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**Socioecology of the red colobus monkey in The Gambia with  
particular reference to female-male differences and transfer  
patterns**

**Starin, Erica Dawn, Ph.D.**

**City University of New York, 1991**

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**SOCIOECOLOGY OF THE RED COLOBUS MONKEY IN  
THE GAMBIA WITH PARTICULAR REFERENCE TO  
FEMALE-MALE DIFFERENCES AND TRANSFER PATTERNS**

by

Erica Dawn Starin

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

1991

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## **Abstract**

# **SOCIOECOLOGY OF THE RED COLOBUS MONKEY IN THE GAMBIA WITH PARTICULAR REFERENCE TO FEMALE-MALE DIFFERENCES AND TRANSFER PATTERNS**

by

Erica Dawn Starin

Advisor: John F. Oates

Temminck's red colobus (Procolobus badius temminckii) was the focus of this study, which took place from February 1978-September 1983 in the 107 ha relict forest patch of the Abuko Nature Reserve, The Gambia, West Africa.

In this thesis I examine sexual differences in a population in which (1) there is very little, if any, sex difference in body size; (2) food does not appear to be a limiting factor; (3) there is very obvious climatic seasonality with a distinct dry and wet season; and (4) females generally transfer between troops, whereas males generally remain in their natal troop (except for an adolescent period of exile).

All ages and reproductive stages were represented by transferring females, but juveniles clearly predominated. Males, however, emigrated at a younger age than females. Female departures appeared to be voluntary and not the result of competition and aggression, but young males left because of aggression received while in the confines of their natal troop.

During the transfer process, females appeared to move immediately between troops while males spent months (even years) as solitaires looking for vacancies. Most males, however, returned to their natal troop when a vacancy occurred.

It was found that this population has more prominent female-female bonds than has been described in other populations in which females transfer. I argue that this is due to the fact that females transfer between troops with, or immediately after, their natal troop peers and maintain these relationships with each other in their chosen troop. In fact, attraction among female peers is likely to be an important (if not the most important) factor determining the timing of transfer and eventual troop choice. I found that females who originally shared a common natal troop rarely use aggression against each other, groom each other more than other females, and form subunits which leave the troop for days at a time. Female-female aggression was mostly between those individuals who did not share a common natal troop. Male-male bonds are

not as prominent in this population as they are in most other female-transfer populations. There is very little intramale grooming, proximity and coalitionary support.

A recurring theme in this dissertation is the importance of female peer transfer in the everyday interactions of the colobus in Abuko. I suggest that this practice fosters female bonding in what has traditionally been regarded as a non-female-bonded species. This is clearly at odds with previous ideas regarding female-transfer species in general and the bonding patterns of red colobus monkeys in particular.

The special bonding patterns found amongst individuals in Abuko may be due to both the limited number of troops available in a small, isolated forest patch and to the existence of a birth season which results in a seasonally produced peer group. If so, then the social aspects of this particular society related to special habitat features at Abuko.

## ACKNOWLEDGEMENTS

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## Chapter 1. INTRODUCTION

This study looks at sex differences in Temminck's red colobus monkeys (Procolobus badius temminckii) living in the Abuko Nature Reserve, The Gambia, West Africa, in light of the fact that females are generally not life-long residents of their natal troop whereas males frequently are.

Throughout this thesis I assume that these patterns of intertroop transfer have important effects on intratroop social relationships and female/male differences (Wrangham, 1979, 1980, 1983, 1987; Hrdy, 1981; Harcourt and Stewart, 1983; Lancaster, 1984, 1986; Smuts, 1987; Stewart and Harcourt, 1987).

The focus in this dissertation is on several specific questions. First, since ecology and social systems are likely to be interrelated (e.g. Crook and Gartlan, 1966; Denham, 1971; Eisenberg, Muckenhirn and Rudran, 1972; Altmann, S., 1974; Milton and May, 1976; Clutton-Brock and Harvey, 1977, 1977; Richard, 1981), I sought a basic understanding of the habitat, diet, activity patterns and social organization of the red colobus in the Abuko Nature Reserve. Are there obvious sexual differences in terms of diet and activity patterns within the population? How does this population compare with other red colobus populations living in different habitats? The literature available for comparison is reviewed below (pages 10-14). Next, I sought

to investigate the relationship between transfer patterns in Abuko and the observed female/male differences. What are the exact transfer 'rules'? What are the nature and sources of sexual differences in terms of aggressive, cooperative, and reproductive behaviors within a troop and between troops? How are the observed sexual differences related to transfer patterns? How does the Abuko population differ from other populations in terms of specific transfer patterns and observed female/male differences? Throughout this thesis references will be made to the work of Greenwood (1980) and Wrangham (1979, 1980, 1983, 1987) and discussed in light of the data found in Abuko.

Greenwood (1980) suggested that females and males will have different patterns of dispersal and that philopatry will favor the evolution of cooperative traits between members of the sedentary sex, while disruptive acts will be a feature of the dispersers.

Wrangham (1980) contrasted 'female-bonded' social systems with 'non-female-bonded' social systems in which females transfer between groups more frequently than do males. He characterized non-female-bonded groups as follows:

1. the very existence of social units depends on females being attracted to males rather than to each other;
2. females pay more attention to males than to

females within the group;

3. cooperative relationships among females are developed poorly, if at all;
4. male-male bonds are stronger than female-female bonds;
5. only males participate in intergroup interactions.

Do the basic models put forward by Greenwood (1980) and Wrangham (1979, 1980, 1983, 1987) fit the Abuko population?

This thesis consists of 11 chapters. Following this very brief introduction are three additional preliminary chapters. A description of the study animal (Procolobus badius temminckii) in terms of taxonomy, physical description and geographical distribution, and a review of past field studies of various red colobus throughout Africa is given in Chapter 2. A description of the study area (Abuko Nature Reserve) is given in Chapter 3. At the end of this brief chapter Abuko is compared with some of the other sites where red colobus have been studied. A description of the methods used during this study and how they compared with methods used by other field workers studying red colobus is given in Chapter 4.

The text then continues with a series of chapters that lay out the principal results. Diet and feeding patterns (Chapter 5) and then activity budgets (Chapter 6) are discussed and compared with information collected from other red colobus sites. A summary of basic demographic

information in terms of births, deaths and reproductive parameters is presented in Chapter 7. Data on transfer patterns (the main emphasis is on the difference between females and males) are presented in Chapter 8.

Sexual differences in terms of aggressive, cooperative and reproductive behavior make up Chapter 9. Many of the findings are related to transfer behaviors detailed in Chapter 8. Data on intertroop behavior, emphasizing the difference between females and males during encounters and the impact transfer patterns have on intertroop behaviors, are presented in Chapter 10. In the eleventh chapter I attempt to synthesize what has gone before and answer some of the questions mentioned above. The emphasis in this final chapter is on coordinating data from the previous chapters rather than generating new hypotheses.

Specifically, I try to answer why a basically male resident society with female transfer patterns is not as male-bonded as other societies fitting this description. I also try to answer why the females in the Abuko Nature Reserve are more strongly bonded than most female-transfer species.

## Chapter 2. THE STUDY SPECIES

### Taxonomy

Red colobus monkeys belong to the family Cercopithecidae, subfamily Colobinae. Although Rahm (1970), Dandelot (1968; 1971), Szalay and Delson (1979) and Napier and Napier (1985) consider them as members of the genus Colobus, Kuhn (1967, 1972) and Strasser and Delson (1987) group the red and olive colobus into Procolobus, distinct from the black and black-and-white forms in Colobus. The latter distinction is followed here. The species-level systematics have yet to be resolved. For a discussion of the various opinions see Dandelot (1968, 1971), Rahm (1970), Thorington and Groves (1970), Kuhn (1972) and Oates (1986). I shall use the classification system proposed by Oates (1986) and followed by Lee, et al (1988), which recognizes two species of red colobus in West Africa: Procolobus badius and Procolobus pennantii. P. badius is the only forest monkey to have a distinct form, temminckii, in The Gambia, Senegal, and Guinea-Bissau (Oates, 1988). Since an in-depth study of red colobus taxonomy was beyond the scope of this project, my use of this classification is one of convenience and does not imply any taxonomic judgement on my part.

### Geographic Distribution

Red colobus are spread from Senegambia in the west discontinuously across equatorial Africa to the island of Zanzibar (Figure 1). The geographical distribution of the various subspecies is given in Dorst and Dandelot (1970), Rahm (1970), Haltenorth and Diller (1980), Lee, Thornback and Bennett (1988) and Oates (1988). P.b. temminckii is the most western and northern form of red colobus and probably inhabits the most diverse habitats. While most of the other subspecies are limited to dense evergreen forest or relict forest patches, P. b. temminckii is found in gallery forest, high stature mangrove swamp, tree and shrub savanna, open and closed woodland savanna, rain forest, village perimeters and infrequently residential gardens and agricultural fields throughout the Senegambia region. Recently, (March 1989) the red colobus in western Gambia have started crop-raiding (Starin, 1989). The only other subspecies known to crop-raid is the Zanzibar red colobus (P.b. kirkii) (Omari, pers. comm.).

If all subspecies are considered together it appears to be a very versatile species, able to use a wide variety of habitats. A review of habitat types is given in Wolfheim (1983) and Lee, et al (1988).

### Physical Description

The amount and shade of red in the pelage, body size and weight, the amount and type of sexual dimorphism, the size of the female sexual swelling and the presence of the young male perineal swelling vary considerably from subspecies to subspecies. Description of the various distinguishing external characteristics is given by Dorst and Dandelot (1970), Rahm (1970), Kuhn (1972) and Haltenorth and Diller (1980) for the different subspecies. Diagnostic characteristics for tephrosceles are given by Struhsaker (1975) and those for rufomitratatus appear in Marsh (1978).

The red colobus in Abuko are a mixture of bright rufous, black-grey and white hair (Figure 2). They are predominantly black-grey on the back and crown of the head and back of the arms and legs. They are dull white, often mixed with some orange, from the front of the neck, down the chest, abdomen and the groin, and then down the medial sides of the arms and legs. There is bright rufous hair on the sideburns, outer sides of the arms and the legs and the complete length of the tail. There is much individual variation in the shades of the colors, but the placement of the colors remains the same for all individuals. The most obvious color variation is on the back. Some of the individuals are black, others grey-black and still others salt and pepper colored. There is also some variation in the hair texture. While most of the individuals have



straight hair, one adult female and some of the juveniles had sparse, frizzy hair. The juveniles all eventually lost their frizzy look, but the adult female had hers for at least 7 years.

On most of the individuals, the face is grey-black with pinkish circum-orbital patches and muzzle patches from the lower lip to the top of the nostrils. In adults the soles, palms and ears are the same color as the face, grey-black. In the infants the soles, palms, ears and ano-genital area are bright pink.

Females develop elongated nipples about one month before they give birth for the first time. Before this, the nipples are scarcely noticeable. After the first infant is born, nipple size is no longer a good indicator of age. Both breast size and the distention of nipples may decrease in a female who has not given birth for a few years and has no dependent young. The nipples of some of the very old females closely resembled those of nulliparas just before they gave birth. Males do not have very apparent nipples.

Compared with the weights and measures given for some East African forms by Struhsaker (1975) and Kingdon (1971), the red colobus in Abuko are smaller (Table 1). Marsh (1978) states, however, that rufomitrat appears to be smaller than tephrosceles and Napier and Napier (1985) state that the Zanzibar red colobus is the smallest subspecies.

There may be a habitat divide in terms of body size; that is, the populations in the drier regions such as Senegambia, Tana River and Zanzibar have a smaller body size than the populations found in the wetter habitats.

There may be an east-west cline in terms of body size dimorphism. In at least some of the east African forms, adult females are about 3/4th the size of the adult males (Kingdon, 1971 and Struhsaker 1975 for weights and Marsh, 1978 for visual estimates). My impression was that no body size dimorphism existed in The Gambia; in fact, the two largest animals in the main study troop were adult females. While body size dimorphism was lacking, the canines appeared slightly larger in males than females. My estimates are in agreement with data collected on other West African populations (Leutenegger and Kelley, 1977), which show that body size dimorphism is slight or lacking but canine size dimorphism is moderate.

One of the most obvious advertisements of dimorphism in red colobus is the female sexual swelling. The swellings are variable in size between subspecies (Marsh, 1978) and, at least for teminckii, within subspecies. In the main study troop in Abuko, there was much individual variation in size and color. The size ranged from about 50mm long and 50mm wide to about 100mm long and 100mm wide. The color ranged from bright pink to a pinkish mahogany brown. The variation in color and size did not appear to be related to

age. The two sexually mature females with the largest swellings were a young nullipara and an old multipara.

Allen (1925) first described and Kuhn (1972) and Marsh (1978) reviewed the data on male perineal swellings and note that not all subspecies have this characteristic. In Abuko all infant and juvenile males possess this swelling which can best be described as an obvious knob-like, raised pink pubic cushion. As the males mature, the pubic cushion appears to grade gradually into the rest of the ano-genital region and become less obvious. Adult males do not have a very visible pendulous scrotum and when they are relaxed the penis is retracted and invisible.

From the above information it can be seen that temminckii in Abuko differs from the two best-studied species, rufomitratatus and tephrosceles, in the following physical characteristics:

1. They are more brightly colored.
2. They are smaller in size.
3. They show less body size dimorphism.
4. The young males possess a very obvious pubic cushion which is non-existent in rufomitratatus and relatively small in tephrosceles.

#### Literature Review: Previous Red Colobus Field Studies

While primate field studies began in earnest in the 1950's, it was not until much later that the behavior and

ecology of red colobus monkeys was investigated. A number of incidental references to their behavior existed (Booth, 1956; Kuhn, 1964; Kano, 1971; Kingston, 1971), a five-day study on calls in the Kibale Forest, Uganda on tephrosceles (Marler, 1970) and a note on the general ecology of tephrosceles in the Mahale Mountains, Tanzania made as an adjunct to a study of East African chimpanzees (Nishida, 1972).

The first long-term field study was begun in 1969 by Clutton-Brock (1972). He spent 17 months in the field studying tephrosceles in the Gombe National Park, Tanzania, but also collecting comparative data on tephrosceles and Colobus guereza in Kibale, Uganda. In the main, his work was a detailed 9-month study of activity budgets, habitat use and diet on one troop living in the Gombe National Park (1973, 1974, 1975a, 1975b). There was very little mention of social structure and organization, no individual identification and no mention of transfer patterns, socialization, sexual behavior or social relationships.

In 1970, Struhsaker (1975), after surveying various red colobus populations, mostly in West Africa, began a long-term, in depth study, also on tephrosceles in the Kibale Forest, Uganda. The main focus of this study was a detailed account of calls, diet, activity patterns and habitat use (Struhsaker 1975, 1978a, 1978b; Struhsaker and Oates, 1975). This work included some individual identification and

covered social interactions, behavioral development, transfer patterns and reproductive strategies in more depth than done by Clutton-Brock (Struhsaker and Leland, 1979, 1985, 1987).

Isbell (1983) completed a concentrated and detailed study on another troop of tephrosceles inhabiting the Kibale Forest. She investigated the relationship of daily ranging behavior to numerous social and environmental variables in one troop of approximately 65 red colobus.

In 1973 Marsh began a 37-month detailed study on another species of red colobus. This time the subject was the endangered rufomitratus living along the Tana River in Kenya. Like the other studies it gives detailed accounts of diet, habitat use and activity budgets (Marsh, 1978, 1981a, 1981b), but more attention is paid to social relationships and transfer patterns (1979a, 1979b).

Six studies have been conducted on the red colobus living in West Africa.

In 1976 the waldroni form in the Bia National Park, Ghana was one of the subjects in a study on the problems of primate conservation. Incidental references are made to its behavior and some notes were made on the general ecology. Specific data were collected on reactions to humans and a list of foods for one year was given (Rucks, unpublished).

Galat-Luong and Galat (1979) briefly looked at three troops of oustaleti and provide some data on the ecology of

this subspecies.

Galat-Luong (1983) looked at the badius form in the Tai Forest, Ivory Coast and compared its behavior with that of the sympatric black-and-white and the olive colobus.

Of particular relevance to this project was the first study conducted on temminckii, by Gatinot (1975, 1978), describing the ecology, diet and habitat use of a population living in the Fathala Forest, Senegal. Once again, there was little attention paid to behavior and social relationships.

Gunderson (1977) watched temminckii in the Abuko Nature Reserve for 8 months and described some observations on ecology. She did not recognize individual animals.

Galat-Luong (1988) spent two weeks looking at temminckii in Pirang Forest, a relict forest patch in The Gambia. Interspecific interactions, population density and conservation issues were described. There was very little mention of social behaviors, no individual recognition and no mention of transfer patterns or relationships.

Thus, beginning with Clutton-Brock's study at the Gombe National Park in Tanzania, red colobus have been the subject of five in-depth studies, three on tephrosceles in East Africa (Clutton-Brock, Struhsaker and Isbell), one on rufomitratus in Kenya (Marsh), and one on temminckii in Senegal (Gatinot). Temminckii in The Gambia, waldroni in Ghana, oustaleti in the Central African Republic and badius

in the Ivory Coast have also been the subjects of less intensive studies.

From the above it can be seen that ecology, diet, activity patterns and ranging behavior for red colobus have been examined in detail. It can also be seen that in-depth information on social relations were often missing from these studies. The lack of information on the social behavior of red colobus is addressed in this study. Throughout this thesis comparisons will be made with data reported from previous red colobus field studies. Since the methods used in Abuko (see Chapter 4) were more similar to those used by field workers studying East African forms of red colobus, however, most of the systematic comparisons will be made with East African studies.

### Chapter 3. THE STUDY AREA

#### The Gambia : An Overview

Lying between latitudes 13°N and 14°N, and almost bisected by the 15° W longitude, The Gambia forms a narrow band on either side of the River Gambia for some 320 km, and is bordered on three sides by the Republic of Senegal (Figure 3). The River Gambia is the main physical feature of this country. The river rises in the mountains of Guinea, meanders through Senegal and discharges into the Atlantic at Banjul (the capital) after passing the length of The Gambia. The Gambia itself has little topographical relief, nowhere exceeding an altitude of 90 m.

The country has a total land area of 10,350 sq km and a total human population of 750,000 (UNDP, 1987), resulting in an average density of 72.5 people per sq km. This makes The Gambia one of the most densely populated countries in Africa. Only about 20% of the population is urban, the rest living scattered through the country in small villages. As a result there are virtually no undisturbed forests and very few protected areas.

Based on panchromatic black-and-white aerial photos taken in October/November 1981, The Gambia contains 4,514 km<sup>2</sup> of natural forest made up of the following habitats: tree and shrub savanna (76.8%); open woodland (13.9%);



closed woodland (4.4%); high stature mangroves (3.3%); gallery forest (1.6%) (Forster, 1983).

### Site Selection

Before selecting an area for an intensive study of red colobus in The Gambia it was necessary to survey a number of potential sites. I was looking for a site with the following requirements:

1. Adequate numbers of red colobus, with at least two separate troops so that intertroop behavior could be studied;
2. A habitat at least slightly different from that found at Fathala Forest (Gatinot, 1975), enabling comparison of the same subspecies in two different habitats;
3. Other resident primate species, allowing interspecific behaviors to be studied;
4. A relatively undisturbed area with no burning, hunting, or provisioning of wild animals;
5. Easily accessible throughout the year with good visibility;
6. A protected area where any animals which became habituated to my presence would be guaranteed some measure of safety.

After spending the last half of February and the first week of March 1978 surveying The Gambia and the Cassamance

province in Senegal, it was apparent that the Abuko Nature Reserve was the place best suited for this study.

### Abuko Nature Reserve

#### Introduction

The Abuko Nature Reserve (latitude 13° 24'N, longitude 16° 39'W) is a mosaic habitat slightly different from that found in Fathala and containing numerous red colobus, green monkeys (Cercopithecus sabaeus) and patas monkeys (Erythrocebus patas) . It is relatively undisturbed with no hunting, burning or provisioning of wild animals occurring when the study was initiated. It is easily accessible throughout the year and visibility is excellent. Since a one-meter wide, 2.5 km long path had been cut through the reserve, the animals would be easy to follow. Additionally, there were markers placed every 33 m along this path and all the main trees had been identified and labelled by a member of the Department of Wildlife Conservation.

There were, however, two immediate drawbacks to working in Abuko: the presence of a zoo and tourists. I overcame the first problem by concentrating on the troops whose home ranges did not include the zoo. The tourists were more difficult to avoid. In recent years the number of tourists has greatly increased. According to the reserve gate records, from July 1975 through June 1976 there were 10,020

visitors and from July 1979 through June 1980 there were 14,555 visitors. Most of these visitors were European tourists who were led very quickly through the reserve on guided tours. They spent very little time in the park and frequently did not even see the red colobus. As the study progressed and the colobus became habituated to me, they also got used to tourists moving quickly past.

During the course of this study the Department of Wildlife Conservation began to burn off selected areas (areas not used by the main study troop or its neighbors) and to provision the green monkeys with groundnuts. These actions were taken so that it would be easier to photograph some of the shyer birds and mammals. What effect these management policies had on the red colobus is unknown.

### History of the Reserve

The Abuko Nature Reserve is situated outside the village of Lamin some 15 km by road from the capital, Banjul (Figure 3). In 1916, 77.35 ha were fenced and barred to settlement to protect the water supply of Banjul. Though used for collecting firewood, cattle grazing, rice growing and palm tree tapping (based on interviews I conducted with elders of the Lamin community), an unique sample of gallery forest was preserved together with tall grass tree and shrub savanna and various stages of woodland typical of the area. In 1968 this area was given the status of nature reserve and

has received complete protection since then. In 1978 the reserve was enlarged by the addition of 29.3 ha of basically tree and shrub savanna. Its present size is 106.6 ha. The rectangular-shaped reserve rises from approximately 5.5 to 16 m above sea level. It is completely surrounded by human habitation, fallow and/or cultivated fields and is protected from poaching and invasion by domestic animals by a set of parallel chain link fences which also provides a firebreak. During this study, however, one large pig and two dogs managed to get through holes in the fence and enter the reserve.

### Climate

The Gambian climate consists of a long dry season with a shorter, but intense, rainy season. During the dry season, the days are hot, the nights and early mornings are cold and the "harmattan" blows from the Sahara and dries up the countryside, causing much haze and low humidity.

Generally, the rainy season starts in mid-June and ends in mid-October, with the majority of rain occurring in July, August and September (Table 2). Based on 25 years of records (1955 through 1980) collected from Yundum Meteorological Station, located less than 1.25 km from the reserve, the mean annual rainfall was 1124 mm. During this period, a minimum of 582 mm occurred in 1972 and a maximum of 1854 mm in 1958. During the rainy season, grass and herb

growth is rapid and by the end of the rains visibility is very restricted in the savanna and woodland zones. The reserve is closed to tourists during the latter part of the rainy season, partly because visibility in the savanna zones is so poor and partly because the paths are often impassable. The reserve staff often do repair work on paths and photo-hides at this time.

During the dry season clouds are virtually absent and the temperature is high during the day and low at night. During the rains, clouds are frequently present and the temperature shows less daily variation than it does during the dry season. The mean monthly sunshine duration for the three peak rainy season months (July, August, September) over the years 1950 to 1979 was 181.6 hours while during the other 9 months it was 267.5 with little mean monthly variability (s.d. = 23.77 hours).

Mean hourly temperatures taken in Abuko in both the gallery forest and the tree and shrub savanna from June 1978 through May 1979 on 13 days each month are presented in Figure 4. The mean hourly daytime temperature in the savanna was consistently higher than in the forest for every month. In the savanna the mean for the year was 26.75 C° (s.d. = -1.82), with January and December decidedly cooler than the others. In the forest the pattern was similar with a monthly mean hourly temperature of 24.70 C° (s.d. = -1.53).

## Fauna

Primates resident in Abuko during the study included five troops of P. b. temminckii, two troops of E. patas and at least four and possibly six troops of C. sabaeus.

Table 3 gives the numbers of the three permanently resident monkey species. The density of each species varied greatly due to the fact that the different species spent varying amounts of time in the reserve. The colobus with a density of 123.7 animals/km<sup>2</sup>, spent virtually all their time in the reserve. The green monkeys spent time both in and outside the reserve, while the patas appeared to spend the majority of their time in the fields surrounding the reserve.

Because there are no accurate data on how much time these two species actually spent in the reserve, an accurate measurement of density is not possible.

Over the years there have been reports of a lone Campbell's monkey (Cercopithecus campbelli) in the reserve (Edberg, pers. comm.; Gunderson, 1977). During this study a subadult male Campbell's monkey was observed in the reserve on 17 days between January 22 1982 and July 18 1982. He was always travelling with one of the red colobus troops (not always the same troop) and not as reported by Gunderson (1977), with green monkey troops. It was not possible to determine where he came from or where he eventually went. The closest known troop was approximately 8 km from the reserve and there is no reason to suspect that there is an

as yet unobserved troop of Campbell's monkeys in the area. This species is almost extinct in The Gambia. These lone males may be coming from the Cassamance province in Senegal where they still exist in moderate numbers.

During this study two young baboons (Papio) escaped from the zoo within the reserve and spent a few weeks wandering through the reserve before they disappeared. Galat-Luong (1988) noted the existence of a young baboon in the reserve in 1986. I have been informed by reliable sources that this was probably another baboon which escaped from the zoo. Although colobus and baboon overlap in other areas of The Gambia, they do not do so in the Abuko Nature Reserve.

Although small in size, Abuko contains a diverse mammal, bird and reptile population, of which many are normally found in the true rain forest further south (e.g. Nandinia binotata: two-spotted palm civet, Gastropylis smaragdina: the emerald snake). All the mammals observed in Abuko during this study are listed in Appendix A. There were no carnivorous mammals in the reserve capable of killing a red colobus. Reliable sources stated that there had not been any such carnivores for at least 10 years and possibly much longer.

Over 250 bird species have been recorded in the reserve according to Jensen and Kirkeby (1980). Birds of prey capable of killing a colobus were not observed during this

study and have only rarely been observed by members of the Gambian Ornithological Society, either before or during this study (Edberg, pers. comm.; C. White, pers. comm.). The colobus, however, frequently gave alarm calls at low-flying helicopters, large falling leaves, and various kingfishers, hornbills, vultures, hawks and eagles.

The most commonly encountered snakes in Abuko were the black cobra, green mamba, African beauty snake, emerald snake and rock python. Both the Nile and dwarf crocodiles were seen daily in the pools and puddles scattered throughout the reserve in the swamp and gallery forest. The rock python and the Nile crocodile preyed on red colobus in the reserve before (A. Jallow, pers. comm.) and during this study (see section on deaths in Chapter 7).

### Habitat Types

In order to define the various types of habitat present in the reserve as accurately as possible, time was spent making strip enumerations of trees throughout the main study troop's range in the major habitat zones. These results are given in Appendix B.

Basically the reserve can be divided into five gross habitat types. The majority of the reserve consists of tree and shrub savanna (56.6% of the reserve) and woodland savanna (24.8%) with smaller patches of gallery forest (16%), a man-made zoo (1.3%), crocodile-inhabited pools



(0.8%), swamp (less than 0.3%) and clearings (less than 0.3%). The habitat types are described and compared in Table 4. The placement and amount of the different habitat types are mapped in Figure 5.

### Study Troops

The main subjects of this thesis are members of a troop named 'Focal troop'. The size and composition data on Focal troop and a neighboring troop, named 'PWD' are provided in Table 5. During the 1978 - 1983 study period Focal troop ranged in size from a minimum of 22 to a maximum of 32 while PWD ranged in size from 18 - 29 individuals. There were three other troops named 'Middle troop', 'Question troop' and 'Zoo troop'. The less-well-studied Middle troop ranged in size from 14 - 21 members (based on 18 surveys ranging from 1 hour to 6 hours in duration).

The adult male composition of the Abuko troops is variable in that there are both one-male and multi-male troops (Eisenberg et al., 1972) represented. One of the troops, 'Middle troop', never contained more than one adult male at any time, while PWD always had two adult males in residence and Focal troop contained 2 - 5 adult males (two adult males were present for 33 months, three adult males for 22 months, four adult males for 5 months and five adult males for one month. Both Question troop and Zoo troop always contained 2 - 3 adult males. In all five troops

females always outnumbered males and in the Focal troop they ranged from a minimum of 9 to a maximum of 14.

#### Comparison with Other Red Colobus Study Sites

Since throughout this study comparisons will be made with red colobus studied elsewhere, a brief description of the most well-studied sites will be given here. The information for the Gombe National Park is taken from Clutton-Brock (1972), Teleki (1973), Goodall (1986) and Collins and McGrew (1988). The information for Kibale Forest in Uganda is taken from Struhsaker (1975) and Ghiglieri (1984). Marsh (1978) provides the data for the Tana River site in Kenya and Gatinot (1975, 1977) for the Fathala Forest in the Republic of Senegal. Troop size and composition data from the various sites are compared in Table 6.

All five study sites consist of mosaic habitats where the colobus are presented with habitat choice. No two study sites, however, consist of the same vegetation types. Furthermore, the combination of climate, sympatric primates, predators and fire is not comparable from site to site (Table 7).

The Abuko habitat is drier than the Gombe National Park and the Kibale Forest, but is much wetter than the Tana River site. Fathala Forest is most like Abuko in terms of rainfall and temperature, but the intense fires which sweep

through Fathala every year create an environment unlike that found in Abuko where there has not been a major fire since 1966 (Dept. of Wildlife Conservation staff, pers. comm.). There were, however, isolated patches burned off but not in the area used by Focal troop or any of its neighbors. The mean annual rainfall recorded at Gombe National Park and Kibale Forest is less than the maximum recorded at Abuko while the mean annual rainfall recorded at Tana River is less than the minimum recorded at Abuko. One very obvious difference between Abuko and Tana River on the one hand and all other sites on the other, is that Abuko and Tana River are small pockets of forest, while the others are larger expanses of forest. The animals living in these larger forests can easily transfer from troop to troop and they have a larger number of troops to choose from when they transfer. The animals living in Abuko and Tana River are more restricted.

The only two sites where predation has been commonly observed are Gombe National Park and Abuko. The predation rates at Gombe National Park (estimated rate 15%, based on 59 predatory episodes over 6 years, Cheney and Wrangham, 1987; but possibly as high as 41.6%, Wrangham and Riss, 1990) and at Abuko (estimated rate 15%, see section on predation in Chapter 7) are comparable. Furthermore, the high density and diversity of resources at Gombe National Park may be most similar to the Abuko situation. Possibly

related to this is the fact that the lowest population densities are found at Gombe National Park (100 - 200 red colobus per km<sup>2</sup>) and Abuko (123.7 red colobus per km<sup>2</sup>) and not at the drier, resource-restricted areas such as Fathala and Tana River, where the impact of predation is negligible, nor, at the rain forest site in Kibale Forest where the estimated predation rate is 1-2% and the population density is approximately 250-300 red colobus per km<sup>2</sup>.

### Summary

1. The Abuko Nature Reserve is a mosaic habitat of 106.6 ha with an estimated 132 red colobus (equivalent to 123.7 colobus per km<sup>2</sup>).

2. The Focal troop ranged in size from a minimum of 18 to a maximum of 32 individuals. The four other troops inhabiting the reserve were of a similar size. Both one-male and multi-male troops are represented in Abuko.

3. The combination of climate, vegetation, predation and intense fires found at the various red colobus sites is not comparable from site to site. Abuko appears to be most like the Gombe National Park in terms of predation rates, density and diversity of resources and red colobus population densities. It is most like Tana River in terms of total forest size. Both Tana River and Abuko are small relict forest patches surrounded by land which is not usable for colobus.

## Chapter 4. METHODS

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### Study Program

The field study started in mid-February 1978 and lasted through September 1983. The study can be divided into five periods:

1. February - March 1978 (3 weeks): brief survey of western Gambia and western Cassamance province in southern Senegal, to search for a suitable site.

2. March 1978 (1 1/2 - 2 weeks): survey of the Abuko Nature Reserve familiarizing myself with the reserve, its plants and animals and selecting a troop to use as the main study troop ('Focal troop').

3. March 1978 - mid-January 1980: habituating Focal troop and taking systematic scan-samples (Altmann, J., 1974) on habitat use, daily activity patterns and social behavior. Scan-sampling was begun immediately because I felt that the colobus had to become accustomed to my presence and movements from the start. I also wanted to try out various observational techniques and see which would be the most useful and reliable. During this period quarter-hourly scan-samples were collected and information was obtained on habitat use, diet, activity patterns and social behaviors. All unusual behaviors were recorded whenever they occurred (aggression, appeasement, sexual interactions, object use,

intertroop encounters, interspecific encounters, and so forth.

During this period several environmental measurements were taken (temperatures, strip enumerations of trees, mapping of home ranges: methods used are described on the appropriate maps, charts, figures).

The total amount of time spent collecting scan-samples on Focal troop during this period is given in Table 8. Time spent censusing other troops in Abuko, examining forests and populations elsewhere, collecting botanical specimens, taking photographs and non-systematic observations on Focal troop and other troops both in and outside Abuko are not included in this table.

4. mid-January 1980 - mid-March 1982: while information on diet, daily activity patterns and habitat use was no longer collected, quarter-hourly scan-samples continued on all social behaviors. Behaviors such as mountings, matings, fights, object use, interspecific and intertroop encounters were also collected on an ad lib basis (Altmann, J., 1974). The total amount of time spent collecting scan-samples on the social behavior of Focal troop is given in Table 9. Only the unusual use of habitat (such as entering a new area) or new food items were noted during this period.

5. April 1982 - September 1983: The majority of this time was spent taking color 16 mm cine film of Focal

troop. During this period, observations were basically confined to monitoring the composition of Focal troop, censusing neighboring troops and recording only unusual events (births, deaths, troop transfers, object use). When an unusual event did occur, however, detailed notes would be taken, and observation would take precedence over filming.

#### Techniques of Observation and Analysis

All field work was on foot. During observations I used 10 X 40 Leitz Trinovid binoculars. All information was recorded in notebooks. A cassette recorder was occasionally used to tape red colobus calls. Some of the recordings have been deposited with the National Sound Archives in London, England.

Throughout periods 3 and 4, and sometimes during period 5, daily range maps were made, reproductive state of different females was noted and a 35mm camera was used to record as many postures and behaviors as possible.

Demographic data for Focal troop and PWD troop were collected whenever they were observed and the presence (or absence) of all members was noted. Thus, the numbers given for these two troops in Table 5 are considered reliable.

PWD was studied on an opportunistic basis. That is, on days when I could not find Focal troop I often spent time with PWD until I heard or saw Focal troop members. Also, it was frequently possible to watch both Focal troop and PWD at



the same time if they were inhabiting opposite sides of Bamboo pool (Figure 6). From July 1979 through August 1982 I had contact with PWD on 96 separate occasions totalling a minimum of 119 hours of observation.

During the gradual process of habituation to the observer all Focal troop members and most of the PWD members became individually known. A number of other adults, subadults and juveniles in the remaining three troops were individually recognizable in any situation as were most of the solitary males.

Statistical tests of significance often could not be used, especially with scan data, because of the violation of the assumption of independence of observations (Siegel, 1956; Clutton-Brock, 1972). Those tests which were used are listed where appropriate, and were all done by C. Berry, Department of Statistics, Imperial College, London.

#### Classifying Individuals

Because most birthdays were known and the birth season was fairly well-defined, all young colobus were assigned ages in terms of months instead of being classified according to size (i.e. small, medium, large infant or juvenile). It was possible to determine the sex of the infants and juveniles only if they could be seen urinating. Only Focal troop youngsters were accurately sexed. Youngsters outside Focal troop were classified as being the

same age as Focal troop youngsters if they were the same size. This meant, of course, that a large or small individual would have been incorrectly categorized as being older or younger than it really was. In this thesis an animal is referred to as an infant if it is 0 - 13 months of age.

Individuals became juveniles when they reached the age of 13 months and remained classified as juveniles until they began to develop obvious sexual characteristics. Females were reclassified as subadults when they developed their first adolescent swelling. Males were reclassified as subadult when their testes first became obvious.

Differentiating between subadults and adults entailed some problems. In the case of females, the presence of pendulous nipples, which were acquired during the last month of pregnancy, was used to distinguish subadults from adults. This meant, of course, that a sterile adult female would have been incorrectly categorized as a subadult.

Classification of males was more questionable because it depended on a gradual range of characteristics, such as the size of the canines and scrotum, whereas with females, classification depended solely on the presence or absence of the pendulous nipples.

The dividing lines between the various age classes are rather arbitrary, and probably vary both from subspecies to subspecies, and from worker to worker. Thus, care is needed

in making comparisons between various red colobus populations. Errors that occur, in terms of classification, both within and between populations, do not necessarily balance each other out, and can lead to unwarranted conclusions (Caughley, 1977).

#### Activity Budget Data

This section describes methods for determining red colobus monkeys' use of time in different activities. Since it was not possible to keep individual monkeys in sight continuously, I used the scan-sampling technique described by J. Altmann (1974) and also used by Clutton-Brock (1972), Struhsaker (1975), Marsh (1978) and Isbell (1983) in their field studies of red colobus. Every month for 23 months (March 1978 through mid-January 1980), I observed Focal troop at 15-minute intervals for a five minute period and recorded the activity and placement of all visible animals. Whenever possible, I noted the age, sex, reproductive stage and identity of the target animal.

Since the main sources of comparative material for this study are Struhsaker (1975) and Marsh (1978), all scan-sampling records were collected on sustained activities (that activity first performed by the animal under observation for a duration of at least 5 continuous seconds) as opposed to instantaneous activities. However, 600 paired observations of instantaneous activities and sustained

activities were made on Focal troop. Members of the pair differed in 35 cases (5.8%). On summation, some of the differences cancelled out, producing a total difference in 22 cases (3.7%). Of these 22 cases, 18 of them involved moving activity being collected for the instantaneous sample changing to either resting (11 cases) or feeding (7 cases) activity when being collected for the sustained sample. Comparing the two methods there was no significant difference between frequency distribution of scores (chi square = 1.77; d.f. = 5).

The following categories of activity were distinguished and defined:

Feeding included the active inspection of food, bringing it to the mouth, chewing and swallowing. Like the red colobus in Gombe Stream (Clutton-Brock, 1974), the Abuko colobus were almost always stationary when feeding. Marsh (1978) states that, in the Tana River red colobus, feeding commonly coincided with another activity, such as moving, and that both he and Struhsaker (1975) scored this activity as feeding. I, like Clutton-Brock, scored this activity as moving, but found it extremely rare (four times during the entire year of scan-sampling for activity patterns). With the Abuko colobus there was one activity which would have been difficult to categorize. Occasionally, during day-time 'sleep', the colobus would chew for 5-10 seconds with their eyes closed and their bodies motionless. This behavior was

very similar to that shown by animals with cheek pouches or ungulates chewing their cud. It could have been due to forcing a toxic, yet extremely nutritious vomit back down (Altmann, Post and Klein, 1987). The problem of categorization did not arise since this behavior did not occur during scan-samples.

Resting included times when an animal was in an inactive state and also when an animal was calling but physically motionless. This category was subdivided into sitting and lying because it was apparent that there were individual differences in posture choice and also hourly differences. That is, certain individuals chose to sit, others to lie and lying occurred only during certain times of the day.

Moving included both short bodily displacements and progressions (where an animal covered longer distances on its own or with others). Frequently, a moving animal had to be watched for almost 10 seconds in order to determine whether the activity was to be scored as moving, play, fleeing or displacement.

Auto-grooming included an animal grooming or scratching its own body.

Allo-grooming included the same motor patterns as autogrooming, but was a social interaction. Allo-grooming was further subdivided into groomer and groomee.

Play included chasing, wrestling, leaping and

bouncing about, pulling, tugging, banging each other and inanimate objects.

Nursing included all cases when an infant or juvenile had a female's nipple in its mouth. Only the nursling was included in this category. The female was scored as either resting, feeding, grooming, depending on her activity.

Social Activities included mounts, fights, copulations, displacements, embraces, threats, displays. For the purposes of the time budget they are all lumped together.

Five continuous days in which Focal troop was followed continuously from dawn to dusk were extracted for 12 month's (February 1979 - January 1980) data at Abuko. The data collected during each of the extracted five days were analyzed by summing the number of records in each category of activity and expressing these totals as percentages of the total number of records made.

The activity records collected by the above-mentioned methods are given in Table 10. Also given in this table is the annual activity budget for infants (0 - 13 months of age). Two separate activity budgets are given because the number of infants at Abuko was not small and their presence would have affected the monthly scores as they matured. Furthermore, by separating the two activity budgets, it allows for more accurate comparisons with the other red

colobus populations where either the infants were not included (Gombe National Park colobus data) or separate activity budgets are given (Tana River colobus data).

#### Diet and Feeding Data

For the observations on diet I used the same dawn-to-dusk 15-minute interval, scan-sampling technique used to determine activity budgets. Whenever the activity was recorded as feeding, the item eaten was noted.

The identity of most items (in terms of plant part) was usually obvious and could easily be categorized (i.e. flower, flower bud, fruit, leaf bud, etc.). The relative maturity of leaves, however, was sometimes difficult to assess and so some subjectivity was involved in this decision.

If I did not see an item actually being put into the mouth or being handled by the feeder then the item would be categorized as unidentified. For example, an animal might be sitting in a tree, chewing or picking an unseen item from a branch and putting the item in its mouth. In both cases the activity would be scored as feeding on an unidentified item. All plant species, except for Ficus, were collected, dried in the field, sent to the Royal Botanic Gardens, Kew, England and identified by F.N. Hepper. Figs were collected, preserved in formalin and identified by C.C. Berg at the Institute voor Systematische Plantkunde, Utrecht, Nederlands.

Insects were preserved in formalin and identified by the United States Department of Agriculture, Bethesda, Maryland or the Tropical Development and Research Institute at the British Museum of Natural History, London, England. Soils and termite mounds and runway sheets were analyzed by S. Taal at the Soils Laboratory, Yundum, The Gambia.

While the activity budget data was limited to five extracted days each month, the diet data contain all the information collected from July 1978 through the middle of January 1980 on dawn-to-dusk follows. The number of dawn-to-dusk follows and the number of feeding observations collected each month are given in Table 11. The first four months of the study (March 1978 - June 1978) were eliminated, since I felt that the colobus were not sufficiently habituated and may have ignored some items at or near ground level because of my presence.

#### Social Behavior Data

Since it was not possible to keep individual animals in sight continuously, focal animal (continuous) sampling was not a realistic method. In gathering behavioral data, therefore, I used the same dawn-to-dusk, 15-minute interval, scan-sampling technique used to determine activity budgets and diet and feeding behavior. The social behavior data were collected from March 1978 through March 1982. The total amount of time spent collecting scan-samples on the



social behavior of Focal troop (total time = 7950] hours) is given in Table 8 plus Table 9.

During the period from March 1978 through mid-January 1980, social behavior was collected along with information on activity budgets, diet and feeding behavior and the environment. From mid-January 1980 through March 1982 only social behaviors were recorded during scan-samples. Additional unusual behaviors were collected during the fifth period of the study when filming was taking place (see pages 30 - 31).

Certain behaviors were recorded on an ad lib basis while others were only collected during scan-samples. Consequently, for some analyses I used data obtained on an ad lib basis; for others, only data obtained during scan-samples. Details as to which type of method and analyses are provided as appropriate in relevant sections.

To obtain reproductive and demographic data, each day I recorded the size and state of sexual swellings, the presence or absence of troop members, the presence of any new individuals within the troop or as shadowers, any wounds, illnesses and the occurrence of any developmental milestones reached by immature individuals within Focal troop. The presence or absence of all PWD members was noted whenever contact was made with this troop. Case history descriptions of Focal troop members (and some key extratroop and PWD troop individuals) are given in Appendix C.

## Chapter 5 DIET AND FEEDING PATTERNS

### Introduction

While feeding was not the main focus of this study, dietary data are provided because feeding has important consequences for the monkeys' day-to-day behavior and long-term reproductive strategies. This chapter describes the diet of the Abuko red colobus and compares it with other red colobus populations. Some questions I attempt to answer in this chapter include: Are there age/sex differences in feeding behavior? If so, what is the significance? Are any feeding behaviors related to transfer patterns?

### Species Eaten by the Red Colobus in Abuko

During the scan-samples for one annual cycle (February 1979 - January 1980) Focal troop members fed on 89 identified plant species. A list of the 89 species, the items selected and the percent of each item in the annual diet is given in Table 12. These 89 species accounted for approximately 94% of the total feeding time. Unidentified species accounted for 6% and non-plant items such as soil, water, insect, galls accounted for 0.4%. A further 4 species were eaten by members of Focal troop outside this scan-sampling period.

The five most frequently eaten plants (Parinari

excelsa, Ficus trichopoda, Detarium senegalense, Parkia biglobosa, Pseudospondias microcarpa) belong to five different families (Rosaceae, Moraceae, Caesalpinaceae, Mimosaceae, Anacardiaceae respectively) and occur in different habitat types. They are found in gallery forest, savanna, swamp/clearing edge, gallery forest/ savanna edge. They do, however, share some common traits. They could all be described as large trees with wide-spreading crowns and large horizontal branches. Furthermore, they bear very dense crops of either fruit, young leaf, flower or all three, and are spatially clumped. They are all used as sleeping sites and daytime resting sites.

#### Seasonal Variation of Food Items

In Abuko, members of Focal troop spent 41.6% of their time feeding on fruits and/or seeds, 8.6% on floral parts and 46.7% of their time on leaf parts (leaf buds, young leaves, mature leaves, chlorotic leaves, dying leaves, leaf petioles) (Table 13). Young leaves (defined as the same shape, but not the same color and/or texture as mature leaves) comprised 26% of all records (Table 13). Not only were fruits the major food item on an annual basis, but they were also the main food item for 14 of the 19 months of the time spent collecting diet data (July 1978 through mid-January 1980: Table 14). During the peak of the dry season (January - April) young leaves and leaf buds take over as

the major food source with fruit becoming the second most frequently eaten item. Although their digestive system can cope with large amounts of leaves, behaviorally the Abuko red colobus have a highly diverse diet with seasonally available fruit, flowers and leaf parts making up the majority of their diet. It is also apparent, however, that mature leaves (see August 1979: Table 14) can be eaten in large numbers if seasonally available preferred items, such as fruits, are not available.

#### Feeding Data From Other Colobus Troops in Abuko

When other troops in Abuko were observed, a note was made of all food sources. The feeding techniques and postures used by the colobus in other troops appeared similar to those used by Focal troop members. The general food habits of the other troops in Abuko did not appear to differ substantially from those of the Focal troop. In terms of the species they shared in common, all troops fed on the same item during the same months.

Members of PWD troop fed on 32 separate items from 24 plant species and one type of terrestrial termite mound. They also fed on four items from four separate species not used by Focal troop. These four species were not found in Focal troop's range in a mature form and thus could not have been a part of their diet. Three subadult females who transferred from Focal troop (their natal troop) to PWD

troop were frequently observed eating one of these items and thus were obviously able to add new items to their diet after reaching subadulthood.

Members of Zoo troop were seen feeding on 17 separate items from 10 species. Again, the only new item in the diet was from a species (Delonix regia) which did not grow in Focal troop's range.

While the general habits of the various troops were similar, there may be substantial quantitative differences in the ranking of various food items. Because of the lack of vegetational heterogeneity in Abuko (see pages 23-24 and Appendix B) and the fact that many of the important food species appeared to exhibit fidelity to microhabitats, different troops had different plant communities within their ranges.

One of the most obvious differences between Focal troop's range and PWD's range was that PWD did not have access to a tree and shrub savanna. An obvious difference between PWD and Focal troop as opposed to the other three troops, was that PWD and Focal troop had access to year-round swamps while the others had no swamps or year-round natural water sources within their ranges. Some of the top-ranking food trees and the total number found in various ranges are listed in Table 15. It is clear from these data that the Focal troop's range is quite different from those of PWD or the Zoo troop's range, in terms of the numbers of

some of the important food sources (at least important to Focal troop). It would seem that when females transferred from Focal troop to other troops, they entered ranges where the species they once 'depended' on for food and sleeping sites may be either unimportant, nonexistent or areas of intense competition.

#### Feeding on Non-Plant Items

During the course of this study the ingestion of non-plant items was rare. Adults and subadults were not observed deliberately seeking out and eating insects, galls, dead wood, but juveniles were seen feeding on these items five times.

A 21-month-old female picked a mature Vitex grandifolia leaf, held it in her hands, bit off three pea-sized fungus-caused galls, ate them and dropped the leaf. A one-year-old male ate a Pseudospondias microcarpa fruit which had been obviously infected by a torymid-caused gall. A 17-month-old male put his mouth to a Calamus deeratus vine, bit off an unidentified insect (probably an ant), and ate it. An 18-month-old female sat on the savanna watching green monkeys jump up in the air and catch termite alates (Pericapritermes sp.). Twice she reached up, caught an alate in midair and ate it. She then play-scrampered off, put her mouth to the ground and ate another alate which had dropped its wings. A 24-month-old female pulled apart and ate dead pith from

inside the top of a dead, frondless oil palm (Elaeis guineensis). On two occasions juvenile females sat in dead trees, pulled off pieces of dead bark or pith and dropped them to the ground. They did not, however, eat anything while they did this.

Since only these few sightings were made and adult colobus were not seen to use motor patterns usually associated with insect feeding it may be assumed that insects are not a significant part of their diet. It is likely, however, that the colobus inadvertently ingested thrips (Gigantothrips sp.) which were abundant on many Ficus trichopoda leaves, ticks (Amblyomma sp.) which reached epidemic proportions in the dry season, and various termite species which were very infrequently in the soil they ate (see section below).

### Soil Feeding

From July 1978 through mid-June 1981 soil feeding was recorded whenever it occurred. During this period, members of Focal troop fed on arboreal termite mounds four times (three different mounds, all Macrotermitinae), terrestrial termite mounds 30 times ( 13 different mounds: five unidentified mounds, five Cubitermes sp. mounds, one inactive mound invaded by Pericapritermes sp., one Trinervotermes sp. mound and one Anoplotermes sp. mound) and arboreal 'runway' sheets 260 times (all

Macrotermitinae).

I checked the sites used during 271 of the 294 termite soil feeding records and in 265 cases there were no termites present at the feeding site when the colobus fed.

#### Ingestion of Body Fluids

The colobus licked their own blood whenever they were injured. Mothers, seen after having given birth, licked themselves and their infants free of all blood. One multiparous females ate her 12-day-old daughter's milk stool. On five occasions males ejaculated and ate the ejaculate after masturbating. One male vomited up a palmful of dark green semi-solid matter, looked at it and then ate it.

#### Drinking

The colobus seemed to obtain most of their water indirectly from their food. Drinking was a rare event. During the course of this study drinking and licking was seen only 25 times. Eighteen of these observations occurred during the rainy season. This was because the most common method of obtaining water involved licking rain water or drinking rain water which had collected in tree bowls. I did not see the colobus use the crocodile inhabited pools to obtain water. Even during the height of the dry season, when the colobus would come down to the water's edge to feed on



vines and herbs, they still did not drink from these sources. The green monkeys, frequently drank from these pools.

Adults used different water sources from juveniles. Six times adults licked rain from their arms and hands for 1-5 seconds as they sat hunched over during heavy downpours; three adults licked dew off leaves during the height of the dry season (two of them were mothers who had just given birth). Juveniles and subadults used different methods and sources. Nine times juveniles drank water from tree bowls during the rainy season and four times they drank from a puddle. On three occasions juveniles licked rain water but they varied the method used by adults. While adults only licked for 1 - 5 seconds, one juvenile licked for over 10 seconds while another did so for over one minute: one subadult female licked rain as it cascaded down a palm frond.

The adults did not actively seek out water. They simply bent down and licked water off their arms or reached out for a dew-covered leaf. In fact, they only licked water, they did not drink it. The young colobus, however, actively sought out water in the swampy ground or in tree bowls. This could suggest that while taking in water is not very important for colobus, it may be slightly more important for young colobus than it is for adults.

### Feeding Development

The age at which infants were first observed taking solid foods varied greatly (Table 16). The youngest was nine days old and the oldest was 50 days old. This large range of ages was probably due to observational oversight and not to actual individual feeding differences. Quite simply, I probably did not get a chance to observe all the infants when they first sampled food. It was clear, however, that the Abuko colobus started tasting food at a young age and that males began feeding on solid food at a younger age than females, although it is not significant at one or two-tailed level (Kolmogorov Smirnov test:  $Z = 18$ ; d.f. = 6.6: Table 16).

Very young infants did not always eat what and when their mothers ate. Seventeen-day-old Wid and 20-day-old Vaby moved about 12 cm from their resting mothers, picked an item off the tree and fed. They picked items which their mothers had not eaten for at least the past hour.

The most common item picked by infants the first feed time were leaf parts (84.6% of cases - Table 16). This was probably because fruits, the number one item for the group as a whole, were not always easy for young colobus to harvest. Many of the fruits required strength to detach and/or were too heavy for an infant to hold (e.g. Raphia, Detarium, Elaeis, Mangifera). The youngest colobus seen eating a Raphia fruit was 8 1/2-months-old, the youngest

with a Detarium was 8-months-old, with an Elaeis was 5 1/2-months-old and with a Mangifera was 5 months. As the colobus grew older they grew more adept at harvesting or 'taking' these items from others and the number of hard-to-harvest items increased in their diet. The only two infants listed in Table 16 as taking fruit or flower as their first item simply reached up and took pieces of food held by their own mothers. The other 11 infants who ate leaf parts picked their own items from the trees.

Table 17 lists the percentages of the major items in the infants' diet compared with the adults' diet. A comparison of these two diets shows that over an annual cycle, the infants fed less on fruits and seeds, more on floral parts, less on leaf buds, more on both young and mature leaves and that there is a significant profile difference in the infants' diet compared to the adults' diet (based on raw data: chi square = 40.8; d.f. = 5;  $p = <0.0005$ ).

The age differences in selecting dietary items makes sense nutritionally. Proteins are essential for growth and are particularly important during the growing period (Munro, 1969). Fruits are often protein and mineral poor (Bogert, et al, 1973), besides sometimes being difficult to harvest/process. Leaves (Hladik, 1978) and pollen-rich flowers (Howell, 1974) are protein rich, as well as being easy to locate and process and usually more available than

fruits. The richest source of vitamins and a good supply of calcium is often found in leaves. Thus it would seem that infants, who are growing rapidly, would benefit by consuming less fruit and more flowers and leaves than the animals who are not growing rapidly. However, leaves may contain high levels of some secondary compounds. The infant may then need a way of coping with this extra supply of toxins. Termite soils could be a way of absorbing them.

The infant shows some independence from its mother by feeding at different times or on different items. What appeared to be important to the infant was imitative foraging with peers or slightly older individuals. For example, if one infant or juvenile was feeding from a termite mound or drinking water from a tree bowl, other infants or juveniles would rush over and immediately take part. This was particularly true for items which were large, took a long time to consume and thus were exposed for a long period. Large fruits and leaves were the two items which attracted groups of youngsters. Immatures were the only ones to actively share items (6 times). They were also the only ones to rush up and eat items discarded by others (four times). They were the only ones to enter new microhabitats, such as sticking their arms in tree holes (three times) and arboreal termite mounds (four times), peeling off dead tree bark and peering at the exposed areas (five times), or copying green monkey feeding techniques

like catching flying alates (once), dragging plants across ponds (twice) or pulling plants off the bottom of pools (three times). Young females were the most frequent users of these microhabitats. Of the 18 observations made, 15 involved young females while only three involved males.

As infants matured and entered juvenile and subadulthood, they began to copy their peers less frequently. That is, while they were infants they probably relied on imitative foraging first from their mothers and then from their peers. During juvenilehood they probably relied more on their peers and as they entered subadulthood they began to forage independently. For females, however, it may be necessary to revert back to a period of imitative foraging when they transfer troops. This would be especially true in a situation when they transferred into a troop where the residents were consuming items which they had never seen. For example, three Abuko females who transferred from Focal troop where there were no Anacardium fruits began eating them when they found them being eaten by their new troop mates in PWD troop.

### Food Sharing

Active food sharing, where two or more individuals sat and ate from the same item with no aggression, was seen 6 times. The participants were always infants and the item was always too large for an infant to detach, hold in its

hands and eat. Once it was a 75 cm long Anthocleista mature leaf, twice it was a Mangifera fruit and three times a Detarium fruit. In all 6 cases the infants took turns taking bites from the still-attached item without any aggression. Food sharing probably occurred because the items were difficult to process and, because of their size and the time needed to eat them, were difficult to consume without exposing them to other infants, an age class which practiced imitative foraging, particularly imitating their peers.

Successful food transfer, not involving an element of harassment or aggression, was seen only 9 times and always involved mothers tolerating the 'scrounging' of their offspring. Seven of the nine scroungers were sons, one was a daughter and one was unidentified. All of the scrounged items were common and not difficult for an adult to locate or process, but were difficult for a young colobus to process. Food sharing seems to occur when it is the least costly alternative for the original possessor. This has been found to be true for chimpanzees (Wrangham, 1975) and titi monkeys (Starin, 1978) as well.

Information on unsuccessful food transfer and aggressive interactions regarding food items is given in Chapter 9.

Species Eaten by Red Colobus Living Outside Abuko

As I censused troops in other parts of The Gambia and Senegal I made a note of all food items. In only 7 cases did I note new food sources and in all cases the species consumed did not occur in the Focal troop's range. At Tendaba, on the south bank of the Gambia river, a troop spent a morning resting, playing, grooming and feeding on radicles in a mangrove tree, Avicennia africana. In the River Gambia National Park, an island-dwelling troop of colobus spent less than hour feeding on Machaerium lunatum young leaves. Two wild adult females living in residential gardens in a Banjul suburb, frequently are Bauhinia sp. flowers and Lagerstroemia speciosa young leaves. In Bijilo Forest Park, a rhun palm coastal forest on the edge of the Atlantic Ocean, two separate troops of colobus fed on 18 different plant species during 112 hours of observation. Three of these plant species were not located in Focal troop's home range.

Thus when plant species from all non-sampling and non-Focal troop sightings are added up, 16 more species (7 from outside Abuko, five from other troops in Abuko and four from Focal troop outside the scan-sampling period covered in Table 12) are added to the total food list for temminckii in The Gambia. Differences in the diet items of different temminckii populations appear to be largely related to availability.

There is some evidence, however, to suggest that availability is not sufficient to explain all differences in food selection. Some plant species appear to be eaten by some Procolobus subspecies but not by others. At Tana River, rufomitatus commonly encountered the very abundant Phoenix reclinata but never used it. At Abuko colobus frequently fed (it ranked 20 on an annual basis) on this rarely encountered palm. Also at Tana River, Ficus sycamorus was the most frequently eaten species in the diet, while at Abuko this fig was virtually ignored. A mature leaf was rejected by an infant and the young leaves were eaten only twice during this study. At Kibale tephrosceles clearly selected against Parinari excelsa while at Abuko it was the top-ranking species. At Gombe Stream the dense gallery forests are dominated by Elaeis guineensis (Ransom, 1981) and yet this is not mentioned as a food source by Clutton-Brock (1975). In Abuko this very common tree supplied many fruits (it ranked 24 on an annual basis).

The reasons for these differences are not known. They might be related to (1) subspecific differences amongst the colobus themselves in processing and detoxifying abilities, or (2) geographical differences in the chemistry of the food item, or (3) some populations feeding on suboptimal diets, or (4) 'cultural' variations in diet in the sense used by Kummer (1971).



### Comparisons with Red Colobus Studied Elsewhere

#### Number of Species in Diet

Compared to the other red colobus populations, the Abuko colobus has a far richer diet in terms of the total number of species eaten (Table 18).

Is the high diversity of the Abuko diet due to methodological differences? The dietary data collected over an annual cycle on all dawn-dusk follows consisted of 14,938 feeding records, while the Kibale data consisted of 2,898 records and the Tana River data were derived from 2,361 records. Limiting the amount of data to records collected on only five days each month for 12 months as was done by Struhsaker (1975) and Marsh (1978), I ended up with 4,856 records instead of 14,938 records. Taking this five-day, scan-sample diet data over one year, Focal troop ate from 70 identified plant species. This is less than the recorded 89 species, but still more than that collected at the other study sites. Thus it would seem that the difference in dietary breadth is real and not simply due to the number of days spent collecting data.

Are differences in dietary diversity due to differences in the density and diversity of vegetation available to the colobus at different sites? The Tana River (Marsh, 1978) and Fathala (Gatinot, 1975; pers. obs.) populations have access to a much less dense and diversified vegetation than

the Gombe (Clutton-Brock, 1975a) and Kibale (Struhsaker, 1975) populations (Table 7) and this could account for their limited food species list (Table 18). Using the same criteria as the other researchers, that is, counting only trees over 10 meters height, Abuko would contain an extremely low density and diversity of trees. However, counting all savanna trees over 5 meters and all gallery forest trees over 10 meters (which is the height used by colobus in Abuko), then Abuko contains an extremely dense and diverse vegetation (Table 7). In 1/2 hectare I counted 32 identified species (not including 15 unidentified trees) among 338 trees. The relevant data are given in Appendix B.

#### Species Domination

The single top food species comprised 15% of records at both Kibale and Gombe, 29% at Tana River and 44% at Fathala. At Abuko, the top species, Parinari excelsa, made up 13% (11.3% young leaves and 1.3% fruits without seeds) of the annual diet (Table 18). The difference between Abuko and the other sites becomes more obvious when the top five ranking species are considered and again even more when the top ten ranking species are considered. Clearly, the Abuko diet is not only broader in terms of species eaten, but it is also less dominated by any one species.

The number of species recorded each month during one annual cycle ranged from 27 to 49 with a mean of 40.5

species. Thus, in any one month at Abuko, the number of species chosen was more than the number chosen at Tana River in an entire year (Tana River mean = 15.2; range = 11-18 species). Although not as extreme, the number of species chosen at the other red colobus sites was also less than that chosen each month at Abuko.

#### Percentage of Items in Diet

One obvious difference between the diet in Abuko and the diets of other populations is in the percent of time spent feeding on various items (Table 18). None of the other populations fed on such a large amount of non-leaf parts.

In terms of dietary items, the Abuko population most closely resembles Tana River and Fathala populations. At all three sites the colobus spent an overwhelming percent of time feeding on seasonal foods - fruits, floral parts, young leaves, leaf buds. In contrast, the colobus at Gombe and Kibale (the less seasonal sites) spent a much larger percent of time feeding on mature leaves and mature leaf petioles (nonseasonal items).

Although dietary composition obviously reflects an interplay of preference and availability, the red colobus data from the various sites do not support the suggestion that a rain forest habitat (Kibale Forest) provides a richer, more stable source of fruit than more open habitats

(Gaulin, 1979). In fact, the only rain forest population studied consumed less fruit than any other population.

#### Effect of Competition and Predation on Amount of Fruit in Diet

Although interspecific competition was not a major concern of this study, limited observations support the view that competition was absent between colobus and Campbell's monkeys and colobus and patas monkeys. The colobus rarely spent time with these two species. There may have been limited competition between the colobus and green monkeys, with the colobus indirectly limiting some of the green's food sources. For example, the colobus ate flowers from a species (Mangifera indica) which appeared to be a major fruit source for the greens, and seeds from unripe dates (Phoenix reclinata), while ripe fruits were eaten by the greens. As with all the other red colobus sites, there is no information available on the diets of bats and birds and whether they are competing with the resident primates.

Three of the red colobus study sites are apparently without obvious competition from other primates for fruits. At Abuko and Fathala where the colobus spend the majority of their time feeding on fruits, there is no mention of other major fruit eaters nor are there any frugivorous predators. At Tana, where the colobus spend 25% of their time feeding on fruits, there does not appear to be any serious

competition or predation centered on fruit trees. At Gombe Stream, where the colobus only fed 11.4% of their time on fruit, there are two major fruit eaters. The baboon (Ransom, 1981) and the chimpanzee (Goodall, 1986; Wrangham, 1975) spent the majority of their time feeding on fruits. Furthermore, the chimpanzee preyed on the colobus. Busse (1977) recorded 39 kills by chimpanzees over a two-year period, a figure estimated to represent 8-13% of the total population. Cheney and Wrangham (1987) put the estimate at an even higher 15% while Wrangham and Riss (1990) actually maintain that the red colobus in Abuko lose 41.6% of their population to chimpanzee predation each year. This could mean that not only were these two species limiting the colobus monkeys supply, but, fruit trees were centers of potential danger. At the Kibale Forest, where the colobus spent only 5.7% of their time feeding on fruit, there were also primate frugivores. Chimpanzees (Ghiglieri, 1984), manglebeys (Waser, 1975) and blue monkeys (Rudran, 1976) are all frugivores potentially competing with and limiting the red colobus fruit supply in the Kibale Forest. Furthermore, at Kibale, the chimpanzee preys on red colobus (Ghiglieri, 1984; Leland, 1987), although this may not be of major importance since the colobus appears to ward off many of the attacks (Leland, 1987). It remains to be seen whether the amount of fruit in the different diets is related to interspecific competition and/or predation.

### Summary

1. The Abuko colobus have a highly diverse diet with seasonally available fruit making up the majority of the diet. It is also apparent that leaf parts can be eaten in large amounts if necessary.

2. The general food habits of the troops in Abuko were similar, but the ranking of various species probably differ due to the availability of various foods in the different troops' home range. When females switch troops they may have to alter their diet to fit the availability of resources in their new range.

3. Soil feeding is restricted to termite soil products. The vast majority of the mounds and runways were vacant when they were consumed.

4. Drinking is not important for colobus, but it is slightly more important for young and for females who have just given birth than it is for others.

5. Feeding begins at a very young age with males beginning before females. The infant diet differs from the non-infant diet and this could be due to different nutritional needs. Furthermore, infant foraging relies on a completely different set of social behaviors than the other age groups. Transferring females, may revert back to a period of imitative foraging if they switch to a range where they are confronted by new (to them) resources.

6. Active food sharing was rare and only occurred between infants. Non-aggressive food transfer only occurred between mothers and offspring and probably occurred because it was the least costly alternative. Sons scrounged more than daughters.

7. Availability of items is not sufficient to explain all differences in food selection by various red colobus elsewhere.

8. The Abuko population has the richest diet in terms of total number of species eaten. The diet at Abuko is also less dominated by any one species. This could partially be due to the fact that Abuko is one of the more dense and diverse sites in terms of colobus resources.

9. The sites at which there is clearly no obvious competition for fruits are those where fruits are the major food source for colobus. The sites where there are many other primates feeding heavily on fruits are those where fruits are minor items in the colobus diet. Furthermore, at these sites the main fruit eaters are also colobus predators and therefore fruit trees may be potentially more dangerous than other trees.

## Chapter 6. ACTIVITY BUDGETS

### Introduction

In order to understand the constraints within which an individual lives, it is necessary to consider how that individual distributes its time among various activities and procures food. A basic description of the Abuko red colobus monkey's use of time in different activities, and the ways in which these monkeys compare with other red colobus populations, are presented in this chapter. Some specific questions addressed in this chapter include: Do the red colobus in Abuko spend more or less time feeding, resting and socializing than red colobus at other sites? In Abuko are there age/sex differences in activity patterns? If so, what are the possible explanations for these differences?

Comparative activity budget data on red colobus come from three other sites. At the Kibale Forest, Struhsaker (1975) has estimated that the red colobus spend 91.9% of their time in maintenance activities and 8.2% of their time in social interactions. Clutton-Brock's (1972) study of red colobus in the Gombe National Park showed that the animals spent 87% of their time in maintenance activities and 8.6% of their time in social activities (the Gombe data are based



on medians). During the study on the Tana River red colobus, Marsh (1978) found that the animals spent 94.1% of their time in maintenance activities and 5.9% of their time in social activities. The specific percentages for each activity at each site are given in Table 19.

### General Overview

The percent of time spent in maintenance activities (defined here as feeding + resting + moving + nursing + auto-grooming) accounted for 86.6% of the annual activity budget while 12.6% of the time was spent socializing (defined here as play + social grooming + social interacting) (Table 10). This is generally very similar to the activity budgets collected at the other sites (Table 19).

Across activities, sitting (one or more ischial callosities contacting substrate) was the predominant position. 5036 of the 5039 (99.9%) feeding records, 11,904 of the 12,402 (95.9%) resting records, 56 of the 56 auto-grooming records, 1,145 of the 1,290 (88.8%) grooming records, all of the 50 nursing records and 16 of the 171 (9.4%) social interaction records took place in the sitting position. That is, 18,207 of the 23,687 records (76.9%) collected pertained to animals in a sitting position. Sitting, therefore, was the predominant posture and appeared similar to those described by Ripley (1970) and

Fleagle (1978) for Asian colobines.

In comparing the budgets of different colobus populations the most obvious pattern is the similarity in feeding/resting ratios shared by the three populations inhabiting the more seasonal sites (Tana River, Gombe, Abuko), while the population in the less seasonal Kibale Forest, exhibits the opposite pattern (Table 19). The three populations in the more seasonal sites spent the majority of their time resting while the rain forest population in the Kibale Forest spent most of its time actively engaged in feeding. All the populations, throughout the year, regardless of fluctuations in temperature, rainfall, humidity and resource availability, maintained similar feeding/resting ratios.

Across populations very little time is recorded as being spent in auto-grooming, nursing or interacting. The most common social interactions are grooming and play which vary from site to site but do not display any large differences in terms of time spent in such activities.

### Feeding

In Abuko feeding ranged from 13.8% of the budget in August to 34.7% in January with a mean of 21.3%. Marsh showed a positive correlation between the amount of leaf buds in the diet and time spent feeding (1981b). While differences in activity percentages varied from month to

month, as did dietary make-up (Table 14), no correlation was apparent at Abuko between percentage of leaf parts in the diet and time spent feeding ( $r_s = 0.04$ , d.f.=12,  $p = >0.05$ ). Also, there was no correlation between amount of fruit in the diet and amount of time spent feeding ( $r_s = 0.20$ , d.f.=12,  $p = >0.05$ ).

### Resting

Resting in a sitting position was the predominant positional behavior during every month of the year. When the data are pooled, it is also the predominant activity during every hour of the day. On 6 occasions when I visited the troop at night I found all the members to be sitting still, apparently asleep, not moving, feeding, or lying on branches.

Resting postures were probably influenced by a number of factors such as substrate configuration, climatic conditions, individual positional preferences and possibly even subtle psychological factors. During resting periods an animal could either sit or lie. Lying only occurred on horizontal or slightly diagonal branches with a minimum estimated diameter of 6 cm. Lying did not occur during rain or wind storms, early morning chilly periods, in the sun during the heat of the day, intertroop conflicts (except twice by juvenile females who were in the process of transferring troops), python presence or during the first 4

months of the study (when presumably my presence influenced their choice of posture). This would suggest that lying occurred under certain climatic conditions in relaxed situations and not in situations where an animal felt threatened or had to remain alert.

Certain individuals chose a lying position far more than others (Table 20) and each one of these individuals probably had its own specific reason.

Punk's lying (Figure 7) may have been part of her general lethargy, which in turn may have been due to the fact that she was orphaned when she was only 9 months old. Solid and Droopy either preferred lying because they found it more comfortable, or because their status as the two top-ranking females allowed them to relax more frequently than any of the other females. During the mid-afternoon resting period both of them, as soon as they found a suitable site, flopped down and appeared to go to sleep. Simp may have been imitating her mother's behavior. If Solid was lying, Simp would either lie next to or on top of her. Round, a large subadult female, who transferred into Focal troop half-way through the scan-sample period, frequently had a full sexual swelling; she may have chosen to lie because it was more comfortable to do so with a swelling, or perhaps it was a good way to advertise her receptivity, because the swelling could be seen more clearly and for a further distance in the lying position. In fact, Round had a full

sexual swelling during 77% of her lying records.

An interesting use of lying was made by mothers weaning their young. They frequently lay down on a branch as soon as their weanling approached, thereby effectively hiding their nipples and making it difficult for the weanling to nurse. This may have been related to Pelf's high rate of lying. She had adopted her sister Punk and they frequently rested together. On 9 occasions they fought over Pelf's barely visible nipples. By assuming a reclining position, Pelf was able to keep her nipples out of Punk's reach.

### Moving

Moving ranged from 5.5% of the budget in February to 16.5% in December with a mean of 12.5% (Table 10). There was typically an early morning progression occurring sometime between awakening and noon. The exact time of the morning progression depended on whether the colobus had spent the night in, or near, a major food source. A later afternoon progression occurred after 1600h, and usually between 1700 and 1900h; this took the colobus either to their last major food source or to their sleeping tree. Often their last major food source was the sleeping tree, in which case this tree was generally the first major food source the next morning. This pattern had some interesting variations. For example, on three separate occasions in three separate areas of woodland savanna during two

different dry seasons, the entire Focal troop spent an entire day and two nights in an area less than 2,500 m<sup>2</sup>. On two of these occasions it appeared that the temperature was extremely high (temperature data was not recorded on any of these days).

### Play

During the five-day scan-sample, 748 play bouts involving 1,534 players were recorded. Adults were not seen playing during this scan-sample period. Play accounted for 6.5% of the annual budget collected on all troop members or 23.2% of the budget collected on only the colobus below the age of 13 months (Table 10).

Play was both a solitary and a social event. Solitary play accounted for 30% of the 748 play bouts. Play involving two participants accounted for 37% of the bouts while play involving three or more participants (Figure 8) accounted for 32% of the bouts.

Solitary play was basically an infant activity. The only non-infant to engage in solitary, non-object play was the orphaned female, Punk.

Play took place at all heights from the ground to the third storey. Most occurred in the trees, however, with only 1.4% of it taking place on the ground. When play did occur on the ground it either took place in the riverine zone where there was no ground cover or on the savanna where

the grass was compacted or non-existent so that ground visibility was excellent. This was probably quite important considering that play invitations involved the inviter closing its eyes and wobbling its head around for up to 10 seconds and virtually rendering itself unable to see any potential danger in the shape of predators.

### Social Grooming

Social grooming, the major friendly interaction, made up 5.4% of the annual budget on all troop members but only 1.5% of the budget on the infants (Table 10).

The areas most frequently groomed (N=493 observations where parts of the body were noted) were the inaccessible ones, such as the back (28%), various parts of the head (21%) and the rump (19%).

### Social Interactions

During scan-samples, 171 social interactions (excluding play and social grooming) were observed. This accounted for 0.7% of the total activity budget for all members and 0.4% of the budget for those under 13 months of age (Table 10). The most frequently observed social interactions involved those behaviors related to reproduction - particularly the female courtship display (27.5% of all interactions: Table 21).

### Auto-Grooming

The colobus spent very little time auto-grooming. Of the total activity observations collected for one year only 0.2% were auto-grooming bouts (Table 10).

The areas most frequently auto-groomed were the accessible ones, various parts of the legs (85%) and arms (8%). Only one individual was observed attempting to groom a clearly inaccessible area. A ten-month-old tried to groom its own rump. The infant kept turning around in circles, chasing its tail, trying to see what its hands were doing.

### Nursing

Nursing was an infrequently observed, but probably a frequently occurring event. During scan-samples 50 nursing bouts were observed. This accounted for 0.2% of the annual budget on all troop members or 0.6% (N=30) of the budget collected on only those members below 13 months of age.

The nursing data should be viewed with caution because it was so difficult to observe. This was due to the fact that the infant's head and face was often hidden by the mother's body, vegetation, and so forth. Unless I actually saw the female's nipple inside the infant's or juvenile's mouth I did not record the behavior as nursing.



### Sex Differences in Activity Patterns

Because of differences in reproductive patterns faced by each sex, I expected to find sexual differences in activity patterns.

All individuals in Abuko, regardless of sex, spent significantly more time resting than feeding (Table 22: binomial test:  $z = 3.9$ ; two-tailed,  $p = <0.01$ ). After pooling the feeding and resting data on the Abuko colobus, the differences among individuals within age-sex classes are greater than the differences among classes (chi square = 30.1; d.f.=17;  $p = 0.05$ ). Furthermore, females at the same reproductive stage did not have particularly similar activity budgets. For example, Inca, Nene, and Metoo all had dependent infants born within one nine-day period, Solid and Button had infants born on the same day, Droopy and Yundum had juveniles of the same age and yet a close look at Table 22 shows that these females do not have comparable budgets.

There was the possibility that mastication rates varied and that an in-depth investigation would more accurately determine differences in energy in-take. As can be seen from the limited available data in Table 23, males ate more quickly than females (likelihood ratio test: d.f. = 1;  $p = 0.025$ ). Although the sample was small, limited to unripe mango fruit only, and was significant at the 0.025 level only, it suggests that feeding rates may play a part

in determining energy intake and activity patterns between sexes. Throughout the study, regardless of food item, however, it was clear that red colobus had a much faster mastication rate than humans or green monkeys.

There were sex differences in the frequency of play behavior. Male infants (mean = 57.5 bouts; range = 30-81 bouts) took part in more play bouts than female infants (mean = 43.6 bouts; range = 34-53 bouts). The difference, however, was not significant (t test:  $t = 0.94$ ; d.f. = 5;  $p = 0.2$  one-tailed and 0.4 two-tailed).

With the three juveniles who were present in the troop during scan-samples, the case was not as clear-cut. The female, Dunk took part in 9.9% of all observed play bouts ( $N = 743$ ) while the orphaned female Punk took part in 3.4% and the male, Yunk took part in 4.3%. The females were involved in both the most and the least number of play bouts. I assumed that the difference between being orphaned and having a 'normal' infancy and juvenilehood created the differences in play frequencies between the two juvenile females. Other evidence collected during the course of this study on these juveniles suggested that the orphaned female Punk did not display 'normal' behaviors. She was frequently more lethargic (note the amount of time she spent in the lying position: Table 20), stopped from playing by her adoptive sister (11 times) and a 'wallflower' (52 times she sat on the edge of a play session without taking part

although players actually bumped into her - a behavior not displayed by any other young colobus).

None of the subadult males or older juvenile males (above the age of 20 months) were ever seen playing while all the subadult and older juvenile females played at least once a day for every day they were observed in the troop.

Outside the scan-samples, 18 adults were seen playing. Twelve of these adults were mothers of infant sons, one was the mother of an infant daughter, one was the top-ranking male, Captain Crook, two were females with no dependent young and one was a mother in PWD troop playing with her unsexed infant. This suggests that adults females were more likely to play than adult males and that mothers of sons are the most likely players.

Females groomed at a significantly younger age (Nimp = 5.75 months; Simp = 6 months; Nimp = 7 months) than males (Imp = 7.75 months; Mimp = 8 months; Wimp = 10 months; Bimp = 10.5 months) (Two-sample t test:  $t = 2.99$ ; d.f. = 5;  $p = 0.025$  one-tailed and  $p = 0.05$  two-tailed), There is always the possibility that this is due to observational bias in that females groomed more frequently (mean = 2.3 bouts per female infant compared to 1.25 bouts per male infant based on data collected during scan-samples). It would therefore be easier to see females grooming at a younger age.

On rare occasions (6 of the 624 grooming bouts recorded during scan-samples) two monkeys groomed a third monkey

simultaneously. This 'double-grooming' was also seen on 101 occasions during the study outside the scan-sample period and young and adult males received far more double-grooming than females (Table 24). This suggests that a male who is being groomed is more attractive than a female groomee. Certainly, males received far more grooming than females although females groomed more than males (Tables 25 and 26).

All self-grooming bouts involving identified individuals in Focal troop on all observation days between November 1978 and mid-January 1980 inclusive are given in Table 27. There were obvious age-sex differences in the frequency of self-grooming. Adult males self-groomed far more than any other class and infants self-groomed far less. Colobus were not seen self-grooming before their 10th month and only rarely before their 16th month. The one exception was the female orphan, Punk. She self-groomed far more than any other individual with the exception of the adult males. Although without a mother she lacked a consistent grooming partner, she still received more grooming than the other two juveniles her age (Table 25). Her high frequency of self-grooming may not be related to a high ectoparasite rate but to some subtle psychological factor.

#### Population Differences in Activity Budgets

Table 19 lists the activity budgets for the colobus populations inhabiting the various study sites. One of the

obvious differences is that the Kibale Forest population spends the majority of its time feeding, while the other populations spend most of their time resting.

Within populations both the Gombe (Clutton-Brock, 1974) and the Tana River (Marsh 1981b) red colobus females spent more time feeding and less time resting than the males. Clutton-Brock suggested that this could be due to the fact that males appeared to have a faster rate of food intake than females.

Grooming patterns at all sites are similar. That is, females (of all ages) groomed more than males, yet males (of all ages) received more grooming.

The amount of time spent social grooming, playing and socially interacting varied from site to site and obviously depended on a number of variables (e.g. socioeconomic sex ratio, presence of mating/birth season, amount of sexual dimorphism in the subspecies, behavior of adolescent males and females, relationships between females and between males). Auto-grooming and social interactions (excluding social grooming and play) were infrequent in all populations and this was probably not related to environmental or specific life history factors; rather, it may be a common red colobus trait. Nursing was infrequently observed but this is probably an observational problem and not a common trait.

### Discussion of Sex Differences

Although it has been estimated that a female primate's energy requirements increase by 25% during pregnancy and 50% during lactation (Portman, 1970), the data collected and analyzed on the Abuko females did not suggest that females compensate for this by increasing their time spent feeding (Table 22). I am not suggesting that the energy requirements of Abuko females do not vary with reproductive cycles. I am suggesting, however, that it may be necessary to take into account the age, size, maternal experience and social status of the female when trying to determine if and how the energy requirements vary within a reproductive cycle. For example, some of the females were considered quite old, while others were much younger. In fact, there could have been at least a 12-year difference between Yundum on the one hand and Head, Button and Nene on the other. There was also a tremendous variation in size. Nene was the largest monkey in the troop and probably larger than all the PWD troop members as well. Wild was extremely thin, even when she was pregnant. Solid was very small, smaller than her three-year-old daughter. It would seem that some, if not all of these factors would influence the energy requirements. It is also possible, of course, that some factors (i.e. thinness, low social status) are the result of inadequate energy intake.

In Abuko infant males play more frequently than females

and this is similar to most Old World monkeys (see review in Mitchell, 1977). Amongst juveniles and subadults, however, the opposite occurs and this may be due to opportunities that result from specific transfer patterns. Females either remain within the natal troop (rarely) or transfer immediately to another troop where they are surrounded by age mates and infants and have frequent opportunities to play. Most males are expelled (see following chapter) from their natal troop during this stage in their development and lead solitary lives with little opportunity to play. The one male (Yunk) who remained with his natal troop did so as the sole member of his peer group. Therefore, all his play mates were either female or much younger and not as rough in their play behavior. The limited play I observed between infants and this large juvenile male was extremely rough and always ended with one of the infants screaming and the infant's mother, other adult females and adult males threatening and chasing off the offending juvenile male. Since the juvenile/subadult male who is allowed to remain within or return to the confines of the troop must form bonds with the resident adults, particularly with the females, it would seem best not to antagonize them by upsetting their offspring. Therefore, the male should limit his play - since it can only result in being threatened and chased by older troop mates.

### Discussion of Population Differences

Environmental conditions may impose limitations on the amount of time an animal can be active. This is particularly relevant when looking at feeding/resting ratios across populations.

Marsh (1978) felt that the difference in the activity budgets between the Kibale Forest and the Tana River populations was related to dietary diversity. The Tana River colobus, with its more monotonous diet, had more detoxification problems, thereby permitting only smaller quantities to be eaten, leaving more time for rest. While this may be a viable hypothesis for explaining the Kibale Forest-Tana River contrasts, it does not work for either Gombe National Park or Abuko. Both the Gombe and the Abuko populations have highly diverse diets and spend the majority of their time resting. In fact, these two populations have the most diverse diets and spend the most time resting and the least time feeding.

An alternative hypothesis, suggested by Oates (1977) to explain the differences in activity budgets among guereza populations, may help explain the differences between red colobus populations. Colobus subjected to higher environmental temperatures function on a different activity budget from colobus subjected to Kibale-like situations where the environment is consistently wetter and cooler. The climatic hypothesis seems to be the most plausible one



to explain the similarities at the seasonal sites and their dissimilarity with the Kibale activity budget (Table 19). Troop size and composition, population density, the 'quality' of the home range and dietary composition and diversity are not at all similar at the 3 seasonal sites (Tables 6, 7, and 18). Only the gross climatic factors appear to be similar at these sites and quite different from those at Kibale. Data collected on geladas also clearly show that populations living in cooler habitats spent more time feeding and less time resting because their metabolic costs of maintaining body temperature increased (Dunbar, 1984). This explanation could also hold true for the different red colobus populations.

Across populations, social time (social interactions + play + social grooming) is limited, suggesting that (1) they do all the socializing they can do, or (2) resting in physical contact with other animals may serve the same function as interacting and should actually be considered socializing and not a maintenance activity (see Chapter 8).

### Summary

1. Of the total activity records collected during five full days each month for one year (February 1979 through mid-January 1980) on all visible members of Focal troop, 52.4% were resting, 21.3% were feeding, 12.5% were moving, 6.5% were playing, 5.4% were grooming, 0.2% were auto-grooming and 0.2% were nursing (N = 23,687 records).

2. Resting was the most common activity for all age-sex classes every month of the year. Feeding was the second most common activity.

3. There were age-sex differences in the frequencies of some behaviors and individual differences in others. With feeding and resting the differences between individuals was greater than the differences between classes. This may have been due to the fact that the factors responsible for determining individual activity budgets were not fully investigated (e.g. size, weight, social status, health, age, reproductive status and history). With auto-grooming and play behavior age-sex differences were obvious. Adult males were the most frequent auto-groomers. Females were the major social groomers while the males were the main recipients of social grooming. Females played more than males as juveniles, subadults and adults, while males played more when they were infants.

4. The colobus at Tana River, Gombe and Abuko all have feeding/resting ratios similar to each other and quite dissimilar from that of the Kibale colobus. A possible explanation is that the colobus at the seasonal sites spend less time feeding, because they need less energy to maintain body temperatures in a warm climate, while the Kibale colobus spend more time, because, in their consistently cooler and wetter climate, they need more energy to maintain body temperature. Across habitats, among the red colobus, social time is limited.

## Chapter 7. DEMOGRAPHY

### Introduction

A troop's size and composition can be influenced by births, deaths, various reproductive parameters and migration patterns. These life-history phenomena influence a troop member's social behavior by determining the potential interactees that it has available. All these phenomena are displayed in Figure 9.

A description of basic demographic information on births, deaths and reproductive parameters is given below. Migration patterns are discussed in detail in the following chapter (8).

### Births: Sex Ratios

During the course of this study 28 infants were born into Focal troop. No sex bias was evident: 10 infants were females, 9 were males and 9 were of undetermined sex (Table 28). Clutton-Brock and Albon (1982) have pointed out, however, that the variance in sex ratios at birth is often very fine; consequently, large samples are needed to demonstrate statistically the presence of any differences. Nonetheless, it is clear that in Abuko the ratio of adult males to adult females in each troop is far from unity and that the great predominance of adult females (Table 5) probably cannot be explained by an unequal birth ratio.

### Birth: Seasonality

The distribution of colobus births at both Kibale Forest (Struhsaker, 1975) and the seasonal Tana River site (Marsh, 1978) do not show any strict birth seasonality. Birth peaks, however, are indicated for the red colobus in Kibale (Struhsaker and Leland, 1987). In the highly seasonal environment of Fathala, Gatinot (1975) recorded births from mid-August to December, while I recorded Focal troop births over a 5-year period from October 31st until July 14th (Table 28: births varied significantly throughout the year; chi square = 17.89, d.f. = 5,  $p = 0.005$ ). Within the Abuko dry season birth peak, there was an even more pronounced synchrony in the time of births within a particular troop. That is, within the dry season, different Abuko troops had their infants at different times. For example, Zoo troop females had 8 infants between December 1980 and February 1981, while Focal troop females gave birth to six infants from the 6th of April until the 11th of May, 1981.

### Deaths: Sex Ratios

Ten individuals are known to have died and a further 13 disappeared and are presumed to have died during this study (Table 29). The infants born during this study (28 infants) suffered a mortality rate of 21.4% (based on both known and presumed deaths) during the first five months of life. The

mortality rate drops to zero in the several years thereafter. The mortality rate rises again for males during their 3rd and 4th year, while it does not do so for females. For example, of the five females and six males who were born in 1978 and 1979, all of the females survived well into adulthood, while three of the 6 males died when they were 41 - 47 months old. These data agree with data collected elsewhere in Abuko. Of the 13 non-Focal troop deaths, the majority were young males (Table 30).

#### Deaths: Mortality Factors

Little information is available on the causes of death in red colobus populations. Struhsaker (1975), however, postulated that falls, disease and predation were the three main factors responsible for death in the Kibale Forest population. Falling, infanticide and disease are given as proximate causes of death for the Tana River population by Marsh (1978). The determinants of mortality in the Abuko population are discussed below.

#### Falls

Struhsaker (1975) suggested that falling was responsible for the majority of the deaths in the newly independent colobus while Marsh (1978) stated that falling was also a major proximate cause of mortality in infants and juveniles in the Tana River population.

In Abuko, 31 falls were observed from mid-August 1979

through April 1982 and in only two cases did the individual catch itself before reaching the ground. In spite of this, none of the falls were fatal or even serious. I never saw any wounds or dislocations occur as a result of a fall. This may have been due to the fact that the height from which they fell was never more than 12 meters (approximately) and usually less than 8 meters.

Furthermore, they would have landed on either sand if they fell in the savanna zones or leaf litter if they fell in the gallery forest. There were no rocks in Abuko. Falling into one of the crocodile-inhabited ponds, however, would have probably been fatal.

Below the age of three months, a fallen colobus was retrieved by its mother. Older than three months, they climbed back on their own. Falling was most common during infancy and juvenilehood. Twenty-four of the 31 individuals who were seen falling were between the ages of 1.5 - 26 months of age. Once a colobus matured and perfected its locomotor techniques, falling was less common. There did not appear to be any sexual differences. Males fell just as frequently as females. There was, however, one interesting individual difference. One of the young males, Bimp, fell five times more than any of his age mates and was coincidentally subjectively categorized as 'rash' and 'reckless'.

### Predation

In Abuko there were no wild mammalian carnivores large enough to prey on the colobus and probably very few avian predators. There were a number of reptiles, however, which did prey on the colobus.

Although the crocodile population is high (I counted 19 separate crocodiles ranging in size from 1.5 - 5 meters in one pool in February 1985 during a drought), I do not believe that the crocodiles are very important as red colobus predators. When the crocodiles kill an animal as large as a colobus, the body is visible for at least five days and even as long as nine days. Everyday that I was in the reserve I checked all the crocodile inhabited pools once and sometimes twice, looking for kills. Because of the length of time it takes for a crocodile to finish a kill and the constant surveyance of the pools, I think it likely that if there had been more cases of predation during this period I would have seen them or been told about them by the park guards.

During the study period two young males were eaten by Nile crocodiles. Four-year old Bimp was eaten in December 1982 and another male (not a member of Focal troop or PWD - but in an area used only by these two troops - thus probably a potential intruder male) was eaten in July 1983. In neither instance was the actual attack observed.

The colobus did not drink from this pool or feed along



its banks. In order to get from one side to the other, however, they frequently moved along a narrow land bridge where well camouflaged crocodiles frequently lay in the herbs and grasses. It is quite possible that a crocodile could have surprised a colobus and knocked it into the water as it attempted to cross this narrow land bridge. When moving in this area they were normally quite clumsy and not very cautious. Because it was a 'disputed' area between two troops, the colobus appeared to be more concerned with watching for other colobus than looking out for the crocodiles hidden in the grass.

Beside feeding on these two young male colobus, the crocodiles also fed on an adult male green monkey, a marsh mongoose, four rock pythons, one domestic dog (which must have entered the reserve through a hole in the fence) and an innumerable amount of birds, fish and frogs. In the ten years previous to this study, the park guards remember only one case of crocodiles eating red colobus (A. Jallow and A. Jatta, pers. comm.).

Rock pythons killed at least two red colobus during this study period. In April 1978 I found the body of an old adult female inside the dead body of a 3.6 meter long rock python. In August 1981 the conservation director collected a 4-meter-long python, placed it in a burlap bag and deposited it outside the reserve in an agricultural field. When the python was taken out of the bag it was found that

it had vomited up an adult female (C. Ball, pers. comm.).

Besides preying on red colobus, the rock pythons also preyed on newborn harnessed antelope. During this study pythons frequently slid into the enclosures in the zoo and killed caged animals (i.e. patas monkeys, harnessed antelope, Mauritanian gazelles). In the two years preceding this study, pythons were twice observed preying on red colobus (A. Jallow and A. Jatta, pers. comm.).

Although only a few cases of red colobus predation were seen, I believe that pythons may be of particular importance in the population dynamics of the Abuko red colobus. Firstly, pythons were very abundant in the reserve. From April 1978 through March 1981 35 pythons (size range 2 - 7.3+ meters in length) were observed in Focal troop's home range. Secondly, the colobus appeared clumsy and not cautious on the ground, the pythons major habitat. The colobus did not often notice pythons until either the green monkeys gave their snake chatter call or I unintentionally gave a startled reaction or call. Only then did the colobus react. Twice I found pythons only one meter away from colobus. The colobus did not seem to notice the python while I found it quite noticeable. In general, the colobus left me with the impression that they were somehow less aware of their immediate surroundings when they were on or near the ground. On three occasions I had unhabituated and healthy looking adult males run right into me as I walked on

the savanna. Twice the old and probably ailing female Pug Ugly, actually touched my feet before seeing me and once the old female Noam bumped into me.

Snakebite accounted for two deaths in Focal troop. Noam, an old adult female who had just recently transferred into Focal troop was found early one morning in February 1981 just after having died. She was immediately examined by a visiting veterinarian, Dr. L. Mohl, who performed an autopsy. Because of puncture marks to her jugular vein, internal haemorrhaging and the nonclotting of blood, Dr. Mohl diagnosed snakebite. Early in the morning in April 1981 I found the adult female Round lying dead on the savanna. Her seven-day-old infant was missing, she had puncture marks to her jugular and internal haemorrhaging. Because of the similarities between Round's condition and Noam's condition, I assumed that Round also died of snakebite. In fact it was possible that the seven-day-old infant had been eaten by the snake. The only other case of snakebite was an adult male green monkey found in March 1981 lying on the savanna with puncture marks in his femoral artery and internal haemorrhaging.

Zoo troop came into daily contact with caged hyaenas and lions. On one occasion an adult male colobus ran across the ground in the hyaena cage, was caught, killed and eaten by the captive hyaenas. The guards informed me that the colobus was caught because 'he was clumsy and was not

watching where he was going' (A. Jatta, pers. comm.).

The colobus in Abuko are probably free of arboreal predators. All the known predators are terrestrial and it is on the ground where the colobus are the most vulnerable and also the least careful. Reptilian predation accounts for all observed predatory interactions in Focal troop. All the victims were full adults and there did not appear to be any sexual selection taking place; two males and three females were selected as prey with an unsexed seven-day-old infant as a probable victim. In conclusion, predation by reptiles was probably a major proximate cause of mortality in adults in Abuko. Of the 10 Focal troop members who died and the 13 who disappeared and were presumed dead, four were definitely killed by reptiles (this includes the seven-day-old infant, but does not include the intruder male killed by crocodiles). This is 40% of all known deaths. Furthermore, some of the 13 colobus that disappeared and were presumed dead could well have been python victims since this form of predation leaves no evidence unless the actual predation is witnessed or the python dies/is caught with stomach contents that can be identified.

#### Infanticide

During this study six infants below the age of six months died or disappeared and were presumed dead. Two of these infants were almost surely victims of infanticide. Both of them were observed immediately after having died and

they both had canine puncture wounds which were most likely caused by other colobus. In neither case was the sex of the infant ascertained. A third infant may have been a victim because it disappeared at the time of an intruder males death (Bully) (see Chapter 8, section on immigrating males). The mother of this third infant was later seen to join PWD troop. Two more infants simply disappeared with their mothers and the cause of their disappearance /presumed death is unknown. Of the 28 infants born in Focal troop, 6 of them died before they were 0.5 years old. Of these 6, two and possibly even three were victims of infanticide. All three of these deaths occurred during the breeding season so that the mother could have gone straight into receptivity. In only one case, however is it known that the mother immediately cycled and conceived. In the other two cases, the mother actually left Focal troop and transferred into PWD. This suggests that the infanticide not only eliminated the infant, it also eliminated the mother from the immediate breeding pool of females. Assuming that the main function of infanticide is to mate with females, it did not seem to be a reproductive strategy of value to most males.

#### Intraspecific Fighting

Fighting accounted for at least three and probably four deaths in Abuko (pages 203-209). No Focal troop member died in this way. This form of death only occurred in males. None of the known females died from fighting and none of the

female cadavers showed any signs of fighting.

#### Miscellaneous Factors

One of the deaths was due to electrocution. Imp, a 41-month-old male was found at the base of high tension wire. His hair was singed and for the most part had fallen out while his skin was badly burned. He probably fell or jumped onto the wire and was electrocuted. None of the other animals were ever seen to go near these wires, although they actually went through a number of their feeding trees.

#### Summary

The main causes of death amongst Focal troop members were presumed infanticide, old age and predation (Table 29). These factors were clearly age and sex specific with females living longer and dying of old age (old age is discussed in detail in Appendix D) while males appeared to take more risks and died at a younger age. One way to characterize this sexual difference is to say that males, especially young males, are relatively 'risk-prone' (Daly and Wilson, 1983). In fact, the entire life history strategy of males is probably a higher-risk, higher stakes adventure than that of females (Alexander, 1979).

## Female Reproductive Processes

### The Menstrual Cycle

Ovulation in the Abuko red colobus is heralded by the occurrence of a sexual swelling. The age at which females first cycled is known in 4 cases; Simp was 30.75 months old, Nimp was 32.5 months old, Dunk was 35 and Punk was 38.75. The average age was 34.25 months of age. The onset of menarche may have been related to psychological state or status. The orphaned young female Punk, who received more aggression from adult females than the other resident young females (Table 31), was the oldest when she started cycling.

The length of time between the onset of menarche and first births on average was 14.9 months ( $N = 10$  females, range = 9-27 months; median = 15.5 months of age). Subtracting 5.25 months (estimated mean gestation length: Starin, 1988) from each of the 10 cases results in an average adolescent pre-fertility period of 11.7 months (range = 3.75 - 21.75 months).

The age at which females first gave birth is known in four cases: Nimp was 42, Dunk was 48, Simp was 49 and Punk was 61 months old. Furthermore, ages of six more females were known to be definitely more than 33 months and less than 60 months.

The sexual cycle was divisible into four separate cycle states, according to the appearance of the female's perineal region. Average duration for each cycle state were

determined by taking the means of those states recorded for all cycling, nonpregnant females, whether or not the entire cycle was observed (although the entire state was observed). They were INFLATING, 8.66 (range = 6 - 11; median = 9; N = 15); FULLY SWOLLEN, 5.39 (range = 4 - 8; median = 5; N = 23); DEFLATING, 7.8 (range = 6 - 10; median = 7; N = 5); FLAT, 6.5 (range = 4 - 9; median = 6.5; N = 8). Menstrual bleeding (blood seen on the sexual skin obviously coming from the vagina and not from an external cut) was observed 9 times for a period ranging from 1 - 2 days (mean = 1.1; median = 1).

The cycle length was determined by counting the number of days from first swelling till the first day of the next swelling. The number of days between normal, nonpregnant, menstruation cycles (based on 23 cycles) ranged between 23 and 33 days with the mean being 27.7 days and the median 27 days. This is close to the average 28 day cycle of the Mt. Abu langurs (Hrdy, 1977) and falls within the 25 - 35 day range of most apes and Old World monkeys (Hrdy and Whitten, 1986).

#### Interbirth Interval

Data from Tana River are not strictly comparable since no individual female gave birth to more than one individual during the study (Marsh, 1978). It was clear, however, that the females at Tana River are not annual breeders. At



Kibale the mean interbirth interval is approximately 24 - 27 months (Struhsaker and Leland, 1987).

The mean interval between successive births, when the previous infant was still alive, for four females in Abuko was 29.4 months (range = 27.75 - 32 months). If an infant died the birth interval can be much less. When Metoo's infant died (suspected infanticide) Metoo began cycling 19 days later and gave birth to a son 193 days later (approximately 11 month interval as compared to 29.4 months). The death of an infant, however, did not automatically reduce the interbirth interval. When Tara's 8-week-old infant died (also suspected infanticide) during the breeding season, she began cycling within two weeks, but still had not given birth 19 months later.

At all three sites, therefore, it appears that the red colobus female displays a long birth interval - a trait which may in fact be a typical colobine characteristic (Sugiyama, 1957; Hrdy, 1977).

The time it takes a female to resume her sexual cycle after giving birth is a major determinant of the interbirth interval. In Abuko there was very little variation in the length of postpartum amenorrhea (mean = 17.6 months; median = 18 months; range = 14-19 months; N = 9 females). There was, however, much variation in the amount of time a female cycled before giving birth again. Four females conceived during the end of their first breeding season experienced

after their infants reached 12 months of age. One female cycled through two breeding seasons before she conceived while three other females cycled through at least three, and possibly more seasons without conceiving a second time. In some of these cases it is possible, of course, that conception took place but was then followed by an abortion.

The causes of this variation are probably varied. The age of the female may play some role in determining the length of the interbirth interval. For example, all three females (Wild, Droopy, Solid), who experienced cycling through three or more breeding seasons without conceiving, were judged to be far older than the four females (Inca, Garuda, Nene, Button) who conceived during their first or second breeding season.

A final point about interbirth intervals is that the size of the sample is not big enough to say if the sex of the present infant significantly affects its mother's subsequent reproductive history in terms of birth intervals as has been found to be the case with captive rhesus monkeys (Simpson et al., 1981). One of the females who conceived during her first breeding season had a daughter while three of the females had sons. The three females who experienced three or more breeding seasons without conceiving had previously had two daughters and one son respectively. There was a tendency, however, for mothers of sons to conceive sooner than mothers of daughters.

### Male Reproductive Processes

At approximately 28 months a young male's testes become obvious and he immediately begins to approach and initiate matings successfully with sexually mature fully-swollen females ( $N = 3$ ; range = 26-30 months). Yunk began to approach females when he was 26 months old and for the first few months his mounts were disoriented; he either mounted the female's head, her side or too high on her back. When he was 33 months old he was mating correctly, and in fact, was probably responsible for fathering most, if not all, of the infants conceived during the 1980 breeding season.

Bimp, Imp and Wimp began to approach and initiate correct matings with fully swollen females when they were 29, 30 and 34 months old respectively. Bimp was probably responsible for the infants conceived during the 1981 breeding season. Thus, the Abuko male appears to reach sexual maturity before his 3rd birthday which is younger than the Kibale male who reaches maturity at 38-46 months (Struhsaker and Leland, 1987). The differences in maturation rates between the two sexes in Abuko is less than in most cercopithecines and is probably related to the lack of size dimorphism (Willner, 1989). Furthermore, unlike most cercopithecines (Melnick and Pearl, 1987) reproductive maturity (defined here as age at which females conceive and males impregnate) occurs in Abuko at a younger age amongst males than amongst females.

### Seasonality

The number of copulations with fully-swollen females (Figure 10), courtship displays (Table 32) and the number of females who had sexual swellings (Figure 11) varied significantly throughout the year. There was a positive correlation between these three factors for each month (Kendall's Concordance test:  $W = 45.6$ ; d.f. = 11;  $p = 0.001$ ).

Virtually no matings occurred during the period of lowest rainfall (Table 2) and lowest daily and nightly temperatures (Figure 4). It was also during this period that leaf parts comprised a major part of the diet (Table 14).

In general, the timing of the majority of conceptions shows some association with high levels of precipitation, a rise in daily and nightly temperatures and a diet rich in fruit and flower parts. Furthermore, during this same period there is a rise in humidity and an increasing day length (Edberg, 1982). Any or all of these factors could be critical in determining the onset of the general breeding season. It was not, however, possible to evaluate them during this study.

### Summary

1. During the course of this study 28 infants were born.
2. The distribution of births shows a strict birth seasonality.
3. Ten individuals are known to have died and a further 13 disappeared and are presumed to have died during this study. The mortality rate is highest for young males.
4. The main causes of death amongst Focal troop members were presumed infanticide, old age and predation.
5. The menstrual cycle is similar to that of most apes and Old World monkeys lasting on average 27.7 days. Females begin to cycle at 34 months of age, give birth at 50 months of age, have an interbirth interval of 29.4 months and a gestation period of 5.1 - 5.3 months with a postpartum amenorrhea of 17.6 months.
6. Males begin to approach and initiate matings successfully with fully-swollen females when they are approximately 28 months old. This period corresponds with the descent of their testes.
7. The differences in maturation rates between the two sexes is less than in most cercopithecines. Furthermore, males appear to reach sexual maturity before females which is very unusual for primates.

8. A breeding season occurred during the period of highest rainfall, temperatures and humidity, and increasing day length. It also corresponds with the period when the diet was high in fruit and flower parts.

## Chapter 8. INTRATROOP SOCIAL BEHAVIOR

### Introduction

The main focus in this chapter is the social milieu of Focal troop, addressing the basic question of how a female's social life differs from that of a male's social life. Throughout, it is assumed that males and females in different reproductive states all have different social needs and these varying needs force individuals to act differently. Aggressive and cooperative patterns are described and sex differences are discussed. How transfer patterns influence sex differences in these two gross behavioral patterns are also examined. This chapter is divided into two separate sections, one for each of the above-mentioned behaviors. The data used in this chapter were taken on an ad lib basis throughout the study. Since the majority of the comparisons in this chapter are made with data collected at Kibale Forest, basic social information will be summarized from this site.

At the Kibale Forest a distinct linear dominance hierarchy, based on priority of access, exists amongst males (Struhsaker and Leland, 1979; 1987), while among females aggression is usually infrequent and dominance hierarchies are weakly developed (Struhsaker, 1975).

The majority of aggression observed at Kibale Forest is between males and generally involves harassment during copulation (Struhsaker and Leland, 1979). Usually copulations are initiated by males approaching females. A subadult male killed one and perhaps two other infants in his natal group; this subadult, however, is thought to have been sired outside his natal group. In none of these attacks did females form counteractive coalitions (Struhsaker and Leland, 1985).

Based on their proportional representation in the group, adult females were groomed less than expected and groomed one another less than expected. Adult males, though not common groomers, groomed one another more and adult females less than expected (Struhsaker and Leland, 1979; 1986). Adult males remained spatially close to one another, formed a cohesive and coordinated subgroup when fighting other groups and gave a stylized form of presentation among themselves which never involved other age-sex classes (Struhsaker and Leland, 1979).



## AGONISTIC BEHAVIOR

### Introduction

The main aim in this section is to examine the relationship between sex and aggression. The type, frequency and quality of aggressive acts are examined in terms of female-male differences. More specifically, what are the contexts in which aggression is most likely to occur and does this differ for females and males? Which sex is more aggressive and is there a qualitative difference in the form of the aggression? Does one sex intervene in disputes more frequently? Does one sex form alliances more than the other? Is aggression basically an intrasexual interaction? What is the relationship between transfer and aggression?

### Descriptions of Aggressive Behaviors and Sex Differences

Actions considered as aggressive are staring, facial threats, shaking and/or jumping on branches, lunging, chasing and supplanting. Tug-of-war contests with branches and leaping-about displays with and without branches were seen on a number of occasions and are also considered as aggressive non-contact actions. Non-contact aggressive behaviors may be followed by physical contact in the form of hitting, pulling hair and/or skin, grappling, mouthing (presumably nipping with teeth), holding down and biting.

Some of these forms of aggression appeared to be sex-specific. When using facial threats, for example, females

stared at their victim, jerked their head forwards, opened their mouths and puckered their lips without exposing their teeth. Males varied the pattern by staring, jerking their heads forward, opening their mouths by dropping their lower jaws and not puckering their lips and thereby exposing their lower canines. One obvious explanation for this difference is that females do not have obvious canines and were avoiding exposing them. Males made a point of exposing their larger canines and thus flashing a warning.

Another difference was that females of all ages relied on aggressive contact forms slightly more frequently than males (Table 33). Tug-of-war contests and leaping-about displays with branches were generally male activities. A possible explanation for these differences is that males attempt to settle conflicts through ritualized signals more often than do females, possibly because the risk of injury through physical contact are slightly more if a male is involved and he uses his canines (males have larger canines but similar body sizes).

Regardless of the sexual differences, conspicuous elements of all observed aggressive interactions were (a) the disproportionate frequency of instances of older individuals being aggressive towards younger ones, and (b) the fact that aggression was largely an intrasexual activity (Tables 34 and 35).

### Aggressive Contexts

Table 36 shows the major contexts in which aggression was observed. The picture for the females is different from that for the males. Protection of offspring and weaning/punishment were the two major contexts that elicited aggressive behavior in females. Major contexts for male aggression were sexual access and food competition, two areas which were clearly not important for females.

A brief description of each context is given below:

#### 1. Unknown

Due to problems in observation, 166 (14%) of the 1184 cases of aggression, the cause could not be determined. It is known, however, that these unknown cases were not due to tug-of-war contests, presence of shadowers, competition for sexual access, protection of offspring, or weaning punishment.

#### 2. Harassment

Harassment (bothering/pestering) was frequently observed. It was mostly intrasexual and not between peers (Table 37). Harassment consisted of continually threatening and displacing, or, in the case of younger males, pulling of tails, grabbing faces or continual approaching and withdrawing.

The majority (61%) of harassment initiated by older females and directed toward young females was from long-time residents to newly-arrived juveniles and subadult females

(during their first two months in Focal troop). On only five occasions did younger females harass older females and in all cases the harassment was initiated by Focal troop native daughters and directed toward newly-arrived subadult females. Thus, of the 58 cases of harassment, the most common targets were newly arrived transferees (26 times), young males (15 times), young native daughters (14 times) and unidentified (3 times).

In male harassment there was a positive correlation between status and the frequency with which an adult male was harassed (non-sexual harassment). During the period October 1978 to August 1980, Captain Crook (chief copulator) received 6 of the 8 harassments. During the period October 1980 to May 1981, Yunk (chief copulator) received all 13 of the harassments initiated by younger males. This means that the chief copulator is the recipient of most, if not all, harassment.

### 3. Protection

Protection of offspring by mothers was the number one reason for initiating aggressive behavior (Table 36). Mothers protected their sons significantly more than they protected their daughters (Two-sided binomial test:  $Z = 3$ ;  $p = <0.004$ ). This is based on the males Wimp, Imp, Mimp and Bimp being protected 14, 12, 5 and 4 times respectively and the females Nimp, Simp and Himp being protected 4, 0 and 5 times respectively for the first 18 months of their lives.

Male infants were also protected more frequently than females by nonrelatives. For example, of the 25 times infants were protected by nonrelatives, 18 times the infant was a male, twice it was a female and five times it was unsexed. Furthermore, three times juveniles were protected by nonrelatives and in all three cases the protected juvenile was a male. All of this may be related to the fact that young males simply received more attention than young females from all members of the troop. For example, young males received significantly more grooming than young females (Table 38). Males were also carried by nonrelatives more frequently than female infants. For the first 12 months of their lives, the males Wimp, Imp, Mimp, Bimp and Gimp were carried 5, 2, 5, 7 and 80 times. In contrast, the females Nimp, Simp and Himp were carried 3, 2 and one time. Performing a binomial test without using the data collected on Gimp,  $z = 1.905$  and  $p = <0.06$  two-tailed. If Gimp's data had been included, it would have obviously been highly significant. It is not clear why Gimp was so popular. It is interesting to speculate that his 'popularity' may have been due to his mother's low rank ( see section on Adult Female Rank, page 125) and the fact that he could more easily be pulled away from her than other infants could be pulled from their mothers.

Furthermore, of the 18 times adult females were observed playing with their offspring, 17 times it involved

a mother playing with her infant son - only once did it involve a mother playing with her daughter.

#### 4. Food

Competition for food items and feeding sites was observed on 116 occasions in 7309 hours (about one instance every 63 hours of observation). This is probably an underestimate of how often it occurs, since most competitive food situations were probably resolved without any overt competition.

In 84 of the 116 competitive situations, the food item was noted. In 69 of these cases (comprises 25 separate items from 21 separate species) the item was large (larger than a colobus fist), took at least 30 seconds to consume, and/or required some processing skill. It therefore appeared that there was more competition when they were feeding on large food sources than when they were feeding on small sources. Furthermore, this increase in competition was probably a consequence of the items greater visibility and ease of grabbing.

In terms of the distribution of food competition over age-sex classes the most frequent aggressors were adult males (41.4%) with juvenile males (31.9%) being the most frequent targets, followed by adult female aggressors (29.3%) and juvenile female targets (27.9%). Furthermore, seniors behaved aggressively more frequently toward juniors than juniors did toward seniors (70

interactions as opposed to 6 (ages were only known in 76 of the aggressive food interactions). In all 6 instances the aggressor was a son and the target was his mother.

#### 5. Space

On 85 occasions individuals were observed to compete for resting space or threaten an individual who attempted to move close. There was apparently a particular distance within which another individual was not welcome, but my observations did not quantify this distance; it may have varied across individuals. There did not appear to be a shortage of resting sites, but some individuals favored certain resting sites. For example, on four consecutive mornings the adult female Solid ran into a specific fig tree, went to a specific 26 + cm horizontal branch, lay down and immediately appeared to go to sleep. The same pattern was observed for another adult female, Julie, on five mornings in a different area. It could be that parts of certain branches were more comfortable in terms of form, size, shade, breeze and so forth and that these branches were worth fighting for. This competition did not involve food or access to resting patterns; rather, it simply involved access to a place.

#### 6. Sexual Access

There were 204 observations of competition for sexual access. This includes not only cases where there was harassment of copulating couples, but also cases where (a)

males were threatened if they sat near a fully swollen females, or attempted to inspect a female's genitalia, and (b) copulating individuals threatened harassing individuals.

Adult and young males were more frequently involved in aggressive interactions in sexual access contexts compared with adult and young females (two-sided binomial test:  $Z = 7.037$ ;  $p = <0.0002$ ). Young males most frequent context of aggression was sexual access (comparing sexual access with displays and therefore with all other contexts -Table 36) (two-sided binomial test:  $Z = 6.22$ ;  $P = <0.0002$ ). Adult males were not significantly more involved in aggression over sexual access than they were over food (two-sided binomial test:  $Z = 0.59$ ;  $P = 0.56$ ). It is significant, however, when sexual access is compared with aggression over space and therefore over all other contexts (Table 36:  $Z = 2.96$ ;  $P = <0.004$ ).

On four occasions mothers were observed to chase off males who were mounting their daughters. The mothers chased off only those males who were older than their daughter, not males who were the same age or younger. That is, males who could not have fathered their daughters and/or were not dominant to their daughters when their daughters were immature were not threatened.

## 7. Weaning

Mothers threatened and gently attacked their own offspring at the time of weaning. This maternal punishment



took the form of facial threats, pushing, grabbing, nipping (and presumably biting), and hitting. It was first seen when an infant was in its eighth month and if the offspring was still in the same troop as its mother, the weaning aggression continued well after the second year.

Seventy-seven cases of weaning aggression were observed in 7309 hours, equivalent to one case every 94.9 hours. This makes it one of the most commonly observed types of aggression and the second most common reason for adult female aggression (Table 36). This high frequency may reflect observational bias, because weaning aggression was easy to notice from the squeals and screams of the distraught infant/juvenile. In comparison, many of the forms of interadult aggression were silent and could have been missed.

Occasionally (25 of the 77 cases = 32.5%) offspring were allowed to nurse after a rebuff by their mothers. During the first 18 months of their lives, daughters received significantly more weaning punishment than sons (two-tailed binomial test:  $Z = 2.43$ ;  $p = <0.01$ ), while sons retaliated significantly more frequently (two-tailed binomial test:  $z = 2.04$ ;  $p = <0.05$ ) (Table 39).

#### 8. Retaliation

Only 5.8% of the aggressive cases were due to target animals retaliating. Females, however, retaliated more frequently than males -and this was true for all ages

(Table 36). Of the 42 times that adult females retaliated, 34 of them occurred during adult female-adult female interactions (this was actually the reason for 25.4% of all aggression between adult females). In contrast to this only 1 of the 45 (2.2%) cases of adult male-adult male aggression was due to retaliation.

#### 9. Lone Shadowers ('Aliens')

Aggression towards shadowing strangers occurred about once every 122 hours and was more severe than any intratroop aggression. In all instances the initial aggressive response was made by immatures or adult females. Although adult males eventually took part in all fatal attacks on shadowers, they never initiated the attacks or chases.

While all intratroop aggression was limited to threats, chases and mild physical contact, all aggression directed toward lone aliens (always males) involved chasing and/or physical contact. None of the aggression directed toward aliens was limited to just threats. The behavior of established group members to shadowing/alien individuals is discussed in detail in Chapter 10.

#### 10. Tug-of-War contests

On 33 occasions a male sat down, broke off a large stick (70-180 cm in length) with his hands, held the detached stick and stared at another male. The challenged male either ignored the challenge (11 times) and the stick was dropped after a few seconds, or grabbed the stick and

the two males then engaged in a tug-of-war contest (22 times). This was clearly an adult male activity. The only female who ever took part was a mother who tried to grab the challenging stick away from her low-ranking son before a higher-ranking male engaged in a tug-of-war with him. These stick intimidation displays and tug-of-war contests were considered to be dominance interactions amongst males of the same troop and were a way to settle hierarchical differences without resorting to physical contact. These contests appeared to be final settlements since they never led to fighting; rather, one male always backed off. This form of aggression is only listed 9 times (Table 36) (note that this means 18 interactors), because the remaining tug-of-war interactions occurred outside the period covered by this table.

#### 11. Alliance Formation

While coalitions were common during intertroop encounters (see Chapter 11) and when dealing with lone shadowing males (see pages 203-209), they were not that common during intratroop aggressive encounters. Only 17 of the 1184 aggressive encounters resulted in alliance formation. Solicitations for aid were never observed.

Following Cheney (1977), a distinction is recognized between two types of alliance formations: aids and coalitions. In aids, the interferer allies itself with the victim of the agonistic interaction (15 of the 17 alliance

formation were of this form), whereas in coalitions the interferer allies itself with the aggressor. Clearly, aiding carries greater risks than coalition formation (Colvin, 1983).

Of the 17 alliances formed, none of them were male-male and only three of them were female-female (2 of these were the two cases of siding with the aggressor). The rest of them were mixed age/sex alliances with the majority (10 of the 17) being composed of an older individual coming to the aid of a younger nonrelated individual.

#### 12. Intervention

On 20 occasions one individual ran to the scene of an interaction between two other individuals and used aggression to terminate their interaction. This behavior did not involve coalitions or aiding, it simply involved interference in someone else's behavior. On 13 of these occasions, an individual threatened a groomee, broke up the grooming sequence and immediately presented to the groomer for grooming. Such interference in these cases always resulted in the interfering individual being groomed and were probably due to social competitiveness. In 10 of these cases the aggressor threatened an offspring of the groomer - in none of these cases did the mother retaliate, she simply groomed the aggressor when her offspring ran off.

On 3 occasions an adult male ran up and threatened an infant male until he stopped sucking from his mother; the

interfering adult male was Captain Crook, the top-ranking male at the time of interference.

Twice an adult female broke up a fight between two infants (neither one related to the interfering female). In both of these "impartial policing" instances (Kurland, 1977), the motivation appeared to be due to the fact that the 'umpire' simply disliked the disturbance and wanted it stopped.

Once a juvenile female threatened a younger juvenile male who was playing with a group of infants. In this case the motivation was not completely clear. The young female may have acted from feelings of protectiveness toward the infants; when this juvenile male played with younger animals, the younger ones often ended up screaming.

Once one adult male, Captain Crook, threatened the other adult male, Mr. Mean, as Mr. Mean was reassuring an adult female. The motivation underlying this intervention is not clear. Captain Crook may have been attempting to stop Mr. Mean from strengthening an alliance with a troop member. DeWaal (1982) has described similar behavior in a colony of chimpanzees and has labelled it "alliance breaking".

Adult males were responsible for 7 of the 20 intervention episodes and in all cases the interfering male was Captain Crook during his tenure as top-ranking male. Adult females were responsible for 9 of the cases and in 6

of these cases, adult females threatened newly-arrived juvenile and subadult transferees. In the other three cases adult females threatened females who ranked below them in status.

### 13. Redirected Aggression

From July 1978 through May 1981, only two cases of redirected aggression were observed (equivalent to one every 3654 hours). In one of these cases an adult female who was threatened by another adult female, turned and threatened the more dominant, threatening adult female's infant son. In the second case an adult female threatened another adult female who immediately turned and threatened the observer.

In June 1978, during the period not covered by Table 36 Mr. Mean threatened by the more dominant adult male, Jungi, turned and pulled food out of three juvenile's mouths in succession. In each case of redirected aggression, the individual responsible for redirection always chose an individual who was clearly subordinate, or in the case of the observer, known not to interact with monkeys. In other words, the chosen victim was unlikely to retaliate.

### 14. Displays

During 7309 hours of observation young colobus gave intraspecific agonistic displays on 48 occasions. Forty-six of the displayers were young males and twice they were young females. Brandishing of branches during these agonistic displays was seen 20 times (41.6% of the displays involved

brandishing). In all instances, the young displayer wrapped its palm and fingers around a dead branch, detached it from a tree and waved the branch about as it squealed/leapt tripedally through a tree. None of the branches were thrown after use. The grip on the branch was simply released and the branch fell. A further 36 cases of stick brandishing occurred outside the time period covered by Table 36. In all these cases the displayer was also a young male. Since all the other colobus appeared to ignore the displaying young males it can not be said that incorporating branches into displays enhanced the effectiveness of the displays.

#### Competitive Exclusion

Not included in any of the charts which quantify aggressive behaviors is a subtle manifestation of competition termed 'competitive exclusion' by Hardin (1960). It was seen 9 times when a more dominant male fed on a food source while another less dominant male sat watching. Though no interactions occurred, the animals were clearly competing, as shown by the fact that as soon as the more dominant male left, the less dominant male ran up and immediately ate the same source from the exact same site. This type of competition is considered typical of species with well-established dominance relations (Walters and Seyfarth, 1987). It is not considered here because it literally did not involve interactions and its occurrence

depended solely on observer luck.

#### Male Aggression Toward Females

Adult males were aggressive to adult females 30 times. This represents 15.4% of all aggression received by the adult females and 13.5% of all the aggression given by adult males (Table 34),

Adult male aggression toward adult females occurred in the following contexts: feeding competition (9 times); space competition (6 times); defense of one female against another female (3 times); retaliation (once); competition for a grooming partner (once); unknown reasons (10 times).

None of the aggression directed toward adult females involved physical contact; rather, it was limited to calls, facial threats, lunging and/or chasing.

Adult females were the recipients of aggression from adult males on 30 occasions and on only four occasions was the victim (always the adult female Volley) a fully-swollen female. On all other occasions the target was either lactating (6 times), noncycling (16 times - always during the nonbreeding season), inflating or deflating (4 times). Because all of the attacks on noncycling females occurred during months when there were no cycling females, no courtship displays and no copulations, it suggests that males are not aggressive to females during the breeding season. The one female who was threatened when she was



swollen was threatened because she threatened other females. In other words, she was a victim of an alliance formation between one of the males and another female.

Most of the aggression adult males directed at younger females was toward newly-arrived females. Of the 21 times adult males were aggressive to subadult and juvenile females, 14 times (66.6%) the female victim had been resident in the troop for a maximum of three weeks. The most frequent context of adult male aggression to younger females was food (9 times - 42.9%). This probably is a result of the fact that, in general, food competition was one of the most common reasons for male aggression (Table 36).

Most of the aggression subadult and juvenile males gave to females involved competition for food (13 times - 35%), harassment (8 times - 21.6%), competition for space (6 times - 16.2%). One major difference between young males and young females was that 55.5% of young males' aggression was directed at his own mother, while females never attacked their own mothers.

In general, males of all ages were more aggressive to males than they were to females (Table 34). At Abuko, dyadic dominance relationships between females and males of all ages appeared to be relatively unimportant in terms of the total number of aggressive acts given and received.

### Female Aggression Toward Males

Adult females were aggressive to adult males 34 times, which is equivalent to 30.4% of all aggression received by adult males and 7.2% of all aggression given by adult females (Table 34).

Adult female aggression toward adult males occurred in the following contexts: repulsion of alien males (28 times - 82.4%); protection of offspring (5 times - 14.7%); threatening male for mounting prepubescent daughter (once - 2.9%).

None of the aggression directed toward resident adult males involved physical contact. Such aggression, only occurred 6 times and is equivalent to only 1.3% of all aggression given by adult females and 5.4% of all aggression received by resident adult males. The aggression directed toward alien males, however, resulted in the males being fatally attacked. The females clearly differentiated between known and unknown males. With known males they merely used facial threats, lunges and chases without contact. With alien males they chased, caught, held down and mauled them until they were so damaged they could not survive. All of the attacks against alien males were initiated by females; they are assumed to have succeeded because they involved coalitions of females, often with help from one of the resident males. In contrast, none of the aggressive acts directed toward resident males involved

coalitions; rather, they were all acts of one female against one male. In only one case did a male retaliate. Thus, it is difficult to know the extent to which females may have needed support from other females. That is, females did not support one another against a male, but then, they did not need it since only once did a male retaliate instead of backing down.

Adult females were aggressive to younger males 100 times which is more than they were aggressive to older males but less than they were aggressive to younger females (Table 34). The major context for aggression was protection of offspring, the main form of aggression for all adult females.

Young females were aggressive to males 39 times. The subadult female aggressive pattern mimics the adult female pattern in that most of the aggression they give is intrasexual (Table 34: 67.7% of their identified targets were other females). The juvenile females, however, have the opposite pattern in that most of their aggression was directed toward males (Table 34: 59.1% of their known targets are males).

The major contexts for young female aggression were: aggression toward alien males (11 times), competition for food (7 times), sexual access (4 times) and protection of infants and juveniles (3 times). Like the adult females, younger females restricted their aggression toward

residential males to non-contact forms such as facial threats, chasing and lunging.

#### Male Aggression toward Other Males

Adult males were aggressive to other males 45 times (19 times to alien shadowing males and 25 times to troop mates) which is equivalent to 20.2% of all aggression given by the adult males.

Adult males were aggressive to other males in two major contexts: alien males shadowing their troop (19 times) and competition for sexual access to females with fellow resident males.

Like the females, the males did not use contact aggression when aggressing upon fellow residents; rather, they relied solely on non-contact forms of aggression such as threatening calls/expressions, chasing, lunging and tug-of-war contests.

There was a positive correlation between the male who received the least amount of aggression from other adult males and gave the most to other adult males and the male who was responsible for the majority of the copulations each breeding season (Table 40).

Adult males were aggressive to younger males 59 times. This exceeds the frequency with which they were aggressive to their peers, but is less than the frequency with which they were aggressive to young females (Table 34). The major

contexts for aggression were harassment and competition for sexual access, food and space.

Young males were aggressive to other males 72 times. The major contexts were competition for sexual access and general harassment. Table 34 shows clearly that the main victims were young males.

Most male aggression occurs during months when copulations occurred. During the months when there were no copulations, male aggression occurred once every 45.3 hours, compared with once every 11.9 hours during the months when one or more copulations were observed (copulatory data is given in Figure 10 and Table 41). Gunderson (1977) also observed that fighting among Abuko males is most frequent during the mating season.

#### Female Aggression toward Other Females

Adult females were aggressive to other adult females 134 times, representing 69.7% of all aggression received by the adult females and 28.5% of all aggression given by adult females (Table 34). Clearly an adult female's number one victim was another adult female.

Adult female aggression toward other adult females occurred in the following contexts: retaliation (34 times - 25.4%); protection of offspring (29 times - 20.9%); space (16 times 11.9%); food (5 times - 3.7%); coalitions (5 times - 3.7%); intervention (3 times - 2.2%); sexual

access ( 2 times - 1.5%); unknown ( 41 times - 30.6%).

Most of the intrafemale aggression involved non-contact aggression. Occasionally, however, residents were observed to grapple with other adult females to protect their offspring. This seems to suggest that a female only risks a fight when her offspring's safety is at risk. Of the 23 grappling interactions (Table 33) observed, all of them involved an offspring's immediate protection from another adult female or an offspring's potential danger from an alien male.

#### Adult Female Rank

Table 42 shows that some females (Droopy and Solid) consistently win intrafemale aggressive interactions while others (Garuda and Round - the two most recent transferees) consistently lose. The females who rank in the middle of the hierarchy are not as easy to categorize. In ranking females, priority was given to the 'rule of least reversals'. That is, females were arranged along a vertical axis of each matrix so that the fewest possible number of females were ever displaced by a female listed below them (Figure 12). Females were displaced by females ranked lower than they on only 3 occasions and in all 3 cases the interaction involved protection of offspring. The proportion of the data not amenable to the 'rule of least reversals' was small. The low proportion of rank reversals

appears to suggest that a stable hierarchy exists among female red colobus in Abuko. This suggestion receives further support from the fact that the females listed in Table 42 as the females who consistently win aggressive interactions, are also the same females who give the least number of submissive gestures and the most number of reassuring gestures while receiving the most number of submissive gestures and requesting the least number of reassuring gestures (Table 43).

Previous troop membership and en masse movement of female peers must be considered when female rank is determined. For example, three young females (Cisco, Quecha and Tara) who all joined Focal troop from Middle troop, never used aggression against each other and never gave submissive gestures to each other even though they frequently gave submissive gestures and received aggression from females who were not natal troop mates of theirs (Table 44). Also, Pelf, Lip, Velf and Scarty were all originally Focal troop females who joined PWD troop. During the 65 hours PWD troop was observed when all four were members of PWD, they were never seen to interact with each other in aggressive or submissive ways; rather, they only engaged in friendly interactions with each other.

### Rank and Reproductive Outcome

Under some circumstances dominant females in social groups of primates start to breed significantly earlier in life than do subordinate ones, produce significantly more offspring per year, and mate significantly earlier in the breeding season, if there is one (Harcourt, 1987). In Abuko the correlation between copulation frequency and aggression received by male peers is clear for adult males [Table 40], but there is no correlation between reproductive outcome and aggression received by female peers. For example, high-ranking females did not give birth earlier or more frequently than lower-ranking females (Table 45). In fact, of the five top-ranking females (Table 43), one of them (Yundum) was probably experiencing menopause, and two of them (Droopy and Solid) did not conceive through two breeding seasons (there were sexually competent males available).

There was no correlation between female dominance rank and total number of surviving offspring (Spearman Rank test:  $r_s = 262.5$ , d.f. = 13; Table 45) or birth order during the 1978 - 1979 birth season (Spearman Rank test:  $r_s = 85.5$ , d.f. = 8; (Table 45). There was a correlation between dominance rank and the possibility of having a male or female. For this test, each female offspring was given the value of 1, each male was given the value of -1 and no offspring was given the value of 0. Higher-ranking females



had daughters more frequently. (Spearman Rank test:  $r_s = 115$ , d.f. = 13,  $p = 0.01$  ; Table 45). This is similar to male-transfer species where high-ranking females also have daughters more frequently than they have sons (Altmann, 1980; Silk et al, 1981; Simpson and Simpson, 1985) and not similar to findings in a female-transfer species where exactly the opposite pattern was found (Symington, 1987).

#### Mother-Offspring: Status

There may have been a slight relationship between a mother's status and her offspring's eventual status in the troop. Of the five top-ranking females (Table 42), two of them (YuDum and Button) had sons. YuDum's son, Yunk became the chief copulator and top-ranking male during one of the breeding seasons while Bimp, Button's son, became chief copulator and too-ranking male during another breeding season (Table 41 for copulation frequencies and Table 40 for data on male status). Wild, one of the low-ranking females had a son Wimp and he was the lowest-status male and the least frequent copulator during the last breeding season of the study. Mimp never rejoined Focal troop after his initial exile and since he was the only young male who never rejoined and the only one whose mother had disappeared (presumed dead), it is assumed that the lack of a mother made it too difficult for him to rejoin. Interestingly, however, he eventually ended up as the chief copulator in

Question troop - a troop which had no common borders with Focal troop and none of his natal troop mates as members.

In terms of daughters, there may also be a relationship between mother's rank and daughter's status. Daughters of high-ranking females received less aggression from adult females than daughters of lower-ranking females and orphans (Table 31).

Only 13 times were young females aggressive towards adult females and five of these cases involved daughters of top-ranking females retaliating when the bottom-ranking adult females were aggressive toward them. This suggests that like male-transfer species, Abuko females may in some way pass status from mother to daughter - at least for the short period that they stay in their natal troop. There is a further possibility that once this status is passed on, it stays with them when they transfer and that the high rank gives them an assurance or confidence that helps them during and just after their transfer. The eight remaining cases all involved young females harassing older, newly-transferred females.

Young females were aggressive to each other infrequently and when they were (26 times), the majority of interactions were either against the orphaned female, Punk (7 times - 26.9%) or newly-arrived females (during their first three weeks only - 14 times - 53.8%) who had no mother present in the troop. The number of times Focal troop young

females were aggressive to each other was insignificant (Table 44 for data on Simp and Nimp) compared to the number of times they used aggression against females with whom they did not share a common natal troop.

## COOPERATIVE BEHAVIOR

### Introduction

The Abuko colobus display a complicated system of gestural and vocal cooperative communication, including kissing, touching, embracing and mounting. These behaviors are performed in the context of reunions, dominance interactions, reconciliations, excitement and fear. The most conspicuous and time-consuming cooperative behavior, however, is grooming (Table 10) and it is this behavior which, for the most part, is used to illustrate the sexual differences and the impact transfer patterns have on bonds within a troop. This section is based on the assumption that individuals who groom most with each other have stronger bonds than individuals who rarely groom (Washburn and DeVore, 1961; Seyfarth and Cheney, 1984; Gouzoules and Gouzoules, 1987; Dunbar, 1988). It is further based on the assumption that individuals who rest together or form subgroups and absent themselves from the main body of the troop for long periods of time (2 days or more) are more closely bonded than individuals who do not exhibit such behaviors.

### Male Grooming Patterns: An Overview

Table 26 presents the number and percent of times the adult males, Captain Crook and Mr. Mean, groomed and were groomed by different age-sex classes from August 1978

through August 1980. The scores show clearly that the adult males are groomed far more than they groom. They also show that the two males receive the same amount of grooming from adult females although they do not give equal amounts of grooming. There is a possibility that these differences reflect 'personality differences' between the two males (Harcourt, 1979; Hinde, 1983). It is also possible that they reflect status differences, with Captain Crook (because of his higher status during the time covered by Table 25) more able and/or willing to initiate grooming on females. For example, on 4 occasions females walked away while Mr. Mean was still in the process of grooming them. Females were not observed doing this to any other individual. On 8 occasions Mr. Mean presented for grooming to females and was rejected. Captain Crook was never rejected.

Table 46 presents the number of times the resident males groomed and were groomed from June 1981 - October 1981. The results are basically the same as in Table 26, although the number of males present has more than doubled: (1) males groom less than they are groomed; (2) the majority of their grooming is from females; and (3) males never groom their male peers.

In younger individuals a similar situation occurs; males groom significantly less and receive significantly more grooming than females (Table 47). Young males distribute their grooming differently from females of

comparable ages (Table 47). Young males direct most of their grooming toward adult males particularly the dominant male Captain Crook. In contrast, adult males direct most of their grooming toward adult and young females (Tables 26 and 46).

From June 1981 to October 1981, the three native sons returned to their natal troop and were in the process of reforming bonds with their previous troop mates. During this time the three male age-mates, Wimp, Imp and Bimp never groomed each other although they groomed and were groomed by others (Table 46).

Further support for the lack of male-male grooming bouts comes from the 63 hours of observation on PWD troop and 15 hours observation on Zoo troop. During these periods males were never observed grooming each other although over 100 grooming bouts were observed in PWD and 10 in Zoo troop.

Adult males clearly preferred grooming some adult females more frequently than they groomed others (Table 48) and the preferred females were not the high-ranking females. In fact, they tended to be the lower-ranking females. This is in contrast to some primates where high-ranking females appear to be the most attractive social partners (Seyfarth, 1977; 1980). While Mr. Mean clearly chose Volley (ranked 8 out of 13) who overwhelmingly reciprocated by giving Mr. Mean twice as much grooming as she gave Captain Crook (Table 49). Captain Crook clearly preferred the adult female Inca

(ranked 7 out of 13) and the juvenile female orphan Punk. Inca gave Mr. Mean and Captain Crook the same amount of grooming (Table 49), while Punk clearly preferred Captain Crook. She groomed Captain Crook 9 times and Mr. Mean 0 times.

Ovulation did not appear to make a female more 'desirable' as a grooming partner for a male (Table 50). Females were more often not ovulating when they were groomed by males.

#### Female Grooming Patterns: An Overview

The number and percent of times adult females groomed and were groomed by others is presented in Table 49. The scores show that adult females generally groom more than they are groomed and that their own offspring and adult males are the main recipients. Like the males, however, there are individual differences which are not easily explainable. For example, while most females gave Captain Crook and Mr. Mean an equal amount of grooming, Nene and Volley clearly preferred one male over the other.

Like most other primates (Hrdy, 1976; Altmann, 1980) grooming patterns are affected by whether or not a female possesses a newborn infant (Table 51). Comparing data for 10 females during the month immediately preceding the birth with the month immediately after the birth they received significantly less grooming after the birth (Sign test:

$p = 0.04$  two-tailed). While they did not give grooming more frequently after the birth (Sign test:  $p = 0.508$  two-tailed) they do groom adult males relatively more frequently after the birth compared to before the birth (Sign test:  $p = 0.004$  two-tailed) (Table 51). In fact, the proximity of new mothers to an adult male was very obvious (Table 52). The male chosen was usually the male of highest status (Table 53). In the cases of Yunk and Bimp, it is highly likely that they were also the fathers. In the case of Captain Crook he was clearly not the father since he was incapable of intromission. The actual father was probably Jungi who disappeared and was presumed dead before any of his assumed offspring were born (during the time of Jungi's assumed offsprings' birth, Captain Crook was the male of highest status and Mr. Mean was the other resident male in the troop at this time).

In western lowland (Yamagiwa, 1983) and mountain gorillas (Stewart and Harcourt, 1987) new mothers also spent more time with adult males than they did before their infants were born.

It is normally assumed that mothers spend more time grooming their younger offspring than they spend grooming their older offspring. With the Abuko red colobus, however, the mothers groomed their older offspring significantly more frequently than they groomed their younger offspring (Table 54).



No obvious correlation between rank and the percentage of time spent grooming and being groomed was apparent in terms of grooming relationships between females (Figure 13). Within the female grooming system, individuals were equally likely to groom someone above them or below them in the dominance hierarchy (Table 55). Using the data in this table and testing for deviations away from it, it was clear that there were some quite large deviations, but they are not all in the same direction and therefore they cancel each other out. Some individuals consistently groom above, some below, and therefore the group is not homogeneous in terms of grooming rules because they are behaving in such wildly different ways.

Whilst grooming amongst females was not correlated with rank, amount of grooming received from males was correlated with low rank. The females who received the most grooming from adult males were either natal troop immature females who had not yet left their natal troop or low to middle ranking adult females (Table 48). For example, the five most popular groomees were either immature females (Punk, Ilf, Jiggaty Jaggaty) or adult females from the bottom half of the dominance hierarchy (Round ranked 12th and Inca ranked 7th out of a total of 13 females). Three of the five top ranking females (Droopy, Solid and YunDum) were the females groomed least by adult males.

In younger individuals females groom more and are

groomed less than males of comparable age (Table 38) and their grooming profiles are different, both in terms of grooming given (Table 47) and grooming received (Table 56). Two interesting patterns emerge from these tables. Males receive more grooming from their mothers than females do, while young females groom their peers and the next higher female age group more than they groom any other group.

In terms of siblings grooming each other, there were only two pairs of sisters (Pelf and her younger sister Punk, and Self and her younger sister Simp). In both cases, the older sister groomed the younger sister more than she groomed her own peers (Page 112). This makes it all the more intriguing that maternal sisters were not known to follow each other into troops when they transferred (pages 176-177).

When females first transferred into Focal troop they received very little grooming from the resident females compared to the grooming received by Focal troop age mates (Table 57). Furthermore during 63 hours of observing PWD troop, the four females who originally came from Focal troop only groomed each other, their own offspring, each other's offspring and adult males. They were not seen grooming females with whom they had not shared a common natal troop. Twice when PWD juvenile females joined Focal troop, on their first day they ran directly to previous PWD troop members (and their peers), embraced and groomed. They did not

interact in a friendly manner with any other Focal troop members. Furthermore, during the 15 hours of observation on Zoo troop, three females who originally came from Focal troop only groomed each other or adult males.

#### Male-Female Grooming Differences

Of the male's grooming time, an average of 7.3% is spent grooming adult males, 52.8% with adult females, 36.6% with young females and 3.25% with young males (Table 26). Captain Crook spent 16.5% of his total grooming time grooming Punk (a young orphaned female - Table 48), while Mr. Mean spent 15% of his total grooming time with Volley and 15% of his total grooming time with Punk. Males, regardless of age receive most of their grooming from females and rarely from each other (Tables 26, 46 and 56).

Of the female's grooming time, an average of 42.5% is spent grooming other females, 25.8% with adult males, 26.0% with their own offspring and 8.8% with nonrelated immatures (Table 49). Mothers spent more time grooming sons than they spent grooming daughters. Young females spent the majority of their grooming time grooming other young females. Immatures and low-to-middle ranking females receive more grooming from adult males than high-ranking females receive.

#### Social Resting

Following Carpenter (1964) and Kummer (1968), it is

assumed that interindividual distances among group members can be used as a measure of their social affinities, representing lasting summaries of individuals' previous interactions. Resting in physical contact with one or more animals, therefore, may serve as a socially integrating behavior. In Abuko individuals spent the majority of their time resting within touching distance of another animal.

Each scan-sample recorded an animal within touching distance of another animal. Individuals interacting socially were not recorded as nearest-neighbors but were treated separately. During the year of scan-samples (Table 10) a total of 64.6% of the resting + lying time was spent in physical contact by all members of the population. Infants spent 96.6% of their resting + lying time in physical contact with another individual (96.2% with their own mother and 0.4% with an individual who was not a known relative). The adult males spent much less time in physical contact with other individuals and never with each other. Captain Crook spent 26.6% of his time within touching distance of another individual. The data on the adult females was very different. Adult females (on average) spent 44.0% of their time within touching distance of another adult female, 6% of their time within touching distance of one of the two adult males and 62% of their time within touching distance of their offspring. Obviously, the totals add up to more than 100% because an individual can

sit within touching distance to a number of animals at the same time.

These social resting data contrast sharply with the data collected on the Kibale population (Struhsaker, 1975) where a red colobus usually has no other colobus within 2.5 m. There is one similarity in that in both populations adult males have fewer neighbors than do adult females.

### Reconciliations

Like chimpanzees and rhesus monkeys (de Waal and van Roosmalen, 1979; de Waal and Yoshihara, 1983), the Abuko red colobus also engage in reconciliation after conflict by kissing and embracing.

Amongst adult males, 15.4% of their conflicts were resolved within one minute, and amongst adult females 21.6% of their conflicts were resolved within one minute. In intrasexual conflict, females never initiated reconciliation with males while males did so after 33.3% of their conflicts with females. Amongst juveniles, reconciliation was more common. Juvenile males resolved 52.4% of their conflicts within one minute while juvenile females resolved 42% of their conflicts within one minute.

### Miscellaneous Cooperative Behaviors

Although grooming, social resting groups and reconciliation are the most obvious measures of cohesion and

affinitive behavior, there are other forms. One form of cooperative behavior is the giving of warning calls that signal the presence of predatory danger. This was heard 6 times (when the caller was correctly identified) in correct situations and on five occasions the caller was the adult female Inca (ranked 7th in the dominance hierarchy). The sixth caller was the dominant male Captain Crook. Immatures frequently gave inappropriate warning calls at large falling Anthocleista procera leaves, low flying planes and helicopters, kingfishers killing frogs, nonpredatory birds and the observer's knapsack.

Another form of cooperative behavior was food sharing. This occurred 6 times between infant peers and nine times between mothers and their offspring (7 of the sharers were sons, one was a daughter and one was unidentified (see pages 52-53)).

### Summary

1. Aggressive behavior includes both contact and non-contact forms with some obvious sexual differences apparent.

2. Protection of offspring and weaning punishment were the two major contexts which elicited aggressive behaviors in females while the major contexts for males were sexual access and food competition. The majority of the aggressive interactions were intrasexual.

3. Females directed the majority of their harassment toward newly-arrived females while males directed most of their harassment toward the dominant male.

4. Male and female infants were protected by their mothers, but not with equal frequency. Male infants and juveniles were protected more than females by both mothers and nonrelatives.

5. There was more competition when feeders were feeding on large items than when they were feeding on small items.

6. In terms of weaning aggression, daughters received more maternal punishment than sons while sons retaliated more frequently.

7. Females retaliated twice as frequently as males and this was true for all ages (except for weanlings). Alliance formations, interventions and redirected aggression were not frequently observed and are assumed not to play a large part in the social organization.

8. Aggressive displays and tug-of-war contests were a form of ritual aggression virtually specific to males.

9. Males infrequently attacked females and they appear not to be aggressive toward females during the breeding season. In general, males were more aggressive to other males than they were to females.

10. Females very infrequently attacked resident males. The majority of their aggression was directed toward other females and extratroup males.

11. There was a positive correlation between the role of chief copulator and dominant male.

12. There is a female dominance order with some females consistently winning aggressive interactions and others losing. High rank was not associated with greater fecundity. If the male offspring's mating success is computed, however, then ultimately high female status does appear to increase genetic investment in the future.

13. Female aggressive interactions are probably based on past natal troop histories, with females who shared a common past being less aggressive with each other than with females who do not share a common past.

14. Adult males are groomed far more than they groom and this same situation holds true for young males. Males, of all ages, rarely groom each other.

15. Adult and young females groom more than they are groomed. Most of a females grooming is directed to males,



their own offspring or to other females.

16. A young female spends most of her time grooming her peers and females of the next older age group. Young males spend most of their time grooming older males - particularly the dominant male. Sons receive more grooming from their mothers than do daughters.

17. There was no apparent correlation between rank and intrafemale grooming patterns or intramale grooming patterns. While high-ranking males sometimes received more grooming from females than low-ranking males, this was not always the case. Adult males tended to groom low-ranking or immature females more than high-ranking females.

18. Female grooming patterns probably reflect past troop histories; that is, females who shared a common natal troop groom more than females who did not share a common history.

19. Cooperative behaviors such as social resting bouts, reconciliations. the giving of alarm calls and food sharing are more common to females than to males.

## Chapter 9. SEXUAL BEHAVIOR

### Introduction

The principal aim in this chapter is to present data on, and discuss, mate competition and mate choice in terms of female and male strategies. More specifically, the aim is to look at what factors determine the distribution of matings among individuals. Is there evidence of female choice? Whom do females chose? Is there evidence of female-female competition? male-male competition?

### Signalling Sexual Receptivity

Females signal their receptivity in a variety of ways: sexual swellings, olfactory cues and audio-visual displays.

#### Sexual Swellings

To solicit copulations, ovulating females must signal their fertility and receptivity to males, and apparently sexual swellings do that (Dixon, 1983). The female in Abuko has a conspicuous sexual swelling which advertises her fertility and sexual receptivity. Male sexual interest seems to be related to cyclical changes in sexual swellings with the most genital inspections (Table 58), copulations (Table 59) and copulatory harassment (Table 60) occurring with inflating and fully-swollen females. It is therefore

assumed that ovulation occurs sometime during this period and that the swelling is important in attracting males. In contrast to this, males were more aggressive to non-cycling females than they were to ovulating females (see page 119). Furthermore, ovulation did not appear to make a female more 'desirable' as a grooming partner for a male (Table 50).

#### Olfactory Signals

It is assumed that olfactory cues play some part in indicating a female's sexual receptivity since they do so in other primates (Dixson, 1983; see list in Hrdy and Whitten, 1987). From July 1978 through March 1982 (7251 hours of observation) inspection of female genitalia occurred 234 times which is equivalent to once every 31 hours. In all but four cases, a male touched and/or muzzled and/or peered very closely (and probably sniffed) at a female's perineum. The four unusual cases involved immature females (twice) and adult females (twice) investigating other females' perinea. Sixty-five inspections were part of the copulatory act: thirty-seven immediately preceded a mount, 24 of them occurred between mounts and four of them occurred shortly after a mount. The remaining 183 were not an immediate part of the copulatory act.

The initiator of the interaction was observed 186 times. Significantly more inspections were initiated by males (147 times) than by females (39 times): binomial two-tailed test ( $Z = 7.9$ ,  $p = <0.0002$ ) (Table 58). Genital

inspection appeared to be directly related to assessing the female's reproductive state. Males were most interested in a female's perineum when she was in the inflating or fully swollen state and least interested in investigating a noncycling female (Table 58).

#### Female Courtship Audio-Visual Displays

Cycling females frequently leapt about, bounced on and ricocheted off branches while giving highly audible quaver calls. These audiovisual female courtship displays were not given by pregnant (with the exception of Volley), lactating or prepubescent females. In four cases, in fact, females gave their very first display on the first day of their very first adolescent swelling (mean age: 34.25 months of age - see page 94).

The displays appeared to induce contagious displays in that often a displaying female immediately set off a chain reaction and one to six or more cycling females immediately displayed. This often made it difficult to count accurately and identify all the displaying females. In spite of this difficulty, however, it was clear that these displays were the most common social interaction observed during the collection of daily activity patterns (Table 26). Of course, they were also the most obvious and noisiest social interactions.

During the breeding season the number of displays recorded in two-week periods totalled well over 100 while it

fell drastically during the non-breeding season to well under 20 (Table 32).

Because 26% of all heterosexual mounts between adult males and inflating or fully swollen females ( $N = 362$ ) were immediately preceded by an audio-visual display, it is assumed that this display is actually an advertisement for receptivity and an invitation to copulation. Unfortunately in all other cases it was not noted whether the display occurred or not before copulation. This means that in the remaining 74% there was no record made on whether a display occurred. It does not mean that a display did not occur.

These displays are not reported as being given by any other red colobus population. Why this subspecies (it was seen/heard in other populations in the Senegambia region) has developed it is unclear. It is possible that it is used to attract males from other troops, shadowing males and males from one's own troop and inform all of them of the displayer's sexual receptivity and fertility. These calls might function to increase access to several males and thereby allow females to observe the nature of subtle, aggressive and cooperative interactions between males.

Of these three different signals, only the olfactory cues are limited to short-distance messages. The audio-visual courtship displays and the highly conspicuous sexual swellings function on both a short and long distance level and probably function to incite interest amongst males both

within and without the troop.

In contrast to the obvious messages of sexual receptivity, no signs of male sexual solicitation were seen.

### Copulations

Although 644 copulations were observed, many were not seen in their entirety, while for others I was too far away to determine the occurrence or nonoccurrence of various components of the behavioral pattern. Thus, the base numbers for the various positional components are different.

Copulation was defined as a heterosexual mount between adults/subadults with thrusting. Since intromission was only observed 10 times (Mr. Mean = 5; Imp = 4; Bimp = 1) it did not seem reasonable to use it as part of the definition of copulation. The red colobus are multiple mounters. Some bouts lasted for nearly 30 minutes and contained over 6 separate mounts. Vaginal plugs, assumed to consist of congealed ejaculate, were seen only 6 times. All of them after fully swollen females had mated with Yunk.

Copulation is initiated by either sex. The male may approach the female and then mount. If the female is seated or lying down he may push against her back or rump with his hand, and then mount when she assumes a quadrupedal standing position. The female may approach the male and present her rear to the male with her tail slightly elevated and deviated, sometimes looking back. Alternatively, she may

give a courtship display (see above). The initiation of a copulation was seen 267 times. Males initiated 148 (55.4%) while females initiated 119 (44.6% - 93 by courtship displays and 26 by presenting hindquarters). Females most frequently initiated copulations when they were sexually swollen and thus assumed to be ovulating, while males most frequently initiated copulations when the females were inflating and thus assumed to be not quite ready to conceive but certainly worth monopolizing from other males (Table 61: Females initiated significantly more copulations in a swollen state: chi square test, d.f. = 1;  $p = 0.05$ . Males initiated significantly more copulations when females had an inflating sexual skin: chi square test, d.f.= 1;  $p = <0.005$ ).

During most mounts the male holds the female's back or rear with his hands while the exact placement of his feet varied, probably depending on the type and size of substrate and possibly on the size of the male and female involved. Captain Crook who was smaller than Mr. Mean and the majority of the females and had a deformed penis and was incapable of intromission, used a position unused by any of the other males. For 13.9% of his 277 mounts, he sat down, pulled the female into his lap and she thrust backwards while he remain seated with both his feet and his rump on the supporting branch and his ventrum hunched over the female's back.

In 44 cases females gave copulation quavers while being mounted and they did not give them in 28 cases; their presence or absence was not noted in the remaining cases. These quavers were given by fully swollen, inflating, deflating and flat females and during mounts which included thrusts and those which did not. Once a female gave a copulation quaver while standing quadrupedally and being inspected by Mr. Mean. Thus, the quaver could not be used as a means of identifying a mount with intromission. The quaver did, however, immediately advertise the fact that a female was being mounted or inspected and always resulted in the couple being harassed.

Usually it was not possible to see the male's face while he was mounting. However, on 187 occasions it was obvious that the male displayed a threat face (Figure 14) and that the threat was directed toward anyone who might be looking at him, but not to anyone in particular. In 18 cases the mounted male mouthed the female's tail and in 4 cases he mouthed her back while he thrust on her. The intruder male, Bully and the subadult male Imp were responsible for all the mouthing episodes.

None of the observed mounts were seen to terminate with a pause. In fact, in two cases where Captain Crook was seen to ejaculate into mid-air (because the female pulled away just as he was ejaculating) there was no pause. He simply continued ejaculating and thrusting at the same time.



Furthermore, during five separate male masturbation episodes, there was no posture pause during ejaculation.

Grooming was associated with 75 mounting bouts. In 49 of these the female groomed the male and in 26 the male groomed the female. Females obviously gave more grooming than males after a copulation (binomial test:  $Z = 1.94$ ;  $p = 0.10$  two-tailed). Individual differences amongst males were not obvious in determining variations in grooming frequencies (Table 62). All males were groomed equally (chi square test; d.f. = 4;  $p = 0.5$ ). All males groomed equally (chi square test, d.f. = 5;  $p = 0.3$ ). Fully-swollen females were groomed more frequently than they groomed males. Twenty-six per cent of the females who were groomed by males after a mount were fully swollen, while only 4.8% of the females who gave post-copulatory grooming were fully swollen. These differences may be due to the fact that swollen females did not 'need' to groom males in order to keep them attracted to them, while males needed the added attraction of being a groomer in order to keep the fully-swollen female from approaching other males.

Seventy cases of copulation harassment were observed and in all cases the mount was curtailed. Forty-three of these were preceded by a female giving a copulation quaver and announcing the mount. Females were, therefore responsible for 61.4% of the curtailments. Harassment was responsible for 32.9% of all the 88 observed multiple

mounts.

The adult harassment consisted of calls and/or lunging toward (but not touching) the mating pair. The immature harassment consisted of slapping, grabbing, butting and/or climbing on the mating pair.

Of the 70 separate copulation harassments observed, 15 involved 2 harassers, two of them involved three harassers, two of them involved four harassers and the remaining 50 episodes involved only one harasser. This means that a total of 94 individuals harassed 70 copulating couples. All of the episodes (except one) involving two or more harassers included immature males only. Mature males and females (except one) of all ages acted on their own when they harassed copulating couples.

The majority of the harassers were males ( 81 out of 94) while females rarely interfered with copulations and those females who did were usually related to the female mountee. Of the 6 adult/subadult females who interfered with copulations, four of them were related to the copulating female while 6 of the 7 juvenile female harassers were related to the copulating female. In contrast, only 14 of the 69 juvenile male harassers were related to the copulating female. Clearly, female juvenile-harassers were more frequently related to the copulating female than male juvenile harassers were (t test:  $t = 7.01$ ; d.f. = 65;  $p = <0.0001$ ).

The function of sexual harassment is not known, but its occurrence in juveniles may represent a form of parent-offspring conflict. Such harassment may also enable subordinate juvenile males to approach, examine and threaten older (and therefore more dominant) males at a time when they are unlikely to retaliate (Walters, 1987).

It appeared that males harassed copulating couples in different contexts than females harassed the couples. All the adult and subadult males who harassed couples did so only when the female mountee was fully swollen and thus most likely to conceive. Four of the six adult female harassers directed their antagonism toward males mounted on their prepubescent (and thus not able to conceive) daughters. One of the adult females joined her harassing subadult son as he called and lunged toward an adult male mounted on a fully swollen female who the son then mounted. Thus, this female appeared to be helping her son to increase his chances of fathering offspring. The other adult female lunged and called at a newly-transferred fully swollen female mounted by an adult male.

In summary while mounts involving fully swollen females were interfered with more than any other mounts (Table 60), females and males interfered for different reasons. Simply, males appeared to compete sexually with other males, while females did not appear to do so - at least not in terms of putting an immediate stop to conception.

### Masturbation

Five times adult males (Captain Crook = 3; Mr. Mean = 1; Kinky = 1) were observed masturbating, ejaculating and eating the ejaculate. During each observation, the male sat and rubbed, stretched, and scratched his penis until it became erect, after which additional rubbing produced ejaculate which was eaten. As with mounting and incomplete copulation where ejaculate was seen to land in mid-air, there was no pause. In all five cases, masturbation occurred during intertroop encounters when the situation could be considered 'tense'.

Female masturbation, such as that frequently seen in Japanese macaques, and accompanied by muscular contractions of the vaginal muscles, sphincter, base of the tail and thighs (Wolfe, 1986) was not observed.

### Chief Copulator

Males mounted and copulated with females in all cycle states. The large majority of copulations for all males, however, occurred with fully-swollen and inflating females (Table 59). This suggests that males distribute their copulations in ways that will ensure fertilization. The great majority of copulations with fully-swollen and inflating females were performed by one male (Table 41). The role of chief copulator, however, usually changes from

breeding season to breeding season (Table 41).

Males varied in their ability to attract and repel females. Table 63 lists the total number of approaches made by each male to fully-swollen and inflating females and the total number of times each male was rejected. Chief copulators each breeding season received the least number of rejections. Over time, a males popularity with females can change as can be seen in Table 63, if one looks at the number of advances made by Captain Crook over three breeding seasons and the number of times he was rejected.

In terms of immediate and direct male-male competition for fully-swollen females, there was very little harassment of copulating couples by male competitors - only 12 of the 94 harassers were adult or subadult males. On an individual basis, however, one male was responsible for the majority of the harassing each breeding season and the male was the chief copulator for that season. For example, from May 1979 - August 1980, the dominant male Captain Crook was responsible for all 6 harassments. From October 1980 - May 1981 the dominant male Yunk was responsible for all three harassments and from May 1981 - September 1981 the dominant male Bimp was responsible for all three sexual harassments.

#### Consort Behavior - 'Safaris'

The formation of consort pairs occurred four times during this study and never involved the chief copulator.

Once Mr. Mean spent two days sitting by Metoo's side as she remained by her dead infant's side. She was not cycling and showed no signs of moving into another troop's area.

Simply, she did not stay with her troop; rather, she stayed next to her dead infant, and Mr. Mean stayed with her. On another occasion, Mr. Mean spent 28 hours following Inca around the home range as she ran from one end to the other over and over again apparently looking for her lost 10-month-old son, Imp. As soon as she found him, Inca stopped wandering frantically around the range and rejoined the main body of the troop, and Mr. Mean stopped following Inca. In both cases the females were not cycling and Mr. Mean made no attempt to mate with them. The loss of an infant, however, does bring on an early resumption of sexual cycling.

Twice, a 'number-two' male formed a consort relationship with a fully-swollen female. Once, Mr. Mean went off with the fully-swollen female, Metoo and her 18-month-old son, Mimp in June 1980, for 1.5 days. During this period the three of them remained out of sight and sound of the rest of the troop. Four of the seven copulations Mr. Mean engaged in during this month actually occurred during this 1.5 day safari. The fourth consort pair involved the young male Imp and the fully-swollen female Kana who went off for one day in June 1981 and remained out of sight and sound of the rest of the troop members. During their consortship they mated twice which accounts for the majority

of Imp's copulations during this month (Table 41: he only mated three times with fully swollen females during June 1981).

Although there are only limited data on consort behavior, it was clear that all four consort formations involved no aggression. The males simply followed the females as the females either stayed put (as in the case of Metoo and her dead infant) or moved continually away from the rest of the troop. In fact, it was my impression in the two cases involving fully-swollen females that the females initiated the consortship. Furthermore, these two females appeared to be particularly interested in mating with these two males. Metoo was seen initiating five sexual advances and four of them were directed toward Mr. Mean. Also, Kana initiated two sexual advances and both of them were toward Imp. During their periods of copulating neither one of these males were chief copulators. Both of them may have been able, however, to copulate more frequently and with less harassment by consorting with females outside the troop environment rather than inside the troop's social space.

Like yellow baboons (Hausfater, 1975), when a consortship involving a sexual attractive female occurred, the female and male showed continual attraction to, and awareness of, each other's location, and both animals moved so as to maintain close proximity with each other. In contrast, when a consortship involved a female who had lost

an infant (both permanently and temporarily) the male tagged behind the moving female who appeared to ignore him. She made all movement decisions and he followed immediately behind. In these two cases it appeared that the male was anticipating her departure from the troop or the occurrence of receptivity -both of which are related to the loss of an infant.

Like chimpanzees (Goodall, 1986) when a female and male are 'on safari', females did not give copulation quavers even though they did exhibit facial expressions characteristic of copulation. Similarly, females on safari did not give audio-visual courtship displays. The females appeared to withhold information regarding their location and sexual activities from other troop members.

From the above, it would appear, that males have two strategies. The chief copulator mates with females while remaining within the confines of the troop. Other males, leave the troop in order to mate with fully-swollen females. In general, however, the chief copulator is still responsible for the majority of the matings each breeding season.



### Female Mating Patterns

#### 'Pseudoestrus'

Not all cycles fell within the typical 4-8 day peak swelling period. One case involved the pregnant female, Volley, who was fully swollen from November 25 through December 22 1979 (for a total of 28 days) and gave birth on April 26 1980. During this exceptionally long swollen period, Volley spent time with the alien male, Flattop, who was shadowing Focal troop and she continually travelled back and forth between Focal troop and PWD troop. Volley was not ovulating during most of this period, and yet she sported a full sexual swelling, solicited males for mating, was mated and frequently gave courtship displays. In another case, in May 1981 one day after the disappearance (and presumed death) of Yimp, Garuda began swelling and maintained a full swelling for 14 days while Droopy maintained a full swelling for 21 days. Both females gave frequent courtship displays and solicited copulations yet did not become pregnant.

Clearly sexual receptivity during pregnancy or periods of social upheaval cannot be an adaptation to enhance the probability of conception. This 'pseudoestrus' behavior may have served to placate ('trick') all the males Volley encountered (Flattop, PWD and Focal troop males). Irregular cycles may be caused by a variety of social factors; one of the most common being the presence of unfamiliar males (Loy,

1974). In Volley's case the alien male and/or the frequent visits to a semi-alien range may have elicited the 'pseudoestrus' state. And, as hypothesized by Hrdy (1981) this pseudoestrus may be an investment in future offspring by the female and is particularly important in situations where infanticide is a real possibility; since, it might encourage males to behave 'paternally' toward the female's future offspring should they happen to have contact with it. In Garuda's and Droopy's case the situation was different in that they were not pregnant. Given the fact that all adult male disappearances were immediately followed by replacements, were these females 'anticipating' the arrival of extratroup males? Or, were they 'inviting' extratroup males by 'announcing' their receptivity and the occurrence of a male 'vacancy'?

#### Female Choice

It is usually assumed that female primates do not mate indiscriminately. Rather, it is suggested that they should carefully choose their mates (Trivers, 1972; Halliday, 1978; Parker, 1979). There is, however, no general agreement about the basis of female discrimination among potential mates (Mayr, 1972; Selander, 1972).

Table 64 lists copulation and genital inspection initiation by fully-swollen and inflating females and shows that the dominant male received significantly more advances

than other males.

During the 1979 and part of the 1980 breeding season they chose Captain Crook. When Yunk, a native son, began to assume the correct mating posture and became dominant to both Captain Crook and Mr. Mean, their choice switched to him and Captain Crook was relegated to second choice. Furthermore, when Yunk disappeared and was presumed dead, and three young males returned to their natal troop, the females choose Bimp and Imp over Captain Crook, Mr. Mean and Wimp. Comparing the information in Table 64 with the information in Table 63, it is clear that females are specifically choosing some males and rejecting others. Furthermore, this process changes over time and the male who is selected one season may not be selected the next season.

Since females are obviously choosing specific males to mate with, it is assumed that they are choosing partners of the highest possible quality who are at the very least sexually competent (Trivers, 1972). In fact, for 1.5 breeding seasons, females were selecting Captain Crook who was obviously incapable of intromission and thus were rendering themselves incapable of conceiving.

What quality is a female looking for when she chooses a mate? Halliday (1983) suggested that females prefer older males, if the ability to survive has a heritable basis. In fact, the Abuko female consistently chose the youngest available male. O'Donald (1983) has suggested that females

may choose the most persistent male. If persistence is defined as attempting to mate with females in all cycle states more frequently than other males, then persistence itself may be a quality that females select for. For example, the chief copulator with fully-swollen females was also the chief copulator with females in the inflating state during each breeding season (Table 41) and in all other states as well (Figure 15).

Among primates, there is considerable variation within and between species, in the extent to which high-ranking males, obtain a majority of matings (Bernstein, 1976; Fedigan, 1983; Smuts, 1987). While the importance of male dominance as a determinant of female choice may have been overemphasized (Hausfater, 1975; Andelman, 1985), it may play some part in Abuko as it does in Kibale (Struhsaker and Leland, 1985) and Tana River (Marsh, 1978).

Firstly, each breeding season the majority of females mated preferentially with the male who had the highest status (defined as receiving the least amount of aggression and giving the most to other males). And, even more importantly, the females were seen to choose the top-ranking male over all others (Tables 63 and 64). This was particularly interesting in the case of Captain Crook who, although he was of high status, was incapable of intromission. The advantage the female gains by mating with the high-status male was immediate, in that matings with the

dominant male received no harassments. Because a male had a very brief career as chief copulator (see Table 41 for lengths of various tenures), it was hard to see what long-term advantage the female would gain since her progeny would not benefit from the father's high status through paternal care and protection except for the first few months. In fact, new mothers spent more time with adult males than they did before their infants were born (Table 52) and the male chosen was usually the male of highest status (Table 53). In two cases (Yunk and Bimp) it is highly likely that the chosen male was also the father. It would seem, therefore, that the young received some protection in the form of extra-companionship during the first few months of life - a time of probable infanticide.

Females appear not only to be able to discriminate between high- and low-status males, but actually to create situations whereby males compete with each other for a female's favor. The female's courtship display and copulation quaver attracted the attention of males and incited male-male aggression. Interestingly enough, the two females who went on 'safari' with the number-two males never gave copulation quavers or courtship displays when they were with these males. As soon as they returned to Focal troop however, they began displaying.

### Summary

1. Females signal sexual receptivity in a variety of ways; sexual swellings, olfactory signals and courtship displays. There were no male signals of sexual solicitation.

2. Copulation was initiated by either sex. There were individual differences in postures, copulatory rates and harassment.

3. Males appeared to compete with other males more than females competed with other females.

4. The large majority of copulations for all males occurred with inflating and fully-swollen females and the majority of copulations each breeding season were performed by one male. The role of chief copulator changed from season to season.

5. Each breeding season the chief copulator received the least number of rejections and the most number of advances by females.

6. Consort pairs were observed and they always involved a male who was not the chief copulator.

7. Females show mate choice, consistently picking the chief copulator each breeding season. They do not pick the most sexually competent or oldest male. They pick the male of highest status.

8. Through the use of copulation quavers and audio-visual courtship displays, females may actually create a situation whereby males compete with each other for a female's sexual favor.

9. The absence of overt female-female competition in conjunction with a high level of female consensus in terms of mate choice is possibly due to the short-lived tenure of the chief copulator and his lack of parental involvement.

## Chapter 10. GROUP CHANGES

### Introduction

In most social species of birds and mammals that have been studied, it has been found that, as time passes, some individuals leave and others join the group (Greenwood, 1980; Wilson, 1975). The group, for most such species then, is clearly not a closed unit.

Among social primates it is generally males who leave their natal group (Wrangham, 1980; Pusey and Packer, 1987). With the increased number of field studies on well-habituated groups, it is now becoming clear that females also transfer (Moore, 1984; Crockett and Eisenberg, 1987; Pusey and Packer, 1987; Bennett and Sebastian, 1988).

Of particular relevance to this study is the information collected on red colobus transfer patterns. At two red colobus study sites (Kibale Forest and Tana River), where at least some amount of individual recognition of animals was achieved, females routinely and voluntarily transferred between troops. It was also found that the process was fairly rapid and involved little intrasexual aggression and competition (Marsh, 1979b; Struhsaker and Leland, 1985). The most obvious difference was the age of the migrants with the Kibale Forest females moving as



juveniles and the Tana River females migrating as adults. In both populations, males also moved between groups but not as frequently as females. Furthermore, amongst mountain gorillas (Harcourt, 1978; Stewart and Harcourt, 1987; Watts, 1990), hamadryas baboons (Kummer, 1968, 1971), mantled howler monkeys (Clarke, 1982; Clarke and Glander, 1984), and red howler monkeys (Crockett, 1984, 1987), males and females both move between social units.

In the Abuko Nature Reserve both sexes commonly emigrated. Of all known individuals born during the 1978-1980 birth seasons, and observed throughout subadulthood, 80% of the females and 83% of the males emigrated. Thus, it is not the fact of emigration that distinguishes the sexes. Rather, as I intend to show, it is the process leading up to, and the result of, emigration which distinguishes the Abuko female from the Abuko male.

Some of the major questions addressed in this chapter include: Who transfers? Where do the transferees go? Are there age/sex differences in terms of transfer behaviors and troop choice? How does the Abuko population differ from other red colobus populations in terms of specific transfer patterns?

The transfer process (i.e. migration) and the characteristics and fates of many of the migrants are detailed. The factors involved in migration of both sexes are discussed and comparisons are made.

## Characteristics of Transferring Females

### Age of Females

Both Packer (1979) and Greenwood (1980) distinguished between natal dispersal, applied to individuals who had not yet reproduced and thus are assumed to be juveniles or subadults, and breeding dispersal which referred to individuals who had reproduced and thus are considered to be adult. In most species natal dispersal of the young is more common than breeding dispersal of the sexually mature (Greenwood, 1980; Wilson, 1975) and the Abuko red colobus is no exception. Over a five-year period, of the 22 permanent and 6 temporary females who transferred, nineteen were juveniles, five were subadults and four were adults (Table 65). In four cases actual ages at time of transfer were known. Himp was 27-28 months old, Nimp was 29-30 months old, Dunk was 31-33 months old and the orphan Punk was 40-41 months old.

Moore (1984) suggested that the predominance of young adults who transfer is partially due to the numerical predominance of this age class. This suggestion does not adequately account for the patterns of transfer in Abuko. The rate of migration in Focal troop was the highest (both in absolute and relative terms) among juveniles. During the first three years of the study, 11 of the 12 resident juveniles (91.6%) of this age group left Focal troop; ten left permanently, while one left for only a short period.

In contrast, only one of the 13 resident adult females (7.7% of this age group) spent time travelling between Focal troop and the neighboring PWD troop, taking part in the social life of both troops.

#### Reproductive State of Transferring Females

Seven of the juvenile emigrants left Focal troop before developing sexual swellings (see page 94), three of them left immediately after developing their first adolescent swelling, while one left after experiencing infrequent adolescent swellings for five months. Of the 8 juveniles who joined Focal troop all of them looked and behaved as though they had not yet developed any of the traits associated with the beginning of puberty, whether physical (sexual swellings) or behavioral (sexual leaping-about courtship displays).

In contrast to the juveniles' lack of obvious sexuality, all of the subadults and one of the two adults observed in the process of migrating displayed full sexual swellings and were assumed to be sexually receptive at the time of transfer.

#### Female's Kin Network and Its Influence on Transfer Patterns

While the majority of the females born in Focal troop left permanently and joined other troops, two young females, Nimp and Simp, did not make this permanent move. A comparison with all the other immature females who had ever been resident in Focal troop showed that Nimp and Simp were

the only ones who had a mother still present in their troop, and at the same time all the males who were older than they were had disappeared or were no longer allowed by females to take part in mating activities. That is, they were the only two females who had their mother still present in the troop and all older males absent or sexually inactive. In contrast, if both the mother and an older, sexually active male were present, young females emigrated. Furthermore, they also emigrated when their mother was absent but the older male was present.

Both Nimp and Simp eventually mated with their probable half-sibling (different mother, probable same father - assuming one male was responsible for all conceptions of their peer group - Table 41), gave birth, and successfully reared young in their natal troop.

#### Female Transfer and Female Relationships

##### Mother-led Investigative Forays

Mothers appeared to influence their daughters' transfers: which troops to join and when to join. For example, one mother, Volley, spent 6 3/4 months leading her pubescent daughter Velf, and Scarty, a close age-mate of Velf's, into the center of various resting, socializing and feeding groups in PWD troop where they frequently spent a few days. During each foray into PWD's range Volley was always the first to interact with PWD members. Velf, with

to Volley or grooming with PWD females (Lip and Pelf) who had previously been Focal troop members. Volley was always the first to return to Focal troop and a day or two later, Velf and Scarty also returned.

Volley was probably sexually receptive during all her visits to PWD troop and may even have conceived during one of these forays. Eventually, Volley gave birth to an infant within the confines of Focal troop while Velf conceived, gave birth twice and successfully reared one young in PWD troop, the troop her mother 'introduced' her to.

Another Focal troop mother, Solid, led her just-pubescent daughter, Self, to Middle troop's border on three separate occasions. Unlike Volley, Solid was not sexually receptive and made no attempt to enter Middle troop's social space. Solid and Self simply sat and watched, possibly unnoticed by Middle troop's members. Eventually, Self joined, conceived, and successfully reared one young in Middle troop, the only troop toward which her mother led her.

Approximately two years later Solid twice led her just-pubescent daughter, Simp, into PWD's home range. Solid, who was not sexually receptive on either occasion, made no attempt to socialize with any PWD members. Neither, did Simp. On both occasions they sat 15-30 meters from PWD members for about one hour. During this time they appeared to watch the troop members interact. Both times they

returned to Focal troop, Solid leading with Simp directly behind her. Eventually, Simp remained in Focal troop where she gave birth and successfully reared young.

Twice sexually receptive Droopy led her pre-pubescent daughter, Dunk into PWD's range where they stayed for at least 1/2 day each time. Eventually, Dunk joined Zoo troop, where she successfully reared young. Unfortunately, the troop was not observed during the period before or during Dunk's transfer and thus there is no information on whether Droopy also led Dunk into Zoo troop's area.

Dunk transferred when she was 31-33 months old. Her age-mate, Punk, who was orphaned at 9 months of age, did not transfer until she was 40-41 months old. When Punk was orphaned, she was adopted by her older sister Pelf for 6 months until Pelf emigrated to PWD troop, leaving Punk behind in Focal troop. While Punk displayed all the other apparently age-related behavior patterns, like interacting in a friendly manner with green monkeys and solitary male and alien female colobus monkeys, she was not seen to stray into neighboring ranges prior to her transfer.

Pelf's transfer was also slightly delayed compared to her age-mates. All her age-mates (Lip, Jiggaty Jaggaty and Ilf) left to join PWD on the same day, while Pelf left 8 weeks later. There is a possibility that her 'drive' to transfer was delayed because she had developed a strong temporary bond with her orphaned, younger sister, something

none of the other females were observed to do. The bond with her sister, Punk, however, was only temporary and 8 weeks later she joined the same troop as her previous troop mates. There is the stronger possibility, however, that Pelf's transfer was delayed, albeit slightly, because she was orphaned before her mother introduced her to the practice of investigating alien ranges.

These observations suggest that a daughter first samples ranges of other troops by following her mother. If an infant is orphaned and has no mother to imitate, such investigations are delayed. The presence of a mother may make it easier or less distressing for a young female to visit and explore a new territory. Research on chimpanzees and human children suggests that the presence of an attachment figure moderates or eliminates fearfulness in a new setting and, moreover, provides the opportunity for exploration (Rheingold, 1969; Rheingold and Eckerman, 1969; Ainsworth and Bell, 1970; Miller, Bard, Juno and Nadler, 1986).

#### Peer-led Migrations

Co-migration of male age peers has been documented in vervets (Cheney and Seyfarth, 1977; 1983), sifakas (Richard, 1974) and various species of macaques (Boelkins and Wilson, 1972; Drinkamer and Vessey, 1973; Sugiyama, 1976; van Noordwijk and van Schaik, 1985; Paul and Kuester, 1985). In

contrast, in species where females transfer voluntarily and routinely, emigrants usually move on their own and not in the company of peers (chimpanzees: Nishida, 1979; Pusey, 1979; gorillas: Harcourt, 1978). The females in Abuko are an exception. Of the 11 immature females who left Focal troop, 8 of them first travelled in the immediate company of peers while only three of them travelled first on their own.

Harcourt (1978) suggested that the synchrony of emigration, in species which have a clear-cut breeding season, could be mere coincidence. Pusey and Packer (1987) further suggested that seasonally breeding species display peer migration more frequently than non-seasonally breeding species because in seasonally breeding species, cohorts of individuals of the same age are likely to reach the same physical stage at the same time as well as experience the same external stimuli. Since the majority of transfers in Abuko occur during the breeding season (Table 65) this suggestion cannot be completely ruled out. It must be remembered, however, that peer migration only occurs amongst immature females who are not yet capable of breeding. Sexually-receptive females, whose immediate purpose for moving could be to breed, do not move en masse.

Cheney (1983) suggested that transfer in the company of natal group peers occurs because it facilitates integration into the new group by providing allies whose presence reduces aggression and increases the rate at which one can



reduces aggression and increases the rate at which one can climb the social hierarchy. For example, with rhesus macaques (Meikle and Vessey, 1981), brothers who transferred together, supported each other and attained a higher rank sooner than males who transferred alone. Like the suggestions mentioned above, this one is not applicable to the sexually-receptive subadult or the mature female since none of them transferred with peers. There is a possibility, however, that this hypothesis is relevant to immature female transfer. The data available show that females give and receive aggression to females with whom they do not share a common natal troop past more frequently than females with whom they do share a common natal past (Table 44). It is also possible that peer group migration like mother-led migration, could be related to the need for an attachment figure to eliminate or, at least moderate, the fear of an unknown area (Miller, et. al, 1986).

#### Sister Migration

Two known sets of sisters were members of Focal troop during this study. One set consisted of Pelf who joined PWD and her younger, orphaned sister Punk who, two years later, joined Zoo troop - both of them joining their age peers in their chosen troops. The other matrilineal sister set consisted of Self, who joined Middle troop on her own, and the younger sister Simp, who never transferred and eventually bred in her natal troop. In both cases the

younger sisters knew where their older sisters had gone and yet never made an attempt to join the same troop. It is assumed that the bonds between maternal sisters were strong since they never used aggression against each other and older sisters groomed younger sisters significantly more than they groomed their own peers. Pelf groomed her younger sister Punk 30 times. During the same time period she groomed her peer Lib 3 times, Jiggaty Jaggaty once and Ilf once. Self groomed her younger sister Simp 8 times. During the same time period she groomed her peers Velf and Scarty once each.

In contrast to the strong, albeit temporary, ties uniting maternal sisters, the bond between peers, who were possibly paternal sisters, were maintained. Of the 11 young females who first transferred with peers or joined a troop which contained peers, all of them were still with at least one peer four years later (and possibly longer). Furthermore, from 1981-1983 and possibly longer at least 50% of the PWD females were originally Focal troop native daughters and at least 33% of Zoo troop females were Focal troop native daughters. The history of the other female troop members is unknown. Thus, it appeared that the social relationship formed around a common social and environmental background and resulting in age cohorts was stronger than

that formed from sharing the same mother. The interesting point is that, regardless of whether the matrilineal or presumed patrilineal bonds are maintained during the process of female transfer, a similar situation occurs. That is, a troop ultimately consists of nonaggressive groups of females, many (but not all) of whom once shared a common background during their youth.

#### Reasons for Female Emigration

Various explanations have been proposed to explain troop transfer with most authors focusing on the ultimate causes of emigration and incest avoidance (Itani, 1972; Harcourt, 1978; Maynard-Smith, 1978; Packer, 1979; Greenwood, 1980; Pusey, 1980; Cheney, 1983; Stewart and Harcourt, 1987). This section focuses on proximate causes. In particular, five factors will be discussed: overt competition between females, choice of range, the successful rearing of young, the search for 'strange' mates and psychological drives.

#### Overt Competition between Females

In some species, females are actively expelled or peripheralized from their natal troop (Aloutta palliata: Jones, 1980; A. seniculus: Rudran, 1979; Crockett, 1984; Crockett and Pope, 1988; Pygathrix nemaeus: Lippold, 1977)

and thus are probably transferring to avoid aggression. This suggestion did not appear to apply to the Abuko females since forced expulsions or peripheralizations were never observed, aggression was rarely directed toward migrating females before they left their natal troop and all female departures appeared to be voluntary. The amount of aggression received by 5 females for a four-month period before they left their natal troop was totalled. Dunk received 3, Jiggaty Jaggaty 2, Ilf 2, Lib 1 and Pelf no cases of aggression. Furthermore, no wounds, injuries or scratches were ever seen on any females of any age during their period of transfer. This suggests that the rate of intense physical aggression against females during the transfer process is low.

Data collected on the female orphan Punk indicate (Table 31) that intrasexual aggression was not sufficient to account for female transfer. Punk was subjected to significantly more aggression than any other Focal troop native daughter. This was probably because she had no mother to protect or defend her. If female transfer was due to competition and aggression between females then Punk should have been the first to leave her natal troop. In fact she was the oldest to so do (see page 169).

### Choice of Range

Another hypothesis advanced to account for female transfer is choice of range (Moore, 1984). That is, a female switches troops because she is seeking to improve the quality of available resources in the daily environment.

While range choice is apparently important in some species of birds (Verner and Willson, 1966; Wittenberger, 1976), it has not been considered significant in any primate species where large numbers of females transfer between social units (Marsh, 1978; Harcourt, 1978; Struhsaker and Leland, 1979). There were a number of observations which pointed to the fact that this hypothesis was probably not applicable to the Abuko situation either.

First, if the quality of the five different home ranges varied significantly to attract more females, these ranges might support a larger number of infants because it might be a more successful place to breed. In Abuko no one range supported a larger number of infants/breeding females. For example, in the beginning of 1981 Focal troop females produced 6 infants, Zoo troop females produced 8 infants and PWD troop females produced 6 infants. During the next birth season Focal troop and PWD females each produced 5 infants while Zoo troop females produced 6 infants. During the following birth season Focal troop females produced 3 infants, PWD females produced 5 infants and Zoo troop females produced 2 infants.

Secondly, if the ranges did not differ sufficiently then the hypothesis would not apply, because it would not make any difference which range a female selected - they would all be similar. In fact, there was a large difference in the sizes of the various ranges (Figure 6), with Middle troop (a troop only chosen by one Focal troop female) having a range at least three times larger than PWD troop (a troop chosen by the majority of Focal troop females (Table 65)).

This hypothesis is difficult to deal with in detail due to the lack of vital data collected during this study. No attempt was made to map the exact number and placement of resources in all five ranges. Nor, was an attempt made to census and accurately identify all individuals in all five troops and track every transfer between troops. As Marsh (1978) and Harcourt (1978) have both pointed out, however, with more quantitative data on resource distribution and population dynamics, this hypothesis is a reasonably testable one.

#### Successful Rearing of Young

A third hypothesis advanced to account for whether a female emigrates or not is the successful rearing of her young (Harcourt, 1978). During the entire study there were 28 births. In three instances an infant died (all probable infanticide - see page 92) while the mother survived. Two of these three mothers then left Focal troop, transferred to

and eventually raised young in PWD troop, while no mother with a dependent young transferred (although Garuda spent +6 months moving between both PWD and Focal troop with her infant son Gimp). Therefore, while this factor only pertains to adult females who have given birth and failed to raise young, it is possibly very important amongst this class in Abuko as it is with mountain gorillas (Harcourt, 1978) and the Tana River red colobus (Marsh, 1979).

#### Search for Strange (Unrelated) Males)

A fourth hypothesis is that females transfer to search for strange males in another troop because of an inhibition to mate with familiar individuals (Packer, 1979; Pusey, 1990; Sugiyama, 1976). There were a number of lines of evidence which suggest that this factor may not be important in explaining transfer patterns of females in Abuko.

1. Individuals who matured together and were probably paternal half-siblings freely mated with one another. Furthermore, adult females freely mated with younger males whom they had known from birth. In both situations the females conceived after mating with these highly familiar males. For example, after three native sons, Wimp, Imp and Bimp returned to Focal troop in June 1981, Bimp and Imp took over most of the mating activities (they were involved in 17 of the 22 matings with fully swollen females and 11 of the 13 matings with inflating females - see Table 41). Simp and

Nimp mated only with them. They conceived, gave birth and successfully reared young in their natal troop with a male who was not their father, but was almost certainly their paternal half-sibling and definitely a well-known childhood acquaintance. A similar situation occurs in mountain gorillas who also mate with peers (Stewart and Harcourt, 1987).

2. If females were transferring to strange troops simply to meet and form bonds with strange males, then it would probably (although not necessarily) be advantageous for them to be fully swollen and sexually receptive and thus, presumably most attractive to the males (Teneza, 1989). This can only occur, however, when the females are mature. In most cases the females who transfer are not sexually mature (Table 65) and make no attempt to form bonds with males when they first join. None of the new migrants were observed grooming males during their first month in Focal troop. Rather, their time was mostly spent with other females, particularly with the females who were previously members of their natal troop. For example, when Quecha and Tara joined Focal troop they were only seen grooming with Cisco or with each other (all three were originally Middle troop females).

This suggests that a general inhibition to mate with familiar individuals does not apply to the Abuko population. Nor does there appear to be a lack of sexual interest



because of early habituation as suggested by Demarest (1977). Thus females in Abuko were not simply leaving because they were sexually uninterested in their male troop-mates. Since young females remain in their natal troop only when all males who were one or more years older than they had disappeared or were no longer allowed by the females to take part in mating activities, this strongly suggests that there is a specific inhibition to mate with a familiar but dominant male.

#### Psychological Drives

A fifth factor in the transfer patterns of the Abuko juvenile females is the psychological element. Juvenile females in the pre-transfer and the immediate post-transfer stage were the only individuals to initiate friendly interactions with alien males and females who strayed into their range. The one exception was a sexually-receptive female, Volley, who once groomed the young 'strange' male, Flattop. Furthermore, they were the most active age/sex class to initiate friendly interactions with green monkeys, make physical contact with the researcher and investigate unusual and possibly even 'dangerous' objects and areas such as closed knapsacks and deep tree holes (Table 66).

Juvenile females appeared to be far more adventurous and have a higher degree of 'curiosity' than any other age class. Something in the specific make-up of this age/sex

class made it easier, more rewarding, more interesting and/or more compelling for them to engage in novel situations with novel individuals and explore novel areas. Furthermore, all of these exploratory behaviors are closely related to each other (see collection of papers in Archer and Birke, 1983). In all cases the individual is seeking out change and this age/sex class appears to actively solicit more change of various sorts than any other class. Whether this is due to an 'exploratory drive' (Montgomery, 1953; Berlyne, 1950) or a 'boredom drive' (Myers and Miller, 1954) or certain aspects of each (Berlyne, 1960) is an extremely important question, but one beyond the scope of this study; in any case, it could not be determined in a study on a wild population. Whatever the exact 'drive' may be, it is a drive that may be at least partially responsible for transferring out of the natal troop at the juvenile stage. Once an individual reaches sexual maturity of course, the 'drive' disappears and thus this factor would not pertain to adult transfer patterns.

### Summary

It is unlikely that one factor alone is responsible for female transfer. Rather, a wide range of social, psychological and possibly as yet undetermined ecological factors probably influence transfer patterns. Furthermore, the key factors appear to vary with age, reproductive state,

reproductive history, social and kin relationships and individual circumstances.

Whatever the exact factors may be which are directly or indirectly responsible for female emigration, it is not something within the group (such as aggression or inhibition to mate with familiar peers), which forces immature females to leave. Rather, something outside the troop attracts them. In only one situation does it appear that internal factors force a female out of the group; an adult female who loses her infant within the confines of her present troop will be more likely to leave and join another group. In this case, the female may be leaving because of aggression directed toward her infant (in both cases - Kunkle and Tara - the dead infant was presumed to have been the victim of infanticide).

#### Characteristics of Chosen Troop

An Abuko female had four social troops from which to choose upon leaving her natal troop. Where did she go? Did she simply transfer to the nearest troop? Did she transfer to the troop with the most number of previous troop mates?

In Abuko all five troops were well-established and contained all age and sex classes throughout the study. Furthermore, no new troops were formed during the study. Since newly-established troops did not exist, an Abuko female did not have this option. She was confronted only

with well-established troops and had to choose amongst them. Furthermore, observed extratroop associations were all-male groups and rarely was a female seen to spend any time with these groups (Table 67). This suggests that females were not interested in forming bonds with males in male-only associations. Rather, an Abuko female appeared to be interested only in troops which contained all age and sex classes.

#### Familiarity of Chosen Troop

Whereas the mature females selected the best known troop (PWD troop) and the youngest females chose the least familiar troop (Zoo troop), the older juveniles and subadults who were either just beginning to swell sexually or were fully swollen and ready to conceive also chose well-known troops (Table 65).

Two troops (PWD and Middle troops) had ranges which greatly overlapped with the range of Focal troop (Figure 6). Because of this large (60%) range overlap with these two neighboring troops, females knew and had access to many resources used by these two other troops. Indeed, so frequently were some of the food and sleeping sites (Table 68) used by Focal troop and one of the two neighboring troops that these resources would have to be described as actually 'belonging' to both troops.

Furthermore, a Focal troop female was able to monitor

social events and changes in composition in both PWD and Middle troops without leaving the confines of her present troop's social and physical space and thereby possibly wasting time and/or energy in perhaps futile investigations. In particular, the views which Focal troop and PWD had of each other when they were in their core areas at Bamboo pool (Figure 6) were unhindered. Certainly, I was frequently able to watch social interactions in both troops at one time and I assume the colobus, who were up in the trees, had an even better view than I did from the ground or a photo-hide. Thus, if a female wanted to transfer to a troop with which she was most familiar than she would pick either PWD or Middle troop. In fact, Ali (1981) has suggested that because the cost of switching to an unknown troop, female Macaca radiata transfer is a direct consequence of their highly-overlapping home ranges.

In contrast to the above, if an Abuko female wanted an unfamiliar social and resource situation and was seeking out obvious change, then she would have picked either Question or Zoo troop. Neither one of these troops shared common borders, resources or views of social interactions with Focal troop and are assumed to be more alien than PWD or Middle troop.

The Abuko data appeared to show that mature and immature females selected troops which varied in terms of familiarity. All four adult females (Volley, Kunkle, Noam,

Tara) who transferred during this study selected troops with overlapping home ranges. This suggested that the mature females were not simply seeking out the unknown or unfamiliar. Rather, they selected troops where the type, amount and placement of many resources and the social structure and membership composition was well known.

None of the 11 juveniles and subadults who left Focal troop joined Question troop, 1 joined Middle troop, 5 joined PWD troop and another 5 joined Zoo troop. Thus, with the youngest females six of the 11 transferees chose troops (Middle and PWD) whose ranges overlapped extensively with their natal troop's range (Figure 6), while 5 individuals chose Zoo troop which was the most distant and thus assumed to be the least familiar. The three youngest females (Dunk, Nimp and Himp) to transfer between social units were among the five females who chose Zoo troop. The fact that the youngest females selected the most distant and alien troop may be related to their 'need' for more change than any other classes (see pages 184-185). Greenwood (1980) has stated that amongst most animals, natal dispersal is more extensive and over longer distances than breeding dispersal.

These data suggest that, like many other transfer behaviors, the importance of selecting a well-known or unfamiliar troop appeared to carry different weights for each class of female depending on her age and immediate reproductive state.

### Presence of Previous Troop mates in Chosen Troop

Another factor possibly influencing troop choice may have been the presence in that troop of previous (and thus assumed known and possibly even related) troop mates. Certainly, this was found to be an important factor with immature male Cercopithecus aethiops who transferred between troops in Amboseli National Park, Kenya (Cheney, 1983).

All of the Focal troop female emigrants (except the pubescent Self) either transferred to troops where previous troop mates were residing or transferred in the immediate company of peers (in two cases - Kunkle and Ilf - it is not known whether previous troop mates were in their chosen troops since the study had just begun). Whether one transfers in the immediate company of troop mates or transfers to a troop with previous troop mates, the end result is the same: the female immigrant ends up being surrounded by a social group of known and possibly-related females. What was rather unexpected was the fact that maternal half-sisters did not select the same troop (see pages 176-177).

From the above data on troop choice it could be argued that mature females choose the nearest and best known troop (PWD) while the very youngest females prefer the least known troop (Zoo troop) (Table 65). It could also be argued that all females select troops where there are known female allies and avoid troops where there are no previous troop

members. Unfortunately, both arguments are circular because there was no way to prove whether it was the degree of familiarity or the presence of allies which attracted the immigrant. For example, Focal troop females were never observed joining Question troop. Whether this was due to its unfamiliarity or whether its unfamiliarity was due to the fact that Focal troop females never attempted to join presents an intriguing problem which merits further study. An interesting point is that the only Focal troop native son who transferred to another troop actually chose Question troop - the only troop assumed not to have any Focal troop females.

In general, the juvenile females made their first move in the company of peers as opposed to moving alone (Table 65). Furthermore, females do not choose amongst troops with equal frequency (Table 69). Rather, they tend to choose troops with peers present. The synchronized reproductive cycles among females and the mating and birth seasons in Abuko resulted in a community of age mates, or peers, for most infants and juveniles. Indeed, precise timing of birth peaks in Abuko could be an adaptation for the production of peer groups.

#### Switching Troops

How many times does a female switch troops? In some cases the first choice made by a female was not the final



one (Table 65). That is, after their first known move, females sometimes transferred again. Two of the Focal troop juvenile females made two moves before settling down in a troop where they bred and reared young. Ilf left Focal troop with two peers for PWD troop and then immediately left for Zoo troop, where she finally remained. Nimp left Focal troop with two peers for Zoo troop and then returned to Focal troop (her natal troop) where she remained.

Furthermore, three juveniles and one sexually mature subadult female joined Focal troop for periods of time ranging from three days to five months (Table 65) before they moved on to other troops. It is also highly likely that females joined for periods of a few hours or days without having been seen before moving on to other troops. In Ilf's case it is not known whether there were any original Focal troop females in Zoo troop when she joined. Eventually, however, she was joined by other, younger Focal troop females. Nimp also eventually ended up with peers when she rejoined her natal troop since Simp never left.

Two adult females, Kunkle and Tara, made a second move after the death of an infant. These were the only instances where the 'reason' for retransfer was known.

#### Dual Membership

Five females appeared to maintain membership in two troops before settling in one. Volley and her daughter Velf

and Velf's age-mate, Scarty spent 6 months travelling back and forth between Focal troop and PWD before Volley settled in Focal troop and Velf and Scarty settled in PWD. During this time Volley spent 17% of her time with PWD while both Velf and Scarty spent 51% of their time with PWD (based on 136 days of observation between August 1 1979 and February 22 1980). The juvenile female Cisco spent 3 1/4 months travelling back and forth between her natal troop (Middle troop where she frequently suckled from her mother) and Focal troop where she finally settled. During these 3 1/4 months she spent 10% of her time with Focal troop (based on 60 observation days). The fifth female, Garuda originally joined Focal troop as a subadult. She then spent her pregnancy and the first 6+ months of her sons life moving between Focal troop and PWD. From the time Garuda was first seen with an infant, she spent 35% of her time with Focal troop and the rest with PWD (based on 80 observation days). When her son, Gimp was approximately 6+ months old, Garuda permanently joined Focal troop. The maintenance of two memberships at one time appears to be common in other species be they predominantly female transfer species such as gorillas (Harcourt, 1978) or male transfer species such as Papio anubis (Packer, 1979; Ransom, 1981) or Presbytis entellus thersites (pers. obs.).

### Solitary and Extratroop Females

There were no solitary or long-term extratroop females observed in Abuko. During this study, however, 3 of the 7 observed solitary juveniles were not accurately sexed and thus could have been females. Their numbers, however, would have been insignificant.

These patterns contrast greatly with red howler monkeys in particular. Although in both cases, females leave their natal troop, a high proportion of red howler females fail to join established troops and are forced into tenuous extratroop associations (Crockett, 1984).

Outside Abuko, however, solitary and extratroop females did exist. In areas where it was not possible to move easily between neighboring troops due to the geographical isolation of the troops themselves, solitary females did exist and they did so for long periods of time. In the Banjul suburb of Fajara, where there were no colobus troops, two juvenile females frequented a garden for over two years and appeared to have no contact with troops, the closest-known troop being over 1.5 km away from their garden cul-de-sac. In fact, these two females started their extratroop life as juveniles, but were fully mature females when last observed.

There were also two cases of females living in villages near Abuko. In one case a young female with no sexual

swelling spent three days in Lamin, a village which borders the reserve. She was then beaten to death by the villagers for eating mango flowers. The second female, of indeterminate age, with no sexual swelling, spent two days in Banjulunding, another village bordering the reserve. She was chased and stoned for two days and then disappeared. Both of these females were moving toward Abuko and probably came from the closest troop which was at least 1 3/4 km from the border of the reserve. I never witnessed, nor was told about, any red colobus attempting to move in the other direction through the bordering villages and fields, away from the reserve. Regardless of the direction, however, the move through villages and fields, is probably not a very safe one. In contrast to the infrequent movement of red colobus outside Abuko, patas and green monkeys were seen moving into, out of and around the neighboring fields and villages on a daily basis.

#### Subunit Formation - An Overview

Female troop members in Abuko sometimes formed subunits which separated from the main body of the troop for days at a time and then joined up again. In this respect the Abuko red colobus could be said to display a form of fusion-fission organization (Kummer, 1968). The form found in Abuko, however, does not appear to be as formalized and regimented as the hamadryas or gelada baboons (Kummer, 1968;

Dunbar and Dunbar, 1975; Dunbar, 1984). Nor, however, is it as prominent as that of the chimpanzees (Goodall, 1986), Ateles, and perhaps also Brachyteles (Robinson and Janson, 1987). What is intriguing here is the fact that all these species also exhibit female transfer. What the exact connection is, is not yet clear. Nothing approaching this form of organization has been reported for any other red colobus population. None of the other red colobus populations break up into subgroups that move independently of one another.

In Abuko mothers with their young were the main individuals who broke off from the troop and went their separate ways. Occasionally, these mother-young groups were joined by non-swollen adult and subadult females.

All Focal troop subunits observed from January 1979 through March 1982 are listed in Appendix E. It is clear from this that these subunits were basically nursery units (only one subunit - no. 9 - was not a nursery group) and that the same females tended to form subunits over and over again. Furthermore, comparing the data in Appendix E with the grooming information in Table 55 it is clear that the subunits are not random associations; rather, they tended to contain individuals who were favorite grooming partners. Furthermore, all three female-female alliances observed (page 115) are represented in these subunits. Nene once assisted Inca, Wild once assisted Garuda and Button once

assisted Inca.

All the PWD subunits formed from January 1980 through March 1982 are also listed in Appendix E. In all cases where individuals could be identified, the subunit members consisted of individuals who were once members of the same natal troop (in this case they were always previous Focal troop members).

### Emigrating Males

#### Age of Males

Like the females, the males in Abuko generally emigrated before sexual maturity. All Focal troop members with known birth dates and the age at which they emigrated are listed in Table 70. It is clear from these data that males emigrated at a significantly younger age than females (Two sample t test:  $t = 2.463$ ; d.f. = 8;  $p = <0.025$ ).

#### Expulsions

Unlike the females, the young Abuko males received overt aggression from older animals and it was assumed that this aggression led directly to their emigration. All of the antagonism directed toward four of the emigrating young males and five emigrating females were totalled for approximately 4 months before they left Focal troop. The four males received aggression 61 times ( 29 threats, lunges, chases directed at Bimp, 11 at Mimp, 11 at Wimp and 10 at Imp). In contrast to this five young females who transferred received a total of 8 threats (Dunk received 3, Jiggaty Jaggaty 2, Ilf 2, Lib 1 and Pelf 0).

Like most other interactions observed in Abuko, the aggression directed at the young males was mostly intrasexual. That is, the three older males were responsible for 40 (65.5%) of the 61 episodes directed at the young males. Mr. Mean was responsible for 18 (29.5%),

Captain Crook for 8 (13.1%) and the subadult male Yunk for 14 (22.9%) of the aggressive episodes directed at the four young males. None of the aggression involved physical contact and thus never resulted in obvious wounds. However, it may have created psychological changes in the young males which in turn caused them to emigrate.

All 6 males who were evicted were evicted by adult males who were almost certainly not their father. For example, Wimp, Imp, Bimp and Mimp were conceived at a time when Jungi was the chief copulator. Gimp was possibly conceived outside Focal troop and Cid was almost certainly fathered by Yunk. All of the supposed fathers were dead by the time their own son reached late juvenilehood. The only male who was not expelled was Yunk and there is no way of knowing who his father was, since he was conceived before the study began. It is always possible, however, that Mr. Mean was his father and he was not expelled because his father was still alive (although certainly not of very high status - see Chapter 8, section on Aggression for Mr. Mean's status).

#### Exile Period

Once the Abuko young males were expelled, they spent months on their own, with each other or with alien males. The number of observations made on all known extratroop males, their group composition and the minimum amount of



time spent as extratroup males are listed in Table 67. Most of their time was spent alone, in single sex groups or as members of green monkey troops. Females rarely associated with these extratroup males. Given the number of males observed and the amount of time they spent in a state of exile, this situation was probably a regular and important feature of the life-history and development of most males in Abuko. In contrast to this there were no known solitary females or long-term extratroup females associated with male groups or other species.

During their exile, the young males appeared to spend their time shadowing other troops and their natal troop, monitoring the various social environments and looking for a 'vacancy'. The males were very well-attuned to the immediate existence of a vacancy. In all cases when males rejoined their natal troop, they did so quite soon after the disappearance or death of a resident male. For example, 41-month-old Yunk disappeared and was presumed dead on May 23, 1981; Bimp rejoined June 1st, Imp on June 15th and Wimp on June 17th. The same awareness of vacancy was shown in 1982 when the 41-month-old Imp died from falling on high tension wires. Sixteen days later Gimp rejoined Focal troop. The same was found in non-Focal troop males. Kinky spent 26 months travelling on his own and as a member of a green monkey troop. During this time he shadowed both Focal troop and PWD, neither one of which was originally his natal

troop. Within one month of one of the two PWD adult males disappearing, Kinky joined PWD and took over as chief copulator. All of the above observations suggest that the exiled males were in fact actively looking for vacancies during their exile and that they were well aware of what was occurring in various troops, although they were not physically present.

None of the males appeared to loose weight or suffer from any nutritional deficiency either before, during or after their exile. In fact, they were in what appeared to be obvious robust health. Given the constraints of working with a completely wild population, accurate measurements of stress, weight loss and nutritional deficiencies were not attempted. Information collected on a solitary male yellow baboon in Amboseli National Park, however, indicated that a solitary mode of life was not necessarily a period of ill health, low reproductive potential or nutritional deficiencies (Slatkin and Hausfater, 1976).

#### Immigrating Males

##### Aggression Received by Returning Males

There are obvious sexual differences in immigration procedures and results. These differences are very obvious when returning native daughters are compared with returning native sons. In June 1981 one native daughter, Nimp and three native sons, Wimp, Imp and Bimp returned permanently

to Focal troop. The data on returning males were completely different from those on Nimp (Table 71). Nimp was involved in significantly fewer aggressive interactions than Imp was involved in and therefore fewer than the other two males, Wimp and Bimp (Fisher's Exact test;  $p = <0.0001$ ).

The majority of the aggression was intrasexual with all of the aggression directed at the young males coming from other males, mostly from Captain Crook (highest status male at the time) who was responsible for 43 of the 48 aggressive acts received by the young males. It is assumed that Captain Crook, being the highest status male, had the most to lose by allowing these young males to re-enter their native troop and this accounts for his high rate of aggression.

#### Aggression Received by Alien Males

In spite of the high rate of aggression both given and received by native sons, all of those who attempted to return to their natal troop were 'permitted' to stay. This was not the case with non-native males who attempted to join Focal troop. In two cases males, who were either known or assumed to have come originally from other troops, attempted to join Focal troop. The detailed events surrounding the attempted transfer of each of these males is given below.

1. Bully, a young adult male in robust health, was first seen on June 27 1978 and remained in Focal troop for 25 days. A total of 193.75 hours of observation took place while he was there. During this time he engaged in no friendly interactions with the other three males, infants, juveniles, or mothers with dependent young. In contrast to the other three resident males, Bully was the only one to direct aggressive acts toward females. Furthermore, he was involved in less friendly interactions and significantly more aggressive interactions than the other adult males (Table 72: Fisher's Exact Test;  $p = <0.02$  for Crook and Mr. Mean;  $p = <0.004$  for Jungi). Bully was in no way spatially peripheral. Every night he slept with the main body of the troop, always 5-6 meters away from either a subadult or adult female. He was socially peripheral, however, compared to most other members.

On his 25th day with Focal troop, Bully was chased down to the ground by two adult females, Julie who had no known offspring, and Droopy (mother of +6-month-old female Dunk and the highest status female at the time), and an adult male Captain Crook (not the highest status male, but probably tied for joint second-place with Mr. Mean - see Chapter 8, section on Aggression) pinned Bully down to the ground and bit his head, thigh and scrotum for 10 minutes without stopping. During the entire biting session Bully could not move or retaliate because he was completely pinned

down. The attackers moved off after 10 minutes due to my presence and Bully stayed exactly where he was and died approximately 24 hours later.

A post-mortem showed that his right testicle was hanging by a thread and his left testicle had been completely ripped off. Severe multiple lacerations covered his tail and both sides of his thighs exposing bones and ripping major tendons and muscles. He appeared to have broken no bones and there were no wounds on his ventrum, which was not exposed during the attack. I was left with the impression that the attack only stopped because the attackers became aware of my presence.

2. Flattop, a young adult male, first seen on October 30 1979, proceeded to shadow Focal troop for 41 days. During this time he was groomed by the sexually-receptive adult female Volley and juvenile females, mounted juvenile females and was chased off whenever he was observed following Focal troop. In general, Flattop was involved in more antagonistic interactions than friendly interactions (Table 73: Binomial Test;  $Z = 1.46$ ; significant only at  $p = 0.1$  level).

On December 12 1979, after what appeared to be peaceful acceptance of Flattop's presence, I suddenly heard infant squealing and adult screaming and saw Solid (number-two female and mother of 11-month-old Simp) chase Flattop. Solid was immediately joined by 8 other females and the

adult male, Mr. Mean. Flattop was pinned down to the ground and the 9 attackers took turns biting and resting for a full fifteen minutes. It was a very coordinated attack, with all of them getting a chance to rest, and yet there was always a minimum of four individuals attacking at all times.

After 15 minutes the attackers realized that I was standing 1 m away and they stopped biting and rushed up trees. Flattop slowly sat up, dizzily moved off and disappeared until 16 hours later when I found him obviously hiding and well-camouflaged in a dense vine tangle. As the Focal troop passed within 10 m of him he did not move. As soon as they passed, however, he dragged himself slowly further into the vine tangles and disappeared. At one point I saw his wounds clearly; his left eyelid and eyeball were missing, copious amounts of thick fluid were continually dripping from his empty eye socket and there were massive cuts on his face. Furthermore, he appeared to have badly damaged his thigh and/or groin, which was covered with dried blood, and he was unable to move properly, having to drag himself around by his arms. I never saw him again and assumed that he either died or left Abuko permanently. It is doubtful, however, if he would have survived such severe mauling. Furthermore, the dangers found outside the reserve (see page 195) make it unlikely that he could have survived there.

In the attack on Flattop, I was again left with the distinct impression that they meant to kill him when they pinned him to the ground. After the attack I noticed Julie had lost half her lower lip, Mr. Mean had a 7.5 cm long scratch on his tail, Solid had a 7.5 cm cut in her groin and Nene's lip was swollen to at least twice it's normal size. The attacker's wounds were either caused by Flattop fighting back which seemed impossible since he was always pinned down to the ground or they were due to the fact that the attackers in their absolute frenzy sometimes bit each other without realizing it.

There were a number of similarities in both Bully's and Flattop's failed attempts to transfer. First both males received friendly overtures from immature females. The same situation occurred at the Gombe National Park between newcomer olive baboon males and resident females. Ransom (1981) suggested that this was due to the needs of the relatively unsocialized young females, with poorly developed non-familial bonds, to reduce the 'alienness' of the new male and the tension surrounding his presence and at the same time attempt to initiate the process of bond formation with them. Whatever the reason for the attraction, it was clear that juvenile females were not in danger when they associated with 'aliens'. This may not have been true, however, for other classes of individuals such as mothers and their infants.

The second similarity in both these cases was that attacks were initiated by mothers with immediate backup from other troop members. During the time Bully and Flattop were with Focal troop they were never approached by mothers or immature individuals younger than 1.75 years. Furthermore, during both attacks all infants and juveniles ran off and hid for the duration of the attacks and were seen nowhere near the scene of the attacks. In contrast, infants and juveniles did not disappear during intertroop aggressive encounters or aggressive interactions between resident members of the troop.

What precipitated these attacks? In both cases there is indirect evidence that these males were possibly involved in attempted, or even successful, infanticide. Bully's fatal attack came on the same day that Kunkle and nine-day-old, Kunk, disappeared. The next day Kunkle was later seen to join PWD troop without Kunk. Both the day before and immediately preceding Flattop's probably-fatal attack he was bitten and chased by Solid because her 11-month-old daughter, Simp, squealed.

Did Bully and/or Flattop attempt infanticide and were the coordinated attacks by the troop members a response to an infanticide attack? Not being Focal troop males and almost certainly not siring any of the Focal troop young, their degree of relatedness was quite low and thus they had no genetic investment in them. The quickest way for these



intruder males to invest genetically in the troop was to kill an infant, which would hasten sexual receptivity in the mother and then impregnate the mother (Sugiyama, 1967). Were the intruder males in Abuko attempting and failing to increase their reproductive success through infanticide? Certainly, two infants in Abuko (Munk and Tissue) had what looked like canine bites all over them when they died and the populations at Tana River (Marsh, 1979b) and Kibale Forest (Struhsaker and Leland, 1985) are either assumed or known to contain infanticidal males, as in fact, do most populations where female transfer is a regular part of the social system (e.g. mountain gorillas, chimpanzees, red and mantled howler monkeys, and the purple-faced monkeys).

#### Aggression Received by Assumed Alien Males

During this study two other cases of fatal male transfer were assumed from indirect evidence and the case histories are given below:

1. In October 1980 there was a tremendous amount of screaming and stranger-squeals (a particular vocalization given only when an alien male was in the vicinity) coming from PWD. When I arrived 15 minutes later, I found a dead young male lying on the ground. He had puncture wounds in his groin and an 11 cm long gash on his thigh exposing bones and ripped muscle and tendons. There were no marks on his ventrum and no blood underneath his fingernails indicating

that he was probably pinned down and not able to fight back.

2. Bend, a young adult male was first seen on October 18 1980, with green monkeys. He spent the next 5 months shadowing both Focal troop and PWD and was chased off whenever he was within sight of either troop. On April 11 1981 he was lying dead on the ground in an area used by both Focal troop and PWD. He had bite marks along his upper thigh, the back of his neck and scrotum. Again there were no marks on his ventrum and no blood under his fingernails.

In both these cases, the placement and number of wounds pointed to the fact that both victims must have been pinned down and that the attacks were coordinated by a number of individuals and not the work of a lone attacker. Furthermore, the lack of blood under the fingernails suggested that neither victim fought back.

All of these cases of known and assumed attempts at male transfer that failed contrasted greatly with the data collected on female transfer. There were no female bodies found with wounds which resembled colobus-inflicted wounds.

#### Successful Male Transfer

Occasionally non-native males are able to join troops and integrate themselves successfully into the social life of the troop. During this study two cases of successful male transfer occurred and a brief history of each is given below:

1. Mimp, who was originally from Focal troop and orphaned when he was 19.5-months-old, joined Question troop after a 15-22 month period as an extratroop male. The process he went through to become a member of this troop was not observed and, therefore, no data are available on how much aggression he received. Since he was the only orphaned male and the only male not to return to his natal troop, it is assumed that having a mother present makes it easier to return and that joining a non-natal troop for a male is no more dangerous than joining one's own troop without maternal support.

2. After spending 26 months as an extratroop male, Kinky joined PWD troop and spent at least two years as its resident male and chief copulator. Like Mimp, Kinky's transfer process was not observed so data are not available on how many antagonistic encounters were involved. It was assumed, however, that Kinky was not involved in serious fighting since he never displayed any wounds, injuries or displaced limbs or digits. Furthermore, none of the other PWD members displayed any signs of fighting. The only interactions observed were either friendly ones directed by and toward Kinky, or occasionally Kinky harassed young juveniles who attempted to interfere with his mounting of both receptive and nonreceptive females.

Although Mimp and Kinky successfully transferred to alien troops, this was unusual for Abuko males. Of the 6

males born during the 1978 - 1980 study period, and observed through subadulthood, only one joined an alien troop. Based on these data young Abuko males do not appear to be seeking change, unfamiliar troop mates on a permanent basis or unfamiliar ranges. Given the opportunity, they preferred to affiliate with the most familiar troop possible - their natal troop. This was probably because the effort involved in rejoining one's natal troop was strenuous but was never observed to involve serious injuries. The process of joining an alien troop, however, could well be fatal. Males, whether they rejoined their natal troop or an alien troop, appeared to have a more difficult time during the transfer period than did females.

With Mimp and Kinky it was assumed that their success in joining alien troops was not based on relationships and previous alliances; rather, it was probably based on their individual personalities and successful episodes and interactions which took place at the time of transfer. This assumption is based on the fact that Mimp joined a troop where there were none of his previous troop mates and this troop's range shared no common borders or resources. Thus his emigration from Focal troop and transfer into the alien Question troop led to a radical restructuring of all his relationships including the breaking of all previous bonds and the building and cementing of new bonds with aliens in strange environmental settings. Mimp resided in Question

troop for at least one year and possibly longer and thus obviously succeeded in cementing bonds with aliens.

Furthermore, Mimp was observed for a total of six hours after he joined Question troop and during this time he mated with fully-swollen females twice, was groomed by females 6 times and chased off members of a neighboring troop (Zoo troop) three times. This would suggest that he was fully accepted as a member of his chosen troop.

In contrast to Mimp and probably Kinky's situation, female transfer did not usually involve the breaking of all previous alliances. In fact, previous relationships and alliances held by the females were so strong that they may even have determined troop choice. Of course, the transfer of females also involved the complex process of change entailing the loss of some old relationships and the formation of new ones and the process of switching 'allegiance'. The main difference, however, was the fact that females did not sever all relationships since normally they either transferred with peers or selected a troop which contained previous troop mates from their natal troop. In short, the females used old relationships as buffers in new environments, while the males who actually did transfer went without buffers.

### Shadowing and the Male Perineal Organ

The male perineal organ closely mimics the first adolescent swelling of a young female colobus and becomes progressively less obvious as the male matures. This organ is the most obvious from birth through juvenilehood and thus, of the most use, behaviorally as well.

The function of this organ has not yet been determined. Kuhn (1972) suggested that it might help juvenile males share the social advantages conferred by a sexual swelling. Clutton-Brock and Harvey (1976) suggested that it might help subordinate males appease dominant animals in conflict situations. Both these suggestions assume that the advantage to the young male occurs during intratroup agonistic encounters amongst known individuals who are temporarily 'tricked'. While these suggestions are possible, particularly since young females receive less aggression than young males (Table 34), it is also likely that the organ might contribute to facilitating shadowing behavior during a young male's exile period.

During the shadowing of troops a young male was often watching, and possibly being watched by unknown individuals. In this situation he was viewed from a distance by 'aliens' who could have assumed that he was a young female with her first adolescent swelling in the process of transferring troops. This would have been to his advantage because it would have allowed him to get closer and determine, what if

any, vacancies were available. By treating him as a female engaged in the process of transferring troops he would not have been subjected to aggression. If he was immediately identified as a young male looking for a vacancy he would probably be chased and/or attacked since all shadowing males were chased off by troop members. During the shadowing of troops a young male would frequently be dealing with individuals who were unknown to him and thus could have been more easily 'tricked' by the presence of his perineal organ. Furthermore, the shadowing was frequently done at a distance making it even more difficult to distinguish the mimic from its model.

#### Inbreeding Avoidance Hypothesis

Dispersal of juveniles in birds and mammals generally (Greenwood, 1980), and in chimpanzees (Nishida and Kawanaka, 1972; Wrangham, 1975; Pusey, 1979), hamadryas baboons (Kummer, 1968) and gorilla (Harcourt, 1978; Stewart and Harcourt, 1987) females in particular, it is assumed to be a behavioral strategy to avoid inbreeding.

Originally I interpreted female transfer in Abuko as of no importance to the avoidance of inbreeding (Starin, 1981). This was based on the assumption, now known to be incorrect, that males as well as females routinely and permanently leave their natal troop. Much of the evidence collected since, however, indicates that while both sexes do indeed

leave their natal troop, males routinely return to assume breeding roles. Therefore, since females accounted for the majority of genetic migration, at least some inbreeding was avoided or outbreeding was accomplished, through the movement of females away from their natal troop. In theory, three forms of deleterious inbreeding could have occurred: mother-son, sister-brother and father-daughter.

In Abuko, transfer patterns had no effect on the avoidance of mother-son inbreeding. In the Focal troop there were five potentially-incestuous pairs of sexually-receptive mothers and their mature sons and at no time were they observed displaying any sexual interest in each other. In fact, it was not unusual for a mature son to lie with his face less than a few mm. away from his mother's swelling and not attempt to poke and/or sniff the swelling. If the mother had been another female this would have been an automatic and constant activity. As with male rhesus monkeys (Sade, 1968) when each male matured, he copulated with friends of the same age and status as his mother, but not with her.

In mother-immature son pairs, the avoidance of sexual activity was discouraged by the mother. On three occasions mothers were observed threatening their large infant and small juvenile sons when they attempted to mount and thrust. In all three cases the sons immediately dismounted and either nursed or presented for grooming. Thus, either role



conflict or mother-son dominance-submission was ultimately responsible for the inhibition. Transfer patterns played no role in the avoidance of mother-son mating simply because mothers and sons frequently ended up as members of the same troop.

Sister-brother mating occurred, but was infrequent and it only involved probable half-siblings. Most of these matings were avoided by the separation of most of the immature females through migration and the attachment of most of their probable paternal half-brothers to their natal troop. When the sexually-mature half-siblings did reside in the same troop at the same time, they mated and two females (Nimp and Simp) are assumed to have conceived after mating with their half-siblings, since all of their observed matings which took place when they conceived were with Bimp or Imp (their probable half-siblings). Of the three forms of inbreeding, however, the mating of half-siblings is genetically the least deleterious and, in Abuko the most commonly practised.

The third form of inbreeding, that between fathers and daughters, appeared to be infrequent because most young females had dispersed from their natal troop before they could possibly mate with any male old enough to have fathered them. Furthermore, it is unlikely that a father would be high enough in reproductive rank to mate with his daughter or even alive when she matured, making father-

daughter mating even less likely.

From the beginning of the study until March 1982 each breeding season a different male was responsible for the majority of matings with sexually receptive females (Table 41) suggesting a short tenure as chief copulator. For example, during the 1978 breeding season, Jungi was the chief copulator, during 1979 and the first half of 1980 Captain Crook was the chief copulator, Yunk took on the role for the later half of 1980 and Bimp took on the roll in 1981. These data appear to suggest that each breeding season one male is the progenitor of the following birth season's offspring. This would mean that infants born during the same birth season share a common patrilineage and thus are not merely peers but also half-sibs. These data further suggest that fathers are rarely, if ever, in a position to mate with their own daughters. By the time their daughters are sexually mature they are no longer chief copulators. The suggestion that one male is basically responsible for most of the copulations, receives further support when the data in Table 41 are studied with the birth data in Table 28. When Captain Crook, who was incapable of achieving intromission, was actually the chief copulator, no infants appeared in the following birth season except for Volley's infant (Vaby) who was probably conceived in PWD troop (see pages 171-172).

In summary, mother-son inbreeding was possible but

actively prevented by the mother and quickly learned by the son. In contrast to this, father-daughter inbreeding was virtually impossible primarily due to transfer of females out of the natal troop, but also for demographic reasons similar to those proposed for Neolithic humans (Slater, 1959) Amboseli baboons (Hausfater, 1975) and Venezuelan red howler monkeys (Crockett, 1984). The mating of half-siblings was possible, although due to transfer of most females away from their half-sib brothers it was infrequent. When circumstances permitted, however, the mating of half-siblings was neither actively prevented nor avoided. It is interesting to note that the only form of inbreeding which was frequently possible, but had both an active discouragement and learning component, involved individuals who had a known and recognized relationship - mother and son. In the father-daughter and half-sibling relationships, where the kin ties were probably not recognized, external circumstances such as transfer and demography played an important role in the avoidance of inbreeding. In any case, it has been argued that a degree of inbreeding may, in fact, be beneficial (Shields, 1982; Bateson, 1983). While it remains clear that emigration helps to minimize any costs that inbreeding might incur, it is probably fair to say that avoidance of inbreeding is not a significant cause of emigration in primates (van Schaik, 1983; Crockett, 1984; Waser et al, 1986; Dunbar, 1988).

Use of Other Species During Transfer

On three occasions members of Focal troop chased a troop of patas monkeys out of the reserve. During one of these chases, the young female, Velf, who had originally been one of the active chasers, actually joined the running patas. She ran with the patas for over 50 meters until they all reached the PWD colobus troop where she remained for the rest of the day. Velf ran in the middle of the patas troop. It appeared as if she was using the patas as a shield or shelter against any potential danger and/or a screen against being seen by PWD members before she saw them. The road she was running on was not an area generally used by her troop although it was frequently used by cars, people, dogs - possible dangers from a colobus viewpoint. Presumably she was safer being flanked by patas than she was making this journey on her own. On another occasion a young female left her natal troop, joined a patas troop as it foraged through her home range and left the patas troop as it merged with a neighboring colobus troop.

Two other young females were also seen to spend brief periods with green monkeys in the months immediately before their transfer out of their natal troop. The young female, Nimp spent three hours on one day and two hours and one night with a troop of green monkeys two months before she left her natal troop to temporarily join Zoo troop. On another occasion, Simp spent five hours with a troop of

green monkeys just three weeks before she left her natal troop to join Middle troop.

Young colobus males spend up to two years on their own before they locate a 'vacancy' and either return home to their natal troop or join a new troop. During their exile period all young males were seen associating with green monkeys from time to time (Table 67). One young male, Kinky, actually spent over two years as a full-fledged member of a green monkey troop. feeding, resting, playing and sleeping with them day after day. In fact, it was only when he was surrounded by green monkeys that he was able to successfully 'spy' without being seen. On the rare occasion when he was on his own he was immediately spotted and chased off by screaming females.

By traveling with another species instead of travelling on their own, the young colobus are increasing the number of vigilant eyes and individuals and so there is obviously less chance of predation. However, it is also possible that transferring females and exiled males need a screen when they travel on their own between troops. By travelling with another troop - albeit another species - they would be less visible and their own locomotor sounds and odours would be camouflaged. Certainly, I could tell the difference between the sound made when a colobus leapt through the trees and a green monkey leapt through the trees. I could also smell where colobus had been. I assume that the colobus were far

better than I at differentiating sounds and smells. Therefore if a colobus - male or female - needed to shadow a troop without being seen, heard or smelled, it would have a better chance if it travelled with a group of patas or green monkeys where presumably the other species' smells and sounds predominated.

#### Some Comparisons with Other Red Colobus Populations

Like the red colobus females in Kibale Forest and Tana River, the Abuko females routinely and voluntarily transfer between social units. At all three sites the process was fairly rapid and involved a minimal amount of aggression and competition. One obvious difference between sites, was the age of the migrants with the Abuko and Kibale females moving as juveniles and the Tana River females migrating as adults. While the movement of juveniles is routine in both male and female migrants throughout the animal world (Greenwood, 1980; Wilson, 1975), the wholesale movement of adult females is unusual. Marsh (1979b) has suggested that this is due to the females' effort to counteract infanticide and effect mate choice. While Marsh's hypothesis may be appropriate for the Tana River red colobus, it may not be valid for all other cases. For example, at Kibale Forest infanticide occurred but it was not followed by mass adult female transfer (Struhsaker and Leland, 1985). At Abuko native son and alien male replacements did not lead to substantial

female emigrations and females did not form bonds with males suspected of being infanticidal. Furthermore, intruder males were not observed to join Focal troop successfully and, therefore, gained no direct reproductive advantage by their infanticidal actions. In fact, they were attacked and fatally wounded by the resident troop members and thus risked far more than they gained.

Coincidentally, four other species exhibit the pattern of female transfer between social units, infanticide by adult males and killing of intruder males by residents (chimpanzees: Goodall, 1977; 1986; purple-faced langurs: Manley, 1986; mantled and red howler monkeys: Crockett and Eisenberg, 1987; Clarke, 1983; Crockett and Sekulic, 1984). The functional connection, if any, among these three behavioral actions is not clear. However, a look at the other red colobus populations may help to detect connections between some of these actions.

At red colobus sites where males generally matured and remained within their natal troop (Kibale Forest) or left for varying lengths of time and then returned (Abuko and Gombe Stream), troops consist of a closely-related group of males who were not observed to attempt infanticide and were not in turn fatally wounded by their co-residents. The one exception was in Kibale Forest where a male who was raised, but not conceived in the study troop, committed infanticide (Struhsaker and Leland, 1985). In contrast to this, at

sites where alien males attempted to join strange troops (Tana River and Abuko), infanticide was observed or suspected and females either left their troops (Tana River and Abuko) or fatally attacked the intruder (Abuko). Either migrating or attacking led to the same result: females did not associate with certain males and actively selected others.

The Abuko strategy of attacking probably involved more risks, but perhaps not as many as would occur in other populations of red colobus. Firstly, the red colobus in Abuko is less sexually dimorphic than the other observed populations and therefore females are better able to fight males and defend their young. Secondly, Abuko females allied themselves against intruder males. In this, they resemble the patrilocal, matrilineal, multimale baboon groups where females are closely related (Busse and Hamilton, 1981; Collins, Busse, and Goodall, 1984) as opposed to the other red colobus populations which are assumed to contain unrelated groups of females (Struhsaker and Leland, 1987).

What is clear from the Abuko data is that probably-unrelated males attempt infanticide and that probably-related females cooperate in defending their young. Furthermore, related males are not suspected of attempting infanticide. This would tend to suggest that infanticide is not an 'automatically inherited trait' as suggested by Hrdy



(1981). Rather, it is a behavioral strategy used by unrelated males in certain situations and thus by either killing or boycotting these males, the females are not destroying their sons chances of inheriting such a trait.

The one generalization that does appear to hold is that males and females pursue different sex-specific strategies and tactics for successful reproduction in terms of troop affiliation. However, it is virtually impossible to generalize about what red colobus males do or how females act. Each population of red colobus presents a complex pattern of intersexual variation representing its own specific evolutionary history and current socioecological context.

### Summary

1. During the course of this study 12 females permanently emigrated, 10 females permanently immigrated, 6 females temporarily moved into or out of Focal troop, 6 young males were expelled and four of these males returned home to Focal troop.

2. All ages and reproductive stages were represented by transferring females, but juveniles clearly predominated. Males, however, emigrated at a younger age than females.

3. Social and possibly psychological factors appeared to influence female transfer patterns and mate choice.

4. Female departures appeared to be voluntary and not the result of competition and aggression, but young males left because of aggression received within the confines of their natal troop.

5. Juvenile female peer migration (which resulted in females maintaining bonds in their chosen troop) may have helped combat the mild aggression young immigrants experienced when they first joined a new troop. This peer migration resulted in a group of probably-related, allied females inhabiting the same troop at the same time.

6. In terms of troop choice the search for 'strange' males did not appear the most important factor. The search

for familiar females may on the other hand, have been an important factor. Upon joining a troop females used previous alliances and relationships as 'buffers' against mild aggression, while males did not have such relationships and thus their success in transforming troops was based on their individual personalities and successful episodes and interactions which took place at the time of the transfer. Given the opportunity and the necessary 'vacancy', however, males preferred to join their natal troop, probably because joining a 'strange' troop could be fatal. Sexually immature females preferred non-familiar troops and mature and sexually-receptive females preferred semi-familiar troops.

7. Red colobus in Abuko display a form of fusion-fission whereby nursery groups break off from the main body of the troop and travel on their own for days at a time. The females which make up these subunits may, in fact, be originally from the same natal troop and maintain long-term bonds.

8. During the transfer process, females appeared to move immediately between troops while males spent months (even years) as solitaries looking for vacancies. There is a possibility that the male juvenile's perineal organ affords him some advantage during his period of exile and shadowing by allowing him to get close to strange troops.

9. It is assumed that female transfer has a role to play in the avoidance of certain forms of inbreeding in

Abuko. It is not, however, the only reason for, nor the major cause of, transfer. Rather, it is assumed that social factors are immediately responsible for transfer and the avoidance of inbreeding is an indirect result of this.

10. Transferring females and exiled males may be using patas and green monkeys as screens so that they can get close to other red colobus troops and determine the suitability of the troop as a potential place to reside.

11. It is assumed that an alien male's attempts to kill infants and the killing of intruder males are related.

12. The lack of sexual dimorphism and unusually high degree of female cooperation at Abuko against alien males reduces the risks to females of fighting males.

## Chapter 11. INTERTROOP ENCOUNTERS

### Introduction

Since red colobus troops do not exist in isolation from one another, and encounters between troops can be as complex, subtle and important as any encounters that occur within the troop, it was considered essential to characterize these behaviors accurately.

In this chapter the home range of the Focal troop and intertroop encounters are described. More specifically, what type of encounters occur? Who takes part in the encounters? How does female behavior differ from male behavior during the encounters? How do transfer patterns relate to intertroop encounters? How does the situation compare at the various red colobus sites?

The data used in this chapter were taken on an ad lib basis throughout the study. Since comparisons in this chapter are made with data collected at Kibale Forest, Gombe National Park and Tana River, I will summarize basic information on intertroop relations from these three sites.

At Kibale Forest several troops shared the same range with no sign of territoriality (Struhsaker, 1975). Relations between these troops were variable and ranged from apparent tolerance to spatial supplantation. The outcome of

the encounter did not depend on the location; rather, it seemed to depend on the number of males and/or on the identity of the particular individuals taking part. Only adult and subadult males took part in intertroop encounters; females and immatures actually appeared to avoid these encounters. During the intertroop encounters, the cohesion within the male coalitions was most prominent. It has been argued that these male coalitions defend females as reproductive resources against other male coalitions (Struhsaker and Leland, 1987), which is analogous to the hypothesis offered for chimpanzee male coalitions (Wrangham, 1979).

At Gombe National Park the amount of overlap was not quantified, but appears to have been restricted to the peripheral parts of the range (Clutton-Brock, 1972). Relations between troops were variable and ranged from peaceful intermingling to spatial supplantation.

The Tana River red colobus display relatively little overlap (about 33% overlap with the most intensively-used areas not shared) (Marsh, 1978). Relations between troops were variable and ranged from apparent tolerance ('neutral' encounters) to spatial supplantation. Only males took active parts in the encounters; females only called.

In many other species where females transfer between social units, home ranges overlap to a considerable extent: *P. hamadryas* (Sigg and Stolba, 1981), *A. seniculus* and *A.*

palliata (Glander, 1980; Crockett and Eisenberg, 1987), gorillas (Fossey, 1974; Fossey and Harcourt, 1977), chimpanzees (Goodall, 1986), and Nasalis (Bennett and Sebastian 1988).

#### Home Range Size and Overlap with Neighboring Troops

The known home range size and shape for Focal troop, PWD and Middle troop are given in Figure 6. From July 1978 through September 1982, Focal troop used an area of 33.5 ha, PWD used an area of 10.9 ha (2 ha were outside the reserve but still in a protected area) and Middle troop used an area of at least 21.3 ha (their total range was not known)

There was extensive home range overlap (Figure 6). Focal troop overlapped with PWD in 6.0 ha, with Middle troop in 13.4 ha and with PWD and Middle troop for a further 0.1 ha. Of the 33.5 ha home range, only 40% was used exclusively by Focal troop. PWD with its much smaller range of 10.9 ha used 38.5% exclusively. The data presented contain no lacunae since every part of all the home ranges was criss-crossed over and over again.

Troop densities were quite variable; ranging from approximately 0.79 animals/ha for Focal troop to 2.3 animals/ha for PWD. Ecological variables, particularly in terms of food availability, probably account for much of the difference. For example, unlike Focal troop, PWD did not have a wet-weather clearing (see Table 6 for description of

various habitat types). Focal troop had more types of habitat than PWD, but far less swamp and no access to the 2 ha cashew plantation bordering the reserve but still protected by the conservation department.

The troops in Abuko are living in a relict forest patch - virtually isolated on an island. Focal troop used 0.03 ha outside the reserve. This small area bordered the reserve, contained two Parkia biglobosa trees and was used three times. Each time it was visited by no more than 5 individuals - always Captain Crook and pubescent or about-to-transfer females. None of the other troops were ever seen using unprotected areas outside the reserve or crop-raiding from the surrounding fields.

#### Form and Type of Encounter

##### Neutral Encounters

If the Focal troop was within 50 m of one of its neighbors without resorting to aggressive/friendly interactions, gestures, displays or calls, then a 'neutral' encounter was assumed to have taken place. This distance (50 m) is for comparison with Struhsaker (1975), Marsh (1978) and Isbell (1983) only and does not imply any particular behavioral significance. Neutral encounters were recorded whenever they occurred. Focal troop was involved in a neutral encounter with at least one of its neighbors (PWD or Middle troop) on the majority of the days they were



observed. From March 1980 through March 1981 158 days were spent recording intertroop encounter data. During this time there were 56 neutral encounters with PWD and 46 neutral encounters with Middle troop. This is equivalent to one encounter every 2.8 days with PWD and every 3.4 days with Middle troop. Statistically a neutral encounter occurred with PWD and Middle troop with equal frequency (binomial test:  $z = 0.99$ ;  $p = 0.32$  two-tailed). During these neutral encounters the neighboring troops appeared to be tolerant of one another. Members of different troops watched each other and occasionally responded to one another's alarm calls. These neutral encounters were obviously less costly/time-consuming and possibly more informative than an active hostile encounter. About-to-transfer females, who can sit and watch PWD and Middle troop residents interact within their own special network and assess the infrastructure, size and composition of the troops, probably find these neutral encounters particularly important.

#### Hostile Encounters

From January 1980 through March 1982, Focal troop was observed in 39 hostile encounters with PWD and 30 with Middle troop. The Focal troop had hostile encounters with their two neighbors with equal frequency (Table 74: two-sided binomial test:  $Z = 1.08$ ;  $p = 0.30$  - components of a hostile encounter are given in this table). A hostile encounter occurred every 46.8 hours and ranged from

avoidance to chasing and spatial supplantation. It is probable, however, that the passive encounters such as avoidance and detouring, without intertroop calls occurred more frequently but were not observed as easily as the more aggressive and vocal encounters.

An interesting component of most of the hostile encounters was the alternation between hostility and neutrality.

The following description by Hrdy (1977) for the Hanuman langurs at Abu fits perfectly for the Abuko red colobus intertroop encounters:

"Furious spats during which nothing appears to be either won or lost, interspersed with periods of adjacent foraging so calm that a monkey watcher on survey .... would record a single large troop .... typifies the relations between .... troops"

The capacity to ignore (accept?) the presence of a neighboring troop may be due to familiarity which is probably due to the frequent neutral encounters where individual recognition, at least by some members of neighboring troops, occurs.

Because of the large overlap (over 60% of Focal troop's range was shared with PWD and Middle troop - Figure 6) and sharing of major food and sleeping trees (Table 67), the

Abuko red colobus did not appear to be territorial as defined by Burt (1943) or Wilson (1975). While all encounters occurred in overlap zones, the exact location of the encounter did not affect the outcome. The Focal troop supplanted Middle troop throughout Middle troop's range, even in the most heavily-used areas up until February 1981. After this period Focal troop never won an encounter against Middle troop, regardless of where they occurred. Furthermore, in April 1981 Focal troop had four encounters with PWD troop in the same area. Focal troop lost one, won one, and two encounters resulted in stalemates. Clearly, the outcome of an encounter between PWD and Focal troop was not rigidly dependent on the location.

Larger troops, or troops containing more males, did not have an advantage over smaller troops or troops with fewer males. All the encounters lost by Focal troop occurred when it was larger in total size and contained more males than both its opponents. In fact, Focal troop was always larger than Middle troop, which never contained more than 19 individuals and never had more than one resident adult male at any time.

Generally, it was impossible to show what colobus were gaining or losing when they engaged in conflicts. However, during one 7-8 hour encounter Middle troop slowly and constantly displaced Focal troop throughout its range. During this encounter, Focal troop was never able to gain an

advantage; rather, each time Middle troop moved toward Focal troop, Focal troop moved off. This resulted in an immediate gain for Middle troop for one day. The next day, however, Focal troop was back using the same area and continued to do so for at least four months without another intertroop encounter in this area. Despite the expenditure of much time and energy by Middle troop members, there were no permanent gains or losses for either side. Middle troop, however, gained knowledge of Focal troop's resources and was able to demonstrate its ability to dominate Focal troop. The outcome of intertroop encounters was often unpredictable; a troop could be aggressive with its neighbor in the morning and neutral in the afternoon.

#### Behavior of Males

All males from the age of 13 months upwards took part in intertroop encounters. Young males did not initiate encounters on their own. During a conflict, subadult and adult males called, threatened, displayed, chased and counterchased. Squealing younger males followed closely behind, often forming a 'cheer-leader squad' during the chasing and counterchasing. In some cases the young males followed so close that the older males actually tripped over them during the chases.

The males' aggression generally appeared to be directed to other males in the opposing troop. None of the Focal

troop males were seen singling out females from other troops and chasing toward or displaying at them. Their movement always appeared to be directed toward another male or the main body of the troop which contained the male. On three occasions, however, the PWD male, Kinky, singled out Focal troop females and chased them away from his troop. In all three cases the adult female, Solid (second highest-ranking female), followed by other Focal troop females had purposefully moved toward PWD long before Kinky chased them. Thus, it is difficult to pinpoint who initiated the conflict.

Once two troops were in close proximity, if an aggressive encounter was going to occur, Captain Crook (both during his reign as alpha male and after his fall from this position) was usually (93% of the time) the first male to display, threaten and/or chase. Mr. Mean provided the physical and/or vocal back-up, but never got as close to the opposing troop as Captain Crook. In the PWD troop, one male, Midfin (the highest ranking male), initiated all the aggressive encounters while the other male, Budha, provided the back-up. After Buddha disappeared and Kinky joined PWD troop, Kinky became the highest-ranking male, chief copulator and the initiator of intertroop encounters while Midfin assumed the back-up position during intertroop encounters. In all cases, when two males took part in an intertroop encounter, the back-up male also appeared to keep

an eye on the resident females. If a juvenile or sexually receptive subadult or adult female began to run toward the opposing troop, the back-up male ran after her and groomed and/or mounted her. he never attempted to use aggression or herding.

Focal troop clearly won 35 encounters and lost 6 (Table 75 ) All but two of the winning encounters involved Captain Crook as the primary antagonist and Mr. Mean in the back-up position. Most of the losing conflicts, and the majority of the avoidances, occurred after January 1981 (Table 75 when Mr. Mean began to deteriorate physically and socially (see Appendix D) and his back-up position was taken up by the returned younger native sons who, although they were of higher status than Mr. Mean, possibly lacked experience, practice and/or knowledge of the opponents. Focal troop won significantly more encounters from January to December 1980 than from January 1981 to March 1982 and lost more during the second period than during the first period (Table 75 - This statistical analysis does not include encounters which consisted only of avoidances, since this is probably a factor of observer luck and not of actual behavior).

Before January 1981, engaged in a common action against another troop, Captain Crook and Mr. Mean frequently shifted closer together before Captain Crook initiated his attack. These two males were never observed exchanging aggressive gestures when threatened by or threatening

outsiders; rather, they united together against the outsiders. During the entire study, these two males were only observed to sit within touching distance on 7 occasions and all of these occasions occurred during intertroop encounters.

In contrast, the period during and after Mr. Mean's deterioration contained daily aggressive interactions between all the resident males. These intratroop fights sometimes continued during intertroop encounters. In two cases (June 1981 when Bimp, Imp and Mimp returned to Focal troop) younger males were attacked by Captain Crook and the female Round just before and during an intertroop encounter and in both cases the attacked younger male did not offer support for his troop during the encounter. In one of these cases the Focal troop clearly lost, while in the other case the encounter ended in a stalemate. The instability continually present within the male hierarchy could easily have been noticed by members of the neighboring troops and may have been responsible for Focal troop losing intertroop encounters.

The negative outcome of the encounters, which occurred after Mr. Mean's deterioration (Table 75), could have been due to his inability to give immediate back-up support, a lack of coordination, cooperation or cohesion between Captain Crook and the younger males and/or a general instability within the troop due to the influx of the three

younger returned males and the deteriorating relationship between Captain Crook and the ailing Mr. Mean.

Coincidentally, while Focal troop was undergoing a period of instability, Kinky, a long-time shadowing male (see, page 143) joined PWD troop and became the main protagonist during intertroop encounters. Thus, it is also possible that Kinky's ability as leader in intertroop encounters was superior to his predecessors. Though it is not possible to know exactly what Kinky was watching when he was shadowing Focal troop and PWD for 26 months, it is assumed that he had an opportunity to frequently and accurately assess opponents and perhaps gain fighting experience. Certainly, he was observed shadowing Focal troop on 24 occasions and each time he was seen by Focal troop members he was chased off. Also, he was younger and possibly stronger than Captain Crook, his main opponent.

Affiliative interactions between adult males and infants took place during intertroop encounters. Of the 105 times infants were carried by nonrelatives adult males were the carriers and initiators of the carrying 12 times and during 11 of these carrying instances, an intertroop encounter was actually taking place. Furthermore, on three occasions a PWD adult male was seen carrying a PWD infant during encounters with Focal troop. A similar type of behavior has been seen in Barbary macaques (Deag and Crook, 1971; Taub, 1980) and various baboon populations (Parker,



1980; Smuts, 1982; Strum, 1984).

Affiliative interactions were also observed to take place between adult males and immature and cycling females during intertroop encounters. Of the 110 times Mr. Mean and Captain Crook groomed adult and young females, 27 (24.5%) of these interactions occurred during intertroop encounters or immediately after hearing calls from a neighboring troop. In this case the friendly interactions may be an attempt to stop females from transferring to the opposing troop.

#### Behavior of Females

Like the males, females did not take part in intertroop encounters until they were 13 months of age. The young females only took part if their own mother was taking part in the encounter; they did not automatically run squealing after the combatants like the young males. Females in all reproductive states, except for mothers with dependent young, took part in intertroop encounters.

The females' aggression appeared to be directed to males in opposing troops. None of the females were observed singling out females from other troops and chasing toward or displaying at them. Like the males, the females directed their aggression toward the resident male/males or the main body of the troop which contained the males. On one occasion Nene and her 11-month-old daughter and Head and her

9-month-old daughter spent two days out of sight and sound of their own troop but within 25 meters of Middle troop. They appeared to completely ignore Middle troop and all the Middle troop members appeared to ignore them as they foraged, groomed, played and slept.

The behavior of different females during conflicts was variable. Solid (second highest-ranking female) was responsible for initiating counterchases with PWD when no Focal troop males were present on 3 separate occasions. Nine times sexually mature, but not receptive, females (Solid once, Droopy twice, Round 6 times) partnered Captain Crook during his initiation of an encounter. In fact, Captain Crook (no longer highest-ranking male) and the respective females were so well coordinated in all nine cases, that it was not possible to determine which of the two actually initiated the encounter. In three of these nine conflicts, Round (once when she was pregnant) and Captain Crook, with vocal assistance but no physical assistance from other troop members, were able to spatially supplant an entire troop on their own. On two occasions mothers provided vocal and physical support for their subadult sons during encounters with Middle troop. The mothers, Wild and Inca, screamed, displayed and followed closely behind Mimp and Imp, providing audio-visual and physical support for over 30 minutes.

The reaction of females toward an opposing troop

appeared to depend on whether or not an individual had previously been a member of the opposing troop. For example, during two encounters with Middle troop, all the females, except for Self who had previously been a Focal troop member, ran off when Focal troop aggressively approached. Self, with a one-month-old infant, continued feeding, appearing to be unconcerned about the displaying, screaming, and threatening which went on around her.

Furthermore, during 4 encounters with PWD, the females who had once been part of the Focal troop did not move off when Focal troop arrived. In all 4 cases, all the other adult females (7+) ran off leaving the previous Focal troop adult females (Lip, Pelf and Jiggaty Jaggaty) sitting amidst their previous troop mates, feeding but not interacting.

On three other occasions, PWD females (Lip, Pelf, Jiggaty Jaggaty) who had once been Focal troop members, threatened, screamed and displayed at their previous troop mates. Only females who did not have mothers left in the Focal troop showed aggressive behavior toward Focal troop. Self and Velf, whose mothers were resident in Focal troop, ignored all encounters. If they were feeding when an encounter occurred they kept feeding. If they were resting, they kept resting. Regardless of whether they had relatives present or not, however, no previous Focal troop female was seen to run off when the Focal troop chased her new troop; she simply was not intimidated by well-known aggressors.

She either threatened (if no mother was present in opposing troop) or ignored her previous troop mates (if her mother was still a member of the opposing troop).

Females about to transfer may have used encounters (neutral and agonistic) as an easy way of closely assessing the social environment of a troop. On three occasions Middle troop females did not move off when their troop was engaged in an encounter with Focal troop. Within one week all 3 of these females had left Middle troop - one of them joined PWD while two of them joined Focal troop.

Newly-transferred females initiated encounters on three occasions. Twice females who had just joined from PWD initiated an encounter with Middle troop, while once a female who had just joined from Middle troop initiated an encounter with PWD troop. In all 3 cases the newly-transferred females (they had been resident in Focal troop for less than one month) ran toward the neighboring troop, 3-5 other members of the female's new troop rushed after and then past her and the two troops engaged in agonistic interactions until the newly-transferred females ran back to Focal troop. As soon as the female returned to Focal troop, all aggressive acts stopped and both troops fed and rested quietly without interacting for a further 1.5 - 3 hours. During these encounters no spatial supplantation occurred and no aggression was directed toward the initiating females.

Transferring females initiated encounters and used these interactions as a time and place to transfer between troops. Seven (50%) of the female immigrants were observed in the process of transferring and all did so during an intertroop encounter. In three of these cases, the immigrating female initiated the encounter by moving away from her own troop into the Focal troop. She was immediately followed by an adult male and 1-5 females of her own troop and these individuals engaged in screaming, threatening, displaying, chasing and/or counterchasing with members of Focal troop. As the immigrant moved further away from her old troop and moved closer to Focal troop females, the conflict lessened. It ended with the immigrant leaving her troop, moving into and then off with Focal troop individuals while her old troop gradually moved off in the opposite direction.

Focal troop emigrants were also seen initiating encounters during their transfer period. Volley, Velf and Scarty spent months travelling between Focal troop and PWD (see pages 171-172 and 192-193) and on 4 occasions they switched troops during encounters. On three of these four occasions the transfer was the reason for the encounter. The switching females were followed by others and when the members of the opposing troops met, screaming, displaying and threatening occurred immediately. The encounter ended when the females had moved out of sight of one of the two

troops.

Data presented above suggest that females moving between troops create a situation where members from neighboring troops move closer and scream at, display, threaten, chase and counterchase each other. The females who initiated the encounter through their movement, appear to be immune to the aggression. In all 9 encounters initiated by the transferring females, spatial supplantation did not occur; rather, the two opposing sides gradually moved off in opposite directions with one side gaining a female and the other side obviously losing a female. During this study it was difficult to determine why neighboring troops seek each other out. In only 9 of the active aggressive encounters ( $N = 65$ ) was there a 'reason' and in all cases it was assumed to be a transferring female who was bringing the troops together.

There is a suggestion that the relationships between various troops could be based to some extent on how many females in a troop originally came from the opposing troop. Since females are not intimidated by previous troop mates, a large influx of Focal troop females into one of the neighboring troops might create a situation where Focal troop would consistently be unable to intimidate the females and thus might even lose many of their encounters. There was some evidence that this, in fact, does not occur. Between April and June 1979 four Focal troop females

transferred to PWD and all the conflicts between the two troops for a 6-month period after their transfer either resulted in a stalemate or were won by Focal troop. A possible explanation for this is that when females first transfer into a troop they have very little influence on the older residents. However, as they mature and acquire more status, they have more influence. This might mean that, as they acquire influence, their lack of fear of Focal troop members during conflicts would have more impact than when they first transferred. There is some evidence, in fact, that this may occur. From January 1981 when Focal troop began to lose encounters with PWD, at least 33% of the adult females in PWD were originally Focal troop members. None of these females ran off when Focal troop approached. Their lack of intimidation may have had some impact on the other residents, which in turn may have affected the outcome of the conflict. This would not, however, account for the fact that during the same time period, Focal troop lost encounters with Middle troop, yet Middle troop only had one adult female who was originally from Focal troop.

#### Comparison with Other Red Colobus Populations

One of the obvious differences between Abuko and the other sites is the active involvement of females in virtually all agonistic intertroop encounters. A possible correlate for this difference in female behavior is the

degree of sexual dimorphism between the various subspecies (see pages 8-9) with the Abuko population showing little or no body size dimorphism while the other subspecies display an obvious body size dimorphism. If a female's ability to act aggressively toward adult males depends upon the degree of sexual dimorphism within a given species, then the Abuko female would be expected to be more aggressive than the other, more sexually dimorphic females. As a consequence of this difference in sexual dimorphism, it is possible that Abuko females exert more of an influence than do other females during intertroop encounters. An in-depth study of what causes sexual dimorphism in the first place and whether it is a cause or consequence of certain behavioral patterns was beyond the scope of this thesis.

A second explanation for this difference in female behavior is the degree of relatedness between females in opposing troops and this may be related to the fact that Abuko is virtually an island where the five troops contained within it are more closely related to each other than are troops at other study sites. This high degree of relatedness means that the individuals on opposing sides are known to and not intimidated by, each other and are thus more willing to threaten than flee from each other. Furthermore, individuals on the same side are perhaps more willing to come to their troop mates defense.



### Transfer Patterns

There appears to be a relationship between particular behaviors observed during intertroop encounters and the specific transfer patterns found in Abuko.

It is possible that the affiliative interactions between adult males and immature and cycling females during intertroop encounters stop females (at least during this particular encounter) from transferring to the opposing troop.

Smuts (1987) has speculated that the males' use of infants in 'agonistic buffering' signals to females that he will take good care of her infant if she mates with him. Carrying this speculation a step further for the Abuko colobus, it could be that the male is signalling females in the opposing troop that if they transfer to his troop he will take good care of their infants, that this is a 'good, safe' place to mate and raise young and that he is not an infanticidal male.

All of the affiliative behaviors displayed by males at intertroop encounters suggest that they use the encounters as advertisements to potentially-transferring females, signalling those which belong to neighboring troops that they should join and those who belong to their own troop that they should stay.

Females, on the other hand appear to use the encounters to assess other troops' suitability. Furthermore, females appear to create intertroop encounters and use them as points in time to transfer.

There is some evidence to suggest that a female's past troop allegiance may affect the actual outcome of the intertroop encounter.

All of the evidence on female behaviors during the intertroop encounters in Abuko appears to contradict the suggestions put forth by Wrangham (1980) and Cheney (1987). They predict that females who transfer between social units should ignore encounters and take no part in defense. This prediction, of course, is based on the assumption that patrilocal groups are never female-bonded - a point refuted in this thesis.

### Summary

1. Neutral intertroop encounters were an everyday occurrence while aggressive encounters occurred once every 46.8 hours. Friendly interactions between members belonging to different troops were not seen until actual migrations took place.

2. While all encounters took place in overlap zones, the location of the encounter did not appear to affect the outcome.

3. The number of adult males resident in the troop and the total number of individual members did not affect the outcome of the conflict. That is, larger troops did not always dominate smaller troops, nor did troops with more males dominate troops with fewer males.

4. During intertroop encounters the two resident males in Focal troop took on separate roles. One of them was the main protagonist while the other provided back-up and also kept watch on the female members of Focal troop.

5. The amount of stability, coordination and cohesiveness within the male hierarchy of an individual troop may affect the outcome of intertroop encounters.

6. Females not only took part in conflicts, they actually initiated them and used the intertroop encounter as a point of transfer.

7. A female's past history, in terms of her troop

residency, may affect the outcome of the conflict.

8. Only Abuko is reported to have a population where female colobus take an active aggressive role in intertroop encounters. It is possible that this is related to (a) the lack of sexual dimorphism making it less dangerous and/or advantageous for females to get involved and/or (b) the high degree of relatedness amongst females in opposing troops and within the same troop.

9. There appears to be a direct relationship between particular behaviors observed during intertroop encounters and the specific transfer patterns found in Abuko.

## Chapter 12. CONCLUDING DISCUSSION

In this thesis I have tried to show that the social behavior of the Abuko red colobus can best be understood in terms of sexual differences, and that these differences can best be understood by detailing the structure of the society within which the animal lives and the ecological, demographic, physiological constraints that act on the animal.

In this final chapter, some of the findings from other chapters are considered and an attempt is made to relate them to each other and to the practice of female transfer and patrilocality which occurs in this population. Also these findings are compared with those of other populations where males are generally the resident sex and females normally emigrate to another area.

From the outset it is important to remember that the population in Abuko consists of a group of individuals which show very little, if any body size dimorphism. Furthermore, the environment in which they live does not appear to be poor in terms of food availability or sleeping sites (comparing vegetation density and diversity at various red colobus field sites). The social unit in Abuko is composed of males who are usually life-long residents (except for their adolescent period of exile) and females who generally transfer between social units with, or after, their natal troop mates.

It has usually been assumed that female-transfer, male-resident social structure has as a nucleus a cluster of strongly-bonded adult males characterized by intramale grooming, proximity and coalitionary support while female-female relations lack cohesion, involve few cooperative interactions and are less prominent than male-male bonds (Greenwood, 1980; Wrangham, 1980; Smuts, 1987; Struhsaker and Leland, 1987; Walters, 1987). It is further assumed that when a female leaves her natal troop she leaves her natal troop mates behind and enters a new group where the adult females are largely unrelated and have not known one another from birth (Harcourt and Stewart, 1983; Wrangham, 1983). It is also assumed that in most female-transfer species the proximate causes of group composition are female attraction to particular males or male herding of females and that the existence of social units depends on females being attracted to males rather than to each other (Wrangham, 1987).

Contrary to these former suggestions the transfer patterns in Abuko do not result in an organization where male bonds are stronger and less aggressive than female bonds. Rather, in Abuko they result in an organization where aggression is basically intrasexual with males using aggression against each other slightly more frequently than females use it against each other. Furthermore, there is a clear dominance order with some females being high-ranking and others clearly low-ranking. Like many colobines, the level of

aggression observed was low. This low level of aggression has often been indicated as evidence that dominance and rank order is unimportant in a species social system (Struhsaker and Leland, 1987). This, however, is not necessarily true (Dunbar and Dunbar, 1975). The point of dominance may be that when an individual needs to exert power/influence it can and not that an individual will always exert dominance.

The particular dominance system probably reflects the fact that females enter a troop with already-formed-alliances and that a troop ultimately is made up of various alliances formed from various troops whose members transfer together. Furthermore, these alliances are probably not based on active coalitions but mostly on nonaggressive interactions and socially integrating behaviors such as grooming and resting closely together. For example, females take part in more grooming episodes, subunit formations and cooperative, socially-integrating behaviors than males.

Some of the grooming patterns observed in Abuko are probably directly related to the transfer patterns. For example, mothers groom their sons more than their daughters, because in the long run sons generally spend their adulthood in their natal troop while daughters do not and therefore the relationship between the mother and son is more long-lasting than the relationship between the mother and daughter. Thus, the mother-son relationship is 'worth more' and receives a higher investment. Probably related to this is the fact that

mothers share food more with sons and give less weaning punishment to sons than to daughters. Male infants were also protected more frequently than female infants by both relatives and nonrelatives. Furthermore, mothers played with their male infants more than they played with their female infants and young males were carried and groomed by nonrelatives more than females. Young males simply received more friendly attention than young females from all members of the troop. Again, because of the male's tendency to remain in his natal troop, it would seem a reasonable investment in terms of time and energy for adults to form bonds with the young males who will eventually become their troop mates on an equal footing.

Young females groom their peers and the next oldest female age group because these are the individuals with whom they will form their long-lasting bonds with when they transfer. Therefore, this is the group that is 'worth more' and receives a higher investment.

Grooming amongst females is not correlated with rank. This is possibly because bonds with low-ranking females are just as beneficial as bonds with high-ranking females. Only the bond itself is important. Of course, bonds with well-known females may be more reliable and it may be that the number-one grooming partner was originally a member of one's natal troop. Ultimately, alliances against alien 'potentially infanticidal' males benefit all females and their offspring



and since animals of all ranks are equally effective alliance partners, the benefits each individual has to offer are symmetrical. The observations made on subunit formations in PWD and the brief grooming observations made on PWD and Zoo troop members suggests that bonds formed in natal troops are carried into the transfer troop.

Adult males spend the majority of their grooming time on immature and low-to-middle ranking females. If males use grooming as a way to strengthen bonds with the most-likely-to-leave females then it makes sense that they spend more time grooming these females as opposed to the more dominant females (who are probably the least-likely-to-leave females).

In general the grooming patterns observed in Abuko appear to be distributed in such a way that the groomer derives maximum benefit in terms of the distribution. In other words, they are optimal grooming patterns as discussed by Seyfarth (1983).

One of the most obvious principles underlying grooming patterns, subunit formations and cooperative, socially integrating behaviors is that females are more bonded with females (especially particular females - probably peers) than males are with other males.

In terms of general sexual patterns, females exercise choice in favor of high-status males when mating. In specific cases, however, some females form consorts with the number-two male and move away from the main body of the troop where their

matings will not be interrupted and where they do not give behavioral signals (e.g. copulation quavers and audio-visual courtship displays) which signal their position and activities to the number-one male. It appears that in Abuko both competition amongst males (often initiated by the female) and female choice go hand in hand in determining mating patterns and that one does not preclude the other.

In terms of immediate and direct female-female competition for copulating males, there was very little harassment of copulating couples by adult females. Of the 6 instances involving adult and subadult females harassing fully-swollen copulating females, only one of these instances could be considered female-female competition.

The absence of overt female-female competition in conjunction with a high level of female consensus in terms of their choice of mates is possibly due to the particular mating system and the short-lived tenure of the chief copulator. Because male parental effort is virtually limited to fertilising eggs (and possibly protecting the new mother and infant for the first few months), females will not incur significant costs if they all choose and mate with the same male.

All of this information on female sexual patterns must be viewed in conjunction with the fact that females are not only choosing particular males, they are choosing specific home ranges with specific members in those ranges and they are also

playing a part in determining which males will be allowed to join them in their chosen troop.

Looking at the data presented in this thesis, the red colobus in Abuko do not appear to fit most of the common descriptions of female-transfer species. This would seem to indicate that behavioral patterns such as transfer systems which appear similar on a very gross level (eg. chimpanzees, howler monkeys, gorillas, hamadryas baboons, purple-faced langurs, red colobus all display female-transfer) often differ considerably when examined in detail, particularly in the distribution of social bonds within the social unit. These differences in group infrastructure indicate strongly that different evolutionary pathways involving different ecological selection pressures, have led to a superficially similar pattern, i.e., the transfer of females between social units. Some of the specific differences found within female-transfer species will be looked at in the rest of this chapter in an attempt to explain two major questions:

1. Why are the Abuko red colobus males less strongly bonded than those of most other female-transfer, male-resident species?
2. Why are the females more strongly bonded than those of most other female-transfer, male-resident species?

Why are the Abuko males not strongly bonded?

From the results presented in chapter 8 it is clear that the Abuko males are not strongly bonded with each other. There is very virtually no intramale grooming, proximity and coalitionary support. The only time intramale grooming or proximity were observed was when there was either an alien male or a neighboring troop threatening the social integrity of the troop. Adult males were involved in only 7 coalitions, and none of these involved assisting or aiding another adult male. Although most of the data come from Focal troop, other troops in Abuko also showed the same lack of male-male bonding. PWD males were never seen grooming or resting within touching distance. Nor were the males in Zoo troop seen interacting with each other or cooperating on any level. Middle troop displayed the ultimate lack of male-male bonding by containing only one adult male at any time throughout the entire study period (March 1978 - September 1983).

In contrast to the situation in Abuko, the Kibale males spend much of their time close to each other and may even be in physical contact while feeding from the same branch (Struhsaker, 1975). Furthermore, only males actively participate cooperatively in intertroop encounters where the outcome actually depends on the number of adult and subadult males (only) in the troop and on their general physical condition (Struhsaker, 1980). Adult males groomed each other more than expected and the strong coalition of males is

assumed to be strengthened through this grooming (Struhsaker and Leland, 1986).

In other female-transfer species, male-male bonds are also obviously strong. In chimpanzees, males from the same community often groom each other while adult females groom each other proportionately less (Nishida and Hiraiwa-Hasegawa, 1987). Furthermore, while males frequently share meat, females do not (Teleki, 1973). Male cooperation is reflected in the high degree of cohesion among males to the extent that all-male parties are common (Halperin, 1979; Nishida, 1968). Furthermore, females spend the majority of their time alone or in the company of their own dependent offspring while males are more gregarious (Goodall, 1986). In short there is a high degree of tolerance among male chimpanzees and cooperation - particularly in terms of patrolling border areas of their communal territories (Bygott, 1979; Goodall *et al.*, 1979) where the outcome is determined by the number of adult males in the patrolling party (Nishida, 1979).

These simple comparisons suggest that these populations, although superficially similar in terms of transfer patterns, are in fact quite different when social relationships and interactions are considered. The question which obviously needs to be answered is why do the red colobus males in Kibale and chimpanzee males form strong bonds with other males while the males in Abuko basically ignore each other? The theory underlying this question is that if males derive maximum

benefit by cooperating with other males, then each male will cooperate and there will be minimal conflict between the interests of the individual males involved. In short, if it is selectively advantageous for males to cooperate, they will. If they do not 'need' to, they will not.

At both Kibale and Abuko, red howler monkey sites in Venezuela and various chimpanzee sites, threats from outside are considerable in that infanticide either definitely or most probably occurs. During these attacks by infanticidal males the response varied from site to site. At Kibale coalitions against infanticidal males involved only adult males (presumably the sire and his male allies: Leland, Struhsaker and Butynski, 1984). In Venezuela male invasions and associated infanticides resulted in males dying of injuries received while fighting other males (Crockett and Sekulic, 1982).

At Gombe National Park and the Mahale Mountains, chimpanzees are subjected to intercommunity infanticide and fatal aggression against adults, and Wrangham (1979) suggested that male-male bonding benefits each male by providing allies in defense of the community range. Males from the same community certainly cooperate to chase or attack males or other communities (Nishida, 1979; Goodall et al., 1979) suggesting that intercommunity interactions are probably a key factor in the maintenance of male-male bonds. Nishida and Hiraiwa-Hasegawa, 1987 have argued that the chimpanzee alpha-

male 'needs' male subordinates to help defend the group while the subordinates 'need' to cooperate with each other and the alpha-male while waiting for a chance to usurp the alpha rank which is reproductively valuable (Nishida, 1983; Tutin and McGinnis, 1981).

In contrast to the red colobus in Kibale, red howler monkeys and chimpanzees, coalitions against potentially infanticidal males at Abuko involved a number of females with only one of the adult males forming a coordinated attack and sometimes killing the assumed infanticidal male. The situation in Abuko is more similar to multimale, matrilineal, matrilocal groups (e.g. baboons: Busse and Hamilton, 1981; Collins, Busse and Goodall, 1984) than to female-transfer, male-resident groups.

If amongst red colobus in Kibale, red howler monkeys and chimpanzees, the counterattacks on infanticidal males are avoided by females, then males need to cooperate. On the other hand, if females initiate and coordinate the attacks (as happens in Abuko) then males do not need to cooperate since they are being aided by females and thus are not solely responsible for maintaining the social integrity of the troop. Furthermore, since body size dimorphism is lacking in the Abuko population, the female is 'worth' just as much as the male when a fighting partner is considered. In Kibale and amongst red howler monkeys and chimpanzees, there is more obvious difference in terms of body size dimorphism and a

female would not be 'worth' as much as a male in terms of a fighting partner. All of this tends to suggest that the Abuko males 'need' each other less than many of the animals which display female transfer patterns.

Why are Abuko females more strongly bonded than in most other female-transfer species?

From the results presented in Chapter 10 it is clear that the females in Abuko are generally moving between social units with peers (who are possibly half-sibs) and that these relationships are important to them when they transfer troops. Females who share a common natal troop rarely use aggression against each other and groom each other more than they groom other females.

Theoretically, the Abuko females who transfer with peers have the opportunity to choose a new troop with a new male and simultaneously to remain with their peers (kin?). The proximity of female peers is regarded as a result of the need not just for companions but for particular companions, namely individuals who can be relied on to provide support against conspecifics. Why natal troop peers? Basically, individuals who are familiar with each other from birth have repeated opportunities to test each other's reliability as partners, allowing the development of a reciprocally beneficial relationship. A critical feature of the Abuko social unit is that females are probably bonded by the need for support



against the outside infanticidal male.

During all invasions and shadowings by alien males, resident females were always responsible for initiating and maintaining the attacks.

In a number of female-resident, male-transfer species, females unite to chase males away from their groups (E. patas; Kaplan and Zucker, 1980; C. ascanius: Cords, 1984; C. aethiops: Cheney, 1983). Hall (1967), Packer and Pusey (1979) and Cheney (1981) concluded that female aggression is a major determinant by which some males achieve or do not achieve group membership. The Abuko colobus are unusual because they are not female-resident, male-transfer, and yet they display cooperative patterns typical of this form of social structure. The question then remains why Abuko females should risk themselves by chasing away alien males or attacking potentially infanticidal males? One explanation suggests that female mobbing of males provides benefits similar to those proposed for mobbing of predators (Harvey and Greenwood, 1978): because mobbing serves to warn the 'predator' (in this case a conspecific male) that hostility toward females and infants is costly, it may reduce the chances that the mobbing female (or one of her infants, relatives, peers) will be the victim of male aggression in the future. And if the male is killed then certainly the female will not be bothered by him again. Because infanticide lowers the reproductive success of females, females should be

expected to develop counterstrategies (Hrdy, 1974, 1977, 1979; Chapman and Hausfater, 1979; Struhsaker and Leland, 1985; 1987). What is unusual about the counterstrategy used by the females in Abuko is that they form aggressive coalitions against the presumed infanticidal male before he attacks. This counterstrategy is more similar (and more successful) to ones employed in one-male groups where females do not transfer groups and are presumably closely related to one another (Hrdy, 1977; Struhsaker, 1977; Butynski, 1982). The females in Abuko did not limit themselves, however, to just this one strategy. They also used postconception estrus behaviors which are assumed to reduce the risk of infanticide (Hrdy, 1974; Hrdy, 1979; Struhsaker and Leland, 1985). And, those most at risk - mothers with dependent young - avoided all alien males and intertroop encounters. Therefore, it would seem that the females in Abuko are simultaneously using various counterstrategies to eliminate the possibility of infanticide.

The social unit in Abuko appears to be founded on various female social networks (albeit, translocated passive networks) with males adapting to and not substantially changing the pattern of female relationships. Whenever a male died or disappeared and was presumed dead, the group of females stayed intact and continued to behave as a discrete self-contained social unit. They did not desert the troop. For example, Jungi, Mr. Mean, Captain Crook, Yunk, Bimp and Imp all died/disappeared and there were no desertions by the females.

This suggests that females have stronger bonds with each other than they have with males. In a sense then the male(s) is a social supernumerary whose role is mainly that of breeder and assister (but not initiator or main protagonist) in times of attacks on potentially infanticidal males.

It could be argued that Abuko females cooperate with each other more than males cooperate with each other because the females in any given group are, on average, more closely related to each other for a longer period of time. There are two factors suggesting this. First, rates of mortality in Abuko for males are high. Most adult males probably have few living, close male relatives for any length of time. In fact, most males who achieve a position of chief copulator only maintain this position for one breeding season and after this they either die or disappear. Second, and most important, patterns of transfer among females are remarkably non-random, with the result that at least some (if not most) females may be more closely related to other females for a longer period of time than males are to each other.

There is one other very obvious way in which the Abuko red colobus social unit resembles male-transfer, female resident species. The unit itself is recognized by its female membership and not its male membership. While it is true that females in Abuko transfer between troops, they are still the basic core of the troop in that they live longer and spend more time as members of a troop as an adult than do the males.

Certainly, over a period of years it was always the females who alerted me as to which troop I was watching in an area where three troops overlapped in home ranges. Of the three adult males (Jungi, Mr. Mean and Captain Crook) who were members of Focal troop when the study began in March 1978, all three had died by July 1982. Of the 13 adult females who were members of the troop when the study began, four of them (Wild, Inca, Nene, Solid) were still members of Focal troop in June 1986.

Obviously, the Abuko red colobus grooming, bonding, aggressive and cooperative patterns contrast sharply with Kibale red colobus and chimpanzees who have as a nucleus a cluster of strongly bonded, cooperating, coordinated males with relatively detached females forming no long-lasting relationships. It would seem therefore that not all female-transfer species show the same type of bonding patterns within the social unit. This finding is clearly at odds with most of the ideas regarding female-transfer species in general (Wrangham, 1980; Smuts, 1987) and the bonding patterns of red colobus monkeys (Struhsaker, 1975; Struhsaker and Leland, 1985; Struhsaker and Leland, 1987) in particular.

These differences may be a reflection of differences in the actual relationships amongst females within a social unit. For example, it is assumed that Kibale red colobus females and females from various chimpanzee populations transfer on their own and do not have any long-term enduring bonds with each

other. On the other hand, it is obvious that the Abuko transferring female is known to (and probably even related to) other females in her chosen troop. Furthermore, like gorillas (Stewart and Harcourt, 1987) attraction among female peers is likely to be an important factor determining the extent and timing of actual transfer and females join particular troops because they contain known females who transferred there previously. Byrne et. al. (1989) have shown that not all matrilocal primates form female-bonded groups. Similarly not all patrilocal primates form non-female-bonded, male-bonded units.

It must be borne in mind, of course, that there are two very obvious ways in which the Abuko red colobus (like all female-transfer species) do not resemble male-transfer, female-resident species like macaques, baboons, and so forth. First, the long-term maintenance of territories (note the lack of mutually exclusive territories with defended boundaries) do not reside in female lineages. Second, female dominance positions are probably not permanently determined by matrilineages, although a high-ranking mother could instill an element of 'self-assurance' in her offspring.

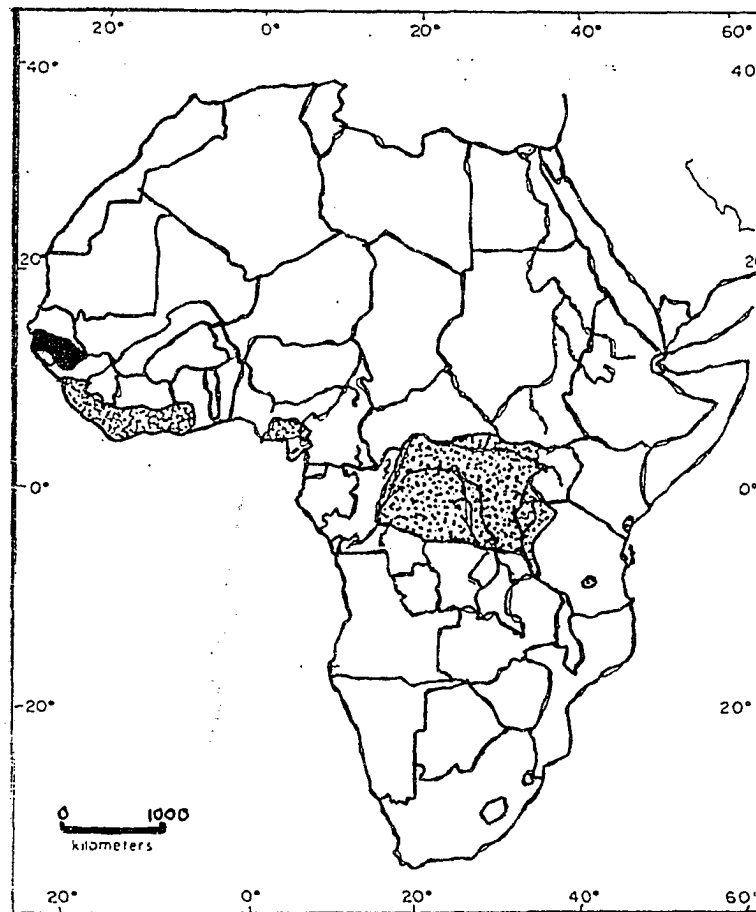
When discussing the differences between the Kibale and the Abuko situation, it must also be remembered that ecologically there is one very important difference. The red colobus in Kibale inhabit a large forest block with access to many, very large troops. When a female in Kibale transfers

she has many troops to choose from and each troop has many potential female and male interactees for her to develop bonds with. In contrast, the Abuko forest is small, isolated and contains only five troops with the largest troop containing less than 35 individuals. When a female in Abuko transfers, she often just moves 'next door' and joins neighbors. The females in Kibale, therefore have more social and spatial choices available. It is possible that this ecological difference may partially account for many of the observed differences in interrelationships both within and among troops.

There is one other obvious difference between these two populations. In Kibale there is no seasonal breeding and birth season. In Abuko there is a very clearly defined birth season. In a seasonally breeding/birthing population like Abuko, cohorts of individuals of the same age are likely to reach the same physical stage at the same time as well as experience the same external stimuli. If, in fact, peer migration is due to the creation of a seasonally produced peer group, then many of the differences in female bonding patterns could actually be attributable to the birth seasonality found in the population. If forest size and breeding/birth seasonality are, in fact, responsible for the specific bonding patterns found in Abuko, then these social aspects of the society are a direct result of the environmental set up, pressures and opportunities found in this habitat. In summary

then, this suggests that ecological pressures do in fact help to determine the spatial distribution and social networks of females (Wrangham, 1980; Clutton-Brock, Guinness and Albon, 1982) and the behavior of males depends on the distribution and behavior of females (Trivers, 1972; Wrangham, 1987).

**Figure 1**  
Distribution of *P. badius* group



*P.b. temminckii* ■

All other *P. badius* subspecies  
modified from Wolfheim (1983) ■



**Figure 2**

Photograph of mothers and their infants climbing down an oil palm trunk and creating a 'traffic jam'.

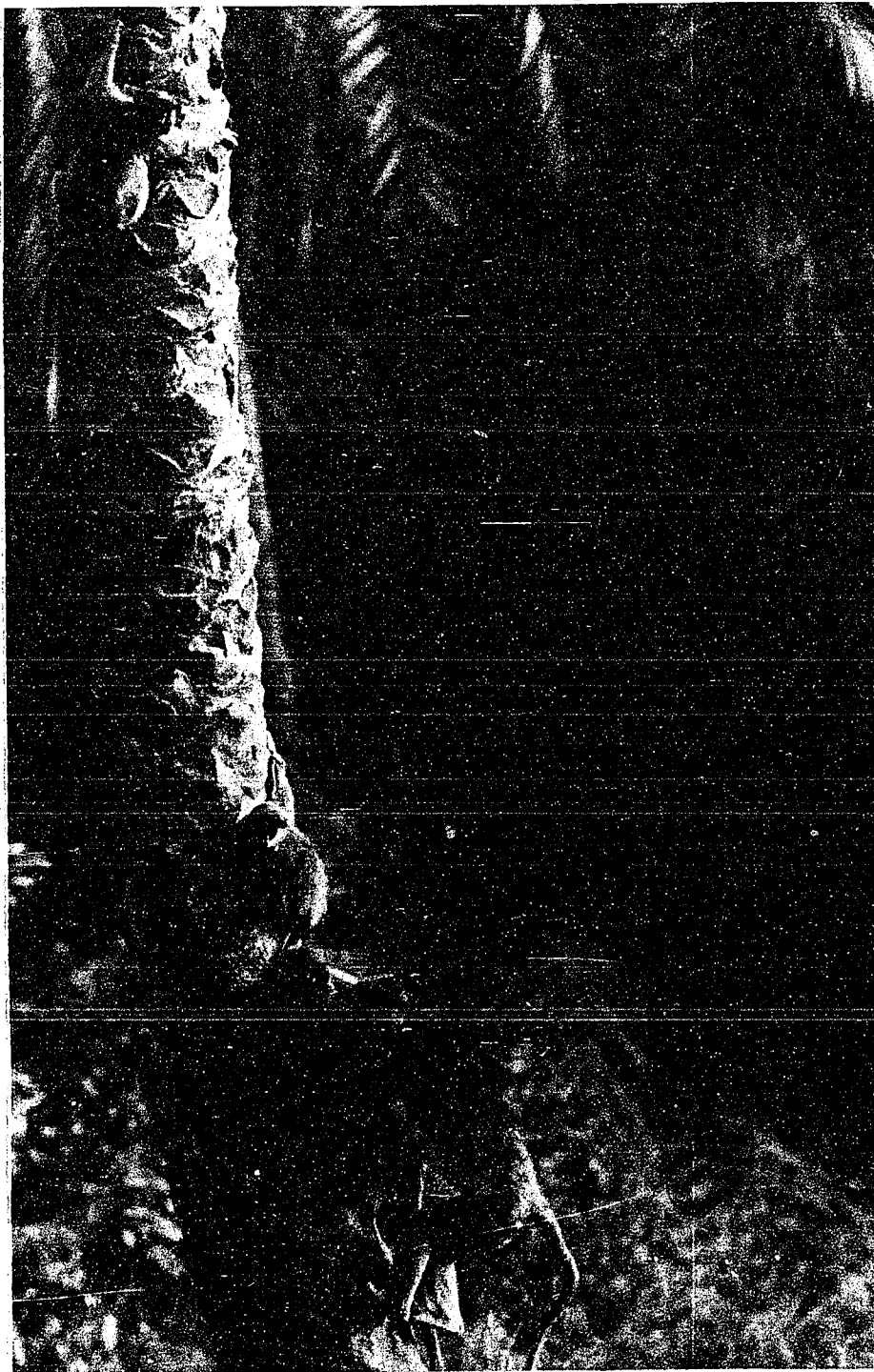


**Figure 3**

Map of The Gambia within West Africa and an enlargement of the extreme western section of The Gambia showing the Abuko Nature Reserve and its relation to the capital Banjul, Senegal, the airport and the river Gambia.

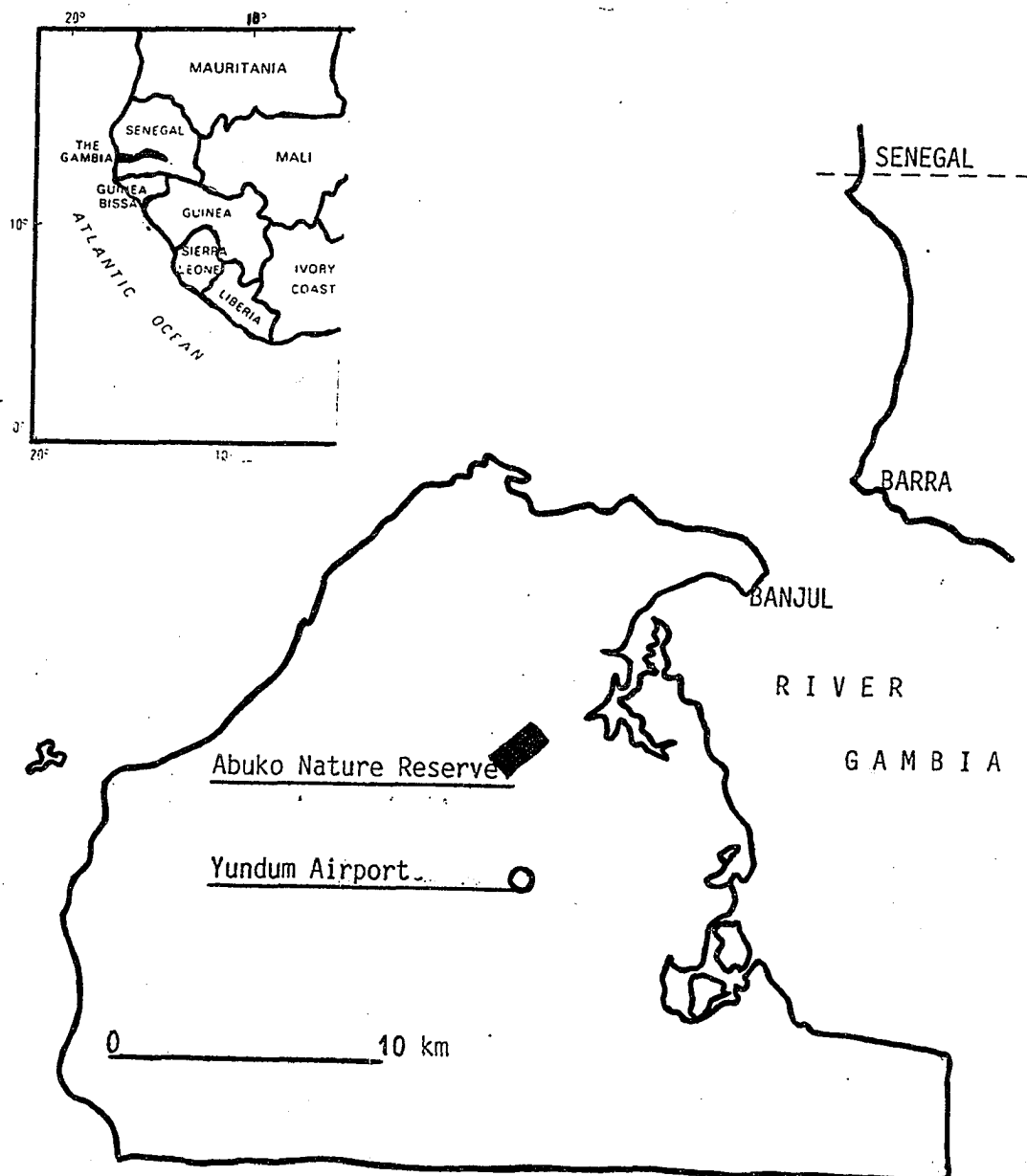
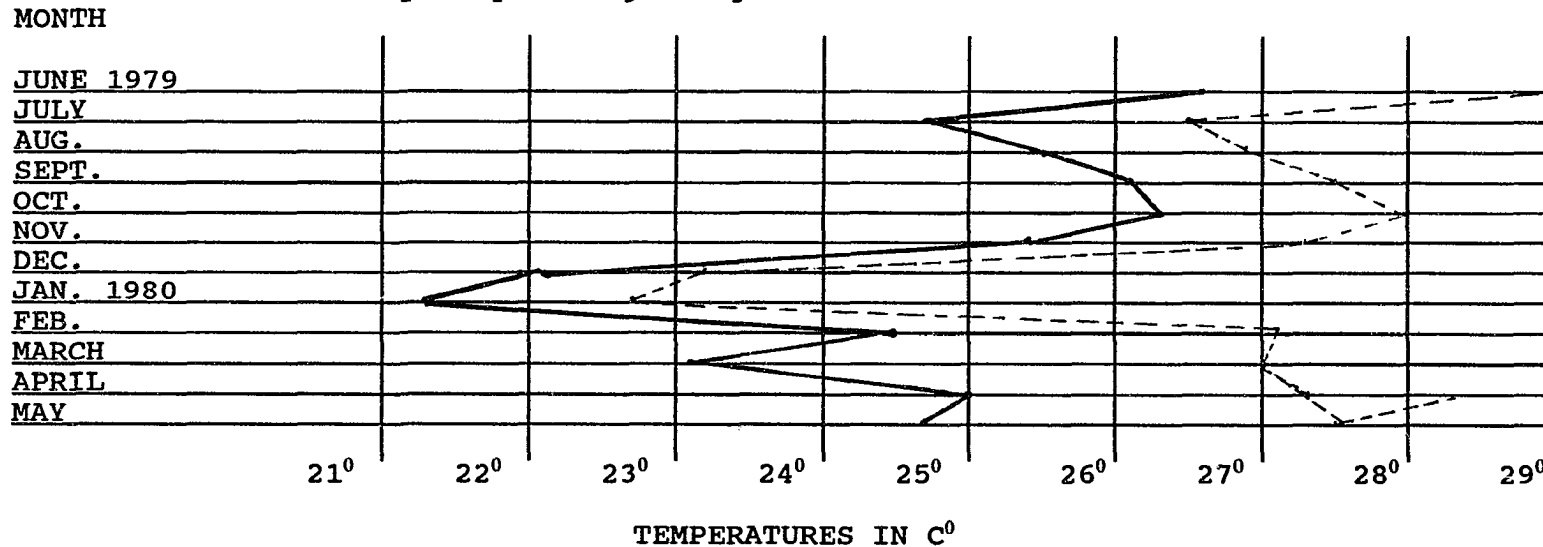


Figure 4

Temperature data collected in the Abuko Nature Reserve

Mean hourly temp. for gallery forest and tree and shrub savanna



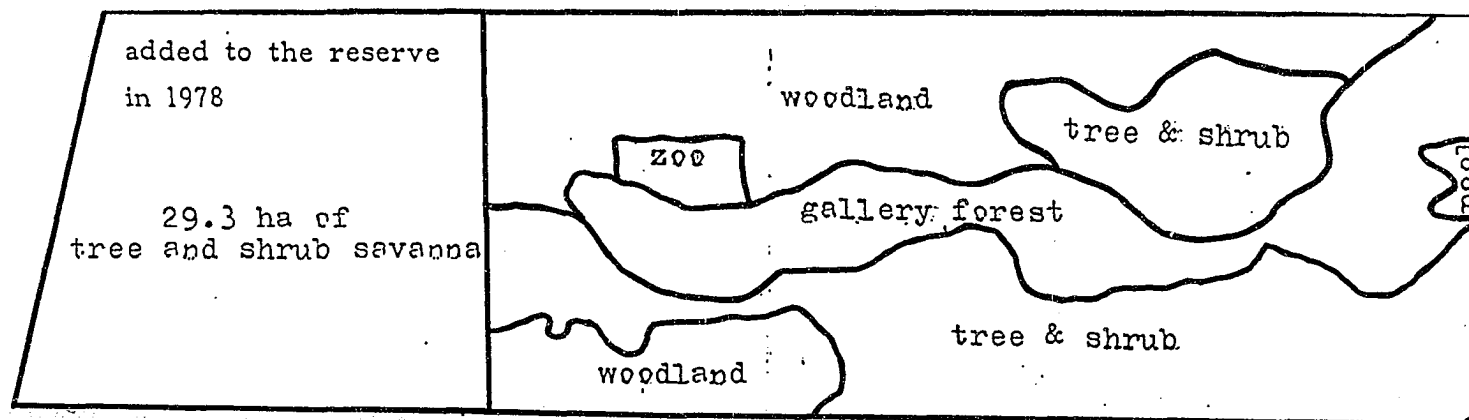
Gallery forest temperatures

Tree and shrub savanna temperatures - - - - -

The mean hourly temperatures are based on hourly records taken from 0700 to 1900 on 13 days each month. the thermometers were placed in complete shade 1.2 meters above the ground. The temperatures were recorded to the nearest .5 degree and the calculations are to the first decimal point.

**Figure 5**

Map of the Abuko Nature Reserve showing amount and placement of major habitat zones.



1 : 10,000

Based on an October 1980 aerial survey commissioned by the Forestry Department. The Gambia (scale 1:25,000: roll 2, line 00019 and 000192, October 1980). The map was made by G. Thaller, Gambian-German Forestry Project.

The swamp and clearings were too small to show up on the photograph. They are surrounded by gallery forest and together they make up less than 0.6% of the reserve. Tree & shrub savanna = 57%; Woodland savanna = 25%; Gallery Forest = 16%; Zoo = 1.3%; Pool = 0.1%.

Figure 6

Size and placement of various home ranges.

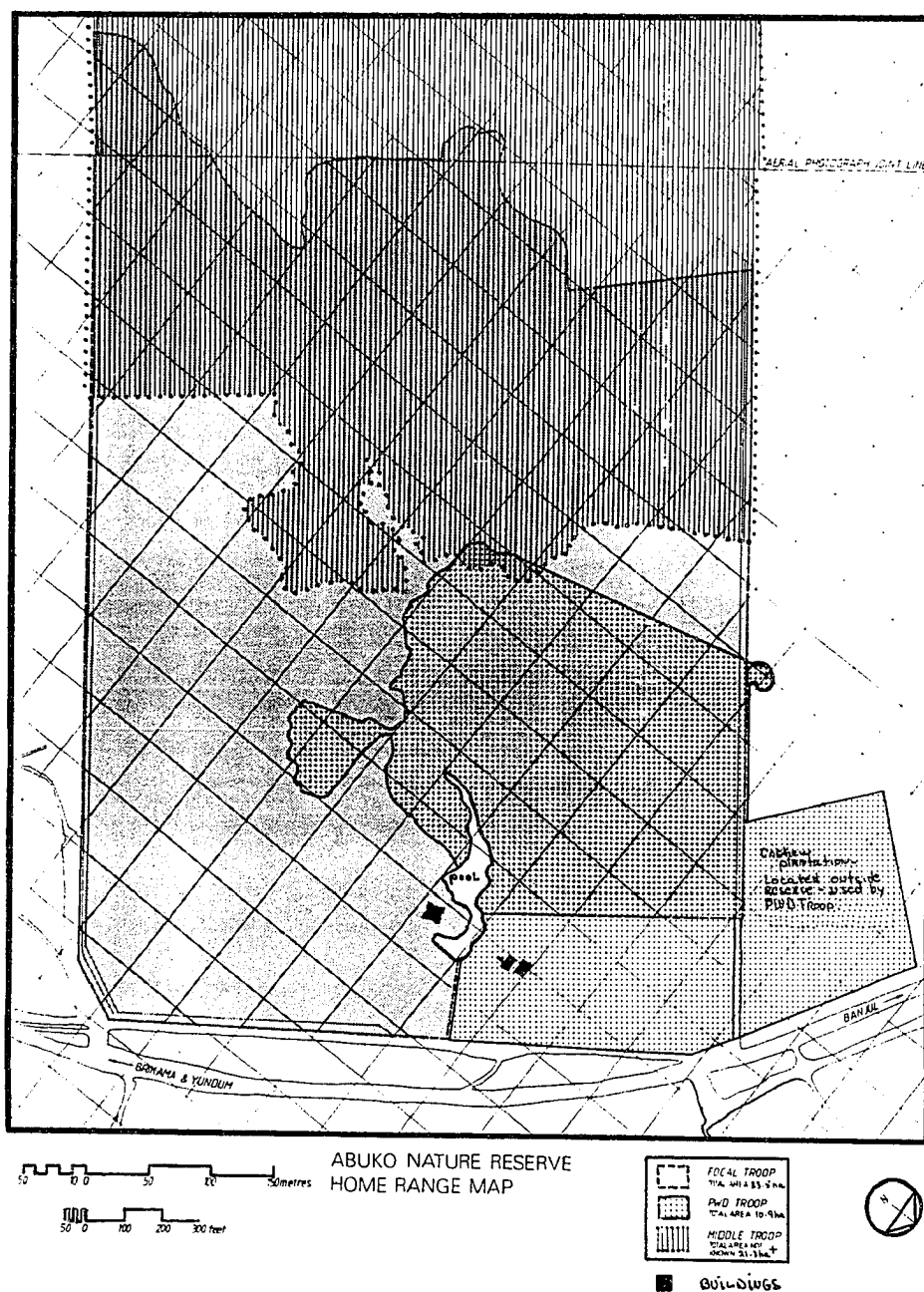


Figure 7

Photograph of the lethargic, 'wallflower' orphaned young female, Punk lying on a Ficus trichopoda branch.



**Figure 8**

Photograph of juveniles playing in one of the clearings.

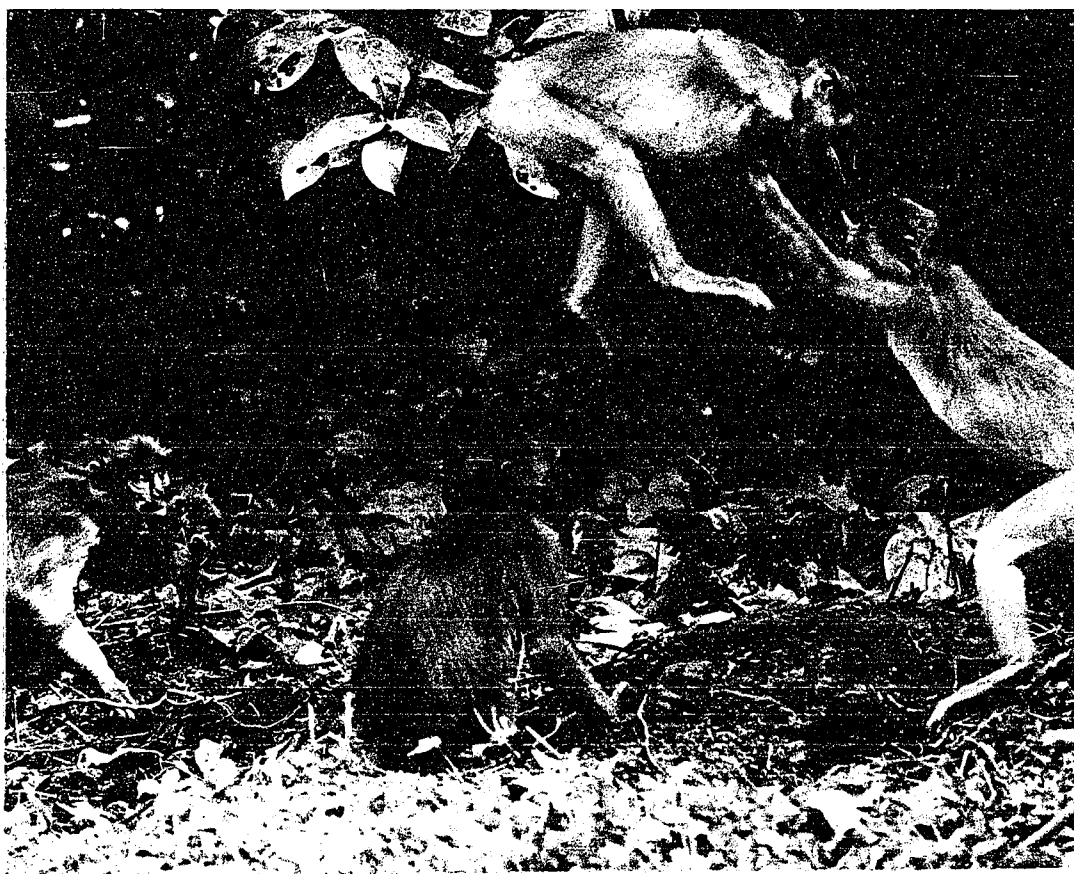


**Figure 9**  
**Demographic data for focal troop in Abuko**

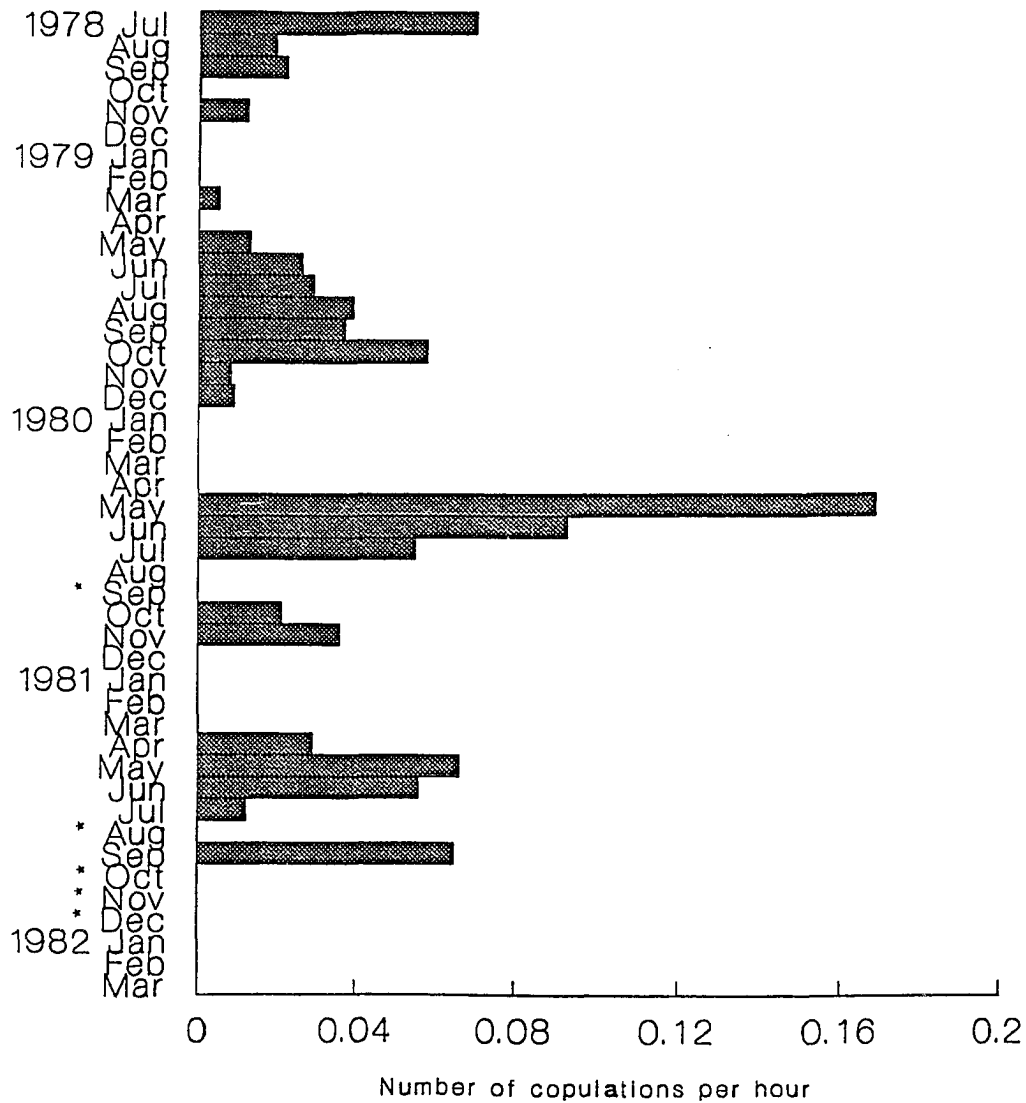
|           | Births    | Deaths | Emigrations<br>Female | Immigrations<br>Female | Expulsions<br>Male | Rejoinings<br>Male |
|-----------|-----------|--------|-----------------------|------------------------|--------------------|--------------------|
| Jan. 1978 | ■ ■ ■ ■ ■ |        |                       |                        |                    |                    |
| Feb.      |           |        |                       |                        |                    |                    |
| Mar.      |           |        |                       |                        |                    |                    |
| Apr.      |           |        |                       |                        |                    |                    |
| May       |           |        |                       |                        |                    |                    |
| June      |           | ■      |                       |                        |                    |                    |
| July      | ■         | ■      | ■                     |                        |                    |                    |
| Aug.      |           |        |                       |                        |                    |                    |
| Sept.     |           |        |                       |                        |                    |                    |
| Oct.      | ■         | ■ ■    |                       |                        |                    |                    |
| Nov.      |           |        |                       |                        |                    |                    |
| Dec.      | ■ ■ ■     |        |                       |                        |                    |                    |
| Jan. 1979 | ■ ■       |        |                       |                        |                    |                    |
| Feb.      | ■         |        |                       |                        |                    |                    |
| Mar.      |           |        |                       |                        |                    |                    |
| Apr.      | ■         |        | ■ ■ ■                 |                        |                    |                    |
| May       |           |        |                       | ■                      |                    |                    |
| June      |           | ■      | ■                     |                        |                    |                    |
| July      |           |        |                       |                        |                    |                    |
| Aug.      |           |        | ■ ■ ■                 |                        |                    |                    |
| Sept.     |           |        |                       |                        |                    |                    |
| Oct.      |           |        |                       | ■                      |                    |                    |
| Nov.      |           |        |                       |                        |                    |                    |
| Dec.      |           |        |                       | ■                      |                    |                    |
| Jan. 1980 |           |        |                       |                        |                    |                    |
| Feb.      |           |        |                       | ■                      |                    |                    |
| Mar.      |           |        |                       |                        |                    |                    |
| Apr.      | ■         |        |                       |                        |                    |                    |
| May       |           |        | ■ ■                   |                        |                    |                    |
| June      |           |        |                       | ■                      |                    |                    |
| July      |           | ■ ■ ■  |                       | ■                      |                    |                    |
| Aug.      |           |        |                       |                        |                    |                    |
| Sept.     |           |        | ■                     |                        | ■                  |                    |
| Oct.      |           |        |                       |                        | ■                  |                    |
| Nov.      |           |        |                       |                        | ■ ■                |                    |
| Dec.      |           |        |                       |                        |                    |                    |
| Jan. 1981 |           | ■      |                       |                        |                    |                    |
| Feb.      |           | ■      |                       |                        |                    |                    |
| Mar.      |           |        |                       |                        |                    |                    |
| Apr.      | ■ ■ ■ ■ ■ | ■ ■ ■  |                       | ■ ■                    |                    |                    |
| May       | ■         | ■      | ■ ■ ■                 |                        |                    |                    |
| June      |           |        |                       | ■ ■ ■                  |                    | ■ ■ ■              |
| July      |           |        |                       |                        |                    |                    |
| Aug.      |           |        |                       |                        |                    |                    |
| Sept.     |           | ■ ■    |                       | ■                      |                    |                    |
| Oct.      |           |        |                       |                        |                    |                    |
| Nov.      |           |        |                       |                        |                    |                    |
| Dec.      |           |        |                       |                        |                    |                    |
| Jan. 1982 | ■ ■       | ■      |                       |                        | ■                  |                    |
| Feb.      |           |        |                       |                        |                    |                    |
| Mar.      | ■         |        |                       |                        |                    |                    |
| Apr.      | ■         |        |                       |                        |                    |                    |
| May       |           | ■ ■    |                       |                        |                    |                    |
| June      | ■         |        |                       |                        |                    | ■                  |
| July      |           | ■ ■    |                       |                        |                    |                    |
| Aug.      |           |        |                       |                        |                    |                    |
| Sept.     |           |        | ■                     |                        |                    |                    |
| Oct.      |           |        |                       |                        |                    |                    |
| Nov.      |           |        |                       |                        |                    |                    |
| Dec.      |           | ■      |                       |                        |                    |                    |
| Jan. 1983 | ■         |        |                       |                        |                    |                    |
| Feb.      | ■         |        |                       |                        |                    |                    |
| Mar.      | ■         |        |                       |                        |                    |                    |
| TOTAL     | 28 born   | 23 die | 16 leave              | 16 join                | 6 expelled         | 4 rejoin           |

Each box represents one individual. Birth data is accurate from January 1978 because it was possible to estimate dates. All other data is accurate from June 1978. Before this date colobus were not well known and deaths, transfers, etc. could have gone unnoticed. Only emigrations and immigrations which lasted 30 days or longer are noted here.



**Figure 10**

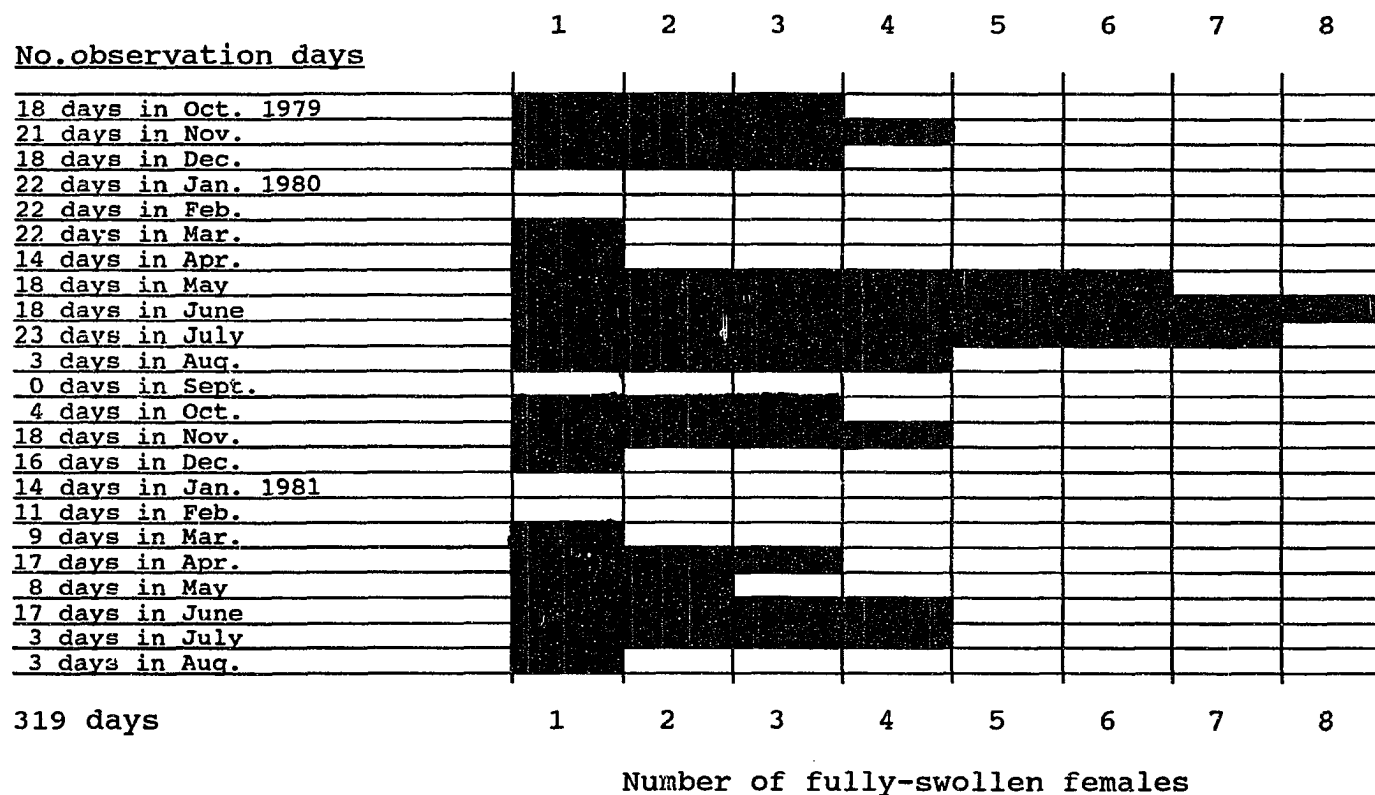
Number of copulations with fully swollen females  
(corrected for hours of observation).



\* denotes no data collected

The number of copulations varied significantly throughout year  
(likelihood ratio test: d.f. = 10;  $p = <.0001$ ).

**Figure 11**  
Number of females displaying sexual swellings each month



Number of swollen females varied significantly throughout the year.  
Likelihood ratio test: d.f. = 10;  $p = < 0.001$ .

Figure 12

## Matrix of Adult Female Aggressive Interactions

## ABSOLUTE WINS

|        | Droopy | Solid | Nene | Button | Yundum | Head | Inca | Volley | Metoo | Julie | Wild | Round | Garuda | Other | TOTAL |
|--------|--------|-------|------|--------|--------|------|------|--------|-------|-------|------|-------|--------|-------|-------|
| Droopy |        |       |      |        |        |      |      |        |       |       |      |       |        |       | 0     |
| Solid  |        |       |      |        |        |      |      |        |       |       |      |       |        |       | 0     |
| Nene   |        |       |      |        |        |      |      |        |       |       |      |       |        |       | 1     |
| Button |        |       |      |        |        |      |      |        |       |       |      |       |        |       | 1     |
| Yundum |        |       |      |        |        |      | 2    |        |       |       |      |       |        |       | 2     |
| Head   |        | 1     | 2    | 1      | 1      |      |      |        |       |       |      |       |        |       | 5     |
| Inca   |        |       | 1    |        | 2      |      |      |        |       |       |      | 1     |        |       | 4     |
| Volley |        |       |      | 1      |        |      |      |        |       |       |      |       |        |       | 1     |
| Metoo  |        |       |      | 1      |        |      |      |        |       |       |      |       |        |       | 1     |
| Julie  | 1      |       |      |        |        |      |      |        |       |       |      |       |        |       | 1     |
| Wild   | 1      |       |      |        | 2      |      |      |        |       |       |      |       |        |       | 3     |
| Round  | 1      | 1     | 1    | 4      |        |      |      | 1      |       |       |      |       |        |       | 8     |
| Garuda | 1      |       | 3    | 2      |        | 2    |      |        |       |       |      | 1     |        |       | 9     |
| Other  |        |       |      |        |        |      | 1    |        |       |       |      |       |        |       | 2     |
| TOTAL  | 6      | 3     | 7    | 9      | 5      | 2    | 3    | 1      | 0     | 0     | 0    | 2     | 0      | 0     | 38    |

Significantly more numbers below diagonal than above (two-tailed binomial test:  $z = 5.2$ ;  $p = 0.00002$ ).

**Figure 13**  
Relationship between dominance rank and grooming rank

| FEMALE NAME | DOMINANCE RANK | RECEIVES GROOMING RANK | RECEIVES GROOMING FROM OTHER FEMALES % | GIVES GROOMING TO OTHER FEMALES % |
|-------------|----------------|------------------------|----------------------------------------|-----------------------------------|
| Droopy      | 1st            | YumDum (1st)           | 74.0                                   | 25.9                              |
| Solid       | 2nd            | Droopy (2nd)           | 58.7                                   | 41.3                              |
| Miff        | 3rd            | Miff (3rd)             | 57.1                                   | 42.85                             |
| Button      | 4th            | Wild (4th)             | 55.8                                   | 44.2                              |
| YumDum      | 5th            | Inca (5th)             | 55.2                                   | 44.8                              |
| Head        | 6th            | Julie (6th)            | 54.9                                   | 45.1                              |
| Inca        | 7th            | Solid (7th)            | 52.8                                   | 47.1                              |
| Volley      | 8th            | Metoo (8th)            | 47.8                                   | 52.1                              |
| Metoo       | 9th            | Round (9th)            | 44.8                                   | 55.2                              |
| Julie       | 10th           | Garuda (10th)          | 42.5                                   | 57.5                              |
| Wild        | 11th           | Volley (11th)          | 38.2                                   | 61.8                              |
| Round       | 12th           | Button (12th)          | 37.4                                   | 62.6                              |
| Garuda      | 13th           | Head (13th)            | 34.1                                   | 65.9                              |

No correlation between dominance rank and grooming rank in terms of percent of time spent being groomed (Spearman Rank:  $r_s = 252$ ,  $N = 13$ ).

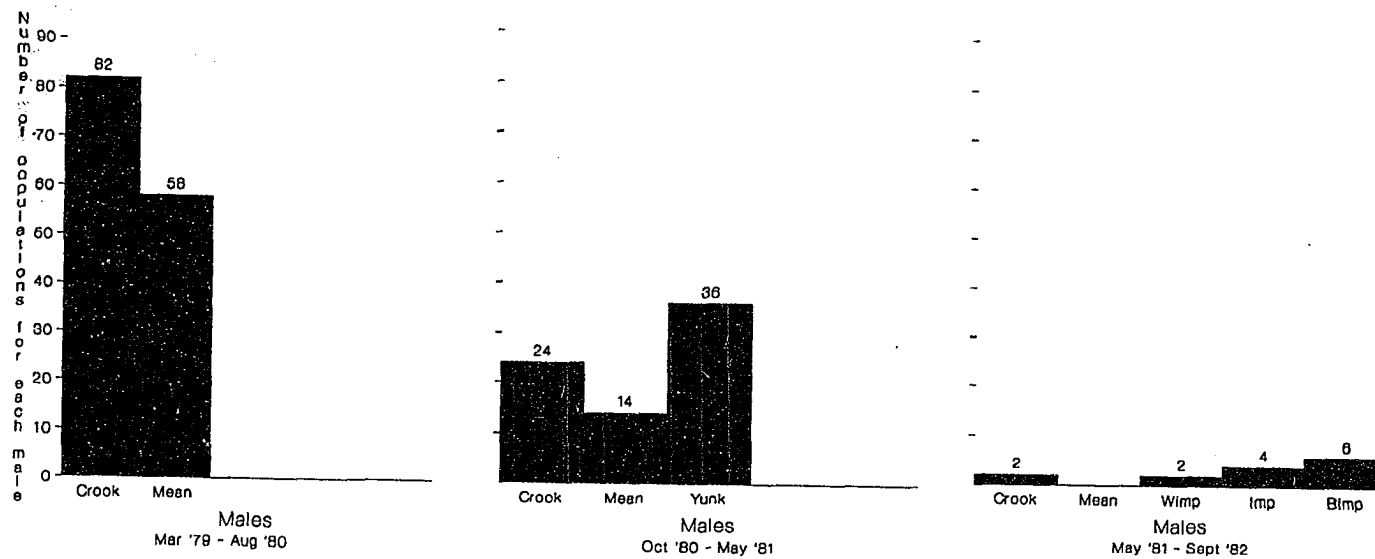
**Figure 14**

Young adult male, Imp, mates fully swollen adult female, Nene.  
Imp displays threat face.



Figure 15

Copulations with Females in all other\* cycle states each breeding season.



Total mounts counted = 228

\* not including fully swollen and inflating states, mounts by immature males or the adult male Jungi.

TABLE 1

Measurements and weight collected on various red colobus living in Abuko

| Age/Sex      | Name  | Weight    | Tail Length | Face Length | Torso Length | Foot Length |
|--------------|-------|-----------|-------------|-------------|--------------|-------------|
| Adult Female | Round |           | 63cm        | 7.5cm       | 51cm         | 11.5cm      |
| Adult Female | Noam  |           | 69.5cm      | 6cm         | 45cm         | 10.5cm      |
| Adult Female | Julie |           | 62cm        | 6cm         |              |             |
| Adult Male   | Bend  |           | 63cm        | 6cm         | 48cm         | 11cm        |
| Adult Male   | Bully | 6.5 kilos | 63cm        |             |              |             |

Face length refers to measurement from base of chin to top of forehead; Torso length refers to measurement from top of spine to base of tail; Foot length refers to measurement from heel to base of longest digit (only sole of foot - not the digit).

All measurements and the one weight were collected on animals which died a natural death.

TABLE 2

34 Year Rainfall Total (1946 through 1979) collected at Yundum Meteorological Station (1.25 km from the Abuko Nature Reserve).

| MONTH            | TOTAL RAINFALL mm | MEAN RAINFALL mm |
|------------------|-------------------|------------------|
| January          | 33.1              | 0.9              |
| February         | 25.6              | 0.7              |
| March            | trace*            | trace            |
| April            | trace             | trace            |
| May              | 141.4             | 4.0              |
| June             | 2364.3            | 69.5             |
| July             | 9071.5            | 266.8            |
| August           | 15207.6           | 447.3            |
| September        | 9820.9            | 288.9            |
| October          | 3232.4            | 95.1             |
| November         | 218.9             | 6.4              |
| December         | 37.7              | 1.1              |
| 40153.4 mm total |                   | 1180.9 mm mean   |

\*trace equals less than 0.3mm



TABLE 3

Number of monkeys present in Abuko Nature Reserve

| SPECIES                             | No. of Monkeys | No. of Troops |
|-------------------------------------|----------------|---------------|
| <u>Cercopithecus campbelli</u>      | 1              | 0             |
| <u>Cercopithecus sabaues</u>        | 110**          | 4 - 6         |
| <u>Erythrocebus patas</u>           | 40             | 2             |
| <u>Procolobus badius temminckii</u> | 132            | 5             |
| TOTAL MONKEYS PRESENT               | 283+           |               |

\*\* The green monkey count of 110 is considered the most inaccurate. I know that there were at least four troops whose combined membership was approximately 110. It is possible that two more troops inhabited the western section of the reserve, an area infrequently visited.

**TABLE 4**
**Summary of Major Habitat Types**

|                                                | SAVANNA ZONES<br>TREE & SHRUB      WOODLAND |                          | GALLERY FOREST            | SWAMP                   | CLEARING              |
|------------------------------------------------|---------------------------------------------|--------------------------|---------------------------|-------------------------|-----------------------|
| PERCENT OF<br>TOTAL AREA                       | 56.6%                                       | 24.8%                    | 16%                       | 0.3%                    | 0.3%                  |
| TREE DENSITY                                   | 1 species<br>in 0.19 ha                     | 7 species<br>in 0.185 ha | 22 species<br>in 0.203 ha | almost<br>treeless      | virtually<br>treeless |
|                                                | 3 trees only                                | 9 trees only             | 198 trees                 |                         |                       |
| No. OF TOP 10<br>FOOD SPECIES<br>FOUND IN ZONE | 5                                           | 7                        | 6                         | 2                       | 1                     |
| SOIL TYPE                                      | sandy loam                                  | sandy loam               | loam                      | water-logged            | silt loam             |
| SOIL pH (range)                                | 4.3 - 6.5                                   | 4.8 - 6.0                | 5.3 - 6.1                 | 5.6 - 6.8<br>(water pH) | 4.1 - 5.5             |
| SOIL - % OF<br>ORGANIC MATTER<br>(range)       | 0.9 - 1.6%                                  | 1.9 - 3.4%               | 5.9 - 16.8%               |                         | 10.1%                 |
| (N =)                                          | 5                                           | 3                        | 4                         |                         | 1                     |

TABLE 5

FOCAL TROOP SIZE AND COMPOSITION

| DATE       | SIZE<br>TOTAL | ADULT |    | SUBADULT |   | JUVENILE |   | INFANT |   |
|------------|---------------|-------|----|----------|---|----------|---|--------|---|
|            |               | M     | F  | M        | F | M        | F | M      | F |
| Sept. 1978 | 26            | 3     | 13 | 0        | 4 | 0        | 3 | 1      | 2 |
| Sept. 1979 | 30            | 2     | 14 | 0        | 3 | 1        | 2 | 5      | 3 |
| Oct. 1980  | 26            | 2     | 12 | 0        | 2 | 5        | 5 | 0      | 0 |
| Sept. 1981 | 24            | 2     | 10 | 4        | 3 | 0        | 0 | 1      | 4 |

mean =                26.5    2.2 12.2        1        3            1.5    2.5        1.7   2.2

adult male/adult female ratio ranges from 1:4.3 to 1:7 with a mean of 1:5.5.

PWD TROOP SIZE AND COMPOSITION

| DATE |      | SIZE  | ADULT |    | SUBADULT |   | JUVENILE |   |   | INFANT |   |   |
|------|------|-------|-------|----|----------|---|----------|---|---|--------|---|---|
|      |      | TOTAL | M     | F  | M        | F | M        | ? | F | M      | ? | F |
| Jan. | 1980 | 26    | 2     | 8  | 0        | 5 |          | 8 |   |        |   | 3 |
| Jan. | 1981 | 25    | 2     | 10 | 0        | 3 |          | 5 |   |        |   | 5 |
| Jan. | 1982 | 25    | 2     | 10 | 0        | 3 |          | 5 |   |        |   | 5 |

mean =                25.3        2    9.3        0        3.6            6                    3.6

adult male/adult female ratio ranges from 1:4 to 1:5 with a mean of 1:4.6.

Sept. 1978 was chosen as the first month for Focal troop because it was the first time all individuals were positively identified. January 1980 was the first time an accurate and complete count of all PWD members was made.

TABLE 6

Population Information on Five Red Colobus Study Sites

| Form                     | GOMBE STREAM<br><u>tephrosceles</u> | KIBALE FOREST<br><u>tephrosceles</u> | TANA RIVER<br><u>rufomitratu</u> s | FATHALA FOREST<br><u>temminckii</u> | ABUKO<br><u>temminckii</u> |
|--------------------------|-------------------------------------|--------------------------------------|------------------------------------|-------------------------------------|----------------------------|
| Colobus/km <sup>2</sup>  | 100 - 200                           | 250 - 300                            | 200 - 300                          | c. 400                              | 123.7                      |
| Troop Structure          | multi-male troops                   | multi-male troops                    | one & two male troops              | one, two & multi-male               | one, two & multi-male      |
| Mean Size of Troop (N=)  | c.55<br>5                           | 45 - 50<br>15                        | 17.5<br>3                          | 29<br>14                            | 26.2<br>2                  |
| Range of Troop Size (N=) | 35 - 82<br>5                        | 19 - 70+<br>15                       | 13 - 30<br>13                      | 9 - 62<br>14                        | 18 - 32<br>2               |
| % Adult (N=)             | 47.6%<br>1                          | 49.5%<br>1                           | 64.6%<br>3                         |                                     | 0.9%<br>2                  |
| Male:Female Ratio (N=)   | 1:2.5<br>1                          | 1:2.1<br>1                           | 1:7.5<br>3                         | 1:2<br>14                           | 1:5.2<br>2                 |
| Extratroup Males         | present                             | present                              | present                            | present                             | present                    |
| Infanticide              | ?                                   | present                              | probable                           | ?                                   | probable                   |

Two troops at Abuko, three at Tana River, and one each at Gombe and Kibale were accurately censused and involve NO estimates. Fathala data are estimates only.

**TABLE 7**  
**A Comparison of Five Red Colobus Study Sites**

|                                         | SITES                                |                                   |                       |                           |                                                                          |
|-----------------------------------------|--------------------------------------|-----------------------------------|-----------------------|---------------------------|--------------------------------------------------------------------------|
|                                         | GOMBE STREAM                         | KIBALE FOREST                     | TANA RIVER            | FATHALA FOREST            | ABUKO                                                                    |
| Altitude (m.)                           | 780                                  | 1300 - 1500                       | 30                    | 10                        | 5.5 - 16                                                                 |
| Annual Rainfall (mm.)                   | 1450                                 | 1475                              | 550                   | 1050                      | 1181                                                                     |
| TEMPERATURE+                            |                                      |                                   |                       |                           |                                                                          |
| Mean Daily Minimum                      | 19°                                  | 12.7°                             |                       |                           | 19.4° - 20.4°                                                            |
| Mean Daily Maximum                      | 28°                                  | 25.5°                             |                       |                           | 28.1° - 32°                                                              |
| Fires                                   | Absent                               |                                   | Severe++              | Absent                    | Absent                                                                   |
| Predation +++                           | Noticeable<br>15%                    | Not Important<br>1 - 2%           | Not<br>Important      |                           | Noticeable<br>15%                                                        |
| RESOURCE DENSITY<br>trees/ha. 10 m tall | 360 trees<br>in 1 ha.                | 328 trees<br>in 1 ha.             | 48 trees<br>in 1 ha.  | 100-200 trees<br>in 1 ha. | 210 trees in<br>0.58 ha or<br>338 trees in<br>0.58 ha*                   |
| Percent of top 3<br>tree species        | 24%                                  | 48%                               | 60%                   |                           | 55.7% or 44.4%*                                                          |
| Total No.<br>of Spp.                    | 79 among<br>3049 trees<br>in 1.43 ha | 51 among<br>469 trees<br>in 9 ha. | 26 among<br>430 trees | 22 in<br>8.5 ha.          | 27 among 210<br>trees in 0.58ha.<br>or 32 among 338<br>trees in 0.58 ha* |

Marsh states that Tana River is 10° warmer than Kibale and slightly warmer than Gombe Stream. Gatinot states that the mean annual temperature in Fathala is 26.5°.

++ In 1978 fires swept through Fathala killing at least five adult red colobus (pers. obs.).

+++ If predation was not observed it is listed as not important. At Kibale Ghiglieri (1984) saw a chimpanzee eating meat from what appeared to be the skin of a red colobus and Leland (1987) mentions that it occurs. The percentages for Kibale are given as determined by Cheney and Wrangham (1987).

\* The resource data for Gombe Stream are based on all trees over 4" in diameter at breast height. The data for Kibale Forest, Tana River, Fathala and the first numbers given for Abuko are based on all trees over 10 meters in height. The second set of numbers for Abuko are based on all savanna trees over 5 meters in height and all gallery forest trees over 10 meters in height. Details are give in Appendix B.

TABLE 8

Time Spent Collecting Systematic Scan-Samples on Diet  
and Activity Budgets

| MONTH     |      | NUMBER OF HOURS           |
|-----------|------|---------------------------|
|           |      | (to the nearest .25 hour) |
| March     | 1978 | 165                       |
| April     |      | 158.25                    |
| May       |      | 171                       |
| June      |      | 205                       |
| July      |      | 202.50                    |
| August    |      | 207.25                    |
| September |      | 175.75                    |
| October   |      | 212.75                    |
| November  |      | 315.50                    |
| December  |      | 264.25                    |
| January   | 1979 | 250.25                    |
| February  |      | 242.75                    |
| March     |      | 217.75                    |
| April     |      | 205.75                    |
| May       |      | 225.75                    |
| June      |      | 77.75                     |
| July      |      | 204.75                    |
| August    |      | 259                       |
| September |      | 180.50                    |
| October   |      | 206.75                    |
| November  |      | 241.25                    |
| December  |      | 204.25                    |
| January   | 1980 | 125.25                    |
| TOTAL     |      | 4719 hours                |

TABLE 9

Time Spent Collecting Systematic Scan-Samples  
on Social Interactions

| MONTH            |             | NUMBER OF HOURS<br>(to the nearest .25 hour) |
|------------------|-------------|----------------------------------------------|
| <u>January</u>   | <u>1980</u> | <u>106.25</u>                                |
| <u>February</u>  |             | <u>235.25</u>                                |
| <u>March</u>     |             | <u>241.50</u>                                |
| <u>April</u>     |             | <u>166.50</u>                                |
| <u>May</u>       |             | <u>219</u>                                   |
| <u>June</u>      |             | <u>216</u>                                   |
| <u>July</u>      |             | <u>273.25</u>                                |
| <u>August</u>    |             | <u>31.25</u>                                 |
| <u>September</u> |             | <u>0</u>                                     |
| <u>October</u>   |             | <u>46.50</u>                                 |
| <u>November</u>  |             | <u>168.50</u>                                |
| <u>December</u>  |             | <u>186.25</u>                                |
| <u>January</u>   | <u>1981</u> | <u>156</u>                                   |
| <u>February</u>  |             | <u>134</u>                                   |
| <u>March</u>     |             | <u>111.75</u>                                |
| <u>April</u>     |             | <u>207</u>                                   |
| <u>May</u>       |             | <u>90.75</u>                                 |
| <u>June</u>      |             | <u>214</u>                                   |
| <u>July</u>      |             | <u>17</u>                                    |
| <u>August</u>    |             | <u>6</u>                                     |
| <u>September</u> |             | <u>121.5</u>                                 |
| <u>October</u>   |             | <u>0</u>                                     |
| <u>November</u>  |             | <u>0</u>                                     |
| <u>December</u>  |             | <u>0</u>                                     |
| <u>January</u>   | <u>1982</u> | <u>96.5</u>                                  |
| <u>February</u>  |             | <u>82.5</u>                                  |
| <u>March</u>     |             | <u>104.5</u>                                 |
| TOTAL            |             | 3231.75<br>observation<br>hours              |

**TABLE 10**
**Daily Activity Budgets for Various Age-Sex Classes During One Year in Abuko**
**TOTAL NUMBER OF RECORDS COLLECTED ON THE FOLLOWING ACTIVITIES FOR ALL INDIVIDUALS**

| MONTH         | ?          | FEED        | SIT          | LIE        | MOVE        | AUTO-<br>GROOM | GROOM      | GROOMED    | PLAY        | NURSE     | SOCIAL     | TOTAL        |
|---------------|------------|-------------|--------------|------------|-------------|----------------|------------|------------|-------------|-----------|------------|--------------|
| Feb '79       | 89         | 411         | 851          | 14         | 182         | 3              | 42         | 42         | 86          | 1         | 5          | 1726         |
| March         | 0          | 391         | 1139         | 47         | 107         | 2              | 56         | 54         | 148         | 1         | 8          | 1953         |
| April         | 60         | 400         | 919          | 2          | 245         | 0              | 39         | 39         | 199         | 6         | 4          | 1913         |
| May           | 25         | 388         | 1078         | 13         | 214         | 3              | 39         | 39         | 151         | 2         | 14         | 1966         |
| June          | 3          | 281         | 1214         | 48         | 188         | 3              | 58         | 59         | 124         | 3         | 14         | 1995         |
| July          | 0          | 402         | 1165         | 47         | 294         | 3              | 38         | 38         | 131         | 4         | 33         | 2155         |
| Aug           | 0          | 270         | 1196         | 59         | 198         | 4              | 61         | 60         | 86          | 7         | 1          | 1953         |
| Sept          | 0          | 350         | 933          | 84         | 312         | 5              | 53         | 51         | 90          | 2         | 6          | 1886         |
| Oct           | 0          | 335         | 1110         | 92         | 308         | 13             | 66         | 66         | 91          | 6         | 2          | 2110         |
| Nov           | 0          | 485         | 764          | 54         | 292         | 11             | 74         | 72         | 147         | 5         | 20         | 1924         |
| Dec           | 0          | 547         | 654          | 27         | 306         | 6              | 72         | 70         | 163         | 6         | 7          | 1858         |
| Jan '80       | 0          | 779         | 881          | 11         | 322         | 3              | 52         | 50         | 118         | 7         | 25         | 2248         |
| <b>TOTAL</b>  | <b>177</b> | <b>5039</b> | <b>11904</b> | <b>498</b> | <b>2968</b> | <b>56</b>      | <b>650</b> | <b>640</b> | <b>1534</b> | <b>50</b> | <b>171</b> | <b>23687</b> |
| <b>MEAN</b>   |            |             |              |            |             |                |            |            |             |           |            |              |
| %             |            | 21.3        | 50.3         | 2.1        | 12.5        | 0.2            | 2.7        | 2.7        | 6.5         | 0.2       | 0.7        | 99.75        |
| <b>MEDIAN</b> |            |             |              |            |             |                |            |            |             |           |            |              |
| %             | 0.0        | 19.9        | 50.9         | 2.1        | 13.2        | 0.2            | 2.8        | 2.7        | 6.1         | 0.2       | 0.7        |              |



TABLE 10 Continued

| ANNUAL ACTIVITY BUDGET FOR ALL INDIVIDUALS 0-13 MONTHS OF AGE IN THE FOCAL TROOP         |     |      |      |     |      |               |       |         |      |       |        |       |
|------------------------------------------------------------------------------------------|-----|------|------|-----|------|---------------|-------|---------|------|-------|--------|-------|
|                                                                                          | ?   | FEED | SIT  | LIE | MOVE | AUTO<br>GROOM | GROOM | GROOMED | PLAY | NURSE | SOCIAL | TOTAL |
| TOTAL                                                                                    | 0   | 439  | 3000 | 35  | 562  | 0             | 12    | 70      | 1259 | 30    | 22     | 5429  |
| MEAN %                                                                                   | 0.0 | 8.1  | 55.2 | 0.6 | 10.4 | 0.0           | 0.2   | 1.3     | 23.2 | 0.6   | 0.4    |       |
|                                                                                          |     |      |      |     |      |               |       |         |      |       |        |       |
| ANNUAL ACTIVITY BUDGET FOR ALL INDIVIDUALS 13 MONTHS OF AGE AND OLDER IN THE FOCAL TROOP |     |      |      |     |      |               |       |         |      |       |        |       |
| TOTAL                                                                                    | 177 | 4600 | 8904 | 463 | 2406 | 56            | 638   | 570     | 275  | 20    | 149    | 18258 |
| MEAN %                                                                                   | 6.9 | 25.2 | 48.8 | 2.5 | 13.2 | 0.3           | 3.5   | 3.1     | 1.5  | 0.1   | 0.8    |       |

There is a significant profile difference between the infants budget and the budget of all those 13 months of age and older ( $\chi^2 = 1549$ ; d.f. = 10;  $P = <0.001$ ).

TABLE 11

## Observation Times for Feeding Data

|                |      | Total No.       | Mean No.        | TOTAL              |
|----------------|------|-----------------|-----------------|--------------------|
|                |      | Feeding<br>Obs. | Feeding<br>Obs. | all-day<br>follows |
| MONTH          |      |                 |                 |                    |
| July           | 1978 | 1533            | 139.4           | 11                 |
| August         |      | 876             | 67.4            | 13                 |
| September      |      | 1066            | 96.9            | 11                 |
| October        |      | 1407            | 100.5           | 14                 |
| November       |      | 1777            | 71.1            | 25                 |
| December       |      | 1549            | 91.1            | 17                 |
| January        | 1979 | 1873            | 104.1           | 18                 |
| February       |      | 1536            | 80.8            | 19                 |
| March          |      | 1355            | 79.7            | 17                 |
| April          |      | 1232            | 82.1            | 15                 |
| May            |      | 1189            | 74.3            | 16                 |
| June           |      | 362             | 60.3            | 6                  |
| July           |      | 992             | 66.1            | 15                 |
| August         |      | 1029            | 51.5            | 20                 |
| September      |      | 929             | 71.5            | 13                 |
| October        |      | 1223            | 76.4            | 16                 |
| November       |      | 1842            | 87.7            | 21                 |
| December       |      | 1823            | 101.3           | 18                 |
| January        | 1980 | 1426            | 142.6           | 10                 |
| <u>TOTAL</u>   |      | 25019 Obs.      |                 | 295                |
| <u>follows</u> |      |                 |                 |                    |
| MEAN           |      |                 | 84.8 Obs.       |                    |

TABLE 12

Percentages for each specific food item eaten February 1979 - mid-January 1980

| SPECIES                      | ITEM                  | TOTAL No.<br>FEEDING<br>RECORDS | PERCENT<br>ANNUAL<br>DIET | SPECIES<br>in ANNUAL<br>DIET | RANK |
|------------------------------|-----------------------|---------------------------------|---------------------------|------------------------------|------|
| <u>Parinari excelsa</u>      | young leaf            | 1679                            | 11.2                      |                              | 1    |
|                              | fruit                 | 197                             | 1.3                       |                              |      |
| <u>Ficus trichopoda</u>      | fruit                 | 1034                            | 6.9                       |                              | 2    |
|                              | young leaf            | 357                             | 2.4                       |                              |      |
|                              | leaf bud              | 144                             | 0.96                      |                              |      |
|                              | mature leaf           | 127                             | 0.85                      |                              |      |
|                              | young aerial root tip | 14                              | 0.09                      |                              |      |
|                              | leaf petioles only    | 2                               | 0.01                      |                              |      |
| <u>Detarium senegalensis</u> | fruit                 | 1139                            | 7.6                       |                              | 3    |
|                              | leaf bud              | 426                             | 2.9                       |                              |      |
|                              | flower bud            | 48                              | 0.3                       |                              |      |
|                              | young leaf            | 2                               | 0.01                      |                              |      |
|                              | flower                | 1                               | 0.01                      |                              |      |
|                              | chlorotic leaf        | 1                               | 0.01                      |                              |      |
| <u>Parkia biglobosa</u>      | leaf bud              | 292                             | 1.9                       |                              | 4    |
|                              | flower bud            | 174                             | 1.2                       |                              |      |
|                              | fruit                 | 147                             | 0.9                       |                              |      |
|                              | young leaf            | 116                             | 0.8                       |                              |      |
|                              | flower                | 10                              | 0.07                      |                              |      |
|                              | mature leaf           | 3                               | 0.02                      |                              |      |

|                                  |                      |     |      |    |
|----------------------------------|----------------------|-----|------|----|
| <u>Pseudospondias microcarpa</u> | fruit                | 276 | 1.8  | 5  |
|                                  | young leaf           | 184 | 1.2  |    |
|                                  | flower               | 175 | 1.2  |    |
|                                  | leaf bud             | 40  | 0.3  |    |
|                                  | flower bud           | 13  | 0.08 |    |
|                                  | mature leaf          | 3   | 0.03 |    |
|                                  | leaf petioles only   | 2   | 0.01 |    |
|                                  | chlorotic leaf       | 1   | 0.01 |    |
| <u>Prosopis africana</u>         | fruit and seed       | 586 | 3.9  | 6  |
|                                  | leaf bud             | 34  | 0.2  |    |
|                                  | young leaf           | 15  | 0.1  |    |
|                                  | flower               | 2   | 0.01 |    |
|                                  | flower bud           | 2   | 0.01 |    |
|                                  |                      |     |      |    |
| <u>Raphia palma-pinus</u>        | fruit                | 526 | 3.5  | 7  |
|                                  | flower bud           | 19  | 0.1  |    |
|                                  | flower               | 10  | 0.07 |    |
|                                  | flower peduncle      | 7   | 0.05 |    |
|                                  |                      |     |      |    |
| <u>Pterocarpus erinaceus</u>     | young leaf           | 315 | 2.1  | 8  |
|                                  | mature leaf          | 159 | 1.1  |    |
|                                  | flower bud           | 35  | 0.2  |    |
|                                  | leaf bud             | 18  | 0.1  |    |
|                                  |                      |     |      |    |
| <u>Ficus ovata</u>               | fruit                | 361 | 2.5  | 9  |
|                                  | leaf bud             | 67  | 0.4  |    |
|                                  | young leaf           | 17  | 0.1  |    |
|                                  | fruit calyptrate bud | 17  | 0.1  |    |
|                                  | mature leaf          | 16  | 0.1  |    |
|                                  |                      |     |      |    |
| <u>Dichrostachys glomerata</u>   | mature leaf          | 262 | 1.8  | 10 |
|                                  | fruit                | 67  | 0.4  |    |
|                                  | young leaf           | 26  | 0.2  |    |
|                                  | leaf bud             | 14  | 0.09 |    |
| <u>Dialium guineense</u>         | fruit                | 362 | 2.4  | 11 |
|                                  |                      |     |      |    |

|                               |                    |     |      |    |
|-------------------------------|--------------------|-----|------|----|
| <u>Mangifera indica</u>       | flower bud         | 166 | 1.1  | 12 |
|                               | young leaf         | 69  | 0.5  |    |
|                               | flower             | 55  | 0.4  |    |
|                               | fruit              | 36  | 0.2  |    |
|                               | leaf bud           | 11  | 0.07 |    |
|                               | leaf petioles only | 9   | 0.06 |    |
|                               | bark               | 1   | 0.01 |    |
| <u>Cleistopholis patens</u>   | fruit              | 290 | 1.9  | 13 |
|                               | flower             | 25  | 0.2  |    |
|                               | flower bud         | 4   | 0.03 |    |
| <u>Anthocleista procera</u>   | mature leaf        | 246 | 1.6  | 14 |
|                               | chlorotic leaf     | 31  | 0.2  |    |
|                               | dying leaf         | 15  | 0.1  |    |
|                               | flower             | 11  | 0.07 |    |
| <u>Landolphia heudelottii</u> | young leaf         | 232 | 1.6  | 15 |
|                               | leaf bud           | 59  | 0.4  |    |
|                               | flower bud         | 6   | 0.04 |    |
|                               | fruit              | 3   | 0.02 |    |
|                               | flower             | 1   | 0.01 |    |
| <u>Khaya senegalensis</u>     | young leaf         | 191 | 1.3  | 16 |
|                               | leaf bud           | 26  | 0.2  |    |
|                               | fruit              | 8   | 0.05 |    |
| <u>Ficus sur</u>              | fruit              | 186 | 1.2  | 17 |
|                               | young leaf         | 33  | 0.2  |    |
|                               | leaf bud           | 5   | 0.03 |    |
| <u>Paranari macrophylla</u>   | fruit              | 128 | 0.9  | 18 |
|                               | young leaf         | 91  | 0.6  |    |
|                               | mature leaf        | 3   | 0.02 |    |
|                               | leaf bud           | 1   | 0.01 |    |
| <u>Ficus thonningii</u>       | fruit              | 164 | 1.1  | 19 |
|                               | young leaf         | 24  | 0.2  |    |
|                               | mature leaf        | 6   | 0.04 |    |
|                               | leaf bud           | 6   | 0.04 |    |
| <u>Phoenix reclinata</u>      | seed only          | 166 | 1.1  | 20 |
|                               | flower             | 23  | 0.2  |    |
|                               | flower bud         | 2   | 0.01 |    |

|                               |                    |     |      |    |
|-------------------------------|--------------------|-----|------|----|
| <u>Alstonia boonei</u>        | flower             | 93  | 0.6  | 21 |
|                               | flower bud         | 44  | 0.3  |    |
|                               | young leaf         | 15  | 0.1  |    |
|                               | fruit              | 8   | 0.05 |    |
|                               | mature leaf        | 3   | 0.02 |    |
| <u>Lannea acida</u>           | flower             | 76  | 0.5  | 22 |
|                               | flower bud         | 47  | 0.3  |    |
|                               | mature leaf        | 28  | 0.2  |    |
|                               | dying leaf         | 2   | 0.01 |    |
|                               | young leaf         | 2   | 0.01 |    |
|                               | leaf bud           | 2   | 0.01 |    |
|                               | fruit              | 1   | 0.01 |    |
| <u>Albizia ferruginea</u>     | young leaf         | 73  | 0.5  | 23 |
|                               | leaf bud           | 58  | 0.4  |    |
|                               | flower             | 9   | 0.1  |    |
|                               | flower bud         | 5   | 0.03 |    |
|                               | mature leaf        | 3   | 0.02 |    |
| <u>Elaeis guineense</u>       | fruit              | 146 | 0.9  | 24 |
| <u>Indigofera macrophylla</u> | mature leaf        | 133 | 0.9  | 25 |
|                               | flower             | 5   | 0.03 |    |
|                               | flower bud         | 1   | 0.01 |    |
|                               | young leaf         | 1   | 0.01 |    |
| <u>Tetracera potatoria</u>    | fruit              | 110 | 0.7  | 26 |
|                               | flower bud         | 23  | 0.2  |    |
|                               | young leaf         | 5   | 0.03 |    |
|                               | leaf petioles only | 1   | 0.01 |    |
| <u>Ficus lutea</u>            | fruit              | 89  | 0.6  | 27 |
|                               | leaf bud           | 39  | 0.3  |    |
|                               | mature leaf        | 4   | 0.02 |    |
|                               | young leaf         | 1   | 0.01 |    |
| <u>Vitex grandifolia</u>      | young leaf         | 53  | 0.4  | 28 |
|                               | leaf bud           | 28  | 0.2  |    |
|                               | bark               | 1   | 0.01 |    |
| <u>Ficus glumosa</u>          | fruit              | 59  | 0.4  | 29 |
|                               | young leaf         | 16  | 0.1  |    |

|                                |             |    |      |    |
|--------------------------------|-------------|----|------|----|
| <u>Dioscorea bulbifera</u>     | mature leaf | 31 | 0.2  | 30 |
|                                | fruit       | 29 | 0.2  |    |
|                                | young leaf  | 10 | 0.1  |    |
|                                | flower      | 1  | 0.01 |    |
| <u>Hibiscus rostellatus</u>    | flower bud  | 48 | 0.3  | 30 |
|                                | flower      | 19 | 0.1  |    |
|                                | mature leaf | 4  | 0.03 |    |
| <u>Alchornea cordifolia</u>    | young leaf  | 42 | 0.3  |    |
|                                | mature leaf | 17 | 0.1  |    |
| <u>Saba senegalensis</u>       | mature leaf | 28 | 0.2  | 31 |
|                                | young leaf  | 24 | 0.2  |    |
|                                | flower      | 7  | 0.05 |    |
| <u>Leptoderris brachyptera</u> | young leaf  | 51 | 0.3  | 32 |
|                                | flower      | 2  | 0.01 |    |
|                                | leaf bud    | 1  | 0.01 |    |
|                                | fruit       | 1  | 0.01 |    |
|                                | stem only   | 1  | 0.01 |    |
| <u>Cassia sieberiana</u>       | flower      | 33 | 0.2  | 33 |
|                                | fruit       | 8  | 0.05 |    |
|                                | mature leaf | 7  | 0.05 |    |
| <u>Combretum paniculatum</u>   | flower bud  | 34 | 0.2  | 33 |
|                                | flower      | 14 | 0.1  |    |
| <u>Macaranga heudelottii</u>   | young leaf  | 43 | 0.3  | 34 |
| <u>Paullinia pinnata</u>       | young leaf  | 15 | 0.1  | 35 |
|                                | fruit       | 10 | 0.1  |    |
|                                | mature leaf | 4  | 0.03 |    |
|                                | flower bud  | 2  | 0.01 |    |
|                                | flower      | 1  | 0.01 |    |
| <u>Terminalia albida</u>       | mature leaf | 25 | 0.2  | 36 |
|                                | young leaf  | 9  | 0.1  |    |

|                                 |                    |    |      |    |
|---------------------------------|--------------------|----|------|----|
| <u>Nauclea latifolia</u>        | fruit              | 18 | 0.1  | 37 |
|                                 | mature leaf        | 6  | 0.04 |    |
|                                 | leaf petiole only  | 2  | 0.01 |    |
|                                 | young leaf         | 2  | 0.01 |    |
|                                 | flower             | 1  | 0.01 |    |
| <u>Lophira lanceolata</u>       | young leaf         | 28 | 0.2  | 38 |
| <u>Philiostigma thonningii</u>  | fruit bud and seed | 10 | 0.1  | 39 |
|                                 | leaf bud           | 8  | 0.05 |    |
|                                 | flower             | 5  | 0.03 |    |
|                                 | young leaf         | 1  | 0.01 |    |
| <u>Hibiscus sterculiifolius</u> | flower bud         | 17 | 0.1  | 40 |
|                                 | flower             | 3  | 0.02 |    |
| <u>Combretum mucronatum</u>     | young leaf         | 18 | 0.1  | 41 |
|                                 | mature leaf        | 1  | 0.01 |    |
| <u>Mezoneuron benthaminum</u>   | young leaf         | 12 | 0.1  | 42 |
|                                 | mature leaf        | 6  | 0.04 |    |
| <u>Ipomoea cairica</u>          | mature leaf        | 17 | 0.1  | 43 |
| <u>Lantana camara</u>           | flower             | 13 | 0.1  | 44 |
|                                 | mature leaf        | 2  | 0.01 |    |
|                                 | flower bud         | 1  | 0.01 |    |
| <u>Salacia senegalensis</u>     | fruit              | 9  | 0.1  | 45 |
|                                 | flower             | 3  | 0.02 |    |
|                                 | mature leaf        | 2  | 0.01 |    |
|                                 | young leaf         | 1  | 0.01 |    |
| <u>Daniella oliveri</u>         | leaf bud           | 13 | 0.1  | 46 |
|                                 | young leaf         | 1  | 0.01 |    |
| <u>Mikania cordata</u>          | flower             | 8  | 0.05 | 46 |
|                                 | mature leaf        | 4  | 0.03 |    |
|                                 | flower bud         | 2  | 0.01 |    |
| <u>Annona senegalensis</u>      | young leaf         | 8  | 0.05 | 47 |
|                                 | fruit              | 5  | 0.03 |    |



|                                  |             |    |      |    |
|----------------------------------|-------------|----|------|----|
| <u>Ficus scott-elliottii</u>     | fruit       | 5  | 0.03 | 48 |
|                                  | young leaf  | 5  | 0.03 |    |
|                                  | mature leaf | 2  | 0.01 |    |
| <u>Ficus platyphylla</u>         | leaf bud    | 12 | 0.1  | 48 |
| <u>Azadirachta indica</u>        | mature leaf | 7  | 0.05 | 49 |
|                                  | young leaf  | 4  | 0.03 |    |
| <u>Leptadenia hastata</u>        | mature leaf | 9  | 0.1  | 50 |
|                                  | leaf bud    | 1  | 0.01 |    |
| <u>Syzgium guineense</u>         | fruit       | 10 | 0.1  | 50 |
| <u>Albizia zygia</u>             | young leaf  | 5  | 0.03 | 51 |
|                                  | leaf bud    | 4  | 0.03 |    |
| <u>Cassytha filiformis</u>       | fruit       | 6  | 0.04 | 51 |
|                                  | stem only   | 3  | 0.02 |    |
| <u>Ficus elegans</u>             | mature leaf | 7  | 0.05 | 51 |
|                                  | young leaf  | 1  | 0.01 |    |
|                                  | fruit       | 1  | 0.01 |    |
| <u>Calamus deeratus</u>          | fruit       | 8  | 0.05 | 52 |
| <u>Ampelocissus multistriata</u> | young leaf  | 6  | 0.04 | 53 |
|                                  | flower bud  | 1  | 0.01 |    |
| <u>Bridelia micrantha</u>        | young leaf  | 4  | 0.03 | 54 |
|                                  | leaf bud    | 2  | 0.01 |    |
| <u>Bourgainvillea sp.</u>        | mature leaf | 4  | 0.03 | 55 |
|                                  | flower      | 1  | 0.01 |    |
| <u>Treculia africana</u>         | mature leaf | 5  | 0.03 | 55 |
| <u>Ceibia pentandra</u>          | young leaf  | 4  | 0.03 | 56 |
| <u>Celtis integrifolia</u>       | mature leaf | 3  | 0.02 | 56 |
|                                  | young leaf  | 1  | 0.01 |    |
| <u>Triumfetta cordifolia</u>     | flower      | 4  | 0.03 | 56 |

|                                 |             |   |      |    |
|---------------------------------|-------------|---|------|----|
| <u>Acacia sp.</u>               | mature leaf | 2 | 0.01 | 57 |
|                                 | leaf bud    | 1 | 0.01 |    |
| <u>Cola cordifolia</u>          | mature leaf | 2 | 0.01 | 57 |
|                                 | young leaf  | 1 | 0.01 |    |
| <u>Craterispermum laurinum</u>  | young leaf  | 3 | 0.02 | 57 |
| <u>Entada africana</u>          | mature leaf | 2 | 0.01 | 57 |
|                                 | young leaf  | 1 | 0.01 |    |
| <u>Zizyphus jujuba</u>          | young leaf  | 2 | 0.01 | 57 |
|                                 | mature leaf | 1 | 0.01 |    |
| <u>Cephaelis peduncularis</u>   | flower      | 2 | 0.01 | 57 |
|                                 | mature leaf | 1 | 0.01 |    |
| <u>Clerodendrum thyrsoideum</u> | mature leaf | 1 | 0.01 | 58 |
|                                 | flower      | 1 | 0.01 |    |
| <u>Jasminum paniculatum</u>     | flower bud  | 1 | 0.01 | 58 |
|                                 | mature leaf | 1 | 0.01 |    |
| <u>Newbouldia laevis</u>        | mature leaf | 1 | 0.01 | 58 |
|                                 | flower      | 1 | 0.01 |    |
| <u>Quisqualis indica</u>        | young leaf  | 2 | 0.01 | 58 |
| <u>Pavetta corymbosa</u>        | mature leaf | 2 | 0.01 | 58 |
| <u>Strophanthus sarmentosus</u> | flower      | 2 | 0.01 | 58 |
| <u>Acacia albida</u>            | mature leaf | 1 | 0.01 | 59 |
| <u>Allophylus africanus</u>     | young leaf  | 1 | 0.01 | 59 |
| <u>Cissampelos mucronata</u>    | mature leaf | 1 | 0.01 | 59 |
| <u>Cnestis ferruginea</u>       | young leaf  | 1 | 0.01 | 59 |

|                            |             |   |      |    |
|----------------------------|-------------|---|------|----|
| <u>Ficus sycomorus</u>     | young leaf  | 1 | 0.01 | 59 |
| <u>Gardenia erubescens</u> | flower bud  | 1 | 0.01 | 59 |
| <u>Gmelia arborea</u>      | mature leaf | 1 | 0.01 | 59 |
| <u>Hoslundia opposita</u>  | mature leaf | 1 | 0.01 | 59 |
| <u>Cissus sp.</u>          | mature leaf | 1 | 0.01 | 59 |
| <u>Jacaranda sp.</u>       | flower      | 1 | 0.01 | 59 |

89 species identified

13980 feeding records

OTHER ITEMS:

|                                       |    |      |
|---------------------------------------|----|------|
| <u>termite soil</u>                   | 37 | 0.2  |
| <u>bite on twigs</u>                  |    |      |
| <u>(infants &amp; juveniles only)</u> | 10 | 0.07 |
| <u>drink water</u>                    | 6  | 0.04 |
| <u>unidentified insect</u>            | 1  | 0.01 |
| <u>unidentified gall</u>              | 1  | 0.01 |

UNIDENTIFIED SPECIES:

|                      |     |      |
|----------------------|-----|------|
| <u>Vine species</u>  | 512 | 3.4  |
| <u>Tree species</u>  | 370 | 2.4  |
| <u>Herb species</u>  | 4   | 0.03 |
| <u>Liana species</u> | 2   | 0.01 |
| <u>Ficus</u>         | 15  | 0.1  |

TOTAL FEEDING RECORDS COLLECTED IN ABUKO

14938

|                                          |                                                               |            |             |
|------------------------------------------|---------------------------------------------------------------|------------|-------------|
| OTHER FOOD ITEMS:                        | <u>termite soil</u>                                           | <u>37</u>  | <u>0.2</u>  |
|                                          | <u>bite on twigs</u><br><u>(infants &amp; juveniles only)</u> | <u>10</u>  | <u>0.07</u> |
|                                          | <u>drink water</u>                                            | <u>6</u>   | <u>0.04</u> |
|                                          | <u>unidentified insect</u>                                    | <u>1</u>   | <u>0.01</u> |
|                                          | <u>unidentified gall</u>                                      | <u>1</u>   | <u>0.01</u> |
| UNIDENTIFIED SPECIES:                    |                                                               |            |             |
|                                          | <u>Vine species</u>                                           | <u>512</u> | <u>3.4</u>  |
|                                          | <u>Tree species</u>                                           | <u>370</u> | <u>2.4</u>  |
|                                          | <u>Herb species</u>                                           | <u>4</u>   | <u>0.03</u> |
|                                          | <u>Liana species</u>                                          | <u>2</u>   | <u>0.01</u> |
|                                          | <u>Ficus</u>                                                  | <u>15</u>  | <u>0.1</u>  |
| TOTAL FEEDING RECORDS COLLECTED IN ABUKO |                                                               | 14938      |             |

TABLE 13

Distribution of food items of 14,938 feeding records collected during scan-sampling from February 1979 - mid-January 1980.

| ITEMS                                                | PERCENT<br>of ANNUAL<br>DIET |
|------------------------------------------------------|------------------------------|
| <u>Fruits</u>                                        | <u>38.8</u>                  |
| <u>Seeds Only</u>                                    | <u>2.85</u>                  |
| <u>Flowers</u>                                       | <u>4.1</u>                   |
| <u>Flower Buds</u>                                   | <u>4.5</u>                   |
| <u>Mature Leaves (green)</u>                         | <u>11.4</u>                  |
| <u>Chlorotic Leaves (yellow)</u>                     | <u>0.2</u>                   |
| <u>Dying Leaves (brown)</u>                          | <u>0.1</u>                   |
| <u>Young Leaves</u>                                  | <u>26.2</u>                  |
| <u>Leaf Buds</u>                                     | <u>8.7</u>                   |
| <u>Leaf Petioles only</u>                            | <u>0.1</u>                   |
| <u>Vine Stems only</u>                               | <u>0.05</u>                  |
| <u>Young Aerial Root Tips (all Ficus trichopoda)</u> | <u>0.1</u>                   |
| <u>Bark (no insects)</u>                             | <u>0.03</u>                  |
| <u>Calyptrate Buds (all Ficus ovata)</u>             | <u>0.1</u>                   |
| <u>Flower Peduncle (all Palme)</u>                   | <u>0.1</u>                   |
| <u>Herb Stalk</u>                                    | <u>0.01</u>                  |
| <u>Galls on Mature Leaf (caused by Fungus)</u>       | <u>0.01</u>                  |
| <u>Unidentified Insect (probably ant)</u>            | <u>0.01</u>                  |
| <u>Termite Soil from Mounds</u>                      | <u>0.02</u>                  |
| <u>Termite Soil from Runway Sheets</u>               | <u>0.2</u>                   |
| <u>Drinking Water/Rain/Dew</u>                       | <u>0.04</u>                  |
| <u>Unknown</u>                                       | <u>2.2</u>                   |
| <u>TOTAL</u>                                         | <u>99.8</u>                  |

TABLE 14

Seasonality of major items in Focal troop's diet for 19 months

| MONTH        | REPRODUCTIVE PLANT PARTS<br>% of |                 | VEGETATIVE PLANT PARTS<br>% of |               | TOTAL        |       | TOTAL No. of<br>SPECIES<br>RECORDED |
|--------------|----------------------------------|-----------------|--------------------------------|---------------|--------------|-------|-------------------------------------|
|              | Fruits &<br>Seeds                | Floral<br>Parts | Mature<br>Leaf                 | Young<br>Leaf | Leaf<br>Buds | %     |                                     |
| July 1978    | <b>44.9%</b>                     | 2.7%            | 8.5%                           | 33.1%         | 2.5%         | 91.7% | 33                                  |
| August       | <b>42.8</b>                      | 1.8             | 20.8                           | 20.9          | 1.2          | 87.5  | 37                                  |
| September    | <b>65.75</b>                     | 1.1             | 17.0                           | 7.1           | 0.3          | 91.2  | 26                                  |
| October      | <b>55.5</b>                      | 0.9             | 14.4                           | 12.2          | 4.7          | 87.7  | 36                                  |
| November     | <b>52.8</b>                      | 7.1             | 7.8                            | 25.3          | 3.7          | 96.7  | 42                                  |
| December     | <b>46.2</b>                      | 15.6            | 9.3                            | 13.5          | 11.0         | 95.6  | 36                                  |
| January 1979 | <b>30.75</b>                     | 8.0             | 8.7                            | <b>34.0</b>   | 15.75        | 97.2  | 38                                  |
| February     | 14.4                             | 12.1            | 5.1                            | <b>35.7</b>   | 27.8         | 95.1  | 40                                  |
| March        | 22.6                             | 19.3            | 4.8                            | <b>44.9</b>   | 4.6          | 96.2  | 48                                  |
| April        | <b>33.1</b>                      | 6.1             | 6.2                            | 23.7          | 28.4         | 97.5  | 41                                  |
| May          | <b>55.2</b>                      | 3.9             | 3.9                            | 28.9          | 6.9          | 98.8  | 49                                  |
| June         | <b>69.9</b>                      | 2.8             | 3.0                            | 19.1          | 2.8          | 97.6  | 27*                                 |
| July         | <b>46.1</b>                      | 1.6             | 21.9                           | 27.3          | 0.9          | 97.8  | 49                                  |
| August       | 39.9                             | 0.6             | <b>41.7</b>                    | 13.4          | 1.5          | 97.1  | 46                                  |
| September    | <b>50.6</b>                      | 0.9             | 24.9                           | 15.3          | 1.2          | 92.9  | 39                                  |
| October      | <b>43.25</b>                     | 9.5             | 11.0                           | 26.7          | 4.1          | 94.6  | 38                                  |
| November     | <b>60.9</b>                      | 5.2             | 7.1                            | 20.1          | 5.5          | 98.8  | 34                                  |
| December     | <b>53.1</b>                      | 12.5            | 13.7                           | 12.9          | 5.4          | 97.6  | 40                                  |
| January 1980 | 29.4                             | 17.3            | 6.2                            | <b>44.0</b>   | 1.6          | 98.5  | 36                                  |

The major food item for each month is written in bold lettering. Fruits and seeds were the major items for 14 of the 19 months; young leaves for 4 months and mature leaves for one month. Since items such as soil, water, unidentified parts, and so forth are not counted in each monthly total, none of the months add up to 100.0%.

\* The month of June is based on 6 days of scan-sampling as opposed to 10 - 25 days (mean= 16.1) for the other months.

TABLE 15

Number of top-ranking food trees in three different troop's home ranges.

| TREE SPECIES                 | RANK IN<br>ANNUAL<br>DIET | NUMBER OF TREES IN VARIOUS RANGES |              |              |
|------------------------------|---------------------------|-----------------------------------|--------------|--------------|
|                              |                           | FOCAL<br>TROOP                    | PWD<br>TROOP | ZOO<br>TROOP |
| <u>Parinari excelsa</u>      | 1st                       | 18                                | 3            | 3            |
| <u>Ficus trichopoda</u>      | 2nd                       | 12                                | 3            | 2            |
| <u>Detarium senegalensis</u> | 3rd                       | 18                                | 3**          | 2 - 9        |

\*\* One of these Detarium trees is actually outside the reserve and is frequently harvested by the local villagers.

TABLE 16

Age at which infants were first observed taking solid food.

| INDIVIDUAL  | SEX    | AGE<br>(in days) | ITEM EATEN                 |
|-------------|--------|------------------|----------------------------|
| <u>Wimp</u> | male   | 43               | <u>mature leaf petiole</u> |
| <u>Imp</u>  | male   | 22               | <u>leaf bud</u>            |
| <u>Bimp</u> | male   | 18               | <u>young leaf</u>          |
| <u>Cid</u>  | male   | 12               | <u>fruit</u>               |
| <u>Gid</u>  | male   | 9                | <u>flower bud</u>          |
|             |        |                  |                            |
| <u>Id</u>   | female | 50               | <u>young leaf</u>          |
| <u>Bid</u>  | female | 33               | <u>mature leaf petiole</u> |
| <u>Nimp</u> | female | 30               | <u>leaf bud</u>            |
| <u>Simp</u> | female | 28               | <u>leaf bud</u>            |
| <u>Himp</u> | female | 24               | <u>young leaf</u>          |
| <u>Quid</u> | female | 17               | <u>mature leaf</u>         |
|             |        |                  |                            |
| <u>Vaby</u> | ?      | 20               | <u>young leaf</u>          |

Although there is a slight tendency for males to begin feeding on solid food at a younger age than females, it is not significant at one or two-tailed level (Kolmogorov-Smirnov test:  $Z = 18$ , d.f. = 6.6).



TABLE 17

A comparison of annual diets collected on Focal troop members from February 1979 through mid-January 1980.

|                                                 | ALL INDIVIDUALS<br>ABOVE 13 MONTHS<br>OF AGE | ALL INDIVIDUALS<br>BELOW 13 MONTHS<br>OF AGE |
|-------------------------------------------------|----------------------------------------------|----------------------------------------------|
| <hr/>                                           |                                              |                                              |
| Percent of Various Items<br>in the Annual Diet: |                                              |                                              |
| <u>Fruits and Seeds</u>                         | 43.7%                                        | 31.9%                                        |
| <u>Floral Parts</u>                             | 6.0                                          | 11.6                                         |
| <u>Leaf Buds</u>                                | 7.5                                          | 7.9                                          |
| <u>Young Leaves</u>                             | 29.1                                         | 30.4                                         |
| <u>Mature Leaves</u>                            | 11.1                                         | 13.4                                         |
| <u>Other Items</u>                              | 2.5                                          | 4.7                                          |
| <hr/>                                           |                                              |                                              |
| TOTAL PERCENT                                   | 99.9%                                        | 99.9%                                        |
| TOTAL (N)                                       | 4600 records                                 | 439 records                                  |

There is a significant profile difference in the two diets ( $\chi^2 = 40.8$ , d.f. = 5,  $p = < 0.0005$ ) with the major difference occurring in the fruit and seed category.

TABLE 18

A comparison of *P. badius* diets on five populations

|                                                    | TANA RIVER | GOMBE STREAM | KIBALE FOREST | FATHALA FOREST | ABUKO  |
|----------------------------------------------------|------------|--------------|---------------|----------------|--------|
| Percent of major Items in Diet:                    |            |              |               |                |        |
| FRUIT & SEED                                       | 25.0%      | 11.4%        | 5.7%          | 35.9%          | 41.6%  |
| FLORAL PARTS                                       | 6.2        | 6.8          | 11.9          | 8.7            | 8.6    |
| LEAF BUDS                                          | 16.4       | 2.8          | 11.2          | 17.5           | 8.7    |
| YOUNG LEAF                                         | 36.0       | 32.0         | 39.4          | 24.0           | 26.2   |
| MATURE LEAF                                        | 11.5       | 44.1         | 23.1          | 5.4            | 11.7   |
| TOTAL No. of ABOVE ITEMS*                          | 95.1       | 97.1         | 91.3          | 91.5           | 96.8   |
| Total No. of Species Recorded during scan-Samples: | 22         | 58+          | 56            | 39             | 89+    |
| Percent of Records made up by:                     |            |              |               |                |        |
| The Top-Ranking Species                            | 29.4       | 15.4         | 15.4          | 43.9           | 12.6   |
| The Top Five Species                               | 78.0       | 52.0         | 55.9          | 77.5           | 44.1   |
| The Top Ten Species                                | 92.3       | 78.4         | 75.0          | 89.9           | 61.2   |
| SAMPLE TIME (in months)                            | 12         | 8            | 12            | 12             | 12     |
| No. of FEEDING RECORDS                             | 2,361      | 7,346        | 2,898         | 3,322          | 14,938 |

\*Percentages do not add up to 100.0% because only major items are considered. Unidentified items, water, soil, insects, and other minor items or items specific to certain populations (for example aerial root tips eaten by the colobus in Abuko) were eliminated from this analysis.

The above data were extracted from Marsh (1978), Clutton-Brock (1975), Struhsaker (1975), and Gatinot (1977). The basic format of the table is taken from Marsh (1978).

**TABLE 19**

Per cent of time different populations spend in different activities

|                                 | TANA RIVER<br>KENYA<br>(mean)          | GOMBE<br>TANZANIA<br>(median)              | KIBALE FOREST<br>UGANDA<br>(mean)      | ABUKO<br>THE GAMBIA<br>(mean) (median) |                                        |
|---------------------------------|----------------------------------------|--------------------------------------------|----------------------------------------|----------------------------------------|----------------------------------------|
| Per cent of time<br>Spent in:   |                                        |                                            |                                        |                                        |                                        |
| Feeding                         | 30.0%                                  | 25.0%                                      | 45.3%                                  | 21.3%                                  | 19.9%                                  |
| Inactive<br>(includes clinging) | 54.9                                   | 54.0                                       | 37.6                                   | 52.4                                   | 54.7                                   |
| Moving                          | 7.2                                    | 8.0                                        | 9.0                                    | 12.5                                   | 13.2                                   |
| Social +<br>Auto-grooming       | 4.1                                    | 5.6                                        | 5.3                                    | 5.6                                    | 5.7                                    |
| Play                            | 3.4                                    | 3.0                                        | 2.7                                    | 6.5                                    | 6.1                                    |
| Total of Above                  | 99.6                                   | 95.6                                       | 99.9                                   | 98.3                                   | 99.6                                   |
| Sample Time<br>in months        | 12                                     | 8                                          | 12                                     | 12                                     | 12                                     |
| Methods                         | Sustained<br>Quarter-hour<br>intervals | Instantaneous<br>Quarter-hour<br>intervals | Sustained<br>Quarter-hour<br>intervals | Sustained<br>Quarter-hour<br>intervals | Sustained<br>Quarter-hour<br>intervals |
| Source                          | Marsh<br>1978                          | Clutton-Brock<br>1974                      | Struhsaker<br>1975                     |                                        |                                        |

TABLE 20

Per cent of total resting time various individuals spent in a lying position during twelve month period.

| INDIVIDUAL                        | PER CENT OF TIME | NUMBER OF RECORDS |
|-----------------------------------|------------------|-------------------|
|                                   | %                | N                 |
| <u>ADULT MALES</u>                |                  |                   |
| Captain Crook                     | 4.6%             | 30                |
| Mr. Mean                          | 0.1              | 1                 |
| <u>JUVENILES</u>                  |                  |                   |
| Punk - female                     | 15.4             | 53                |
| Dunk - female                     | 3.4              | 14                |
| Yunk - male                       | 4.0              | 13                |
| <u>MOTHERS of INFANTS</u>         |                  |                   |
| Wild                              | 2.3              | 9                 |
| Inca                              | 3.3              | 22                |
| Nene                              | 5.2              | 24                |
| Metoo                             | 4.4              | 17                |
| Button                            | 4.9              | 21                |
| Solid                             | 7.0              | 28                |
| Head                              | 2.6              | 11                |
| <u>ADULT FEMALES</u>              |                  |                   |
| Droopy                            | 12.8             | 62                |
| YumDum                            | 1.0              | 4                 |
| Julie                             | 5.4              | 25                |
| Volley                            | 3.6              | 13                |
| <u>JUVENILE-SUBADULT FEMALES*</u> |                  |                   |
| Round                             | 38.3             | 51                |
| Pelf                              | 8.2              | 11                |

MEAN PER CENT 7.0

MEDIAN PER CENT 4.5%

In the above analysis N refers to the total number of records made on the individual while in the lying position during the scan-sampling period. The per cent refers to total per cent of resting time spent in the lying position. For example, Punk spent 15.4% of her resting time in a lying position and 84.6% of her time in a sitting position.

\*The data based on Round is based on 7 months of observations and the data on Pelf is based on 5 months. The rest of the data is based on 12 months of scan-sampling.

TABLE 21

## Types of Interactions Observed During Scan-sample Period

TYPE OF INTERACTION  
OBSERVED

|                                                  | No. | %    |
|--------------------------------------------------|-----|------|
| <u>Female Courtship Display</u>                  | 47  | 27.5 |
| <u>Chases</u>                                    | 24  | 14.0 |
| <u>Male Mounts Female</u>                        | 22  | 12.9 |
| <u>Female Mounted by Male</u>                    | 22  | 12.9 |
| <u>Chased</u>                                    | 7   | 4.1  |
| <u>Gives Facial Threat</u>                       | 7   | 4.1  |
| <u>Gives Branch Bounce Threat</u>                | 6   | 3.5  |
| <u>Male Inspects Female Genitalia</u>            | 4   | 2.3  |
| <u>Female Presents Rump to Male</u>              | 4   | 2.3  |
| <u>Male Mounted</u>                              | 4   | 2.3  |
| <u>Unidentified Individual Mounts Male</u>       | 4   | 2.3  |
| <u>Gives Submissive Facial Expression</u>        | 4   | 2.3  |
| <u>Displaced from Food Site</u>                  | 2   | 1.2  |
| <u>Displaces from Food Site</u>                  | 2   | 1.2  |
| <u>Embraces</u>                                  | 2   | 1.2  |
| <u>Ignores Facial Threat and Looks Away</u>      | 2   | 1.2  |
| <u>Fight with Physical Contact</u>               | 2   | 1.2  |
| <u>Mother push Infant off Nipple</u>             | 1   | 0.6  |
| <u>Infant throws Weaning Tantrum</u>             | 1   | 0.6  |
| <u>Infant Interfers with Mating</u>              | 1   | 0.6  |
| <u>Infant hides from Tourists</u>                | 1   | 0.6  |
| <u>Female Mounts Unidentified Individual</u>     | 1   | 0.6  |
| <u>Unidentified Individual Mounted by Female</u> | 1   | 0.6  |
| <u>TOTAL INTERACTIONS OBSERVED</u>               | 171 |      |

Of the 41 actively aggressive interactions listed above, 8 of them were directed toward other species and 17 of them were directed toward colobus from other troops, not toward Focal troop members.

Therefore, only 16 of the 41 aggressive acts were intertroop interactions.

**TABLE 22**

Per cent of time individuals spent feeding and resting during one year.

| INDIVIDUAL                       | PER CENT OF TIME<br>FEEDING | PER CENT OF TIME<br>RESTING | No. OF RECORDS<br>COLLECTED<br>FEED + REST |
|----------------------------------|-----------------------------|-----------------------------|--------------------------------------------|
| <u>ADULT MALES</u>               |                             |                             |                                            |
| Captain Crook                    | 23.1                        | 74.9                        | 867                                        |
| Mr. Mean                         | 31.5                        | 68.5                        | 986                                        |
| <u>JUVENILES</u>                 |                             |                             |                                            |
| Punk - female                    | 38.9                        | 61.1                        | 563                                        |
| Dunk - female                    | 31.7                        | 68.4                        | 597                                        |
| Yunk - male                      | 34.3                        | 65.7                        | 492                                        |
| <u>MOTHERS</u>                   |                             |                             |                                            |
| Wild                             | 35.2                        | 64.8                        | 600                                        |
| Inca                             | 32.5                        | 67.5                        | 996                                        |
| Nene                             | 37.2                        | 62.8                        | 729                                        |
| Metoo                            | 30.1                        | 69.9                        | 555                                        |
| Button                           | 41.2                        | 58.8                        | 729                                        |
| Solid                            | 28.2                        | 71.8                        | 563                                        |
| Head                             | 27.9                        | 72.1                        | 595                                        |
| <u>ADULT FEMALES</u>             |                             |                             |                                            |
| Droopy                           | 27.1                        | 72.9                        | 665                                        |
| YumDum                           | 35.5                        | 64.5                        | 595                                        |
| Julie                            | 30.9                        | 69.1                        | 676                                        |
| Volley                           | 30.8                        | 69.2                        | 516                                        |
| <u>JUVENILE-SUDADULT FEMALES</u> |                             |                             |                                            |
| Velf                             | 31.5                        | 68.5                        | 343                                        |
| Pelf                             | 36.4                        | 63.6                        | 209                                        |
| <u>TOTAL RECORDS</u>             |                             |                             | 11,276                                     |
| MEAN PER CENT                    | 32.0                        | 68.0                        |                                            |

All animals spent significantly more time resting than feeding (binomial test, two-tailed  $p = <0.01$ ;  $z = 3.9$ ). There is a significant ratio difference overall between individuals (chi-square = 30.1; d.f. = 17;  $p = 0.05$ ). Captain Crook, the dominant male, spent more time resting than Mr. Mean (binomial test, one-tailed  $p = <0.001$ ,  $z = 3.24$ ). \* The data on Velf is based on 10 months scan-sampling and on Pelf is based on 5 months only.

TABLE 23

Mastication rates for six animals feeding on unripe mangos.

| INDIVIDUAL           | No.<br>Separate<br>Records | Mean No.<br>Chews<br>per<br>Second | Median No.<br>Chews<br>per<br>Second | Range<br>Chews<br>per<br>Second |
|----------------------|----------------------------|------------------------------------|--------------------------------------|---------------------------------|
| <u>ADULT MALES</u>   |                            |                                    |                                      |                                 |
| Captain Crook        | 6                          | 2.7                                | 2.55                                 | 2 - 3.4                         |
| Mr. Mean             | 2                          | 3.1                                | 3.1                                  | 2.8 - 3.5                       |
| <u>ADULT FEMALES</u> |                            |                                    |                                      |                                 |
| Metoo                | 3                          | 2.65                               | 2.75                                 | 2.4 - 2.8                       |
| Nene                 | 3                          | 2.1                                | 2.15                                 | 2.1 - 2.3                       |
| Volley               | 2                          | 2.2                                | 2.2                                  | 2.2 - 2.3                       |
| YumDum               | 3                          | 2.4                                | 2.2                                  | 1.8 - 2.7                       |
| MEAN                 |                            | 2.5                                |                                      |                                 |
| MEDIAN               |                            |                                    | 2.35                                 |                                 |

To determine mastication rates, individuals were timed as soon as they took their first bite of an unripe mango and all chews made on that first bite were counted. For example, YumDum was seen 3 separate times entering a mango tree and starting to feed. Once she took 33 chews in 17½ seconds, once 22 chews in 9 seconds and once 22 chews in 8 seconds. This gave her a mean of 2.23 chews per second. This data only pertains to the first bite on a food source. Presumably, after they had been eating for a while the rate declines.

TABLE 24

Recipients of Double Grooming from January 1979-June 1980 and April 1981-June 1982

| CLASS OF INDIVIDUALS   | RECEIVES DOUBLE GROOMING |       |
|------------------------|--------------------------|-------|
|                        | (No.)                    | (%)   |
| <u>Adult Male</u>      | 61                       | 57.0  |
| <u>Adult Female</u>    | 27                       | 25.2  |
| <u>Subadult Male</u>   | 5                        | 4.7   |
| <u>Subadult Female</u> | 1                        | 0.9   |
| <u>Juvenile Male</u>   | 9                        | 8.4   |
| <u>Juvenile Female</u> | 3                        | 2.8   |
| <u>Unsexed Infant</u>  | 1                        | 0.9   |
| TOTAL                  | 107 records              | 99.9% |



TABLE 25

## Focal troop grooming patterns for one annual cycle

| INDIVIDUAL              | GROOMED<br>Bouts |      | GROOMS<br>Bouts |      | TOTAL<br>Bouts<br>No. |
|-------------------------|------------------|------|-----------------|------|-----------------------|
|                         | No.              | %    | No.             | %    |                       |
| <hr/>                   |                  |      |                 |      |                       |
| <u>ADULT MALES</u>      |                  |      |                 |      |                       |
| Captain Crook           | 73               | 77.7 | 21              | 22.3 | 94                    |
| Mr. Mean                | 86               | 97.7 | 2               | 2.3  | 88                    |
| <u>JUVENILES</u>        |                  |      |                 |      |                       |
| Punk - female           | 16               | 57.1 | 12              | 42.9 | 28                    |
| Dunk - female           | 13               | 35.1 | 24              | 64.9 | 37                    |
| Yunk - male             | 9                | 60.0 | 6               | 40.0 | 15                    |
| <u>MOTHERS</u>          |                  |      |                 |      |                       |
| Wild                    | 20               | 30.8 | 45              | 69.2 | 65                    |
| Inca                    | 36               | 43.9 | 46              | 56.1 | 82                    |
| Nene                    | 21               | 35.6 | 38              | 64.4 | 59                    |
| Metoo                   | 7                | 18.9 | 30              | 81.1 | 37                    |
| Button                  | 15               | 25.4 | 44              | 74.6 | 59                    |
| Solid                   | 45               | 52.3 | 41              | 47.7 | 86                    |
| Head                    | 16               | 36.4 | 28              | 63.6 | 44                    |
| <u>ADULT FEMALES</u>    |                  |      |                 |      |                       |
| Droopy                  | 22               | 48.9 | 23              | 51.1 | 45                    |
| YunDum                  | 15               | 50.0 | 15              | 50.0 | 30                    |
| Volley                  | 29               | 28.2 | 74              | 71.8 | 103                   |
| Julie                   | 17               | 32.7 | 35              | 67.3 | 52                    |
| <u>SUBADULT FEMALES</u> |                  |      |                 |      |                       |
| Round*                  | 28               | 45.9 | 33              | 54.1 | 61                    |
| Pelf*                   | 9                | 42.9 | 12              | 57.1 | 21                    |
| Velf                    | 19               | 46.3 | 22              | 53.7 | 41                    |
| <hr/>                   |                  |      |                 |      |                       |
| MEAN %                  |                  | 45.6 |                 | 54.4 |                       |
| MEDIAN %                |                  | 43.9 |                 | 56.1 |                       |

Data on Round is based on 7 months and for Pelf on 5 months observation; the rest are based on 12 months of scan-sampling

**TABLE 26**

No. and % of times adult males groom and are groomed by different age-sex classes  
August 1978 - August 1980

|               | RECEIVES GROOMING FROM |       |       |       | TOTAL |
|---------------|------------------------|-------|-------|-------|-------|
|               | FEMALES                |       | MALES |       |       |
|               | ADULT                  | YOUNG | ADULT | YOUNG |       |
| Captain Crook | 543                    | 108   | 1     | 54    | 706   |
| Mr. Mean      | 533                    | 47    | 8     | 20    | 608   |
| TOTAL (No.)   | 1076                   | 155   | 9     | 74    | 1314  |
| TOTAL (%)     | 81.9%                  | 11.8% | 0.1%  | 5.6%  |       |

|               | GIVES GROOMING TO |       |       |       | TOTAL |
|---------------|-------------------|-------|-------|-------|-------|
|               | FEMALES           |       | MALES |       |       |
|               | ADULT             | YOUNG | ADULT | YOUNG |       |
| Captain Crook | 58                | 36    | 8     | 1     | 103   |
| Mr. Mean      | 7                 | 9     | 1     | 3     | 20    |
| TOTAL (No.)   | 65                | 45    | 9     | 4     | 123   |
| TOTAL (%)     | 52.8              | 36.6  | 7.3   | 3.3   |       |

Captain Crook grooms Mr. Mean more than Mr. Mean grooms Captain Crook  
(Fisher's Exact test:  $p = 0.019$ ).

Captain Crook and Mr. Mean receive the same amount of grooming from adult females  
(two-sided binomial test,  $z = 0.3$ ;  $p = 0.76$ ).

Captain Crook receives more grooming from young females and young males than Mr. Mean  
(two-sided binomial test,  $z = 6.3$ ,  $p = <0.0002$ ).

Captain Crook gives more grooming to adult and young females than Mr. Mean does  
(two-sided binomial test,  $z = 6.9$ ;  $P = <0.0002$ ).

TABLE 27

## Auto-Grooming Bouts

| GROOMER                   | BOUITS |       |
|---------------------------|--------|-------|
|                           | (N)    | (%)*  |
| <u>ADULT MALES</u>        |        |       |
| Captain Crook             | 26     | 21.7% |
| Mr. Mean                  | 23     | 20.7  |
| <u>JUVENILES</u>          |        |       |
| Punk - female             | 12     | 30.0  |
| Dunk - female             | 5      | 11.9  |
| Yunk - male               | 1      | 6.3   |
| <u>MOTHERS OF INFANTS</u> |        |       |
| Wild                      | 3      | 4.4   |
| Inca                      | 9      | 9.9   |
| Nene                      | 5      | 7.8   |
| Metoo                     | 5      | 11.9  |
| Button                    | 5      | 7.8   |
| Solid                     | 4      | 4.4   |
| Head                      | 4      | 8.3   |
| <u>ADULT FEMALES</u>      |        |       |
| Volley                    | 6      | 5.5   |
| Droopy                    | 5      | 10.0  |
| YumDum                    | 8      | 21.1  |
| Julie                     | 8      | 13.3  |
| <u>SUBADULT FEMALE</u>    |        |       |
| Round**                   | 9      | 12.9  |

\*The per cent refers to the per cent of total grooming bouts the individual was observed to participate in (auto-grooming + grooming others + being groomed). For example, Captain Crook auto-groomed 26 times, groomed others 21 times and was groomed 73 times during 12 months of quarter-hourly scan-samples. Therefore his 26 auto-grooming bouts are equal to 21.7% of his total observed grooming bouts. The total number of social grooming bouts for each individual can be found in Table 25.

\*\* Data on Round is based on 7 months of scan-sampling; the rest is based on 12 months of scan-sampling.

TABLE 28

Birth information for all 28 Focal troop infants in Abuko

| DATE OF BIRTH      | SEX    | MOTHER'S NAME | INFANT'S NAME | MORTALITY |
|--------------------|--------|---------------|---------------|-----------|
| ± 1 January 1978   | ?      | Metoo         | Munk          | died      |
| ± 1 January        | Female | Droopy        | Dunk          |           |
| ± 1 January        | Female | Porkpie       | Punk          |           |
| ± 1 January        | Male   | YumDum        | Yunk          |           |
| 14 January         | ?      | Kunkle        | Kunk          | died      |
| 31 October         | Male   | Wild          | Wimp          |           |
| 4 December         | Male   | Inca          | Imp           |           |
| 7 December         | Female | Nene          | Nimp          |           |
| 13 December        | Male   | Metoo         | Mimp          |           |
| 3 January 1979     | Female | Solid         | Simp          |           |
| 3 January          | Male   | Button        | Bimp          |           |
| 9 February         | Female | Head          | Himp          |           |
| ± 1 April          | Male   | Garuda        | Gimp          |           |
| 20 April 1980      | ?      | Volley        | Vaby          | died      |
| 0 April 1981       | Male   | Cisco         | Cid           |           |
| 8 April            | Female | Quechua       | Quid          |           |
| 17 April           | ?      | Round         | Rid           | died      |
| 18 April           | Female | Inca          | Id            |           |
| 25 April           | Female | Button        | Bid           | died      |
| 7 - 11 May         | Female | Nene          | Nid           |           |
| 23 January 1982    | ?      | Kama          | Kissue        |           |
| 31 January         | Male   | Garuda        | Gissue        |           |
| 27 Mar. - 3 April  | ?      | Tara          | Tissue        | died      |
| 27 April           | Male   | Nimp          | Nissue        |           |
| 13 June            | ?      | Falafel       | Fissue        |           |
| 25 January 1983    | ?      | Zorro         | Zirth         |           |
| 12 Feb. - 22 March | ?      | Eisel         | Eirth         |           |
| 12 Feb. - 22 March | Female | Simp          | Sirth         |           |

During this study the exact birth dates for 18 infants were recorded and a further 10 birth dates were estimated.

± is used to denote two weeks more or less. For example, ± 1 January means the birth occurred between December 15 to January 15. In the cases where actual dates are given as estimates such as 12 Feb. - 22 March it means that the mother was seen on the 11th of February with no infant and by the 22nd she had an infant.

Died is used to signify that an infant died before it's first birthday. In fact, all the infants so listed died before they reached 6 months of age.

TABLE 29

Information on mortality for all Focal troop members: dates, names, age/sex class and causes.

| DATE OF DEATH | NAME          | AGE        | SEX            | CAUSE OF DEATH                 |
|---------------|---------------|------------|----------------|--------------------------------|
| June 1978     | Munk          | ±5 months  |                | Infanticide                    |
| July          | Kunk          | 1 week     | ?              | Infanticide (?)                |
| October       | Porkpie       | adult      | F; lactating   | Disappear                      |
| June 1979     | Pug Ugly      | old adult  | F; acyclic     | Old age (?)                    |
| July 1980     | Metoo         | adult      | F; cycling     | Disappear                      |
| July          | Volley        | adult      | F; lactating   | Disappear with Vaby            |
| July          | Vaby          | 3 months   | ?              | Disappear with Volley (mother) |
| November      | YumDum        | adult      | F; acyclic     | Disappear; Old age             |
| January 1981  | Julie         | adult      | F; acyclic     | Old age (?)                    |
| February      | Noam          | adult      | F; acyclic     | Snake bite                     |
| April         | Head          | adult      | F; pregnant(?) | Disappear                      |
| April         | Round         | adult      | F; lactating   | Snake bite                     |
| April         | Rid           | 9 days     | ?              | Disappear (mother dies)        |
| May           | Yunk          | 41 months  | M              | Disappear                      |
| September     | Button        | adult      | F; lactating   | Disappear with Bid             |
| September     | Bid           | 4.5 months | F              | Disappear with mother (Button) |
| January 1982  | Mr. Mean      | old adult  | M              | Disappear; Old age (?)         |
| May           | Imp           | 41 months  | M              | Electrocuted                   |
| May           | Tissue        | 1 month    | ?              | Infanticide (?)                |
| July          | Droopy        | adult      | F; cycling     | Disappear                      |
| July          | Captain Crook | adult      | M              | Disappear                      |
| December      | Bimp          | 47 months  | M              | Crocodile                      |

During the course of this study 10 individuals died and a further 13 disappeared from Abuko and were presumed dead. The individuals listed as having disappeared, were all well-known and would have been immediately recognized if they had been seen anywhere in Abuko. A complete search and continual censusing in Abuko without any sign of them appearing seemed to indicate that they had died, or, at least left Abuko. Two infants, Munk and Tissue are presumed to have been infanticide victims because of the type and number of wounds. Old age is listed as cause of death when the individual was clearly very old and incapacitated. Rid, a nine-day-old infant disappeared when her mother died from snake bite. Although Rid was never found, this disappearance is counted as a known death since it seems unlikely that a 9-day-old could survive without its mother. It is even possible that Rid was eaten by the snake which bit Round.

**TABLE 30**
**Mortality Information on Non-Focal Troop Members in Abuko**

| <b>AGE</b>  | <b>SEX</b> | <b>TIME OF DEATH*</b> | <b>CAUSE OF DEATH</b>                           |
|-------------|------------|-----------------------|-------------------------------------------------|
| Juvenile    | ?          | ?                     | ?                                               |
| Juvenile    | Male       | July 1983             | Slash wound - possible infanticide              |
| Subadult    | Female     | February 1979         | ?                                               |
| Subadult    | Male       | October 1980          | Fighting - probably killed by PWD               |
| Subadult    | Male       | ?                     | ?                                               |
| Young Adult | Male       | July 1978             | Fighting - Bully killed by Focal troop          |
| Young Adult | Male       | April 1981            | Fighting - Bend probably killed by PWD          |
| Young Adult | Male       | July 1983             | Crocodile feeds on 'alien '                     |
| Adult       | ?          | ?                     | ?                                               |
| Adult       | Male       | July 1982             | Caged hyenas in zoo kill member of Zoo troop    |
| Adult       | Female     | August 1981           | vomited up by captured python                   |
| Old Adult   | Female     | April 1978            | Python - female's body found inside dead python |
| Old Adult   | Female     | ?                     | ?                                               |

\*If the actual death was seen or the body was discovered shortly after death.

TABLE 31

Number of times young females receive aggression from resident adult females

| YOUNG FEMALE | MOTHER'S RANK | No. of AGGRESSIVE<br>ACTS RECEIVED | BASED ON<br>No. of<br>MONTHS | No. of Aggressive<br>ACTS RECEIVED<br>EACH MONTH |
|--------------|---------------|------------------------------------|------------------------------|--------------------------------------------------|
| Punk         | Orphan        | 26                                 | 19                           | 1.4                                              |
| Dunk         | 1st           | 7                                  | 19                           | 0.4                                              |
| Himp         | 6th           | 14                                 | 16                           | 0.9                                              |
| Simp         | 2nd           | 5                                  | 16                           | 0.3                                              |
| Nimp         | 3rd           | 7                                  | 16                           | 0.4                                              |

The data on the peers Punk and Dunk pertains to the time from Punk's being orphaned to Dunk's leaving Focal troop and joining Zoo troop.

The data on Himp, Simp and Nimp (peers) pertains to the time from their first receiving aggression to Himp and Nimp leaving Focal troop and joining Zoo troop.

TABLE 32

## Seasonality of courtship displays by Focal troop females

| MONTH        | TOTAL No. OF DAYS<br>DISPLAYS RECORDED | TOTAL No. OF<br>DISPLAYS | MEAN No. OF DISPLAYS |
|--------------|----------------------------------------|--------------------------|----------------------|
| October 1979 | 15                                     | 73                       | 4.9                  |
| November     | 15                                     | 36                       | 2.4                  |
| December     | 15                                     | 12                       | 0.8                  |
| January 1980 | 15                                     | 9                        | 0.6                  |
| February     | 15                                     | 23                       | 1.5                  |
| March        | 15                                     | 12                       | 0.8                  |
| April        | 13                                     | 12                       | 0.9                  |
| May          | 15                                     | 121                      | 8.1                  |
| June         | 15                                     | 166                      | 11.1                 |
| July         | 15                                     | 159                      | 10.6                 |
| August       | 2                                      | 18                       | 9.0                  |
| September    | 0                                      | ---                      | ---                  |
| October      | 4                                      | 34                       | 8.5                  |
| November     | 11                                     | 81                       | 7.4                  |
| December     | 15                                     | 50                       | 3.3                  |
| January 1981 | 12                                     | 6                        | 0.5                  |
| February     | 11                                     | 5                        | 0.5                  |
| March        | 9                                      | 17                       | 1.9                  |
| April        | 15                                     | 14                       | 1.1                  |
| May          | 6                                      | 38                       | 6.3                  |
| June         | 15                                     | 101                      | 6.7                  |

The above table lists the minimum number of female courtship displays heard and recorded for a certain number of days each month. Courtship displays varied significantly throughout the year: likelihood ratio test, d.f. = 10;  $p = <0.0001$ .



**TABLE 33**  
Aggressive forms used by females and males in all contexts.

|                                      | ADULT MALES |      | ADULT FEMALES |      | TOTAL |
|--------------------------------------|-------------|------|---------------|------|-------|
|                                      | No.         | %    | No.           | %    | No.   |
| <u>NONCONTACT FORM OF AGGRESSION</u> |             |      |               |      |       |
| Vocalizations only                   | 6           | 3.2  | 3             | 1.1  | 9     |
| Facial Threats only                  | 26          | 14.1 | 119           | 43.8 | 145   |
| Supplantation                        | 8           | 4.3  | 6             | 2.2  | 14    |
| Branch Shake/ Branch Jump            | 2           | 1.1  | 5             | 1.8  | 7     |
| Chase                                | 66          | 35.7 | 56            | 20.2 | 122   |
| Lunge                                | 24          | 12.9 | 13            | 4.7  | 37    |
| Tug-of-war with dead branch          | 10          | 5.4  | 1             | 0.03 | 11    |
| Grab Food                            | 4           | 2.2  | 4             | 1.4  | 8     |
| <u>CONTACT FORMS OF AGGRESSION</u>   |             |      |               |      |       |
| Hit, Slap, Pull Hair                 | 32          | 17.3 | 42            | 15.2 | 74    |
| Bite                                 | 5           | 2.7  | 5             | 1.8  | 10    |
| Grapple, Combination of Bite and Hit | 2           | 1.1  | 23            | 8.3  | 25    |
|                                      | YOUNG MALES |      | YOUNG FEMALES |      | TOTAL |
|                                      |             |      |               |      |       |
| <u>NONCONTACT FORM OF AGGRESSION</u> |             |      |               |      |       |
| Vocalizations Only                   | 0           | 0.0% | 0             | 0.0% | 0     |
| Facial Threat Only                   | 3           | 3.1  | 17            | 27.9 | 20    |
| Supplantation                        | 2           | 2.0  | 1             | 1.6  | 3     |
| Branch Shake/Branch Jump             | 7           | 7.1  | 11            | 18.0 | 18    |
| Chase                                | 6           | 6.1  | 12            | 19.7 | 18    |
| Lunge                                | 4           | 4.1  | 1             | 1.6  | 5     |
| Tug-of-War                           | 7           | 7.1  | 0             | 0    | 7     |
| Grab Food                            | 10          | 10.2 | 4             | 6.6  | 14    |
| Display                              | 46          | 46.9 | 2             | 3.3  | 48    |
| <u>CONTACT FORM OF AGGRESSION</u>    |             |      |               |      |       |
| Hit, Slap, Pull Hair                 | 13          | 13.3 | 8             | 13.1 | 21    |
| Bite                                 | 0           | 0.0  | 2             | 3.3  | 2     |
| Grapple, Bite, Hit, Pull, Slap       | 0           | 0.0  | 3             | 4.9  | 3     |

The above numbers refer only to interactions where the form of aggression was noted.

TABLE 34

Distribution of aggression over age-sex classes

## A G G R E S S O R

|                      | ADULT |        | SUBADULT |        | JUVENILE |        | TOTAL | MEAN No.   |
|----------------------|-------|--------|----------|--------|----------|--------|-------|------------|
|                      | Male  | Female | Male     | Female | Male     | Female | (N)   | PER ANIMAL |
| MEAN No. OF ANIMALS  | 2.35  | 12.3   | 0.2      | 0.8    | 1.9      | 7.0    |       |            |
| <u>T A R G E T S</u> |       |        |          |        |          |        |       |            |
| Adult Male           | 45    | 34     | 6        | 4      | 15       | 8      | 112   | 47.6       |
| Adult Female         | 30    | 134    | 4*       | 9      | 14**     | 4      | 195   | 15.9       |
| Subadult Male        | 9     | 17     | 1        | 1      | 2        | 2      | 32    | 160.0      |
| Subadult Female      | 11    | 48     | 2        | 4      | 1        | 6      | 72    | 90.0       |
| Juvenile Male        | 59    | 83     | 28       | 5      | 20       | 15     | 210   | 110.5      |
| Juvenile Female      | 10    | 101    | 3        | 8      | 13       | 8      | 143   | 20.4       |
| Unsexed Juvenile     | 59    | 53     | 0        | 15     | 0        | 0      | 127   |            |
| TOTAL                | 223   | 470    | 44       | 46     | 65       | 43     | 891   |            |
| MEAN No. PER ANIMALS | 94.9  | 38.2   | 220      | 57.5   | 34.2     | 6.1    |       |            |

\*Two of the four cases involved a subadult male attacking his mother. None of the nine acts of subadult female aggression were directed toward their mothers.

\*\*Eight of the fourteen cases involved males attacking their own mothers. None of the four acts of juvenile female aggression were directed toward their mothers.

The rates at which juveniles received aggression was far higher than is indicated by the above table. The highest number of acts received were by juveniles who were not accurately sexed.

1. Juvenile males receive significantly more aggression than juvenile females (chi-square = 309,  $p = <0.00001$ ).
2. Subadult males receive significantly more aggression than subadult females (chi-square = 7.5,  $p = <0.01$ ).

The above were collected on an ad lib. basis (July 1978 - May 1981). They do not correspond with the numbers in Table 36. Table 36 refers to context. This table is based on identity of the aggressor and the target regardless of context.

TABLE 35

Shows how many times each age-sex class were aggressive to any age-sex class.

## A G G R E S S O R

|                 | <u>A D U L T</u> |        | <u>S U B A D U L T</u> |        | <u>J U V E N I L E</u> |        |
|-----------------|------------------|--------|------------------------|--------|------------------------|--------|
|                 | male             | female | male                   | female | male                   | female |
| <b>TARGETS</b>  |                  |        |                        |        |                        |        |
| Adult male      | 19.1             | 2.76   | 30                     | 5      | 7.9                    | 1.1    |
| Adult female    | 12.8             | 10.9   | 20                     | 11.25  | 7.4                    | 0.6    |
| Subadult male   | 3.8              | 1.4    | 5                      | 1.25   | 1.1                    | 0.6    |
| Subadult female | 4.7              | 3.9    | 10                     | 5      | 0.5                    | 0.9    |
| Juvenile male   | 26.1             | 6.75   | 140                    | 6.25   | 10.5                   | 2.1    |
| Juvenile female | 4.25             | 8.2    | 15                     | 10     | 6.8                    | 1.1    |
| MEAN            | 11.6             | 5.65   | 36.6                   | 6.5    | 5.7                    | 1.1    |

The above is corrected for different age-sex classes. Comparing all males with all females it is clear that aggression is intrasexual (chi-square = 78.5, d.f. = 1,  $p = <0.001$ ). Juvenile males are more aggressive than juvenile females ( $z = 7.72$ ,  $p = <0.0002$  two-tailed). Adult males are more aggressive than adult females ( $z = 11.58$ ,  $p = <0.0002$  two-tailed).

TABLE 36

Frequency of aggression for females and males in all contexts in the focal troop.

|                           | A G G R E S S O R S |       |      |       |    | TOTAL<br># | TOTAL<br>% |
|---------------------------|---------------------|-------|------|-------|----|------------|------------|
|                           | AF                  | AM    | YF   | YM    | ?Y |            |            |
| Mean # of individuals     | 12.3                | 2.35  | 7.8  | 2.1   |    |            |            |
| <u>CONTEXT</u>            |                     |       |      |       |    |            |            |
| 1. UNKNOWN                | 80                  | 30    | 22   | 25    | 9  | 166        | 14.0       |
| 2. HARASSMENT             | 43                  | 27    | 15   | 41    | 1  | 127        | 10.7       |
| 3. PROTECT INFANT         |                     |       |      |       |    |            |            |
| BY MOTHER                 | 104                 |       |      |       |    | 104        | 8.8        |
| BY OTHERS                 | 8                   | 8     | 8    | 1     |    | 25         | 2.1        |
| 4. PROTECT JUVENILE       |                     |       |      |       |    |            |            |
| BY MOTHER                 | 45                  |       |      |       |    | 45         | 3.8        |
| BY OTHERS                 |                     |       | 3    |       |    | 3          | 0.02       |
| 5. FOOD                   | 34                  | 49    | 12   | 20    | 1  | 116        | 9.8        |
| 6. SPACE                  | 42                  | 28    | 6    | 9     |    | 85         | 7.2        |
| 7. SEXUAL ACCESS          | 12                  | 55    | 9    | 128   |    | 204        | 17.2       |
| 8. WEANING                | 77                  |       |      |       |    | 77         | 6.5        |
| 9. RETALIATION            | 42                  | 10    | 12   | 5     |    | 69         | 5.8        |
| 10. SHADOWING MALE        | 28                  | 19    | 11   | 2     |    | 60         | 5.1        |
| 11. TUG-of-WAR            | 1                   | 10    |      | 7     |    | 18         | 1.5        |
| 12. COALITION             | 6                   | 7     | 2    | 2     |    | 17         | 1.4        |
| 13. INTERVENTION          |                     |       |      |       |    |            |            |
| STOP GROOMING             | 7                   | 3     | 1    | 2     |    | 13         | 1.1        |
| STOP NURSING              |                     | 3     |      |       |    | 3          | 0.02       |
| STOP FIGHTING             | 2                   |       |      |       |    | 2          | 0.02       |
| STOP PLAYING              |                     |       | 1    |       |    | 1          | 0.01       |
| STOP REASSURING           |                     | 1     |      |       |    | 1          | 0.01       |
| 14. REDIRECTION           | 2                   |       |      |       |    | 2          | 0.02       |
| 15. DISPLAY               |                     |       | 2    | 46    |    | 48         | 4.1        |
| TOTAL NUMBER RECORDED     | 531                 | 250   | 104  | 288   | 11 | 1184       |            |
| mean # of acts/individual | 43.2                | 106.4 | 13.3 | 137.1 |    |            |            |

The above were collected on an ad lib basis from July 1978 through May 1981 (7308.75 hours). 1184 aggressive acts were observed which is equivalent to once every 6.2 hours.

AF = adult female; AM = adult male; YF = juvenile and subadult female; YM = juvenile and subadult male; ?Y = unsexed juvenile and subadult.

TABLE 37

FREQUENCY OF NON-SEXUAL HARASSMENT / AGE OF INTERACTOR

INDIVIDUAL HARASSED

|                  | OLDER MALE | YOUNGER MALE | OLDER FEMALE | YOUNGER FEMALE | TOTAL |
|------------------|------------|--------------|--------------|----------------|-------|
| H OLDER MALE     |            | 42           |              | 5              | 47    |
| A YOUNGER MALE   | 21         |              |              |                | 21    |
| R OLDER FEMALE   |            | 15           |              | 35             | 50    |
| A YOUNGER FEMALE |            |              | 5            |                | 5     |
| S                |            |              |              |                |       |
| S                |            |              |              |                |       |
| E                |            |              |              |                |       |
| R                |            |              |              |                |       |
| TOTAL            | 21         | 57           | 5            | 40             | 123   |

The above refers to interactions where both the harasser and harassed were accurately identified and the ages are given as relative figures between two individuals and therefore does not correspond with the numbers given in Table 36.

**TABLE 38**
**Young colobus grooming patterns**

Data is taken from scan-samples for each individual from 0-18 months of age

|                 | No. of times<br>individual<br>grooms | No. of times<br>individual<br>is groomed | TOTAL |
|-----------------|--------------------------------------|------------------------------------------|-------|
| <u>FEMALES:</u> |                                      |                                          |       |
| <u>NIMP</u>     | 15                                   | 57                                       | 72    |
| <u>SIMP</u>     | 26                                   | 42                                       | 68    |
| <u>HIMP</u>     | 28                                   | 47                                       | 75    |
| <u>MALES:</u>   |                                      |                                          |       |
| <u>WIMP</u>     | 9                                    | 66                                       | 75    |
| <u>IMP</u>      | 15                                   | 82                                       | 97    |
| <u>MIMP</u>     | 10                                   | 65                                       | 75    |
| <u>BIMP</u>     | 4                                    | 53                                       | 57    |

Young females groom more and are groomed less compared to males  
(chi-square test:  $p = <0.001$ ).

Young females groom more than young males groom  
(two-tailed binomial test:  $z = 4.52$ ,  $p = <0.00002$ ).

Young females are groomed less than young males  
(two-tailed binomial test:  $z = 3.04$ ,  $p = <0.002$ ).

**TABLE 39**

FREQUENCY OF MATERNAL AGGRESSION FOR FEMALES AND MALES FROM 0 - 19 months

| NAME   | SUCKLES | RECEIVES MATERNAL<br>AGGRESSION. |              | RETALIATES &<br>WINS LOOSES |     | TOTAL |        |
|--------|---------|----------------------------------|--------------|-----------------------------|-----|-------|--------|
|        | No.     | No.                              | % of Sucking | No.                         | No. | No.   | %      |
| WIMP   | 35      | 4                                | 11.4%        | 1                           | 2   | 3     | 75.0%  |
| IMP    | 63      | 5                                | 7.9%         | 1                           | 1   | 2     | 40.0%  |
| MIMP   | 48      | 5                                | 10.4%        | 3                           | 1   | 4     | 80.0%  |
| BIMP   | 60      | 5                                | 8.4%         | 3                           | 1   | 4     | 80.0%  |
| Mean   |         |                                  | 9.6%         |                             |     |       | 68.75% |
| Median |         |                                  | 9.4%         |                             |     |       | 77.5%  |
| NIMP   | 77      | 11                               | 14.3%        | 3                           | 1   | 4     | 36.4%  |
| SIMP   | 39      | 8                                | 20.5%        | 3                           | 1   | 4     | 50.05% |
| HIMP   | 51      | 11                               | 21.6%        | 3                           | 1   | 4     | 36.4%  |
| Mean   |         |                                  | 18.8%        |                             |     |       | 40.9%  |
| Median |         |                                  | 19.7%        |                             |     |       | 38.7%  |

The above data was derived from scan-samples and covers the first 18 months of each individual's life.

TABLE 40

Amount of aggression given and received by each male during three breeding seasons in Abuko.

|                            |       | BREEDING SEASON<br>May 1979-Aug. 1980 |             |       |              |                 |
|----------------------------|-------|---------------------------------------|-------------|-------|--------------|-----------------|
|                            |       | AGGRESSOR                             |             |       |              |                 |
| T<br>A<br>R<br>G<br>E<br>T |       | Capt.<br>Crook                        | Mr.<br>Mean | Other | Total<br>No. | Total<br>% Lost |
|                            | Crook |                                       | 3           | 1     | 4            | 17%             |
|                            | Mean  | 7                                     |             | 2     | 9            | 60%             |
|                            | Other | 12                                    | 6           |       | 18           |                 |

|                            |       | BREEDING SEASON<br>Oct. 1980- May 1981 |             |      |              |                 |
|----------------------------|-------|----------------------------------------|-------------|------|--------------|-----------------|
|                            |       | AGGRESSOR                              |             |      |              |                 |
| T<br>A<br>R<br>G<br>E<br>T |       | Capt.<br>Crook                         | Mr.<br>Mean | Yunk | Total<br>No. | Total<br>% Lost |
|                            | Crook |                                        | 0           | 4    | 4            | 66.6%           |
|                            | Mean  | 5                                      |             | 3    | 8            | 100.0%          |
|                            | Yunk  | 2                                      | 0           |      | 2            | 22.2%           |

|                            |       | BREEDING SEASON<br>May 1981-Sept. 1981 |             |      |     |      |            |                    |
|----------------------------|-------|----------------------------------------|-------------|------|-----|------|------------|--------------------|
|                            |       | AGGRESSOR                              |             |      |     |      |            |                    |
| T<br>A<br>R<br>G<br>E<br>T |       | Capt.<br>Crook                         | Mr.<br>Mean | Wimp | Imp | Bimp | Total<br>N | Total<br>%<br>Lost |
|                            | Crook |                                        | 1           | 0    | 3   | 3    | 7          | 35.0               |
|                            | Mean  | 8                                      |             | 0    | 1   | 1    | 10         | 100.0              |
|                            | Wimp  | 2                                      | 0           |      | 2   | 10   | 14         | 100.0              |
|                            | Imp   | 1                                      | 0           | 0    |     | 3    | 4          | 36.4               |
|                            | Bimp  | 2                                      | 0           | 0    | 1   |      | 3          | 15.0               |

In each breeding season, the chief copulator (first Captain Crook, then Yunk and finally Bimp) gave the most aggression and received the least aggression. The chief copulator also had the highest percentage of wins.



TABLE 41  
Number of times each male mates with swollen and inflating females (July 1978 - March 1982)  
MATES WITH SWOLLEN FEMALES      MATES WITH INFLATING FEMALES

|           | J  | C  | M  | Y  | W | I | B  | G | Total | J | C  | M  | Y  | W | I  | B  | G | Total |
|-----------|----|----|----|----|---|---|----|---|-------|---|----|----|----|---|----|----|---|-------|
| July 1978 | 11 | 0  | 4  |    |   |   |    |   | 15    | 4 |    |    |    |   |    |    |   | 4     |
| Aug       | 3  | 1  | 0  |    |   |   |    |   | 4     | 2 | 1  | 1  |    |   |    |    |   | 4     |
| Sept      | 0  | 3  | 0  |    |   |   |    |   | 3     | 0 | 0  | 0  |    |   |    |    |   | 0     |
| Oct       | ■  | 0  | 0  |    |   |   |    |   | 0     | ■ | 0  | 0  |    |   |    |    |   | 0     |
| Nov       |    | 3  | 1  |    |   |   |    |   | 4     |   | 0  | 0  |    |   |    |    |   | 0     |
| Dec       |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| Jan 1979  |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| Feb       |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| Mar       |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| April     |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| May       |    | 3  | 0  |    |   |   |    |   | 3     |   | 0  | 0  |    |   |    |    |   | 0     |
| June      |    | 2  | 0  |    |   |   |    |   | 2     |   | 0  | 0  |    |   |    |    |   | 0     |
| July      |    | 1  | 5  |    |   |   |    |   | 6     |   | 2  | 1  |    |   |    |    |   | 3     |
| Aug       |    | 6  | 4  |    |   |   |    |   | 10    |   | 1  | 0  |    |   |    |    |   | 1     |
| Sept      |    | 3  | 4  |    |   |   |    |   | 7     |   | 0  | 0  |    |   |    |    |   | 0     |
| Oct       |    | 12 | 0  |    |   |   |    |   | 12    |   | 8  | 0  |    |   |    |    |   | 8     |
| Nov       |    | 1  | 1  |    |   |   |    |   | 2     |   | 8  | 0  |    |   |    |    |   | 8     |
| Dec       |    | 2  | 0  |    |   |   |    |   | 2     |   | 0  | 0  |    |   |    |    |   | 0     |
| Jan 1980  |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| Feb       |    | 0  | 0  |    |   |   |    |   | 0     |   | 0  | 0  |    |   |    |    |   | 0     |
| Mar       |    | 0  | 0  |    |   |   |    |   | 0     |   | 3  | 0  |    |   |    |    |   | 3     |
| April     |    | 0  | 0  |    |   |   |    |   | 0     |   | 2  | 0  |    |   |    |    |   | 2     |
| May       |    | 20 | 6  | 11 |   |   |    |   | 37    |   | 10 | 2  | 6  |   |    |    |   | 18    |
| June      |    | 8  | 7  | 5  |   |   |    |   | 20    |   | 17 | 5  | 0  |   |    |    |   | 22    |
| July      |    | 3  | 8  | 4  |   |   |    |   | 15    |   | 21 | 3  | 13 |   |    |    |   | 37    |
| Aug       |    | 0  | 0  | 0  |   |   |    |   | 0     |   | 10 | 3  | 0  |   |    |    |   | 13    |
| Sept      |    | /  | /  | /  |   |   |    |   | /     |   | /  | /  | /  |   |    |    |   | /     |
| Oct       |    | 0  | 0  | 1  |   |   |    |   | 1     |   | 2  | 2  | 6  |   |    |    |   | 10    |
| Nov       |    | 0  | 0  | 6  |   |   |    |   | 6     |   | 0  | 1  | 2  |   |    |    |   | 3     |
| Dec       |    | 0  | 0  | 0  |   |   |    |   | 0     |   | 0  | 0  | 0  |   |    |    |   | 0     |
| Jan 1981  |    | 0  | 0  | 0  |   |   |    |   | 0     |   | 0  | 0  | 0  |   |    |    |   | 0     |
| Feb       |    | 0  | 0  | 0  |   |   |    |   | 0     |   | 0  | 0  | 0  |   |    |    |   | 0     |
| Mar       |    | 0  | 0  | 0  |   |   |    |   | 0     |   | 0  | 0  | 0  |   |    |    |   | 0     |
| April     |    | 2  | 0  | 4  |   |   |    |   | 6     |   | 0  | 0  | 0  |   |    |    |   | 0     |
| May       |    | 6  | 0  | ■  |   |   |    |   | 6     |   | 0  | 0  | ■  |   |    |    |   | 0     |
| June      |    | 4  | 0  |    | 0 | 3 | 5  |   | 12    |   | 0  | 0  |    | 0 | 3  | 5  |   | 8     |
| July      |    | 1  | 0  |    |   |   | 1  |   | 2     |   | 0  | 0  |    | 0 | 0  | 0  |   | 0     |
| Aug       |    | /  | /  |    | / | / | /  |   | /     |   | /  | /  |    | / | /  | /  |   | /     |
| Sept      |    | 0  | 0  |    | 0 | 3 | 5  |   | 8     |   | 0  | 0  |    | 2 | 1  | 2  |   | 5     |
| Oct       |    | /  | /  |    | / | / | /  |   | /     |   | /  | /  |    | / | /  | /  |   | /     |
| Nov       |    | /  | /  |    | / | / | /  |   | /     |   | /  | /  |    | / | /  | /  |   | /     |
| Dec       |    | /  | /  |    | / | / | /  |   | /     |   | /  | /  |    | / | /  | /  |   | /     |
| Jan 1982  |    | 0  | ■  |    | 0 | 0 | 0  |   | 0     |   | 1  | ■  |    | 0 | 2  | 0  |   | 3     |
| Feb       |    | 0  |    |    | 0 | 0 | 0  |   | 0     |   | 0  |    |    | 0 | 8  | 5  |   | 13    |
| Mar       |    | 0  |    |    | 0 | 0 | 0  |   | 0     |   | 0  |    |    | 0 | 4  | 1  | 1 | 6     |
| Total (N) | 14 | 81 | 42 | 31 | 0 | 6 | 16 | 0 | 185   | 6 | 86 | 18 | 27 | 2 | 18 | 13 | 1 | 171   |

J=Jungi Y=Yunk B=Bimp C=Captain Cook W=Wimp G=Gimp M=Mr Mean I=Imp ■=Individual dies /=No data collected

TABLE 42

## Adult Female Aggressive Interactions

| ADULT FEMALES | ABSOLUTE WINS |       | ABSOLUTE LOSSES |       | IGNORE/ STALEMATE |       | TOTAL AGGRESSIVE INTERACTIONS | RANK BASED ON THIS TABLE |
|---------------|---------------|-------|-----------------|-------|-------------------|-------|-------------------------------|--------------------------|
|               | #             | %     | #               | %     | #                 | %     |                               |                          |
| Droopy        | 6             | 100.0 | 0               | 0     | 0                 | 0     | 6                             | 1st                      |
| Solid         | 3             | 75.0  | 0               | 0     | 1                 | 25.0  | 4                             | 2nd                      |
| Nene          | 7             | 63.6  | 1               | 9.0   | 3                 | 27.3  | 11                            | 3rd                      |
| Button        | 9             | 60.0  | 1               | 6.6   | 5                 | 33.3  | 15                            | 4th                      |
| YumDum        | 5             | 91.4  | 2               | 28.6  | 0                 | 0     | 7                             | 5th                      |
| Head          | 2             | 20.0  | 5               | 50.0  | 3                 | 30.0  | 10                            | 6th                      |
| Inca          | 3             | 15.8  | 4               | 21.1  | 12                | 63.1  | 19                            | 7th                      |
| Volley        | 1             | 11.1  | 1               | 11.1  | 7                 | 77.7  | 9                             | 8th                      |
| Metoo         | 0             | 0     | 1               | 25.0  | 3                 | 75.0  | 4                             | 9th                      |
| Julie         | 0             | 0     | 1               | 20.0  | 4                 | 80.0  | 5                             | 10th                     |
| Wild          | 0             | 0     | 3               | 21.4  | 11                | 78.6  | 14                            | 11th                     |
| Round         | 2             | 12.5  | 8               | 50.0  | 6                 | 37.5  | 16                            | 12th                     |
| Garuda        | 0             | 0     | 9               | 52.9  | 8                 | 47.1  | 17                            | 13th                     |
| Others        | 0             |       | 2               |       | 1                 |       | 3                             |                          |
| TOTAL #       | 38            |       | 38              |       | 64                |       | 140                           |                          |
| MEAN %        |               | 33.3% |                 | 20.9% |                   | 44.2% |                               |                          |

Rank determined by data collected on only the 13 identified females and not including data collected on 'others'.

TABLE 43

ADULT FEMALE DOMINANCE/SUBMISSIVE INTERACTIONS

| TOP FIVE RANKING FEMALES         | ABSOLUTE WINS | SUBMISSIONS |          | REASSURANCE |          |
|----------------------------------|---------------|-------------|----------|-------------|----------|
|                                  |               | GIVES       | RECEIVES | GIVES       | RECEIVES |
| <u>DROOPY</u>                    | 100.0%        | 0           | 3        | 5           | 1        |
| <u>SOLID</u>                     | 75.0          | 0           | 3        | 2           | 0        |
| <u>NENE</u>                      | 63.6          | 1           | 0        | 0           | 2        |
| <u>BUTTON</u>                    | 60.0          | 0           | 1        | 0           | 5        |
| <u>YUMDUM</u>                    | 71.4          | 0           | 3        | 7           | 0        |
| OTHER FEMALES                    |               |             |          |             |          |
| <u>Head</u>                      | 20.0          | 1           | 1        | 0           | 2        |
| <u>Inca</u>                      | 15.2          | 1           | 1        | 1           | 2        |
| <u>Volley</u>                    | 11.1          | 2           | 0        | 1           | 1        |
| <u>Metoo</u>                     | 0.0           | 0           | 0        | 1           | 0        |
| <u>Julie</u>                     | 0.0           | 3           | 1        | 4           | 2        |
| <u>Wild</u>                      | 0.0           | 2           | 1        | 0           | 1        |
| <u>Round</u>                     | 12.5          | 2           | 0        | 0           | 1        |
| <u>Garuda</u>                    | 0.0           | 2           | 0        | 0           | 1        |
| <u>Others (not listed above)</u> | 0.0           | 0           | 0        | 0           | 3        |
| TOTAL                            |               | 14          | 14       | 21          | 21       |
| MEAN (divided by 13 )            | 33.0%         | 1.1         | 1.1      | 1.5         | 1.4*     |

\*The three instances received by 'others' is not counted in the mean since the data above refers to the thirteen females listed here and not to extra 'others'.

**TABLE 44**

Frequency of dominance interactions for females who shared a common natal troop compared with females with whom they did not share a common natal troop.

| FEMALES ORIGINALLY<br>FROM:     | DATES OF<br>OBS. | RECEIVES AGGRESSION FROM    |                  | GIVES AGGRESSION TO         |                  |
|---------------------------------|------------------|-----------------------------|------------------|-----------------------------|------------------|
|                                 |                  | FELLOW NATAL<br>TROOP MATES | OTHER<br>FEMALES | FELLOW NATAL<br>TROOP MATES | OTHER<br>FEMALES |
| <u>MIDDLE TROOP<br/>FEMALES</u> | 6/80 - 4/82      |                             |                  |                             |                  |
| Cisco                           |                  | 0                           | 19               | 0                           | 10               |
| Quechua                         |                  | 0                           | 12               | 0                           | 16               |
| Tara                            |                  | 0                           | 9                | 0                           | 5                |
| <u>FOCAL TROOP<br/>EMALES</u>   | 6/81 - 4/82      |                             |                  |                             |                  |
| Simp                            |                  | 1                           | 20               | 0                           | 3                |
| Nimp                            |                  | 1                           | 11               | 0                           | 3                |
| TOTAL                           |                  | 2                           | 71               | 0                           | 37               |

The numbers are of such high value that the formality of a statistical test is not necessary in this case. Therefore, it can be said that females give and receive aggression to females with whom they do not share a common natal troop past more frequently than females with whom they do share a common natal troop past.

TABLE 45

## Female Rank and Reproductive Success

| FEMALE | RANK | # & SEX OF OFFSPRING<br>WHICH LIVE<br>BEYOND INFANCY | BIRTH ORDER DURING<br>1978 - 1979 BIRTH<br>SEASON |
|--------|------|------------------------------------------------------|---------------------------------------------------|
| DROOPY | 1st  | 1 female                                             | -0-                                               |
| SOLID  | 2nd  | 2 females                                            | 5th - tied                                        |
| NENE   | 3rd  | 2 females                                            | 3rd                                               |
| BUTTON | 4th  | 1 male                                               | 5th - tied                                        |
| YUMDUM | 5th  | 1 male                                               | -0-                                               |
| HEAD   | 6th  | 1 female                                             | 7th                                               |
| INCA   | 7th  | 2 females, 1 male                                    | 2nd                                               |
| VOLLEY | 8th  | 1 female                                             | -0-                                               |
| METOO  | 9th  | 1 male                                               | 4th                                               |
| JULIE  | 10th | -0-                                                  | -0-                                               |
| WILD   | 11th | 1 male                                               | 1st                                               |
| ROUND  | 12th | -0-                                                  | -0-                                               |
| GARUDA | 13th | 2 males                                              | 8th                                               |

-0- = no infants born.

**TABLE 46**

Amount of time males groom and are groomed by others (June 1981-October 1981)  
G R O O M E R S

|                      | Captain<br>Crook | Mr.<br>Mean | Wimp | Imp | Bimp | Mother | Adult<br>Female | Young<br>Female | TOTAL |
|----------------------|------------------|-------------|------|-----|------|--------|-----------------|-----------------|-------|
| <u>Captain Crook</u> |                  | 0           | 2    | 2   | 1    |        | 15              | 10              | 30    |
| <u>Mr. Mean</u>      | 0                |             | 0    | 1   | 0    |        | 9               | 0               | 10    |
| <u>Wimp</u>          | 1                | 0           |      | 0   | 0    | 26     | 6               | 5               | 38    |
| <u>Imp</u>           | 0                | 2           | 0    |     | 0    | 18     | 32              | 29              | 81    |
| <u>Bimp</u>          | 0                | 1           | 0    | 0   |      | 15     | 33              | 24              | 73    |
| <u>Mother</u>        |                  |             | 2    | 2   | 0    |        |                 | 5               | 9     |
| <u>Adult Female</u>  | 2                | 0           | 0    | 0   | 3    |        | 46              | 7               | 58    |
| <u>Young Female</u>  | 5                | 0           | 1    | 1   | 0    | 9      | 2               | 8               | 26    |
| <u>Total (N)</u>     | 8                | 3           | 5    | 6   | 4    | 68     | 143             | 88              | 325   |

It is clear from the above that the young males, Wimp, Imp and Bimp never groom each other and that Crook and Mean never groom each other showing quite clearly that male peers do not interact in terms of grooming. Also, it is clear that males receive most of their grooming from females (young, adult and mothers).

**TABLE 47**

Young males and young females and the ways in which they distribute their grooming. Data is taken from scan-samples for all individuals from 0 - 18 months of age.

**G R O O M E R S**

|                | Own Mother | Adult Male | Subadult & Juvenile Male | Adult Female | Subadult & Juvenile Female | Peers | Infant | Total |
|----------------|------------|------------|--------------------------|--------------|----------------------------|-------|--------|-------|
| <u>MALES:</u>  | #          | #          | #                        | #            | #                          | #     | #      | #     |
| Wimp           | 3          | 3          | 0                        | 1            | 2                          | 0     | 0      | 9     |
| Imp            | 5          | 2          | 2                        | 3            | 1                          | 2     | 0      | 15    |
| Mimp           | 2          | 5          | 2                        | 0            | 0                          | 1     | 0      | 10    |
| Bimp           | 1          | 2          | 0                        | 0            | 0                          | 1     | 0      | 4     |
| Total          | 11         | 12         | 4                        | 4            | 3                          | 4     | 0      | 38    |
| <u>FEMALES</u> | #          | #          | #                        | #            | #                          | #     | #      | #     |
| Nimp           | 5          | 5          | 2                        | 1            | 2                          | 0     | 0      | 15    |
| Simp           | 0          | 5          | 3                        | 4            | 9                          | 5     | 0      | 26    |
| Himp           | 1          | 2          | 4                        | 2            | 7                          | 11    | 1      | 28    |
| Total          | 6          | 12         | 9                        | 7            | 18                         | 16    | 1      | 69    |

Females and males distribute their grooming in the same way: chi-square = 13.7, d.f. = 2, p = .001 - therefore reject null.

Females groom subadult and juvenile females and peers more than they groom other groups: two-sided binomial test: Z = 3.97, P = <.001.

TABLE 48

Number of times each adult male groomed each adult female and each young females: August 1978 through August 1980.

| <u>ADULT FEMALES</u> | Captain Crook Grooms |        | Mr. Mean Grooms |        |
|----------------------|----------------------|--------|-----------------|--------|
|                      | N                    | %      | N               | %      |
| Wild                 | 4                    | 8.2%   | 0               | 0%     |
| Inca                 | 11                   | 22.4   | 0               | 0      |
| Nene                 | 4                    | 8.2    | 0               | 0      |
| Metoo                | 2                    | 4.1    | 0               | 0      |
| Solid                | 1                    | 2.0    | 0               | 0      |
| Button               | 7                    | 14.3   | 0               | 0      |
| Head                 | 4                    | 8.2    | 1               | 14.3   |
| Garuda               | 1                    | 2.0    | 1               | 14.3   |
| Droopy               | 2                    | 4.1    | 0               | 0      |
| YumDum               | 0                    | 0      | 0               | 0      |
| Volley               | 2                    | 4.1    | 3               | 42.9   |
| Julie                | 2                    | 4.1    | 1               | 14.3   |
| Round                | 9                    | 18.4   | 1               | 14.3   |
| TOTAL                | 49                   | 100.1% | 7               | 100.1% |

The above refers to identified groomees only. This means of the 58 adult females Captain Crook groomed (Table 26), only 49 of them were identified. All 7 of the adult females groomed by Mr. Mean were identified.

#### YOUNG FEMALES

|             |    |        |   |        |
|-------------|----|--------|---|--------|
| Punk        | 17 | 54.8%  | 3 | 60.0%  |
| Simp        | 1  | 3.2    | 0 | 0      |
| Velf        | 1  | 3.2    | 0 | 0      |
| Self        | 2  | 6.5    | 0 | 0      |
| Scarty      | 3  | 9.7    | 0 | 0      |
| Ilf         | 4  | 12.9   | 2 | 40.0   |
| Jiggaty Jag | 3  | 9.7    | 0 | 0      |
| TOTAL       | 31 | 100.0% | 5 | 100.0% |

The above refers to identified young females only. This means of the 36 young females groomed by Captain Crook only 31 of them were properly identified and only 5 of the 9 groomed by Mr. Mean were properly identified. Punk receives significantly more grooming than Ilf and therefore more than all the others (Binomial two-tailed test:  $Z = 2.75$ ,  $P = <.01$ ).



**TABLE 49**  
Female Grooming Patterns: How females distribute their grooming.

| Females arranged according to rank | Grooms <u>ALL</u> other adult females | Grooms adult males | Grooms offspring | Grooms young female non-relatives | Grooms young male non-relatives | Total Grooms |      | Total Groomed |      |
|------------------------------------|---------------------------------------|--------------------|------------------|-----------------------------------|---------------------------------|--------------|------|---------------|------|
|                                    | %                                     | %                  | %                | %                                 | %                               | No           | %    | No            | %    |
| Droopy                             | 34.3                                  | 16.6               | 30.9             | 6.6                               | 1.7                             | 242          | 62.7 | 144           | 37.3 |
| Solid                              | 41.1                                  | 17.7               | 37.7*            | /                                 | 2.8                             | 180          | 61.6 | 112           | 38.4 |
| Nene                               | 37.9                                  | 37.1               | 23.6             | /                                 | 1.3                             | 229          | 64.9 | 124           | 35.1 |
| Button                             | 53.8                                  | 24.5               | 18.2             | 2.1                               | 1.4                             | 286          | 74.5 | 98            | 25.5 |
| Yumdum                             | 34.3                                  | 10.1               | 44.4             | 10.1                              | 1.0                             | 99           | 55.6 | 79            | 44.4 |
| Head                               | 69.0                                  | 13.9               | 15.5             | /                                 | 1.6                             | 262          | 72.6 | 95            | 27.4 |
| Inca                               | 47.1                                  | 27.4               | 21.9*            | 3.2                               | 0.03                            | 314          | 63.8 | 178           | 36.2 |
| Volley                             | 36.3                                  | 38.9               | 13.2*            | 7.5                               | 4.1                             | 491          | 76.8 | 148           | 23.2 |
| Metoo                              | 37.9                                  | 28.6               | 29.1             | 3.5                               | 0.1                             | 227          | 75.9 | 72            | 24.1 |
| Julie                              | 56.0                                  | 17.2               | /                | 25.5                              | 1.3                             | 157          | 58.0 | 113           | 41.9 |
| Wild                               | 37.2                                  | 31.4               | 25.2             | 5.4                               | 0.1                             | 258          | 69.7 | 112           | 30.3 |
| Round                              | 26.3                                  | 55.2               | /                | 13.2                              | 5.3                             | 281          | 74.5 | 96            | 25.5 |
| Garuda                             | 39.2                                  | 16.6               | 26.8             | 16.6                              | 0.1                             | 186          | 76.5 | 57            | 23.5 |
| Total (N)                          | 1349                                  | 933                | 647              | 209                               | 64                              | 3202         |      | 1428          |      |
| Mean (%)                           | 42.4%                                 | 25.8%              | 26.0%            | 7.2%                              | 1.6%                            |              |      |               |      |

\* denotes two offspring  
All females, except Volley, spent most of their grooming time grooming their own offspring.

TABLE 49 Continued

| GROOMED<br>only those<br>identified | GROOMERS % of grooming given to ALL ADULTS |            |             |            |            |             |            |            |            |             |            |            |             |               |            |                                          |
|-------------------------------------|--------------------------------------------|------------|-------------|------------|------------|-------------|------------|------------|------------|-------------|------------|------------|-------------|---------------|------------|------------------------------------------|
|                                     | Droopy                                     | Solid      | Nene        | Button     | Yumdum     | Head        | Inca       | Volley     | Metoo      | Julie       | Wild       | Round      | Garuda      | Capt.<br>Cook | Mr<br>Mean | *No of<br>times<br>chosen as<br>favorite |
| Droopy                              | /                                          | 1.1        | 0           | 4.5        | 4.0        | 3.6         | 5.7        | <u>7.9</u> | 1.8        | 3.8         | 5.4        | 0.1        | 2.7         | 1.9           | 0          | 1                                        |
| Solid                               | 1.2                                        | /          | 1.7         | 2.8        | 3.0        | 6.7         | 1.3        | 1.4        | 3.1        | 5.7         | 1.6        | <u>4.3</u> | 1.6         | 0.1           | 0          | 1                                        |
| Nene                                | 1.2                                        | 2.2        | /           | 1.4        | 4.0        | 5.9         | <u>8.6</u> | 2.4        | 3.1        | <u>13.4</u> | 1.6        | 2.8        | 1.1         | 3.9           | 0          | 2                                        |
| Button                              | 2.5                                        | 2.8        | 2.2         | /          | 0          | 6.7         | 4.5        | 2.6        | 3.9        | 2.5         | 2.3        | 1.8        | 2.2         | 6.8           | 0          | 0                                        |
| Yumdum                              | <u>6.2</u>                                 | 0.1        | 3.1         | 0.1        | /          | 4.8         | 5.7        | 2.2        | 2.6        | 1.3         | <u>6.2</u> | 1.1        | 1.6         | 0             | 0          | 2                                        |
| Head                                | 2.5                                        | <u>6.7</u> | 4.4         | 3.1        | 3.0        | /           | 5.7        | 1.2        | 1.8        | 4.5         | 0.04       | 2.8        | 2.7         | 3.9           | 5.0        | 1                                        |
| Inca                                | 4.1                                        | 3.3        | <u>12.7</u> | <u>9.1</u> | 5.1        | <u>21.0</u> | /          | 2.2        | 4.8        | 3.2         | 5.0        | 1.1        | 4.8         | 10.7          | 0          | 3                                        |
| Volley                              | 5.4                                        | <u>6.7</u> | 0.04        | 4.9        | 2.0        | 3.9         | 3.2        | /          | 2.2        | 10.2        | 3.5        | 2.8        | 3.8         | 1.9           | 15.0       | 1                                        |
| Metoo                               | 1.7                                        | 1.7        | 1.3         | 2.4        | 5.1        | 1.9         | 4.1        | 2.4        | /          | 3.2         | 2.3        | 3.6        | 2.2         | 1.9           | 0          | 0                                        |
| Julie                               | 1.7                                        | 4.4        | 4.4         | 1.4        | 1.0        | 2.8         | 2.5        | <u>7.9</u> | 2.6        | /           | 4.3        | 1.1        | 3.2         | 1.9           | 5.0        | 1                                        |
| Wild                                | 5.4                                        | 2.8        | 2.2         | 2.8        | <u>7.1</u> | 3.6         | 2.5        | 2.0        | <u>9.7</u> | 3.8         | /          | 1.8        | <u>10.2</u> | 3.9           | 0          | 3                                        |
| Round                               | 0.1                                        | <u>6.7</u> | 2.6         | 1.4        | 0          | 3.6         | 1.3        | 1.6        | 1.8        | 2.5         | 0.04       | /          | 3.2         | 8.7           | 5.0        | 1                                        |
| Garuda                              | 0.1                                        | 1.7        | 1.7         | 0.1        | 0          | 3.9         | 1.9        | 1.6        | 0.04       | 1.9         | 3.1        | 2.5        | /           | 0.1           | 5.0        | 0                                        |
| Capt. Cook                          | 12.4                                       | 8.8        | 28.4        | 12.6       | 5.1        | 3.2         | 13.4       | 12.4       | 14.1       | 9.6         | 16.7       | 27.8       | 10.2        | /             | 5.0        |                                          |
| Mr. Mean                            | 14.0                                       | 9.4        | 11.5        | 11.9       | 5.1        | 6.7         | 13.1       | 26.5       | 14.5       | 7.6         | 13.6       | 23.8       | 6.4         | 7.8           | /          |                                          |
| Offspring                           | 30.0                                       | 37.7       | 23.6        | 18.2       | 44.4       | 15.5        | 21.9       | 13.2       | 29.1       | /           | 25.2       | /          | 26.8        | /             | /          |                                          |
| Total %                             | 90.3                                       | 95.1       | 99.8        | 76.7       | 88.9       | 93.8        | 95.4       | 87.5       | 95.1       | 73.2        | 90.9       | 77.4       | 82.7        | 53.5          | 40.0       |                                          |

Female's favorite partner is underlined. If there is a tie then all are underlined. \*Favorite partner refers to adult female most frequently groomed

In total: Crook 5½ times favorite  
Mean 4

Inca 2 times favorite  
Nene 1

Wild 1½ times favorite  
Volley 1

(Numbers do not correspond with numbers in Tables 25 & 26. The numbers in this table only involve interactions where both parties were identified. Also numbers do not correspond with those in Table 47 & 56 because numbers in 47 & 56 are corrected for age differences amongst young.)

TABLE 50

Female's reproductive state during time she was groomed by adult males

| FEMALE'S NAME | GROOMED BY MALES<br>No. of Times | CYCLE STATES                                            |
|---------------|----------------------------------|---------------------------------------------------------|
| INCA          | 11                               | Lactating (5), Flat (4), Fully Swollen (2)              |
| ROUND         | 10                               | Flat (5), Fully Swollen (4), ? (1)                      |
| UNIDENTIFIED  | 9                                | Flat (3), Fully Swollen (1), ? (5)                      |
| BUTTON        | 7                                | Flat (5), Lactating (2)                                 |
| VOLLEY        | 5                                | Fully Swollen (3), Pregnant (2)                         |
| HEAD          | 5                                | Flat (2), Lactating (1), Pregnant (1),<br>Inflating (1) |
| WILD          | 4                                | Lactating (2), Flat (2)                                 |
| NENE          | 4                                | Flat (2), Lactating (1), Pregnant (1)                   |
| JULIE         | 3                                | Inflating (2), Flat (1)                                 |
| DROOPY        | 2                                | Fully Swollen (1), ? (1)                                |
| GARUDA        | 2                                | Lactating (2)                                           |
| METOO         | 2                                | Lactating (2)                                           |
| SOLID         | 1                                | Lactating (1)                                           |
| YUMDUM        | 0                                |                                                         |

65 : 24 were flat(negative), 16 were lactating (also flat),  
11 were fully swollen, 7 were unknown, 4 were pregnant,  
3 were inflating.

TABLE 51

Comparison of grooming patterns for one month before and one month after a female gives birth.

| Female                                 | GROOMS              |                    | GROOMED             |                    |
|----------------------------------------|---------------------|--------------------|---------------------|--------------------|
|                                        | one month<br>before | one month<br>after | one month<br>before | one month<br>after |
| WILD                                   | 2 (0)               | 3 (3)              | 4                   | 0                  |
| INCA                                   | 5 (1)               | 4 (3)              | 2                   | 2                  |
| NENE                                   | 4 (1)               | 1 (1)              | 6                   | 4                  |
| METOO                                  | 1 (0)               | 1 (1)              | 0                   | 0                  |
| BUTTON                                 | 0 (0)               | 2 (1)              | 0                   | 2                  |
| SOLID                                  | 3 (0)               | 4 (4)              | 4                   | 1                  |
| HEAD                                   | 3 (1)               | 7 (2)              | 5                   | 2                  |
| VOLLEY                                 | 21 (7)              | 29 (19)            | 6                   | 14                 |
| CISCO                                  | 3 (0)               | 8 (8)              | 3                   | 0                  |
| QUECHA                                 | 3 (0)               | 2 (1)              | 1                   | 1                  |
| TOTAL #                                | 45                  | 61                 | 31                  | 26                 |
| TOTAL # OF TIMES<br>MALES WERE GROOMED | 10                  | 43                 |                     |                    |

The grooming bouts listed above refer to all the grooming females gave and received from other adults, subadults and juveniles. The numbers in parenthesis refer to the number of times females groomed adult males.

TABLE 52

Number of scan-samples females spend grooming, embracing or resting within touching distance of adult males immediately before and then immediately after they give birth.

|           | BEFORE BIRTH          |                  | AFTER BIRTH           |                  |
|-----------|-----------------------|------------------|-----------------------|------------------|
|           | No. of times interact |                  | No. of times interact |                  |
|           | with others           | with adult males | with others           | with adult males |
| FEMALES   |                       |                  |                       |                  |
| Inca      | 1                     | 0                | 7                     | 7                |
| Wild      | 4                     | 0                | 2                     | 10               |
| Garuda    | 2                     | 1                | 4                     | 12               |
| Button    | 4                     | 5                | 3                     | 7                |
| Round     | 2                     | 3                | 2                     | 6                |
| Inca      | 2                     | 0                | 5                     | 12               |
| TOTAL     | 15                    | 9                | 23                    | 54               |
| TOTAL (%) |                       | 37,5             |                       | 70.1             |

The above data are based on two days immediately before the birth and the two days immediately after the birth. During both the before and after period there were no antagonistic interactions observed.

Inca is listed above twice. The first entry refers to April 1981 when she gave birth to Id and the second entry refers to December 1978 when she gave birth to Imp.

**TABLE 53**

Males chosen as resting and grooming partners by new mothers

| FEMALE        | Male of Highest Status Chosen |       | Other Male Chosen |        |
|---------------|-------------------------------|-------|-------------------|--------|
|               | No.                           | %     | No.               | %      |
| <u>INCA</u>   | 5 (YUNK)                      | 71.4% | 2                 | 28.6%  |
| <u>WILD</u>   | 1 (CROOK)                     | 10.0  | 9                 | 90.0   |
| <u>GARUDA</u> | 8 (BIMP)                      | 66.6  | 4                 | 33.3   |
| <u>BUTTON</u> | 7 (YUNK)                      | 100.0 | 0                 | 0.0    |
| <u>ROUND</u>  | 5 (YUNK)                      | 83.3  | 1                 | 16.6   |
| <u>INCA</u>   | 10 (CROOK)                    | 83.3  | 2                 | 16.6   |
| <u>TOTAL</u>  | 36                            |       | 18                |        |
| <u>MEAN %</u> |                               | 69.1% |                   | 30.85% |

TABLE 54

Total number of times mothers groomed their younger and older offspring. The data below is based on time periods when mothers had both offspring in the focal troop at the same time.

| Mother Grooms           | Older Offspring |          |              | Younger Offspring |          |              |
|-------------------------|-----------------|----------|--------------|-------------------|----------|--------------|
|                         | Name            | Sex      | # of Times   | Name              | Sex      | # of Times   |
| <u>Button Grooms</u>    | <u>Bimp</u>     | <u>M</u> | <u>15</u>    | <u>Bid</u>        | <u>F</u> | <u>6</u>     |
| <u>Inca grooms</u>      | <u>Imp</u>      | <u>M</u> | <u>18</u>    | <u>Id</u>         | <u>F</u> | <u>1</u>     |
| <u>Nene</u>             | <u>Nimp</u>     | <u>F</u> | <u>3</u>     | <u>Mid</u>        | <u>F</u> | <u>1</u>     |
| <u>Porkpie</u>          | <u>Pelf</u>     | <u>F</u> | <u>3</u>     | <u>Pimp</u>       | <u>F</u> | <u>1</u>     |
| <u>Solid</u>            | <u>Self</u>     | <u>F</u> | <u>38</u>    | <u>Simp</u>       | <u>F</u> | <u>20</u>    |
| <u>Total # of Times</u> |                 |          | <u>77</u>    |                   |          | <u>29</u>    |
| <u>Total %</u>          |                 |          | <u>72.6%</u> |                   |          | <u>27.4%</u> |

Clearly by inspection of the above table mothers groom their older offspring significantly more than they groom their younger offspring.

TABLE 55

Grooming and Rank Order Amongst Females in the Focal troop - August 1978 through August 1980.

| GROOMERS NAME                                                     | GROOMERS RANK | FAVORITE GROOMING PARTNER<br>NAME | RANK     | % OF TIME SPENT GROOMING<br>UP HIERARCHY | DOWN HIERARCHY |
|-------------------------------------------------------------------|---------------|-----------------------------------|----------|------------------------------------------|----------------|
| DROOPY                                                            | 1             | YUMDUM                            | 5        | 0.0%                                     | 100.0%         |
| SOLID                                                             | 2             | HEAD, VOLLEY, ROUND               | 6, 8, 12 | 2.7                                      | 97.3           |
| NENE                                                              | 3             | INCA                              | 7        | 4.8                                      | 95.2           |
| BUTTON                                                            | 4             | INCA                              | 7        | 16.3                                     | 83.7           |
| YUMDUM                                                            | 5             | WILD                              | 11       | 67.6                                     | 32.3           |
| HEAD                                                              | 6             | INCA                              | 7        | 40.5                                     | 59.5           |
| INCA                                                              | 7             | NENE                              | 3        | 66.9                                     | 33.1           |
| VOLLEY                                                            | 8             | DROOP, JULIE                      | 1, 10    | 56.25                                    | 43.7           |
| METOO                                                             | 9             | WILD                              | 11       | 61.6                                     | 38.3           |
| JULIE                                                             | 10            | NENE                              | 3        | 85.2                                     | 14.7           |
| WILD                                                              | 11            | YUMDUM                            | 5        | 90.3                                     | 9.7            |
| ROUND                                                             | 12            | SOLID                             | 2        | 90.5                                     | 9.5            |
| GARUDA                                                            | 13            | WILD                              | 11       | 100.0                                    | 0.0            |
| MEAN %                                                            |               |                                   |          | 52.5%                                    | 47.5%          |
| MEAN DISTANCE IN RANK BETWEEN PARTNERS                            |               |                                   |          | +.37                                     |                |
| MODAL DISTANCE IN RANK BETWEEN PARTNERS                           |               |                                   |          | - 4                                      |                |
| MEDIAN DISTANCE IN RANK BETWEEN PARTNERS                          |               |                                   |          | - 2                                      |                |
| MOST POPULAR GROOMING PARTNER: WILD (ranked 11) & INCA (Ranked 7) |               |                                   |          |                                          |                |



**TABLE 56**

Grooming received by young males and young females. Data is taken from scan-samples for all individuals from 0 - 18 months of age.

**G R O O M E R S**

|                 | Own | Mother | Adult | Subadult              | Adult  | Subadult                | Peers | Infants | Total |
|-----------------|-----|--------|-------|-----------------------|--------|-------------------------|-------|---------|-------|
|                 |     |        | Male  | &<br>Juvenile<br>Male | Female | &<br>Juvenile<br>Female |       |         |       |
| <b>MALES:</b>   | #   | #      | #     | #                     | #      | #                       | #     | #       | #     |
| Wimp            | 53  | 0      | 2     |                       | 2      | 7                       | 2     | 0       | 66    |
| Imp             | 52  | 0      | 0     |                       | 8      | 19                      | 3     | 0       | 82    |
| Mimp            | 59  | 1      | 1     |                       | 0      | 4                       | 0     | 0       | 65    |
| Bimp            | 42  | 0      | 0     |                       | 2      | 7                       | 2     | 0       | 53    |
| Total #         | 206 | 1      | 3     |                       | 12     | 37                      | 7     | 0       | 266   |
|                 |     |        |       |                       |        |                         |       |         |       |
| <b>FEMALES:</b> | #   | #      | #     | #                     | #      | #                       | #     | #       | #     |
| Nimp            | 43  | 0      | 0     |                       | 2      | 10                      | 2     | 0       | 57    |
| Simp            | 26  | 1      | 0     |                       | 1      | 12                      | 2     | 0       | 42    |
| Himp            | 33  | 0      | 0     |                       | 1      | 8                       | 5     | 0       | 47    |
| Total #         | 102 | 1      | 0     |                       | 4      | 30                      | 9     | 0       | 146   |

Grooming to young males and young females is distributed in the same way (Reject null: chi-square = 6.77, d.f. = 2, P = .05).  
Males receive more grooming from their mothers than females receive from their mothers: two-sided binomial test: Z = 3.45, P = <.002.

TABLE 57

Total grooming received by newly arrived juvenile females (Cisco and Round) compared to resident juvenile females.

| Individual                              | No. of Times Individual Groomed<br>During First Month Resident in Chosen Troop |                                            |
|-----------------------------------------|--------------------------------------------------------------------------------|--------------------------------------------|
| <u>Cisco</u>                            | <u>1</u>                                                                       |                                            |
| <u>Punk (during same time period)</u>   | <u>6</u>                                                                       | Cisco receives significantly less          |
| <u>Dunk (during same time period)</u>   | <u>7</u>                                                                       | grooming (Fisher's Exact Test: $P = .03$ ) |
| <hr/>                                   |                                                                                |                                            |
| <u>Round</u>                            | <u>0</u>                                                                       |                                            |
| <u>Velf (during same time period)</u>   | <u>6</u>                                                                       | Round receives significantly less          |
| <u>Self (during same time period)</u>   | <u>6</u>                                                                       | grooming (Fisher's Exact Test: $P = .01$ ) |
| <u>Scarty (during same time period)</u> | <u>4</u>                                                                       |                                            |

From the above it is clear that the newly arrived females Cisco and Round receive less grooming than resident females of a comparable age when they first join their chosen troop.

**TABLE 58**
**State of Female's Sexual Skin During Genital Inspection and Identification of Initiator**

| FEMALE'S STATE         | STATE OF SEXUAL SKIN |       | IDENTIFICATION OF INITIATOR |                 |                    |              |
|------------------------|----------------------|-------|-----------------------------|-----------------|--------------------|--------------|
|                        | #                    | %     | Female<br>#                 | Adult Male<br># | Juvenile Male<br># | Unknown<br># |
| <b>ADULT FEMALE</b>    |                      |       |                             |                 |                    |              |
| <u>Flat-noncycling</u> | 21                   | 9.1%  | 3                           | 4               | 6                  | 8            |
| <u>Inflating</u>       | 57                   | 24.8  | 7                           | 19              | 30                 | 1            |
| <u>Fully Swollen</u>   | 44                   | 19.1  | 7                           | 21              | 13                 | 3            |
| <u>Deflating</u>       | 23                   | 10.0  | 1                           | 9               | 3                  | 10           |
| <u>Menstruating</u>    | 5                    | 2.2   | 3                           | 1               | 1                  | 0            |
| <u>Flat-pregnant</u>   | 5                    | 2.2   | 1                           | 1               | 3                  | 0            |
| <u>Flat-lactating</u>  | 6                    | 2.6   | 1                           | 2               | 3                  | 0            |
| <u>Not Recorded</u>    | 21                   | 9.1   | 3                           | 4               | 14                 | 0            |
| <b>IMMATURE FEMALE</b> | 48                   | 20.9  | 13                          | 9               | 4                  | 22           |
| <b>TOTAL</b>           | 230                  | 100.0 | 39                          | 70              | 77                 | 44           |
| <b>TOTAL %</b>         |                      |       | 16.9%                       | 30.4%           | 33.5%              | 19.1%        |

Significantly more inspections are initiated by males (147) than by females (39): binomial two-tailed test:  $Z = 7.9$ ,  $P = <0002$ .

TABLE 59

Total No. of Mounts July 1978 - March 1982

| Female's Sexual State         | Mounts Observed |           |
|-------------------------------|-----------------|-----------|
|                               | No.             | %         |
| <u>Immature Female</u>        | 106             | 16.5%     |
| <u>Adult Female:</u>          |                 |           |
| <u>Menstruating</u>           | 1               | 0.02      |
| <u>Inflating</u>              | 177             | 27.5      |
| <u>Fully Swollen</u>          | 185             | 28.7      |
| <u>Deflating</u>              | 10              | 1.6       |
| <u>Negative (not swollen)</u> | 111             | 17.2      |
| <u>Pregnant</u>               | 8               | 1.2       |
| <u>Lactating</u>              | 16              | 2.5       |
| <u>Not Recorded</u>           | 30              | 4.7       |
| <br>TOTAL                     | <br>644         | <br>99.9% |

TABLE 60

STATE OF FEMALE'S GENITALIA DURING SEXUAL HARASSMENT EPISODES

| FEMALE'S STATE                               | TOTAL # HARASSED | TOTAL FEMALES ENGAGED IN COPULATION<br>IN THIS STATE |            |
|----------------------------------------------|------------------|------------------------------------------------------|------------|
|                                              |                  | TOTAL #                                              | % HARASSED |
| <u>Deflating</u>                             | 0                | 10                                                   | 0.0%       |
| <u>Negative (flat)</u>                       | 2                | 111                                                  | 1.8        |
| <u>Menstruating, Pregnant,<br/>Lactating</u> | 0                | 25                                                   | 0.0        |
| <u>Inflating</u>                             | 21               | 177                                                  | 11.9       |
| <u>Fully Swollen</u>                         | 41               | 185                                                  | 22.2       |
| <u>Immature Female</u>                       | 4                | 106                                                  | 3.8        |
| <u>Not Recorded</u>                          | 2                | 30                                                   | 6.6        |
| TOTAL                                        | 70 harassed      | 644 copulations                                      |            |

Using a Two sample T test it was possible to test whether fully swollen females received more harassments than other females when they were engaged in copulating.

Fully Swollen compared with inflating:  $t = 2.6$ , d.f. = 362,  $P = 0.01$  two-tailed.  
 Fully Swollen compared with immature :  $t = 4.11$ , d.f. = 291,  $P = 0.00002$  two-tailed.  
 Fully Swollen compared with negative :  $t = 4.81$ , d.f. = 296,  $P = <.0002$  two-tailed.  
 Fully Swollen compared with deflating:  $t = 1.68$ , d.f. = 195,  $P = 0.10$  two-tailed.  
 Fully Swollen compared with menstruating/lactating/pregnant females:  $t = 2.62$ , d.f. = 210,  $P = 0.01$  two-tailed.

**TABLE 61**  
**COPULATION INITIATIONS**

| INITIATED BY     | STATE OF FEMALE'S SEXUAL SKIN |           |              |        | TOTAL |
|------------------|-------------------------------|-----------|--------------|--------|-------|
|                  | SWOLLEN                       | INFLATING | PREPUBESCENT | OTHER* |       |
| <u>FEMALE</u>    | 43                            | 28        | 24           | 24     | 119   |
| <u>MALE</u>      | 31                            | 61        | 23           | 33     | 148   |
| <u>TOTAL No.</u> | 74                            | 89        | 47           | 57     | 267   |
| <u>TOTAL %</u>   | 27.7%                         | 33.3%     | 17.6%        | 21.3%  | 99.9% |

\*OTHER refers to flat, deflating, pregnant, lactating phases of a female's sexual cycle.

Females initiated significantly more copulations in a swollen state than in other states (chi-square test,  $p = .05$ , d.f. = 1).

Males initiated significantly more copulations when females had an inflating sexual skin, (chi-square test,  $p = .005$ , d.f. = 1).

TABLE 62

Direction of Post-Copulatory Grooming Bouts for Focal Troop Males

|               | Receives Grooming<br>from Female<br>After Copulation | % of Total<br>Copulations | Gives Grooming<br>to Female<br>After Copulation | % of Total<br>Copulations |
|---------------|------------------------------------------------------|---------------------------|-------------------------------------------------|---------------------------|
|               | No.                                                  | No.                       | No.                                             | No.                       |
| Captain Crook | 22                                                   | 7.9                       | 16                                              | 5.8                       |
| Mr. Mean      | 9                                                    | 6.6                       | 5                                               | 3.7                       |
| Yunk          | 13                                                   | 12.7                      | 3                                               | 2.9                       |
| Imp           | 3                                                    | 9.7                       | 0                                               | 0.0                       |
| Bimp          | 2                                                    | 5.7                       | 2                                               | 5.7                       |
| Wimp          | 0                                                    | 0.0                       | 0                                               | 0.0                       |
| TOTAL         | 49                                                   |                           | 26                                              |                           |

All males are groomed equally (chi-square test: d.f. = 4;  $p = 0.5$ ). All males groom equally (chi-square test: d.f. = 5;  $p = 0.3$ ). Females give more grooming than males give after a copulation (binomial test:  $z = 1.94$ ;  $p = 0.10$  two-tailed).

TABLE 63

Number of times females reject sexual advances

|                                 | Capt.<br>Crook | Mr.<br>Mean | Yunk | Wimp  | Imp | Bimp | TOTAL |
|---------------------------------|----------------|-------------|------|-------|-----|------|-------|
| B R E E D I N G S E A S O N # 1 |                |             |      |       |     |      |       |
| Rejec<br>tions                  | 2              | 5           |      |       |     |      | 7     |
| Appro<br>aches                  | 145            | 54          |      |       |     |      |       |
| % Rejec<br>ted                  | 1.4%           | 9.3%        |      |       |     |      |       |
| B R E E D I N G S E A S O N # 2 |                |             |      |       |     |      |       |
| Rejec<br>tions                  | 12             | 7           | 1    |       |     |      | 20    |
| Appro<br>aches                  | 16             | 10          | 20   |       |     |      |       |
| % Rejec<br>ted                  | 75%            | 70%         | 5%   |       |     |      |       |
| B R E E D I N G S E A S O N # 3 |                |             |      |       |     |      |       |
| Rejec<br>tions                  | 1              | 1           | dead | 1     | 1   | 1    | 5     |
| Appro<br>aches                  | 13             | 1           |      | 3     | 25  | 25   |       |
| % Rejec<br>ted                  | 7.9%           | 100%        |      | 33.3% | 4%  | 4%   |       |

\*Includes month of May when females did not have a choice. Yunk was dead; Mean made no advances; Wimp, Imp and Bimp had not yet returned. If May is eliminated than Crook's percentage rises to 14.3%.

Chief copulator receives significantly less rejections than other males. Breeding Season # 1: t test:  $t = 2.68$ ; d.f. = 198;  $p = 0.008$  two tailed. Breeding Season # 2: two-tailed binomial test:  $z = 3.47$ ;  $p = 0.0004$ . Breeding Season # 3: two-tailed binomial test:  $z = 0.659$ ; not significant.



TABLE 64

Females make sexual advances to each male during each breeding season.

## BREEDING SEASON

## ADULT MALES

|                         | <u>Crook</u> | <u>Mean</u> | <u>Yunk</u> | <u>Wimp</u> | <u>Imp</u> | <u>Bimp</u> | <u>TOTAL</u> |
|-------------------------|--------------|-------------|-------------|-------------|------------|-------------|--------------|
| May 1979 -<br>Aug 1980  | 26           | 7           |             |             |            |             | 33           |
| Oct 1980 -<br>May 1981  | 7            | 3           | 14          |             |            |             | 24           |
| May 1981 -<br>Sept 1981 | 2            | 0           | dead        | 0           | 8          | 13          | 23           |
| TOTAL                   | 35           | 10          | 14          | 0           | 8          | 13          | 80           |

This is based on all interactions where fully swollen and inflating females approached and sexually presented to identified males. It includes cases where females were rejected by males, where they were inspected but not mounted and where they were mounted.

Chief copulator receives more advances than other males during breeding season:

Breeding Season # 1: Crook receives more (binomial two-tailed:  $Z = 3.31$ ,  $P = <0.0002$ ).

Breeding Season # 2: Yunk receives more (binomial two tailed:  $Z = 2.6$ ,  $P = 0.01$ ).

Breeding Season # 3: Bimp receives more (binomial two-tailed;  $Z = 4.38$ ,  $P = <0.0002$ ) against all other males. However, Bimp does not receive more compared only to Imp (binomial two-tailed:  $Z = 1.09$ ,  $P = 0.28$ ).

**TABLE 65**

Names, ages, and transfer information on all known female migrants in Focal troop

| <b>EMIGRANTS</b> |          |                     |                                                    |                              |              |
|------------------|----------|---------------------|----------------------------------------------------|------------------------------|--------------|
| NAME             | AGE      | REPRODUCTIVE STATE  | TRANSFER FORM                                      | TIME                         | TROOP CHOICE |
| Kunkle           | Adult    | ?                   | Solo- after her infant died                        | July 1978                    | PWD          |
| Volley           | Adult    | Swollen             | Leads daughter back and forth                      | August 1979                  | PWD          |
| Tara             | Adult    | ?                   | Solo - after her infant died                       | Aug. - Nov. 1982             | PWD          |
| Lib              | Juvenile | Adolescent Swelling | Moves with peers                                   | April 1979                   | PWD          |
| Jiggaty Jaggaty  | Juvenile | Pre-pubescent       | Moves with peers                                   | April 1979                   | PWD          |
| Ilf              | Juvenile | Pre-pubescent       | Moves with peers<br>Goes Alone                     | April 1979<br>April 1979     | PWD<br>Zoo   |
| Pelf             | Juvenile | Pre-pubescent       | Joins peers but moves on her own                   | June 1979                    | PWD          |
| Scarty           | Juvenile | Pre-pubescent       | moves with peer                                    | August 1979                  | PWD          |
| Velf             | Juvenile | Adolescent Swelling | moves with mother and peer                         | August 1979                  | PWD          |
| Self             | Juvenile | Adolescent Swelling | mother-led<br>no peers                             | May 1980                     | Middle       |
| Dunk             | Juvenile | Pre-pubescent       | ?                                                  | Aug. - Oct. 1981             | Zoo          |
| Punk             | Juvenile | Adolescent Swelling | moves with peers and joins peer                    | May - June 1981              | Zoo          |
| Himp             | Juvenile | Pre-pubescent       | Moves with peers                                   | May - June 1981              | Zoo          |
| Nimp             | Juvenile | Pre-pubescent       | Moves with peers<br>Moves Alone and Rejoins Mother | May - June 1981<br>June 1981 | Zoo<br>Focal |

Table 65 continued

# IMMIGRANTS

| NAME      | AGE      | REPRODUCTIVE STATE | TRANSFER FORM                              | TIME       | TROOP ORIGIN |
|-----------|----------|--------------------|--------------------------------------------|------------|--------------|
| Noaf      | Very Old | Acyclic            | Moves Alone                                | Nov. 1980  | Middle       |
| Garuda*   | Adult    | Lactating          | Joins with + 5 month old son               | Oct. 1979  | PWD          |
| Round     | Subadult | Swollen            | Solo                                       | May 1979   | ?            |
| Quechua   | Subadult | Swollen            | Joins previous Troop Mates                 | July 1980  | Middle       |
| Spectacle | Subadult | Swollen            | Solo- stays only 5 months                  | Dec. 1979  | Middle       |
| Kana      | Subadult | Swollen            | Moves with peers                           | April 1981 | PWD          |
| Zorro     | Juvenile | Pre-pubescent      | Moves with peers                           | April 1981 | PWD          |
| Eisel**   | Juvenile | Pre-pubescent      | Moves with peers                           | June 1981  | PWD          |
| Heart     | Juvenile | Pre-pubescent      | Moves with peers                           | April 1981 | PWD          |
| Bel       | Juvenile | Pre-pubescent      | Solo- stays only one month                 | Nov. 1980  | PWD          |
| Falafel   | Juvenile | Pre-pubescent      | Moves alone but joins peers                | Sept. 1981 | PWD          |
| Cisco     | Juvenile | Pre-pubescent      | Solo                                       | June 1980  | Middle       |
| Tara      | Juvenile | Pre-pubescent      | Moves alone but joins peer                 | Nov. 1980  | Middle       |
| Witchaty  | Juvenile | Pre-pubescent      | Moves alone but joins previous troop mates | June 1981  | Middle       |

Reproductive state refers to the female's cycle state on the day of transfer.

\* Garuda first visited Focal troop as a subadult; spent pregnancy and first 5 months of motherhood travelling between Focal troop and PWD; permanently joined Focal troop October 1979 with + 5-month-old son, Gimp.

\*\* Eisel travelled to Focal troop with Velf and Self (originally Focal troop females) and another female (Eisel's size). Eisel remained, the others left within 3 hours.

TABLE 66

Types of unusual activities engaged in by juvenile and subadult females and males in Focal troop.

| TYPE OF ACTIVITY                                                                        | TOTAL INVOLVING<br>JUVENILE/SUBADULT | TOTAL INVOLVING<br>JUVENILE/SUBADULT | TOTAL NO.<br>IN THE FOCAL |
|-----------------------------------------------------------------------------------------|--------------------------------------|--------------------------------------|---------------------------|
|                                                                                         | FEMALES                              | MALES                                | TROOP                     |
| Initiate friendly interaction<br>with alien male                                        | 7                                    | 0                                    | 8                         |
| Initiate friendly interspecific<br>interactions                                         | 101                                  | 31                                   | 160                       |
| Initiate physical contact with<br>the observer                                          | 6                                    | 3                                    | 9                         |
| Investigate 'unusual' items<br>e.g. knapsacks, paper, various<br>non-colobus food items | 4                                    | 6                                    | 10                        |
| Climb on human-made structures<br>such as photo-hides                                   | 2                                    | 0                                    | 2                         |
| Investigate deep tree holes                                                             | 9                                    | 3                                    | 12                        |
| TOTAL NUMBER OF OBSERVATIONS                                                            | 129                                  | 43                                   | 201                       |
| TOTAL PERCENT OF OBSERVATIONS                                                           | 64.2%                                | 21.4%                                |                           |

The information listed above pertains to the females Velf, Self, Punk, Dunk, Himp, Nimp and Simp before they transferred and Cisco immediately after she joined Focal troop. It refers to males Yunk, Wimp Imp, Mimp, Bimp and Gimp before they were exiled.

By inspection young females engage in unusual behaviors more frequently than adults.

TABLE 67

Number of sightings made on all extratroup males, the composition of their groups, amount of time spent as extratroup male and their eventual fate, if known.

| NAME                  | AGE            | GROUP COMPOSITION<br>TYPE | No. | TIME SPENT AS<br>EXTRATROOP MALE<br>(IN MONTHS) | OUTCOME                               |
|-----------------------|----------------|---------------------------|-----|-------------------------------------------------|---------------------------------------|
| NON-NATAL TROOP MALES |                |                           |     |                                                 |                                       |
| Chand                 | subadult       | solitary                  | 1   | only seen once                                  | ?                                     |
| Noleg                 | Juv/subadult   | solitary                  | 4   | > 12                                            | ?                                     |
|                       |                | Green monkeys             | 4   |                                                 |                                       |
| Flattop               | young adult    | solitary                  | 7   | > 1½                                            | Dies in fight<br>with<br>Focal troop  |
| Bend                  | young adult    | solitary                  | 22  | > 6                                             | Dies in fight<br>probably with<br>PWD |
|                       |                | male-only                 | 2   |                                                 |                                       |
|                       |                | bisexual                  | 2   |                                                 |                                       |
|                       |                | green monkeys             | 1   |                                                 |                                       |
| Maim                  | very old adult | solitary                  | 11  | > 14½                                           | ?                                     |
|                       |                | male-only                 | 2   |                                                 |                                       |
|                       |                | bi-sexual                 | 1   |                                                 |                                       |
| Kinky                 | juv/subadult   | solitary                  | 6   | > 26                                            | joins PWD                             |
|                       |                | green monkeys             | 14  |                                                 |                                       |
|                       |                | bi-sexual                 | 4   |                                                 |                                       |

TABLE 67 Continued

| NAME              | AGE                | GROUP COMPOSITION<br>TYPE | No. | TIME SPENT AS<br>EXTRATROOP MALE<br>(IN MONTHS) | OUTCOME                 |
|-------------------|--------------------|---------------------------|-----|-------------------------------------------------|-------------------------|
| NATAL TROOP MALES |                    |                           |     |                                                 |                         |
| Wimp              | 24.5-31.5 months   | solitary                  | 2   | 7                                               | rejoins natal<br>troop  |
|                   |                    | male-only                 | 4   |                                                 |                         |
| Imp               | 23 - 31 months     | solitary                  | 2   | 8                                               | rejoins natal<br>troop  |
|                   |                    | male-only                 | 5   |                                                 |                         |
| Bimp              | 22 - 29 months     | solitary                  | 2   | 7                                               | rejoins natal<br>troop  |
|                   |                    | male-only                 | 7   |                                                 |                         |
| Gimp              | 33 - 39 months     | solitary                  | 5   | 6                                               | rejoins natal<br>troop  |
|                   |                    | male-only                 | 1   |                                                 |                         |
|                   |                    | bisexual                  | 2   |                                                 |                         |
| Mimp              | 20/22-35/42 months | solitary                  | 3   | 15 - 22                                         | joins Question<br>troop |
|                   |                    | male-only                 | 5   |                                                 |                         |
| Cid               | 20 months          | solitary                  | 1   | > 1                                             | ?                       |

A total of 112 distinct associations were seen: 66 solitary males; 19 males were part of green monkey groups; 19 groups consisted of 2 - 3 males; 9 groups consisted of 1 male and 2 - 3 females. The above listed groups add up to more than 112 because some male-only groups would be listed under two male's names. For example, Imp and Mimp twice spent time together. The group, however, can only be counted once.

TABLE 68

Sleeping trees used by three separate troops - May 1979 through June 1981

|                                                                 | TROOP NAME |        |       |
|-----------------------------------------------------------------|------------|--------|-------|
|                                                                 | PWD        | MIDDLE | FOCAL |
| Total number of nights troop<br>observed in sleeping trees      | 205        | 122    | 626   |
| Total number of sleeping sites<br>shared with another troop     | 11         | 7      | 17    |
| Total number of sleeping sites not<br>shared with another troop | 12         | 8      | 41    |
| Total number of sleeping sites<br>observed                      | 23         | 15     | 58    |

Focal troop shares 18.9% (11 sites) of its sleeping sites with PWD troop and 12.1% (7 sites) of its sleeping sites with Middle troop. Furthermore, the top 8 most-used sleeping sites were used on 276 of the 626 nights and these 8 different sites were shared sites - not exclusive to the Focal troop. PWD and Middle troop do not have any sleeping sites in common.

TABLE 69

Transfer information on all 12 Focal troop females who transferred as juveniles and the type of troop they chose for their first troop.

|                                                     |                               |
|-----------------------------------------------------|-------------------------------|
| <u>Choose troop of maternal sister</u>              | <u>0 out of a possible 2</u>  |
| <u>Choose troop with age mates present</u>          | <u>9 out of a possible 11</u> |
| <u>Choose troop with no known age mates present</u> | <u>2 out of a possible 11</u> |
| <u>Stays with mother and never transfers</u>        | <u>1 out of a possible 6</u>  |

The above information refers to a females first move and not to her permanent troop choice.

Of the 11 juvenile females who choose to move, significantly more of them moved with peers as opposed to on their own (chi-square test: d.f. = 1; p = 0.05).



TABLE 70

Names of all individuals born during the 1978 and the 1979 - 1980 birth periods their migration history, and their age at time of migration.

| NAME | SEX    | AGE IN MONTHS | MIGRATION HISTORY                                                                                                                                                                      |
|------|--------|---------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Dunk | female | 31 - 33       | transfer to Zoo troop where Ilf, a previous Focal troop member resides.                                                                                                                |
| Punk | female | 40 - 41       | transfer to Zoo troop with peers; Dunk and Ilf are already resident                                                                                                                    |
| Nimp | female | 29 - 30       | transfer to Zoo troop with peers; Dunk and Ilf are already resident. She stays briefly in Zoo troop and then returns to her natal troop where her mother and a peer (Simp) are present |
| Himp | female | 27 - 28       | transfer to Zoo troop with peers; Dunk and Ilf are already present                                                                                                                     |
| Simp | female |               | never leaves her natal troop                                                                                                                                                           |
| Yunk | male   |               | never leaves his natal troop                                                                                                                                                           |
| Wimp | male   | 24.5          | exiled from natal troop and then rejoins natal troop after death of top-ranked male, Yunk                                                                                              |
| Imp  | male   | 22.75         | exiled from natal troop and then rejoins natal troop after death of top-ranked male, Yunk                                                                                              |
| Bimp | male   | 22            | exiled from natal troop and then rejoins natal troop after death of top-ranked male, Yunk.                                                                                             |
| Gimp | male   | 33            | exiled from natal troop and then rejoins natal troop after death of second-ranked male, Imp                                                                                            |
| Mimp | male   | 20 - 22       | exiled from natal troop and then joins Question troop after resident adult male disappears.                                                                                            |

Four of the five Focal troop females left their natal troop three of them permanently. Five of the six natal troop males were expelled from their natal troop. Four of these males eventually returned after spending time as extratroop males. Another young male, Cid, born during the 1981 birth season was expelled when he was 20 months old. None of his female age-mates had left the troop when they were 27 months old, although they probably left afterward.

Males left their natal troop at a significantly younger age than females (Two sample t test:  $t = 2.463$ , d.f. = 8,  $p = 0.025$ ).

TABLE 71

Total number of aggressive interactions given and received by returning native daughter and sons, June 1981.

| RETURNING      | No. OF AGGRESSIVE<br>ACTS<br>RECEIVED | No. OF AGGRESSIVE<br>ACTS<br>GIVEN | BASED ON<br>No. OF<br>DAYS | No. OF AGGRESSIVE<br>ACTS EACH DAY |
|----------------|---------------------------------------|------------------------------------|----------------------------|------------------------------------|
| <b>FEMALE:</b> |                                       |                                    |                            |                                    |
| <u>Nimp</u>    | 0                                     | 0                                  | 6                          | 0                                  |
| <b>MALE:</b>   |                                       |                                    |                            |                                    |
| <u>Wimp</u>    | 5                                     | 2                                  | 3                          | 2.3                                |
| <u>Imp</u>     | 7                                     | 6                                  | 6                          | 2.1                                |
| <u>Bimp</u>    | 36                                    | 21                                 | 16                         | 3.6                                |
| TOTAL (N)      | 48                                    | 29                                 |                            |                                    |
| MEAN (N)       | 12                                    | 7.25                               |                            | 5.3                                |

Nimp was involved in significantly less aggressive interactions than Imp was involved in (Fishers Exact Test:  $P = 0.0001$ ) and therefore less than the other two males, Wimp and Bimp.

TABLE 72

Type and Number of Interactions Bully was involved in during his 25-day stay with Focal troop in July 1978 and a comparison with the other resident males.

|                                     | <u>Bully</u> | <u>Jungi</u> | <u>Crook</u> | <u>Mean</u> | <u>Total</u> |
|-------------------------------------|--------------|--------------|--------------|-------------|--------------|
| <u>Friendly Interactions</u>        |              |              |              |             |              |
| Receives Grooming                   | 1            | 3            | 4            | 3           | 11           |
| Gives Grooming                      | <u>1</u>     | <u>0</u>     | <u>1</u>     | <u>0</u>    | <u>2</u>     |
| <u>TOTAL FRIENDLY INTERACTIONS</u>  | 2            | 3            | 5            | 3           | 13           |
| <u>Agonistic Interactions</u>       |              |              |              |             |              |
| Receives Aggression                 | 5            | 0            | 1            | 1           | 7            |
| Gives Aggression                    | <u>3</u>     | <u>0</u>     | <u>0</u>     | <u>0</u>    | <u>3</u>     |
| <u>TOTAL AGONISTIC INTERACTIONS</u> | 8            | 0            | 1            | 1           | 10           |

Bully was involved in significantly more agonistic interactions than other males (Fisher's Exact Test:  $P = 0.02$  for Crook and Mean;  $P = 0.004$  for Jungi).

TABLE 73

Total number and type of interactions between the shadowing male Flattop and members of the Focal troop during the period he was shadowing the focal troop and before the mass attack where he received probably fatal injuries.

|             |                                  |   |
|-------------|----------------------------------|---|
| Groomed by: | Sexually Receptive Adult Female: | 1 |
|             | Juvenile Females:                | 5 |
| Chases:     | Adult Female:                    | 1 |
| Chased by:  | Adult Males:                     | 7 |
|             | Adult Female:                    | 1 |
|             | Juvenile Males:                  | 3 |
|             | Juvenile Females:                | 3 |
| Mounts      | Juvenile Females:                | 2 |

Flattop was involved in 8 friendly and 15 agonistic interactions. Juvenile females were the participants in 7 of the 8 friendly interactions and only 3 of the 15 agonistic interactions.

Flattop was involved in more antagonistic interactions than friendly interactions (Binomial Test:  $z = 1.46$ , significant only at  $P = 0.1$  level).

TABLE 74

No. of agonistic encounters between Focal Troop and its Neighbors  
(January 1980 - March 1982)

| FOCAL TROOP INTERACTIONS                        | PWD TROOP | MIDDLE TROOP | TOTAL         |
|-------------------------------------------------|-----------|--------------|---------------|
| Focal troop Chases Off                          | 19        | 16           | 35 wins       |
| Focal Troop Chased Off By                       | 3         | 3            | 6 loses       |
| Counterchasing with no Spatial Supplantation    | 2         | 8            | 10 stalemates |
| Counterdisplaying with no Spatial Supplantation | 2         | 9            | 11 stalemates |
| Exchange of Facial Threats                      | 1         | 1            | 2 stalemates  |
| Focal Troop Avoids and Takes Detour             | 2         | 2            | 4 detours     |
| Other troop Avoids and Takes Detour             | 1         | 0            | 1 avoided     |
| Total Agonistic Encounters in 3231.75 hours     | 30        | 39           | 69 encounters |

64 of the agonistic encounters involved active aggressive interactions with much screaming while five of the encounters were silent (the avoid and detour encounters).

The data on intertroop encounters was collected from January 1980 - March 1982 because it was felt that before this period, PWD and Middle troops may have lost encounters because of my presence. Indeed, in 1979 Middle troop initiated 3 encounters but immediately retreated upon seeing me. After January 1980 neither PWD nor Middle troops appeared to be affected by my presence.

TABLE 75

Agonistic intertroop Encounters in Relation to Mr. Mean's Physical and Social Deterioration from January 1981

|                                       | January 1980 - December 1980 | January 1981 - March 1982 |
|---------------------------------------|------------------------------|---------------------------|
|                                       | #                            | #                         |
| <u>Focal Troop Wins Encounter</u>     | <u>27</u>                    | <u>8</u>                  |
| <u>Focal Troop Loses Encounter</u>    | <u>1</u>                     | <u>5</u>                  |
| <u>Focal Troop Stalemates</u>         | <u>11</u>                    | <u>12</u>                 |
| <u>Focal Troop Avoids and Detours</u> | <u>1</u>                     | <u>3</u>                  |
| <u>Other Troop Avoids and Detours</u> | <u>0</u>                     | <u>1</u>                  |
| Total Encounters Observed             | 40                           | 29                        |
| Total Number of Observation Hours     | 1890.25                      | 1341.5                    |

Mr. Mean assisted in the majority of intertroop encounters through 1980. Beginning in January 1981, Mr. Mean began to physically deteriorate and became a social outcast. He no longer assisted in intertroop encounters and became socially peripheral to the rest of the troop members.

The Focal troop won significantly more encounters during January 1980 - December 1980 than during January 1981 - March 1982 (two-sided binomial test:  $Z = 4.68$ ,  $P = <0.0002$ ). The Focal troop lost significantly more encounters during January 1981 - March 1982 than during January 1980 - December 1980 (two-sided binomial test:  $Z = 10$ ,  $P = <0.0002$ ).

## APPENDIX A

## List of mammals seen in the Abuko Nature Reserve

| LATIN NAME                     | COMMON ENGLISH NAME                     |
|--------------------------------|-----------------------------------------|
| <u>Aonyx capensis</u>          | Cape clawless otter                     |
| <u>Atilax paludinosus</u>      | Marsh mongoose                          |
| <u>Cricetomys emini</u>        | Emin's giant rat                        |
| <u>Cephalophus sp.</u>         | Duiker                                  |
| <u>Erinaceus sp.</u>           | Hedgehog                                |
| <u>Euxerus erythropus</u>      | Ground squirrel                         |
| <u>Genetta genetta</u>         | Genet                                   |
| <u>Heliosciurus gambianus</u>  | Gambian sun squirrel                    |
| <u>Herpestes ichneumon</u>     | Egyptian mongoose                       |
| <u>Hystrix cristata</u>        | North African crested porcupine         |
| <u>Mungos sp.</u>              | Either <u>mungo</u> or <u>gambianus</u> |
| <u>Nandinia binotata</u>       | Two-spotted palm civet                  |
| <u>Thryonomys swinderianus</u> | Cane rat                                |
| <u>Tragelaphus scriptus</u>    | Harnessed antelope                      |
| <u>Tragelaphus spekei</u>      | Sitatunga                               |
| <u>Viverra civetta</u>         | African civet                           |
| Unidentified                   | Bat                                     |

The above list includes all mammals seen at least once during this study. It also includes porcupine although only quills were found - 17 times. It does not include mammal fragments found in owl pellets and identified by P. Jenkins at the British Museum of Natural History, London. These are: Arvicanthis, Crocidura (at least three different species), Hylomyseus, Mus, Nycteris, Praomys natatensis, Tatera.

## APPENDIX B

STRIP ENUMERATION DATA  
(trees above 10m)

Results of strip enumeration of all trees greater than 10m in height are given below for the three main habitat zones found in Focal troop's home range.

TREE AND SHRUB SAVANNA

Results: 1 species; 3 trees above 10 m.  
Total Area Covered: 0.193 ha.

| <u>Species</u>          | <u>No. in</u><br><u>Sample</u> | <u>% of</u><br><u>Total</u> |
|-------------------------|--------------------------------|-----------------------------|
| <u>Elaeis guineense</u> | 3 trees                        | 100.0%                      |

WOODLAND SAVANNA

Results: 7 species; 9 trees above 10m.  
Total Area Covered: 0.185 ha.

| <u>Species</u>              | <u>No. in</u><br><u>Sample</u> | <u>% of</u><br><u>Total</u> |
|-----------------------------|--------------------------------|-----------------------------|
| <u>Parinari macrophylla</u> | 3 trees                        | 33.3%                       |
| <u>Elaeis guineense</u>     | 1                              | 11.1                        |
| <u>Ficus ovata</u>          | 1                              | 11.1                        |
| <u>Parkia biglobosa</u>     | 1                              | 11.1                        |
| <u>Prosopis africana</u>    | 1                              | 11.1                        |
| <u>Pterocarpus africana</u> | 1                              | 11.1                        |
| <u>Vitex grandifolia</u>    | 1                              | 11.1                        |

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## APPENDIX B

GALLERY FOREST

Results: 22 species: 198 trees above 10m.  
Total Area Covered: 0.203 ha.

| <u>SPECIES</u>                   | <u>No. in<br/>Sample</u> | <u>% of<br/>Total</u> |
|----------------------------------|--------------------------|-----------------------|
| <u>Elaeis guineense</u>          | 69 trees                 | 34.8%                 |
| <u>Parinari excelsa</u>          | 25                       | 12.6                  |
| <u>Mangifera indica</u>          | 21                       | 10.6                  |
| <u>Pseudospondias microcarpa</u> | 21                       | 10.6                  |
| <u>Anthocleista procera</u>      | 15                       | 7.6                   |
| <u>Dialium guineense</u>         | 9                        | 4.5                   |
| <u>Detarium senegalensis</u>     | 8                        | 4.0                   |
| <u>Cleistopholis patens</u>      | 6                        | 3.0                   |
| <u>Ficus sur</u>                 | 6                        | 3.0                   |
| <u>Ficus lutea</u>               | 3                        | 1.5                   |
| <u>Raphia palma-pinus</u>        | 3                        | 1.5                   |
| <u>Anthostema senegalensis</u>   | 2                        | 1.0                   |
| <u>Ficus ovata</u>               | 1                        | 0.5                   |
| <u>Ficus scott-elliotii</u>      | 1                        | 0.5                   |
| <u>Ficus thonningii</u>          | 1                        | 0.5                   |
| <u>Ficus trichopoda</u>          | 1                        | 0.5                   |
| <u>Philiostigma thonningii</u>   | 1                        | 0.5                   |
| Unidentified Species             | 5                        | 2.5                   |

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**APPENDIX B**  
**COMBINED STRIP ENUMERATION DATA**  
**TREES ABOVE 10m**

Combined results of strip enumerations in all three major habitat zones (Tree and Shrub Savanna, Woodland Savanna and Gallery Forest) for all trees greater than 10m in height are given below.

Results: 27 species; 210 trees above 10m.  
 Total Area Covered: 0.58 ha.

| Species                          | No. in<br>Sample | % of<br>Total | Rank in<br>Annual |
|----------------------------------|------------------|---------------|-------------------|
| <u>Diet</u>                      |                  |               |                   |
| <u>Elaeis guineense</u>          | 73               | 34.8%         | 24                |
| <u>Parinari excelsa</u>          | 25               | 11.9          | 1                 |
| <u>Mangifera indica</u>          | 21               | 10.0          | 12                |
| <u>Pseudospondias microcarpa</u> | 21               | 10.0          | 5                 |
| <u>Anthocleista procera</u>      | 15               | 7.1           | 14                |
| <u>Dialium guineense</u>         | 9                | 4.3           | 11                |
| <u>Detarium senegalensis</u>     | 8                | 3.8           | 3                 |
| <u>Ficus sur</u>                 | 6                | 2.9           | 17                |
| <u>Cleistopholis patens</u>      | 6                | 2.9           | 13                |
| <u>Ficus lutea</u>               | 3                | 1.4           | 27                |
| <u>Parinari macrophylla</u>      | 3                | 1.4           | 18                |
| <u>Raphia palma-pinus</u>        | 3                | 1.4           | 7                 |
| <u>Anthostema senegalensis**</u> | 2                | 1.0           | **                |
| <u>Ficus ovata</u>               | 2                | 1.0           | 9                 |
| <u>Ficus scott-elliotii</u>      | 1                | 0.5           | 48                |
| <u>Ficus thonningii</u>          | 1                | 0.5           | 20                |
| <u>Ficus trichopoda</u>          | 1                | 0.5           | 2                 |
| <u>Parkia biglobosa</u>          | 1                | 0.5           | 4                 |
| <u>Philiostigma thonningii</u>   | 1                | 0.5           | 39                |
| <u>Prosopis africana</u>         | 1                | 0.5           | 6                 |
| <u>Pterocarpus africana</u>      | 1                | 0.5           | 8                 |
| <u>Vitex grandifolia</u>         | 1                | 0.5           | 28                |
| Unidentified Species             | 5                | 2.4           |                   |
| Total                            | 210 trees        |               |                   |

**\*\*Anthostema senegalensis** was not eaten during scan-samples February 1979-January 1980.

**APPENDIX B**  
**COMBINED STRIP ENUMERATION DATA**

Combined results of strip enumerations of all gallery forest trees above 10m and all tree and shrub savanna and woodland savanna trees above 5m in height.

|                         | Tree and<br>Shrub<br>Savanna | Woodland<br>Savanna | Gallery<br>Forest |
|-------------------------|------------------------------|---------------------|-------------------|
| <u>Trees Above 10m</u>  |                              |                     |                   |
| <u>No. of Trees</u>     | <u>3 trees</u>               | <u>9 trees</u>      | <u>198 trees</u>  |
| <u>No. of Species</u>   | <u>1 species</u>             | <u>7 species</u>    | <u>22 species</u> |
| <u>% of Top Species</u> | <u>100%</u>                  | <u>33.3%</u>        | <u>34.8%</u>      |
| <u>Top Species</u>      | <u>Elaeis</u>                | <u>Parinari</u>     | <u>Elaeis</u>     |
|                         | <u>guineense</u>             | <u>macrophylla</u>  | <u>guineense</u>  |

Trees Above 5m

|                         |                    |                    |
|-------------------------|--------------------|--------------------|
| <u>No. of Trees</u>     | <u>27 trees</u>    | <u>113 trees</u>   |
| <u>No. of Species</u>   | <u>8 species</u>   | <u>13 species</u>  |
| <u>% of Top Species</u> | <u>37%</u>         | <u>28.3%</u>       |
| <u>Top Species</u>      | <u>Parinari</u>    | <u>Pterocarpus</u> |
|                         | <u>macrophylla</u> | <u>erinaceus</u>   |

Combined results of strip enumerations in all three zones for all trees above 5m in the two savanna zones and above 10 m in the gallery forest are given below.

|                               |                                               |
|-------------------------------|-----------------------------------------------|
| <u>No. of Species</u>         | <u>32 species</u>                             |
| <u>No. of trees</u>           | <u>338 trees</u>                              |
| <u>% of Top Species</u>       | <u>23% (<u>Elaeis guineense</u>=78 trees)</u> |
| <u>% of Top Three Species</u> | <u>44.4%</u>                                  |

**APPENDIX C**  
**Selective Case History Descriptions**

**Males**

1. **Jungi** was a young adult male when the study began in March 1978. He disappeared in October 1978. During the time he was in the Focal troop he was the chief copulator, never received any aggression or gave any submissive gestures and received more grooming than any other individual.

2. **Captain Crook** was an adult male in March 1978 and disappeared in July 1982. He was extremely small, covered with facial scars, had only one-half of a tail and was incapable of intromission because of a deformed penis. From the time Jungi disappeared until Yunk reached maturity (October 1980), Captain Crook was the chief copulator, top-ranking male, and initiator of intertroop encounters.

3. **Mr. Mean** was an adult male in March 1978 and disappeared in January 1982 when he appeared to be very old. He was never chief copulator, top-ranking male or main initiator of intertroop encounters. From January 1980 he began to physically deteriorate and spent much time on his own, actually moving away from his troop.

4. **Bully** was a young adult male in June 1978 and was killed by members of Focal troop in July 1978. From the time he was first seen until he was killed, he spent 25 days with Focal troop. He was socially peripheral, aggressive toward mothers and young and may have been responsible for one case of infanticide.

5. **Flattop** was a young adult male when first seen in October 1979 and was wounded (probably fatally) by Focal troop members in December 1979. He shadowed Focal troop for 41 days engaging in more antagonistic interactions than friendly interactions. There is indirect evidence that Flattop was possibly involved in attempted infanticide.

6. **Kinky** was a juvenile male when he was first seen shadowing Focal troop and PWD - neither one of which was his natal troop. After 26 months as an extratroop male he joined PWD, became chief copulator and main initiator of intertroop encounters. He spent at least one year in PWD.

7. **Yunk** was born approximately 2 months before field work began on Focal troop. His mother was YunDum and he had no known siblings and no male peers. He was the only male never to be expelled from his natal troop and thus spent his entire juvenile and subadulthood in his natal troop. In October 1980 he became chief copulator and top-ranking male. In May 1981 he disappeared.

8. **Wimp** was born October 1978 to low-ranking Wild. Wimp was always the lowest ranking male and was never seen copulating with fully swollen females. He was still part of Focal troop in June 1986.

9. **Imp** was born in December 1978 to middle-ranking Inca. He had an older sister Ilf who joined Zoo troop when he was 4-months old. He had a younger sister, Id who was born just before he rejoined Focal troop after an 8 month exile period. He then became second-ranking male and number two copulator. He died in May 1982 when he fell on to a high tension wire.

10. **Mimp** was born in December 1978 to middle-ranking Metoo. He had no known siblings although his mother had lost an infant (probable infanticide) exactly 6 months before his birth. His mother disappeared when he was 20 months old and he was then exiled from his natal troop. He spent 15 - 22 months in exile and then joined Question troop - a troop which had no connections with Focal troop. He spent at least 6 months with question troop.

11. **Bimp** was born in January 1979 to high-ranking Button. He had no older siblings but did have a sister, Bid, born when he was in exile. He rejoined Focal troop after 7 months in exile and became top-ranking male and chief copulator. He was killed by a crocodile in December 1982.

12. **Gimp** was born about May 1979 and spent the first + 6 months of his life travelling with his low-ranking mother, Garuda, back and forth between Focal troop and PWD troop. He had no older siblings but did have a younger brother just after he was exiled from Focal troop. He spent 6 months in exile, returned to Focal troop and then remained in Focal troop eventually becoming top-ranking male after the death of Bimp. He was still in Focal troop in June 1986.

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### Females

1. **Wild** was an adult female when the study began in March 1978. She had only one known offspring - an infant son, Wimp, born in October 1978. She was a low-ranking female. She was still in Focal troop in June 1986.
2. **Inca** was an adult female in March 1978 with a juvenile daughter, Ilf. She had a son, Imp, in December 1978 and another daughter, Id, in April 1981. She was still in Focal troop in June 1986.
3. **Metoo** was an adult female in March 1978 with a + 2 month old infant, Munk, who died (probable infanticide) in June 1978. She then gave birth to a son, Mimp, in December 1978. Metoo was a middle-ranking female who disappeared in July 1980.
4. **Nene** was a subadult female in March 1978. She had her first infant, a daughter - Nimp, in December 1970 and a second daughter Nid in May 1981. Nene was the largest animal in Focal troop, was a high-ranking female and was still present in August 1989.
5. **Button** was a subadult female in March 1970, gave birth to a son, Bimp, in January 1979 and a daughter, Bid in April 1981. Button was a high-ranking female who disappeared in September 1981 with her five month old daughter.
6. **Solid** was a very small, adult female in March 1978 with a juvenile daughter, Self. In January 1979 she had another daughter, Simp. Solid, the number-two ranking female was still present in June 1986.
7. **Head** was a subadult female in March 1978, gave birth to a daughter, Himp, in February 1979. Head was a middle-ranking female who disappeared in April 1981.
8. **Garuda** was a subadult female in March 1978. Garuda spent the first 6 months of her first offspring's life, travelling between PWD and Focal troop. When her son, Gimp, was + 6 months old she joined Focal troop permanently. Garuda was a low-ranking female. In January 1982 Garuda gave birth to another son, Gid. In June 1986, Garuda, Gimp and Gid were all still present in Focal troop. Garuda was still in Focal troop in August 1989.
9. **Droopy** was the top-ranking adult female with a 2 month old daughter, Dunk, in March 1978. She had no other known offspring and disappeared in July 1982.

10. **Yundum** was an old adult female in March 1978 with a + 2 month-old male, **Yunk**. Yundum was a high-ranking female who disappeared in November 1980. Her son **Yunk** became top-ranking male after her death.

11. **Julie** was an old adult female with no known offspring in March 1978. Julie was a low-ranking female who spent much of her time on her own. She had numerous facial ulcers and a constant loss of hair on her arms and legs. She died in February 1981.

12. **Volley** was a middle-ranking adult female with a juvenile daughter in March 1978. Volley and her daughter **Velf** spent one breeding season travelling between Focal troop and PWD. Volley gave birth to a second offspring (unsexed) in April 1980 and both mother and infant disappeared in July 1980.

13. **Noaf** was an old adult female who left Middle troop and joined Focal troop in November 1980. After three months in Focal troop, Noaf died from snake bite.

14. **Round** was a subadult female who joined Focal troop in May 1979. She gave birth to an unsexed infant in April 1981, was bitten by a snake and died 7 days later (infant disappeared). Round was a low-ranking but very active member of Focal troop. She was the main female initiator of intertroop encounters.

15. **Self** was a juvenile female in March 1978. She developed her first adolescent swelling in October 1979, joined Middle troop in May 1980, gave birth to her first infant in January 1982. Self joined a troop which had no previous Focal troop females.

16. **Pelf** was a juvenile female in March 1978. She adopted her orphaned infant sister, **Punk**, in October 1978 and left her orphaned sister in May 1979 and joined her peers in PWD when she developed her first swelling. She has her first infant in April 1980 and her second infant in May 1983. She was still in PWD troop in August 1989.

17. **Velf** was a juvenile when the study began in March 1978. From August 1979 through February 1980, Velf and her mother, **Volley**, travelled between PWD and Focal troop with Velf eventually joining PWD. She had her first swelling October 1979 and her first infant in January 1982. This infant died before it's first birthday and Velf had a second infant in May 1983. She was still in PWD troop in August 1989.

18. **Cisco** was a Middle troop juvenile in March 1980 when she was first seen. She spent three months travelling back and forth between Middle troop and Focal troop. She joined Focal troop (which contained none of her peers) in June 1980, had her first adolescent swelling in July 1980 and gave birth in April 1981 to a son, Cid. She was still in Focal troop in August 1989.

19. **Quecha** was a subadult female from Middle troop who joined Focal troop in July 1980 (she joined her previous troop mate, Cisco). She had a daughter, Quid in April 1981 and was still present in Focal troop in August 1989.

20. **Tara** was a Middle troop juvenile who joined Focal troop in November 1980 (where she joined Cisco and Quecha). She developed her first swelling in November 1980 and her first infant was born in March - April 1982 and died 4 weeks later (probable infanticide). Sometime between August and December 1982 Tara disappeared and at the end of December she was found in PWD troop where she remained until at least July 1986.

21. **Dunk** was born about January 1978 to the top-ranking female, Droopy. Dunk was the most adventurous of all the colobus. Sometime between August and October 1980 Dunk joined Zoo troop which contained a previous troop mate ([If - not an age peer]). Dunk developed her first adolescent swelling when she was 35 months old and had her first infant when she was 48 months old. Dunk was still in Zoo troop in August 1989.

22. **Punk** was orphaned when she was 9 months old. She was adopted by her older sister, Pelf, who was overly protective. Punk was a lethargic, withdrawn young female who developed her first swelling when she was 38.75 months old, transferred to Zoo troop where she joined her age peer Dunk and gave birth when she was 61 months old. Punk was still in Zoo troop in August 1989.

23. **Simp** was born in January 1979 to 2nd-ranking Solid. Simp never left her natal troop. She developed her first swelling at 30.75 months of age and gave birth when she was 49 months old. Simp was still in Focal troop in August 1989.

24. **Nimp** was born to high-ranking Nene in December 1978. She developed her first swelling when she was 32.5 months old and gave birth when she was 42 months old. Nimp left Focal troop for a brief period and joined Zoo troop. She then returned to Focal troop where she remained until at least August 1989.



## APPENDIX D

OLD AGE

The effect of age on the social behavior of female and male wild primates is largely unknown. This is probably because not many animals in any studied population survive until senescence is well established.

In the Focal troop, one male, Mr. Mean, and four females, Julie, Pug Ugly, YumDum and Noam, were all characterized as attaining and then dying in old age during this study. Aging in all five individuals was characterized by a number of physiological changes such as balding, particularly on the joints, wrinkling and puckering of the facial skin, extreme weight loss and obvious locomotor and visual degeneration. Furthermore, the skeletons of Julie, Pug Ugly and Noam showed bone deterioration with pitting and extreme tooth wear. And, before YumDum disappeared, and was presumed dead, her lower incisors were virtually non-existent causing a loss of liquid whenever she ate fruits.

The four females showed either non-existent or irregular menstrual cycles. From the time I first recognized Pug Ugly in March 1970 until she died in June-July 1979 she never had a sexual swelling. Noam joined the troop in mid-November 1980 and died from snake bite in mid-February 1981. During this time she never showed any signs of sexual swelling (but then this was not the mating season and most females showed no signs of sexual receptivity during this period). While Julie and YumDum appeared to have irregular cycles during the beginning of the study, they both stopped cycling seven and six months respectively before they died. Furthermore, while YumDum gave birth to a son, Yimp, in January 1978, none of the other females gave birth or were associated with young during this study. This data appears to indicate that reproductive success declines with age in the Abuko female due to irregular or non-existent cycles and a period of apparent infertility.

Aging in the Abuko colobus was also characterized by peripheralization. The reasons for this peripheralization, however, appeared to be different for male and females.

For about one month before Julie and Pug Ugly died and one week before Noam died, they spent more time alone than they did with other troop members. During this time they all stopped taking long leaps through the canopy. They also spent more time on the ground, particularly in the savanna zones, where food was located at lower levels than it was in the

other habitat zones. Their senses also appeared to be dulled: Both Pug Ugly and Noam, neither one of whom was particularly habituated to my presence, actually bumped into me as they walked on the ground leaving me with the distinct impression that they neither saw nor heard my approach. It was these physical handicaps which appeared to lead to their spatial separation from the troop. They were simply unable to keep up with other troop members and thus had to spend time alone. None of them appeared to be actively peripheralized nor was there any apparent reduction in their status. For the three months before she died of snake bite (she was only a member of the Focal troop for three months - having just transferred in from Middle troop), Noam received no aggression. Nor, did Julie receive any aggression in her last seven months. YumDum was displaced once in the six months before she disappeared and was presumed dead while Pug Ugly received only one facial threat in the eight months before she died. Therefore, it would appear that none of the four old females were victimized by other troop members during the time they began to show physical signs of old age. Furthermore, none of them appeared to avoid contact with their troop mates. When they were on their own and they heard or saw other troop members nearby, they either moved toward them or stayed and waited to be joined. They were not observed moving away from other colobus.

While the female's spatial separation became obvious, at the most, only a month before they died, Mr. Mean's separation was obvious for nine months before he was last seen and presumed dead. It was my impression that his physical decline was directly responsible for a reduction in his status among the males and females and that the status reduction led to his self-imposed peripheralization.

From February 1979 through January 1980, when Mr. Mean possessed none of the physical characteristics associated with old age, and appeared in perfect health, he received more grooming than any other individual (Table 25), no aggression from Focal troop females or juveniles and took part in matings with fully swollen females. From January 1981, when Mr. Mean began showing signs of physical degeneration and was frequently described in field notes as 'frail' and 'lethargic', he began to lose status. He received the least number of friendly (grooming) interactions, the most number of rejections when he attempted to mount females and was harassed ten times by Focal troop members. Furthermore, unlike the old females, Mr. Mean actively avoided his troop mates on occasion. It was not unusual for him to move off when he heard or saw members of his troop move in his direction. Also, on four occasions he was found resting with juvenile males who had been ousted from his troop. He was the only individual (except for the juvenile males own mothers) observed with these males in a non-aggressive context. It seemed as though

he was forced to rely on relationships with expelled males because his present troop members either ignored his friendly overtures or threatened him.

Although these data are limited to only five individuals, it would appear that females fared better in their old age than males (or at least this one male). The nature and extent of the females relationships with others did not seem to differ as they aged. The males differed drastically. If, as Ransom (1981) has suggested for the Gombe Stream baboons and, as I believe for the Abuko colobus, the status-base of a female differs from that of a male in that it is derived more from relationships with others than from individual characteristics and episodes, then her physical decline would have much less effect on her status. Furthermore, this is probably true for females who belong to both female and non-female transfer species because a female either takes her relationships with her in the form of peer groups or keeps her relationships by not transferring.

In the Abuko population, females were able to outlive males but the reasons for this remain unclear. This phenomenon is probably the result of a combination of factors. Various factors to be considered are females (1) have wider social networks to help relieve stress, (2) take less risks, and (3) have an inherent resistance to life-threatening disease due to a more efficient immune system.

Old age, like disease (which was not obviously present in any of the animals), is probably not a common proximate cause of death. However, it may work together with other factors to cause death. For example, an old animal may be more susceptible to predation, falling, etc. than a young animal.

APPENDIX EAll Focal troop subunits formed January 1979 - March 1982

1. Inca, Imp, YumDum, Yunk, Nene, Nimp went off on their own for at least three and possibly five days. During this time they were joined by Button and Bimp for 1.5 days. They never saw any other troop members during this period. This group formed during the mating season. None of the females involved in this group were cycling at the time.
2. Head, Himp, Nene, Nimp went off for two days on their own. They did this twice: once during the mating season and once outside the mating season. None of the females were cycling during the times they formed these subunits.
3. Nene, Nimp, Julie went off once for two days during the mating season. Neither female was cycling at the time.
4. Volley, Velf, Droopy, Dimp went off for two days on their own. They did this 3 times; once during the mating season, twice outside the mating season. Neither female was cycling at the time of subunit formation.
5. Wild, Wimp, Garuda, Gimp went off for four days on their own and again for two days. They did this during the mating season. Neither female was cycling at the time.
6. Solid and her two daughters Self and Simp went off for a period of two days during the mating season when Solid was not cycling and once for two days during the non-mating season. Solid and her daughter Simp went off for 1.5 days on their own during the non-mating season. Also, on at least 10 occasions the three females would disappear for up to 5 hours during the day. On two occasions they were joined by the non-swollen subadult female Round.
7. Metoo, Mimp, Volley, Vaby went off for three days on their own and once for two days during the mating season when neither female was cycling.
8. Cisco, Cid, Quecha, Quid went off twice for over two days on their own; once during the mating season and once during the non-mating season. Neither female was cycling during subunit formation.
9. Julie and Noam went off once for 2.5 days during the non-mating season. Neither female was cycling.

APPENDIX EAll PWD troop subunits formed January 1980 - January 1982

1. Lip and Pelf and their infants went off 3 times on their own without any other PWD troop members. During all three times they wandered back into Focal troop's range (their original natal troop). They made no attempt to contact their previous troop mates just as they made no attempt to contact their present PWD troop mates during these 'jaunts' which lasted from 1-2 days.

2. Lip, Pelf and Velf went off on their own for at least 1 day on two different occasions. During both of these occasions none of the females were cycling. During these 'jaunts' wandered back into Focal troop's range but made no contact with Focal troop members.

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