

* = Canopy species.

Table 5.4: *Vegetation enumeration Gbanraun study area: swamp subsample;*

DBH ≥ 30 cm.

SPECIES	N	DENSITY	RELATIVE DENSITY	BASAL AREA	RELATIVE DOMINANCE
Uapaca staudtii	128	25.60	31.68	3.90	19.37
Ctenolophon englerianus	81	16.20	20.05	8.71	43.44
Uapaca heudelotii	60	12.00	14.85	1.85	9.17
Xylopia staudtii	23	4.60	5.69	0.67	3.36
Funtumia africana	16	3.20	3.96	0.33	1.63
Hexalobus crispiflorus	13	2.60	3.22	0.30	1.50
Symphonia globulifera	10	2.00	2.48	0.30	1.47
Macaranga spp.	10	2.00	2.48	0.24	1.18
Klaineanthus gaboniae	9	1.80	2.23	0.28	1.03
Pycnanthus marchalianus	8	1.60	1.98	0.27	1.36
Oxystigma mannii	7	1.40	1.73	0.33	1.62
Rothmannia megalostigma	7	1.40	1.73	0.17	0.84
Alstonia boonei	6	1.20	1.49	1.89	9.45
Hallea ledermannii	5	1.00	1.24	0.31	1.52
Coelocaryon preussii	4	0.80	0.99	0.17	0.82
Syzygium owariense	4	0.80	0.99	0.12	0.59
Pentadesma butyraceae	3	0.60	0.74	0.10	0.49
Cassipouria barteri	2	0.40	0.50	0.03	0.15
Musanga cecropioides	2	0.40	0.50	0.04	0.18
Spondianthus preussii	1	0.20	0.25	0.03	0.17
Cleistopholis patens	1	0.20	0.25	0.04	0.19
Xylopia sp.	1	0.20	0.25	0.04	0.18
Discoglypremna caloneura	1	0.20	0.25	0.04	0.22
Unidentified	2	0.40	0.50	0.06	0.30
TOTAL	**404**	**80.80**	**100**	**20.22**	**100**

Total area sampled is 5 ha.
Density = relative density species A / total density of all species × 100.
Relative density = # species A / total individuals all species × 100.
Basal area = $m^2.ha^{-1}$
Relative dominance = basal area species / total basal area × 100.

Table 5.5: *Vegetation emmeration Gbanraun study area: transitional subsample; DBH ≥ 30 cm.*

SPECIES	N	DENSITY	RELATIVE DENSITY	BASAL AREA	RELATIVE DOMINANCE
Uapaca staudtii	193	38.60	43.96	5.66	25.65
Ctenolophon englerianus	76	15.20	17.31	8.99	40.75
Uapaca heudelotii	43	8.60	9.79	1.00	4.55
Xylopia staudtii	19	3.80	4.33	0.53	2.41
Funtumia africana	13	2.60	2.96	0.29	1.31
Alstonia boonei	12	2.40	2.73	3.38	15.32
Klaineanthus gaboniae	12	2.40	2.73	0.27	1.24
Symphonia globulifera	9	1.80	2.05	0.18	0.80
Pentadesma butyraceae	8	1.60	1.82	0.18	0.82
Syzygium owariense	8	1.60	1.82	0.21	0.94
Macaranga spp.	8	1.60	1.82	0.19	0.84
Rothmannia megalostigma	7	1.40	1.59	0.14	0.62
Hexalobus crispiflorus	7	1.40	1.59	0.26	1.19
Coelocaryon preussii	5	1.00	1.14	0.21	0.97
Pycnanthus marchalianus	4	0.80	0.91	0.07	0.33
Erythrophleum ivorense	4	0.80	0.91	0.18	0.82
Cassipouria barteri	4	0.80	0.91	0.08	0.35
Spathandra blakeoides	2	0.40	0.46	0.06	0.28
Musanga cecropioides	2	0.40	0.46	0.05	0.21
Anthocleista sp.	1	0.20	0.23	0.02	0.08
Mammea africana	1	0.20	0.23	0.04	0.08
TOTAL	**439**	**87.80**	**100**	**21.99**	**100**

Total area sampled is 5 ha.
Density = relative density species A / total density of all species × 100.
Relative density = # species A / total individuals all species × 100.
Basal area = m^2.ha^{-1}
Relative dominance = basal area species / total basal area × 100.

Table 5.6: *Vegetation enumeration Gbanraun study area; dry subsample: DBH ≥ 30 cm.*

SPECIES	**N**	**DENSITY**	**RELATIVE DENSITY**	**BASAL AREA**	**RELATIVE DOMINANCE**
Uapaca heudelotii	148	29.60	31.42	12.65	45.53
Uapaca staudtii	80	16.00	16.99	2.12	7.62
Klaineanthus gaboniae	67	13.40	14.23	1.56	5.62
Ctenolophon englerianus	27	5.40	5.73	3.38	12.16
Irvingia gabonensis	20	4.00	4.25	1.41	5.07
Rothmannia megalostigma	20	4.00	4.25	0.44	1.60
Pentadesma butyraceae	17	3.40	3.61	0.43	1.55
Symphonia globulifera	13	2.60	2.76	0.29	1.05
Xylopia staudtii	11	2.20	2.34	0.27	0.97
Spondianthus preussii	7	1.40	1.49	0.26	0.92
Hexalobus crispiflorus	7	1.40	1.49	0.38	1.37
Coelocaryon preussii	6	1.20	1.27	0.31	1.12
Erythrophleum ivorense	6	1.20	1.27	0.43	1.56
Macaranga spp.	6	1.20	1.27	0.18	0.66
Funtumia africana	5	1.00	1.06	0.13	0.47
Dacryodes sp.	4	0.80	0.85	0.16	0.57
Sacoglottis gabonensis	3	0.60	0.64	1.22	4.38
Syzygium owariense	2	0.40	0.42	0.34	1.21
Hallea ledermannii	2	0.40	0.42	0.09	0.31
Klainedoxa gabonensis	2	0.40	0.42	0.56	2.03
Spathandra blakeoides	2	0.40	0.42	0.16	0.56
Musanga cecropioides	2	0.40	0.42	0.05	0.17
Anthocleista sp.	2	0.40	0.42	0.16	0.57
Cassipouria barteri	1	0.20	0.21	0.02	0.07
Pycnanthus marchalianus	1	0.20	0.21	0.02	0.06
Cleistopholis patens	1	0.20	0.21	0.05	0.19
Alstonia boonei	1	0.20	0.21	0.20	0.72
Mammea africana	1	0.20	0.21	0.28	1.01
Lovoa trichilioides	1	0.20	0.21	0.02	0.08
Nauclea diderichii	1	0.20	0.21	0.03	0.11
Unidentified (4 spp.)	5	1.00	1.06	0.19	0.68
Total	**471**	**94.20**	**100**	**27.79**	**100**

Total area sampled is 5 ha.

Density = relative density species A / total density of all species × 100.

Relative density = # species A / total individuals all species × 100.

Basal area = $m^2.ha^{-1}$

Relative dominance = basal area species / total basal area × 100.

Table 5.7: *Total number of trees in each family, and rank of the top 10 families at each site.*

FAMILY	GBANRAUN		GBANRAUN 1		GBANRAUN 2		UKUBIE	
	N	RANK	N	RANK	N	RANK	N	RANK
Euphorbiaceae	1702	(1)	972	(1)	428	(1)	302	(1)
Ctenolophonaceae	353	(2)	238	(2)	42	(4)	73	(2)
Annonaceae	307	(3)	106	(3)	129	(2)	72	(3)
Guttiferae	187	(4)	80	(4)	42	(4)	65	(4)
Apocynaceae	135	(5)	69	(5)	38	(5)	28	(6)
Myristicaceae	111	(6)	35	(7)	27	(7)	49	(5)
Rubiaceae	107	(7)	54	(6)	47	(3)	6	(10)
Rhizophoraceae	53	(8)	8		33	(6)	12	(9)
Ceasalpinioideae	41	(9)	19	(9)	22	(8)	-	
Moraceae	33	(10)	9		10		14	(7)
Sterculiaceae	31		2		15	(10)	14	(8)
Irvingiaceae	29		22	(8)	6		1	
Myrtaceae	18		15	(10)	3		-	
Laureceae	16		-		16	(9)	-	
Miliaceae	8		2		1		5	
Ochnaceae	6		-		6		-	
Burseraceae	6		4		2		-	
Melastomataceae	5		4		1		-	
Humiriaceae	4		3		1		-	
Loganiaceae	4		3		1		-	
Sapotaceae	3		-		-		3	
Rutaceae	2		-		2		-	
Verbenaceae	2		-		2		-	
Simaroubaceae	1		-		1		-	
Ebenaceae	1		-		1		-	
TOTAL	**3165**		**1645**		**876**		**644**	

GBANRAUN 1 = DBH ≥ 30 cm.
GBANRAUN 2 = DBH ≥ 10 cm < 30cm.
UKUBIE = DBH ≥ 30 cm.

Table 5.8: *Relative diversity of all tree species with a DBH ≥ 30 cm from the Gbanraun and Ukubie vegetation enumerations.*

FAMILY	GBANRAUN		GBANRAUN 1		GBANRAUN 2		UKUBIE	
	RD	RANK	RD	RANK	RD	RANK	RD	RANK
Euphorbiaceae	16.33	(1)	17.14	(1)	18.18	(1)	23.08	(1)
Ctenolophonaceae	2.04	(5)	2.86	(5)	2.27	(6)	3.85	(4)
Annonaceae	10.20	(2)	11.43	(2)	11.36	(2)	19.23	(2)
Guttiferae	8.16	(3)	8.57	(3)	9.09	(3)	7.69	(3)
Apocynaceae	4.08	(4)	5.71	(4)	2.27	(6)	7.69	(3)
Myristicaceae	6.12	(4)	5.71	(4)	6.82	(4)	7.69	(3)
Rubiaceae	6.12	(4)	8.57	(3)	4.55	(5)	3.85	(4)
Rhizophoraceae	2.04	(5)	2.86	(5)	2.27	(6)	3.85	(4)
Ceasalpinioideae	4.08	(4)	5.71	(4)	4.55	(5)	-	
Moraceae	6.12	(4)	2.86	(5)	4.55	(5)	7.69	(3)
Sterculiaceae	2.04	(5)	2.86	(5)	4.55	(5)	3.85	(4)
Irvingiaceae	4.08	(4)	5.71	(4)	4.55	(5)	3.85	
Myrtaceae	2.04	(5)	2.86	(5)	2.27	(6)	-	
Laureceae	2.04	(5)	-		2.27	(6)	-	
Miliaceae	4.08	(4)	5.71	(4)	2.27	(6)	3.85	(4)
Ochnaceae	2.04	(5)	-		2.27	(6)	-	
Burseraceae	2.04	(5)	2.86	(5)	2.27	(6)	-	
Melastomataceae	2.04	(5)	2.86	(5)	2.27	(6)	-	
Humiriaceae	2.04	(5)	2.86	(5)	2.27	(6)	-	
Loganiaceae	2.04	(5)	2.86	(5)	2.27	(6)	-	
Sapotaceae	2.04	(5)	-		-		3.85	(4)
Rutaceae	2.04	(5)	-		2.27	(6)	-	
Verbenaceae	2.04	(5)	-		2.27	(6)	-	
Simaroubaceae	2.04	(5)	-		2.27	(6)	-	
Ebenaceae	2.04	(5)	-		2.27	(6)	-	

RD: relative diversity = # of species in a family / total # of species × 100.
GBANRAUN 1 = DBH ≥ 30 cm.
GBANRAUN 2 = DBH ≥ 10 cm < 30cm.
UKUBIE = DBH ≥ 30 cm.

Table 5.9: *Tree species diversity indices for all tree species with a DBH ≥ 30 cm included in the Gbanraun and Ukubie enumerations; Shannon-Wiener* (H'), *Evenness* (E), *and Simpson's index* (D).

	GBANRAUN DBH ≥ 30 cm					UKUBIE DBH ≥ 30 cm		GBANRAUN DBH≥10cm <30cm
	SWAMP	**TRANS.**	**DRY**	**S+T+D**	**TOTAL**	**TOTAL**	**S.S.**	**TOTAL**
S	24	21	31	35	36	27	24	43
H'	2.2408	2.0136	2.3821	2.3375	2.3442	2.7362	2.6687	2.588
E	0.7051	0.6614	0.6937	0.6575	0.6513	0.8302	0.8397	0.6881
1/D	6.4893	4.2248	5.8858	6.2267	10.0806	12.1065	11.8765	10.5932

S = # of species. All unidentified species in each sample were included as 1 species.

Table 5.10: *Presence of significant difference in tree species diversity (H') between the subsamples and samples from Gbanraun and Ukubie.*

		GBANRAUN				UKUBIE
		TRANS	**DRY**	**S+T+D**	**TOTAL**	**TOTAL**
GBANRAUN	**SWAMP**	yes (.01)	no	no	no	yes
	TRANS.		yes	yes	yes	yes
	DRY			no	no	yes
	S+T+D				no	yes
	TOTAL					yes

$p < 0.001$ unless otherwise indicated.

Table 5.11: *Sorenson's index indicating the degree of similarity in species composition for all tree species with a DBH ≥ 30 cm included in the Gbanraun and Ukubie enumerations.*

		GBANRAUN			UKUBIE
		TRANS	**DRY**	**TOTAL**	**TOTAL**
GBANRAUN	**SWAMP**	0.96	0.92	0.99	0.89
	TRANS.		0.96	0.97	0.85
	DRY			0.93	0.82
	TOTAL				0.88

Table 5.12: *Morisita-Horn index indicating the degree of similarity in species composition for all tree species with a DBH ≥ 30 cm included in the Gbanraun and Ukubie enumerations.*

		GBANRAUN			UKUBIE
		TRANS	**DRY**	**TOTAL**	**TOTAL**
GBANRAUN	**SWAMP**	0.95	0.72	0.99	0.75
	TRANS.		0.62	0.95	0.65
	DRY			0.84	0.74
	TOTAL				0.79

Table 5.13: *Coefficients of dispersion (variance/mean) for 11 tree species with a DBH ≥ 30 cm included in the Gbanraun and Ukubie enumerations and phenology samples.*

SPECIES	**GBANRAUN**				**UKUBIE**	
	SWAMP	**TRANS.**	**DRY**	**TOTAL**	**TOTAL**	**S.S.**
Uapaca staudtii	1.2781	1.5663	2.8571	2.2759	0.9252	1.2351
Uapaca heudelotii	2.7551	2.8481	3.1083	3.1215	1.2080	0.9660
Ctenolophon englerianus	1.4082	0.9463	1.7543	1.1066	1.1860	1.0617
Klaineanthus gaboniae	1.2902	1.1156	1.4190	2.1992	0.9312	1.0091
Xylopia staudtii	1.3496	1.9216	0.9859	1.4614	1.0732	1.0765
Rothmannia megalostigma	0.8718	1.1691	0.9184	0.8520	—	—
Symphonia globulifera	1.0204	1.0635	1.4564	1.0333	0.9091	1.0000
Funtumia africana	1.2041	0.7551	1.3265	1.1422	0.8788	0.8878
Pentadesma butyraceae	0.9796	0.8571	0.7935	0.9528	1.0790	0.9144
Coelocaryon preussii	0.9388	1.9184	1.0057	0.9146	0.9394	0.8497
Pycnanthus marchalianus	1.3673	0.9390	1.0000	1.1561	0.9572	1.0204

Table 5.14: *Presence of a significant difference, ω, between indices of clumping of the dry land, transition zone and swamp subsamples in Gbanraun and the Ukubie sample for 11 tree species in the DBH ≥ 30 cm enumerations and that were also included in the phenology samples. Those species showing significant differences ($p = 0.05$), when ω lies outside the range ± 2.5 / √(N-1) (where N is the number of samples in each set), are listed. For the other 7 species* Ctenolophon englerianus, Klaineanthus gaboniae, Xylopia staudtii, Rothmannia megalostigma, Funtumia africana, Pentadesma buteraceae *and* Pycnanthus marchalianus *no significant differences were observed.*

Uapaca staudtii

	TRANS.	**DRY**	**UKUBIE**
SWAMP	no	yes	no
TRANS.		no	no
DRY			yes

Uapaca heudelotii

	TRANS.	**DRY**	**UKUBIE**
SWAMP	no	no	yes
TRANS.		no	yes
DRY			yes

Symphonia globulifera

	TRANS.	**DRY**	**UKUBIE**
SWAMP	no	no	yes
TRANS.		no	yes
DRY			yes

Coelocaryon preussii

	TRANS.	**DRY**	**UKUBIE**
SWAMP	no	no	yes
TRANS.		no	yes
DRY			yes

$p = 0.05$

Figure 5.1: *Species area curve for the DBH > 30 cm enumerations of Gbanraun and Ukubie.*

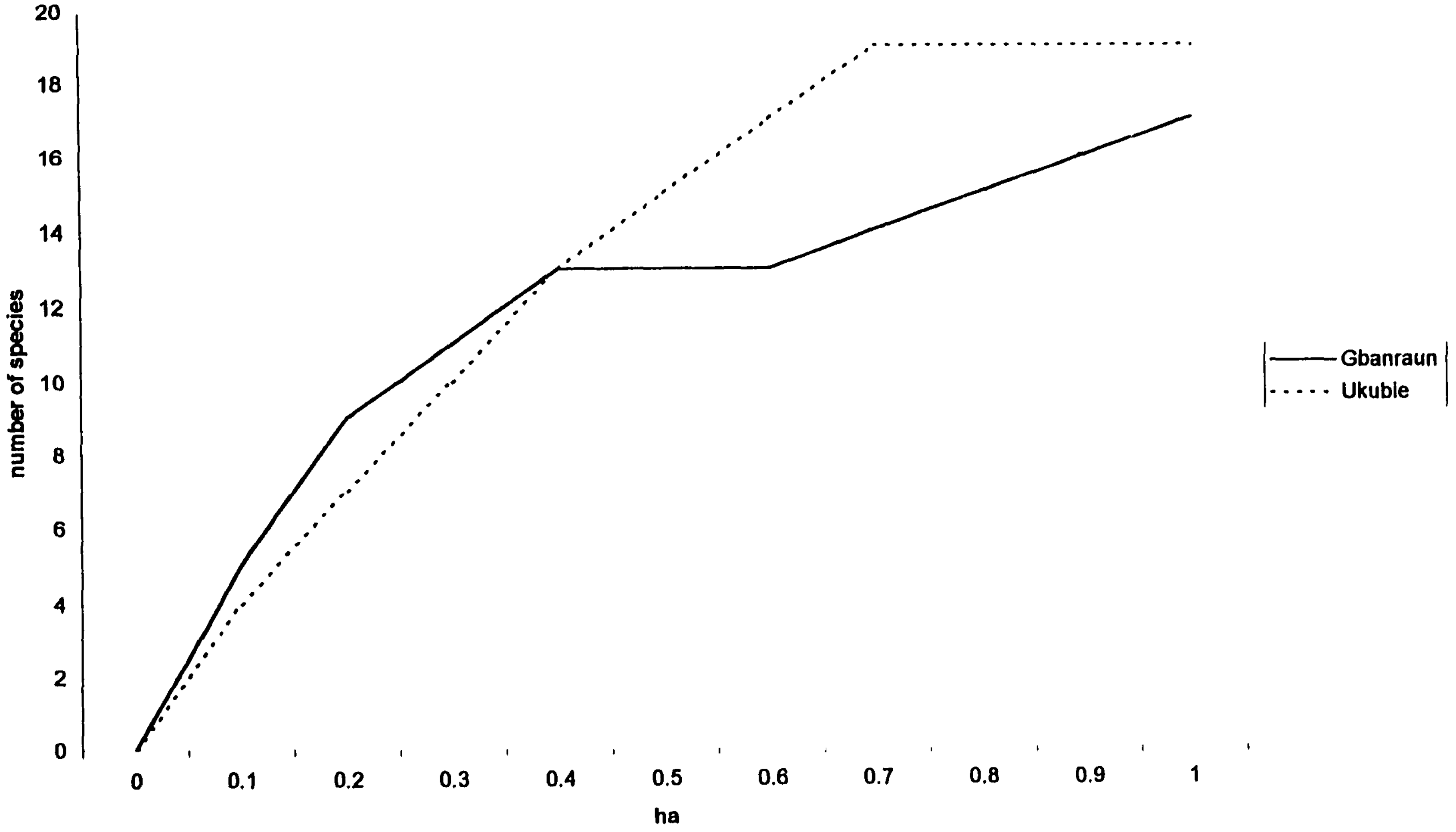


Figure 5.2: *Distribution DBH classes for the DBH · 30 cm enumerations of Gbanraun and Ukubie*

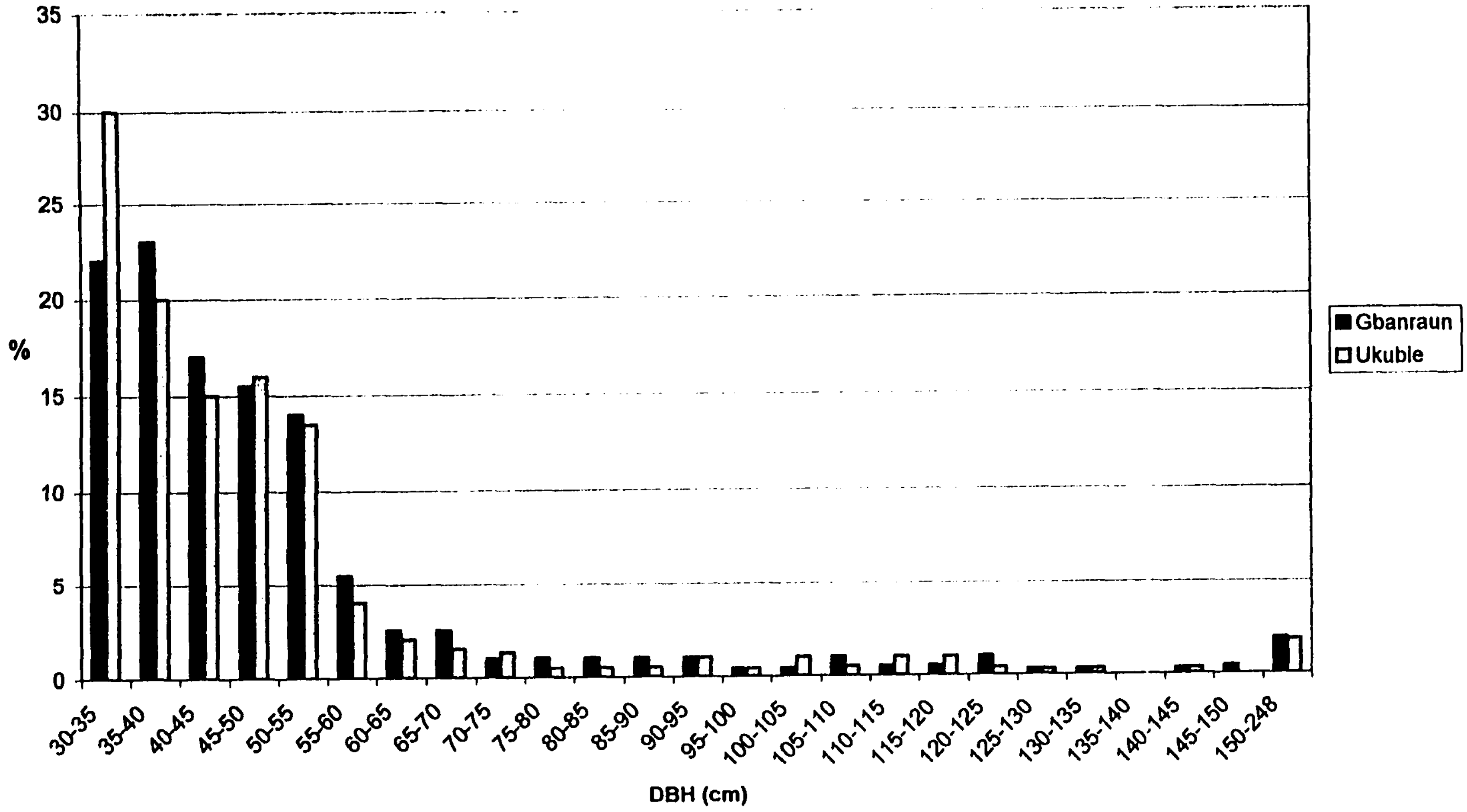


Figure 5.3: *Distribution height classes for the DBH 30 cm enumerations of Gbanraun and Ukubie.*

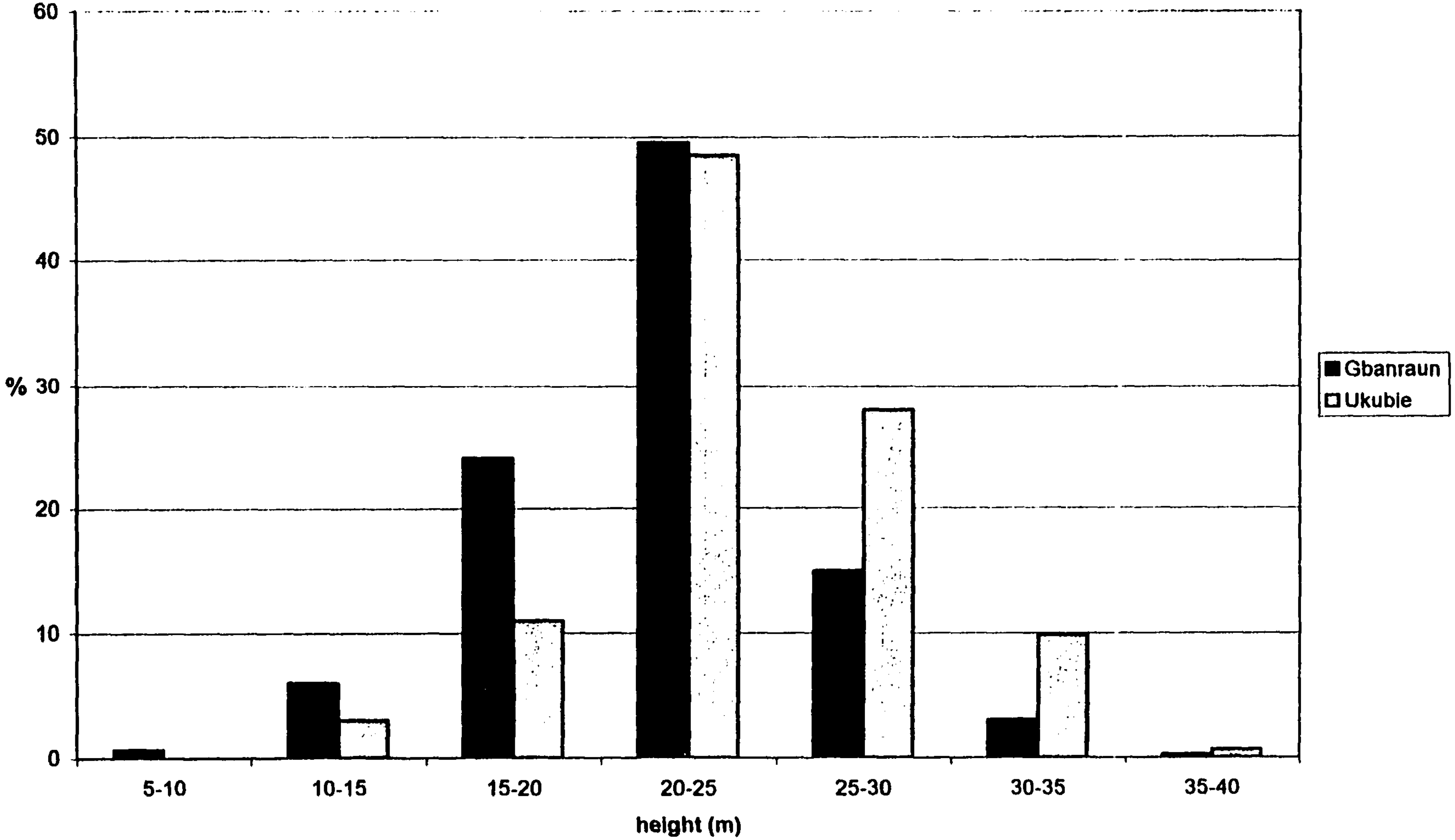
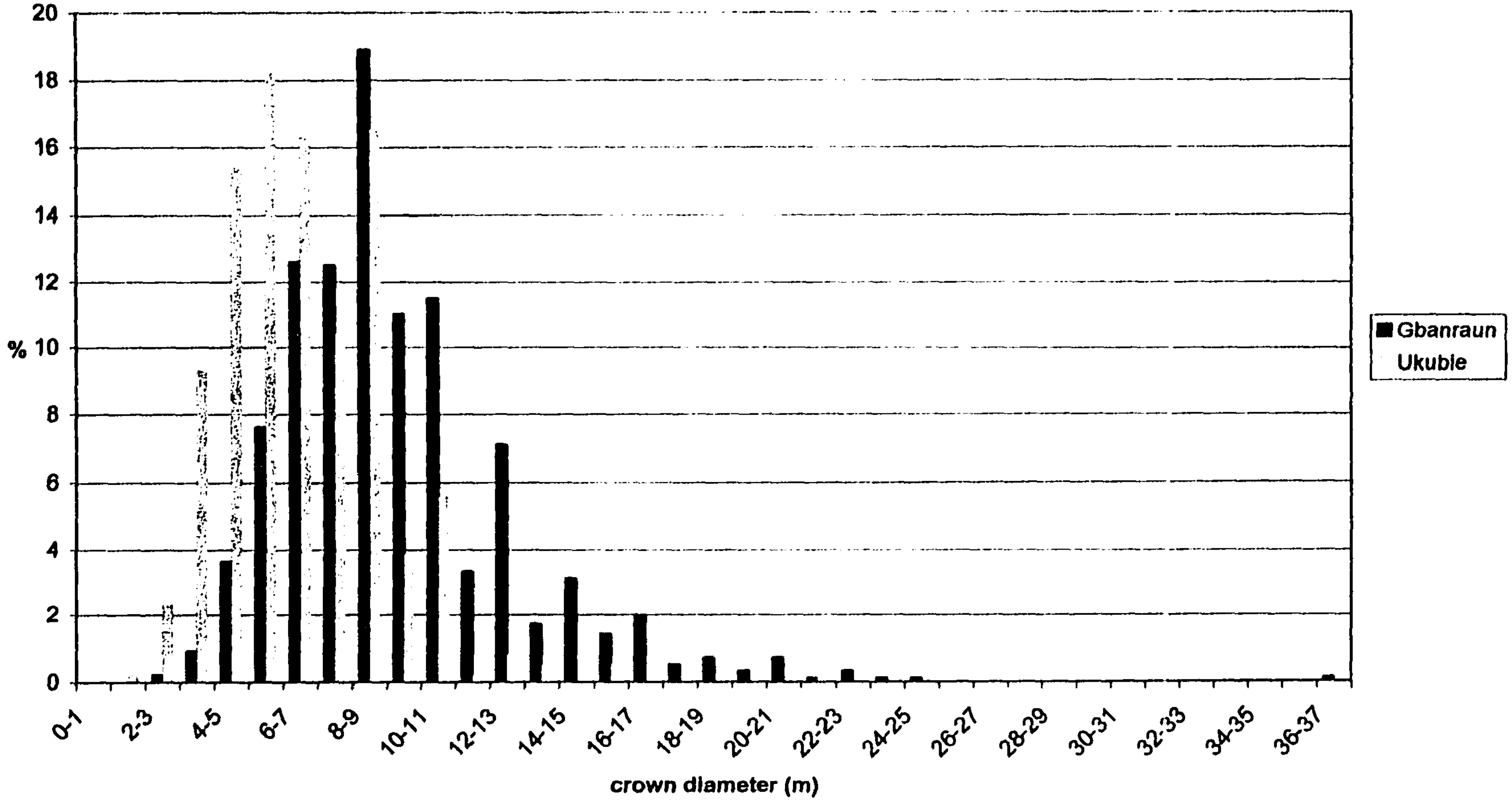


Figure 5.4: *Distribution crown size classes for the DBH > 30 cm enumerations of Gbanraun and Ukubie.*



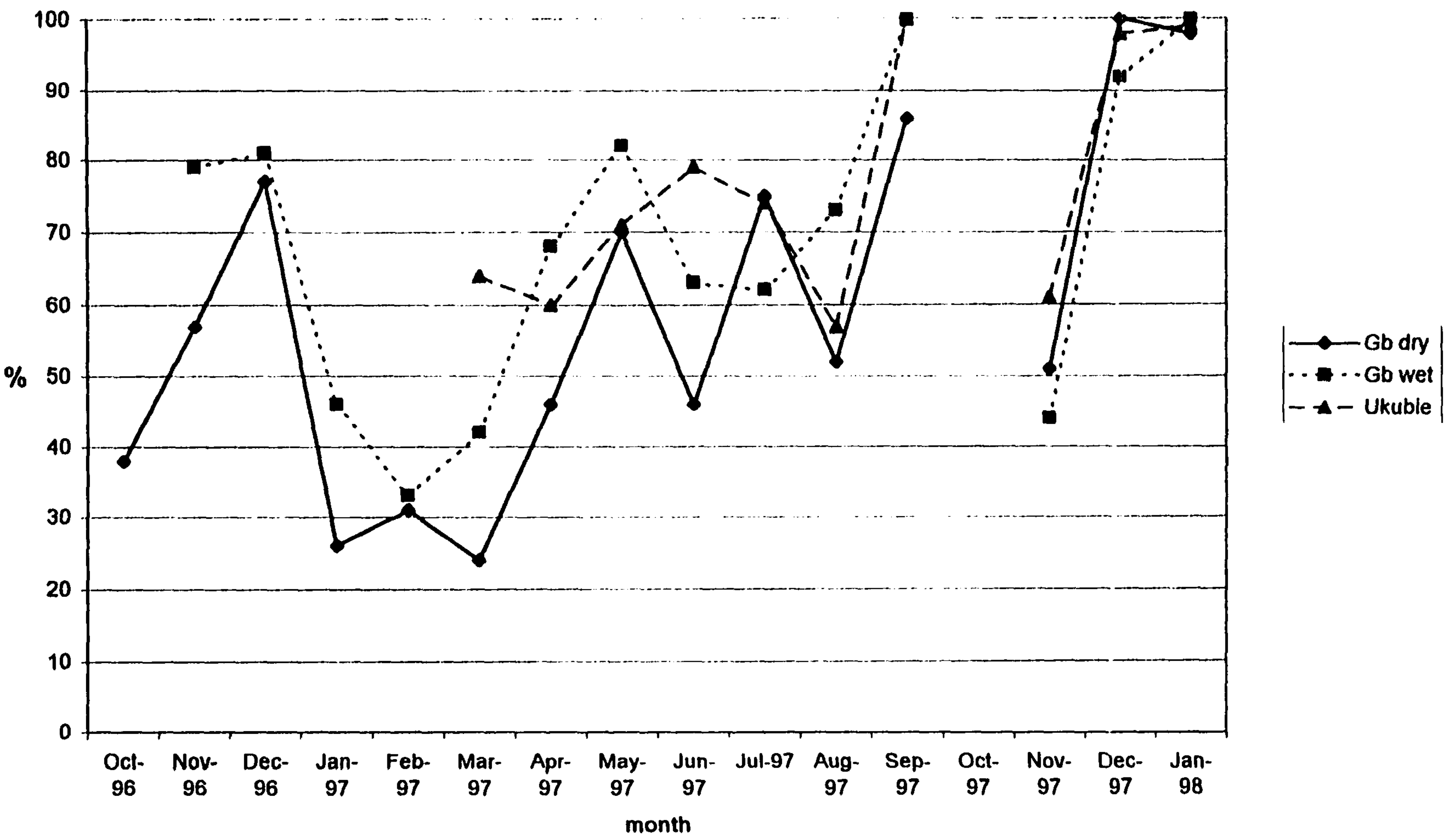


Figure 5.5: *Percent of trees with young leaves in the Gbanraun and Ukubie phenology samples.*

Figure 5.6: *Percent of trees with flowers in the Gbanraun and Ukubie phenology samples.*

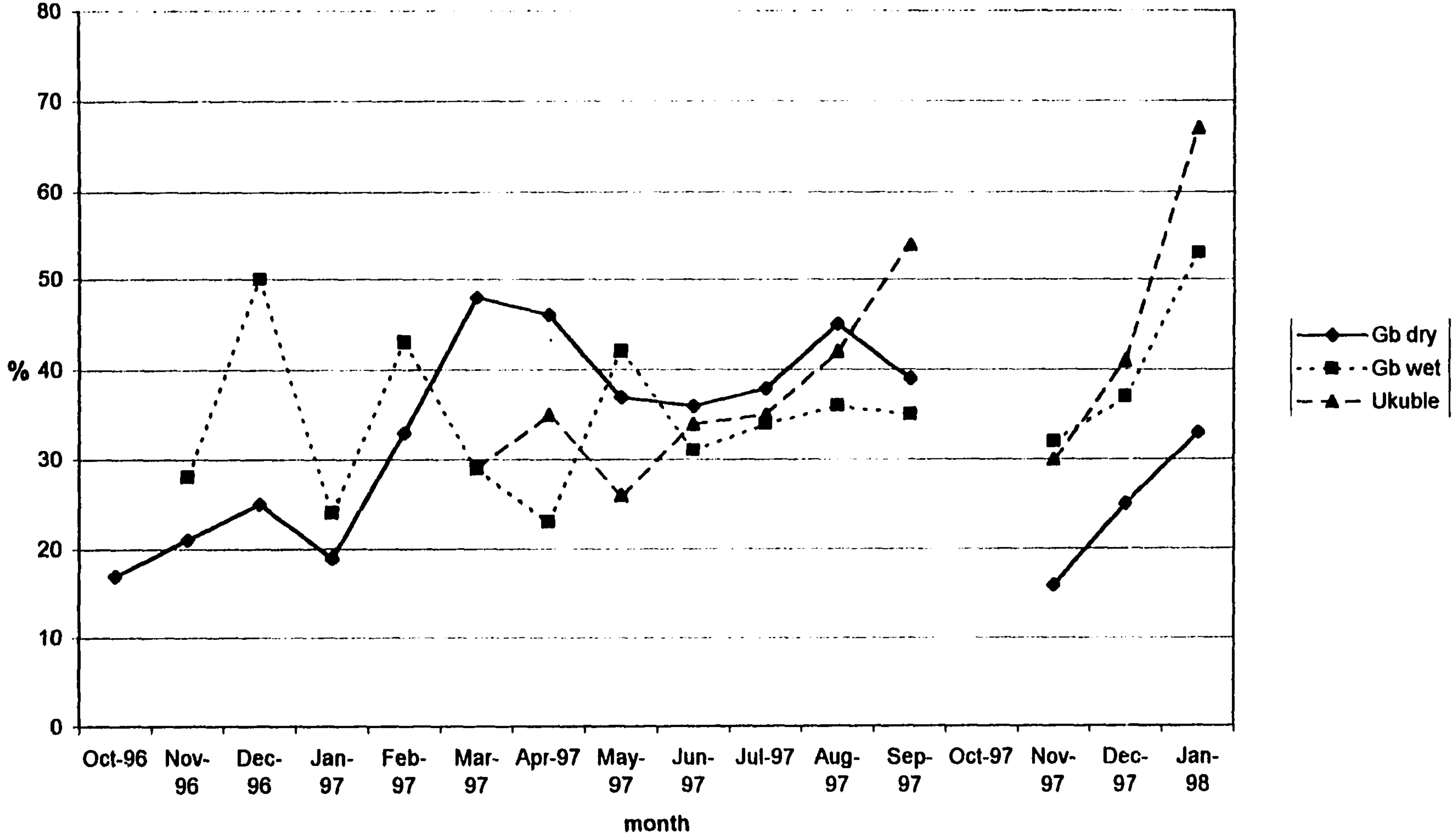


Figure 5.7: *Percent of trees with fruit in the Gbanraun and Ukubie phenology samples.*

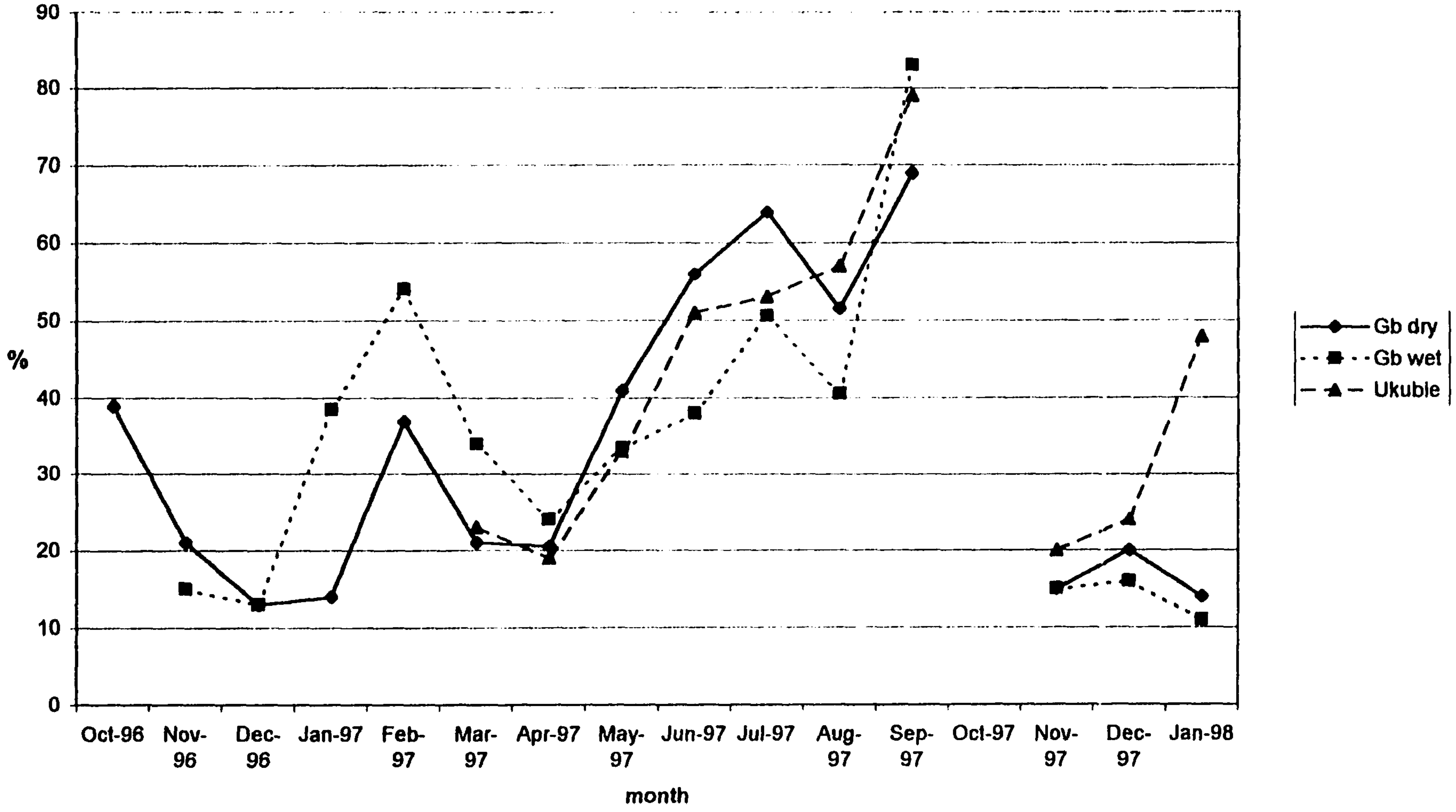
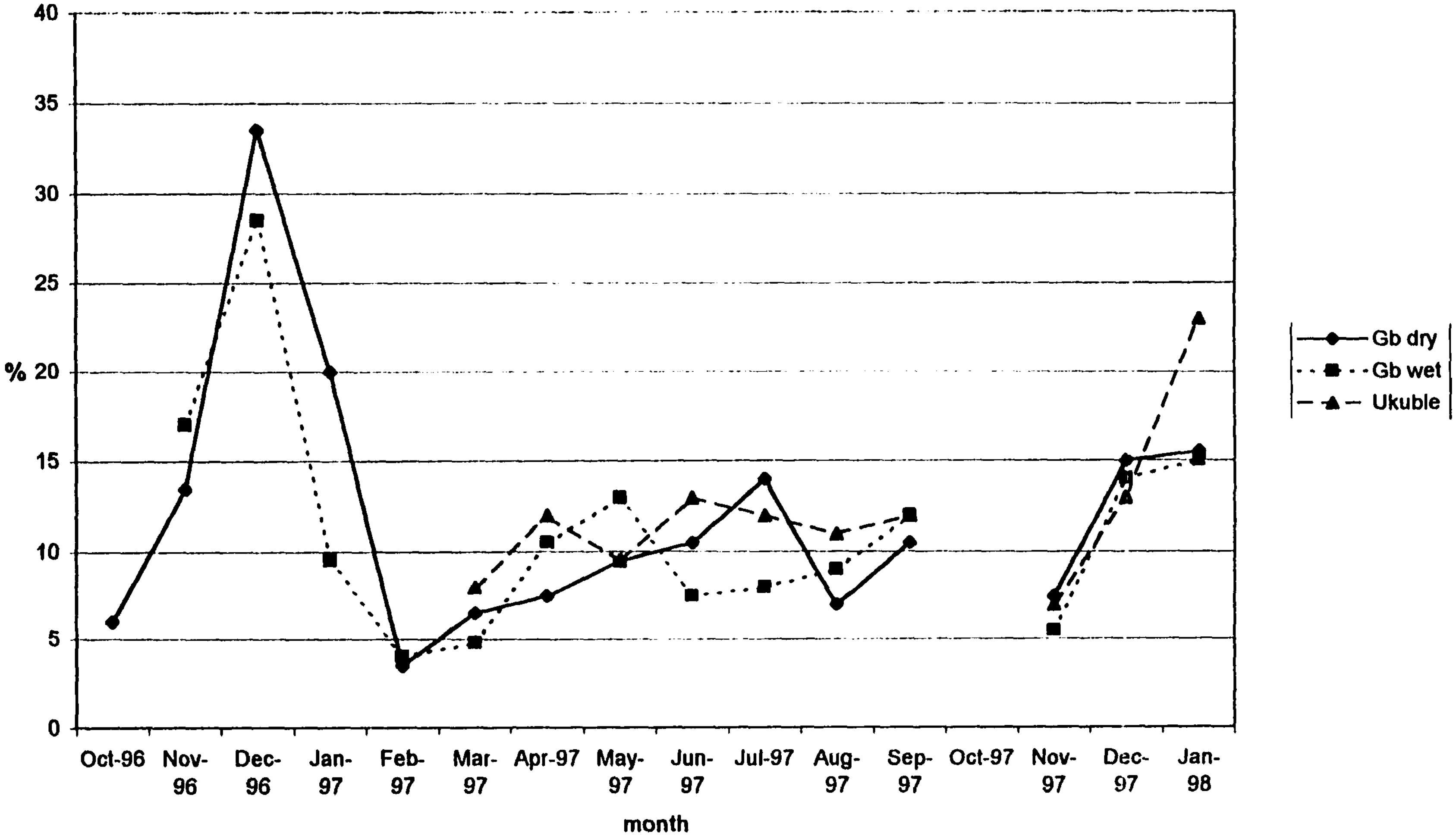


Figure 5.8: *Percent of young leaves present in the Gbanraun and Ukubie phenology samples.*



CHAPTER 6

FEEDING BEHAVIOR

6.1. Introduction

In this chapter I describe the annual diet, monthly variation, and food preferences of the Gbanraun study group, together with a few observations made on other groups. I also compare the feeding behavior of this group with that of other red colobus populations that have been the subject of long-term studies.

6.2. Methods

All observations on feeding behavior in the study group were collected during one 4-day and 12 5-day follows. Following Struhsaker (1975) feeding observations were operationally distinguished from one another by the following criteria: 1) a different monkey feeding on the same item; 2) the same monkey feeding on a different food item (*i.e.*, species and part); 3) the same monkey feeding on a different food species; or 4) the same monkey feeding on the same food item of the same food species at least one hour after any previous such observation. The number of monthly feeding observations ranged from 130 to 395.

Food items were distinguished as follows:

- Young and mature leaves were distinguished by color and size, and though for a number of plant species only certain parts of a leaf were consumed, only leaf stalk consumption was scored separately as petiole.

- Color and/or size were used to distinguish ripeness of fruit.
- Flowers were classified as bud when petals, and in some cases bracts (*e. g.*, *Uapaca*) were closed, and as flower the moment they unfolded.

6.3. Results

6.3.1. *Annual diet*

The study group was very particular in their choice of food items. For example, during feeding on *Coelocaryon preussii* and *Pycnanthus marchalianus* most often only the leaf's distal half was consumed, but in these cases no distinction with the consumption of whole leaves was made. *Hallea ledermannii*, *Rothmannia megalostigma*, and the *Uapaca* spp. all produce new leaves in a similar way, with a leaf bud and a few young leaves sprouting from the soft green terminal end of the stem. This structure will be referred to as a shoot. In most cases the monkeys would focus on obtaining the pith from the shoot, but would sometimes also consume the leaf bud and young leaves in the process. Seeds were in every case obtained from unripe fruits, and the pericarp was always discarded. Only from three food trees (two *Raphia* spp. and *Pycnanthus*) were ripe fruits consumed. I tasted ripe *Pycnanthus* fruits consumed by the monkeys and found them to be sweet. The monkeys would occasionally feed on them by taking one or two bites from the pericarp, discarding the remainder of the fruit. For *Uapaca* spp., the single largest source of flowers, only the flower itself was consumed, and the petal-like bracts discarded.

Only 19 different identified plant species were consumed together with an unknown number of rare, unidentified tree species (these unidentified species comprised only 1.8% of total feeding observations, see **Table 6.2**, p. 136). Of the lianas only 4 *Combretum* spp. were partially identified, as well as two strangler figs (*Ficus* spp.) whose feeding records were included under lianas. A large number of other liana species also contributed to the diet. The two most important families were the Ctenolophonaceae and Euphorbiaceae which contributed 67% to the total diet (**Table 6.1**, p. 136). The only sub-family of the Leguminosae to be included in the diet was the Ceasalpinioideae with 2% of the diet. All food species at Gbanraun were evergreen as were the majority of the other species present. Of all species identified in the study area only *Alstonia* and *Nauclea pobeguinii* were deciduous.

Most of the feeding records came from large or medium-sized tree species, and *Ctenolophon englerianus* was by far the most preferred species (**Table 6.2**, p. 137). Relatively few species formed a large proportion of the diet, with the top 10 species contributing 91% and the top three 67% to the total diet. Food species diversity in the diet is also dependent on the number of species present, and of the 39 species recorded in the DBH ≥ 30 cm enumeration, 19 or 54% were utilized by the study group as food species. The only common tree that was very little utilized was *Xylopia staudtii*, for which only one feeding record was obtained. Of the other tree species with a density of more than 1 tree/ha, another member of the Annonaceae, *Hexalobus crispiflorus*, but also *Alstonia boonei* and *Irvingia gabonensis* were not utilized. For these trees also no feeding observations were made outside the scan samples.

Feeding data for the Gbanraun study group clearly indicates a strong preference for young growth (**Tables 6.1 & 6.2**, pp. 136 & 137). Young leaves constitute 55.9% of the diet, with mature leaves comprising only 4.9%. The next most important food items, seeds (12%), flowers (9.4%), and pith (6.2%) were also young growth. Petioles of mature leaves (5.5%) were basically the only other mature food item consumed by the red colobus making the total contribution of mature leaf items to their diet 10.4%.

On one occasion a female was observed consuming the healthy bark of *Pentadesma buteracea*. The section of the tree affected by the gnawing was too large for it to be the result of the observed feeding bout, suggesting that bark feeding had taken place before. Lichens were also consumed but the three observations made all fell outside scan samples. Gall consumption from mature *Macaranga* leaves were the only records of possible arthropod consumption, but on two occasions two females were observed manipulating rotten wood. It is also possible that the few records of *Symphonia* young leaf consumption made at the beginning of the study were actually gleaning for insects, as described by Struhsaker (1978).

Food item diversity was low, even though a total of 10 different items were consumed, but the top three comprised 77% of the diet. The main reason for this lack of diversity was that young leaf consumption contributed 57% to the study group's annual diet.

6.3.2. *Observations on other groups within the study area*

Observations on two neighboring groups within the study area indicated that a number of other food items, such as the seeds of *Cola nitida* and the unripe fruits (pericarp) of *Klainedoxa gabonensis*, were also consumed. These tree species, however, were very rare or absent within the home range of the study group. Only on one occasion was a feeding record obtained for a food item, *Pentadesma* seeds, which was also available within the study group's home range.

6.3.3. *Monthly variation*

Ctenolophon made up more than 40% of the total diet during eight months and never dropped below 20%. The only other food species that accounted for more than 10% to the diet were *Uapaca* spp. (flowers during November-December 1996; unripe seeds during February-March 1997, and *Klaineanthus gaboniae* (unripe seeds during June, July, and August 1997). *Macaranga* spp. were the only other food source to contribute more than 10% with unripe fruits to the diet during one month (May 1997). For a detailed summary of the monthly diet see **Appendix 3**.

The top four food items in the red colobus' diet, *Ctenolophon* young leaves, *Uapaca* spp. seeds and flowers, and *Klaineanthus* seeds, as well as all other records for young leaves (mainly from lianas, *Pentadesma*, and *Erythrophleum ivorense*) accounted for more than 70% to the diet during most months.

6.3.4. *Feeding in relation to seasonal availability*

Figures 6.1, 6.2, and **6.3** (pp. 141, 142, & 143) illustrate the consumption of major food items in relation to the monthly variation their availability. After *Ctenolophon* young leaves the second largest number of feeding records came from *Uapaca* spp.

flowers and unripe seeds, followed by and *Klaineanthus* unripe seeds. Spearman Rank Correlations were calculated to investigate if a correlation existed between the percentage of feeding records for the most important seasonal food items and their availability in the phenological samples. A significant positive correlation ws found for the percentage of feeding records for *Uapaca* and the percentage of *Uapaca* flowers in the phenology sample ($r_s = 0.9603$, $p > 0.05$). The percentage of feeding records for Uapaca unripe fruits and the percentage of *Uapaca* unripe fruits, and the percentage of feeding records for *Klaineanthus* seeds and the percentage of *Klaineanthus* unripe fruits in the phenology samples showed no significant correlation. This is most likely the result of the red colobus only feeding on unripe fruits of a certain size, thus excluding very young fruits. A distinction not made in the phenology samples. **Figures 6.1** and **6.2** (pp. 141 & 142), however, do indicate that as total *Uapaca* and *Klaineanthus* flower and seed availability increases in the phenology sample, so does the percentage of feeding records for these food items. This suggests that the presence of large quantities of potential food items has a strong influence on the study group's feeding behavior. However, when the percentage of feeding records for *Ctenolophon* is correlated with availability of *Uapaca* spp. flowers and seeds, and *Klaineanthus* seeds no significant correlations are found, suggesting that the presence of these abundant food sources does not significantly change the number of feeding records for *Ctenolophon*.

The phenology samples for Gbanraun show that *Ctenolophon* young leaf availability is basically constant over the sample with an average monthly production between 10 and 20%, indicating that availability is never affected. **Figure 6.3** (p. 143) shows the percentage of feeding records for *Ctenolophon* compared with the availability of both *Ctenolophon* young leaves and of young leaves generally. During November-December 1996 when general young leaf production reached its peak *Ctenolophon* contributed least to the diet, while during January 1997, when general young leaf production reached its lowest point, the second highest level of feeding on this species was recorded. Only during May 1997 did *Ctenolophon* young leaf consumption not drop as much, even though the percent of trees with young leaves was high. Although a large number of trees were producing young leaves at this time the actual quantity available was considerably lower (10%) than in December (30%) (**Figure 5.8**, p. 117). However, when comparing feeding on *Ctenolophon* young leaves with feeding on young leaves of all other sources for all 11 months with phenological data again no significant correlation is found (r_s = -0.167), indicating that the fluctuations in young leaf availability of other food species does not influence the number of feeding records for *Ctenolophon* either. This does, however, suggest that the study group actively selected *Ctenolophon* young leaves, and that the year-round availability of this particular food item was not the deciding factor for its inclusion in the diet.

Diversity in the monthly diet of the study group showed some variation; Shannon's diversity index ranged between 0.8 and 1.8 (**Figure 6.4**, p. 144). However, a Chi-square test indicated that there was no significant variation between months. **Figure 6.4** shows also that the indices of food species diversity and food item diversity are correlated, with food item indices being lower because fewer categories were involved in this index than the number of species included in the diet.

6.3.5. *Food selection in relation to species abundance*

The frequency with which a tree species is included in the diet is likely to be affected by its distribution in time and space. When considering its distribution in space both its average density, and the size of individual crowns will affect its inclusion in the diet (Struhsaker, 1975).

Canopy indices for the most common food species were calculated for Gbanraun and Ukubie (**Table 6.5**, p. 140). I followed Marsh's (1981*b*) method, calculating a total canopy index by:

$$CI_i = \overset{n}{\underset{j=1}{\%}} (B_{ij} \times D_{ij})$$

where CI_i is the total canopy index for n trees belonging to species i.

B_{ij} is the crown breadth of specimen j of species i.

D_{ij} is the crown depth of specimen j of species i.

The canopy index gives an indication of the contribution of each species to the canopy. The *Uapaca* spp. have at all locations the highest canopy index. There was, however, considerable variation in the canopy index for *Ctenolophon*, which was nearly 4 times larger in the Gbanraun swamp then at Ukubie, and three times larger in the Gbanraun swamp subsample then in the dry-land subsample. When food species rank in the diet was correlated with the total Gbanraun canopy indices for these food species a significant positive correlation was observed ($r_s = 0.6391$, $p > 0.05$). However when a distinction between the dry-land sample and the swamp was made a different result was found. For this comparison I calculated the relative contribution of the 11 most important food species present in both samples for those months that the majority of cells occupied fell within the dry-land area and within the swamp. This resulted in a significant positive correlation for the swamp subsample ($r_s = 0.7694$, $p > 0.05$) but no significant correlation for the dry-land area. This suggests that the red colobus depend more heavily on the most common food species in the swamp than they do in the dry-land area.

To get a better grasp on the relative importance of each food species in the diet I calculated selection ratios that take account not only of crown size but also density (**Table 6.6**, p. 140). Though different researchers have used different methods to calculate selection ratios (Clutton-Brock, 1975; Struhsaker, 1975; Mturi, 1993), I use Struhsaker's (1975) method. In this method the percentage of feeding observations recorded for a tree species is divided by the product of their density and crown size. Tree density estimates were based on the DBH ≥ 30 cm enumeration for Gbanraun. Indices of crown size were computed slightly differently from Struhsaker (1975) who measured crown diameter and depth for 10 specimens of each species. In this study only crown diameters were measured during the vegetation enumeration. Therefore, an estimate was made of crown depth using the following method; an average *Uapaca heudelotii*, for example, was estimated to have a crown depth that on average occupied 40% of the tree's total height. Average crown depth was then calculated by multiplying the average height of all trees of this species in the DBH ≥ 30 cm enumeration by 0.4.

The results indicate that *Hallea ledermannii* has the highest selection ratio. This suggests that this species' absolute contribution to the diet is artificially low because most trees of this species had been logged in my study area. *Uapaca* spp. have a low selection ratio reflecting the relatively low number of feeding records in proportion to their density.

Only *Ctenolophon* has both a high selection ratio and a high density. The other species with high selection ratios all have low densities but generally even distributions in the swamp, except for *Erythrophleum* which is mainly found in the drier sections but heavily selected when producing young leaves.

6.4. Patterns in the Study Group's Feeding Behavior

The study group exhibited a number of distinct patterns in their feeding behavior. Young leaves of *Ctenolophon* were the principal component of their diet, followed by seasonal food items from tree species with very high densities. The remaining 25% of feeding records came from two other sources. The first source is a number of tree species that have low densities but a relatively even distribution, and which provide either non-seasonal young growth (*Hallea* and *Rothmannia*), or seasonal and/or non-seasonal, mature, food items (*Funtumia*, *Coelocaryon*, and *Pycnanthus*) on a year round basis. The second source is ripe, but mostly unripe fruits from species that have a very high density (*e.g.*, *Raphia* spp.), or a relatively high density (*e.g.*, *Macaranga* spp.) but which do not produce food items in great abundance.

Table 6.5 (p. 140) illustrates that, with the exception of *Rothmannia*, all food items that are available on a year-round basis (*Ctenolophon*, *Funtumia*, *Coelocaryon*, *Pycnanthus*) have the highest selection ratios. The only exceptions are *Erythrophleum* and *Pentadesma* that contributed between 2% and 3% to the diet when producing young leaves. These two species, however, are mostly restricted to the forest's dry section, resulting in a low overall density that inflates the selection ratio.

These data and other observations indicate that for most of the year the study group moved between patches, areas of high food concentration separated by areas of low concentration (Oates, 1986), consisting of one or more *Ctenolophon* trees. In and around these patches the red colobus also fed from individuals of tree species from the two above mentioned sources, and from lianas, which provided seasonal items or non-seasonal (mature) food items on a year-round basis. The red colobus only deviated from this pattern when young growth or flowers appeared on species that did not produce these on a year-round basis. This did not, however, significantly reduce the consumption of *Ctenolophon* young leaves. Such seasonal young growth was exploited only if it occurred at high density, in great abundance, and of a certain individual size. This could explain why *Klaineanthus* flowers, which are very small, were not included in the diet like the much larger *Uapaca* flowers (although other possibilities, such as the presence of secondary compounds, cannot be ruled out). All other seasonal food items which occurred at lower densities were only included in the diet when encountered during the movement from one *Ctenolophon* patch to another (*e.g.*, *Macaranga* spp., *Musanga cecropioides*), or when the tree species in question happened to be part of such a patch (*Spondianthus preussi*).

Examining the densities of the different tree species recorded in the Gbanraun DBH ≥ 30 cm enumeration, the food species all seem to include most, but not all, of the tree species with densities greater than 0.5 tree/ha. The most notable exception is *Xylopia*, which is the fifth most common species in Gbanraun. The coefficient of dispersion for this tree is 1.35 (**Table 5.13**, p. 108) indicating some degree of clumping, and I also observed that this tree was most abundant in more open spots in the swamp and was, therefore, rarely found in *Ctenolophon* patches. Its crown also has an open whorled structure, something the monkeys appeared to avoid. *Symphonia* was also found in the more open spots. Despite the fact that study animals sometimes would rest in this tree by placing themselves with their back against the trunk, which made them very hard to detect, feeding in the whorled crown would mean full exposure when moving along a branch away from the trunk. Given the frequent observations of attempts by crowned eagles to catch the monkeys, avoidance of exposure is a possible explanation for the exclusion of certain potential food species.

For *Hexalobus*, *Irvingia*, and *Alstonia* no structural or distributional explanation can be identified for their avoidance. Each species occurs at densities comparable to those of the other food species, but they were never utilized. It may be, however, that the avoidance of *Hexalobus* is related to its membership of the Annonaceae, the family to which *Xylopia* also belongs. At Kibale the fourth most common tree species, *Uvariopsis congensis* belongs to this family and is also not utilized (Struhsaker, 1975) suggesting the possibility that they produce feeding deterrents. At most other sites, however, members of the Annonaceae are included in red colobus diet in small quantities (Mturi, 1993; Maisels *et al.*, 1994; Davies *et al.*, 1998), confirming the problems associated with the determination of dietary availability through extrapolating from a few plant species to the entire family (Struhsaker, 1978). Only one, or possibly two *Irvingia* were found on the edge of the study group's home range and this may be why they were not included. *Procolobus badius preussi* in Cameroon has been observed feeding on this tree's young fruits (Struhsaker, 1975), an observation which was also confirmed by my assistants, making it likely that if the trees had been more common in the home range they would have been included. *Alstonia*'s family, the Apocynaceae, is generally considered to be toxic (Janzen, 1974). In some red colobus diets, however, a large percentage of the diet comes from the Apocynaceae suggesting that this family is theoretically available to the monkeys (Clutton-Brock, 1975; Struhsaker, 1978). This does suggest that toxicity is unlikely to play an important role in red colobus food species/item selection. It remains, however, possible that individual variation in toxicity could be a determining factor, but given the favorable growing conditions in the swamp, as indicated by the high levels of young growth production in the phenology sample, a heavy investment in secondary compounds seems unlikely (Janzen, 1974).

6.5. Discussion

Published data on the diet of different red colobus populations indicate considerable variation in the relative proportions of food items in the diet. The only consistent observation is that the contribution of young growth to the diet is the largest component, with the result that seasonally available items often play an important role. The most important food item category is young leaves, with the exception of Gombe, Tanzania (Clutton-Brock, 1975) where mature leaves are most important, and Abuko, Gambia where fruits and/or seeds form the largest dietary component (Starin, 1991). The exception at Gombe may, however, be the result of differences in the categorization of different food items (Struhsaker, 1975). Total contribution of young leaves to the diet shows considerable variation between the studies with 32% in Tiwai (Davies *et al.*, 1998) and 55% in Salonga (Maisels *et al.*, 1994). Mature leaves can contribute from around 6.5% (Gatinot, 1977; Maisels et al., 1994; Mturi, 1993) to more than 20% (Struhsaker, 1975; Oates, 1994*b*) and even as much as 44% if the Gombe results are included (Clutton-Brock, 1975). Flowers show a similar pattern to mature leaves if Salonga, where flowers contributed less than 2% to the diet, is excluded (Maisels *et al.*, 1994). A few sites showed a contribution of more than 10% to the diet (Struhsaker, 1975; Mturi, 1993; Oates, 1994*b*). Fruits, including seeds, are, after young leaves, the most important food item in the red colobus diet. In 6 out of the 8 available studies this food item was second most important and contributed between 6% in Kibale (Struhsaker, 1975) to around 40% in Abuko and Salonga (Starin, 1991; Maisels *et al.*, 1994).

The relative importance of the food items categories in this study, 1) young leaves, 2) fruit (including seeds), 3) mature leaves, and 4) flowers, is the same as in four other studies (Marsh, 1981; Mturi, 1993; Oates, 1994*b*; Maisels *et al.*, 1994) making it the most common pattern (**Table 6.2**, p. 137). The proportion of each category in the diet was considerably different, however, from the proportions in other studies. Young leaves contributed by far the most with 56%, which is 2% more than the next highest record (Maisels *et al.*, 1994). Fruits and seeds (mostly seeds in this study) contributed 16% placing it at the lower end of the observed range. Mature leaves, with 10%, falls in the mid-range, and consists as in most other studies mainly of feeding on leaf-petioles, apical tip, and basal part. Flowers with 10% are at the higher end of the recorded range. It can be concluded, therefore, that this study confirms the considerable variation of the relative importance of different food item categories in the red colobus diet.

With only 19 food species included in the annual diet this study does stand apart. The next lowest observation with 22 of species in the diet comes from Tana River (Marsh, 1981*b*). This is surprising because the number of trees at Tana, where all trees within the red colobus' home range were identified, included 26 species as compared to 39 at Gbanraun. When comparing the results with other sites the difference becomes even more pronounced with 89 species at Tiwai (Davies *et al.*, 1998) and 84 species at Salonga (Maisels *et al.*, 1994). These two sites are composed of lowland rainforest and are considerably more diverse than the freshwater swamp forest at Gbanraun, but not to the degree that it explains the observed difference. This difference does suggest though that red colobus do not attempt to include as many species as possible in their diet, which is confirmed by the exclusion of a number of available species which are not included in the study group's diet but which appear to be suitable food (see **Section 6.4**).

As observed in other studies, my study group concentrated in feeding on the largest, most common tree species in their habitat (*Ctenolophon*, *Uapaca*, and *Klaineanthus*), and they were willing to travel long distances to reach food trees (see **Section 7.6**).

Red colobus food species are also often clumped in their distribution, especially when considering the differences in phenological patterns within certain species, which results in clumping in time as well. The evidence for clumping of food species in the study area, and the resultant feeding on widely separated food patches is also observed for the study group, confirming previously made generalizations of red colobus feeding behavior (Oates, 1994*b*).

6.6. Summary

Red colobus at Gbanraun showed little diversity in the food species or the food items in their diet. Young leaves from one food species, *Ctenolophon englerianus*, were by far the largest component of their diet. Variation in monthly *Ctenolophon* young leaf intake was mostly dependent on the presence of temporarily available young growth from the forest's most abundant species (*Uapaca* spp. and *Klaineanthus gaboniae*), but there was no significant correlation between the inclusion of these abundant food items and *Ctenolophon* young leaves in the diet. These species and young leaves from other relatively common species formed the largest component, 75%, of the study group's diet. The remaining 25% of the diet was mostly obtained from a number of trees which produced young growth on a year-round basis, or that provided the few mature food items included in the monkey's diet. A few species with relatively high densities, but which produced food items at a low abundance, formed the remainder of the study group's diet.

The following patterns were identified for the study group's feeding behavior: For most of the year the red colobus depended on *Ctenolophon* patches and the tree species most commonly associated with these patches. All food species in the patches either produced young items on a year-round basis and/or carried the few mature food items that were included in the diet. The study group deviated to the greatest extent from this pattern when tree species with a high density produced young growth in high abundance. Smaller degrees of deviation from this pattern were observed when tree species with relatively high densities produced young growth in smaller quantities. The remaining food items came from rare trees which happened to be part of a food patch but which were not actively selected.

Available studies for the diet of different red colobus populations indicate considerable variation in the relative proportions of food items in the diet. The results from this study, though different in the distribution of the contribution of food items fall, with the exception of young leaves which fell just outside, broadly within the observed variation. The main distinction between my study group and others is the low number of species included in the diet, which is even lower than at floristically poorer sites.

Table 6.1: *Characteristics of Procolobus badius epieni food species.*

SPECIES	Growth form	#/ha	CD	Sp.tot., % obs.	Cum.%
Ctenolophon englerianus	L	11.90	1.11	43.76	43.76
Uapaca spp.	M-L	41.90	*	15.90	59.66
LIANAS	—	—	—	7.73	67.39
Klaineanthus gaboniae	M	4.75	2.20	5.08	72.47
Funtumia africana	M	2.05	1.14	4.92	77.39
Rothmannia megalostigma	M	2.20	0.85	2.89	80.28
Pentadesma buteracea	M-L	1.80	0.95	2.81	83.09
Unidentified spp.	—	—	—	2.77	85.86
Coelocaryon preussii	M-L	0.90	0.91	2.61	88.47
Hallea ledermannii	M-L	0.45	—	2.28	90.75
Erythrophleum ivorense	L	0.55	—	2.09	92.84
Pycnanthus marchalianus	M-L	0.85	1.16	1.92	94.76
Macaranga spp.	S-M	1.35	—	1.75	96.51
Raphia spp.	S	—	—	1.42	97.93
Syzygium owariense	M-L	0.75	—	1.11	99.04
Symphonia globulifera	M-L	2.10	1.03	0.40	99.44
Spondianthus preussii	M	0.50	—	0.26	99.70
Oxystigma mannii	L	0.40	—	0.14	99.84
Musanga cecropioides	S-M	0.45	—	0.08	99.92
Anthocleista spp.	M	0.15	—	0.03	99.95
Xylopia staudtii	M	0.10	1.46	0.03	99.98

Growth form: S – small tree; M – medium-sized tree; L – large tree. All food-tree species are evergreen in Gbanraun.

Density values (#/ha) are for the trees ≥ 30 cm DBH.

CD = coefficient of dispersion (* for *Uapaca* see also Table 5.13).

Cum. % = cumulative percent.

Sp. tot. % obs = total contribution of the species to the annual diet.

Table 6.2: *Annual diet of Procolobus badius epieni (September 1996–August 1997). Values represent percentages of total feeding observations (n = 3600).*

SPECIES	YL	ML	PET	PITH	SEED	RFR	URFR	FL	BUD	BARK	UI	TOTAL
Ctenolophon englerianus	43.76	—	—	—	—	—	—	—	—	—	—	43.76
Uapaca spp.	—	—	—	1.28	6.25	—	—	8.31	—	—	0.06	15.90
LIANAS	4.50	1.00	0.31	0.06	0.22		0.50	0.44	0.31	—	0.39	7.73
Klaineanthus gaboniae	—	—	—	—	5.08	—	—	—	—	—	—	5.08
Funtumia africana	—	—	4.92	—	—	—	—	—	—	—	—	4.92
Rothmannia megalostigma	—	—	—	2.53	—	—	—	0.36	—	—	—	2.89
Pentadesma buteracea	2.45	0.22	—	—	0.03	—	—	—	0.08	0.03	—	2.81
Unidentified spp.	1.11	0.47	0.08	—	—	—	0.11	—	0.11	—	0.89	2.77
Coelocaryon preussii	0.61	1.89	—	—	—	—	—	—	0.11	—	—	2.61
Hallea ledermannii	—	—	—	2.28	—	—	—	—	—	—	—	2.28
Erythrophleum ivorense	2.09	—	—	—	—	—	—	—	—	—	—	2.09
Pycnanthus marchalianus	0.06	1.25	0.14	—	—	0.25	0.22	—	—	—	—	1.92
Macaranga spp.	0.11	0.06	—	—	—	—	1.25	0.19	—	—	0.14	1.75
Raphia spp.	—	—	—	—	—	1.42	—	—	—	—	—	1.42
Syzygium owariense	1.11	—	—	—	—	—	—	—	—	—	—	1.11
Symphonia globulifera	0.03	—	—	—	—	—	0.06	—	—	—	0.31	0.4
Spondianthus preussii	—	—	—	—	0.26	—	—	—	—	—	—	0.26
Oxystigma mannii	—	—	—	—	0.14	—	—	—	—	—	—	0.14
Musanga cecropioides	—	—	—	—	—	—	—	0.08	—	—	—	0.08
Anthocleista spp.	—	—	0.03	—	—	—	—	—	—	—	—	0.03
Xylopia staudtii	0.03	—	—	—	—	—	—	—	—	—	—	0.03
TOTAL	**55.86**	**4.89**	**5.48**	**6.15**	**11.98**	**1.67**	**2.14**	**9.38**	**0.61**	**0.03**	**1.79**	**100**

Plant parts abbreviated as follows: YL, young leaves; ML mature leaves; PET petioles; PITH a combination of central portion of the terminal end of a stem, leaf bud, and young leaf; SEED unripe seeds; RFR ripe fruit; URFR unripe fruit; FL flower; BUD flower bud; UI unidentified item.

Table 6.3: *Plant species consumed by Procolobus badius epieni from September 1996 through August 1997. Values represent percent of total feeding observations (n = 3600).*

FAMILY	SPECIES	SPECIES TOTAL	FAMILY TOTAL
Ctenolophonaceae	*Ctenolophon englerianus*	43.76	43.76
Euphorbiaceae	*Uapaca* spp.[a]	15.90	
	Klaineanthus gaboniae	5.08	
	Macaranga spp.	1.75	
	Spondianthus preussii	0.26	22.99
Rubiaceae	*Rothmannia megalostigma*	2.89	
	Hallea ledermannii	2.28	5.17
Myristicaceae	*Coelocaryon preussii*	2.61	
	Pycnanthus marchalianus	1.92	4.53
Guttiferae	*Pentadesma butyraceae*	2.81	
	Symphonia globulifera	0.40	3.21
Ceasalpinioideae	*Erythrophleum ivorense*	2.09	
	Oxystigma mannii	0.14	2.23
Palmae	*Raphia* spp.[b]	1.42	1.42
Myrtaceae	*Syzygium owariense*	1.11	1.11
Moraceae	*Musanga cecropioides*	0.08	0.08
Loganiaceae	*Anthocleista* sp.	0.03	0.03
Annonaceae	*Xylopia staudtii*	0.03	0.03
LIANAS[c]		7.73	
UNIDENTIFIED		2.77	
		100	**84.56**

Uapaca spp.[a]: *Uapaca heudelotii* and *U. staudtii*.
Raphia spp.[b]: *Raphia hookeri* and *R. vinifera*.
Lianas[c]: (includes strangler figs) 3 Combretaceae spp., 2 Ficus spp., and a large number of undetermined species.

Table 6.4: *Monthly composition of the Procolobus badius epieni diet. Values represent percent of feeding observations during 5-day follows.*

MONTH	YL	ML	PET	PITH	SEED	RFR	URF	FL	BUD	B	UI
SEP 96	52.7	10.7	12.2	6.1	—	—	—	—	—	—	18.3
OCT 96	77.0	2.9	8.0	7.3	—	—	0.7	—	—	—	4.0
NOV 96	38.5	1.6	4.0	3.6	—	—	2.8	47.6	—	—	2.0
DEC 96	47.2	0.5	0.5	4.1	0.5	0.5	0.8	43.0	—	—	2.8
JAN 97	70.1	1.6	2.6	14.6	1.0	6.5	3.2	0.3	—	—	—
FEB 97	44.6	5.8	4.2	3.1	38.1	1.3	1.6	0.8	—	—	0.3
MAR 97	44.0	8.3	6.6	6.0	21.8	0.3	0.6	6.6	5.7	—	—
APR 97	69.7	1.5	6.7	9.0	5.2	3.7	—	3.7	—	—	0.7
MAY97	70.0	—	3.6	1.8	3.6	4.5	10.3	6.3	—	—	—
JUN 97	64.2	7.0	2.5	6.1	11.2	3.9	3.6	1.1	—	0.3	—
JUL 97	47.3	7.3	11.3	5.8	24.4	—	3.7	—	—	—	0.3
AUG 97	56.7	8.7	8.7	7.6	16.0	0.6	0.9	—	—	—	0.9

Plant parts abbreviated as follows: YL, young leaves; ML mature leaves; PET petioles; PITH a combination of central portion of the terminal end of a stem, leaf bud, and young leaf; SEED unripe seeds; RFR ripe fruit; URFR unripe fruit; FL flower; BUD flower bud; B bark; UI unidentified item.

Table 6.5: *Canopy indices for 12 Procolobus badius epieni food species.*

	CI^M			
SPECIES	**GBT**	**GBS**	**GBD**	**UK**
Ctenolophon englerianus	1796	2446	815	646
Uapaca spp.	3234	2902	3520	1657
Klaineanthus gaboniae	222	83	618	280
Funtumia africana	106	161	50	50
Rothmannia megalostigma	125	80	227	—
Pentadesma buteracea	83	28	158	234
Coelocaryon preussii	70	63	94	131
Hallea ledermannii	49	98	39	36
Erythrophleum ivorense	64	—	127	—
Pycnanthus marchalianus	58	102	13	78
Macaranga spp.	85	122	73	60
Syzygium owariense	52	52	26	—

CI^M: Canopy index calculated using Marsh's (1981) methods, crown depth sp. n × crown width sp. n × Σ sp. n.

GBT: Gbanraun total DBH $\geq$ 30 cm enumeration.

GBS: Gbanraun swamp subsample DBH $\geq$ 30 cm enumeration.

GBD: Gbanraun dry subsample DBH $\geq$ 30 cm enumeration.

UK: Ukubie DBH $\geq$ 30 cm enumeration.

Table 6.6: *Selection ratio for the most common food species (September 1996 - August 1997).*

SPECIES	**CS**	**D**	CI^T	**%FO**	**SR**
Ctenolophon englerianus	25	11.9	297.5	43.8	147.2
Uapaca spp.	17.6	41.9	737.4	15.9	21.6
Klaineanthus gaboniae	13.6	4.8	65.3	5.1	78.1
Funtumia africana	14.5	2.1	30.5	4.9	160.7
Rothmannia megalostigma	15.1	2.2	33.2	2.9	87.3
Pentadesma buteracea	13.7	1.8	24.7	2.8	113.4
Coelocaryon preussii	17.7	0.9	15.9	2.6	163.5
Hallea ledermannii	19.9	0.5	10.0	2.3	230.0
Erythrophleum ivorense	20.7	0.6	12.4	2.1	169.4
Pycnanthus marchalianus	16.0	0.9	14.4	1.9	131.9
Macaranga spp.	15.8	1.4	22.1	1.8	81.4
Syzygium owariense	16.2	0.8	13.0	1.1	84.6

CS: mean spread + mean depth = crown size for an average tree.

D: density (stems/ha).

CI^T: crown size × density = cover index Gbanraun study area (Struhsaker, 1975).

%FO: percent of total feeding observations for 12 month period.

SR: Selection ratio = 1000 × %FO / CI.

Figure 6.1: *Percentage of Uapaca flower feeding records (UA-FL), and the percentage of Uapaca with flowers in the phenology samples.*

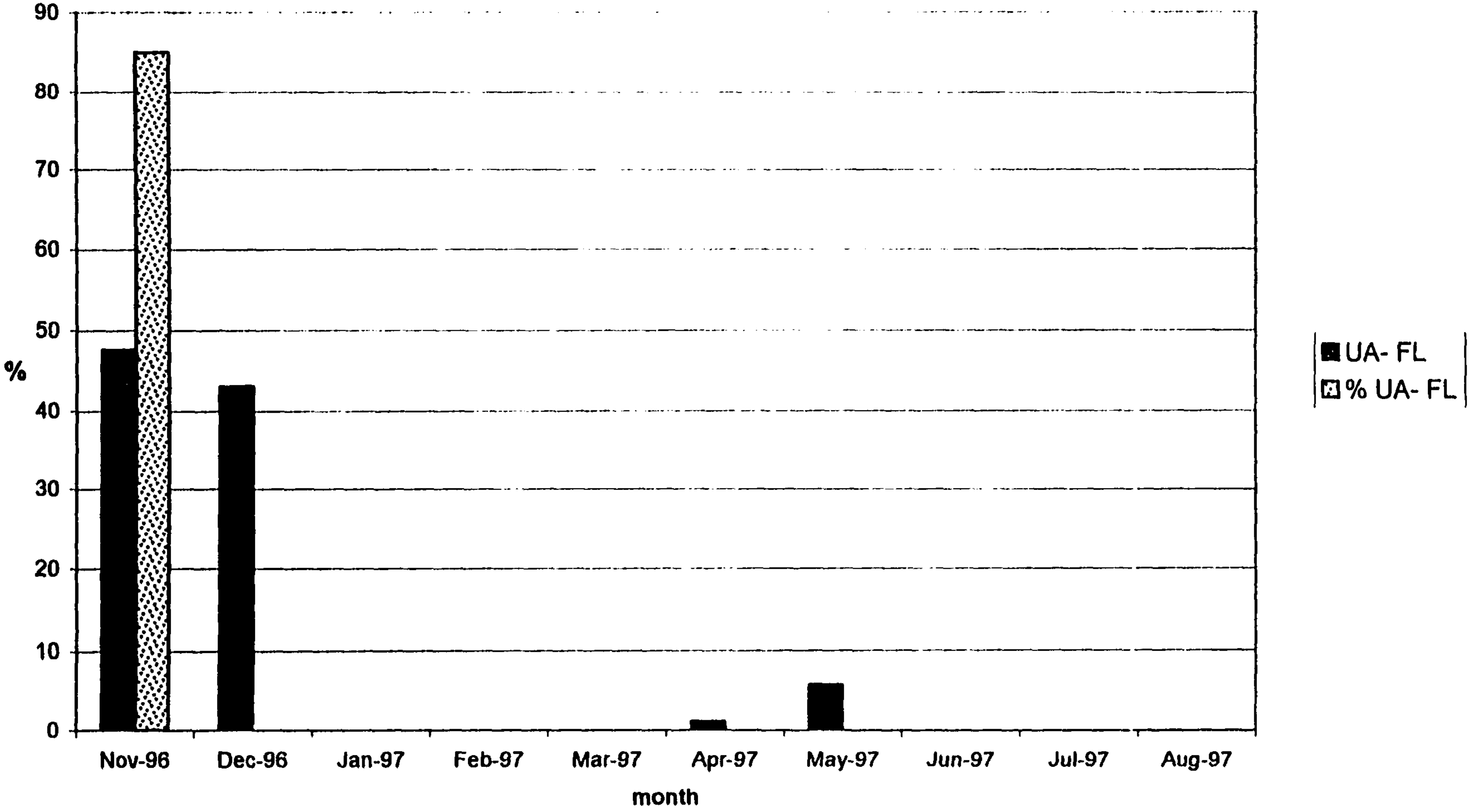


Figure 6.2: *Percentage of feeding records for Uapaca seeds (UA-FR) and Klaineanthus seeds (KLGA-S), and the percentage of Uapaca with unripe fruits and Klaineanthus with seeds in the phenology samples.*

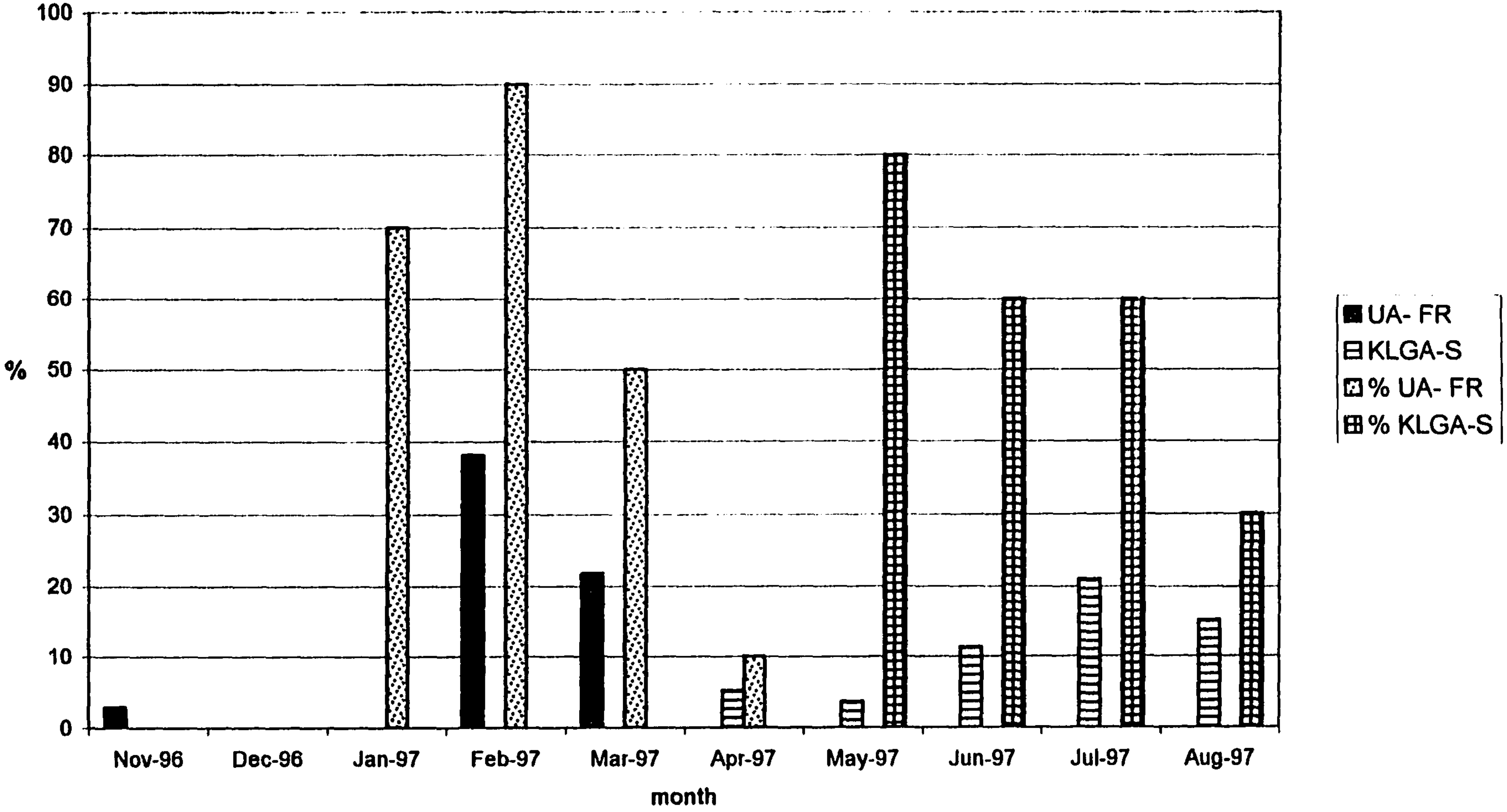


Figure 6.3: *Percent of feeding observations for* Ctenolophon englerianus *(CTEN), and percent of trees with young leaves in the Gbanraun dry (GB dry) and Gbanraun swamp (GB wet) phenology samples.*

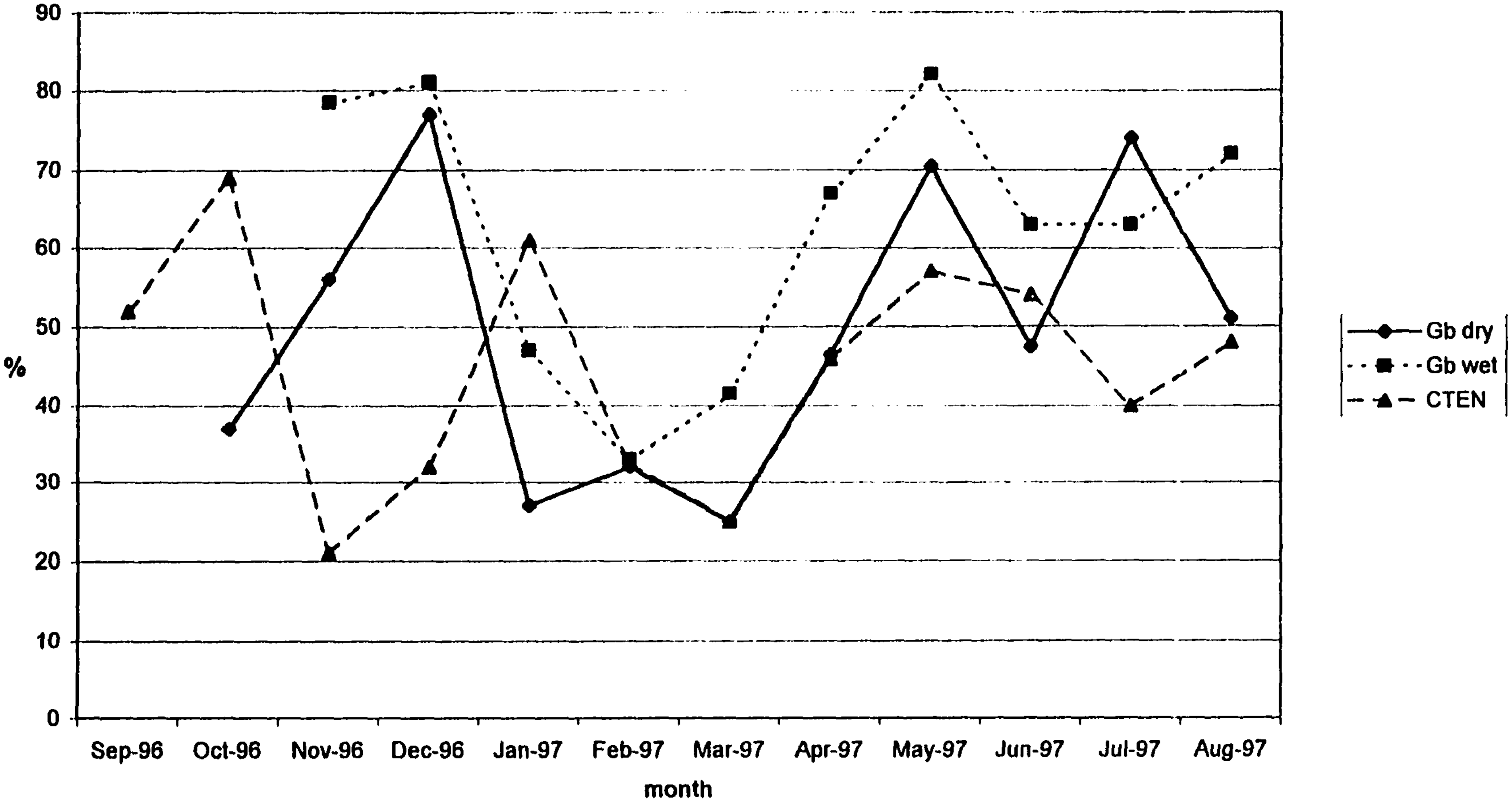
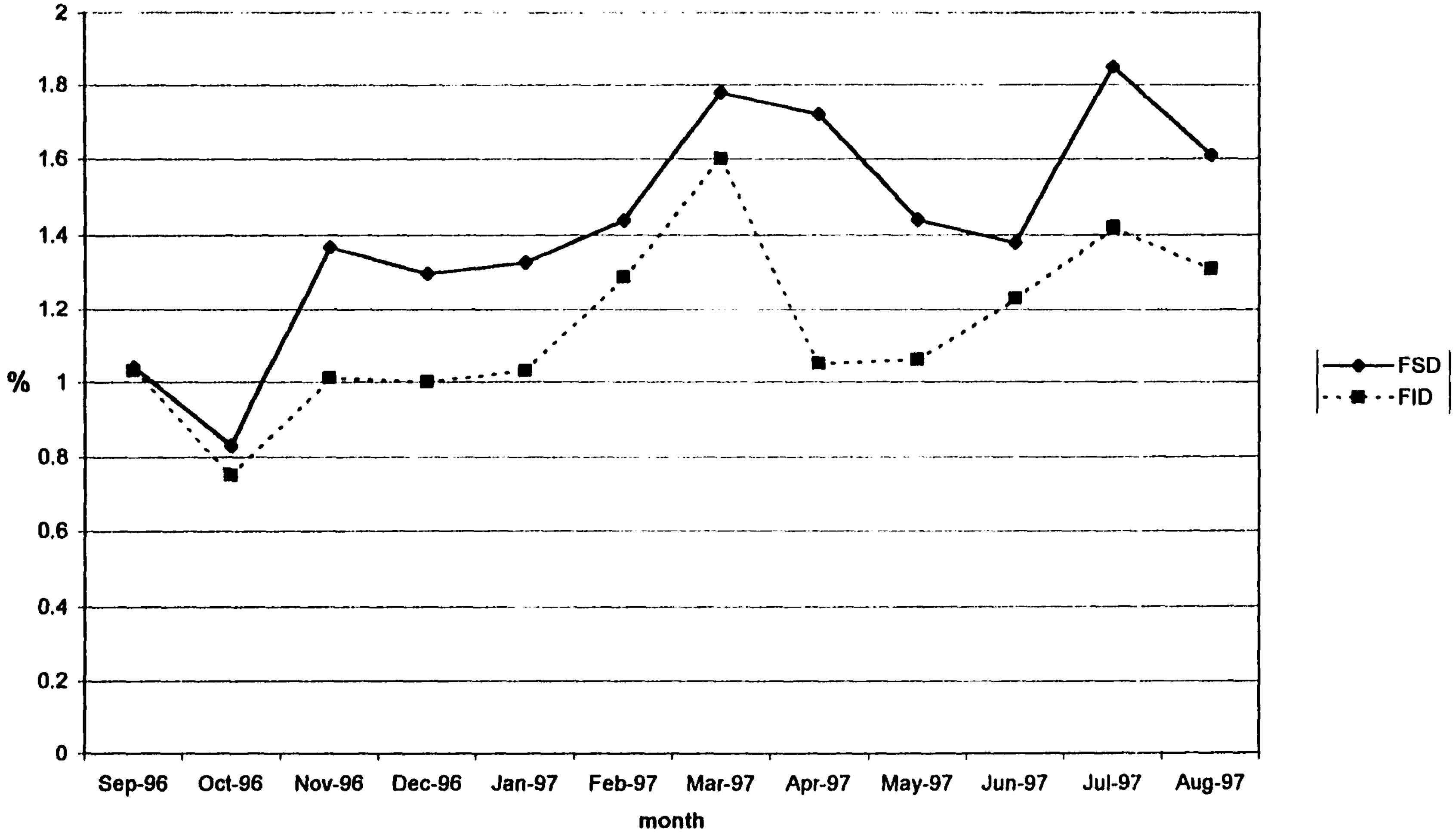


Figure 6.4: *Shannon's diversity index (H') for food species (FSD) and food item (FID) diversity.*



CHAPTER 7

RANGE USE

7.1. Introduction

Taken together, this research confirmed the conclusion that primate ranging behavior is strongly influenced by the way resources are distributed in time and space (Milton, 1980; Sigg & Stolba, 1981; Stanford, 1991), and by features of the primates themselves. Body weight, for example, has been shown to be an important influence on ranging behavior (Milton & May, 1976; Clutton-Brock & Harvey, 1977; Temerin *et al.*, 1984).

Early investigations of primate ranging behavior focused mainly on species living in savanna, or other open habitats, and led to the conclusions about the interaction between social structure and ecology (*e.g.*, DeVore, 1963; Altmann & Altmann, 1970; Struhsaker & Gartlan, 1970). These studies were soon supplemented by research on rain-forest species (*e.g.*, Struhsaker, 1975; Oates, 1977; Waser, 1977; Wrangham 1977).

Beyond these generalizations, field studies have attempted to identify the finer details of the factors responsible for observed variation in ranging patterns (Struhsaker, 1975; Oates, 1977; Marsh, 1981a; Stanford, 1998). Food distribution and abundance, habitat structure, group size, movements on previous days, weather patterns, and inter- and intragroup social interactions have all been suggested as potential determinants of variation in ranging. However, few studies of red colobus have identified significant correlations between one or more of these variables and ranging patterns (Isbell, 1984).

Most long-term studies of red colobus groups have attempted to determine what variables have most influence upon red colobus ranging behavior. Struhsaker's (1975) study of *Procolobus badius tephrosceles* at Kanyawara in Kibale Forest, Uganda identified a positive correlation only between day range length and intergoup encounters. He found no positive correlations of day range length with different aspects of the group's feeding behavior. Marsh (1981*a*), who studied a group of *P. b. rufomitratus* on the Tana River, Kenya did, however, find two positive correlations between aspects of the group's feeding behavior and day range length. During this study information on all larger tree species in the study group's home range was collected which allowed for a more accurate analysis than possible at the much larger study site in Kibale (Marsh, 1981*a*). Marsh (1981*a*) found that the distribution of major food species and daily range length were positively correlated, and that an inverse relationship existed between the diversity of monthly ranging patterns and availability of young growth. Isbell (1984) tested a number of variables to determine how they affected daily ranging behavior for a group of *P. b. tephrosceles* at Kibale. Her analysis indicated that intragroup conflicts between males, rainfall, dietic diversity, and tree species richness in the diet were significantly correlated with daily ranging behavior. As a result Isbell (1984) came to the conclusion that red colobus monkeys are apparently sufficiently flexible in their ranging behavior and that they are not restricted by foraging constraints in the face of more ephemeral pressures.

For this study I will examine if there are any relationships between ranging behavior and a number of aspects of the study group's feeding behavior. Specifically, food item availability, tree species richness in the diet, and food species distribution will be compared with daily ranging behavior and cell use diversity. This comparison will help to determine if feeding on seasonally abundant food items and/or the distribution of food species in time and space plays a significant role as a determinant of daily ranging behavior for the study group.

7.2. Methods

Ranging and activity patterns were derived from observations made during 12 monthly follows, 1 of 4 days and 11 of 5 days, from September 1996 through August 1997. Data were collected by scan sampling at 15 minute intervals between approximately 06:00 and 18:00 hours. During scans the activity of individual animals was scored as one of five mutually exclusive categories: feed, travel, move (all locomotion other than travel), inactive, social interaction, or other. For each record the sampled animal's vertical distance from the ground was estimated in 5 m increments, and the cell occupied by each sampled monkey was recorded. Because the study group was large, approximately 60 animals, and most often distributed over an area between 0.5 and 1 ha, there was a good possibility that the scan samples could be biased. In order to have some idea of their accuracy I also recorded an overall assessment of the activity in which the majority of the whole group was engaged during each scan sample. Though it was always impossible to observe the whole group at a single point in time, information from all visible animals as well as presence or lack of different types of movement were used to arrive at an estimate of the group's main activity. I restricted myself to three different activity states, feed, travel, and inactive. The activity states move and social, which were included in the systematic scan samples, were included in feed (move), and inactive (social), because on no occasion did the majority of group members engage in these activity states.

During follows I recorded the group's daily movements on a prepared map. Day range lengths were then estimated, in 50 m increments, by measuring daily path length with a mapping wheel from this map.

The number of methods to measure a primate group's home range, the entire area occupied over one year, is quite extensive. The first question to be answered is how the area occupied is to be defined. Boundaries can be determined by; a) the area that can be surveyed with all of the animal's senses, thus extending the home range beyond the range of physical occupation (P. Waser, in Struhsaker, 1975; p. 148), b) the area used above a certain level of physical occupation (*i.e.* only those sections of the home range that get visited more than once), or c) as the total area of physical occupation.

Two methods are commonly used to calculate home range size. The first method sums the number of different cells entered by the group. This method is employed in a number of different forms, most commonly the grid method, where a grid of 0.25 ha cells is superimposed on a map of the animal's movements. Most studies of African colobines employ this method (Clutton-Brock, 1975; Struhsaker, 1975; Oates, 1977; Marsh, 1978; Harrison, 1986; Dasilva, 1989). The second method is the taut string method that determines the home range size by placing a line around the outer limit of all areas entered by the study group (Altmann & Altmann, 1970).

Both methods have limitations; the taut string method may include many lacunae, although this problem can be eliminated in certain circumstances (Struhsaker, 1975). The grid method, on the other hand does not allow for partial usage of grid cells (Kool &

Croft, 1992). A record that the study animals entered a particular cell does not imply that all of that cell's area was used. The bias in home range size that this causes increases if the study group is small, and therefore often uses only a small part of any one cell. However, if the study group is large and is often spread over a large area, this type of bias gets reduced. This was the case with my study group that was both large (60 animals), and often spread out over a very large area. My study group would often occupy two to four 0.25 ha cells when feeding or resting, and was only contained, on rare occasions, within a single cell during travel or at night. Though this does not exclude the possibility that the estimated home range includes a number of lacunae, their contribution to the annual home range is reduced.

I decided to use the simplest method, and define the size of the study group's home range as the total area of physical occupation, and calculated its size by adding the number of cells entered during all of the twelve monthly follows. However, because of the group's large size and relative incohesiveness, it was generally impossible to determine the group's center of mass (Altmann & Altmann, 1970). Daily ranges recorded on the maps were, therefore, determined by estimating the group's center of mass.

The same method to calculate home range size as described by Bocian (1997) was followed. I multiplied the cell's area (0.25 ha) by the number of cells entered on the prepared maps, with as result that also all cells entered outside the scan samples are included.

To identify my study group's use of different habitat types, cells within the study area's grid system were identified as swamp, transition zone, or dry land (see **Section 5.3**), and the group's use of these different habitat types calculated.

Shannon-Wiener's index H' was used to calculate monthly indices of cell use diversity:

$$H' = -\Sigma\, p_i \ln p_i$$

where p_i = the proportion of scan samples during which cell i was occupied. I used Spearman Rank Correlation Coefficients (r_s) to compute correlations between different aspects of ranging diversity and various measures of food distribution and diet composition. I calculated Chi Squares to investigate differences in activity budgets of red colobus studies, as well as differences between months in activity states and daily and average monthly path length for the study group.

My results, describing the study group's ranging behavior are compared with those of Struhsaker (1975), and Marsh (1981a) because these studies employ similar methods and were closest in duration to this study.

7.3. Activity Patterns

7.3.1. *Daily activity patterns*

A general pattern was observed in which the study group spent its day. When the group was encountered at dawn most of the group would still be inactive, while a small number had started foraging. The number of foraging animals would increase over the next 30 to 60 minutes until all animals had become active. At this point the group would start traveling, with individual animals occasionally interspersing travel with short feeding bouts. These short foraging bouts would never last longer than 15 minutes, and consisted generally of the monkey feeding on some food items without loosing contact with the majority of traveling animals. The group would generally stop two to three times in a specific area for longer periods of time, varying from 30 to 90 minutes, with the majority of group members foraging. During these periods a number of animals would also be inactive, and a smaller number would engage in social behavior This pattern would generally continue until 12:00 to 13:00 hours. At that point the group would typically become more cohesive, and rest in an area occupying about two 0.25 ha cells for approximately 1.5 hours. During this period most social behavior, especially grooming and infants/juveniles playing, was observed. At approximately 14:00 to 15:00 hours the morning pattern, travel interspersed by short foraging bouts of individual animals, and two to three stops for longer foraging bouts would be repeated. Though generally the largest number of animals would be foraging during these stops, the proportion of inactive animals would be higher than during the morning stops. Occasionally the whole group would be resting around 17:00 hours. This was mostly the case during the wet months since it would nearly always rain around that time. The last hour of the day from 17:30 to 18:30 hours would generally see increased foraging activity under any weather condition. Because I was always forced to leave before dusk I have no data on how the group spent the last 30 minutes of the day. The position where the group would be encountered the next day indicated, however, that this could vary from remaining at the same location to movement of up to 200 m.

7.3.2. *Activity budgets*

The percentage of total samples of individual activities in which the animals engaged in each of four categories (feed, inactive, move, and other) comparable to those of other red colobus studies, together with the results from these red colobus populations are presented in **Table 7.1** (p. 167).

The red colobus in Gbanraun spent 37% of their time feeding, which is only little more than the average of 33% for the other red colobus groups. The red colobus at Gbanraun spent, however, less time resting than the majority of other red colobus populations studied, with exception of Struhsaker's (1975) study group at Kanyawara. The average percentage of inactive for the other red colobus studies is 50%, which is considerably more than the 33% at Gbanraun. Travel, which is an average of 8% outside, but 25% in Gbanraun, shows the greatest difference with the other studies. This is the only category that falls well outside the variation observed in the other listed studies. The 6% for other, which includes mostly social behavior is broadly similar to the 8% for the other studies. This indicates that the study group at Gbanraun spent as much time feeding and socializing as the other groups listed, but spent much more time traveling, which resulted in a lower percentage for inactive.

However, a comparison of all studies for the different activity states indicates that, despite these apparent similarities, most of the observed percentages vary significantly from the mean percentage of each activity state. Chi-square tests show significant variation for the following activity states: feed, inactive, and move when compared to the mean (**Table 7.1**, p. 167). Only other, which includes mainly social behavior, shows no significant variation between all studies. When Gbanraun is excluded however, the other studies show no significant variation for move, indicating that there is a significant difference in travel time between this and the other studies.

The percentage distribution of samples in different categories in the assessment of overall group activity is very similar to that obtained from the scan samples. Feeding was scored at 35.1%, which is comparable with a combined feeding and moving score of 37.3% from the scan samples. Inactive was 42.5% for overall group activity, and 38.2% for inactivity and social interactions from scan samples. Locomote scored 22.3% for overall group activity and 24.5% from scan samples. Though the two methods are dissimilar and do not allow statistical comparison, their similar results suggest that the study group's large size and incohesiveness did not affect the activity scan samples' accuracy negatively.

7.3.3. *Monthly variation in activity*

The monthly distribution of the different activity states for the 12 monthly follows is presented in **Table 7.2** (p. 168). I used Chi-square tests to determine if the observed variation in percentages between the different months was significant. Travel was the only activity state for which significant variation was observed (**Table7.2**). However, if the month October is excluded, which with 12.7% was considerably lower than the observed mean of 24.5%, no significant variation between the other months is observed.

A Spearman Rank Correlation indicated that there was no significant correlation between the monthly percentage of travel records and average monthly path length. This could be explained by differences in the speed with which the animals travel. High travel speed could result in a long path length, but also a low number of travel records because of reduced travel time. Table 7.3 shows that the actual distance traveled during October deviates far less from the mean monthly path length than the percentage of travel records suggests. It may, therefore, have been the case that in October travel speed was higher than during the other months. I have, however, no good explanation for this much higher travel speed in October.

7.3.4. *Vertical distribution of activities*

During scan samples the height of each animal sampled was recorded in 5 m increments. Given the varying distance and height at which the animals were observed, and the fact that my position varied from standing in 1 m of water to standing on top of dry outcrops it was impossible to be more accurate. The average height of animals resting was 20 m. Since the average tree height of all trees with a DBH ≥ 30 cm for the study area was 21.6 m this indicates that the animals selected a covered position as high in the canopy as possible. Most travel and feeding took place at a lower level of 15 m. During feeding animals were often forced to move down in the canopy, not only because of the location of food items, but also because other group members would often occupy all available higher feeding positions. The observation that the adult males, the most dominant members of the group, were generally in the highest feeding positions tends to support the view that the red colobus preferred the highest strata of the forest. The average travel height of 15 m is the result of the forest's structure. The many gaps in the swamp forest often forced the animals to come down to relatively low levels as they traveled.

The red colobus at Gbanraun never came to the ground, with the exception of one animal that was observed to fall, involuntarily, to the ground. Animals were observed only under 10 m in some sections of the forest where the trees did not exceed this height, or when feeding on the few food items included in the diet from tree species which rarely or never exceeded this height (*e.g.* ripe fruits of *Raphia* spp.). The mean height of all activities fell within the 15 to 20 m increment, supporting a strong preference for the top 25% of the canopy

7.4. Home Range

During the study the group entered 295 cells, giving a total annual home range of 72.75 ha (**Table 7.4**, p. 169). Of the 291 cells 27 (9%) were recorded outside the scan samples. **Figure 7.1** (p. 171) shows the cumulative number of 0.25 ha cells entered by the study group with each successive month. The curve never levels of, and though the number of new cells entered after the sixth month decreases during the remainder of the study, new cells continue to be added to the home range. This indicates that the study group's home range is probably larger than observed during the study period.

Though the observed size of the study group's home range size is probably an underestimation, it falls within the range (55-114 ha) observed for other red colobus populations inhabiting mature evergreen forest (Oates, 1994*b*).

7.4.1. *Spatial overlap with conspecific groups*

Map 7.1 (p. 172) indicates that those areas of the home range used most extensively by the study group are concentrated in the central and eastern parts of the group's home range.

In addition to the study group three other red colobus groups were identified as occupying sections of the study site. All three were observed within the study group's home range, and recordings of the locations of these other groups (both during and outside follows) indicated extensive overlap. My limited observations suggested that a minimum 125 cells (42 %) of the home range were also used by each of the three other groups, but the real number is likely to be larger.

A number of the areas used most intensively even fell within a section of the home range that was used by one or more of the other groups. For example the area around the h6 cell saw some of the most intensive use by the study group, but this was also the area were on two occasions the study group and another group, and on one other occasion the study group and two other groups, were observed to pass the night.

7.5. Daily and Monthly Variation in Ranging Behavior

The daily path length of the study group was extremely variable. The mean daily path over the sample of 59 days was 1040 m but showed a wide range (690 m in September to 1110 m in July), and an even wider range between different days (450 m in September to 1900 m in March) (**Table 7.3**, p. 169).

Chi-square tests were calculated in order to determine if the observed differences in daily and average monthly path length were significant. Daily and mean monthly path lengths were converted to their total number of 50 m increments, which were compared against the expected value, the mean daily travel distance (1040 m or 21 increments). The analysis indicated that there was significant variation between the 59 daily path lengths (Chi-square = 89.7, df = 58, p = 0.05), but no significant variation between average monthly path lengths.

7.6. Monthly Ranging Diversity

During all 12 monthly follows the red colobus occupied a large number of cells (range 82 to 159) (**Table 7.3**, p. 169) Shannon-Wiener's index H' was used to calculate monthly indices of cell use diversity, which showed an average of H' = 3.828 with a range between 3.188 to 4.120. The comparatively low cell use diversity of 3.188 was scored for September, and probably reflects my inexperience in following the study group while on the move. As a result the records may have been biased to periods when the group was not moving, thus reducing the number of cells included in the scan samples.

There was significant monthly variation in cell use diversity between the months of highest and lowest cell use diversity ($t = 19.35$, $df = \infty$). Even when excluding the score from September, with the range running from 3.448 to 4.120, there is still significant variation in cell use diversity ($t = 18.6$, $df = \infty$).

7.7. Correlations between Ranging and Foraging

To investigate relationships between the study group's ranging and different aspects of its feeding behavior, I selected 11 variables for a correlation analysis, using data collected during the 12 monthly follows. Spearman Rank Correlation Coefficients (r_s) were calculated to determine if a correlation existed between two range use variables, monthly indices of cell use diversity, and average monthly day range length and six variables of food plant availability;

1. Number of species in the diet
2. Number of items in the diet
3. food species diversity (H', see **Section 6.3.4**)
4. food item diversity (H', see **Section 6.3.4**)
5. dispersion top 4 food species
6. cover of the top 4 food species,

and between the two range use variables and percentages of five different plant parts in the monthly diet:

1. percentage of young leaves
2. percentage of seeds
3. percentage of flowers
4. percentage of flowers and seeds
5. percentage of *Ctenolophon englerianus* young leaves

The results of these correlations are presented in **Table 7.5** (p. 170). Cell use diversity was significantly positively correlated with the number of species in the diet ($r_s = 0.797$, $p > 0.05$), and the number of items in the diet ($r_s = 0.734$, $p > 0.05$). Average monthly day range length was also significantly positively correlated with the number of species in the diet ($r_s = 0.810$, $p > 0.05$), as well as food species diversity ($r_s = 0.598$, $p > 0.05$) and food item diversity ($r_s = 0.631$, $p > 0.05$).

It is not surprising to observe that the number of species and food items in the diet play an important role in determining the study group's ranging behavior. However, the presence of this positive correlation, but not with any of the food item categories and the most important food item suggests that though diet composition may be an important determinant, no single food item or food item category significantly influenced ranging behavior. It should be kept in mind, though, that the lack of a significant correlation might also be an artifact of the resolution of the vegetation enumeration. If a larger percentage of the study area's vegetation would have been included in the enumeration, significant correlations might have been detected (Marsh, 1981a). The lack of a correlation between the number of food items and day range length is probably the result of most food species in the monkey's diet providing more than one food item.

The absence of a significant correlation between two variables of food plant availability (food species and food item diversity) with cell use diversity, but the presence of a positive significant correlation with day range length, suggests that the study group prefers to feed in areas where food species are clumped. The lack of a positive correlation with cell use diversity indicates that as food species diversity and food item diversity in the diet increase, the number of cells used more intensively does not increase. If, as is the case, there is a positive significant correlation with day range length, it is suggested that though a larger number of cells are being occupied as food species and item increase, still only a small proportion of these cells are used to feed in. The remainder of cells is only used when passed through during travel. As the location of available food patches changed during the year the study group adjusted by increasing and decreasing travel distance. This data, therefore, suggests that the study group travels from food patch to food patch, passing through many cells in which it spends little time, and stops in those patches where the diversity of food items and food species is the highest.

7.8. Habitat Composition and Differential Use of the Home Range

7.8.1. *Habitat composition of the home range*

The study group's home range was broadly divided into three different habitat types: swamp, a transition zone, and a dry-land section. The swamp did not dry out during the dry season, while the dry-land section would only become inundated during periods of heavy rain. The transition zone was a mosaic of wet and dry areas, located between the swamp and dry-land section. Because the smaller transition zone was used at similar rates during all 12 months, and lacked a separate phenology sample, unlike the swamp and dry-land section, I decided to exclude this zone from further analysis.

7.8.2. *Variables influencing variation in habitat use*

Cell use over the study period indicated that the swamp section was mostly used during September, October, November and December of 1996, as well as July and August of 1997. During the first three months the number of new cells entered during each month decreased from 34 in September 1996 to 26 in November in 1996. In

December 1996 the number of new cells entered increased by 41 (58%), nearly all of which were located within the dry-land section, but the majority (56%) still fell within the swamp. During the next 6 months the dry-land section was mostly used, with the exception of May 1997 when the number of cells entered was equal for both habitats. In July 1997 the number of swamp cells used increased by 62%, but in August 1997 this number dropped and the study group used the swamp only marginally more (52%).

The data appeared to indicate that the study group used the swamp mostly during the dry months, and the dry-land section during the wet months. In order to examine whether this observed pattern was statistically significant I compared habitat use with precipitation. Because I had no data on rainfall for the study site I used average precipitation for Brass, the closest available location, recorded in *Nigeria in Maps* (Barbour *et al.*, 1982). However, a Spearman Rank Correlation did not find a significant correlation indicating that precipitation did not influence differential habitat use.

The phenology of tropical rain forests is rarely strictly seasonal (van Schaik, 1986; Richards, 1996; Struhsaker, 1997) and precipitation may be a poor indicator of differential habitat use. It could be, therefore, that the direct examination of the phenology of the two different habitat types would provide an explanation for the observed pattern in habitat use. I compared young leaf production (with 56% the study group's most important food item category) in the swamp phenology sample for those months spent in the swamp, and in the dry-land sample for those months spent in the dry-land section. Single Classification ANOVAs, however indicated that there was also no significant relationship, suggesting that young leaf production also did not influence differential habitat use.

The phenological data for the study area was extensive and was separated in a sample of the swamp and of the dry land. This increased accuracy and made it less likely that any existing relationship with habitat use would have been missed. It is, however, possible that the phenological patterns of specific food tree species, some of which are mostly restricted to one of the two habitats, play a significant role. An example of this would be *Kleineanthus gaboniae*, whose seeds were the fourth most important food item, but which is mostly restricted to the dry-land section. This tree only produced fruits during June, July, and August 1997, but was observed to produce none in the same months of 1996. This variation may have resulted in differential habitat use between these two years. Unfortunately I had no data to test this phenomenon because my study did not start until September 1996.

I did, however, find a significant negative correlation between cell use diversity and the number of activity records from cells located in the swamp ($r_s = -0.6723$, $p > 0.05$). This suggests that cell use diversity increases when the study group was feeding in the dry-land section. An increase in cell use diversity indicates that a larger number of cells are used more evenly and for longer periods of time, indicating that the study group's food species in the dry-land section were more evenly distributed than in the swamp.

I also examined if there was a relationship between mean monthly path length and the number of swamp cells used, and I found a significant negative correlation ($r_s = -0.6291$, $p = 0.05$) between the two variables. This indicates that the study group traveled less when feeding in the swamp than when feeding in the dry-land section.

A comparison between the number of species in the diet and the use of swamp or dry-land cells was also made to examine whether number is a factor in differential habitat use. A Spearman Rank Correlation between the number of species in the diet with the number of dry cells used during each month indicated that such a relationship indeed existed. I found a significant positive correlation ($r_s = 0.9265$, $p = 0.01$), indicating that the study group exploited a larger number of food-tree species in the dry-land section.

7.9. Conclusion

7.9.1. *Activity patterns*

A comparison of activity budgets obtained for the different red colobus groups presented in **Table 7.1** (p. 167) indicated significant variation for three activity states; feed, rest, and move. Only the category "other" showed no significant variation between the different studies. This suggests that social behavior, the largest component of this activity state, is least flexible for red colobus. When Gbanraun was excluded the other studies also showed no significant variation for move, indicating that this study deviates significantly from the other studies for this activity state.

The few available long-term studies make it difficult to discern any species wide patterns in the red colobus activity budget, if there are any. This study confirms this with yet another unique distribution of activity states, not closely similar to those found in other studies.

7.9.2. *Ranging patterns*

Available information on red colobus ranging behavior shows the same degree of variation as activity budgets (**Table 7.6**, p. 170). There is tremendous variation in annual home range size from 9 ha on the Tana River (Marsh, 1978) to 114 ha by Clutton-Brock (1974) at Gombe. At Gombe, however, the home range was calculated by adding all 0.8 ha cells and not the more commonly used 0.25 ha cells that reduce the chance of overestimating. Struhsaker (1975) suggests, therefore, that the actual size of the Gombe home range was more likely 50-75% of 114 ha (approximately 60 ha) making it similar to the 65 ha occupied by Struhsaker's Kanyawara study group during one year (based on occupancy of 260 0.25 ha cells [Struhsaker, 1975, table 46; p. 280]). The annual home range size of 73 ha observed in this study, though somewhat larger than at the other mature rain forest locations, appears to fall within the recorded range.

The number of studies providing daily path lengths is much smaller than those giving home range areas. Struhsaker's (1975) group traveled a mean daily path length of 650 m (range 223 m to 1185 m) and Marsh's (1981*a*) group traveled a mean daily path length of 600 m (range 200 m to 1000 m); very similar results from two very different sites. Stanford (1998) records an even shorter mean daily path length of 400 m in Gombe. The results from this study show a much longer mean daily travel distance of 1040 m (range 450 m to 1900 m), almost double that of other populations. Though my methods were slightly different from those employed in the other two studies, they are not sufficiently different to have resulted in the observed ranging difference. This, therefore, confirms the already made observation that travel time for the Gbanraun study group was significantly higher than recorded for the other groups, and that this also resulted in significantly longer daily path lengths.

7.9.3. *Ranging, feeding, and differential habitat use*

The relationship between the study group's ranging and different aspects of its feeding behavior the following pattern emerged: the study group traveled from food patch to food patch where, for at least most of the year diversity of food items and food species is highest. However, when examining differential habitat use and range variation this general pattern turned out to be subtler. Though food-tree species appear to have a clumped distribution in Gbanraun this appeared to be more pronounced in the swamp than in the dry-land section. This was suggested by three observations:

1. A significant negative correlation between swamp cell use and the percent of activity records from cells located in the swamp indicated that a larger number of cells were used more extensively and for longer periods in the dry-land section, suggesting a less patchy distribution of food items.
2. A significant negative correlation between mean monthly path length and the number of swamp cells entered indicates that the group traveled less when in the swamp, perhaps because foraging involved more direct travel from patch to patch. My observations did not show that this pattern might be explained better by frequent movements within a small area of the swamp.
3. A significant positive correlation between the number of species in the diet and dry cell use indicated that a larger number of food-tree species were exploited in

the dry-land section, making it less likely that all were included in patches, with as result that more foraging outside patches was taking place.

Table 7.1: *Activity budgets of red colobus monkeys. Values represent percent of total activity samples.*

Study site	**Feed**	**Inactive**	**Move**	**Other**	**Ref.**	**Notes**
Gbanraun, Niger Delta	37	33	25	6		Samples across 12 months
Gombe, Tanzania	25	54	8	9	Clutton-Brock (1974)	Median percentage scores for 32 sample days over 8 months
Gombe, Tanzania	29	47	14	10	Stanford (1998)	
Bigodi, Kibale Forest	25	60	7	9	Clutton-Brock (1974)	Median of 12 days in 1 month
Kanyawara Kibale Forest	30	61	4	6	Clutton-Brock (1974)	Median of 10 days in 2 months
Kanyawara Kibale Forest	47	35	9	8	Struhsaker (1975)	Samples across 12 months: clinging infant scores excluded
Kanyawara Kibale Forest	46	31	11	12	Marsh (1978)	One 3-day sample, clinging infant scores excluded
Tana River, Kenya	32	51	8	9	Marsh (1978)	Samples across 12 months. clinging infant scores excluded
Abuko, Gambia	25	51	13	10	Starin (1991)	Samples across 12 months. excluding animals one year old or less
Tiwai, Sierra Leone	37	55	5	3	Davies (in Oates. 1994)	Samples across 12 months
Mean (excluding Gbanraun)	33	50	8	8		
Mean (including Gbanraun)	33	48	10	8		
Chi square	18.6*	23.0*	33.4*	7.5		

*significant at $p = 0.05$ (df = 9)

Table adapted from Oates in Davies and Oates (1994*b*)

Table 7.2: *Monthly and yearly activity budget, as well as an overall assessment of group activity (GI) of Procolobus badius epieni. Values represent percent of total activity samples.*

	Monthly mean percentages				
	Feeding	**Inactive**	**Travel**	**Move**	**Social**
Sep 1996	21.4	29.8	23.6	18.6	6.6
Oct 1996	35.2	34.8	12.7	9.0	8.3
Nov 1996	29.4	35.6	16.6	9.2	9.1
Dec 1996	35.8	30.1	21.6	5.3	6.6
Jan 1997	29.2	31.8	25.7	7.1	6.1
Feb 1997	36.1	29.0	21.6	6.8	6.4
Mar 1997	32.4	29.1	26.7	6.0	5.8
Apr 1997	22.2	36.4	30.8	6.6	4.0
May 1997	24.2	40.0	26.5	5.8	3.5
Jun 1997	29.5	34.7	29.5	3.5	2.7
Jul 1997	33.8	26.2	29.4	5.6	5.0
Aug 1997	31.6	33.0	29.4	3.4	2.6
MEAN	**30.1**	**32.5**	**24.5**	**7.2**	**5.7**
SD	5.14	3.81	5.58	3.99	2.07
Chi-square	11.14	4.93	23.07*	17.73	11.22
GI	35.1	42.5	24.5		

*significant at $p = 0.05$ (df = 11)

Table 7.3: *Daily path length measured in 50 m increments, and monthly mean path length.*

	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
1	650	800	800	900	900	900	1250	750	1250	800	900	500
2	750	1000	700	750	1050	1550	1150	700	950	1050	1550	1500
3	450	850	1300	750	1250	1100	1450	900	1150	1250	700	1150
4	900	950	700	1200	1050	1050	1900	1400	1250	1400	1250	1450
5	--	1050	750	900	1250	850	1000	1150	1150	1250	1150	850
M	690	930	850	900	1100	1090	1170	980	1150	1150	1110	1090

M = mean monthly path length

Table 7.4: *Number of cells entered during each monthly follow and Shannon-Wiener's index H' of cell use diversity.*

	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Day 1	15	23	22	24	27	29	29	15	29	23	22	13
Day 2	24	21	15	17	33	53	29	20	19	21	39	37
Day 3	20	18	22	27	32	24	34	24	29	28	15	30
Day 4	23	25	19	27	28	28	40	29	34	31	32	35
Day 5	--	29	24	29	26	25	22	22	29	29	26	22
Total	82	116	102	124	146	159	154	110	140	132	134	137
H'	3.188	3.579	3.448	4.046	3.980	3.935	4.120	3.997	3.997	3.714	3.982	3.970

Table 7.5: *Spearman Rank Correlation Coefficients (r_s).*

	cell use diversity	**mean monthly day range length**
food spp. diversity	0.550	0.598*
food item diversity	0.523	0.631*
# of spp. in diet	0.797*	0.810*
# of items in diet	0.734*	0.547
dispersion top 4 food spp.	-0.294	-0.112
combined cover top 4 food spp.	-0.513	-0.459
% young leaves in diet	0.077	0.169
% seeds in diet	0.476	0.548
% flowers in diet	-0.221	-0.403
% flowers & seeds in diet	0.118	-0.013
% CTEN in diet	-0.016	0.038

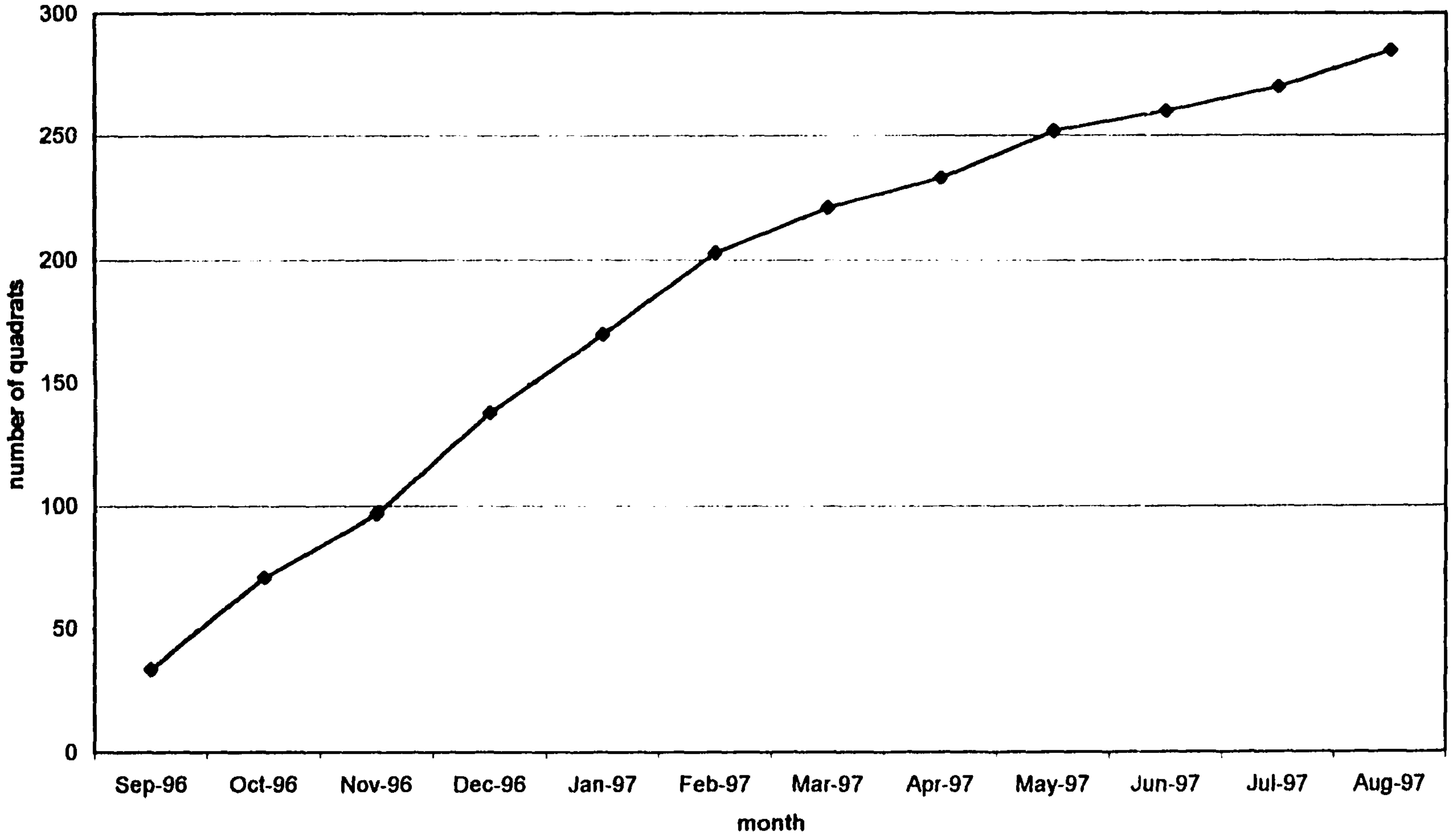
*significant at $p < 0.05$

Table 7.6: *Ranging behavior of red colobus.*

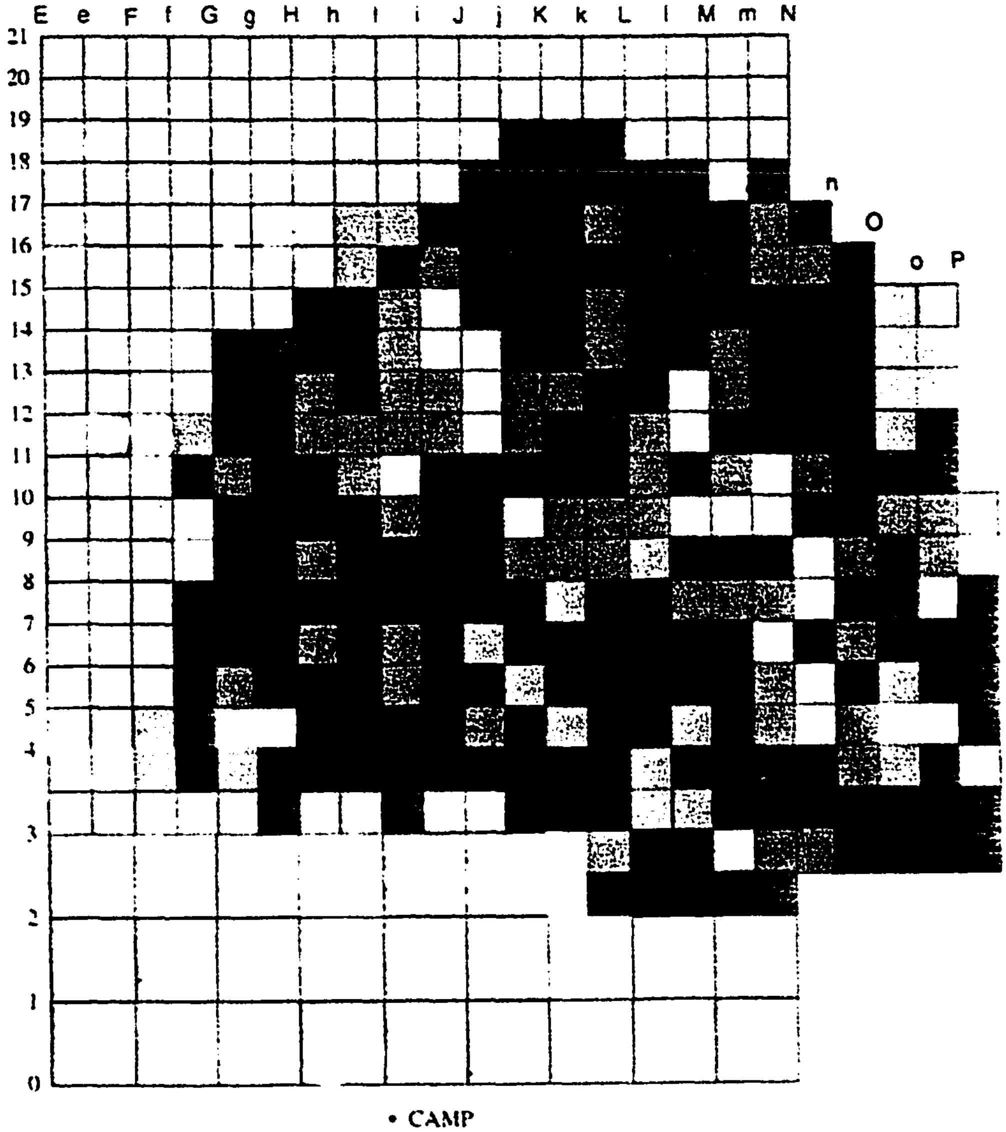
Subspecies	**Study site**	**Annual home range size (ha)**	**Daily path Length (m)**		**Reference**
			mean	**range**	
P. b. epieni	Niger Delta, Nigeria	73	1040	450-1900	
P. b. temminckii	Abuko, Gambia	34	--	--	Starin (1991)
P. b. badius	Tiwai, Sierra Leone	55	--	--	A. G. Davies in Oates (1994)
P. b. tephrosceles	Gombe, Tanzania	114	--	--	Clutton-Brock (1975)
P. b. tephrosceles	Gombe, Tanzania	--	393	0-850	Stanford (1998)
P. b. tephrosceles	Kibale, Uganda	65	649	223-1185	Struhsaker (1975)
P. b. rufomitratus	Tana River, Kenya	9	603	200-1000	Marsh (1981)

Table Adapted from Oates in Davies & Oates (1994*b*).

Figure 7.1: *Cumulative number of new 0.25 ha quadrats entered by the study group during monthly follows.*



Map 7.1: *Home range of the study group.*



Each home range cell occupies 0.25 ha (50 x 50 m).
Dark grey: 1-25% of the maximum number of records recorded in one cell.
Medium grey: 26-50% of the maximum number records recorded in one cell.
Light grey: 51-75% of the maximum number of records recorded in one cell.
Black: 76-100% of the maximum number of records recorded in one cell.

CHAPTER 8

SOCIAL BEHAVIOR

8.1. Introduction

An increasing number of primate studies have found that intraspecific variation in primate social systems is common, and that the colobines are no exception (Richard, 1974; Rudran, 1978; Butynski, 1990; Oates, 1994*b*; Newton & Dunbar, 1994: Bronikowski & Altmann, 1996; Treves & Chapman, 1996; Chapman & Chapman, 1999; Kirkpatrick, 1999).

In this chapter I discuss the social behavior of the red colobus study group at Gbanraun and compare the information I collected with that from other studies of red colobus. I will attempt to determine the following;

- Does the study group provide evidence for unusual patterns in social behavior of red colobus monkeys, or is the observed social behavior similar to that observed in other studies?
- Does this study aid in identifying general patterns in red colobus social behavior, and how might any such patterns be explained?

8.2. Methods

All data presented in this chapter were collected on red colobus groups within the study area. Though red colobus were observed outside the study area, no reliable data on the social behavior of these groups were collected.

Data on social behavior was obtained during 12 monthly follows, one of four days and 11 of five days, from September 1996 through August 1997. Data were collected by scan sampling at 15 minute intervals between approximately 06:00 and 18:00 hours. Records of the social behavior of individual animals fell in the following categories: agonistic, groom, play, and sexual behavior. I augmented the records from scan samples by recording a description of the behavior, that also allowed for further distinction of patterns in each of the behavioral categories. Only the data from scan samples were used for the analysis, but observations made outside scan samples were used to augment descriptions of, and identify patterns in each of the observed behavioral categories.

However, the difficult conditions of working in a swamp, the dense vegetation, and the large size of the study group limited the depth of my observations. Broad comparisons made with other studies conducted under similar conditions should, however, have some validity.

8.3. Social Organization of the Study Group

8.3.1. *Group composition*

The study group at Gbanraun closely fit the structure described for red colobus groups in other populations. There were six adult males in the group during the first six monthly follows, and seven during the remaining six follows (see **Section 8.5**). The remainder of the group contained, approximately, 26 females, 17 monkeys which were either females or subadult males and, on average, six juveniles and four infants.

Though no exact numbers were obtained for the other four groups in the study area the SE group was estimated to be approximately 80 monkeys with a core of at least seven adult males, the SW group approximately 25 animals with a core of at least two adult males, the NW group approximately 50 animals with a core of at least four adult males, and the NE group, which was the smallest, with approximately 15 monkeys and at least two adult males. Apart from these four groups, three subadult males were encountered in the study area on 3 different occasions when no other groups were around. After the fourth monthly follow this small male band was never encountered again.

8.3.2. *Social structure*

As observed in studies of other red colobus populations, the adult males formed the core of the study group (Clutton-Brock, 1972; Struhsaker, 1975; Starin, 1991; Mturi, 1993). The ability of adult males to displace females on most occasions suggested that they were dominant over all other members of the group. The adult males cooperated in the intragroup agonistic interactions, and the percentage of grooming samples between them (13%) was unexpectedly high, indicating a strong bonds (see **Table 8.1** [p. 188] for a break-down of the different categories of social behavior over the different age/sex classes). Females appeared to have weaker social bonds, fewer agonistic interactions were observed between them and they would groom each other much less than did the males. The only consistent interactions observed among the group's adult females were the clustering of all females carrying infants. Though this may in part have been the result of their lower travel speed, they appeared to actively seek each other's company. Within these clusters the interaction between adult females was minimal, and most of the social activity was the result of their offspring playing with each other.

Infants spent all of their time with or within reach of their mothers, and were actively protected from any other group member until they were young juveniles. As the juveniles grew older they would increase the distance from their mothers during most activities, but would still rest with them. I noticed that during rest even subadults would seek the company of adult females who were assumed to be their mothers.

Most of the play behavior observed was between infants and juveniles of the same age group, and consisted mostly of chasing. On occasion juveniles were observed playing a "game" in which they attempted to touch the top of each other's head. During this activity they would make a playface, keeping their mouth open without showing any teeth. On two occasions two adult animals of unidentified sex were observed to play. In one case a red colobus and a *Cercopithecus nictitans* juvenile were observed to play, but the red colobus mother quickly separated the two.

When traveling most animals would move in small clusters of three to six animals, but because I was never able to identify each animal I do not know if these small "bands" consisted of individuals that maintained close long-term relationships.

8.3.4. *Agonistic interactions*

Most intragroup agonistic interactions I observed involved chasing behavior. Of the records that fell within the scan samples (N = 33), participants in chases could not be identified for 21% of samples, 55% involved males chasing males, and 6% males chasing females. All participants were always adults; females were never observed to chase other females, and only in one case a female was observed to chase an adult male away who was interacting in a non-threatening manner with her juvenile offspring. Except in two cases chases never involved any physical contact, but they were always accompanied by loud vocalizations. In one instance two males grappled with one another, continued to chase, grappled another time, and separated when one of the males made a vertical leap of at least 8 m to a crown below him. The second case involved a chase in which at least five monkeys (two adult males followed by what appeared to be three females) participated, and ending with the two males, while grappling with one another, nearly falling to the forest floor. Sometimes chases were preceded by one of the participants making a threatening grimace that showed their teeth at the chasee.

The next most common category of agonistic behavior was branch shaking, which was, however, never recorded during a scan sample. In some cases only one animal, either an adult or subadult male, would engage in this activity but in other cases two adult males would face each other. The shaker would keep his body rigid with limbs fully extended while making rapid vibrations causing the branch to shake. Obvious flexing and extending of the arms as described by Struhsaker (1975) was not observed. On a number of occasions a single monkey was observed to leap about in a manner that created as much disturbance as possible. On two other occasions adult males were observed holding dead branches, one of which was at least 1.5 m long, which they attempted to wield without much success, and the branch was quickly lost, crashing to the ground. On a number of occasions animals were observed to lunge at other animals, but they stopped short from actually chasing or making contact; the animal being lunged at would move away without any further interaction.

Supplantations were also common, and in most cases involved adult males supplanting females and subadult males, and sometimes other adult males. Females and subadult males were also observed to supplant other females and/or subadult males, but on far fewer occasions. On two occasions a female with genital swelling was observed supplanting an adult male. Supplantation generally involved the supplanter approaching in such a way that it was obvious the animal would not stop short. In all observed cases the supplanted animal moved away before physical contact was made. On a few occasions the supplanted animal would grimace with an open mouth but no teeth showing before moving.

8.3.5. *Grooming behavior*

Grooming was the second most common form of social behavior (N = 135) observed for the study group (**Table 8.2**, p. 189). Most solicitations for grooming involved the groomee presenting the body part to be groomed to the groomer. However, not all grooming bouts started in this manner; and on many occasions the groomer moving toward the groomee to start an unsolicited grooming session. On most occasions grooming involved only two animals with the exception that on two occasions both a female and her infant, mimicking the mother's behavior, were observed to groom another monkey. No simultaneous mutual grooming was recorded, and in only a few cases did I record systematic auto-grooming (excluding short self-inspections).

Though in 40% of all grooming bouts observed during the scan samples the sex of the participants could not be established, my observations recorded that females groomed in 40% of the samples while adult males groomed in the remaining 20%. The number of females grooming adult males and the number of males (mostly adult) grooming other males was nearly the same (12% and 13%). The number of adult males grooming females and the number of males grooming females was the same (7%), but the largest percentage for grooming samples was between females and their offspring (21%).

Since adult males were most easily recognized, the number of records in this category is probably inflated and it can be safely assumed that the far majority of the 40% of unidentified groomers and groomees belonged to other age/sex classes. The observation that adult females groom each other less than adult males remains valid though, given their much larger number in the group. Unfortunately I never identified the sex of 17 animals (28%) in the study group making it difficult to determine the relative proportion of each age/sex class in the group. However, if the numbers from **section 8.3.1** are used to determine relative proportion adult males groomed each other approximately four times more often than adult females, supporting Struhsaker's (1975) observation that male bonds in the group are stronger than female bonds.

Most of the grooming between adult males and females involved females with a perineal swelling. In only one case was habitual grooming between an adult male and female observed, and these animals appeared to consort during all 12 follows (see **Section 8.5**).

8.3.6. *Sexual behavior*

Though few observations of sexual behavior fell within the scan samples, a considerable number of observation were made during most of the 12 monthly follows.

Procolobus badius epieni females develop, presumably around ovulation, a large perineal swelling. This swelling is approximately the shape of a doughnut, and on average 12 cm long and 10 cm wide, and pinkish gray in color. This is considerably larger than the swellings observed for *P. b. tephrosceles* (length up to 10 cm) and *P. b. temminckii* (length up to 13 cm), but not as large as observed for this population's closest neighbor *P. b. preussi* with a swelling estimated to be up to 25-33% of body volume (Struhsaker, 1975; Starin, 1991).

All mating behavior observed involved adult females with varying degrees of perineal swellings but never without a swelling, confirming the same observations by Struhsaker (1975) and Starin (1991). The first step in copulation was always an inspection of the female's swelling by the mate. In 55% of all observations the female presenting to the male initiated this. The female would lift her posterior in the direction of the male while pressing the remainder of her body close to the branch. In the remaining 45% of observations adult males approached a female, and often by touching her or lifting her tail, gain access for an inspection of her swelling. In a small number of cases the animals would ignore a presentation or avoid an inspection. Also in some cases the animals would part after inspection, but most often it would result in copulation.

Copulations always followed the same general pattern with only a few minor deviations: the female lifts her posterior and presses her body flat to the branch. The male mounts leaving feet on the branch and holding the female around the waist with his hands while arching over her, often touching her back with his chest. In most cases the male would thrust rapidly 6 to 8 times and dismount without evidently ejaculating. In only one of 15 copulations did I observe what could have been ejaculation because the male thrusted a larger number of times (about 15) and did not dismount immediately after the thrusting had stopped. This supports the observation that red colobus are multiple mounters (Struhsaker, 1975; Starin, 1991). Contrary to observations for most other populations except Kanyawara (Struhsaker, 1975), copulation was completely silent, and the animals involved would not vocalize before, during or after (Oates, 1994*b*). Struhsaker (1975) indicates that adult males would sometimes vocalize (as a form of interference) when other males were copulating, but no such behavior was observed in Gbanraun.

The distribution of copulation over the 12 monthly follows indicates that most of the sexual behavior took place during the rainy season with peaks during April, June, and July 1997. However, females with perineal swellings were observed during all months, and copulations were observed in all months except September 1996, and January and August 1997.

8.3.7. *Births*

Young infants were observed during all of the 12 follows. During the months of December 1996, January, February, and March 1997 a larger number of young infants was seen. Whether this was the result of an actual increase of infants in the group, or an increase of records because of these months falling within the dry season, thus improving observation conditions, remains unclear because I was never able to collect accurate numbers. The number of records for play during this period also increased. Since this activity is mostly restricted to juveniles and older infants, this suggests that visibility conditions influenced the observations of young infants.

Data from Tiwai and Abuko indicate that the majority of births took place during the dry season, as is also suggested by this study (Starin, 1991; Oates, 1994*b*). At Kibale, however, no distinct breeding season was observed, but births were clustered in peaks that coincided with rainy months (Struhsaker & Leland, 1987).

8.4. Intergroup Encounters

During the study's 12 follows six intergroup encounters were observed. During two of these encounters the groups moved through each other without any noticeable changes in behavior. It was only the sudden increase in the number of animals and the subsequent division that made me realize that an intergroup encounter had taken place. During three encounters the groups met but did not mingle. Though no agonistic interactions were observed, the encounters were accompanied by a considerable increase in vocalizations. Two of these encounters took place at the end of the day and upon return the next morning it became clear that the groups had rested next to each other for the night. Only on one occasion was agonistic behavior observed, with the study group supplanting another group, as I will describe in more detail.

As I was trailing the rear of the group on 22 October 1996 I heard unusually loud vocalizations from the front of the group (10:20 hours). I quickly moved to the front were I arrived at 10:30 hours. All this time the vocalizations continued at the same level. A large number of monkeys from the study group were located in the tree above me, while at the same time the NW group was filing in a line past the study group, avoiding contact. A number of females were vocalizing loudly as the NW group continued to file past. Suddenly the males above me, both adults and subadults, charged the NW group while a number of females, even some with infants, charged but stopped short. Only the males reached any of the animals from the other group. No actual physical contact was seen but the NW group appeared to be trying to avoid the study group. One adult male member of the study group was observed to nearly collide with a NW female with infant but avoided physical contact. This action split the NW group. My study group calmed down after the engagement, with only the females continuing intermittent vocalizations. After some time the remaining members of the NW group continued in the direction to which the rest of their group had moved, and at 11:00 hours the study group moved away in the opposite direction.

Data collected in and outside the sample periods, both by my assistants and me, indicate that the majority of encounters are peaceful with at most an increase in vocalizations. Outside the systematic group follows I collected eight reports of groups, both the study group and/or other groups, resting together during the night. On one occasion the study group, SE group, and SW group rested together creating an aggregation of approximately 165 animals. Though I was not able to establish this for all encounters, it appears that the groups, though in close peripheral contact, did not mingle.

The outcome of intergroup interactions in other red colobus studies indicates considerable variation for red colobus. In Abuko aggressive encounters occurred at regular intervals, and because only 3 groups occupied a small restricted area, the outcome of the interactions followed a pattern based on the relative dominance of each group. Marsh (1979) reports a similar situation at Tana where half of the intergroup encounters were neutral with the other half aggressive. Though Struhsaker (1975) observed patterns similar to this study, with some encounters where groups moved through each other without any interaction, the number of aggressive encounters was higher. He also observed a dominance hierarchy in with the largest groups were most dominant. Such a pattern was never observed at Gbanraun, and the largest group, though regularly in close contact with the study group (even resting together for the night), was never observed to supplant the study group.

8.5. Group Merging

During my first follow of September 1996, I lost the study group at the end of day four. This was a consequence of an apparently cohesive group splitting into two sections. While trying to establish what was happening I followed one section for a short period, and then returned to find the other section, and as a result lost both.

During the next month I managed to stay with the group for the full five days. I had the impression that I was observing one large section of approximately 45 animals being trailed by a smaller section of 15 animals. Because of the difficult terrain it was impossible to quickly move around the group to get a better idea of what was actually happening. During the subsequent follows it became, however, clear that I had been right. Because I would often fall behind when the group was traveling I would end up following the smaller section which was far less tolerant of my presence than the main section which I observed mainly when the group slowed down or stopped. As of March 1997 the two sections had fused; this was easily observed since the single dominant male of the small section had a cut upper lip (CUL) and was, therefore, easily recognized. During the remaining months the groups stayed together and CUL was observed to associate freely with other adult males. Though he was not the α-male of the group he was observed to supplant two other adult males on two different occasions.

Male CUL also exhibited a number of behaviors not observed in other males. I often saw him together with what looked to be an old female with a young juvenile. My only grooming records of a male grooming a female without a swelling come from this couple. CUL would also interact regularly with the young juvenile who showed great interest in him and no fear. A number of other juveniles were observed to show interest in adult males, but never to the extent observed here.

There are a few reports of fusion-fission behavior in for red colobus. The earliest reports come from The Gambia (Starin, 1981) and heavily logged compartments of Kibale forest (Skorupa, 1988). Other reports come from *P. b. kirkii* in Zanzibar where groups merge to sleep in the same tree and split when feeding during the day (Mturi, 1991; Siex, 1995, Siex & Struhsaker, 1999*a*).

Two conditions are thought to lead to a fission-fusion social system in primates: 1) the absence of predators, and 2) resource dispersion with evenly distributed, high density resources resulting in cohesive groups and low density, clumped resources being associated with widespread groups (Struhsaker, 1974; Struhsaker & Leland, 1979). In Gbanraun the observation of a relatively large number of attacks by ***Stephanoaetus coronatus*** indicates that predation pressure is present, thus excluding lack of this pressure as a possible explanation. The observation that the Gbanraun study group traveled between widely dispersed food patches (see **Section 7.6**) seems rather to suggest that the pattern of food distribution would most likely fission-fusion system. Whether fusion-fission is actually taking place in Gbanraun remains to be decided. Only fusion was observed but there were a few indications that fission had preceded the event and that fission could also take place again. The observation that the single adult male in the small section was familiar with the other adult males in the large section suggests that at one time they had been part of the same group, and during June and July of 1997 I got the distinct impression that a small section of the group was becoming more peripheral. This observation, however, was not confirmed in August 1997, the month off the last 5-day follow. Confirmation of the presence of a fusion-fission pattern would, therefore, require a much longer study period. This would also allow for a comparison of the fission-fusion pattern with food availability to determine possible cause of this behavior.

8.6. Vocalizations

For the collection of data on vocalizations I was guided by Struhsaker's (1975) description of vocalizations from Kibale. Using his categories I attempted to identify and compare them with vocalizations made by the study group under what I considered to be similar circumstances. This comparison suggested that the call repertoire at Gbanraun and Kibale are similar.

8.7. Discussion

The large number of long-term field studies available for colobines show a high degree of complexity and variation in their social systems. Though most studies have focused on food availability as a determinant of social organization more recent studies have examined other factors that could be responsible for the variability of social organization (Kirkpatrick, 1999).

Initial studies suggested that the one male unit was the most common form of colobine social organization, and though this unit appeared to be the foundation, subsequent studies indicated wide-ranging variation on this pattern. Though many colobine species' one male units have stable memberships over a number of years, some populations show variation in social organization within one year, while others form occasional large aggregations (Rajanathan & Bennet 1990; Newton, 1994; Kirkpatrick, 1999).

Though feeding ecology explains some of the variation, different species with similar diets may have different patterns of social organization; *e.g.*, *Colobus angolensis* and *C. guereza* at Basakwe, Democratic Republic of the Congo (Bocian, 1997). Nevertheless, some patterns in social organization remain robustly associated with aspects of feeding ecology. A high degree of folivory is still associated with smaller groups while populations depending on poor resources or spatially and temporally clumped resources form larger and sometimes less stable groups (Struhsaker & Oates, 1975; Bishop, 1979; Oates 1994*b*). Davies' (1984) study of red leaf monkeys in northern Borneo also indicated that seasonal changes in food availability resulted in group size changes.

However, feeding ecology is but one of a number of factors that explain variation in social organization, which is supported by the observation that similar diets can be associated with different patterns of social organization (Bocian, 1997; Kirkpatrick, 1999). Other factors that have been identified are reproductive cycles (Bishop,1975), predation (Busse, 1977; Stanford, 1998), and phylogeny (Struhsaker & Oates, 1975; Rendall & DiFiore, 1995).

The red colobus at Gbanraun fall within the previously observed range of patterns of social behavior for red colobus this species is no exception to the great degree of variation observed in colobine social systems. They also live in large groups that varied from 15 to 80 animals, with multiple adult males, and a large number of adult females (ratio of males to females is 1:3.5). Despite this, a considerable degree of variation can be observed, including some patterns within the observed variation.

Of all groups for which a long-term study was conducted the Gbanraun study group resembles most closely the Kanyawara group in Kibale Forest (Struhsaker, 1975). A comparison indicated no differences in general patterns of social behavior. There were, however, a number of small variations such as the manner in which males would branch-shake and the lack of vocalization before, during, and after copulation. Less detailed information on other rain forest populations also indicate that group structure and social behavior are similar to that observed at Kanyawara and Gbanraun (Struhsaker, 1975; Clutton-Brock, 1974; Oates, 1994; Stanford, 1998). This suggests that there is little variation between populations in relatively aseasonal rain forest location, and that most of the variation is observed when a comparison with populations inhabiting more seasonal environments is made.

Studies from more seasonal and restricted environments in Tana (Marsh 1979; Decker 1994), Abuko (Starin, 1991), and Jozani (Mturi, 1995; Siex, 1995) indicate that there is considerable variation in a large number of aspects of social behavior compared to populations in less seasonal locations. Some of the major differences were generally smaller group size, fewer adult male members, possibly different patterns of dispersion, and more aggressive intergroup encounters. It is, however, difficult to determine whether the observed differences indeed reflect variation in the red colobus social repertoire, or whether they are artifacts of the extensive habitat reduction and fragmentation which is presently pushing these populations to the brink of extinction (Marsh, 1986; Starin, 1989; Decker, 1994; Oates, 1996). The seasonal character of these habitats remains, and though some aspects of social behavior may have been altered by external pressure, observed behavioral differences must be real since it is unlikely that the same strategies would be adaptive in such dissimilar habitats.

Though the variation in red colobus social behavior is characteristic of the colobines this species' particular patterns appear to be unique in the subfamily. Large permanent groups in which related adult males form the foundation are significantly different from the large, more fluid aggregation based on one male units observed for some other colobines. However, as observed for other populations of colobines not only aspects of feeding ecology explain red colobus social organizations but other factors are identified as well. Predation has been shown, for red colobus in particular, to play an important role in the evolution of their social system. However, despite these advances further research is needed to determine the relative importance of all factors responsible for shaping colobine social systems.

Table 8.1:

Percent of records for the different age/sex classes observed engaging in agonistic behavior (N = 33).

	?-?	M-M	M-F	F-M	Group
Agonistic	21.2	54.5	6.1	3.0	15.2

Percent of records for the different age/sex classes observed engaging in grooming (N = 135).

	?-?	J-J	F-I	F-J	F-F	F-M	M-M	M-F
Groom	40	1.5	11.1	10.4	6.7	11.9	13.3	4.5

Percent of records for the different age/sex classes observed engaging in play (N = 134).

	I-I	J-I	J-J	A-I	A-J	A-A
Play	22.4	18.7	56.8	1.5	0.7	0.7

Percent of records for the different sexual behaviors observed (N = 5).

	Present	Inspect	Copulate
Sexual	40	20	40

? = unidentified, I = infant, J = juvenile, F = adult female, M = adult male, and A = unidentified adult.

Table 8.2: *Percent of records from each monthly sample for each of the categories of social behavior recognized during the 12 monthly follows.*

	Agonistic	Groom	Sexual
N	33	135	5
Sep-96	0	91	9
Oct-96	14	81	5
Nov-96	14	86	0
Dec-96	24	76	0
Jan-97	0	100	0
Feb-97	42	58	0
Mar-97	17	75	8
Apr-97	13	87	0
May-97	25	75	0
Jun-97	18	73	9
Jul-97	32	63	5
Aug-97	8	93	0

CHAPTER 9

DISCUSSION

9.1. Introduction

The data presented in this study suggests that the Niger Delta red colobus' localized distribution is the result of variation in the density and distribution of their primary food species. Even though the surrounding forests contain the same species, the different patterns of food-tree distribution in those forests would require red colobus to form much smaller groups, something the monkeys do not readily do.

The study group's distribution area is characterized by a more clumped distribution of food species resulting in food patches large enough to accommodate a foraging group of red colobus. This observation suggests that the wide, but patchy distribution of this species may, therefore, be the result of variation in spatial composition of Africa's rain forests. Moreover, with red colobus requiring large food patches, it is suggested that being able to feed as a unit becomes an important determinant of habitat availability.

In order to identify whether conclusions drawn about the Gbanraun study group can also be applied to other red colobus population I will first, briefly, discuss general patterns observed for red colobus ecology and how they compare with the results from this study, in order to be able to determine if the results from this study can help answering the following two questions:

1. What variables does this study identify that might be responsible for the red colobus' present distribution in the Niger Delta? and,
2. Do the results obtained help to identify generalities in red colobus habitat requirements, social organization and distribution patterns?

9.2. Red Colobus Distribution and Foraging Strategy

The dominance in the Gbanraun red colobus diet of young growth, mostly from the largest and commonest tree species in the habitat, which are often clumped in distribution, appears to reflect a pattern observed in all studies of red colobus ecology. Beyond that commonality, however, different populations show considerable variation in home range size, day range length, food species and food item diversity, number of food species, and proportion of food items in the diet. Red colobus ranging and feeding behavior also shows considerable variation, and has been observed not only across populations inhabiting different habitat types, but also across groups inhabiting the same forest block (*e.g.*, Kibale; Chapman & Chapman, 1999). The high degree of variation in diet and ranging between groups of red colobus at Kibale, that are separated by no more than 15 km, suggests that red colobus are extremely flexible. At Kibale daily travel distances vary by as much as 75%, and home range sizes can vary by more than 100%.

Although red colobus are clearly ecologically flexible, they do not occur in all African forests. Are there, then, certain minimal requirements that a forest habitat must provide for red colobus to occur there? I addressed this question by comparing a forest where red colobus occur with a nearby section where they do not occur, thus attempting to identify key differences between the two as colobus habitats.

This study's data on feeding behavior and range use (**Chapter 7 & 8**) indicate that *Ctenolophon* food patches are the single most important ecological determinant of habitat availability for the study group. These patches provided the majority of the diet, and the consumption of *Ctenolophon* young leaves (which are available on a year-round basis) was never significantly affected by the presence of other food items. Though the comparison of the two forest blocks at Gbanraun and Ukubie indicates little dissimilarity, the one major difference is a more even distribution of the most common species at Ukubie, and therefore a less patchy environment. Not only is the forest less patchy, but also the density of *Ctenolophon* is much lower, resulting in the few *Ctenolophon* patches being further apart.

My data suggest, therefore, that the forest at Ukubie lacks the single most important ecological requirement for the study group. It is possible, however, that Ukubie supports some other species, similar to *Ctenolophon* in distribution and food item production. The most obvious candidate would be *Hallea*, which has not only the highest selection ratio in Gbanraun but which also provides young growth on a year-round basis (**Table 6.5**). However, when observing the tree species densities in the Ukubie enumeration (**Table 5.3**) *Hallea* occurs at far too low a density to fulfill this role. The only other potential species which produces young growth on a year-round basis is *Anthostema*, which has a density of 4.1 trees/ha, still considerably lower than a density of 11.9 trees/ha for *Ctenolophon* at Gbanraun. *Anthostema* also has copious, very caustic latex that is likely to discourage any feeding on this species. It appears, therefore, that habitat availability in this section of the Niger Delta is indeed determined by an ecological variable, forest structure.

The data for differential habitat use further illustrate the importance of *Ctenolophon* food patches in the study group's ecology. Although the study group depended more heavily on *Ctenolophon* food patches in the swamp, the relative importance of the patches' contribution to the study group's diet during the months that the group occupies mostly dry-land cells was not significantly affected. Because the phenology samples indicate similar year-round levels of food-item production for the *Ctenolophon* patches in the swamp, fluctuations in food-item availability are unlikely to be the cause of the switch between habitat types. The study group must, therefore, prefer to forage in the dry-land area, and since the density and number of food species other than *Ctenolophon* is higher here, allowing for more dietary variation, this may be the deciding factor. However, phenological fluctuations of food species other than *Ctenolophon* young leaves must make this area unavailable during certain months, forcing the group back into the swamp. Because the swamp and dry-land phenology samples do not show significant differences, very subtle differences must have far reaching consequences for habitat availability in this case.

Other than the food items associated with *Ctenolophon* food patches and the food species outside these patches exploited in the dry-land area, two of the three most common tree species in the Gbanraun forest produced, for short periods, highly abundant seasonal food items. Despite the high densities of these food items, the contribution of *Ctenolophon* young leaves to the diet was never significantly affected, altering only the contribution of all other food items. This may have affected range use in the swamp somewhat, because the group spent varying amounts of time feeding on these items while traveling from patch to patch. It does indicate, though, that it is unlikely that the presence of these highly abundant food items is a significant determinant of habitat suitability.

9.3. Red Colobus Distribution

The observation that spatial aspects of the forest played such an important role in the study group's ability to use that habitat sheds some light on a number of patterns observed for the distribution of red colobus generally. If spatial aspects of a forest are indeed as important as is suggested by this study, similarities or differences of habitats in terms of species only composition or phenology are unlikely to shed any light on the suitability of habitats to red colobus. Few rain forests are homogeneous in composition, and structural and spatial aspects can vary significantly over relatively short distances (Reitsma, 1988; Richards, 1996; Struhsaker, 1997). This variation must have significant implications for red colobus populations, affecting their behavior as well as their density. The Niger Delta's discrete hydrological boundaries result in more extreme structural and spatial variation than is observed in most other rain forests where transitions are more gradual. As a result the distribution of red colobus is restricted to a section of the delta that is characterized by a discrete hydrological regimen.

Though the boundaries between habitat types in most forests are not as discrete as in the delta, another study of different red colobus groups in the same forest block, at Kibale, indicates that groups living in close proximity can show a great degree of variation in behavior and density (Chapman & Chapman, 1999). Kibale shows a high degree of variation in habitat types (Struhsaker, 1997) and, if spatial aspects are indeed as important as this study suggests, variation in behavior and density is to be expected.

Moreover, similar degrees of variation would be expected within all red colobus populations inhabiting similar, heterogeneous, environments. As a result, comparisons of groups based on geographical proximity explains little. Spatial variation may, after all, be greater within a forest block than between forest blocks, even if large geographical distances separate these forest blocks. If a forest's species composition plays a less important role, as is also suggested by the enormous variation of food species in the diet of different populations, the only requirements that remain are structural and spatial aspects. The presence of one or more species that show a clumped distribution, appears to be a requirement that is met by all red colobus habitat

Another requirement that is met by all red colobus habitat is the year-round availability of young growth. However, the presence of sufficient young growth in itself is not sufficient, it has to be distributed in a particular way: namely food patches that allow the large groups of red colobus to remain cohesive and forage together.

What this study suggests, therefore, is that even when a forest provides year-round young growth its distribution in space will determine habitat suitability. For red colobus a forest must provide food items in concentrated areas; *i.e.*, patches. The availability of other food items outside these patches will affect feeding behavior and range use, but never to the degree that these food items become the most important component of the diet. This may also explain why red colobus distribution across the African continent shows many gaps (Oates *et al.*, 1994b). Though these gaps consists of forest that can be presumed to be similar to neighboring forest blocks where the red colobus do occur, spatial aspects may make it unavailable.

9.4. Colobine Social Behavior

The colobines as a group show a great degree of inter- and intraspecific diversity in social organization, and the African colobines are no exception. The first studies of two different species of African colobines indicated that a species of black-and-white colobus, *Colobus guereza*, forms mostly one-male groups of 10-15 animals, while red colobus live in much larger multimale groups which varied between 20 to 80 animals in size (Marler, 1969; Dunbar and Dunbar, 1974; Clutton-Brock, 1975; Struhsaker, 1975; Oates, 1977; Gatinot, 1978). Red colobus also live in patrilineal societies, rather than the matrilineal societies observed for *C. guereza*. Subsequent studies of the other black-and-white colobus species indicated that *C. guereza* was actually the only African colobine to form mostly one-male groups. The other forms (*C. angolensis*, *C. polykomos* and *C. satanas*) all form mainly multimale groups that are, however, also matrilineal (Moreno-Black & Maples, 1977; McKey *et al.*, 1981; Harrison, 1986; Dasilva, 1994; Newton & Dunbar, 1994; Bocian, 1997). *C. angolensis* is the only black-and-white colobus that forms, on occasion, groups that rival, or even exceed, those of red colobus in size. These groups are, however, generally aggregations of independently viable groups that disperse after short periods of time, though there are some indications that these groups can remain together for long periods of time (Oates, 1994*b*). Less information on the social organization of olive colobus is available, but multimale groups appear to dominate, though one-male groups occur as well (Galat & Galat-Luong 1985; Oates, 1988; Oates, 1994b). The dominance of multimale groups for the African colobines distinguishes them from the Asian colobines that form mostly one-male groups (Kirkpatrick, 1999). Even for those species (*Pygathrix* spp.) that form large aggregations the one-male group remains the foundation (Bennett & Davies, 1994; Newton & Dunbar, 1994).

Other than variation in social organization between the different species of African colobines there appears also to be a great degree of intraspecific variation. Early on it was observed that ecological variables played an important role in shaping social organization, and many primate studies have focused on aspects of feeding ecology for an explanation of observed patterns of, and variation in social behavior (Clutton-Brock & Harvey, 1977; Oates, 1987; Kirkpatrick, 1999). Though differences in feeding ecology provided some explanations, it has become clear that a number of other variables (*e.g.*, predation, phylogeny) play an important role as well.

Initial explanations of the observed differences in red and black-and-white colobus social organization indicated that feeding ecology provided some explanations for the differences observed between the two species. For instance *C. guereza* in Kibale has a monotonous diet mostly derived from one common tree species, occupies relatively small territories, and lives in small groups. Red colobus, on the other hand, feeds on spatially and temporally clumped resources, located at greater distances from one another, which may lead to large home ranges and groups (Struhsaker & Oates, 1975; Oates, 1994b; Kirkpatrick, 1999). Subsequent studies, however, found that not all colobus populations fit this pattern, and that other ecological factors (*e.g.*, predation) had to play a role as well.

Predation has been another ecological variable, in addition to feeding ecology, that has received extensive attention as a possible determinant of variation in social structure. Predation by chimpanzees on red colobus is even suggested, by some researchers, to have shaped the red colobus social system (Busse, 1987; Wrangham & van Zinnicq Bergmann Riss, 1990; Boesch, 1994; Stanford, 1998). A study of chimpanzee predation at Gombe, Tanzania indicated that red colobus population sizes were significantly decreased by chimpanzee predation (Stanford, 1998). The usually inadequate response of the red colobus to chimpanzee predation, however, provides little evidence of effective adaptation by the red colobus suggesting it is unlikely that this predator-prey relationship has shaped their social behavior. It may be, therefore, that another important variable, phylogeny, is influencing social behavior. It could be that historical events, and none of the present ecological conditions, play an important role in determining a species' social system: "Social characteristics may arise from an evolved genetic substrate that is a response to historic (very long-term) patterns of food availability and other environmental features, rather than the precise conditions of modern habitats" (Oates, 1994b).

9.5. Red Colobus Social Behavior at Gbanraun

The social behavior of the Niger Delta red colobus differed little from that observed for other populations inhabiting mature rain forest (Struhsaker, 1975: Oates, 1994b), although red colobus populations inhabiting more seasonal habitats do show some different patterns. In seasonal environments, groups tend to have fewer adult male members, more aggressive encounters, smaller group sizes, and possibly different patterns of dispersion. However, despite these differences there is still considerable overlap, indicating that the degree of variation possible in red colobus social organization must be limited.

This study suggests that the forest at Gbanraun is available for red colobus because of the spatial organization of its vegetation, which allows the group to feed as a unit. At Ukubie, even though the same food species are present, the forest's spatial structure is different, with the result that there are too few food patches that are large enough to accommodate red colobus groups. Since the same food species are present, Ukubie might be available if the group would divide in smaller groups. In this case, much smaller aggregations of food trees (or even solitary trees) would become available as food patches.

In Gbanraun seasonal variation in home range use was also observed, this was associated with shifts in food availability between the swamp and dry-land section. The data presented in **Chapter 7** indicated that the dry-land section, with its greater diversity of food species, is preferred over the swamp. Again the dry land could theoretically be available to the group on a year-round basis if they were willing to divide into smaller units. Red colobus in Kibale and Zanzibar have been observed to divide into foraging parties that were separated from one another, but only for short periods of time (Struhsaker, 1997; Siex & Struhsaker, 1999). The same was observed during this study but the division of the study group could, possibly, have lasted for more than a month. In all cases, however, the subunits were never separated by more than a few hundred meters, and, given red colobus' almost continuous vocalizations, are likely to have maintained regular contact. The temporary nature of these separations, however, suggests that though there appears to be some degree of flexibility in adapting group size to habitat variables, they never result in any significant, lasting changes in social organization.

It appears, therefore, that red colobus will maintain its large group sizes even if whole sections of forest become unavailable to them. This conclusion is not only supported by the data of this study, but also observations made on red colobus at Gombe, Tanzania. Here, red colobus maintain their large cohesive groups when trying to avoid predation by chimpanzees, a behavior that often enhances the chimpanzees' success (Stanford, 1998). These observations suggest that the present red colobus environment has not played an important role in the determination of their social organization, making it more likely that historic, long-term patterns of food availability and other environmental features, *i.e.*, their phylogeny, are strongly influencing red colobus social behavior.

9.6. Conclusion

The results from this study suggest that red colobus' need to live in large groups is an important variable in determining their social behavior. As a result habitat suitability is determined by the distribution of food species that allow a red colobus group to feed as a unit. If this requirement is not met, red colobus do not change their social organization in order to avoid this obstacle by dividing their groups into smaller units that have no contact with one another for long periods of time. This phenomenon may also explain why red colobus are absent in some forest blocks, which appear to be suitable, within their distribution area.

Further investigation to test the conclusions presented in this study would require the comparison of forest blocks within their distribution area where they do not occur with forest blocks where they do occur, using similar methods to this study. Such comparisons would provide an indication as to whether the results from this study can be applied to red colobus as a whole. Given the precarious position in which the majority of red colobus subspecies find themselves, studies that improve our understanding of the habitat requirements of this primate are essential. Hopefully further research into the topics presented in this study will be undertaken and contribute to red colobus' survival into the future.

APPENDIX

Appendix 1.1. Primate Conservation in Africa

Long-term data collection on the status of primate populations in Africa has been conducted in a relatively small number of locations, resulting in a paucity of data. However, the research conducted at these locations, which are widely distributed over the continent, augmented with data from a large number of surveys conducted in other areas indicates that primate populations are on the decrease.

All over the African continent a growing human population puts the environment under increasing pressure. In most countries subsistence farming is the most important socioeconomic activity, with the result that more and more natural habitat is getting converted into farms. Attempts at developing industry have been relatively unsuccessful, with the result that population growth and the demand for farmland continue to be linked. Efforts at reducing population growth, by both governments and international organizations, as well as attempts to implement more sustainable use of natural resources have only had limited success. Over and above this, in most cases the interactions between widespread political instability and large national debts have hastened the unsustainable exploitation of resources. As a result the forests that harbor the great majority of Africa's primates have reduced significantly in size. Prior to human exploitation Africa was estimated to have 3,620,000 km^2 of forest (Martin, 1991). In

1985 approximately 1,750,000 km^2 was estimated to remain, with most of the deforestation occurring in west and east African forests (Chapman *et al.*, 1999).

Though Africa's forests cover only a small part of the continent they harbor the richest primate communities. The forests are, however, often fragmented not only because of climatic reasons (*e.g.*, rainfall patterns) but also by geographical features (*e.g.*, large rivers) that separate forest blocks. As a result a substantial number of African primate species have restricted distributions, making them even more vulnerable to habitat loss and hunting pressure. Red colobus are a good example: most of the subspecies distribution areas are small, making them extremely susceptible to habitat loss. Moreover red colobus' large groups facilitate hunting, and they are also a favored prey species because of their large body size. As a result red colobus are extremely vulnerable to human pressure, and hunting alone has even been suggested as the primary reason for their disappearance from some forest blocks that appear to be suitable habitat (Struhsaker, 1999).

Primate protection in Africa is limited and inconsistent. Not only do governments often lack the will or ability to enforce conservation laws they have passed, but the political turmoil in which most of Africa finds itself makes continuity, an absolute requirement for any successful conservation project, an absent luxury. Even if the present measures could be effectively implemented, less than an average of 5% of sub-Saharan Africa is designated as national parks or other similar areas (Chapman *et al.*, 1999). This is unlikely to be enough to ensure the survival of all primate forms on the continent.

1.1.1. Southern Nigeria

The primate populations of Africa can be subdivided in a number of different regional primate communities. Southern Nigeria has been identified as such a regional primate community, which stretches from southern Benin to the Cross River in eastern Nigeria (Oates, 1996). Here the flora and fauna of the Upper Guinean and the Cameroon region meet, and in addition to *Cercocebus torquatus*, *Cercopithecus mona*, *Procolobus verus*, *Arctocebus calabarensis*, *Perodicticus potto*, *Galago alleni*, *Galagoides demidoff*, and *Euoticus pallidus* the region also harbors two endemic primate species, *Cercopithecus erythrogaster* and *C. sclateri*. The form of *C. nictitans* in this area is likely to be a different subspecies from that found east of the Cross River (Oates, 1996), as is the subject of this study, *Procolobus badius epieni*, which is also a distinct red colobus subspecies (Grubb & Powell, 1999).

The Southern Nigerian region is under intense human pressure and little of the forest remains. Though agriculture and logging cause most of the damage, hunting pressure is also severe (Oates, 1989; Werre, 1991; Oates *et al.*, 1992; Powell 1997). As a result the pressure on primate populations in this area is even higher than in most other parts of Africa (Oates, 1996).

1.1.2. Conservation and the Niger Delta

The Niger Delta provides a small-scale representation of many of Africa's problems. A growing population, conflicts between different ethnic groups, national political instability, unsustainable exploitation of natural resources; all of these factors play a significant role in the problems the delta is presently facing.

The single most pressing problem facing the delta presently is a lack of development, despite most of Nigeria's revenues coming from the oil found in this area. There is electricity only in a few of the delta's towns and fresh water and health care facilities are basically not present. Rightfully or not, the delta's inhabitants hold the oil industry responsible for this situation, and dissatisfaction has now reached such levels that the seizure and destruction of oil company property, as well as the kidnapping of oil company personnel, has become a common occurrence. As a result it has become extremely difficult to engage in research or conservation activities.

The oil industry, which is not labor intensive, provides only a very small number of the indigenous population with a salary and therefore provides no alternative for government supported development. As a result the only local large-scale economic activities that provides cash come from the exploitation of the delta's other natural resources. Logging is most important, and every community in the delta engages in this activity. The effects of logging on the forest are further exacerbated by the oil industry's activities that open up previously inaccessible areas for exploitation through the creation of canals and seismic lines, much as logging roads do elsewhere.

At the same time the human population of the Niger Delta is growing rapidly. This population increase comes, however, not only from the area's traditional population but also from immigration, both permanent and seasonal. Over the last two decades the population in the delta's surrounding areas has increased dramatically, with the result that most of the natural resources (*e.g.*, fish, timber) there have either been reduced to a level where they are insufficient to meet the local needs, or have been depleted altogether. The areas to the northeast and west of the Niger Delta harbor two of Nigeria's three largest ethnic groups, the Ibo and Yoruba. This southern part of Nigeria has reached one of Africa's highest population densities (20 years ago already between 200 and more than 400 persons/km^2 [Barbour *et al.*, 1982]), with the result that the demand for smoked fish and timber is high, and these commodities come mostly from the delta.

By now the borders of the delta have been mostly depleted of fish and timber. As a result people from as far as Ogoni, located more than 50 km to the east of the delta, have come to its central area for part of the year to fish. As a result fish populations are declining and frozen marine fish, or "icefish", is now for sale in the larger towns of the delta. Buying fish requires money, and as a result the delta's population has been forced to focus more and more on activities that provide cash. This is a significant departure from the barter system that up to not long ago was still the most important form of economic exchange.

With the delta being one of the very few remaining areas with some natural resources left in southern Nigeria, the pressure from the surrounding growing population, pushing further and further into the delta, is increasing rapidly. Tension between different ethnic groups, but also within the same ethnic groups, is now resulting in an increase of communal clashes, which often result in the deaths of people and halt all human activities (*e.g.*, fishing, farming) in the involved communities' vicinity.

1.1.3. Implementing Conservation Efforts in the Niger Delta

Not only has little effort been applied to the collection of biological data from the Niger Delta, but the delta presently also does not contain a single area in which wildlife is formally protected. Moreover, there are hardly any forest reserves, areas under control of the Rivers, Bayelsa, and Delta State Forestry Departments. These forest reserves are not actually protected areas, but the forestry department controls their management. Though this often means conversion into plantations of exotic tree species, a forest block's status as a reserve, theoretically, facilitates the implementation of conservation measures. As a result exploitation of the delta's forests is taking place in a totally unorganized way. Nowhere are any measures applied that would create some form of sustainability. The consequent combination of uncontrolled logging without any replanting has resulted in a rapid reduction of most of the delta's timber trees.

The only government institutions in the delta interested in a more controlled exploitation of the forest are the states' forestry departments, and to a certain degree the Nigerian Federal Environmental Protection Agency (FEPA), but they lack the means to do so. In 1994 the total budget of Rivers State Forestry Department (now divided into Rivers and Bayelsa States) was $US 6750 (Moffat and Linden, 1995), barely enough to pay their employees. The remainder of state and federal institutions are far more concerned with development and economic growth, and see little justification in spending limited resources on managed care of the delta's remaining forests. This absence of governmental interest also has made it very difficult to gain the attention of the local population and governmental institutions that need to be involved in the implementation of a conservation effort.

1.1.4. Conservation and the Niger Delta Red Colobus Monkey

The forests within the red colobus distribution area have all been seriously affected by human exploitation. During the survey no intact forest was observed apart from a few small areas on dry ridges (see **Chapter 2**). None of the swamps, where the red colobus are concentrated, had remained unlogged. Of these swamps only a few sections had been partially logged. In most places all the most valuable timber species were gone, and in quite a few other areas large-scale exploitation of less valuable species had started. This is an alarming development, as very soon no undisturbed sections of an ecosystem that is still largely unknown will remain available for baseline data collection.

The rapid rate of deforestation in the delta has also affected the red colobus population greatly. At none of the visited locations, apart from Gbanraun, were any red colobus observed in great numbers. At most locations the monkeys were well known but had become rare. Even in Gbanraun, a group that had been observed in 1994 (Oates, 1994a) had been reduced to 2 animals by the beginning of 1996. In this case both logging and hunting were the cause. Immigrants had obtained permission from the Gbanraun community to fell large trees in this section of forest that were then used to build canoes. They also brought guns and, even though no permission was given, a number of them started hunting; red colobus were included in the animals shot. It appears, however, that in most cases logging is to blame for the reduction of the red colobus. Most of the swamps in the swamp forest zones contain large numbers of abura (*Hallea ledermannii*), which is the most valuable timber species in the delta and which tends to be extracted first. My survey provided some indications that abura is an important food species for the red colobus in most of the delta, and that the large-scale removal of this species from the swamps renders them uninhabitable to this monkey (Werre & Powell, 1997).

The combination of habitat destruction and their small distribution area has pushed the red colobus population into a precarious position. As indicated in **section 2.5** approximately 125,000 red colobus could inhabit the total available area of 2000 km^2, but I estimate that the present population has dropped below 10,000 animals, which qualifies the population as endangered (Oates, 1996; IUCN, 2000).

Red colobus do not survive well in captivity. Efforts have invariably failed with the result that currently no animals are held in a zoo, and the only way these monkeys can be conserved is *in situ*. It is, therefore, imperative to initiate a conservation effort in the red colobus distribution area. For the duration of my study only the 140 ha of the study area in Gbanraun was protected, containing an estimated population of about 150 red colobus. This is unfortunately no longer the case, and a more enduring conservation effort has to be implemented in the very near future if the Niger Delta red colobus is to survive.

1.1.5. Conservation Plan for the Niger Delta Red Colobus Monkey

During my stay at Gbanraun negotiations for the establishment of a research/conservation area were started. The plan was to start, initially, with an area of about 500 ha on Gbanraun community lands. The first step was to arrive at an agreement with Gbanraun Community about compensation for the loss of such economic benefits as derived from this area of forest. In order to consolidate the community's support a number of, sustainable, high income earning activities would be allowed to continue. A good example of such an activity would be the collecting of the highly priced fruits of the 'bush mango' tree (*Irvingia gabonensis*). Another benefit of participating in the conservation effort for the inhabitants of Gbanraun Community would be the employment of about four to five workers to maintain and supervise the area and extra facilities created. A small building in the town of Gbanraun where researchers/visitors could stay and study would be erected and equipped with a small generator, and possibly a small library, microscopes and a computer.

Though an initial lease length of 10 years for the community's land was proposed, it was suggested that the community would be paid yearly. This would keep the community motivated to maintain the status quo, and would allow the donors to pull out of the project if the community resumed exploitation of the conservation area before the end of the lease. Nigerian Law allows for such a transaction, making legal recourse a valid tool in case of problems.

A management committee would be established to monitor the activities in the area, and it would include representatives from Gbanraun and other interested parties such as a local university, the Ministry of Agriculture and Natural Resources' Forestry Department, Ministry of Education, and foreign conservation organizations who could also provide knowledge and train participants. The committee would monitor the status of the area and the activities in its facilities, but the allocation of funds would be negotiated at the start of the project so that no further financial negotiations would be required.

Unfortunately, after my departure in May 1998 from Nigeria the all too common problems that face conservation in Africa brought this effort to a halt. Communal clashes and tension between the oil companies and local communities made it impossible to continue work in the delta. Outsiders were kidnapped and robbed, making it even impossible to visit Gbanraun. The oil companies that had so far shown strong support for the project no longer allowed any of their workers to enter the delta. Negotiations with the community came to a halt, even though these had reached the stage where the total area to be included was discussed. As a result there continues to be not a single fully protected area in the Niger Delta, outside the few small sacred bushes maintained by a small number of communities.

Given the demands of a rapidly increasing human population in the delta, if no action is taken in the near future to save an area of the delta from exploitation it is unlikely that this ecosystem (and the Niger Delta red colobus) will survive in its present condition for much longer. However, recently the situation in the central Niger Delta appears to be improving and I will visit the area by the end of November 2000 to establish whether the Gbanraun conservation area negotiations can be reopened.

Appendix 1.2. Mammals of the Niger Delta

COMMON NAME	SPECIES	IUCN STATUS	ND STATUS	DECREE 11
MONKEYS	**PRIMATES**			
Angwantibo	*Arctocebus calabarensis*	Vulnerable	Vulnerable	1
Bosman's potto	*Perodicticus potto*		Rare	2
Allen's galago	*Galago alleni*		Vulnerable	2
Demidoff's dwarf galago	*Galagoides demidoff*			
Red-capped mangabey	*Cercocebus torquatus*	Vulnerable	Vulnerable	1
Putty-nosed guenon	*Cercopithecus nictitans*			2
Mona monkey	*Cercopithecus mona*			2
White-throated guenon	*Cercopithecus erythrogaster*	Endangered	Vulnerable	2
Sclater's guenon	*Cercopithecus sclateri*	Endangered	Endangered	2
Green monkey	*Cercopithecus aethiops*			
Olive colobus	*Procolobus verus*	Vulnerable	Endangered	1
Red colobus	*Procolobus badius*	Endangered	Endangered	
Chimpanzee	*Pan troglodytes*	Endangered	Endangered	1
PANGOLINS	**PHOLIDOTA**			
Long-tailed pangolin	*Manis tetradactyla*		Vulnerable	1
Tree pangolin	*Manis tricuspis*		Vulnerable	1
RODENTS	**RODENTIA**			
Derby's flying squirrel	*Anomalurus derbianus*			
Beecroft's flying squirrel	*Anomalurus beecrofti*			
Pygmy flying squirrel	*Idiuris* sp.			
Giant forest squirrel	*Protoxerus stangeri*			
Red-legged sun squirrel	*Heliosciurius rufobrachium*			
Redless tree-squirrel	*Funisciurius anerythus*			
Fire-footed squirrel	*Funisciureus pyrrhopus*			
Orange-headed tree-squirrel	*Funisciureus leucogenys*			
Geoffroy's ground-squirrel	*Xerus erythropus*			
Grass cutter	*Thryonomys swinderianus*			
Brush-tailed porcupine	*Atherurus africanus.*			1
Gambian giant rat	*Cricetomys gambianus*			
Emin's giant rat	*Cricetomys emini*			
CARNIVORES	**CARNIVORA**			
Cape clawless otter	*Aonyx capensis*		Vulnerable	1
Spotted-necked otter	*Lutra macullicollis*		Vulnerable	1
African civet	*Vivera civetta*			2
Two-spotted palm civet	*Nandinia binotata*			2
Crested genet	*Genetta cristata*	Endangered	Endangered	2
Forest genet	*Genetta pardina*		Vulnerable	2
Cusimanse	*Crossarchus platycephalus*			2
Egyptian mongoose	*Herpestes ichneumon*			2
Long-nosed mongoose	*Herpestes naso*			2
Marsh mongoose	*Atilax paludinosus*		Rare	2
Leopard	*Panthera pardus*		Endangered	1
MANATEE	**SIRENIA**			
Manatee	*Trichechus senegalensis*	Vulnerable	Endangered	1
ELEPHANTS	**PROBOSCIDEA**			
African elephant	*Loxodonta africana*	Vulnerable	Endangered	1/2
HYRAXES	**HYRACOIDEA**			

COMMON NAME	SPECIES	IUCN STATUS	ND STATUS	DECREE 11
Western tree hyrax	*Dendrohyrax dorsalis*		Rare	
EVEN-TOED UNGULATES	**ARTIODACTYLA**			
Heslop's pygmy hippopotamus	*Hexaprotodon liberiensis*	Extinct	?	1
African buffalo	*Syncerus caffer*		Endangered	2
Red river hog	*Potamochoerus porcus*			
Water chevrotain	*Hyemoschus aquaticus*		Endangered	1
Sitatunga	*Tragelaphus spekei*		Rare	1
Bushbuck	*Tragelaphus scriptus*			
Black fronted duiker	*Cephalophus nigrifrons*		Endangered	
Maxwell's duiker	*Cephalophus maxwelli*			
Ogilby's duiker	*Cephalophus ogilbyi*			
Bates' dwarf antelope	*Neotragus batesi*		Rare	

Sources: Powell (1993, 1995).

IUCN: International ranking in 1994 IUCN red list.

ND status: Status of the species in the Niger delta as determined by the author. The information collected was augmented with information from Powell (1995).

DECREE 11: Ranking in Federal Endangered Species Decree No. 11 of 1985. 1 = absolute prohibition, 2 = license required.

Appendix 1.3 *Tree species identified within the Gbanraun study area.*

	SPECIES	FAMILY	HABITAT
1	*Cleistopholis patens*	Annonaceae	d,t,s
2	*Xylopia staudtii*	Annonaceae	t,s
3	*Xylopia rubescens**	Annonaceae	t,s
4	*Xylopia* sp.	Annonaceae	t,s
5	*Hexalobus crispiflorus*	Annonaceae	d,t,s
6	*Monodora myristica*	Annonaceae	d,t,s
7	*Beilschmiedia* sp.	Lauraceae	d,t,s
8	*Pycnanthus marchalianus.*	Myristicaceae	d,t,s
9	*Staudtia stipitata*	Myristicaceae	d,t,s
10	*Coelocaryon preussii*	Myristicaceae	d,t,s
11	*Homalium* sp.*	Samydaceae	d
12	*Scottelia mimfiensis**	Flacourtiaceae	d
13	*Barteria fistulosa**	Passifloraceae	d
14	*Ouratea elongata*	Ochnaceae	d,t,s
15	*Ouratea calantha*	Ochnaceae	d,t,s
16	*Rhabdophyllum* sp.	Ochnaceae	d,t,s
17	*Lophira alata**	Ochnaceae	d
18	*Syzygium owariense*	Myrtaceae	d,t,s
19	*Spathandra blakeoides*	Melastomataceae	d,t
20	*Cassipouria barteri*	Rhizophoraceae	t,s
21	*Cassipouria* sp*.	Rhizophoraceae	t,s
22	*Anopyxis klaineana **	Rhizophoraceae	d
23	*Symphonia globulifera*	Guttiferae	t,s
24	*Pentadesma butyraceae*	Guttiferae	d,t,s
25	*Mammea africana*	Guttiferae	d
26	*Garcinia smeathmannii*	Guttiferae	d
27	*Garcinia kola **	Guttiferae	d
28	*Rhaptopetalum* sp.	Scytopetalaceae	d,t
29	*Sterculia tragacantha*	Sterculiaceae	t,s
30	*Cola nitida*	Sterculiaceae	d,t
31	*Ceiba pentandra **	Bombaceae	d
32	*Sacoglottis gabonensis*	Humeriaceae	d,t
33	*Ctenolophon englerianus*	Ctenolophonaceae	d,t,s
34	*Anthostema aubreyanum*	Euphorbiaceae	d,t,s
35	*Macaranga* spp.	Euphorbiaceae	d,t,s
36	*Uapaca staudtii*	Euphorbiaceae	t,s
37	*Uapaca paludosa*	Euphorbiaceae	d,t
38	*Uapaca heudelotii*	Euphorbiaceae	d,t
39	*Tetrorchidium didymostemon**	Euphorbiaceae	d,t
40	*Discoglypremna caloneura*	Euphorbiaceae	d,t
41	*Spondianthus preussii*	Euphorbiaceae	d,t
42	*Klaineanthus gaboniae*	Euphorbiaceae	d,t,s
43	*Maprounea membranacea**	Euphorbiaceae	d
44	*Maesobotrya dusenii **	Euphorbiaceae	d,t

Appendix 1.2: *Continued*

	SPECIES	FAMILY	HABITAT
45	*Parinari excelsa* *	Chrysoblanaceae	d
46	*Oxystigma mannii*	Caesalpinioideae	s
47	*Berlinia auriculata* *	Caesalpinioideae	d
48	*Berlinia* sp.*	Caesalpinioideae	d
49	*Erythrophleum ivorense*	Caesalpinioideae	d,t
50	*Piptadeniastrum africanum**	Mimosoideae	d
51	*Treculia africana*	Moraceae	d
52	*Musanga cecropioides*	Moraceae	d,t
53	*Panda oleosa* *	Pandaceae	d
54	*Zanthoxylum gillettii**	Rutaceae	d,t,s
55	*Pierreodendron africanum* *	Simaroubaceae	d
56	*Hannoa kleineana**	Simaroubaceae	s
57	*Klainedoxa gabonensis*	Irvingiaceae	d
58	*Irvingia gabonensis*	Irvingiaceae	d
59	*Dacryodes* sp.	Burseraceae	d
60	*Carapa procera*	Meliaceae	d
61	*Lovoa trichilioides*	Meliaceae	d
62	*Guarea cedrata*	Meliaceae	d
63	*Turraeanthus africanus**	Meliaceae	d
64	*Trichilia monadelpha**	Meliaceae	d
65	*Diospyros physocalycina*	Ebenaceae	d,t
66	*Diospyros preussii*	Ebenaceae	d,t,s
67	*Chrysophyllum pruniforme**	Sapotaceae	d,t
68	*Anthocleista* sp.	Loganiaceae	d,t,s
69	*Alstonia boonei*	Apocynaceae	t,s
70	*Funtumia africana*	Apocynaceae	t,s
71	*Rothmannia megalostigma*	Rubiaceae	d,t,s
72	*Nauclea diderrichii*	Rubiaceae	d
73	*Nauclea pobeguinii* *	Rubiaceae	d,t
74	*Hallea ledermannii*	Rubiaceae	d,t,s
75	*Massularia acuminata* *	Rubiaceae	d,t
76	*Vitex grandifolia*	Verbenaceae	d
77	*Raphia vinifera*	Palmae	d,t,,s
78	*Raphia hookeri*	Palmae	d,t,s
79	*Elaeis guineensis*	Palmae	d,t

Habitat categories: d = dry, t = transitory, s = swamp, see text for further explanation. Species marked with an * were recorded in the research area but fell outside the enumeration

Appendix 1.4. Monthly Feeding Records of the Study Group

Sep-96

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	69										
UA-			6								2
LIANAS		2	2								
KLGA											
FUAF				16							
ROME											
PEBU											
UNID		12									10
COPR											
HALE											
ERIV											
PYMA											
MA-											2
RA-											
SYOW											
SYGL											10
SPPR											
OXMA											
MUCE											
AN-											
XYST											

Oct-96

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	183										
UA-			14								
LIANAS	1	5									
KLGA											
FUAF				22							
ROME			6								
PEBU	2										
UNID	9	3					2				11
COPR											
HALE	3										
ERIV											
PYMA	2										
MA-	1										
RA-											
SYOW											
SYGL											
SPPR											
OXMA											
MUCE											
AN-											

Nov-96

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	54										
UA-								120			
LIANAS		4									
KLGA											
FUAF				10							
ROME			2								
PEBU	3										
UNID	10										5
COPR											
HALE			7								
ERIV	10										
PYMA											
MA-											
RA-											
SYOW	20										
SYGL											
SPPR											
OXMA											
MUCE											
AN-											
XYST											

Dec-96

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	128										
UA-								166			
UANAS	16	1									
KLGA											
EUAF				2							
ROME			13								
PEBU	36										
UNID											
COPR											
HALE			3								
ERIV											
PYMA		1									
MA-							3				
RA-						2					
SYOW	2										
SYGL											
SPPR					2						
OXMA											
MUCE											
AN-											
XYST											

Jan-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	187										
UA-			1								
LIANAS	20	5					10				
KLGA											
FUAF				8							
ROME			19								
PEBU	4										
UNID	1										
COPR											
HALE			25								
ERIV	1										
PYMA											
MA-	3										
RA-						20					
SYOW											
SYGL											
SPPR					3						
OXMA											
MUCE								1			
AN-											
XYST											

Feb-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	127										
UA-					145						
LIANAS	24			2			1				
KLGA											
EUAF				14							
ROME			9					1			
PEBU											
UNID	2										1
COPR	17	4									
HALE			3								
ERIV											
PYMA		17					5				
MA-		1						1			
RA-						5					
SYOW											
SYGL											
SPPR											
OXMA											
MUCE								1			
AN-				1							
XYST											

Mar-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	92										
UA-			1		76						
LIANAS	15	4						16	11		
KLGA											
FUAF				23							
ROME			17					3			
PEBU		8						3			
UNID	2								2		
COPR		5							4		
HALE			3								
ERIV	43										
PYMA		12				1	2				
MA-								4			
RA-											
SYOW											
SYGL	1										
SPPR											
OXMA											
MUCE											
AN-											
XYST	1										

Apr-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	122										
UA-			14					3			
LIANAS	18										2
KLGA					14						
FUAF				18							
ROME			8					3			
PEBU	25										
UNID	15										
COPR		4									
HALE			2								
ERIV	5										
PYMA	1					7					
MA-								2			
RA-						3					
SYOW											
SYGL											
SPPR											
OXMA											
MUCE								1			
AN-											
XYST											

May-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	127										
UA-								13			
LIANAS	13										
KLGA					8						
FUAF				7							
ROME			3					1			
PEBU	1										
UNID	1			1							
COPR	5										
HALE			1								
ERIV	6										
PYMA											
MA-	1						23				
RA-						10					
SYOW	2										
SYGL											
SPPR											
OXMA											
MUCE											
AN-											
XYST											

Jun-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	193										
UA-			2								
LIANAS	18	1		2			9				
KLGA					40						
FUAF				6							
ROME			10					4			
PEBU	1									1	
UNID											
COPR		24									
HALE			10								
ERIV	7										
PYMA				1							
MA-							4				
RA-						14					
SYOW	11										
SYGL											
SPPR											
OXMA											
MUCE											
AN-											
XYST											

Jul-97

	YL	ML	PITH	PET	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	130										
UA-											
LIANAS	10	12		6	6						
KLGA					69						
FUAF				27							
ROME			1								
PEBU	7										
UNID	3										
COPR		11									
HALE			18								
ERIV											
PYMA		1		4							
MA-							12				
RA-											
SYOW	5										
SYGL											
SPPR											
OXMA					5						
MUCE											
AN-											
XYST											

Aug-97

[illegible]	YL	ML	PET	[illegible]	SEED	RFR	URFR	FL	BUD	BARK	UNID
CTEN	160										
[illegible]			2								
[illegible]	27				2						
[illegible]					52						
[illegible]				30							
[illegible]			4								
[illegible]	7										
UNID	1										
COPR		18									
[illegible]			20								
ERIV											
PYMA		12									
[illegible]							3				3
[illegible]											
SYOW											
SYGL											
SPPR											
OXMA											
MUCE											
[illegible]											
XYST											

CTEN, *Ctenolophon englerianus*; UA-, *Uapaca spp*; KLGA, *Klaineanthus gaboniae*; FUAF, *Funtumia africana*; ROME, *Rothmannia megalostigma*; PEBU, *Pentadesma buteraceae*; UNID, unidentified; COPR, *Coelocaryon preussii*; HALE, *Hallea ledermannii*; ERIV, *Erythrophleum ivorense*; PYMA, *Pycnanthus marchalianus*; MA-, *Macaranga* spp.; RA-, *Raphia* spp.; SYOW, *Syzygium owariense*; SYGL, *Symphonia globulifera*; SPPR, *Spondianthus preussii*; OXMA, *Oxistigma mannii*; MUCE, *Musanga cecropioides*; AN-, *Anthocleista* spp.

YL, young leaves; ML, mature leaves; PET, petioles; RFR, ripe fruit; URFR, unripe fruit; FL, flower; UNID, unidentified.

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