THE DEMOGRAPHY OF THE TANA RIVER RED COLOBUS,

Colobus badius rufomitratus.

M.Sc. Thesis.

By

OCHIAGO, W. ODHIAMBO.

1991.

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THE DEMOGRAPHY OF THE TANA RIVER RED COLOBUS, *Colobus badius rufomitratus*.

BY

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A Thesis submitted in partial
fulfilment for the degree of
Master of Science (Biology of Conservation) in the
University of Nairobi.

1991.

DECLARATIONS

This thesis is based on my original work and has not been presented for a degree in any other University.

OCHIAGO, W.O.

This thesis has been submitted for examination with our approval as University supervisors.

DR. IAN J. GORDON

DR. WARUI KARANJA

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DEDICATION

This thesis is dedicated to my grandparents, Mildred Okola Manyolo and Nicholas Odera Okoth, to whom I owe my interest in education.

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ABSTRACT

This study on spatial and temporal changes in the demographic composition and distribution of the Tana River red colobus, *Colobus badius rufomitratus*, was conducted for 9 months (September, 1988 - June, 1989). The main objectives were to determine the current population status of this primate species and to investigate the distribution and composition of colobus groups.

Environmental variables such as forest size, tree species diversity and density per forest were also studied to show how they varied among different forest patches. Various models and theories were applied to estimate the effective population size and, hence, the viability of the species.

An annual census was carried out in the May-June period throughout the 52 km long geographical range of the species while demographic variables were investigated by carrying out monthly censuses in 16 sample groups for 9 months. The results show that the colobus population consisted of, at least, 264 individuals. The effective population size was estimated as 94. There were at least 22 extant colobus groups living in 17 different forests. The majority of these groups, apparently, were on the western bank of the river. Demographic composition varied in space and time among the groups although adult females dominated most groups. The sex ratio was highly biased in favour of females possibly because some solitary males were missed during the censuses.

The forest refuges inhabited by the colobus were of varying sizes, tree species diversity and density and, of all the environmental variables considered, only forest size correlated significantly with the total number of colobus per forest. The forests were fragmented to an extent that, although the groups appeared to constitute a panmictic population, in some cases inter-forest migration would be difficult due to the presence of geographical and man-made barriers like the Tana River, as well as intervening farmland and villages. The Tana River red colobus is still endangered because such a small population is more prone to genetic drift and loss of genetic diversity than a large population. This may lower their adaptability to environmental changes. The subspecies may be saved from extinction if active and effective conservation and management strategies are adopted now.

CHAPTER 1. GENERAL INTRODUCTION

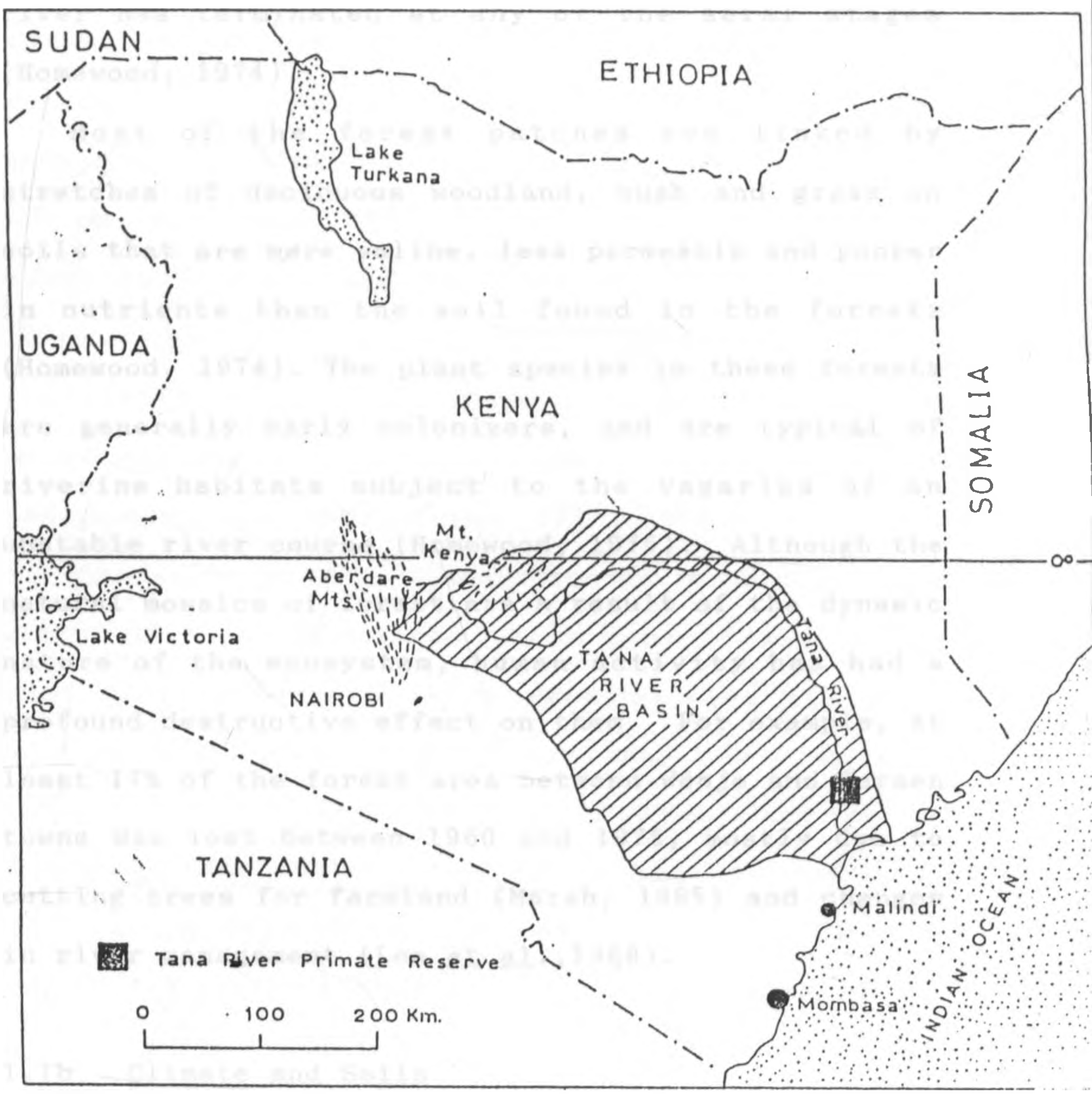
1.1 THE TANA ENVIRONMENT

1.1a Tana River and its Vegetation

The Tana River is Kenya's longest river (Homewood and Redshaw, 1978). From its catchment areas in Mt. Kenya and the Aberdares, the river runs through a course 800 km long (Andrews *et al.*, 1975) before it enters the Indian Ocean through a swampy estuary (Homewood, 1975, Fig. 1). For most of its course the river flows through a semi-arid region of scrub vegetation but in its lower reaches it meanders through a broad flood plain (Andrews *et al.*, 1975). The flood plain is covered by alluvial sediments deposited annually when the river overflows and covers the 8 km wide plain (Homewood, 1974).

As the river nears the ocean, rainfall, humidity and ground-water seepage increase to a level sufficient to support patchy forests and woodland, most of which are not more than a few hectares (Homewood, 1974; Marsh, 1978). These forests are concentrated on raised riverside levees. The water supply is continuously changing due to cyclic changes of the river course. Consequently, the forests form a dynamic mosaic consisting of areas newly exposed to colonization, young forests with limited diversity

Figure 1. TANA RIVER AND TANA RIVER PRIMATE RESERVE



Adapted from Marsh, C. (1976).

and stability, and dying/degrading forests that the river has terminated at any of the seral stages (Homewood, 1974).

Most of the forest patches are linked by stretches of deciduous woodland, bush and grass on soils that are more saline, less permeable and poorer in nutrients than the soil found in the forests (Homewood, 1974). The plant species in these forests are generally early colonizers, and are typical of riverine habitats subject to the vagaries of an unstable river course (Homewood, 1975). Although the natural mosaics of forest are a result of the dynamic nature of the ecosystem, human activity has had a profound destructive effect on them. For example, at least 17% of the forest area between Wenje and Garsen towns was lost between 1960 and 1975, mostly due to cutting trees for farmland (Marsh, 1985) and changes in river management (Lee *et al*.,1988).

1.1b Climate and Soils

The climate is generally hot and dry (Andrews *et al*., 1975; Marsh, 1976). The hottest months are during the Northeast moonson winds when daily maximum temperatures between January and March are about 35^{o} C. The heat is mitigated during the middle six months of the year by the Southeast moonson winds, and the weather is generally cooler during the May-August period. This semi-arid region receives an annual rainfall ranging between 350 and 950 mm. The mean annual rainfall within the Tana River Reserve is 494 mm, most of it falling in the two rainy seasons, March-April and November-December periods (Marsh, 1976). The colobus's geographical range falls within a climatic zone intermediate between that of the humid coastal strip and the semi-arid hinterland (Andrews et al., 1975; Marsh, 1976, 1978).

The soils of the floodplain are generally clay soils which are alkaline. This kind of soil shows poor drainage during rainy seasons when the soil becomes sticky. During dry seasons, the clay soil becomes brittle and develops numerous cracks or fissures. The soils show signs of salt accumulation with high sodium concentration, which can be attributed to the high ratio of evapotranspiration to precipitation. In some places, especially near the river banks, the soil is sandy (raised sandy levees), light in colour and well drained (Andrews, et al., 1975).

1.1c People and their activity

Within the 52 km long geographical range of the Tana red colobus (Lee *et al*., 1988) there are at least 23 villages (Marsh, 1985). These villages had 7,914 people in 1962 and this population has been increasing at a rate of about 3% per annum (Andrews *et al*., 1975). The people belong to 3 main tribal groups, the Pokomo, Orma and Somali.

The Pokomo are riverine people who live by cultivation of rice, maize, bananas and a few other crops. They also keep a few goats, poultry and dogs, and catch fish. The Orma and the Somali depend on large herds of cattle and are semi-nomadic (Andrews *et al*., 1975).

These people affect the Tana ecosystem by illegally hunting, clearing forests for agriculture, and by cutting saplings and undergrowth for buildings and firewood, and bigger trees for canoes. Both the Orma and the Somalis also set dry season fires in the grassland (Marsh, 1976) which sometimes affect the adjacent forests.

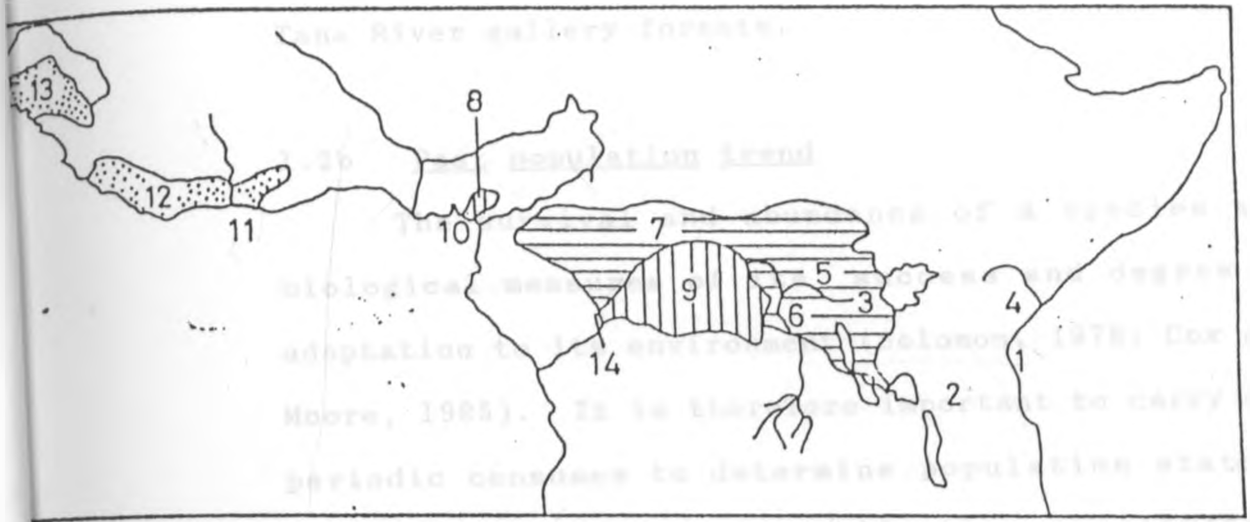
1.2 THE TANA RIVER RED COLOBUS

1.2 a Taxonomy and distribution

The Tana River red colobus belongs to the family Cercopithecidae. This family consist of two subfamilies; the Cercopithecinae and Colobinae. The former include baboons, macaques and guenons while the Colobinae are comprised of langurs, proboscis monkeys and colobus monkeys. The colobus, found only in tropical Africa, are divided into 3 main species; the olive colobus, the black and white colobus, and the red colobus to which the Tana River subspecies belongs (Dandelot, 1968; Struhsaker, 1975).

Forests covered much of tropical African during the Miocene period which could have permitted the original widespread distribution of the red colobus (Andrews and Couvering, 1975). The subsequent dry periods of the Pleistocene resulted in a reduction in forest size and number (Kingdon, 1971). This left small and scattered refugia where the colobus were restricted and probably underwent divergent evolution. As a consequence, the 14 extant colobus subspecies show allopatric distributions (Fig. 2) from Zanzibar to Senegal (Dandelot, 1968; Struhsaker, 1975). The taxonomy and evolution of the colobus monkeys has been reviewed by Struhsaker (1975). The

Figure 2. ALLOPATRIC DISTRIBUTION OF THE SUBSPECIES OF Colobus badius IN AFRICA.



Key

1. Colobus badius kirkii
2. Colobus badius gordonorum
3. Colobus badius tephrosceles
4. Colobus badius rufomitratus (The Tana red colobus).
5. Colobus badius ellioti
6. Colobus badius foai
7. Colobus badius oustaleti
8. Colobus badius preussi
9. Colobus badius tholloni
10. Colobus badius pennanti
11. Colobus badius waldroni
12. Colobus badius badius
13. Colobus badius temmincki
14. Colobus badius bouvieri

Adapted from Struhsaker, T. (1975).

Tana River red colobus subspecies is endemic to the Tana River gallery forests.

1.2b <u>Past population trend</u>

The survival and abundance of a species are biological measures of its success and degree of adaptation to its environment (Solomon, 1976; Cox and Moore, 1985). It is therefore important to carry out periodic censuses to determine population status. This is essential for an effective conservation program (Marsh, 1978), especially for an endangered subspecies like the Tana River red colobus (Struhsaker and Leland, 1980, 1987) whose population is known to have declined by over 80% within a decade (Marsh, 1985). Censuses of the red colobus were carried out in 1979, 1985 and 1989 (this project).

Approximately 50% of all non-human primate species in the world are threatened (Cheney, <u>et al</u>., 1987). This poses a critical threat to the 200 extant primate species (Izard and Simon, 1984) of which East Africa supports 10%. The Tana River red colobus, for example, is listed in the I.U.C.N. Red Data Book as the most endangered colobine subspecies in Africa (Andrews <u>et al</u>., 1975; Struhsaker and Leland, 1987; Lee <u>et al</u>., 1988). In 1975 the Tana

River red colobus population was estimated to be between 1200 and 1800 but by 1985 only about 200 - 300 individuals were found, indicating a population decline of over 80% within a decade (Marsh, 1978, 1985). This was mediated through both declines in group size and local extinction and/or dissolution of whole groups.

Mchelelo forest, for example, had 2 groups in 1975 but in 1985 there was only one group (Marsh, 1985). The proportion of infants and juveniles also declined from 34% to 22% within the same period. Infanticide has been suspected among groups where the dominant males have been replaced (Marsh, 1979a), probably each male would prefer to have his own infants. The frequency of membership changes among colobus groups has been found to be high (Marsh, 1979b).

1.3 OBJECTIVES OF THE STUDY

1.3a General objectives

This study is part of a long term project aimed at determining the current demography of the Tana River red colobus. The project will contribute to the creation of awareness among local people, researchers and administrators about this endangered subspecies. The findings of this study may also show some aspect of the Tana River environment that still need further intensive systematic study. It may also stimulate provision of much needed moral and financial support that will help in adopting effective conservation and management strategies to curb further local extinction and/or dissolution of colobus groups.

1.3b Specific objectives

(1) To determine the current population status of the Tana River red colobus and compare this with data obtained in earlier studies (1975 and 1985) in the same area.

(2) To investigate the current spatial distribution of the colobus and their abundances and to compare these with past distributions among different forest patches. This would show whether there have been any significant changes in distribution and could provide clues as to the causes of any such changes.

(3) To monitor and compare groups' demographic processes (births, maturation, migration and death) in space and time for nine months and determine if there is any significant variation in group size and age-sex composition among groups.

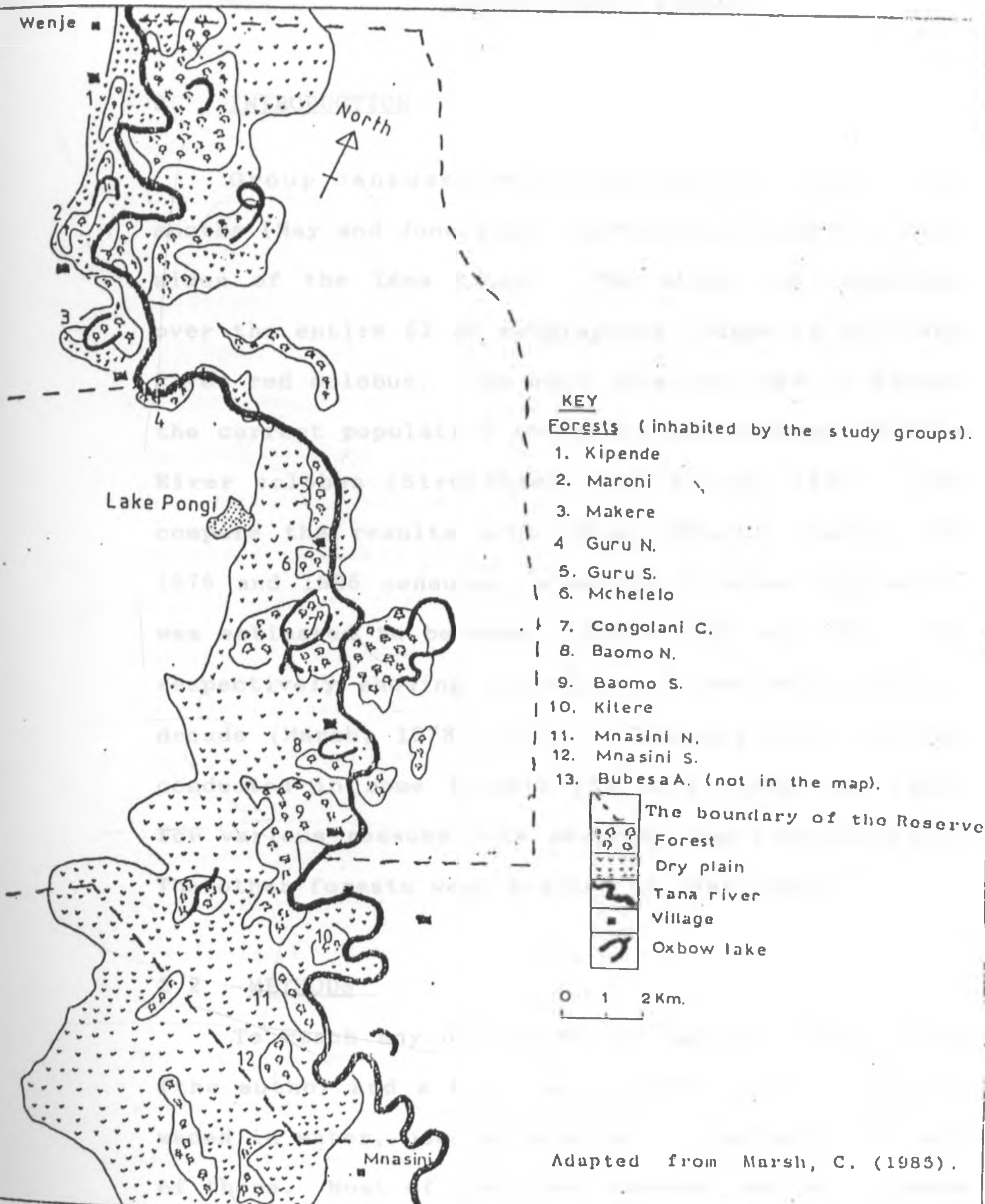
(4) To apply population genetics models to estimate the effective population size in order to assess the dangers of loss of genetic diversity and inbreeding depression.

(5) To employ island biogeography theory, particularly those aspects dealing with the shape, size and the subdivision of habitats, to find out any differences between the actual situation in Tana environment and the ideal states predicted by the theory. The ideal states have been reviewed by Simberloff (1988).

1.4 THE STUDY SITES

This study was conducted near the coast of Kenya within and outside the Tana River Primate Reserve (1^{o} 50'S 40^{o} 10'E, Fig. 1.). Forest, bushland and openland (grassland and farmland) are the three main types of habitats found within the geographical range of the Tana River red colobus. Forest is the least abundant of these habitats, with a total area of not more than 37 sq. km (Marsh, 1978). The size of forested area has been decreasing while both bushland and openland have been increasing mainly due to shifting cultivation, dry season burning of grass and/or changes in the river course (Marsh, 1976, 1985). The forests where censuses were carried out on a systematic monthly basis included Kipende, Maroni, Makere, Guru North, Guru South, Mchelelo, Congolani, Baomo North, Baomo South, Kitere, Mnazini North, Mnazini South, Mbuji and Bubesa A. All these forests are located on the western bank of the river (Fig. 3). Mbuji and Bubesa, which are not included in the map, are located less than 8 km south of Mnazini South. The forests on the east were only visited when the security situation allowed it.

iguro 3. THE STUDY SITES.



Adapted from Marsh, C. (1985).

CHAPTER 2. COLOBUS GROUP CENSUS

2. INTRODUCTION

Group censuses were carried out within two months (May and June 1989) in forests located on both sides of the Tana River. The study was conducted over the entire 52 km geographical range of the Tana River red colobus. The main objective was to assess the current population status of the endangered Tana River colobus (Struhsaker and Leland, 1987), and compare the results with those obtained during the 1975 and 1985 censuses, when the colobus population was estimated to be about 1200 - 1800 and 200 - 300 respectively showing a decline of over 80% within a decade (Marsh, 1978, 1985). Censuses could not be conducted in some forests (in 1975, 1985 and 1989) for various reasons like security and accessibility. The other forests were visited at least once.

2.2 METHODS

To reach any of the forest patches (Fig. 3) we (the author and a field assistant) drove, walked, waded in water, used a canoe or a combination of any of these. Most of the time, however, we had to wade in water or use a canoe since the census period was during the floods. Fresh spoor of humans and wild animals and fresh faeces of the latter, helped in detecting places that were potentially dangerous. Forests where poachers and hippopotami were suspected to be roaming were temporarily avoided, and so were sections of the Tana River and oxbow lakes with high population densities of crocodiles and hippopotami.

Upon reaching a chosen forest we searched the entire forest on foot in a systematic way. This involved walking in a general (avoiding barriers like the river) north-south or east-west direction following compasses and maps, paths being about 100 meters apart. Only the Mchelelo forest had systematic (man-made) trails which were laid out in a 50-meter grid. Occasionally we took advantage of, and used, baboon and/or hippopotamus trails.

Clues used in the search for the red colobus included listening for any vocalizations and shaking tree branches. Questioning people in adjacent farms also helped. Occasionally it was possible to trace a "hiding" group by sensing the odour of their urine or by sighting wet leaves of shrubs and herbs. Places where other primate species like Syke's monkeys, baboons and mangabey were seen or heard vocalizing were also thoroughly checked because the red colobus tended to associate with some of these species when foraging, resting or involved in social activities like grooming and playing.

Since this aspect of the research (i.e. group census) was mainly extensive, it was not possible to habituate all the groups thus most groups were shy. Therefore, although we counted all individuals that we could see before they disappeared, we concentrated mainly on counting groups.

To ascertain the number of groups in a given forest, at times it was necessary to leave one person with an already found group while another person(s) kept on searching the entire forest. Occasionally we teamed up with another researcher and her assistant, who were studying Mangabey monkeys, and worked together. They helped by reporting whatever they saw or suspected whenever we were not working together. In such cases we ascertained the presence of a group or a solitary colobus with our own observations. Twelve of the 27 forests were censused at least twice every month for nine months. The groups in these forests were the colobus sample groups intensively studied to provide detailed demograhic data. The other forests were censused only once during the study period, when they were accessible and/or the security situation allowed it.

2.3 RESULTS

Within the 52 km geographical range of the Tana River red colobus with about 66 forests, the subspecies was distributed among 22 social groups in 17 (25.8%) forests (Table 1). Only 23.5% of the inhabited forests had more than one colobus group. The forests on the east bank had only 6 (27.3%) of the observed 22 groups. Forests on the east bank were, however, only sampled once and some groups could have been missed. About 36.4% of the colobus groups are outside the Tana River Primate Reserve.

The results of this study are compared with those obtained in previous studies (Table 1). The red colobus have been sighted in a total of 27 forests since 1975. It should, however, be noted that the censuses were not carried out every year and also there were some forests that could not be sampled for various reasons. Of the 21 forests visited both in 1975 and 1985, all 21 contained colobus in 1975 but only 12 contained colobus in 1985. Of 17 forests sampled in both 1985 and 1989, ten contained colobus in 1985 and 12 had colobus in 1989. Of the 17 forests visited in both 1975 and 1989, all had colobus in 1975 but only 12 contained colobus in 1989. In general, there were at least 46 groups in 1975 but this had declined to approximately

Table 1. **COLOBUS GROUP CENSUS**

	YEAR OF THE STUDY.		
FOREST	1975	1985	1989
KIPENDE * @	1	1	1
MARONI W * @	2	0	1
MARONI E	1	0	0
MAKERE W * @	1	1	1
GURU N *	6-8 #	1	1
GURU S *	.--	.--	1
GURU E	1 - 2	1	1
MCHELELO W *	2	1	1
MCHELELO E	1	0	.--
CONGOLANI C	3 - 4	1	1
CONGOLANI W	1	0	0
SIFA W	1	0	0
SIFA E	4 - 6	2	1
HADRIBU	1	0	0
BAOMO N *	2 - 3	0	1
BAOMO S *	6 - 8	4	3
KITERE *	.--	.--	1
MNAZINI N *	3	1	2
MNAZINI S *	3	2	1
MNAZINI E @	.--	.--	2
BUBESA A @	.--	.--	1
HEWANI W/1 @	1 - 2	0	.--
HEWANI W/2 @	1	1	.--
HEWANI E/2 @	1	1	.--
HEWANI E/3 @	1	0	0
HEWANI S @	3	.--	.--
WEMA @	.--	.--	2
TOTAL	46 - 56	17	22

* Forests inhabited by the colobus sample groups that were intensively studied in 1989.

.@ Forests located outside the Tana River National Primate Reserve

\# Guru. N and Guru S. were a single undivided forest of over 100 Ha. in 1975 and this figure represents the single forest.

.-- Forests that could not be sampled .

17 groups by 1985. Currently there are at least 22 colobus groups. Although there were at least nine forests with more than one colobus group in 1975, this apparently declined to three forests in 1985. The greatest decline occurred in Guru and Sifa E. forests.

2.4 DISCUSSION

There are at least 22 extant colobus groups living in 17 different forests. These groups show no home range overlap and are still fewer than they were in 1975 (pers. obs.). Since 1973, the red colobus have been sighted in a total of 27 different forest patches out of the 66 that exist within the 52 km long geographical range of the Tana red colobus (Marsh, 1985). The records show that the same forest patches have not been inhabited continuously since then, and that some of the forests that had no colobus group in the past now have (e.g. Baomo N. and Maroni W.). This shows that inter-forest migration has occurred. This may be attributed to many factors. For example, different forests are affected differently by occasional changes of the river's course and the suitability of these forests to the colobus varies concomitantly. The monkeys may migrate to other forests when the ones they are inhabiting senesce.

The apparent decline of the number of existing groups from about 46 to 17 between 1975 and 1985 could have been a result of the 1984 drought (Struhsaker, pers. comm.), the presence of a contagious disease (Else, pers. comm.) or forest senescence due to construction of dams or natural changes in the river's course. The number of surviving groups could also have declined if some smaller groups joined after migration. This possibility, however, is ruled out because the mean group size declined from 18.0 to 9.8 individuals within the same decade (Marsh, 1978, 1985). It is thus most likely that most groups underwent local extinction. Local people maintain that the monkeys migrated but when asked where the monkeys went they can give no answer. Various researchers (Marsh, 1985) think the monkeys died en masse but are unable to explain the absence of skeletons. Colobus bones may decompose quickly or may be eaten or dispersed by scavengers, such as hyenas, which are plentiful along the Tana.

Some forests, like Guru, decreased in size by over 50% between 1975 and 1985. In fact Guru is now divided into two distinct forests with a total area much less that the original single forest. Each of these Guru forests (Guru North and South) has one colobus group while the original, single forest had 6 - 8 groups (Marsh, 1978). This shows that the factors that affected the forest may have affected the colobus by fragmenting and reducing the size of their habitat. Guru North is now very thin and long and is inhabited by a small colobus group. Factors other than reduction in forest size may also have affected the monkey populations as suggested by data for Baomo South, where forest size (220 Ha.) has not changed much since 1975 yet the number of surviving groups has declined, from 6 to 3 groups. The real cause(s) of the colobus population decline should be investigated. The number of colobus groups has stabilized since 1985.

CHAPTER 3. DETAILED DEMOGRAPHY OF SELECTED GROUPS

3.1 INTRODUCTION

Important demographic variables include group size, age-sex composition and rates of birth, maturation, emigration and death (Hutchinson, 1978). Monitoring such variables is important in formulating appropriate conservation and management strategies. For example, it is helpful to know the optimum group size because, theoretically, there is an optimum range of group size for any set of environmental conditions. Such a group would have a reproductive rate that is comparatively higher than that of groups of other sizes in that environment (Altmann and Altmann, 1970; Krebs and Davies, 1987). Also, once a group's size exceeds its food supply or any limiting resource then the group may expand its home range or migrate (Dunbar, 1987). It is important to monitor not only overall population trends but also sex and age ratios, rearing success and survival rates (Downing, 1980).

Detailed data were obtained on 16 groups over two months (May and June, 1989), when an annual census was carried out. Data on temporal variations in demographic parameters were based on 12 groups that were systematically studied over 9 months (September, 1988 to June, 1989). The results of these studies were compared with those obtained in earlier studies, although in this case only one group (Mchelelo group) was investigated in previous studies (Marsh, 1985).

3.2 METHODS

The groups that were selected for determination of demographic studies were those which were most accessible for observation. Since the determination of colobus' age-sex composition requires that groups be habituated, we achieved this by acclimating some groups to our presence. If any group retreated, we also retreated as recommended by Kumar (1968), sat down and avoided looking at them directly. Observations were made using binoculars. Visual contacts with a given group were maintained for at least four hours in a predetermined day, mostly in the morning and late afternoon when the colobus were comparatively active (Marsh, 1978). This was done at monthly intervals over nine months.

Aging of these aboreal primates was based on visible external features like relative body size and coat colour, as well as the presence of canines, reproductive organs, nipples and their relative sizes, following Struhsaker (1975).

Small infants: Young individuals with the smallest body size, not yet weaned, lack red colour on the head and rarely leave their mothers.

Big infants: Slightly larger than small infants, weaned and rarely carried by their mothers. These spend most of their time playing.

Small juveniles: Larger than big infants but smaller than big juveniles. Occasionally engage in play.

Big juveniles: Larger than small juveniles. Males have scrota that are relatively small while females have very short nipples.

Sub-adults: Have body sizes that, although larger than big juveniles and smaller than adults, differ in size depending on sex. Males are larger than females.

<u>Adults</u>: Adult male has fully grown canines and completely descended testes. Adult females have a body size that is almost half as big as that of adult males and have fully developed nipples.

Determination of an individual's sex was based also on visible and auditory features like canines, genitalia, nipples and vocalizations. A few monkeys were known individually, based on peculiar deformities like torn earlobes, bent tails or harelip.

The number of individuals of each sex in each age group was determined on the basis of repeated counts each day the group was followed. Such counts were made when the monkeys were jumping from one tree branch to another, because they were comparatively easy to identify as individuals when they jumped through an open gap in the canopy.

Emigrations were inferred from reduction of group size after searching the entire home range of the group and failing to trace the missing individual or its carcass. Immigrations were recorded when a group's size increased and an unfamiliar and/or shy individual was sighted. Extent of home ranges were plotted each time a group was sighted. Births were assumed whenever an adult female was seen carrying a young infant she never had before. Deaths were only recorded when a group's size decreased and the carcass of the missing individual was traced.

3.3 RESULTS

3.3a Demographic composition of 16 selected groups

The demographic composition of the colobus population varied among groups (Table 2). The 16 sample groups had 192 individuals in May (1989), ranging from 2 to 22 individuals per group with a mean group size of 12.0. Adult females dominated most of the groups. The groups varied in composition but, on average, adult females comprised 53.7% of a group while infants, juveniles, adult males and sub-adults comprised 15.6%, 14.6%, 10.4% and 5.7% respectively. Groups with 18 individuals and above regularly divided into two groups temporarily, especially those with 2 adult males.

All groups had at least one adult female. One group (Baomo North) had no adult male, most groups

Table 2. DEMOGRAPHIC COMPOSITION OF 16 SELECTED GROUPS.

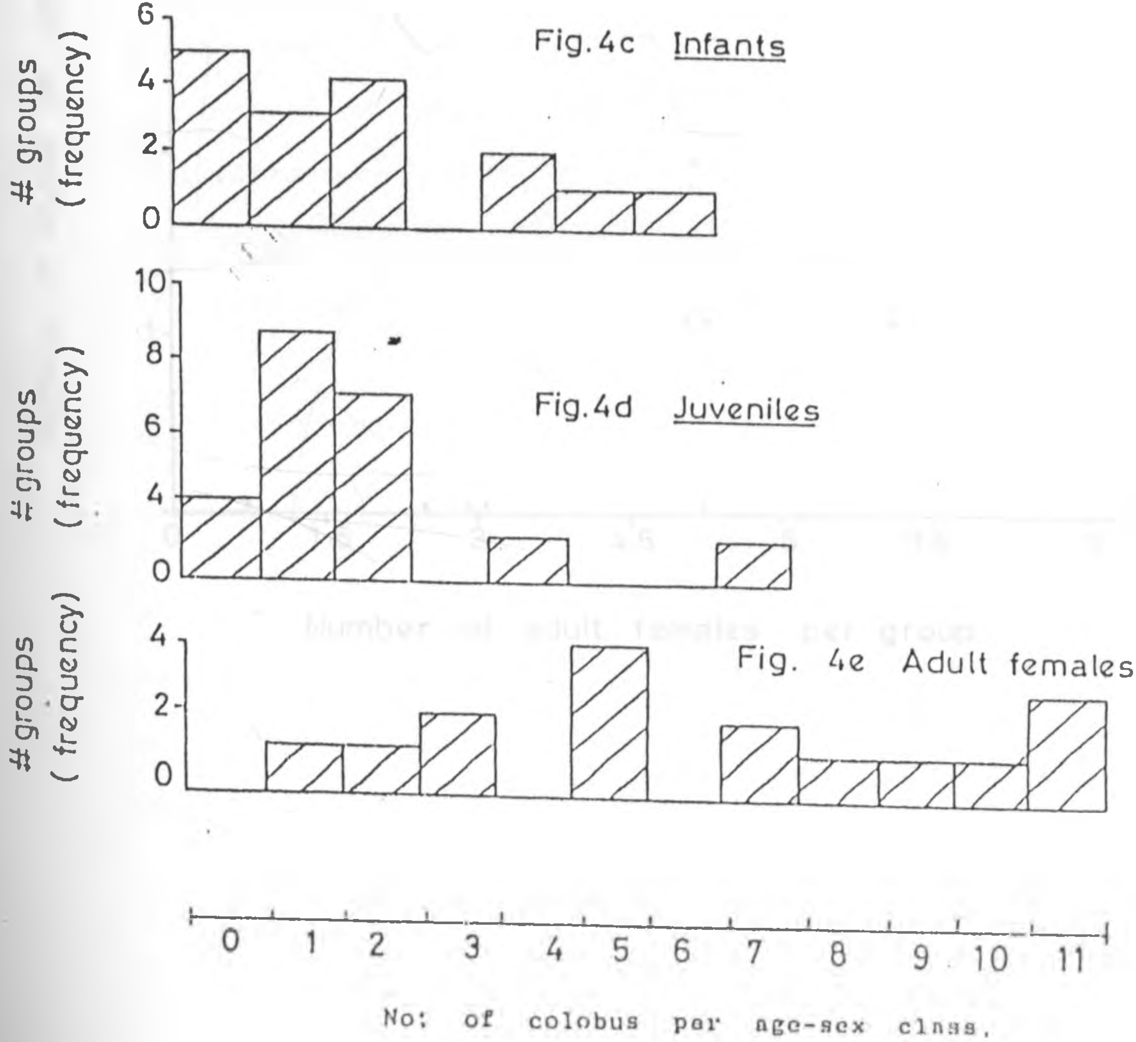
colobus	Adult		Sub-adult		Juvenile		Infants		No. colobus
group	male	female	male	female	Big	Small	Big	Small	per group
Baomo N.*	0	2	0	0	0	0	0	0	2
Bubesa A.*@	1	1	0	0	1	0	0	0	3
Maroni W.*@	1	3	1	0	0	0	0	0	5
Guru N.	1	3	0	0	1	0	0	0	5
Baomo S/2*	1	5	0	0	1	1	0	0	8
Kipende.*@	1	5	0	0	1	1	1	0	9
Mnazini N/2	1	5	0	1	1	0	1	0	9
Kitere.	1	7	0	0	1	0	0	1	10
Mchelelo W.	2	5	0	1	2	0	1	1	12
Baomo S/3	1	11	0	0	1	0	0	2	15
Makere.*@	1	8	0	2	1	0	1	3	16
Mnazini S	1	11	1	1	1	0	2	0	17
Mnazini N/1*	2	9	0	0	1	1	4	1	18
Baomo S/1	2	7	0	1	5	2	2	0	19
Guru S.	2	10	2	0	3	1	2	2	22
Congolani C.	2	11	0	1	1	1	4	2	22
TOTAL	20	103	4	7	21	7	18	12	192
Mean	1.3	6.44	0.25	0.44	1.31	0.44	1.13	0.25	12
S.D.	0.6	3.33	0.58	0.63	1.2	0.63	1.36	1	6.59
Range; Max.	0	1	0	0	0	0	0	0	2
Min.	2	11	2	2	5	2	4	3	22

.@ staying outside the Tana River National Primate Riserve.

* Groups staying near farms/villages (i.e. within about 100 meters).

(62.5%) had one adult male and 31.3% had two. There was, however, no group with more than two adult males. None of the groups with four or fewer adults had infants while all the rest except Baomo S/2 contained infants. The frequency distribution of different age-sex classes were all, except that of adult females, skewed but sample sizes were small (Fig. 4). Since there are 22 extant colobus groups and the mean group size is 12.0, the current population estimate of the subspecies is about 264. It should be noted that this is an estimate because arboreal primates like the Tana River red colobus are notoriously difficult to census because of their mobility and cryptic habits. Also, some forests, especially those in the east bank, could not be censused regularly. All other forests, particularly those containing the 16 colobus sample groups, were censused at least twice a month. The overall female to male ratio for the adults was skewed, being 103:20.

The results (Fig. 5) show that the number of infants in a group is significantly correlated with the number of adult females (Spearman rank correlation test, two-tailed, $r_s = 0.89$, df = 14, $P < 0.05$). Groups with infants have significantly more adult females per group than those without infants



groups (frequency)
6
4
2
0
Fig.4c Infants
10
8
6
4
0
Fig.4d Juveniles
4
2
0
Fig. 4e Adult females
0 1 2 3 4 5 6 7 8 9 10 11
No: of colobus per age-sex class.

Figure 4. FREQUENCY DISTRIBUTION OF DIFFERENT AGE-SEX CLASSES PER GROUP.

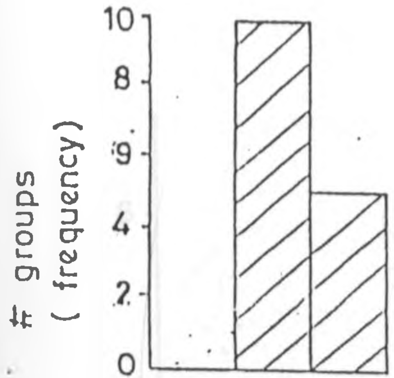


Fig. 4a Adult male

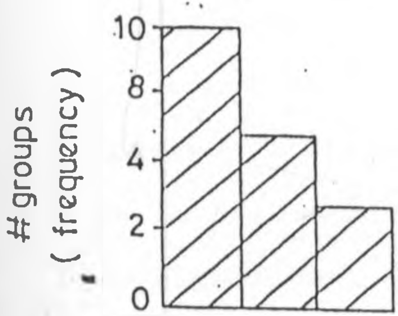
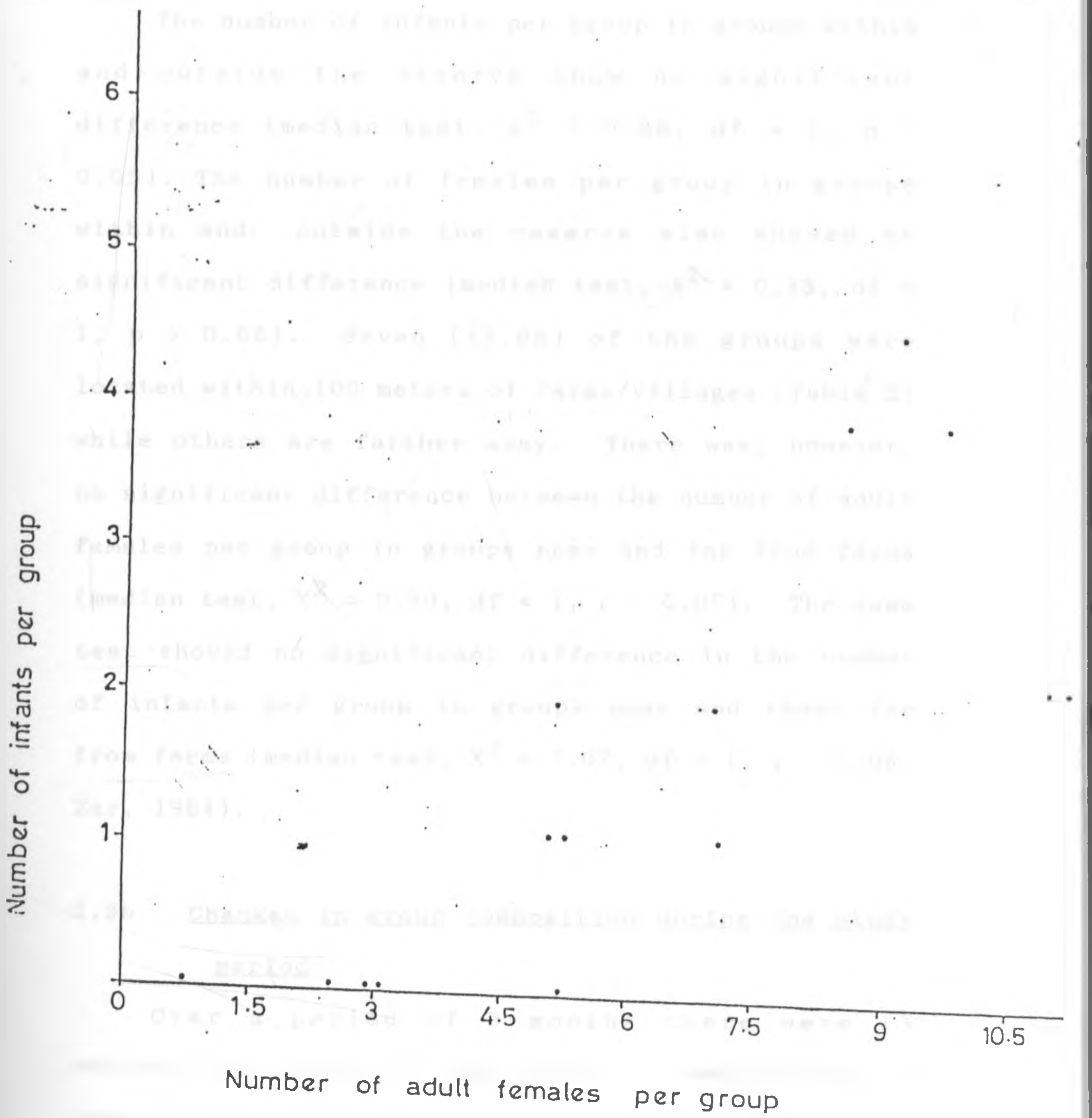


Fig. 4b Sub-adult

Figure 5 The correlation between adult females and infants.



(median test, X^2 = 4.66, df =1, P < 0.05).

The number of infants per group in groups within and outside the reserve show no significant difference (median test, X^2 = 0.86, df = 1, p > 0.05). The number of females per group in groups within and outside the reserve also showed no significant difference (median test, X^2 = 0.33, df = 1, p > 0.05). Seven (43.8%) of the groups were located within 100 meters of farms/villages (Table 2) while others are farther away. There was, however, no significant difference between the number of adult females per group in groups near and far from farms (median test, X^2 = 0.90, df = 1, p > 0.05). The same test showed no significant difference in the number of infants per group in groups near and those far from farms (median test, X^2 = 1.07, df = 1, p > 0.05, Zar, 1984).

3.3b Changes in group composition during the study period

Over a period of 9 months there were 13 maturations (change in age group), 3 emigrations, 6 immigrations, 8 births and one death (I discovered one corpse in Mnazini north forest) among 12 sample groups (Table 3). The colobus population in these

Table 3 ANALYSIS OF CHANGES IN GROUP SIZE AND COMPOSITION IN 12 SELECTED COLOBUS SAMPLE GROUPS.

Colobus group	Births	Number maturing (Age-class)	Migration		Deaths	colobus group size		% Change
			Emigration	Immigration		Initial (Sep, 88)	Final (Jun, 89)	
Baomo N	0	0	0	2(AF)	0	0	2	100
Bubesa A	0	1(SJ)	0	0	0	3	3	0
Maroni W	0	0	3(AF)	0	0	8	5	-37
Guru N	0	1(SJ), 1(SAM)	0	1(SAM	0	4	5	25
Kipende	1	1(SI), 1(BI), 1(SJ)	0	1(BI), 2(AF)	0	6	9	50
Mnazini N/2	0	0	0	0	1(AF)	10	9	-10
Kitere	1	0	0	0	0	9	10	11.1
Mchelelo	2	1(SI), 1(SJ), 1(BJ), 1(SAM)	0	0	0	10	12	20
Makere	1	0	0	0	0	15	16	6.6
Mnazini N/1	1	1(BJ	0	0	0	17	18	5.9
Guru S	1	0	0	0	0	21	22	4.8
Congolani C	1	2(SI)	0	0	0	21	22	4.8
TOTAL	8	13	3	6	1	124	133	181.2
MEAN	0.67	1.08	0.25	0.5	0.08	10.33	11.08	15.1
S.D.	0.65	1.38	0.85	1	0.29	6.87	7.03	33.7
RANGE; MIN.	0	0	0	0	0	0	2	0
MAX.	2	4	3	3	1	21	22	100

AF = Adult female, SAM = Sub-adult male, BJ = Big juvenile,
SJ = Small juvenile, BI = Big infant, SI = Small infant.

groups thus showed a net increase of 7.3%. Infants matured into the juvenile age class quickly within one year. Migrations were witnessed or inferred in only 4 out of the 12 groups. Three adult females emigrated from Maroni. Two adult females and a big infant joined the Kipende colobus group.

3.3c Detailed demographic changes of Mchelelo group

Mchelelo group was a focal group in the studies of 1973/74, 1974/75, 1986/87 and 1988/89 (Marsh, 1978; 1989 the present study). Table 4 shows demographic changes that occurred during these years. There has been a decline in the number of births, maturations, immigrations, emigrations, and deaths, recorded during the September-May period over these years. These variables have declined by 81.8%, 66.7%, 83.3%, 100% and 85.7% respectively.

Considering the data for all the census years, 83% of the colobus that emigrated from Mchelelo group were adult females. Adult males comprised only 8.3% of the 12 recorded emigrations. There were a total of 14 immigrations of which 77.8% were by adult

Table 4. DEMOGRAPHIC EVENTS AFFECTING MCHELELO COLOBUS GROUP
(During the september-may period in 1973/74, 1974/75, 1986/87 and 1988/89)

YEAR / MONTH	Births				Change of age class				Emigration				Immigration				Deaths			
	1973 to 1974	1974 to 1975	1986 to 1987	1988 to 1989	1973 to 1974	1974 to 1975	1986 to 1987	1988 to 1989	1973 to 1974	1974 to 1975	1986 to 1987	1988 to 1989	1973 to 1974	1974 to 1975	1986 to 1987	1988 to 1989	1973 to 1974	1974 to 1975	1986 to 1987	1988 to 1989
September	0	1	0	0	1	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0
October	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0
November	4	1	0	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0
December	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	1	1	0	0
January	0	1	0	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0
February	1	1	0	0	3	0	1	1	0	0	0	0	2	3	0	0	1	1	0	0
March	0	1	0	1	2	4	0	1	0	0	0	0	1	0	0	0	1	1	0	0
April	0	0	0	0	1	1	0	1	2	0	0	0	1	1	0	0	0	0	0	0
May	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	0	1	0	0	0
TOTAL	5	6	0	2	11	7	2	4	10	2	0	0	6	6	2	0	4	3	1	0
Group size*	18.9	23.1	0	10.9	18.9	23.1	8.3	10.9	18.9	23.1	8.3	10.9	18.9	23.1	8.3	10.9	18.9	23.1	8.3	10.9

1973-1975 data is extracted from Marsh, C. 1978 and 1985.
1986-1987 data is based on the results obtained during the preliminary studies by the author.
* Mean group size used because the the group size changed. It should be noted that these figures refers only to the changes that occurred in a 9 month period (i.e. September to may)
Though the study was started in 1973, data was not collected every year.

females while adult males accounted for only 7.7%. Other than sub-adults, younger age groups migrated with their mothers.

3.4 DISCUSSION

I estimated there were approximately 264 individual red colobus in this population, distributed among 22 groups with no overlapping home ranges (pers. obs.). The size and demographic composition of these groups varied in time and space. Various instrinsic and environmental factors might have been the proximate causes of these variations, for example, the size of forest, tree density and species diversity per forest, competition from other primate species including man and the initial number of potential breeders per forest (see chapter 4). Baomo South, for example, is larger (220 ha.) than Guru North forest (6.5 Ha.). In addition, these two forests have different floristic compositions, with *Pachystela brevipes* being numerous in Baomo South forest while *Ficus sycomorus* is plentiful in Guru North. Also, forests to the north of, and including, Guru South have *Cynometra lukei* while the majority of those to the south lack it. All these are major colobus food sources and may therefore affect the distribution of the colobus (pers. obs.).

The number of potential primate competitors also differ in different forests. Mangabey monkeys, for example, are not found in some of the forests such as Guru North, Makere and Kipende. Although the majority of local people depend entirely on firewood for cooking and timber for building, some forests, like Kipende, are subjected to higher rates of tree felling than others, like Baomo South forest (pers. obs.). It is interesting to note that Kipende Forest had most of the immigrants. This may be because there are comparatively more plant species, like Cynometra lukei, which the colobus prefer in Kipende forest than in Guru N. forest. These are some of the environmental variables that may account for variation in the colobus group size, which ranged from 2 to 22 individuals per group, and age-group/sex ratio composition. Possible intrinsic factors that may also play a role include the genetic constitution which helps to determine the intrinsic rate of birth and the initial number of potential breeders in the group. For example, it was observed that none of the four colobus groups with less than a total of 4 adults (groups living in Baomo N., Bubesa A., Maroni W. and Guru N. forests, Table 2) had infants. This may suggest that 4 adults per colobus group could be a threshold value of adults per group below which survival of infants or reproduction is uncertain. The fact that groups with such small number of adults are found in forests that are small in size, lack certain tree species preferred by colobus and/or are long and thin in shape (like Guru North and Maroni West) imply that the threshold value of four may also be taken as an indicator of the quality of the habitat for colobus habitation.

On the other hand, colobus groups with more individuals, particularly those with 9 or more potential (adult) breeders, and especially those with 2 adult males, tend to divide frequently into two distinct one-male groups when foraging. All groups with two adult males tended to show this temporary splitting including those with fewer individuals like Mchelelo group. The groups staying in Mnazini North, Baomo South, Guru South and Congolani Central forests, for example, occasionally divide when they are foraging but join again in the evening (pers. obs.). Small groups with 2 adult males, like the Mchelelo group, differed from large groups with two adult males because the former tended to divide less frequently. A possible deduction from group-splitting is that large group size and/or more than one adult male per group are some of the precursors for the formation of more harem groups. In groups that are small in size, such fissions may be less frequent because there is not much space for new home ranges (such groups occur in small forests like Mchelelo, which is only 14 Ha.) while large groups occur mainly in large forests where there is enough space. The number of surviving groups, apparently, has stabilized within the past four years. The current population estimate of about 264 compared to the 1985's population estimate of about 250 shows that the population has not changed much since then. There are problems with comparing mean group size in these years because the sample size used in 1985 was small (six groups only) compared to 1989 (sixteen groups). Whatever the case, the population seems to have stabilized or grown since 1985. The original population decline between 1975 and 1985 was thought to have been caused by either the 1984 drought, presence of a contagious diseases and/or human influence including interference with the Tana River's flooding regime (Marsh, 1985). The gazetting of the reserve in 1976 (Marsh, 1976) and/or gradual development of immunity to the contagious disease, if it was there, may have accounted for the current stability or growth of the population. Increases in the relative proportions of infants and juveniles (combined) from 1985 to 1989 may also have been due to these reasons.

The fact that different groups have different age-class composition suggests that different forest patches offer optimal condition for different age-classes. The forests, however, were sampled for only nine months. Such a study requires a much longer period. Some forest patches like Guru North are comparatively poor in plant species ause they lack certain tree species used by colobus, for example Pachystela brevipes. (pers. obs.). It is possible that this may lower the forest's carrying capacity, by not providing all the required compounds for reproduction or survival of infants. Comparatively "poor" forests like Guru North, thus, seem not to offer suitable conditions for infant survival.

Adult females occur in almost all groups while sub-adults of either sex seem to be rare in most groups; however there may be some misclassification since differences in adult and sub-adult size may be confused with differences in male and female body sizes in less-habituated groups. The overall adult sex ratio is skewed, the adult female to adult male ratio being 103:20, yet according to the literature (Marsh, 1978) the infant sex ratio is 1:1. Whatever happens to males is still, at best, a matter of conjecture. There may be comparatively high mortality rate among males, but no male corpses were discovered during the 9 month study. Alternatively, more males may be forced to become solitary because of the harem social structure of the species. Since such solitary males are difficult to detect in large forests, probably some may have been missed. The colobus is a quiet species and the only solitary male that was sighted in this study was easily traced since it stayed in an isolated farm where farmers saw it and notified us. Solitary males were seen by Marsh (1978).

The number of infants and juveniles (combined) per group is positively correlated with the number of adult females per group (Spearman rank correlation test, two tailed, $r_s = 0.78$, df = 14, $p < 0.05$). This shows that the total number of potential breeding adults per group is the determinant of the absolute potential growth of the group. The composition of a group also affects the potential for an increase in population size. For example, the two individuals living in Baomo North were adult females.

Unless an adult male joins them, or they migrate to another group with an adult male, there is no way they can reproduce. Few individuals and the absence of one sex may thus constitute a bottleneck for population growth.

The fact that there is not much difference in mean group size and composition between colobus groups within the reserve and those outside the reserve suggests that the reserve forests, currently, offer no advantage to the colobus over forests outside the reserve. This may be because farms and villages are found both within and outside the reserve, and all forests are easily accessible to man. All forests may not be easily accessible to the colobus due to such barriers as the river, farms and villages. Migrations, births and deaths could have been underestimated because it is difficult for two people to monitor 16 colobus groups simultaneously. An individual colobus, for example, may emigrate from a group and be replaced by an immigrant between censuses. An infant also may die soon after birth before its presence has been noted. Tracing a dead monkey in a forest as big as Baomo South forest (220 Ha.) is very difficult. This study was carried out for nine months. Monitoring of demographic variables should be continued for a longer period, to come up with more accurate demographic estimates for this long-lived species (colobus may live for about 30 years, Cheney et al., 1987).

CHAPTER 4 COLOBUS NUMBERS AND HABITAT VARIABLES

4.1 INTRODUCTION

Environmental variables considered here include forest patch size, tree species diversity and density per forest, inter-forest distances and the distribution of villages and farms. All these factors may directly or indirectly account for the distribution and demographic composition of colobus groups. Plant species along the Tana River produce fruits and/or young leaves, which are the colobus major food source (Marsh, 1978), in a synchronous and/or asynchronous pattern depending on the species (Appendix A). Different plant species therefore provide the colobus with food at different times or seasons. This suggests that a good environment for the colobus would be one where there are many edible plant species. The density of each species utilized should be high to reduce intraspecific and interspecific competition. The ideal structure and arrangement of reserves and parks, based on the principles of island biogeography theory (Simberloff, 1988) are compared with the actual structure and arrangement of the forest patches found in Tana. The aim is to determine to what extent the Tana forest refuges differ from the ideal or optimal conditions and suggest, where possible, alternative strategies that may be adopted to make the environment more suitable for the rare and endangered colobus endemic to this region (Marsh, 1978). The gallery forest patches found on either side of the river are thus likened, or taken to be analogous to "islands" or refuges (MacAurther and Wilson, 1967) suitable for colobus habitation in a "sea" of unsuitable areas. Such unsuitable areas include farms, villages, open woodland, grassland, and bush (Marsh 1976, 1978, 1985).

An endangered species like the Tana red colobus may be absent from certain habitats for any of the following reasons: either it cannot reach a patch because of geographical and/or man-made barriers like the Tana River, villages or farms, or it had colonized the habitat but died or emigrated, or it may not have made any attempt to colonize them. Also the population pressure may not be great enough to encourage emigration and/or colonization of other forests.

According to island biogeography theory (MacArthur and Wilson, 1967; Cox and Moore, 1985; Simberloff, 1988), species richness of a forest patch may depend on its size, shape, distance from a source of potential colonists and the number of species present in source areas. The species already present in a forest patch are also important since some may be potential competitors with colonizers. Large forests may have more plant species than small ones. This is because large forests are comparatively more resilient to disturbances and also may provide a large colonizing target (Western, 1984). Forests close to the source of colonists may have more species than remote forests because closeness may facilitate immigration that redresses local extinctions that may have been precipitated by environmental vagaries (Simberloff, 1988). This may affect the colobus directly, or indirectly, if for example a favored food source like Ficus sycomorus disappears in certain forest refuges.

The shape of forest refuges may also affect the number of species in it. An optimal shape would be circular which is thought to be far better than a long thin refuge of the same size (Simberloff, 1988) although this also depends on other factors like the nature of the soil and whether the resident species are competitors. It would also be easier, for example, for predators to track down colobus in long thin forests than in circular forests of the same size. Although large forests are better refuges due to their comparative resilience to disturbances (Western, 1984), there are advantages in having many medium-sized forests instead of one big one of the same size. If there is a catastrophe like an outbreak of a contagious disease or fire, some groups in isolated forests may survive (Cox and Moore, 1985).

Such isolated medium-sized forest refuges, however, may be inhabited by many groups that constitute a metapopulation consisting of subpopulations with minimum interactions among them (Simberloff, 1988) especially if there are physical and/or man-made barriers. Such limited migration among groups may lead to inbreeding depression and genetic drift, which can be avoided by reducing the distances between refuges or occasionally translocating some breeders. The linear arrangement of forest patches limits possible migratory routes to only two directions. It is better if such forests are distributed in such a way that the monkeys can migrate in any direction.

4.2 METHODS

Inter-forest patch distances were estimated from aerial photographs (Marsh, 1985) of the Tana habitat and also by driving, where possible, between adjacent forests while measuring the distance using a car's odometer. The area of each forest patch was determined by laying a transparent paper, with one-hectare squares drawn on it, over the aerial photographs and counting the number of squares within each forest. Adjustments were made for forests that had been cleared for farming since the photographs were taken. The spatial arrangement or pattern of forests was determined from both the photographs and by driving and/or traveling along the Tana River in a canoe.

Tree species diversity and density for each forest was estimated using Point-Centered Quarter (P.C.Q) methods (Mueller-Dombois and Ellenberg, 1974). P.C.Q. methods were only applied to forests located outside the reserve because data for forests within the reserve were available from earlier studies. Plant species diversity was quantified based on the index "Evenness" as elaborated by Zar (1984). This, however, is only one aspect of diversity.

4.3 RESULTS

The area of forests, number of canopy tree species (those equal to or greater than 10 meters tall), tree species evenness and density, and the number of colobus per forest were highly variable (Table 5). The 192 individual colobus (72.7% of the censured population) lived in 16 distinct groups in 13 different forests ranging in size from 4.5 to 220 Ha. The total number of red colobus per forest did not correlate significantly with plant species evenness (Spearman rank correlation test, $r_s = 0.11$, d.f.= 11, $p > 0.05$). Most of the plant species considered were those important to the colobus as a food source and/or provided shelter for them. The number of colobus per forest patch and the density of trees in the forests were not correlated (Spearman rank correlation test, two tailed, $r_s = 0.43$, d.f.= 11, $p > 0.05$). Forest size was the only environmental variable that correlated significantly with the number of red colobus per forest (Spearman rank correlation test, $r_s = 0.78$, df= 11, $p < 0.05$). The mean colobus density per forest was 0.5 ± 0.26 individuals per hectare (approximately 0.0051 colobus per sq. km., Table 5). Baomo South was the largest forest. All other forests inhabited by the colobus

Table 5. FOREST HABITAT VARIABLES.

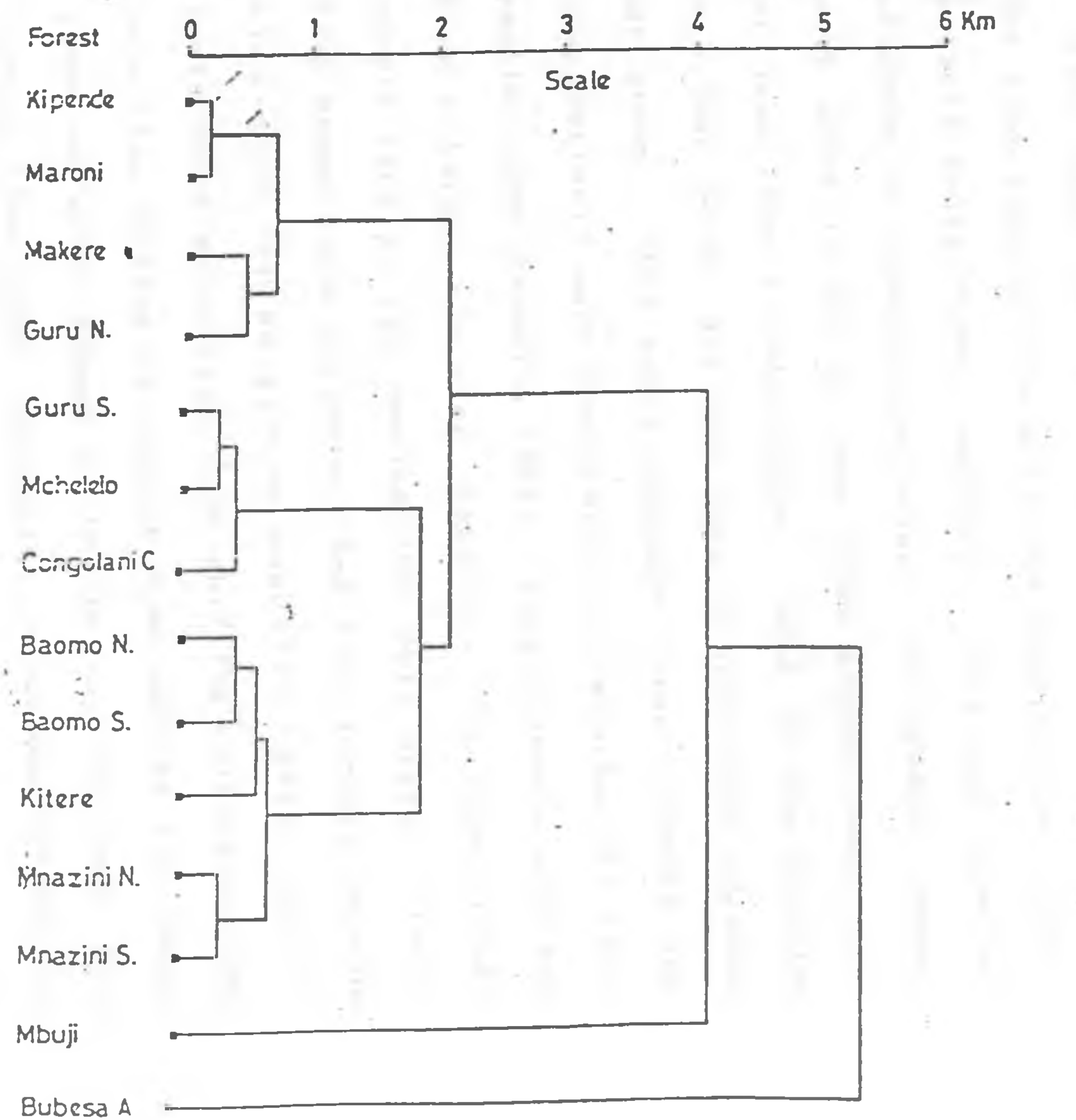
Forest	Forest size	Tree No. species	Tree Density/Ha.	Diversity index (Evenness, J')	Total Colobus per forest	Colobus density/Ha
Baomo N.	21	17	37.1	0.83	2	0.09
Bubesa A.	4.5	8	14.7	0.66	3	0.67
Maroni W.	27	9	18	0.51	5	0.19
Guru N.	6.5	16	21.3	0.92	5	0.77
Kipende.	21	13	107.6	0.42	9	0.43
Kitere.	12	12	66.3	0.52	10	0.8
Mchelelo W.	14	26	42.3	0.78	12	0.86
Makere.	48	8	138.5	0.31	16	0.33
Mnazini S.	36.5	23	69.6	0.75	17	0.45
Congolani C.	32	31	38.2	1.28	22	0.69
guru S.	45	25	34.5	1.51	22	0.45
Mnazini N.*	38	13	58.7	0.62	27	0.7
Baomo S.*	220	25	64.2	0.75	42	0.19
TOTAL	526.5	...	...	...	192	...
Mean.	40	17.1	54.7	0.76	14.8	0.51
S.D.	55.7	8.38	35.9	0.33	11.4	0.26
Range; Min.	4.5	8	14.7	0.31	2	0.09
Max.	220	31	107.6	1.51	42	0.86

* Forests with more than one colobus group.

were not more than one quarter the area of Baomo S. Although there were approximately 62 canopy tree species within the 52 km geographical range of the colobus (Appendix A), each forest contained, on average, only 17.1 + 8.4 species. Evenness ranged from 0.31 to 1.51. Inter-forest distances, which could affect the ease of migration, varied from 0.1 km to 5.25 km. (Fig. 6).

The shapes of forests also varied, and only about 1/3rd tended to be circular. The rest were comparatively thin and long such as Kipende, Guru North and Maroni Forests. Forest patches line either side of the Tana River (Fig. 3). Potential barriers found between adjacent forest patches included villages, farms, grassland, woodland and the river (pers. obs.).

Fig. 6 Dendogram showing hierarchical cluster analysis of inter-forest distances



4.4 DISCUSSION

This study has shown that environmental factors like tree species diversity and density are highly variable among forest patches. This may have an influence on colobus population. For example, Baomo South which is 220 Ha. has three groups, each with not less than 8 individuals. None of the forests less than 30 Ha. has more than 12 individual colobus per group. This may be because larger forests are comparatively more resilient to disturbances than smaller ones (Western, 1984). Large forests also may have a larger carrying capacity. In Tana, local people tend to fear moving deep into bigger forests like Baomo South believing that such forests provide hide-outs for dangerous poachers (pers. obs.). Destructive activities, like shifting cultivation and selective felling of certain tree species for canoes (some of which happen to be the colobus' main food source, like Ficus sycomorus), which may disrupt the structure and function of forests, are restricted to the periphery.

Smaller forests like Bubesa A. and Guru North, on the other hand, have few colobus per group probably because such forests are more sensitive to human activities and are easily penetrated. The major food sources for colobus like Ficus sycomorus and Pachystela brevipes have disappeared from these two forests (Bubesa and Guru North, respectively) due to logging for construction of canoes and paddles. Interspecific interactions may be important in small forests, such as Mchelelo, that happen to contain many primate species including baboons, mangabeys, colobus and Syke's monkeys. Small forests may also promote 'interference' (direct) competition; depending on the densities of interacting species. For example, at Mbuji forest the solitary colobus is occasionally attacked by baboons (pers. obs.). Different primate species also utilize similar resources, for example, fruits of Garcinia livingstonei in Guru North by colobus, baboons and Syke's monkeys. Interspecific interactions, however, are not always competitive (May, 1984). In Tana, for example, Syke's monkeys occasionally groom the colobus (pers. obs.). The reverse, however, was never observed. Also the Tana primate species show mutual dependence in the detection of intruders. In fact in this respect, even pigs, duikers and bushbucks interact with primates.

As opposed to the predictions of island biogeography theory, the number of tree species in

Tana do not increase significantly with increases in forest size (Spearman rank correlation test, $r_s = 11$, d.f. = 11, $p > 0.05$). This may be due to the dynamic nature of the environment. The river occasionally changes its course (Homewood, 1975) and this disrupts plant succession at various seral stages and even promote retrogression and forest senescence. Tree species richness may depend more on the age of the forests. Selective felling of certain tree species may also play a significant role (Marsh, 1976). It is also possible that the number of plant species does not increase with an increase in forest size because only trees equal to or greater than ten meters in height were studied. Inclusion of other physiognomic life forms may have resulted in a different relationship.

Most forests in Tana are narrow, the width being restricted by water availability which, in turn, closely follows the river course (Homewood, 1974). Forests conforming to the presumed optimal circular shape (Simberloff, 1988) are thus few. Water availability tends to decrease with an increase in distance from the river, with the exception of outlying oxbow lakes and smaller lakes like Pongi, near Mchelelo forest. Although some plant species are ecotonal species that may do better if forests are thin and long, the Tana River red colobus, apparently, rarely feed on such species (pers. obs.). More trees should be planted to enlarge smaller forests because, for example,forests like Guru North are so narrow that the few (five) colobus living there can hardly hide themselves from intruders. Their escape/migratory routes are restricted to only two directions, i.e. upstream or downstream. To date, there is no evidence that the colobus can swim across the Tana River which has numerous predatory crocodiles, which commonly catch prey (e.g. men) at the river's edge.

The Tana colobus live in 22 groups in isolated forests on either side of the river. The degree of isolation, however, varies. Isolation of forest refuges can be beneficial in cases where there is an outbreak of a contagious disease or fire. In some case, however, the isolation is so extreme and inter-forest distances are so large that there is little migration (Fig. 6). Mbuji forest, for example, is over 5 km from Mnazini South, the neighboring forest, where there are 17 colobus. At Mbuji, there is one solitary adult male colobus which, according to local farmers, has been living in isolation for the past 9 years. One may logically consider this monkey genetically dead, unless he is translocated into a group of colobus. This may prove difficult because the owner of the farm considers the male colobus as his property.

The isolation of groups, or subpopulations, of the Tana red colobus metapopulation may promote genetic drift and inbreeding depression if inter-group migration, or gene flow, is limited. This may be avoided by creating "corridors", through a re-afforestation program, connecting some forests like Maroni and Kipende, or reducing the gap between forests like Guru North and Makere.

Re-afforestation, however, may necessitate eviction of people from farms, e.g. the farms between Mnazini North and Mnazini South forests, both of which are located inside the "Tana River Primate Reserve". In certain forest, for example Kipende, the colobus are actually harassed by young boys who throw stones at these monkeys.

CHAPTER 5. EFFECTIVE POPULATION SIZE

5.1 INTRODUCTION

Determination of the Tana red colobus' minimum viable population size is difficult because it depends on myriads of genetic, demographic and environmental factors (Simberloff, 1988). Most populations are composed of different age-sex classes some of which are not reproductive. Those that can reproduce contribute to an effective population size which is smaller than the actual population.

The effective size of a population (N_e) is the number of individuals in an ideal population that would undergo the same random genetic drift as the actual population (Lande and Barrowclough, 1987.). An ideal population is that in which the sex ratio is 1:1 and all individuals have equal chances of mating and reproducing (Falconer, 1982). Such a population constitutes the maximum possible effective population especially if there is no variance among individuals in the progeny produced (Lande and Barrowclough, 1987). The ideal population, however, is extremely unusual among primate species. The Tana River red colobus, for example, is a polygynous species (Marsh, 1987). Although both sexes contribute equally to the genes in the next generation in such a breeding social structure (Falconer, 1982), the dominant male contributes more genes than any individual female in his harem. This is because he has access to many females and once a female becomes pregnant, she is sexually unavailable during the gestation period (Krebs and Davies, 1987). The males, therefore, show large variability in the number of progeny produced compared to the females (Lande and Barrowclough, 1987).

As a rule of thumb, effective population sizes of 50 and 500 individuals have been considered, in conservation and management circles, to be the minimum required to avoid inbreeding and loss of genetic diversity by drift respectively (Falconer, 1982; Harris et al., 1984; Lande and Barrowclough, 1987; Simberloff, 1988). The number "50" is based on the experience of breeders of domestic animals which has shown that an increase in the inbreeding coefficient (F), which measures the rate of loss of heterogeneity due to inbreeding, up to 1% for a few generations is the maximum tolerable. Above this level, some deleterious effects of inbreeding may become apparent (Falconer, 1982). Since F increases at a rate that approximates $1/2N_e$ per generation, where N_e is the effective population size, this gives a minimum N_e of 50 individuals over one generation (Harris et al., 1984).

The number "500" refers to the N_e required to maintain polygenic traits and is based on the finding that mutation cannot compensate for a loss of genetic variation exceeding 0.1% per generation (Harris et al., 1984; Lande and Barrowclough, 1987).

A species whose range is composed of isolated patches interconnected through migration and gene flow is called a metapopulation, consisting of several subpopulations (Lande and Barrowclough, 1987). The Tana river red colobus conforms to this definition, showing an almost linear distribution of groups (subpopulations). This predisposes the species to the development of spatial inter-group genetic variation. Under such circumstances each subpopulation or group may eventually acquire specific gene combinations and hence some or all of the subpopulations may have different alleles. The magnitude of such spatial (inter-subpopulation) genetic heterogeneity depends on the subpopulations' sizes, their relative isolation and the geographical range of the colobus (Gilpin and Soule, 1986). This magnitude may be estimated using Malecot's formula once the number of such subpopulations and the effective population size are known (Lande and Barrowclough, 1987). This is an important measure of the genetic diversity of the metapopulation.

5.2 METHODS

Determination of the current effective population size, N_e, of the Tana River red colobus is based on the formula below which corrects for unequal sex ratios (Falconer, 1982; Harris, 1984).

$$N_e = \frac{4Nm\,Nf}{Nm + Nf}$$

Where N_e = The effective population size.

Nm = The number of adult males.

Nf = The number of adult females.

This formula is based on the assumptions that all adults are capable of reproducing while other age-groups cannot and that the generations are discrete, mating is random and the population is closed. The effects of violation of these assumptions are considered in the discussion.

According to Falconer (1982), once the effective population is determined, the rate of inbreeding (F, or inbreeding coefficient) can be estimated using the following formula:

$$F = 1/2N_e$$

The main assumptions involved in this estimation are that there is no mutation, selection or migration, and that mating is random. Although the colobus population may not meet all these assumptions, particularly random mating because of their social structure, this model may help in establishing a range of values of inbreeding coefficients (F). Since the Tana River red colobus groups are isolated, the formula advanced by Malecot (Lande and Barrowclough, 1987) can be used to determine whether the entire population constitutes one panmictic unit.

If $M > (nN_e)^{0.5}$, then the population is a panmictic unit.

Where M = the number of migrants per group per generation.

n = the number of such groups.

N_e = the effective population size of each group (equivalent to the harmonic mean of all group sizes).

It should be noted that violation of assumptions does not mean that models are useless but it is important to understand the effects of such violation on estimates.

5.3 RESULTS

5.3a. Effective population size

The results (Table 2) show that there were 20 and 103 adult males and females, respectively, in the 16 sampled groups (which contained 72.7% of the living colobus). Therefore; using Falconer's (1982) formula, N_e is 67. This indicates that the sampled population with 123 adults is equivalent, in terms of the loss of genetic variation by drift, to an ideal population of 67 monkeys. In addition to the general assumptions outlined above, it also assumes that only the 20 sighted adult males, and none of the solitary males that may have existed, will contribute to the next generation.

The effective population size (N_e) of 67 refers to a sample population of 192 individuals. The current red colobus metapopulation is about 264. Apparently, adult males and females constitute approximately 10% and 54% respectively, of the population. Therefore, a metapopulation of 264 has about 28 and 142 adult males and females respectively. Using these numbers, N_e for the whole population would be 94 individuals. Thus the effective population size amounts to only 36.4% of the colobus metapopulation.

If the colobus population was an ideal one in which the sex ratio is 1:1 and all individuals had the same chances of reproducing, then the effective population would have been equal to actual size. Thus if we assume a 1:1 sex ratio, with Nf = 142 for the entire population, Nm would also equal 142 and Falconer's formula would give Ne = 284. This is equivalent to assuming that there are well over a hundred unsighted adult solitary males which would contribute to the next generation. This represents the maximum possible effective population size. Comparison of N_e based on the actual polygynous social structure of the colobus (N_e = 94) with that based on an ideal (N_e = 284) situation show that the former N_e is smaller than the latter by 67%. Therefore, the actual colobus' effective population size (N_e) is most likely to be between 94 and 284 but probably near 94 since this is a polygynous species.

5.3b <u>Rate of Inbreeding</u>

The rate of inbreeding (F) can be estimated once the effective population is known using the formula;

$$F = \frac{1}{2N_e}$$

For the Tana red colobus population of 264 (N) whose effective population (N_e) estimate is 94 (subject to the validity of the assumptions mentioned earlier);

$$F = \underline{0.0053}$$

If this population was an ideal one, in which case N_e would be 284, then;

$$F = \underline{0.0018}$$

The 0.0018 is the minimum rate of inbreeding possible for the colobus. The actual rate of inbreeding therefore may be between 0.0018 and 0.0053, but social behaviors such as dominance and migration, which ensure outbreeding may result in lower rates.

5.3c Panmicity of the population

Table 3 shows that there were 6 migrants (i.e. the immigrants) among the 12 sample groups within 9 months. This gives 0.67 migrants per group per year. Assuming that the red colobus' longevity is 30 years (Cheney *et al.*, 1987), then each group exchanges about 20 of its members (migration) with other groups per generation (M = 20, a generation may last for 30 years as mentioned before)

For the 12 sampled groups;

n = 12

Ne = 7, taking Ne to be the harmonic mean of all group sizes.

M = 20

$(nNe)^{0.5} = 9.2$

Therefore M (20) is greater than (nNe), suggesting, subject to the validity of the assumptions, that these groups may constitute a panmictic population.

5.4 DISCUSSION

Determination of the Tana River red colobus' minimum viable population is theoretically important if appropriate conservation measures are to be employed. The actual population of such an endangered species may be large but, from the genetic point of view, the most important demographic variation that should be known is the effective population size. Adaptability is conferred on the species by genetic diversity, which depends on the effective population size, the kind of genetic variation, natural selection and mutation (Harris et al., 1984) and environmental changes. This implies that there is a minimum population size below which the population will experience loss of genetic diversity unless appropriate conservation and management strategies are adopted.

As noted in the introduction, the minimum viable population size may be very difficult to determine because it not only depends on genetic factors but is also influenced by a myriad of demographic and environmental factors (Simberloff, 1988). There are various aspects of genetic variability which confer adaptive flexibility. These include the proportion of loci in the colobus population that are polymorphic, the number of different alleles at these polymorphic loci and the average level of heterozygosity per individual in the colobus population.

According to recent developments in conservation biology, effective population sizes of 50 and 500 have been suggested as the minimum below which probabilities of inbreeding and genetic drift, respectively, are very high (Western, 1984; Gilpin and Soule, 1986; Lande and Barrowclough, 1987; Simberloff, 1988). These two population sizes, although still controversial, have been accepted and raised to the status of rules for conservation and management purposes (Salwasser et al., 1984, Simberloff, 1988). Both inbreeding and drift reduce genetic diversity and hence adaptability. The results of this study suggest that the colobus' effective population size is about 94 individuals. This constitutes only 36.9% of the whole population which is about 264. The polygynous social structure of the species contribute to the low effective population size since it lowers the ratio of reproductive males to females. Although the infant's sex ratio has been found to be approximately 1:1 (Marsh, 1978), the adult sex ratio is highly skewed. It is, however, possible that some solitary males could have been missed in the censuses. The colobus' effective population of 94 suggests that, at least, this endangered subspecies endemic to the Tana gallery forests has not reached high levels of inbreeding. In fact this study suggests that the rate of inbreeding is very low, being between 0.2% and 0.5%. These estimates are below the 1% level that is regarded as the maximum tolerable for short term maintenance of genetic diversity. The effective population size, however, is very low compared with the minimum required to maintain polygenic single-locus genetic diversity for a long time (Harris *et al.*, 1984; Lande and Barrowclough, 1987).

The subdivision of the population into 22 groups seems not to affect migration among some groups as indicated by the previous panmicity test. In fact such fragmentation of a metapopulation into isolated refuges minimizes drift (Lande and Barrowclough, 1987). In some cases, however, isolation is so extreme that it is doubtful whether the individuals can interact with adjacent groups. Such isolation is worsened by various geographical and/or man-made features like the Tana River, villages, farms and open grassland. Such isolation may lead to the "Allee effect" whereby there is a decreased reproductive potential not because of any genetic effect but due to the difficulty of finding a mate (Simberloff, 1988). The groups in Mnazini E. and Mnazini N. forests are separated by the Tana River and it is probable that the river acts as a complete barrier to migration between them.

CHAPTER 6. CONSERVATION AND MANAGEMENT OF THE TANA RIVER RED COLOBUS

6.1 DEMOGRAPHY AND POPULATION GENETICS

This study suggests that this colobus population of about 264 out of which only about 94 individuals (35.6%) constitute an effective population, is too small to maintain polygenic traits. Maintenance of such traits requires a minimum effective population of at least 500 individuals (Gilpin and Soule, 1986; Falconer, 1982; Harris et al., 1984; Lande and Barrowclough, 1987). The species, therefore, is still endangered because such a small population is more susceptible to genetic drift and fixation of certain polygenic traits in the population and also any environmental changes or disease could wipe out the population. A trait, for example, that may provide a visible marker for loss of polygenic variation is harelip. The male harem-holder of the Mchelelo group, for example, had a harelip during Marsh's study between 1973 and 1975 (Marsh, 1978). During my work in the field (1986-1989, including 7 months of preliminary study) the group was still led by a male with a harelip (possibly the same male).

Another harelip male is suspected to be in Mnazini forest. There is clear evidence that, in humans, harelip has a genetic component (Clarke, C.A., in litt., pers. comm. Gordon, I.J.). The incidence of harelip in the red colobus should be closely monitored in future studies.

Demographically, such a small population is susceptible to stochastic pertubations, like an outbreak of a lethal contagious disease, that may cause local extinction (Foose et al., 1987). In fact one of the hypotheses advanced to account for the tremendous decline of the colobus population from 1975 to 1985 is that there might have been an outbreak of such a disease (Marsh, 1985). A study should be conducted to check the possible presence of a disease or parasites that may lead to further population declines. Fecal samples should be collected from different groups to monitor changes of parasite loads in time and space.

Although the colobus population is too low to maintain diverse polygenic traits, the current rate of inbreeding may still be within genetically-tolerable levels. This is because the effective population of 94 individuals is above the 50 considered to be the minimum (Harris et al., 1984) below which inbreeding depression may set in (Falconer, 1982). Caution, however, should still be taken because the effective population is subdivided into 22 groups and inter-group migration, and hence gene flow may be restricted. Geneticists should conduct a study on the metapopulation to determine whether there is any level of fixation of alternate alleles among isolated groups. A possible technique that could be used in such a study is the 'tissue dart method' (Gordon, pers. comm.).

In some cases, it is advisable to translocate the colobus, especially those that are completely isolated, like the lone adult male in Mbuji forest, or those in comparatively poor forests (forests that are small and have only a few tree species most of which are not the major colobus food), like Babesa A. forest. The solitary male in Mbuji forest, for example, may be translocated to Baomo North forest where there are only two adult females. To facilitate gene flow across the Tana River, it may be helpful to exchange adult females among different groups, for example between Mnazini North and Mnazini East. The colobus groups in Maroni and Kipende forests may be translocated to Wenje East forest which is large and has numerous tree species. A study should, however, be carried out to determine the effects of translocation on the social structure of the colobus groups. The main problem that may face those trying to translocate the colobus is trapping. The monkeys are shy, difficult to habituate and spend most of their time in the canopy of tall trees like Sterculia appendiculata, especially in the presence of people. During this study, I witnessed colobus walking on the ground on three occasions only. Proposed studies, if possible, should be conducted simultaneously to minimize handling of the colobus.

Another aspect of colobus demography that needs more attention is the cause of the highly skewed adult sex ratio. There are more adult females than males despite the fact that the infant sex ratio is approximately 1:1 (Marsh, 1978). There may be more solitary males, but detecting them requires techniques that may not have been used in this study. Probably the males have a higher mortality rate but the three colobus that died during my stay in Tana (including the preliminary study) were all females. Occasional distribution surveys and population sampling should be carried out to evaluate the status of this species (Brockelman and Ali, 1987).

6.2 HABITAT AND PROBLEMS CAUSED BY PEOPLE

Environmental variables like forest size and the density of the plant species that the colobus prefer may influence the distribution of the colobus. The colobus, for example, may favor forests with high densities of food like *Ficus sycomorus*. Bubesa A. forest, for example, which has an area of about 4.5 Ha., has only 3 colobus while Baomo South forest, with an area of 220 Ha., has 42 colobus. Most forests are located near villages/farms and, unfortunately, some of the current methods of land use, practised both within and outside the reserve, are not compatible with conservation of the endangered colobus and their gallery forest habitat. Shifting cultivation and selective cutting of trees by the Pokomo people, for example, reduces forest area. Browsing and grazing by domestic animals, and burning of grass by the nomadic Orma pastoralists, maintain and/or increase the size of grassland and secondary forests at the expense of primary forests. This leads to changes in the composition of the primate community in favour of species like the baboons which are adapted to open land and secondary forests (Marsh *et al.*, 1987).

Habitat modification and/or destruction has been found to be the major threat to wild populations of non-human primates (Marsh, 1976; Myers, 1979; Marsh, 1985; Mittermeier, 1987). To maintain species diversity of the Tana River ecosystem, there is a need for concerted action and genuine cooperation to safeguard the environment by regulating land use. Maintenance of such diversity is based on the principle that no known species, like the red colobus, should be forced to extinction by human encroachment (Happel et al., 1987). The local people point out that more forest damage was caused by elephants than by humans before poachers reduced elephant numbers. With no elephants and more people, most forests are still undergoing qualitative and quantitative depletion at high rates, especially those near farms like Kipende, Maroni and Mnazini forests (pers. obs.). Such degradation and impoverishment of the forests may reach an extent that recovery may be difficult (Myers, 1987) as is the case with Bubesa A. forest. The shrinkage and fragmentation of forests, like Guru which is now split into two small forests necessitates conservation of the existing forest patches (Marsh, 1976, 1978, 1985). Fragmentation and shrinkage of the forests should be stopped because, according to island biogeography theory, reduction of the total area of such an ecosystem reduces species diversity (MacArthur and Wilson, 1967). The plant species that may be eliminated may be the main food source for the colobus like Albizia gummifera, Ficus bussei and Ficus Sycomorus. The Mnazini North forest, for example, is gradually losing Ficus sycomorus, especially those located at the edge of the forest, as villagers expand their farms (pers. obs.). Removal of selected plant species such as cutting Pachystela brevipes' buttress roots to make canoe paddles in Mnazini forests, and clearance of forest understory and ecotone species like Phoenix reclinata in Mchelelo forest for thatching roofs in adjacent villages, affect regeneration (pers. obs.).

Reduction of forest size and impoverishment of forests like Kipende and Makere may reduce the carrying capacity of such forests. This can be disastrous to the colobus because they tend to expand their home range when food is scarce, such as the Mnazini North groups (pers. obs.). Also, shrinkage of forest size may result in an increase in intraspecific and interspecific competition and also promote the spread of density-dependent ectoparasites and endoparasites. Mchelelo forest, for example, is only about 14 Ha. but contain the home ranges of four troops of baboons, two groups of Sykes monkeys, two groups of mangabeys and one group for the red colobus. A study should be conducted to determine the extent of niche overlap and competition among the primate species within the Tana primate community. Competition may be so stiff that it may lead to competitive exclusion of a species, like the colobus, whose niche breadth is narrow (May, 1984). Probably this is what happened in Hadribu forest where the colobus occurred as recently as 1975 (Marsh, 1978).

The hydrologic regime of the Tana River may be affected by the construction of dams, like Masinga dam, and irrigation schemes, like Bura and Mnazini. Exploitation of the river may stabilize the river course resulting in changes in the floristic composition of the forests. This is because the forests are supported by ground water and seasonal inundation of the Tana flood plain and the plant species are adapted to the vagaries of an unstable river course (Homewood, 1975). Some plant species, like Pachystela brevipes, Cynometra lukei and Populus illiciforlia, which provide colobus with food, are very sensitive to prolonged periods of water stress and will die if deprived of water, as exemplified by the death of most Pachystela species in the Congolani forest (pers. obs.). Such changes in floristic composition may cause changes in primate community composition.

6.3 POSSIBLE SOLUTIONS FOR THE PROBLEMS CAUSED BY PEOPLE

One possible way to check the shrinkage, impoverishment and fragmentation of the Tana River gallery forests, particularly within the reserve, would be to offer people an alternative site for farming and provide incentives and offer generous compensation for moving. This should be discussed with them first so that an optimal solution that is also beneficial to the local people is found. Forceful removal of the people from the reserve would be unfair given that they have also adapted to the vagaries of the unstable river course, and their investment in their villages/farms and the emotional value they attach to their ancestral land is high. In fact a study should be conducted to determine whether the colobus prefer staying close to villages/farms because, apparently, there seem to be more colobus groups in the west bank of the Tana

River, where there are more people, farms and villages than in the east bank forests. If the people know that the endangered species is the cause of their evacuation, they may devise ways of eliminating the species. In fact people outside the reserve are already aggressive toward the species, as exemplified by the frequent stoning of the species in Kipende and Hewani forests because of the rumour that land will be included in the reserve. People with farms within the reserve have resorted to a different strategy. They expand their farms anticipating large compensation, based on the prevailing rumour that there are plans to remove them from the reserve.

An alternative solution would be to let the people stay but stop shifting cultivation within the reserve. Shifting cultivation is practised because of eventual diminishing returns due to the exhaustion of soil nutrients; therefore, fertilizers, which apparently are never used, should be provided at subsidized prices. To stop the use of specific tree species like Ficus for making canoes, aluminum canoes could be made available to the people at affordable prices. Building poles should be brought from less fragile ecosystems, as is done in Malindi and Mombasa towns, and sold in each village. People could be encouraged to collect firewood, which is the main source of energy, in the dry flood plain so that they do not interfere with the structural diversity and nutrient cycles in the riparian forests. Commercial fish traps could be made available so that people stop making them from tree saplings, retarding forest regeneration and succession. Money collected from tourists by local authorities could be used for the proposed subsidies. In fact impact assessment should be done before any implementation of any measure because, without assessment, results may be disastrous. This could include identifying problems, fashioning alternatives, finding optimum solutions, involving the public and resolving conflicts. Impact assessment could take into account the advantages and disadvantages of each alternative. Eviction of the people may be very costly. The use of fertilizers may, on the other hand, affect the aquatic environment. Interactive computer modeling may be of great help in integrating all these variables and generating solutions faster and more cheaply than practical experimentation (Western, 1984).

The Orma pastoralists' practice of burning grass during dry seasons does, at times, damage regenerating forests. This damage may be reduced if field officers are provided. Such officers could coordinate the burning of grass which is currently carried out randomly. In fact conservation strategies should be developed that deal with the Tana environmental problems at a grassroots level and in ways all people understand and accept. Conservation education for the people should be a priority. Although various researchers have tried educating the local people, the main problem, apparently, is communication (pers. obs.). Local people could be trained as environmental officers whose duties could include teaching the people about conservation issues in their own language. Audio-visual aids may facilitate the teaching of ecology.

The survival of the Tana River red colobus, an endangered species endemic to the riverine forests, depends on the efforts of conservationists, researchers, administrators and the local people. There is therefore need, as mentioned earlier, for concerted action and genuine cooperation among these people in conservation efforts. The main suggestion, based on the results of this study, is that measures should be taken now to ensure the survival of <u>Colobus badius rufomitratus</u>, the red colobus.

6.4 ECONOMIC POTENTIAL OF THE TANA COLOBUS AND THE RESERVE

Kenya has well formulated policies that clarify goals, priorities, future trends and human problems that must be addressed to maximize returns from wildlife. Such returns include consumptive uses, tourism, aesthetic, cultural and scientific gains (Jackson, 1979). All these returns may be realized from the Tana River Primate National Reserve once suitable and active conservation and management strategies, based on local realities, are employed. There is a field research station within the reserve, run by the National Museums of Kenya in collaboration with other institutions. The station will help the country in training local scientists in many disciplines. In fact the Tana environments fits Budowski's (1979) definition of a living Museum. The diverse amphibian, bird, reptilian and mammalian assemblages attest to the high economic, aesthetic and scientific potentials of this reserve. This environment deserves to be preserved, at least, as one of the last remaining examples of a riparian ecosystem in East Africa.

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APPENDIX A. CANOPY TREE SPECIES FOUND IN TANA FORESTS

Acacia elator

Acacia robusta*

Acacia ruvumae

Alfezia quanzensis

Alangiure salviiforlium*

Albizia gummifera*

Albizia glabirrema*

Antidesma venosum*

Apporrhiza paniculata

Blighia unijugata*

Borassus aethiiopum

Cassia abbreviate

Celtis philippensis.

Celtis wightii*

Coffea sessiliflora

Colar minor

Cordia goetzi*

Cordia sinensis

Cynometra lukei*

Diospiros ferrea

Diospiros kabuyeana

Diospiros mesipiliformis*

Dobera glabra

*Ficus bussei**

Ficus depauperata

*Ficus natalensis**

Ficus scasselatii

*Ficus sycomorus**

*Garcinia livingstonei**

Huntteria zeylanica

Hyphaene compressa

Ixora narcissodora

Kigelia africana

Lannea stuhlmanii

*Lannea schweinfurthii**

Lamprothamnas zangeubaricus

Lawsonia inermis

Lecaniodeia fraxiniforlius

Lepisanthes senegalensis

Majidea zanguebarica

*Mangifera indica**

*Makhamia zanzibarica**

*Mimosops fruticosa**

Oncoba spinosa

Oxystigma msoo

*Pachystela brevipes**

Pachystela msolo

Pavetta sporerobotys

Phoenix reclinata

Polysphaeria multiflora

Populus illiciforlia*

Salvadora persicea

Sorindeia madagascariensis

Sorindeia obtusiforliolata*

Spirotachyus venerifera

Sterculia appendiculata

Tamarindus indica*

Terminalia brevipes

Thespesia danis

Trema orientalis

Ziziplus pubescene

*Tree species that colobus have been seen eating.
(Sources: Marsh, C. 1976, 1978, 1985, Medley, K. 1988 (pers. com.) and local information.