THE SOCIOECOLOGY AND CONSERVATION OF THE SAMANGO MONKEY (Cercopithecus mitis erythrarchus) IN NATAL

by

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The samango monkey, Cercopithecus mitis erythrarchus. (Photo: E.L. van Hooff).

PREFACE

The data described in this thesis were collected in the Cape Vidal dune forest from January 1986 to August 1987. Experimental work was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from September 1987 to December 1989, under the supervision of Professor Mike Perrin and Professor Peter Henzi.

I declare that the design and execution of the studies on which this thesis is based are my sole and unaided work unless otherwise indicated and acknowledged in the text, and that no part has been submitted for any other degree at any university.

SIGNED: ....
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Last, but foremost, I wish to thank my mother, Lorraine van Hooff, for her encouragement of my interest in things zoological and for her support and belief in my abilities. I dedicate my thesis to my mother, and to the memory of my father, Roger John Lawes, who would have shared her pride.

ABSTRACT

The samango monkey (Cercopithecus mitis erythrarchus) is the southern most representative of the polytypic mitis group. The samango is also the only truly arboreal guenon to have radiated as far as 30°S. At southern latitudes a greater seasonality of climate and an attendant seasonal shift in food availability is expected to restrict the foraging strategy of the arboreal guenon. In the absence of arboreal congenerics and few frugivorous bird and bat species, the samango experiences a level of competitive release at Cape Vidal not found in other equatorially located mitis populations. In this thesis I examine and contrast the diet and feeding behaviour of the mitis species group. In this way I illustrate the consequences of seasonality of food abundance and competitive release on the foraging strategy of the samango, and provide an explanation for the unique distribution of the samango monkey as the only arboreal guenon in southern Africa.

Despite seasonality in climate and abundance of food resources, my data show that, in general, samango monkeys at Cape Vidal are not food limited. For this reason Cape Vidal samangos have large troop sizes (25+), use small home ranges (15 ha) and have the highest density (2.02 ind/ha) of any C. mitis population researched to date. Fruit forms an important part of the diet year-round and therefore, energy and carbohydrate are abundant. There is very little intra-group aggression for food, although interindividual distances are greatest when feeding. There are age-sex differences in the diet, and adult males eat more fruit while females eat more leaves than other age-sex classes.

The most important aspect of the feeding strategy of the samango is concerned with obtaining adequate protein in the diet, and throughout the range of the mitis group, populations differ most in feeding strategies used to secure protein-rich foods, such as young leaves, flowers and invertebrates. In this respect seasonal nutrient (protein) availability, rather than seasonality of food abundance per se, is the most limiting component of the forest environment.

Unlike equatorial populations of mitis that derive most of their protein from insects, samangos are unable to adopt a similar strategy. Insects were available to the monkeys, and then only in low numbers, in the wet summer season at Cape Vidal. Samango

monkeys, therefore, make greater use of a wider variety of plant items for protein acquisition. During the wet summer months, insects, flowers and young leaves are used by samangos to obtain sufficient protein for important reproductive activities, such as lactation, and initial growth of the infant. During the drier winter months only mature leaves and small quantities of young leaves are available as protein resources, consequently samangos use more mature leaf in the diet than other C. mitis populations.

Adaptations of the gut and specialized gut microflora permit this high degree of folivory in the diet (Bruorton and Perrin 1988) of the samango monkey. This is a characteristic that does not appear to be shared with other arboreal guenons. In so far as protein is essential for reproduction, folivory in C. mitis has been important in permitting this arboreal guenon species-group to radiate into southern latitudes where protein is more seasonally available. The ability of samango monkeys to eat large quantities of leaves at any one time, accounts for their unique position as the only arboreal guenon species in southern Africa.

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CHAPTER 1: THE SAMANGO MONKEY

1.1. INTRODUCTION

The samango monkey belongs to the polytypic Cercopithecus mitis species group. The C. mitis species group has an extensive distribution in evergreen forest of Africa from the southern Sudan to the eastern Cape province of South Africa (Fig. 1.1. pp. 11). Two subspecies of the samango, C. m. labiatus and C. m. erythrarchus, are recognized within the southern African subregion (Meester et al. 1986); this thesis is concerned with the ecology of C. m. erythrarchus (Fig. 1.2. pp. 12). Apart from the vervet monkey (Cercopithecus pygerythrus), no other guenon is found within the range of the samango in R.S.A. Since the vervet monkey is not usually a forest dweller there are no diurnal primate competitors within the range of the samango. The samango thus represents the southern most extent of the range of both the mitis species group and the arboreal guenon in Africa.

Although the samango monkey has until now been poorly researched, other subspecies of the C. mitis species group, and particularly the blue monkey (Cercopithecus mitis stuhlmanni), are known from more than one study from different locations. The samango monkey therefore provides a unique opportunity to study a widely distributed, and elsewhere well studied, primate in the absence of competitive congenerics and at the limits of its ecological range.

At the time of this study very little was known about samango ecology. Local interest in the samango monkey stemmed largely from the protestations of foresters. The South African Forestry Research Institute had expressed concern about samango related damage to commercial pine (Pinus taeda) plantations (Von dem Bussche and Van der Zee 1985). Although examples of damage to exotic softwoods plantations by members of the C. mitis species group, had been recorded from elsewhere in Africa (Omar and De Vos 1970, Beeson 1987), there were few solutions. Data, in many cases anecdotal, from unhabituated samango troops (McMahon 1977, Scorer 1980) was of limited value. In view of the rare status of the samango monkey (Smithers 1986), and a corresponding realization that cautious management policies would be necessary to deal with the problem, the need for sound ecological quantification of samango behaviour was of major concern to both science and industry. Proposals for the conservation and management of the samango monkey could then be developed on a sound background of biological knowledge. It was my undertaking to provide this biological knowledge.

My own interest in the samango monkey was more academic than practical. While the economic impact of the monkey on commercial plantations could not be ignored, I did not deliberately concern myself with looking for solutions to the problem. Any answers to the latter problems would, I felt, manifest themselves in the course of a more academic approach to the investigation of the biology of the monkey. Of particular interest to me was the unique position of the samango, as the sole representative of the arboreal guenon in southern Africa. The main thrust of this thesis must therefore be seen as an attempt to elucidate the ecology of the species, especially the feeding ecology, in an effort to explain the successful radiation of the mitis species group into southern Africa.

A brief account of some of the studies that have improved our knowledge of mitis behaviour is given below. A more detailed account of the literature and pertinent issues accompanies each chapter. Not all studies have been concerned with the feeding ecology of mitis.

The first important socioecological study on C. mitis was conducted by Aldrich-Blake (1970). Up until this time the literature on mitis had been largely concerned with distribution and taxonomy of the species (Haddow 1956, Dandelot 1962, Berry 1965, Butler 1966, Booth 1968, Thorington and Groves 1970). Aldrich-Blake (1970) showed that forest monkeys (C. mitis stuhlmanni) exhibited a basic harem-type social organization thought to be characteristic, at that time, of terrestrial primates living in harsh almost semi-arid environments. He was unable to fully habituate a troop and as a consequence the data, in some areas, do not permit confident conclusions. For example, his arguments were centred on issues of social organization, however he recorded the occasional division of the troop for short periods (hours) into smaller groups which would reunite, a behaviour not reliably recorded for mitis since. Rudran (1978a) felt that these 'sightings' by Aldrich-Blake (1970) were artifacts of poor observational conditions as a result of the low level of habituation. However, the value of Aldrich-Blake's (1970) thesis has been the role it has played in generating hypotheses and providing a foundation for other mitis related research.

Discussion of the role of the adult male, and evolution of the single-male troop by Aldrich-Blake (1970) led to a number of mitis studies in recent years covering related issues. Butynski (1982) dealt with harem male replacement and infanticide in blue monkeys, while Tsingalia and Rowell (1984) discussed aspects of adult male behaviour of the blue monkey in the Kakamega forest, Kenya, during the breeding season. They showed that an adult troop male's social position did not necessarily allow him exclusive access of fertile troop females. In addition, Kakamega blue monkey troops regularly experienced breeding season influxes of extra-troop males which competed with the resident male for access to receptive females. Tsingalia and Rowell's (1984) work stimulated considerable interest and Cords et al. (1987) and Henzi and Lawes (1987; 1988) all discuss the problems of promiscuous mating and breeding season influxes into a troop by adult males in C. m. stuhlmanni and C. m. erythrarchus respectively.

Returning to feeding ecology, Aldrich-Blake's (1970) work also showed that the abundance of food for guenon use in a tropical forest varied subject to the combined temporal overlap of food item production between tree individuals of food plant species. This variation in food abundance could only be loosely termed as seasonal. In recent years it has become generally accepted that tropical forests, because of considerable interspecific and intraspecific temporal variation in phytophase production, do not necessarily represent a habitat of continuous superabundance of available food despite high plant diversity. From this Rudran (1978a; 1978b) demonstrated how the peculiarities of food dispersion (in space and time) resulted in space utilization patterns that affected the social structure of blue monkeys in the Kibale forest, Uganda. This thorough study is used extensively in my own work for comparative data, and my methodology therefore closely follows that of Rudran (1978a). Rudran (1978a) also suggested that polyspecific associations with the folivorous red colobus seemed to enhance the acquisition of invertebrates by blue monkeys. Also, blue monkeys may have been able to efficiently locate areas of food abundance by associating with other species (particularly redtails, C. ascanius) during movement. In addition, Rudran (1978a) emphasized the importance of folivory to mitis as a means by which the species group might achieve considerable trophic niche separation from other primates besides the guenons, and thereby account for the extensive distribution and cohabitation of mitis in Africa.

Struhsaker (1978) described food niche separation and discussed the possibility of competition for food among the five most common species of monkeys at Kanyawara, Kibale (blue monkey; redtail monkey, Cercopithecus ascanius schmidti; mangabey, Cercocebus albigena johnstoni; guereza, Colobus guereza occidentalis; red colobus, Colobus badius tephrosceles). He found that blue monkeys had the highest mean dietary overlap of plant foods among these five species. On this basis he classified the blue monkey as a food generalist and suggested that, as a generalist, it might be more adversely affected by interspecific competition with the four more specialized (in terms of diet) species. The advantages of mixed- species associations recorded by both Aldrich-Blake (1970) and Rudran (1978a) seemed questionable, since all other parameters being equal, grouping tends to increase competition among troop members, which blue monkeys could ill afford.

Cords (1987) examined the question of the function of mixed-species associations between redtails and blue monkeys at Kakamega, Kenya. She concluded that mixed-species were not the result of chance encounters of troops of both species moving randomly and independently, but that redtails used blue monkeys as guides to food sources not recently fed upon. By joining a troop of blue monkeys, redtails were also able to avoid areas of the forest exploited by blues earlier on a given day. Avoiding such areas would increase the redtails consumption of ripe fruit whose availability would otherwise be depressed by a passing troop of blue monkeys. The larger blue monkeys frequently contested access to food items or food sources with redtails. The benefits of participating in mixed groups were clearly not symmetrically distributed between the two species. Not surprisingly redtails were found to be primarily responsible for the formation and maintenance of such associations. Benefits to blue monkeys from associations seemed few, if any, but larger size did, however, provide the blue monkey with a competitive advantage over the redtail. Antipredator benefits accruing to members of mixed-species groups, via increased vigilance provided by the larger group, may be one reason for why blue monkeys tolerated these associations at all.

The success of this mixed-species association may in part be due to the ability of blue monkeys to use leaves, as opposed to invertebrates (used heavily by the smaller redtails), as sources of additional dietary protein (Rudran 1978a; 1978b). In this manner competition between the two species is reduced. Bruorton and Perrin (1988) and more recently Bruorton (1989) have shown that the samango (C. m. erythrarchus), has a convoluted caecum and capacious colon, both of which possess taeniae and haustra, which slow down the passage rate of food permitting microbial fermentation. Bacteria degrade leaf material in the hindgut enabling efficient digestion of cellulose thereby enriching the diet in protein. This physiological adaptation has effectively allowed mitis to expand its trophic niche, increasing the food types available in the diet. C. mitis can maximize its use of leaves or invertebrates, or both, depending on which is more conveniently achieved and accounts for the high dietary overlap with other species (Struhsaker 1978). The important advantages derived from gut physiology in mitis are discussed in later chapters on feeding strategy and radiation of the species.

Struhsaker (1978), in addition to showing the blue monkey to be a dietary generalist and thus prone to competitive pressure, hypothesized that the lower density of blue monkeys at Ngogo (Kibale forest) was a response to food competition from other primates; conversely, the higher density of blue monkeys at Kanyawara (Kibale forest) was related to competitive release. Similarly Cords (1986a) showed that blue monkeys at Kakamega (Kenya) had a broader plant diet than the Kanyawara populations at Kibale. One hypothesis suggested to account for the latter, was that Kakamega blue monkeys had undergone competitive release in the absence of Colobus badius and Cercocebus albigena, two larger primates with precedence at feeding sites shared with blue monkeys (Struhsaker 1978). The higher population density of blues in Kakamega relative to Kibale (169 vs. 42 per km^2) supports this hypothesis.

Butynski (1990) examined the ecological correlates of high (Kanyawara) and low (Ngogo) blue monkey densities at Kibale. His data refute Struhsaker's (1978) hypothesis that blue monkey density is related to competition between species. Butynski showed that interspecific competition was higher at Kanyawara than at Ngogo, despite the absence of certain competitor species at Kanyawara. Intraspecific competition for food was apparently absent among blue monkeys at Ngogo but present and affected by food availability at Kanyawara. The subpopulations of blue monkeys at Kanyawara appeared to be stable, at carrying capacity, and food limited. In contrast, the subpopulation at Ngogo was rapidly increasing, below carrying capacity and in a food-rich environment. The density of blue monkeys at Ngogo was not low because of a scarcity of food; it was low in spite of an abundance of food. Obviously, neither food production nor food availability explained the differences in blue monkey densities at Kibale. Competition too, could not explain the differences, for to invoke competition both subpopulations would have had to be at carrying capacity for the purposes of comparison. Butynski concluded that the disparity in density was more likely attributable to some historical, rather than current, factor that resulted in a "population crash" in the Ngogo subpopulation. The two most probable explanations were that hunting by tribesmen or disease greatly reduced the Ngogo subpopulation. Butynski's work emphasized the influence of historical events in shaping ecological situations, and showed the dangers of ascribing inter-population variation to competition and feeding behavioural factors where those populations may not be at carrying capacity. Butynski also cautioned ecologists to be wary of always seeking solutions to ecological problems in the 'here and now', and in so doing ignoring the possible effects of past events.

In Zaire, Schlichte (1978) examined the diet and feeding ecology of two blue monkey troops at Kahuzi-Biega, in an isolated riparian forest habitat of low plant species diversity. Given the food limitations of their environment the blue monkeys showed a remarkable versatility in feeding behaviour. They moved back and forth in a regular pattern within their linear home range. This movement would maximize their knowledge of the availability and timing of food items within the home range. In contrast, Butynski (1990) found that when food availability was low at Kibale blue monkeys increased feeding time, used poorer quality foods from abundant tree species, and conserved energy by moving less. However, the critical factor determining feeding behaviour at Kahuzi-Biega was food diversity. Unlike Kibale blues, Kahuzi-Biega monkeys were unable to increase dietary species diversity while at the same time reducing food quality. Kahuzi-Biega blue monkeys had to maximize their use of food species. They achieved this by a "systematic" ranging pattern, and by making extensive use of most or all food items from plant species seldom used, or used for a single food item type, at Kibale.

Schlichte (1978) had shown that the blue monkey had an astonishing ability to change the diet and feeding behaviour in response to changes in habitat and food availability. Beeson (1987;1989) confirmed these findings when he found that blue monkeys on the Zomba plateau (Malawi) were capable of surviving on foliar material and some flowers, for months at a time, without recourse to any significant amount of fruit. Here the monkeys made frequent use of the cambium of pine trees (Beeson 1987). Undoubtedly the use of commercial plantations by subspecies populations of the mitis species group is a natural manifestation of this dietary versatility.

The samango monkey lives at latitudes where fruit seasonality and, hence, food availability closely follow rainfall patterns. In addition plant species diversity is lower (although not as low as that encountered by blue monkeys at Kahuzi-Biega or Zomba) than most previously studied mitis populations. The samango monkey therefore provides an excellent opportunity to further test the dietary and feeding behaviour versatility of the mitis species group.

During 1984 and 1985 I conducted a study of the feeding behaviour of the samango (subspecies C. m. labiatus) in the Ngoye forest, Natal Province, South Africa (Lawes et al. 1990). This study confirmed the frugivorous nature of the mitis diet at the southern extent of the range. Fruit (or food) seasonality was pronounced at Ngoye. Like the Kibale (Kanyawara) blue monkeys (Rudran 1978a; 1978b, Butynski 1990), the samangos at Ngoye reduced the quality of the diet in favour of diversity in the diet during periods of food shortage. They were, however, more selective of foods high in energy when food was abundant. Habituation of a study troop had proved impossible at Ngoye and had frustrated attempts to answer questions on feeding and foraging behaviour. For instance: (a) how did ranging patterns differ in response to variation in food availability and distribution, (b) were the age-sex class differences in the diet comparable to those observed in tropical mitis counterparts (Rudran 1978a; 1978b, Cords 1986), (c) did the high level of frugivory imply that the samango was not food limited, and if so (d) why had no other guenons radiated as far south? The Ngoye study provided sufficient information to suggest an intricate relationship between seasonality of food supply and feeding behaviour in the samango. It was clear that a habituated study population could well clarify this relationship and provide answers to the questions. In early 1986 I moved to the coastal dune forest at Cape Vidal, and after 4 months was able to confidently began work on a habituated troop of samango monkeys of the _C. m. erythrarchus_ subspecies.

My study at Cape Vidal was designed to investigate hypotheses generated at Ngoye. This study was the first systematic ecological investigation of habituated samango monkeys (and the southern most study of the _mitis_ species group), from which valuable comparative information on the ecological limits of the species group could be obtained. The objectives of the study were:

(1) To investigate the diet, feeding behaviour and feeding strategies of the samango in relation to temporal and spatial variation in food abundance and availability.

(2) To determine the distribution, relative abundance, and status of the samango monkey in Natal, and to relate this to the radiation history of the _mitis_ species group.

(3) To generate sound management and conservation proposals for the samango in Natal.

The organization of the thesis follows what I believe to be the natural order of investigation necessary for elucidating the feeding biology of an arboreal monkey. Of course all chapters are interrelated and there is inevitably a certain degree of repetition of important issues. The initial chapters introduce the samango monkey, the study area and population structure. Food availability and food quality leads to a chapter where the diet of the samango at Cape Vidal is compared to other _mitis_ populations. This is followed by a brief discussion of activity budgets and their importance as part of the feeding strategy. Since the troop comprises a number of individuals of different ages and sexes each with their own trophic requirements, the age-sex differences in the diet and feeding strategy are discussed. The ecological correlates of ranging behaviour, including correlates other than food dispersion, availability and abundance, are then discussed. A chapter on feeding behaviour and foraging strategy in the samango monkey ties together the relationship between activity, diet, ranging behaviour and food availability for the Cape Vidal population. A summary of the salient points introduced in this thesis regarding the samango monkey helps to place the samango monkey in perspective as a member of the mitis species group and its association with the other African guenons in general. The last section describes the status and distribution of the samango monkey in Natal and proposes certain conservation measures for the maintenance and survival of viable populations into the future.

1.2. TAXONOMY, DISTRIBUTION AND RADIATION OF THE SAMANGO MONKEY

1.2.1. Taxonomy

The samango monkey is a guenon. Guenons are the commonest monkeys of Africa and are found throughout sub-Saharan Africa in a variety of ecological niches, both terrestrial (savanna and woodland savanna) and arboreal (tropical forest, swamp forest, mangrove and montane forest). Generally speaking guenons are arboreal forms and, as such, are limited to the forested areas of Africa. There are 20 species of guenon divided into eight species groups. The samango monkey belongs to the C. mitis species group.

The taxonomy of the mitis species group is confused and complex. Hill (1966), Dandelot (1971) and Napier (1981) include C. nictitans, C. mitis and C. albogularis within the superspecies mitis while Kingdon (1980) prefers to place these within the superspecies nictitans. Rahm (1970) regarded nictitans as a separate species group since it was thought that C. nictitans nictitans and C. m. maesi were sympatric, however, this is now thought to be questionable (Lernould 1988, p73). Rahm, Kingdon and Napier all consider albogularis to be a synonym of mitis, because there are cases of hybridization between C. m. stuhlmanni and C. a. kolbi, some kolbi crossing the Rift Valley (Kingdon 1971), and because Booth (1968) considered the population around Lake Manyara as being a hybrid between stuhlmanni and albogularis kinobotensis. Lernould (1988) considers albogularis to be a separate species since unpublished data (Dutrillaux, B. in

Lernould 1988, p 71) show that the chromosome counts of albogularis differ from those of the other mitis forms studied.

In this study albogularis is regarded as a synonym of mitis, thus the samango is regarded as a subspecies of mitis (Roberts 1954, Rahm 1970, Meester et al. 1986), although Lernould (1988) would place the samango with albogularis. For the purposes of this thesis the taxonomic debate need not be resolved since all authors agree that mitis and albogularis are ecologically inseparable.

Two subspecies of the samango, C. m. labiatus and C. m. erythrarchus, are recognized within the southern African subregion (Meester et al. 1986). The subspecies are separated primarily on the extent and colour of the ischial and ventral hairs. C. m. labiatus has white, while C. m. erythrarchus has dark rust red ischial and vent hairs. In labiatus (Karkloof population) the white hairs may extend down the ventral surface of the tail almost to the tip. The saddle and shoulder pelage in erythrarchus has a faint yellow/green tint. Preliminary protein electrophoresis analysis shows a difference of two bands between the subspecies (Appendix 1.1). The subspecies have thus been isolated from one another long enough for some genetic differentiation to have taken place. The subspecies are geographical vicariants in the sense that they occupy distinctly separate geographical regions and even forest types. Based on the protein electrophoresis and the geographical position of the subspecies I propose that the subspecies represent two separate mitis radiation events in southern Africa (see section 1.2.3. Radiation). Body measurements of the subspecies are given in Appendix 1.2.

1.2.2. Distribution

The samango subspecies, representing the southern extent of the C. mitis range (Fig. 1.1), occupy a variety of forest types in southern Africa. C. m. labiatus distribution is confined to Afromontane forest types from the eastern Cape to Natal west of the Ubombo mountain range, and extends no further northward than 27°S. C. m. erythrarchus is found east of the Ubombos and north of the Umfolozi swamp in mainly coastal lowland, coastal dune and sand forest extending onto the Mozambique coastal plain. The north-western limit of this subspecies range appears to be the Vumba mountains in Zimbabwe. The the northern limit is in the region of northern coastal Mozambique/southern Tanzania (Fig. 1.2).

Populations of erythrarchus are found in the mistbelt Podocarpus forest belt of the eastern Transvaal. Although erythrarchus is positively identified from the Soutpansberg and Woodbush areas on the basis of pelage colouration (Roberts 1954, Rautenbach 1982), the subspecific identity of populations to the south have not been clearly established. One reason for this appears to be a negative cline in the intensity of the red of the ischial hairs toward the south. Coastal Mozambique populations have very red ischial hairs and north-eastern Transvaal populations have only a hint of red. Populations further south (Mariepskop, near Pilgrims Rest) show no red at all (Roberts 1954, Hill 1966) and could easily be confused with labiatus were it not for the lighter shoulder and

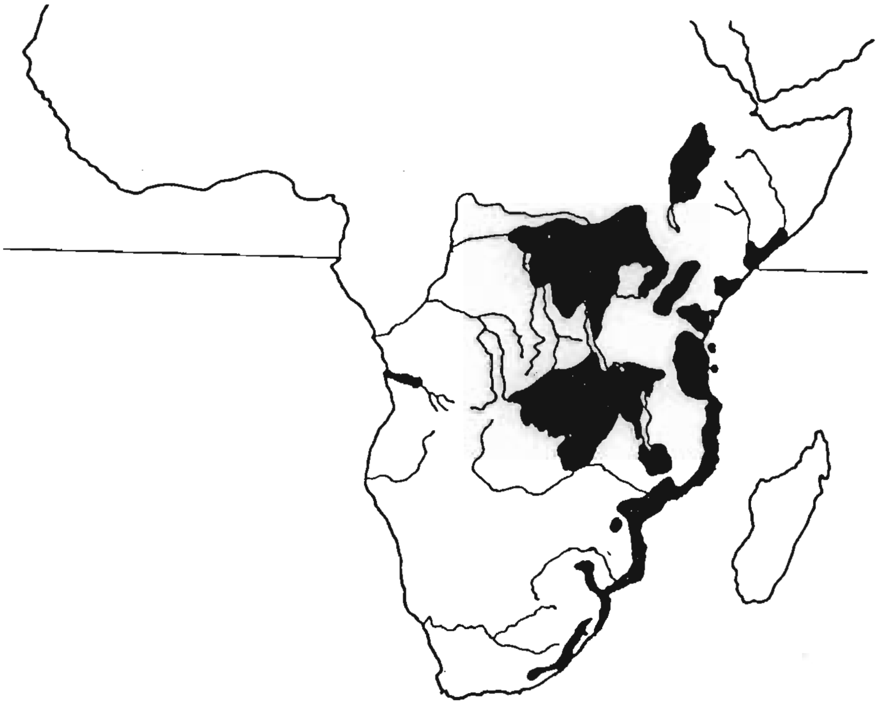

Figure 1.1. Distribution of the Cercopithecus mitis species group in Africa. (from Lernould 1988).

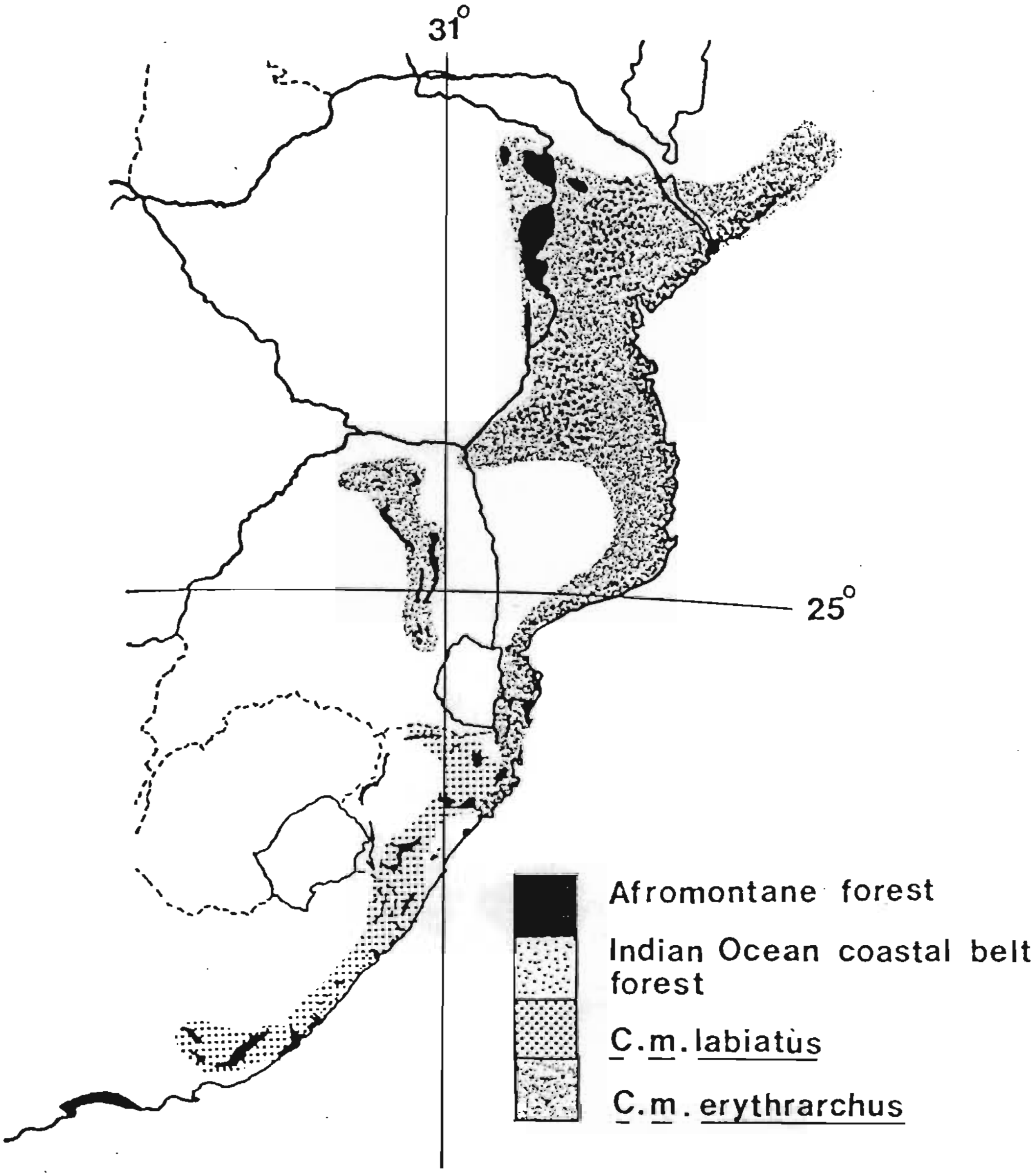

Figure 1.2. Distribution of the two samango monkey subspecies in southern Africa (compiled from pers. obs., K. Cooper unpub. data., Roberts 1956, Scorer 1980, Rautenbach 1982, Bourquin 1988).

rump colouration characteristic of *erythrarchus* (Roberts 1954). For a long time these south-eastern Transvaal populations of the samango were considered sufficiently different to warrant further subspecific division and were called *C. m. schwarzi* (Roberts 1954, Hill 1966, Rahm 1970, Scorer 1980). Current opinion includes the latter populations with *erythrarchus* (Rautenbach 1982, Meester *et al.* 1986) as the southern extent of the chromatic cline. An alternative is to view the south-eastern Transvaal populations as a zone of hybridization between the two subspecies. Interestingly *C. m.*

nyasae found in southern Malawi is similar to labiatus, as opposed to erythrarchus, in pelage colouration (Pers. obs.). The distribution and chromatic variation of the samango pose a number of questions:

(a) Why is erythrarchus, instead of labiatus, found in the eastern highlands of Zimbabwe and in the eastern Transvaal, given that it is likely that labiatus radiated via this route (see Lawes 1990, and this study)?

(b) Why are there no samangos in the coastal dune forest immediately south of the St Lucia/Umfolozi swamp region (e.g. Mapelane dune forest) in Natal? Coastal forest is extensive in places south of this region and of much the same "quality" as forest to the north (MacDevette 1989).

(c) Why are samangos not found in the extensive Knysna and Tsitsikamma forests of the eastern Cape, just further south of the extent of the present distribution of the samango?

1.2.3. Radiation

To clarify some of the above mentioned peculiarities of the distribution and chromatic variation of the samango in southern Africa a short review of the probable radiation history of the samango is presented. The argument is given in full in Lawes (1990).

It is probable that radiation of the guenons began prior to the last glacial maximum, during the hyperthermal (Pickford and Senut 1988, p52). Repeated and drastic changes in climate (Fig. 1.3) and vegetation (Fig. 1.4) characterized the Quaternary in Africa, and forests are likely to have expanded and contracted in extent (Moreau 1966, Van Zinderen Bakker 1978, Hamilton 1988). Although the period 70 000 BP to 20 000 BP was not climatically uniform, and may, on the whole, have been drier than present (Hamilton 1976; 1988), there were episodes of varying degrees of wetness (Perrott and Street-Perrott 1982), suitable for the expansion of forest and woodland and the radiation of the mitis species group. To explain the absence of other arboreal guenons from the greater part of the mitis species group's range Tappen (1960) suggested that the major movement must have taken place during an early spread of montane forest prior to the main Cercopithecus radiation. By Tappen's reckoning the mitis species group therefore

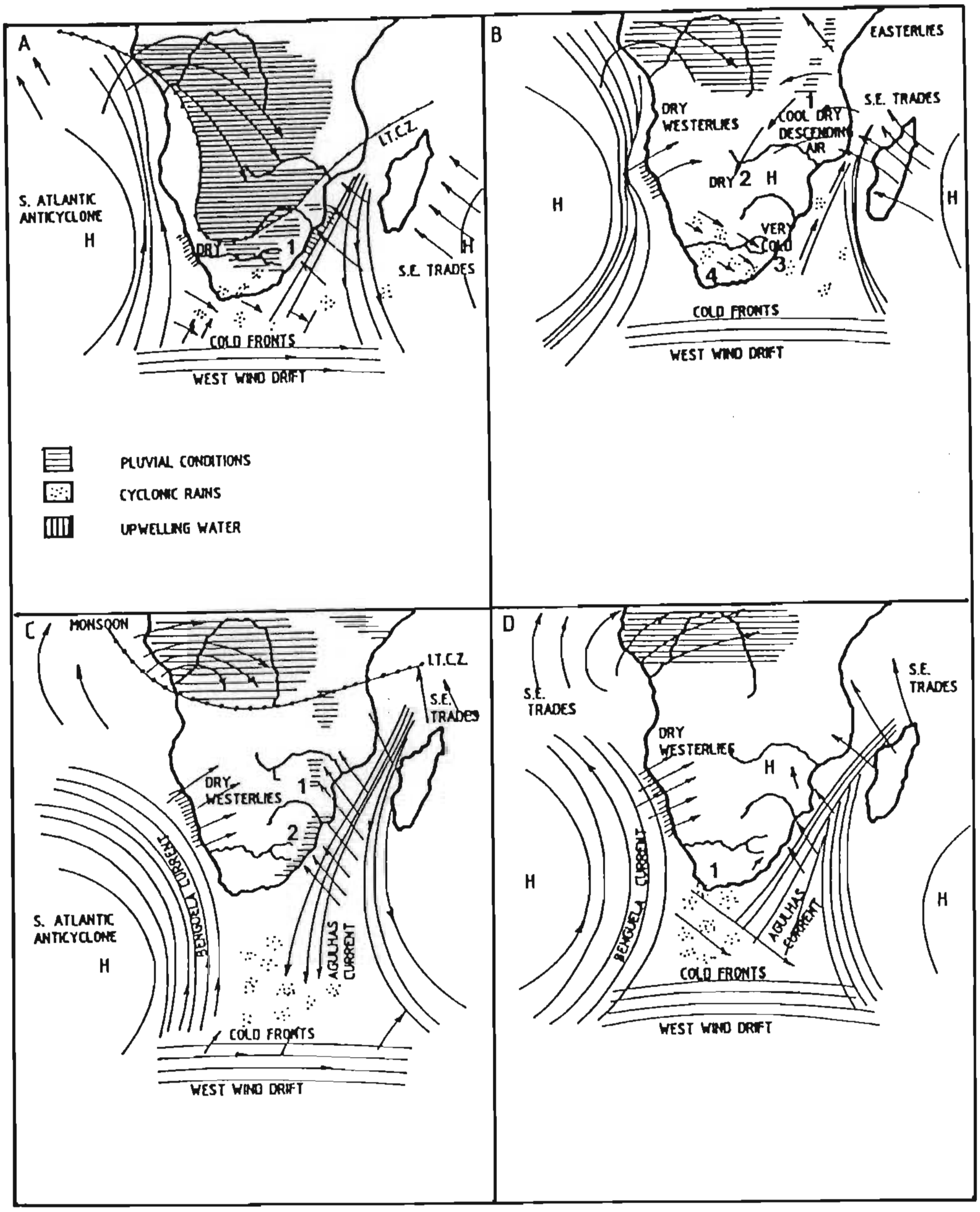

Figure 1.3. Palaeoclimatic events that led to the establishment of forest in parts of southern Africa. Redrawn in part fron Van Zinderen Bakker (1967, 1978). Numbered annotations have been added from Van Zinderen Bakker (1967), Tinley (1985), Deacon and Lancaster (1988).

A. Glacial southern summer: (1) Strong high pressure easterly winds on southeast coast, Agulhas return current strengthened and results in lowered surface water temperature of south Mocambique channel. Dry summer conditions on coast as cold inshore waters inhibit rain development.

B. Glacial southern winter: (1) Region cold, dry; dry subsiding trades and regular influxes of polar air from direction of sea; (2) Dry conditions - redistribution of Kalahari sands; (3) Cool air draining off escarpment close to coast creates very cool zone in region; (4) Westerlies bring winter rainfall to southern and western Cape.

C. Interglacial southern summer: (1) Humid air flows into region due to southward shift of intertropical convergence zone (ITCZ), and weakening of high pressure system over southern Africa because of heating of the land surface; (2) Summer rainfall patterns favour spread of Afromontane forest on the south-east margin of Africa.

D. Interglacial southern winter: (1) Cyclonic rains reach the southern Cape only during winter.

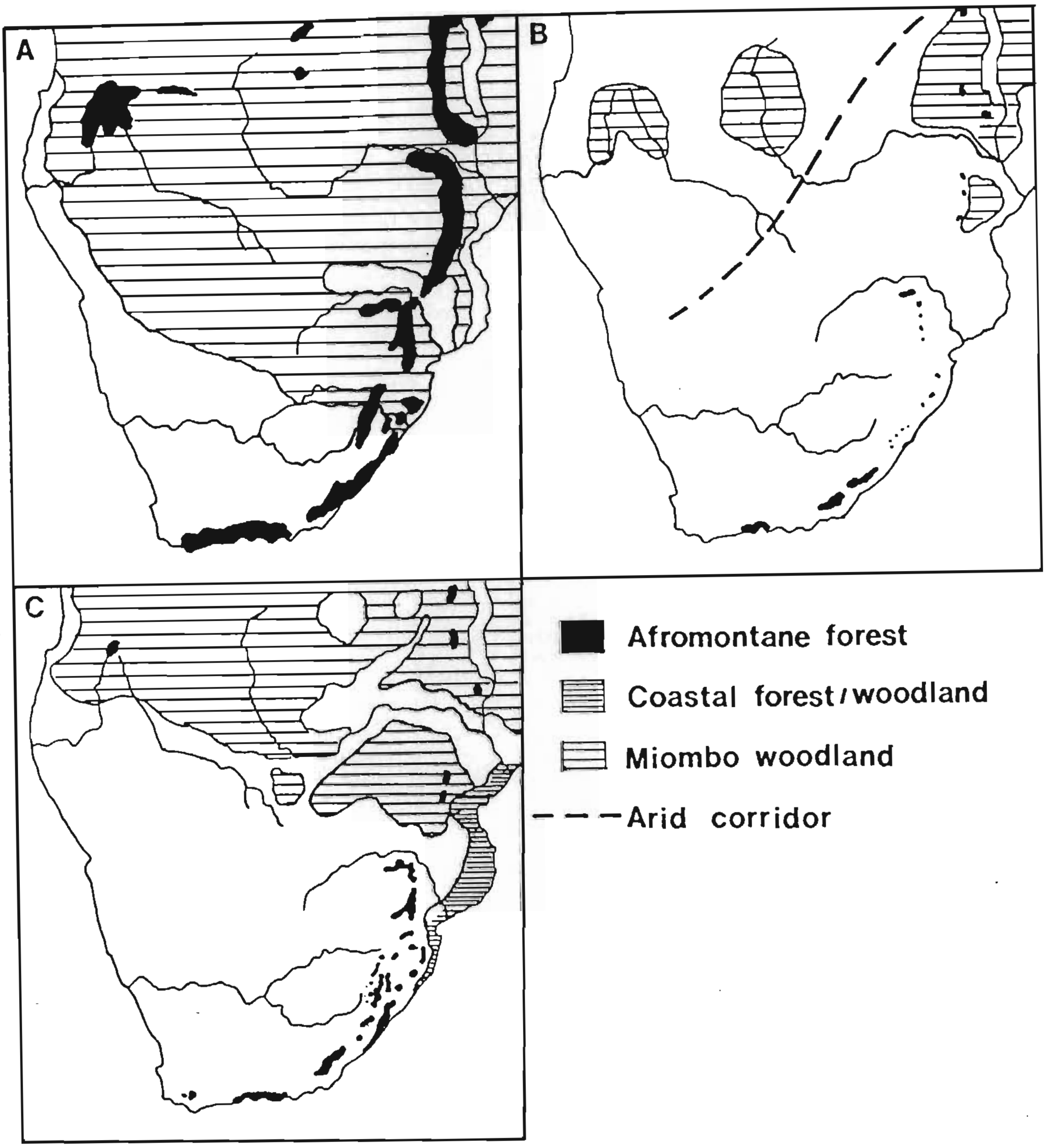

Figure 1.4. Estimates of the distribution of Afromontane and coastal lowland forest over the last 100 000 years in southern Africa. Compiled from Stuckenberg (1969), Cooke (1962), Knapp (1973), Acocks (1953), Van Zinderen Bakker (1978), White (1983), Deacon and Lancaster (1988).

A. Interglacial to preglacial maximum 100 000 - 18 000 BP.

B. Last glacial maximum 18 000 BP.

C. Post glacial maximum, 12 000 BP to present.

represents an ancestral Cercopithecus species group, reaching its southern area of distribution before the differentiation of other species. This is not supported by more recent cladistic analysis based on protein eletrophoretic studies (Ruvolo 1988) and chromosome banding methods (Dutrillaux et al. 1988). They show mitis to be one of the most recently divergent among the Cercopithecini. It is likely therefore that the radiation of the mitis species group down Africa relates to the timing of late speciation events within the Cercopithecini.

The unique structure of the caecum and colon in mitis (Bruorton and Perrin 1988), which permits a high degree of folivory in mitis, undoubtably had an influence on the radiation of the species group. The mitis species group may have been more terrestrial and capable of using fruit-poor woodlands more extensively in the past, ranging much more widely than at present. Today the forest/savanna boundary is usually sharp whereas the types of intermediate vegetation are thought to have been extensively distributed in the past (White and Werger 1978). Palynological work by Livingstone (1971) in Zambia, Clark and Van Zinderen Bakker (1964) at Kalambo falls in Tanzania, and Van Zinderen Bakker (1963) at Dundo in north-eastern Angola, has shown that Brachystegia-type woodlands were widespread before the last glacial. We know from at least one study that mitis will use woodland habitat (Gartlan and Brain 1968). I have seen C. m. nyasae in the Brachystegia woodland of the islands off Cape Maclear, Malawi. The initial radiation of mitis prior to the last glacial is therefore quite possible. Hamilton (1988) suggests that clarification of the forest/savanna boundary could have forced some guenon species to adopt a more strictly arboreal niche which probably accounts for the present confinement of mitis to mostly forest today.

I have proposed four major events in the radiation history of the samango that account for their present distribution (Fig. 1.5; Lawes 1990):

(a) The separation of a mitis form, between the last glacial hypothermals, from a mother population in central Africa. This form radiated deep into southern Africa reaching the eastern Cape via Afromontane forest and interposed woodland. The original population underwent genetic drift in isolation to form a subspecies (see Turner et al. 1988, p149) of mitis, C. m. labiatus.

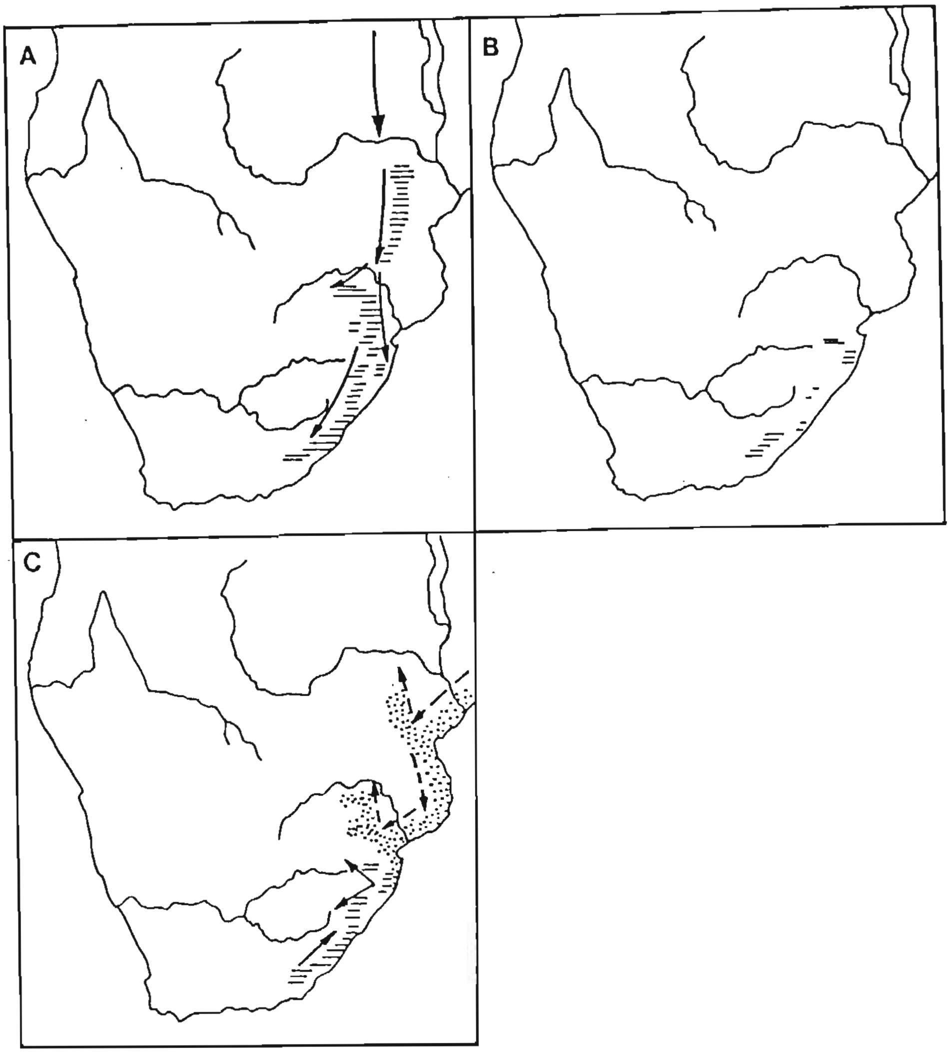

Figure 1.5. The proposed routes by which the samango monkey radiated into southern Africa. Ruled area indicates the extent of C. m. labiatus distribution; stippled area indicates the extent of C. m. erythrarchus distribution; solid arrows indicate the probable radiation routes of C. m. labiatus into southern Africa; and dashed arrows indicate the probable radiation routes of C. m. erythrarchus.

A. Interglacial to preglacial maximum (100 000 - 20 000 years BP). The route most likely used by C. m. labiatus down the Afromontane forest belt.

B. Last glacial maximum (25 000 - 12 000 years BP). C. m. labiatus is isolated in the forests of the eastern Cape and coastal scarp forests of Natal, by the reduction in forest area. Northeastern Zimbabwe is affected by the proximity of an arid zone, while southern Natal is extremely cold.

C. Holocene. Forest expands as warmer conditions return to southern Natal. C. m. labiatus reradiates expanding its range back into southern Natal from the eastern Cape and the larger coastal scarp forests in Natal. In the mid-to-late Holocene (6500 - present) climate ameliorates in highlands of Zimbabwe. C. m. erythrarchus radiates down the eastern seaboard up into the highlands of Zimbabwe and the eastern Transvaal. As dune forest becomes established on the northern Natal coast C. m. erythrarchus moves into Natal as far as the Umfolozi swamp.

(b) The fragmentation of forests and woodland during the hypothermal (18 000 BP) with labiatus populations restricted to forest refugia in the eastern Cape, the south-eastern Transvaal, and possibly the so called coastal scarp forests (which have strong Afromontane forest floristic affinities (MacDevette et al. 1989)) of Natal.

(c) Populations of labiatus in the eastern highlands of Zimbabwe and possibly the north-eastern Transvaal eliminated by harsh dry conditions during the hypothermal (18 000-12 000 BP).

(d) The development of dune and coastal lowland type forest on the Mozambique plain (6000 BP-Present) and the radiation of erythrarchus from eastern into south-eastern Africa. Populations of erythrarchus reached as far south as the Umfolozi swamp where the presence of labiatus to the west in coastal scarp forest (the only available route for further movement) prevented any further movement. In addition the subspecies radiated into the "vacant" eastern highlands of Zimbabwe and also the eastern Transvaal. In the south-eastern Transvaal erythrarchus and labiatus interacted to form a "hybrid" population (Roberts 1954 schwarzi?).

This scenario accounts for the presence of erythrarchus in the Transvaal and Zimbabwe. Samangos, and specifically the erythrarchus subspecies which radiated down the coast, are absent from coastal type forests (as opposed to Afromontane type forests) south of the Umfolozi River. The relatively late development of coastal forest in this region (circ. 6000 BP) would have precluded the opportunity for labiatus to have radiated into coastal forest, and, erythrarchus simply never reached these southern coastal forests in Natal due to the facts explained under point (d) above. The large forests south of the southern extent of the samango range lie southward of the climatically hostile Fish River valley, a feature thought to have been well established by the advent of mitis radition into southern Africa (Geldenhuys 1989). As in the case of some of the coastal dune forest of Natal samangos never reached the Knysna or Tsitsikamma forests due to the presence of an environmental barrier.

It is no coincidence that the diurnal primates (chacma baboon, vervet monkey, samango monkey) of southern Africa are all generalist omnivores. Obviously dietary flexibility has contributed greatly to the ability of these primates to radiate and outcompete their congenerics. The samango with its well developed gut structure and ability to increase the leaf component of the diet has a definite competitive advantage over other guenons, who are confined to tropical latitudes by the availability of invertebrates. Just how unique are the dietary capabilities of mitis? The samango, as the sole representative of the arboreal guenon in southern Africa gives us an insight to the dietary problems faced by a forest guenon in southern Africa.

CHAPTER 2: STUDY AREA AND HABITAT

2.1 INTRODUCTION

During 1984 and 1985 a study of the samango subspecies Cercopithecus mitis labiatus was conducted in the Ngoye forest, 28° 50'S; 31° 42'E (Lawes et al. 1990). This study was a pilot study for research represented in this thesis. The Ngoye forest study allowed me to assess the applicability of field techniques, and provided some ecological data on the monkeys and forest phenology (Lawes et al. 1990). The Ngoye study was terminated when habituation proved impossible. To test hypotheses and ideas raised by my Ngoye work on another samango population, I moved to the Cape Vidal dune forest, some 150 km north and 300 m lower in altitude. At this site habituation of a study troop, in this case of the C. m. erythrarchus subspecies, would be most likely to succeed since the area is well protected by the Natal Parks Board and the monkeys less skittish.

The Ngoye and Cape Vidal forests are broadly classified as Afromontane and Indian Ocean coastal belt forests respectively. Coastal and Afromontane forests within southern Africa have a distinct physiognomy and floristic character (Cooper 1985) that differ from those of central and east African forests where mitis are also found. The importance of these differences and their potential effect on the ecology of the mitis species group had to be investigated before meaningful ecological comparisons could be drawn between widely separated populations of the species group.

2.2 STUDY AREA

2.2.1 LOCALITY

Cape Vidal is located in north-eastern Natal, a province of the Republic of South Africa, and forms part of the Zululand coastal plain generally referred to as Maputaland (Bruton and Cooper 1980). This coastal plain has a maximum elevation of 150m and extends northward into Mocambique where it is extensive in area.

The continuity of a tropical climate down the low-lying Mocambique Plain is largely a result of the southward-flowing warm Mocambique and Agulhas currents. The 18 °C effective temperature isotherm, a useful indicator of the outer limits of the tropics, intersects the south-east African coast near Sodwana some 80 kms north of Cape Vidal (Stuckenberg 1969). To the south and west of this point the tropical association is progressively replaced by a complex of non-tropical elements, hence Maputaland acts as a replacement -transition zone for tropical flora (Tinley 1985, D. MacDevette pers. comm.).

The coast of Maputaland is characterized by a very young, latest Pleistocene and Recent age (Maud 1980), high coastal dune ridge along the shoreline. For the most part this dune ridge has been stabilized by various plant communities, including dune forest. The forest at Cape Vidal (28°05'35" S, 32°33'40" E) forms part of this considerable dune forest block that extends, within the province of Natal, from Kosi Bay in the north as far south as Mbonambi Beach in an almost unbroken belt some 0.2 - 3.5 km wide and about 240 km long.

The study site was located within the Natal Parks Board (NPB) Cape Vidal Recreation Reserve some 35 km north of the town of St Lucia (Fig. 2.1). The dune forest in the region has been under the control of the Department of the Environment, and the presence of the NPB in the immediate vicinity has protected the dune forest from poaching and deforestation. The Cape Vidal dune forest is bounded to the west by Lake Bhangazi, a fresh water system, and to the east by the sea.

2.2.2 THE WOODY COMMUNITIES

In this brief introduction I use Weisser's (1980) classification of the plant communities of the coastal dunes. Five main plant communities occur on the coastal dunes of Maputaland, of which only three were important to the samango monkey at Cape Vidal. These were coastal thicket, dune forest and *Acacia karroo* woodland.

2.2.2.1 Coastal Thicket

This is a dense, unistratal (0 - 5 m high) community of multiple-stemmed dwarf trees and shrubs with a compact canopy (Tinley 1985). The community is situated to seaward of

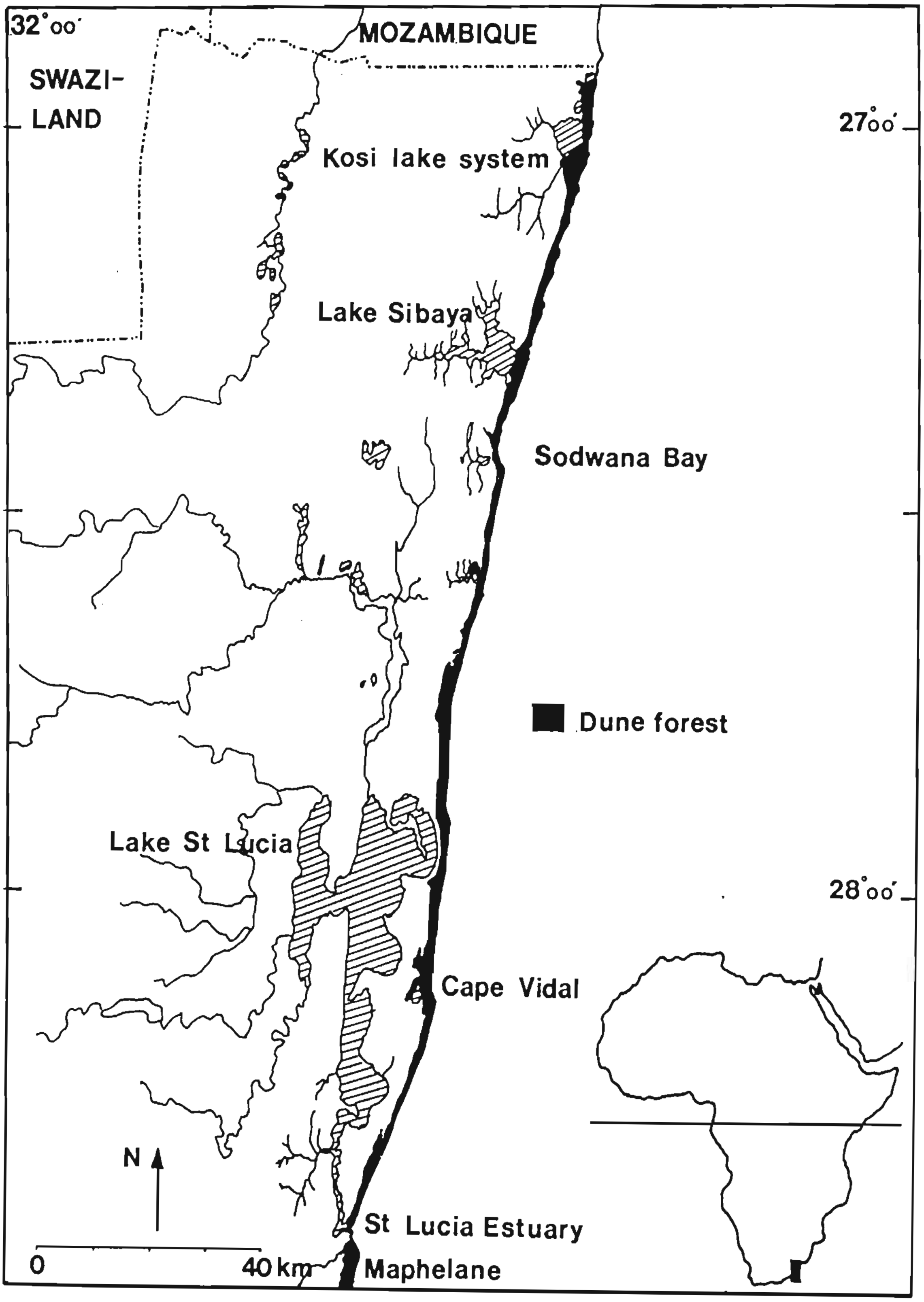

Figure 2.1. The locality of the Cape Vidal dune forest.

the dune forest proper and adjoins the dune pioneers or the beach (Fig. 2.2). The canopy is frequently wind-pruned. The total aerial cover varies from 60% to 100 %. The field layer is usually absent and a litter layer of fallen leaves and twigs is present. At Cape Vidal this community is characterized by the species Mimusops caffra, Brachylaena discolor, Crysanthemoides monilifera and Apodytes dimidiata on the seaward slopes, and included Rhus natalensis and Grewia occidentalis thickets on the leeward slopes.

2.2.2.2 Dune Forest

The dune forest is mostly evergreen, although there are some deciduous species (eg: Celtis africana). On the whole leaves are small (3-10cm) and obovate. They tend to be smooth and shiny with a brittle and hard texture characteristic of the nano-microphyll leaf size class (Tinley 1985). These leaf characteristics are exemplified by Mimusops caffra, Diospyros natalensis, Dovyalis longispina, Euclea schimperi and Rhus natalensis among others, which together form a large component of the trees at Cape Vidal. Most of these have rounded to emarginate apices, and the drip-tip feature of rain forest is absent or rare. These leaf-form characteristics are similar to those of tropical sand forest and miombo savanna woodland (Tinley 1985). The dune forest is therefore physiognomically more similar to dry forest types than to the rain forests of equatorial Africa.

Dune forest is best developed, in terms of height, structure and cover in dune troughs (Fig. 2.2). Here emergents may be found and the canopy is higher (12-18 m), consisting of large Mimusops caffra, Sideroxylon inerme and Erythroxylum emarginatum individuals. On the seaward-facing, landward slopes of the dune the forest canopy is lower (6-12 m) and wind contoured. Common species on these slopes are Olea woodiana, Drypetes natalensis and Diospyros natalensis. Dune crests are characterized, in the Cape Vidal area, by an increase in canopy height and basal area of the canopy trees compared to trees on the seaward facing slopes. The landward facing slopes of the dunes in this area were unusual because of the frequent occurrence of Ziziphus mucronata and Strychnos madagascariensis trees, species more commonly found along the forest edge.

In the dune forest three layers can usually be distinguished (Weisser 1980): canopy trees (7-18 m), understory trees (1.5-6 m), and field layer (0-1.5 m). Over most (80%) of

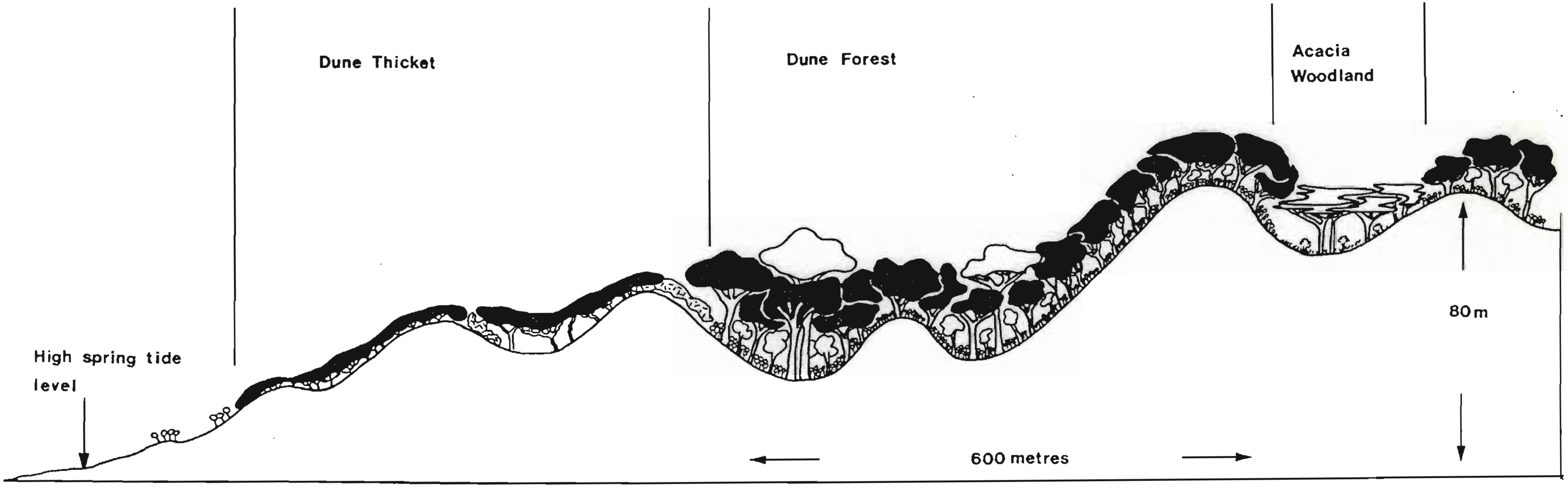

Figure 2.2. Vertical profile of a cross-section through the study area at Cape Vidal. The profile shows the relative position and crude vertical structure of the woody communities.

the study area the shrub component was dominated by Isoglossa woodii, a soft leaved suffrutex which forms a dense shrub layer from about 0.5 m to 1.5 m high.

Unlike the rain forests of equatorial regions (see Whitmore 1975) lianas were not an important structural feature of the dune forest at Cape Vidal. In other parts of the dune forest (Mapelane) lianas are of considerable importance and comprise up to 20% of canopy biomass (MacDevette, pers. com.).

Epiphytes and the semiparasitic Loranthaceae were present only in low numbers. Most large tree individuals have one or two epiphytes individuals present on their boughs.

2.2.2.3 Acacia karroo woodland

Acacia karroo typically forms dense stands on old abandoned fields and is a good indicator of the recent subsistence farming in parts of the dune forest (Weisser 1980, Tinley 1985). These woodlands occur in dune troughs well to landward of the sea. This community represents a successional stage towards the secondary dune forest (Weisser 1980). In the Cape Vidal area the undergrowth of this woodland is characterized by grasses and seedlings of tree species such as Allophylus natalensis, Celtis africana, Teclea gerrardii, and Deinbollia oblongifolia. In terms of the mammalian fauna these Acacia woodlands form an important avenue of access to the dune forest for hippo (Hippopotamus amphibius) and the kudu (Tragelaphus strepsiceros) who feed heavily on the Isoglossa herb layer.

2.2.3 CLIMATE

2.2.3.1 Rainfall

In the absence of a weather station at Cape Vidal all climatic information unless otherwise referenced was collected at St Lucia estuary, 35 km south of Cape Vidal, and supplied by the Computer Centre for Water Research, Univ. of Natal, Pietermaritzburg. The mean monthly rainfall (mm) for the period 1915 to 1987 is illustrated in Figure 2.3 and that for the study period in Figure 2.4. It is clear that there is a single rainfall season during the months November through April and during this 'wet season' the mean monthly rainfall is greater than 100 mm. The mean annual rainfall on the coast is 1155.9 mm (n=60 years, V=29.4%).

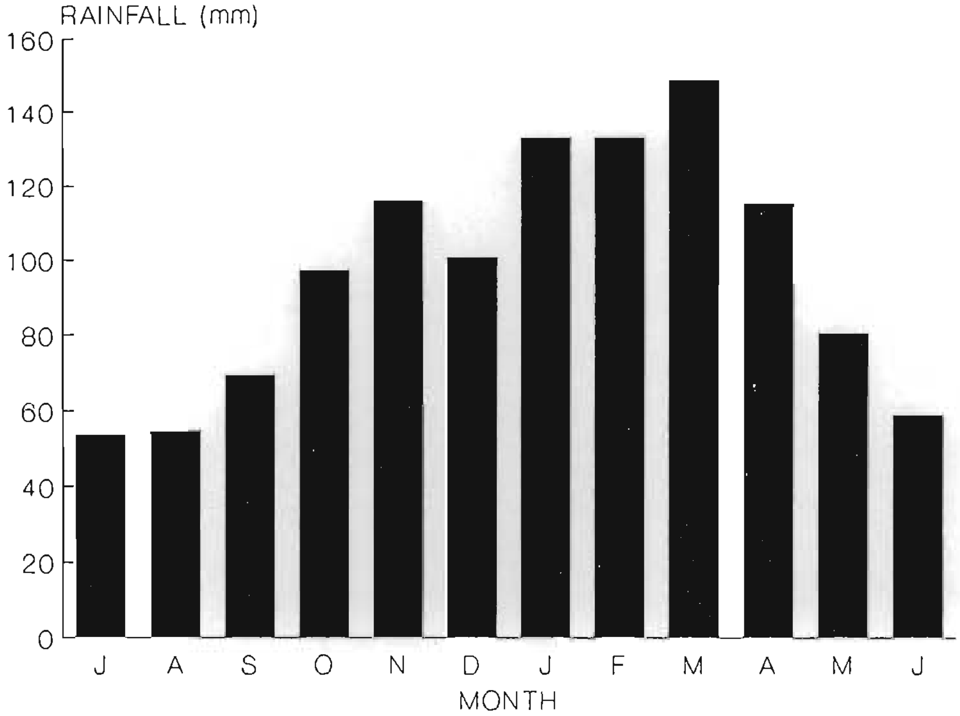

Figure 2.3. The mean monthly rainfall (mm) at St. Lucia estuary during the years 1915 through 1987.

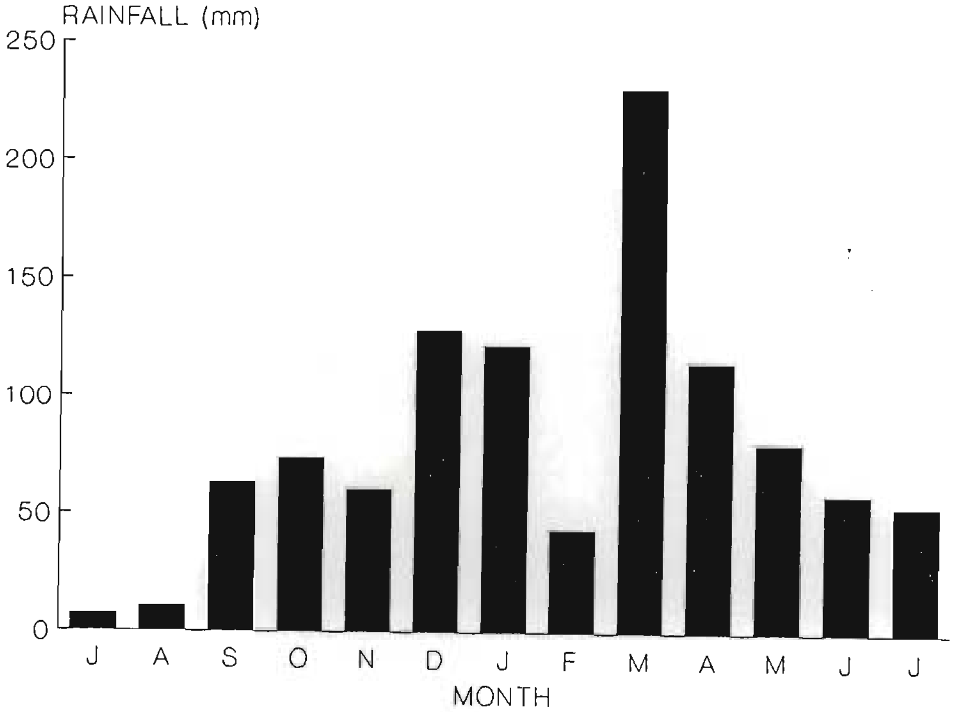

Figure 2.4. The monthly rainfall (mm) recorded from St Lucia estuary for the study period, July 1986 to July 1987.

2.2.3.2 Temperature

The ambient temperature ranged between 13.5 °C and 28 °C while the mean monthly temperature was 21.3 °C. The monthly variation in temperature for St Lucia estuary is given in Figure 2.5. Humidity along the Maputaland coast can reach as much as 88% and as little as 56% (Maud 1980).

2.2.4 THE FAUNAL COMPLEMENT

The faunal complement of the Cape Vidal study area is reasonably diverse although fewer mammal species are found in this area compared to equatorial African forests. Where an ecological niche might support 2 or 3 mammal species in central Africa the niche, if present, seldom has more than 1 or 2 representative species at these southern latitudes. For example, only a single duiker species, the red duiker (Cephalophus natalensis) is found at Cape Vidal as opposed to two duiker species in the Kibale forest (Rudran 1978a). Common mammals that frequented the study area are: red duiker (Cephalophus natalensis), bushbuck (Tragelaphus scriptus), bushpig (Potamochoerus porcus), porcupine (Hystrix africaeaustralis), banded mongoose (Mungos mungo), red squirrel (Paraxerus palliatus tongensis), red veld rat (Aethomys chrysophilus) and the pouched mouse (Saccostomus campestris). The primates are comparatively poorly represented and include only three species: thick tailed bushbaby (Galago crassicaudatus), vervet monkey (Cercopithecus pygerythrus) and the samango monkey (Cercopithecus mitis erythrarchus). Beyond the limits of the study area, hippo (Hippopotamus amphibius) and kudu (Tragelaphus strepsiceros) were seen occasionally in the forest. Large predators were absent although it is quite possible that there are leopard in the region.

Between 200 and 250 birds species are listed from the coastal area around Cape Vidal (Cyrus and Robson 1980). Somewhat fewer species would be scored from the forest itself and the probable total is around 150 species. Frugivorous bird species were not notably abundant and included the purple crested loerie (Tauraco porphyreolophus), four members of the barbet family Capitonidae and the crowned hornbill (Tockus alboterminatus). Although the crowned eagle (Stephanoaetus coronatus) was present it

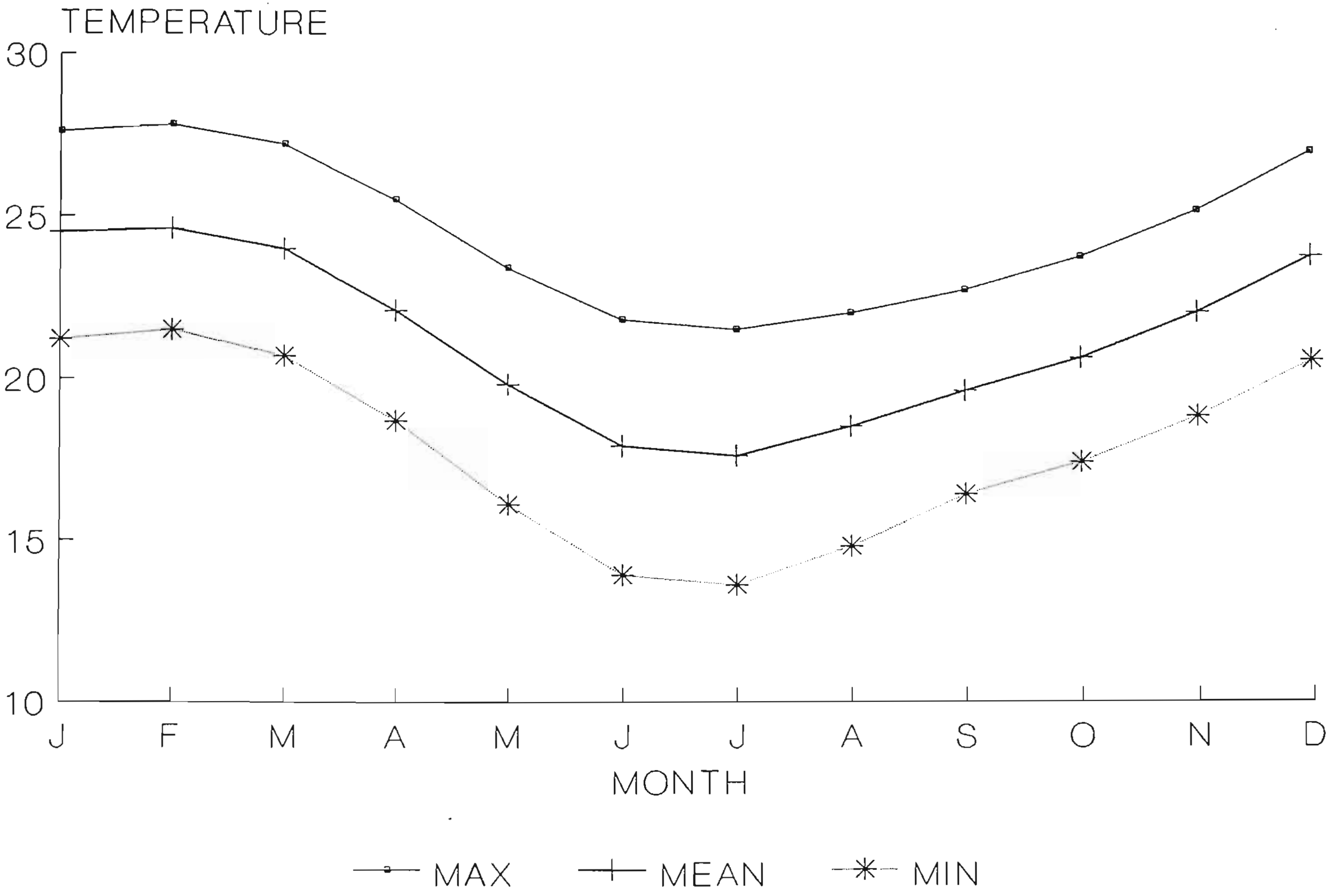

Figure 2.5. The monthly mean, minimum and maximum temperatures recorded from St. Lucia estuary during the years 1915 through 1987.

was seldom seen. The monkeys did, however, react by ducking and dropping into the canopy whenever any bird of similar size flew overhead.

2.3 METHODS

The level of habituation of the monkeys was an important factor in the ultimate selection of the study area. A troop was chosen that was known to enter the public campsite on occasion. This troop was the least skittish of the troops in the area and was named the Camp Troop. After three months (April 1986 - June 1986), the troop was totally habituated and comfortable in my presence and tolerated my presence to within 20-30m in most instances. The home range of the troop was then divided into 50 x 50 m grid cells. Paths were cut to define the boundaries of the cells, the corners of which were marked with yellow marker boards.

The study area or home range of the troop was roughly rectangular in shape (Fig. 2.6). The eastern periphery of the home range was demarcated by the coastal beach and the associated coastal scrub and scrub-thicket communities. Running the whole length of the western edge was a narrow strip of Acacia karroo woodland some 70m wide. The southern limit of the home range was demarcated by an access road while, to the north, parts of the public campsite infringed on the home range boundary.

The primary objective of the study was to determine the ecological relationships between the samango monkey and its habitat, the forest. Thus while the aim of pure botanical investigation might be to determine the density and species composition of the canopy and the understory tree components as accurately as possible for a forest site, I was more concerned with determining the relative density and physiognomic measurements of the representative flora in the study area only. A plotless sampling technique, the point-centred quarter (PCQ) method (Cottam and Curtis 1956, Mueller-Dombois and Ellenberg 1974), was used for these purposes and yielded data on the relative importance of the plant species within the study area.

The home range of the study troop included sixty clearly demarcated 50 x 50 metre quadrats. In each quadrat a point was randomly selected and a single PCQ measurement was made. The axes defining each quarter about the point were determined by fixed compass bearings. Within each quarter the nearest canopy and

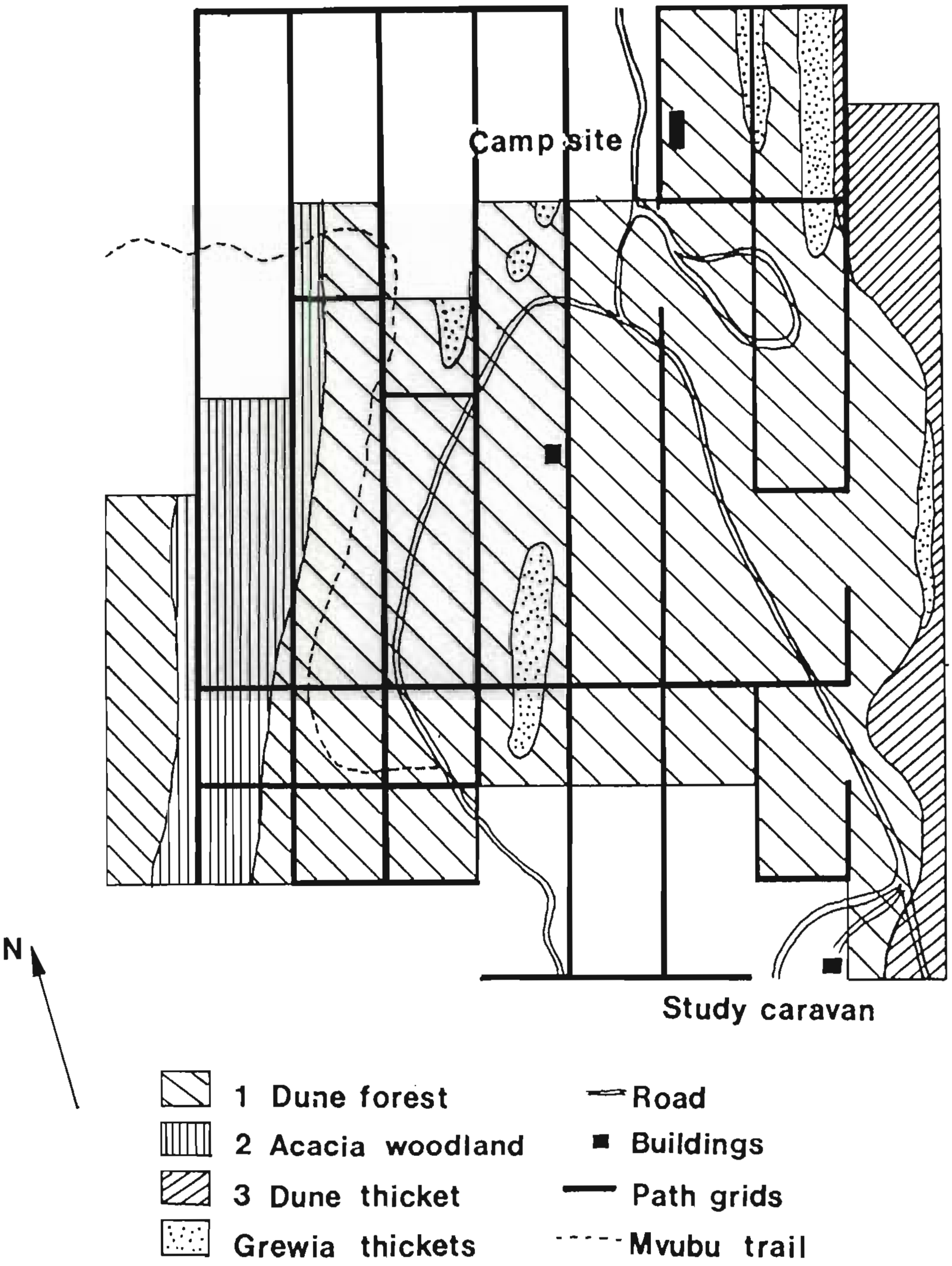

Figure 2.6. Map of the Cape Vidal dune forest study site, showing the distribution of the woody communities, and paths used to follow the monkeys.

understory tree was identified. Canopy trees were distinguished from understory trees on the basis of their circumference at breast height (CBH). Canopy trees had a CBH greater than 25 cm and a crown that contributed to the canopy stratum. Understory trees had a CBH of not less than 5 cm and their crown did not reach the canopy stratum. The species, distance from the point, CBH, height of the tree, depth of the canopy, and the percent canopy overlap were measured for the nearest neighbour trees of both canopy and understory in each quadrat. The following measurements were also recorded from canopy trees:
(1) The percentage proportion of the canopy circumference that was in close contact with neighbouring canopies permitting monkey movement (estimate of canopy perimeter continuity), (2) the diameters D1 and D2 of the canopy at right angles to each other, canopy depth was measured as the height to the lower branches of the canopy subtracted from the height of the tree, (3) the values of D1, D2 and canopy depth were then combined to provide a theoretical rectangular canopy volume. (4) An estimate of the percentage volume of the rectangular canopy volume (percent volume - % vol) actually occupied by the canopy was made for each canopy tree measured.

Within a 25 m^2 area centred at the PCQ point the following measurements were made;

(1) Shrub density - measured along two transects of 12.5 m each from the central point and running at right angles. All 'shrubs' of greater than 3 cm but less than 15 cm CBH that fell within the area beneath the observer's body and outstretched arms were counted along each transect. Counted stems only included the main stem and those branching from the main stem below breast height. Shrub density was represented as the number of stems per unit area covered in this manner.

(2) The vertical structure of the 25 m^2 area was assessed. Eight height classes were chosen and the biomass of the vegetation in each was ranked on a scale of 0 -5. The ranks for each height class were summed and the mean value was used to illustrate the vertical structure of the forest at that point.

0 - 1 m
1 - 3 m
3 - 5 m
5 - 10 m
10 - 15 m
15 - 20 m
20 - 25 m
25 - 30 m

0 - Absent
1 - Rare, 1/20 of stratum
2 - Present, 1/20 - 1/4 of stratum
3 - Numerous, 1/4 - 1/2 of stratum
4 - Abundant, 1/2 - 3/4 of stratum
5 - Dominant, > 3/4 of stratum

2.4 RESULTS

2.4.1 Forest structure

To determine the number of plots required to adequately represent the plant communities within the home range area, I plotted the species/point curves for canopy and understory during the PCQ sampling period (Fig. 2.7). When the curves reached an asymptote and remained unchanged for 10 points of analysis, the data collection was terminated. In the final analysis a total of 48 points within the 15 hectare home range was sampled. A total of 384 individuals (canopy=192 and understory=192) of 33 species was sampled in this manner, and only more intensive quadrat sampling would have included the rarely eaten tree species which were not encountered in this sample.

Table 2.1 and Table 2.2 list the data used in subsequent analyses of the diet and feeding behaviour. These are derived from the PCQ analyses for the canopy and understory tree strata respectively.

Canopy tree density in the home range of the troop was 278.4 individuals/ha. Understory tree density was 320.5 individuals/ha. The total tree density estimate was therefore of the order of 599 individuals/ha.

The total basal area of canopy trees and understory trees at Cape Vidal was 44.06 m^2/ha and 11.47 m^2/ha respectively. The basal area value for understory trees is particularly low. The latter is probably due to the presence of Isoglossa woodii. It has been suggested that this dense vegetation (up to 70% ground cover) could be an important factor in preventing the establishment of seedlings of other species in the dune forest (Ward 1980, Weisser 1980), especially the light demanding thicket and climber elements (Tinley 1985). Isoglossa woodii has a growth periodicity of about 10 years culminating in a single flowering and fruiting period followed by death and new growth from seed (Ward 1980). During 1987 Isoglossa flowered and fruited over most of the study area and was heavily used by the monkeys. Unfortunately this event was not anticipated and as I could not quantify the shrub layer using the PCQ technique no quantitative measurements of the Isoglossa layer were made.

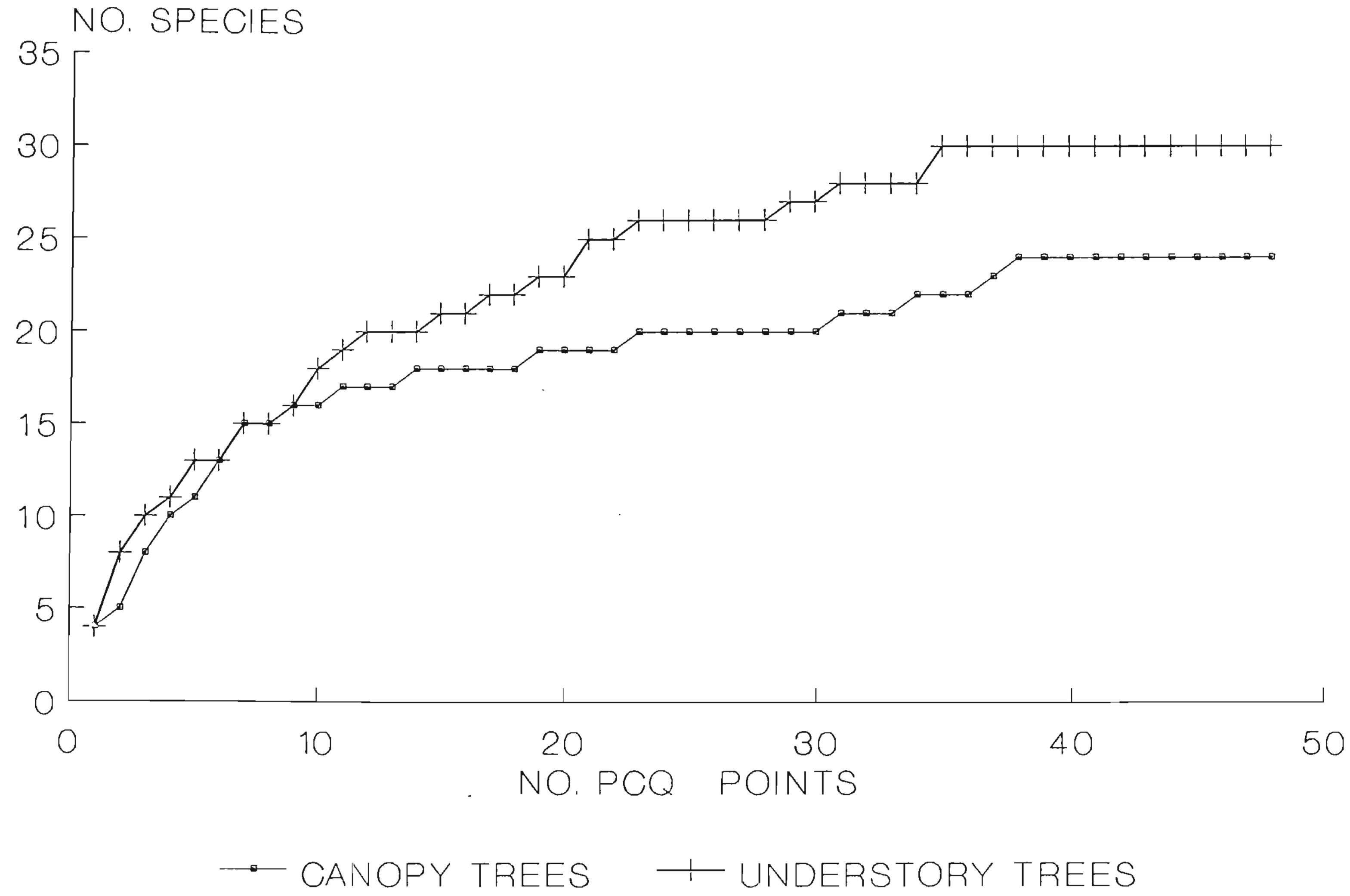

Figure 2.7. The cumulative increase in number of tree species with the increase in PCQ sample points.

Table 2.1. The importance values of the canopy tree species and their canopy biomass, determined from point-centred-quarter analysis of canopy layer within the home range of the study troop.

SPECIES	NO. OF TREES	ABSOLUTE DENSITY/ha	DOMINANCE	RELATIVE DENSITY	RELATIVE DOMINANCE	RELATIVE FREQUENCY	IMPORTANCE VALUE	MEAN CANOPY BIOMASS	RELATIVE CANOPY BIOMASS
Mimusops caffra	41	59.45	67187.82	21.35	25.47	17.24	64.06	550.04	43.25
Sideroxylon inerme	17	24.65	38674.38	8.85	14.66	11.72	35.23	399.35	13.02
Diospyros inhacensis	15	21.75	34506.49	7.81	13.12	8.97	29.90	176.97	5.09
Olea woodiana	15	21.75	21197.88	7.81	8.04	10.34	26.19	217.11	6.25
Acacia karroo	25	36.25	8164.52	13.02	3.10	4.83	20.95	84.65	4.06
Diospyros natalensis	15	21.75	6884.28	7.81	2.61	8.28	18.70	131.23	3.78
Euclea schimperi	11	15.95	4779.50	5.73	1.81	6.90	14.44	57.23	1.21
Apodytes dimidiata	7	10.15	15223.56	3.65	5.77	4.14	13.56	304.47	4.09
Strychnos madagascariensis	6	8.70	14256.82	3.12	5.41	3.45	11.98	304.50	3.50
Ziziphus mucronata	7	10.15	9002.40	3.65	3.41	3.45	10.51	288.60	3.87
Scolopia zeyheri	5	7.25	10205.65	2.60	3.87	2.76	9.23	332.50	3.19
Celtis africana	5	7.25	9072.62	2.60	3.44	2.76	8.80	281.48	2.70
Dovyalis longispina	3	4.35	7616.69	1.56	2.89	2.07	6.52	216.85	1.25
Teclea gerrardii	4	5.80	2648.46	2.08	1.00	2.76	5.84	131.57	1.01
Ochna natalitia	4	5.80	1905.53	2.08	0.72	2.76	5.56	65.51	0.50
Trichelia emetica	2	2.90	3810.69	1.04	1.44	1.38	3.86	211.72	0.81
Allophyllus natalensis	3	4.35	1538.53	1.56	0.58	1.38	3.52	71.06	0.41
Clerodendrum glabrum	1	1.45	3992.03	0.52	1.51	0.69	2.72	675.00	1.29
Drypetes natalensis	2	2.90	407.10	1.04	0.15	1.38	2.57	64.93	0.25
Cordia caffra	1	1.45	1321.10	0.52	0.50	0.69	1.71	138.54	0.27
Euclea natalensis	1	1.45	893.58	0.52	0.34	0.69	1.55	26.50	0.05
Trema orientalis	1	1.45	175.51	0.52	0.07	0.69	1.28	39.94	0.08
Deinbollia oblongifolia	1	1.45	175.51	0.52	0.07	0.69	1.28	42.24	0.08
TOTAL	192 Trees	278.40 IND/ha	263640.65 cm²	99.96 %	99.98 %	100.02 %		9811.99 m^3	99.99

IMPORTANCE VALUE = Relative Density + Relative Dominance + Relative Frequency

Table 2.2. The importance values of the understory tree species and their crown biomass, determined from point-centred-quarter analysis of canopy layer within the home range of the study troop.

SPECIES	NO. OF TREES	ABSOLUTE DENSITY/ha	DOMINANCE	RELATIVE DENSITY	RELATIVE DOMINANCE	RELATIVE FREQUENCY	IMPORTANCE VALUE	MEAN CANOPY BIOMASS	RELATIVE CANOPY BIOMASS
Euclea schimperi	27	45.06	2737.35	14.06	15.12	11.66	13.61	14.00	8.20
Diospyros natalensis	24	40.05	2506.31	12.50	13.85	11.66	12.67	52.19	27.18
Drypetes natalensis	18	30.04	1881.60	9.38	10.39	8.59	9.45	33.06	12.92
Dovyalis longispina	13	21.70	1950.90	6.77	10.78	7.36	8.30	37.44	10.57
Ochna natalitia	16	26.70	1040.17	8.33	5.75	9.20	7.76	19.80	6.88
Teclea gerrardii	13	21.70	1522.11	6.77	8.41	6.13	7.10	30.49	8.61
Diospyros inhacensis	11	18.36	1108.43	5.73	6.12	6.13	6.00	12.68	3.03
Allophyllus natalensis	7	11.68	1519.47	3.65	8.39	3.68	5.24	35.78	5.44
Tricalysia sonderiana	8	13.35	435.67	4.17	2.41	4.91	3.83	12.72	2.21
Mimusops caffra	6	10.01	415.44	3.13	2.30	3.68	3.03	11.20	1.46
Olea woodiana	5	8.34	462.80	2.60	2.56	3.07	2.74	16.92	1.84
Celtis africana	8	13.35	179.55	4.17	0.99	3.07	2.74	11.67	2.03
Deinbollia oblongifolia	5	8.34	435.18	2.60	2.40	3.07	2.69	3.21	0.35
Maytenus heterophylla	4	6.68	578.50	2.08	3.20	2.45	2.58	31.27	2.72
Scolopia zeyheri	4	6.68	223.25	2.08	1.23	2.45	1.92	11.01	0.96
Clerodendrum glabrum	4	6.68	119.52	2.08	0.66	1.84	1.53	12.16	1.06
Clausena anisata	2	3.34	152.99	1.04	0.85	1.23	1.04	3.33	0.14
Sideroxylon inerme	2	3.34	101.00	1.04	0.56	1.23	0.94	29.41	1.28
Canthium inerme	2	3.34	95.89	1.04	0.53	1.23	0.93	6.60	0.29
Trema orientalis	2	3.34	186.53	1.04	1.03	0.61	0.90	9.26	0.40
Kraussia floribunda	2	3.34	76.76	1.04	0.42	1.23	0.90	8.99	0.39
Bauhinia tomentosa	2	3.34	23.97	1.04	0.13	1.23	0.80	17.25	0.75
Erythroxylum emarginatum	1	1.67	119.52	0.52	0.66	0.61	0.60	11.66	0.25
Euclea natalensis	1	1.67	70.25	0.52	0.39	0.61	0.51	32.55	0.71
Acacia karroo	1	1.67	38.38	0.52	0.21	0.61	0.45	0.01	0.00
Acokanthera oppositifolia	1	1.67	34.00	0.52	0.19	0.61	0.44	6.19	0.13
Rothmania globosa	1	1.67	29.88	0.52	0.17	0.61	0.43	3.70	0.08
Trichelia emetica	1	1.67	29.88	0.52	0.17	0.61	0.43	4.69	0.10
Pavetta revoluta	1	1.67	26.03	0.52	0.14	0.61	0.43	2.30	0.05
TOTAL	192	320.45	18101.33	99.98	100.01	99.98		481.50	100.03
	Trees	IND/ha	cm^2	%	%	%		m^3	

IMPORTANCE VALUE = Relative Density + Relative Dominance + Relative Frequency

The circumference of trees at breast height (CBH) in both the canopy and understory tree samples revealed a positively skewed frequency distribution (Fig. 2.8). Some 80.2% of the canopy tree sample (154 trees) had a CBH of less than 150 cm. Most of the canopy trees were thus of relatively small size and mean canopy height was 13.0 m (s=2.82 m, n=192). In the canopy tree sample the median CBH was 94.5 cm and, in the understory tree sample 23 cm. Canopy emergents were rare but could achieve a height of 25 m. Emergents, mostly Mimusops caffra, were found in the dune trough.

The dune forest is characterized by a low, close knit canopy stratum (mean canopy continuity = 83.4%). The canopy crowns were for the most part interlocked and the majority of trees sampled had a high percent canopy continuity value (Fig. 2.9). Furthermore the comparative absence of emergents meant there was little obstruction to movement between crowns. The importance of terminal branches and their limitation on the mechanics of movement by the different age-sex classes was considerably reduced by the interlocking nature of the crowns. The upper crown of the understory layer merges with the lower canopy stratum to provide an almost continuous stratum from understory to canopy crown in some areas (Fig. 2.10). Although the canopy was low in height the dense nature of the crown often made observation difficult.

A consequence of the smaller stature of the Cape Vidal dune forests relative to equatorial lowland rain forest is a reduced canopy biomass. The mean total canopy biomass per hectare was 75605.9 m^3. The mean canopy biomass of an individual tree was 426.6 m^3 (range = 39.94 - 675.0 m^3).

2.4.2 Forest composition

PCQ analysis provides an economical alternative to the time consuming quadrat sampling methods. However, the PCQ method does not provide as complete species-composition information. As a result species diversity indices for the Cape Vidal dune forest could not be calculated from these data with any confidence. Quadrat samples (20x20 m) which included all vegetative components excluding mosses and lichens show a wide range in species richness and diversity from the dune forests in the near vicinity of Cape Vidal (K. MacDevette, unpub. data). At Mapelane (40 km south) species

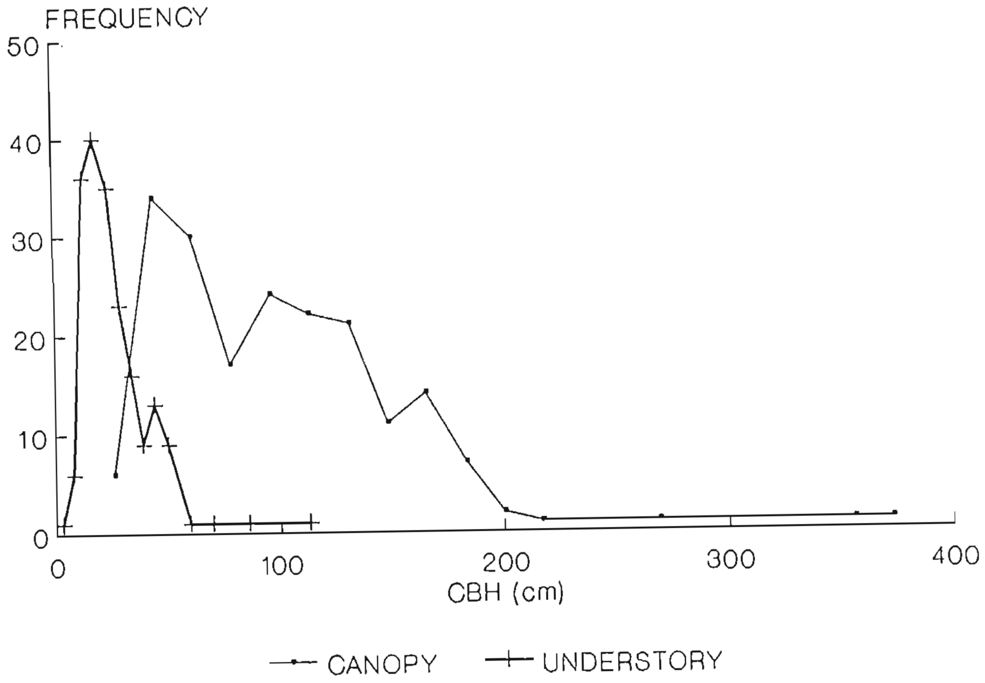

Figure 2.8. The tree frequency distribution of stem circumference (CBH) for canopy and understory trees at Cape Vidal.

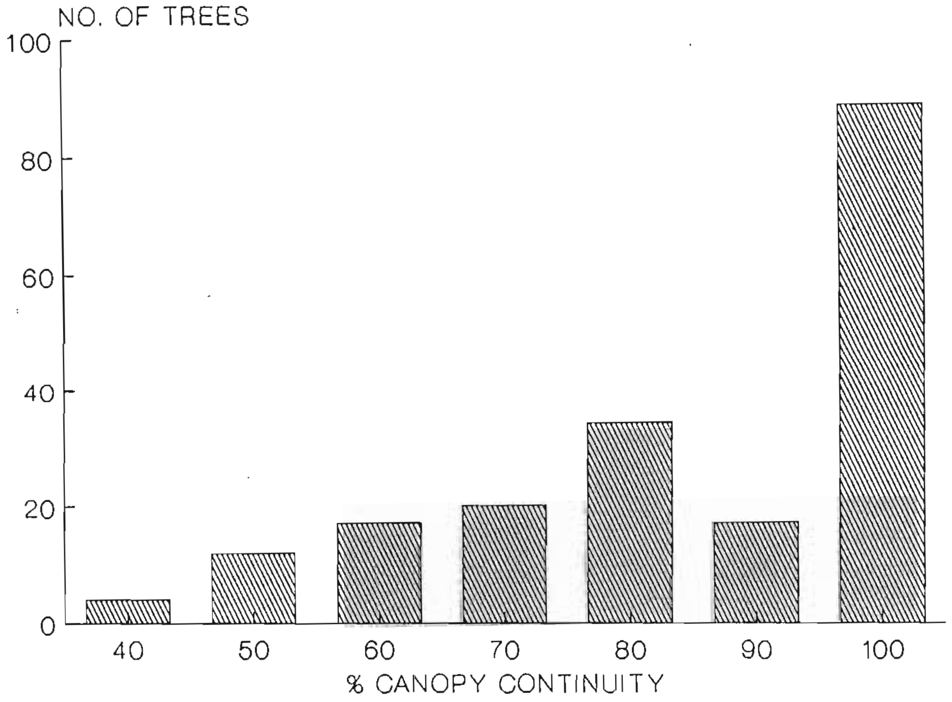

Figure 2.9. The frequency distribution of canopy trees within percent canopy -crown-continuity classes (see text for details).

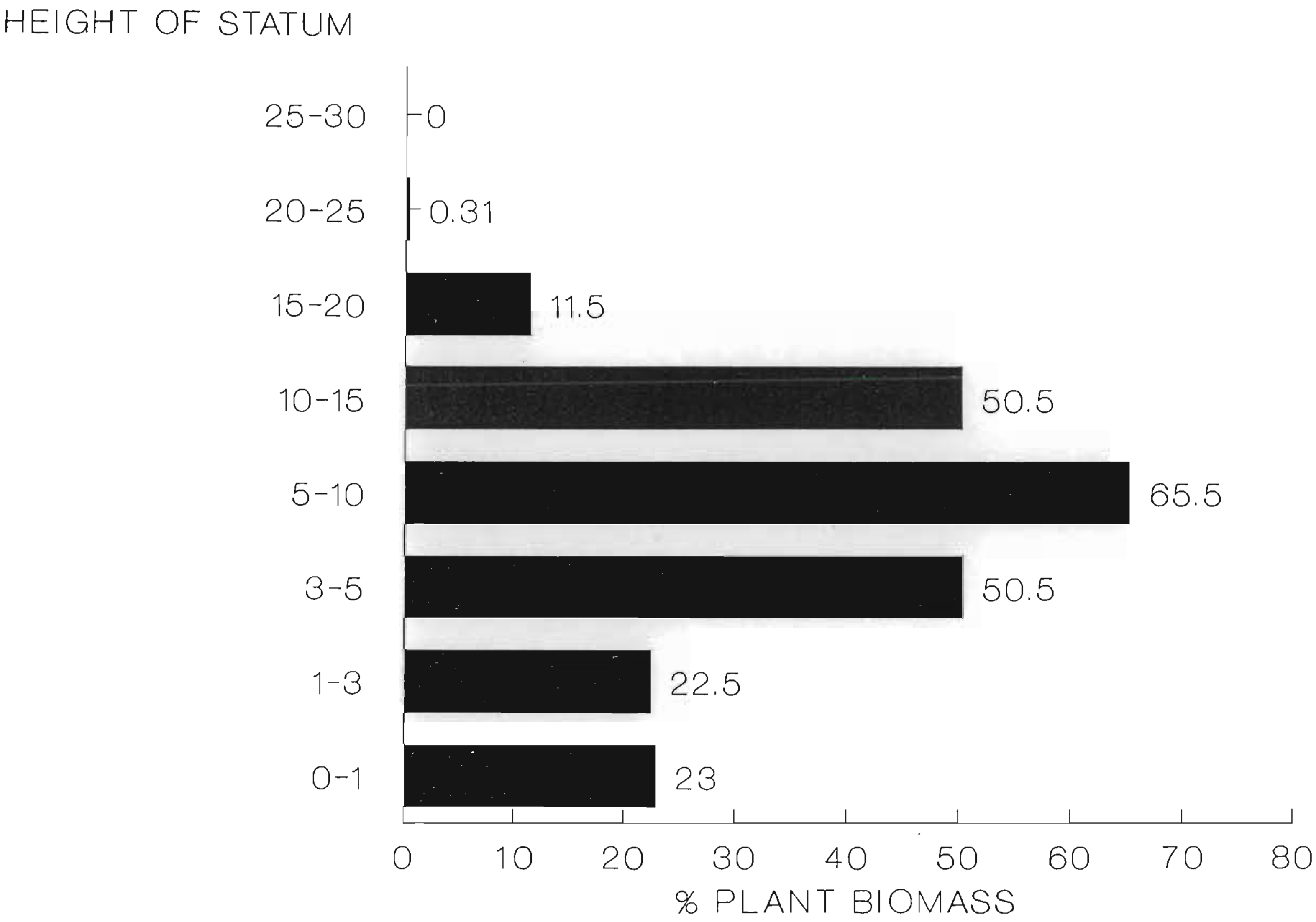

Figure 2.10. The mean percent plant biomass recorded for a canopy stratum (see text for details).

richness ranges from 73.3-86.7 species ha^{-1}, while at Sodwana Bay (80 km north) species richness is 63.0-126.3 species ha^{-1}. A mean of these estimates provides an approximate estimate of species richness for the coast from Sodwana Bay to Mapelane including Cape Vidal, of 87.32 species ha^{-1}. Shannon-Weiner diversity indices for the coastal dune forest based on Whittaker plots, range from 2.99 - 3.65 (K. MacDevette, unpub. data).

A checklist for the woody communities on the dunes of Maputaland by Weisser and Drews (1980) lists 390 species. The species composition of the dune forest in Maputaland varies depending on the environmental conditions, successional stage and topography. A total of 23 canopy species and 29 understory species were recorded during the PCQ analysis. It should be noted that these values represent trees only and do not include either the shrub, thicket, and herb layers or epiphytes and lianas.

Within the study area at Cape Vidal importance values (IV) derived from PCQ analysis for canopy tree species give the following results (Table 2.1): Mimusops caffra 21.4%, Sideroxylon inerme 11.8%, Diospyros inhacensis 10.0%, Olea woodiana 8.7%, Acacia karoo 7.0%, Diospyros natalensis 6.3%, Euclea schimperi 4.8%, Apodytes dimidiata 4.5%. The importance values for understory trees are as follows (Table 2.2): Euclea schimperi 13.6%, Diospyros natalensis 12.7%, Drypetes natalensis 9.5%, Dovyalis longispina 8.3%, Ochna natalitia 7.8%, Teclea gerrardii 7.1%, Diospyros inhacensis 6.0%, Allophyllus natalensis 5.2%, Tricalysia sonderiana 3.8%, and accounted for 74.0% of the total for all understory species.

All of the 23 canopy species recorded during the PCQ analysis were used as food species, and only three of the 29 understory species recorded were not observed in the diet.

Although many lianas were occasionally eaten by samangos, their contribution to the diet was negligible and I did not attempt to quantify their presence. Similarly, I did not attempt to quantify the extent or relative density of Grewia occidentalis thicket (except in crude manner, see Chapter 8) whose fruits and flowers formed a significant fraction of the troops diet (8.6%), but whose physiognomy made such a task impossible using PCQ plots.

2.5 DISCUSSION

2.5.1 Comparisons with other C. mitis study sites

2.5.1.1 Climate

Although all terrestrial environments are seasonal to some extent, climate is more seasonal at Cape Vidal than at lower latitudes. Whittaker's (1975) classification of terrestrial biomes in relation to mean annual temperature and precipitation places the Cape Vidal forest in the tropical seasonal biome. The distinction between wet and dry seasons was defined by mean monthly rainfall of greater and less than 100 mm respectively at Cape Vidal. At Kakamega (Kenya) mean monthly rainfall was greater than 100 mm for all months except December from 1976-1981 (Cords 1987). Mean annual rainfall at Cape Vidal is 300 mm to 1115 mm lower than in the Budongo and Kakamega forests respectively (Aldrich-Blake 1970, Cords 1987). Annual rainfall is also concentrated into 6 months (November to April) at Cape Vidal when monthly rainfall averages 123.9 mm (s = 16.9 mm) as opposed to 68.7 mm (s = 17.1 mm) during the 'dry season' (May to October). Unlike Cape Vidal there is a bimodal peak in the distribution of rainfall at lower latitudes including the Kakamega (Cords 1987) and Kibale forests (Struhsaker 1975).

2.5.1.2 Vegetation

Compared to other forest types within the province of Natal, R.S.A, the dune forest has a comparatively high plant species richness and diversity (Table 2.3). Dune forests and coastal lowland forest are notable among Natal forests for their low canopy height. The vertical structure of dune forest contrasts strongly with that of coastal scarp, mistbelt Podocarpus, swamp and sand forests. The grass and herb layer is poorly represented in coastal forest, while the shrub layer is almost completely dominated by Isoglossa woodii. Although emergents are more common in the other forest types this is in all likelihood related to a recent disturbance history (i.e. logging) especially in coastal scarp and mistbelt Podocarpus forest (e.g. Karkloof forest cf. Fourcade 1889, Rycroft 1944, Cooper 1985; also Marwick 1973, Brink and Van der Zel 1980). The canopy crown is

Table 2.3. Comparative forest composition and structure for forests in Natal where samango monkeys are found. Species richness and diversity values include all plant species from ferns upward to flowering plants.

Forest	Ngome	Karkloof	Fort Nottingham	Hluhluwe	Dukuduku	Cape Vidal[1]		
Forest type	Mistbelt *Podocarpus* forest	Mistbelt *Podocarpus* forest	Mistbelt *Podocarpus* forest	Coastal scarp forest	Coastal lowland forest	Dune forest	Swamp forest	Sand forest
Species richness[3] per Ha	86	73	60	97	90	87	44	66
Species diversity[3] Shannon-Wiener	2.86	2.97	2.87	3.75	3.39	3.35	2.14	2.60
Canopy height[4]	16-20 m	16-18 m	16-18 m	15-18 m	12-16 m	10-16 m	12-18 m	12-14 m
Altitude	1400 m	1000 m	1524 m	750 m	50 m	20 m	40 m	100 m
Rainfall/annum	1200 mm	1400 mm	1200 mm	1000 mm	1300 mm	1100 mm	1100 mm	500 mm
Mean annual temperature °C	18	17	13	21	22	22	21	22

1. Cape Vidal species values are estimates from Macdevette et al. 1988 for dune forest (Sodwana, Mapelane).
2. Swamp forest and sand forest species values represent the mean value derived from two swamp forests (Mfabeni, Richards Bay) and one sand forest (Zinave) respectively.
3. Species richness and diversity values are the highest estimates provided for a forest by MacDevette et al. (1988) and includes all plants from ferns upward.
4. Canopy height estimates from MacDevette et al. 1988.

Climatic data taken from Schulze 1982.
Forest types after Cooper 1985.

therefore more continuous in dune forest. In general, dune forest in Natal forms a well conserved, mature forest type of low stature.

The extent of the dune forest (14 491 ha), its relatively good condition and protected state, favours dune forest as an important forest habitat for the samango monkey in Natal and the *mitis* species group in general.

The Cape Vidal dune forest differs from other forests in Africa in which the *mitis* species group has been studied, mainly in the lower canopy height and biomass, a lack of emergent trees, less woody climbers and lower species diversity (Table 2.4).

The forest canopy is considerably lower than other Central and East African forests (Table 2.5) and emergents are rare. The canopy crown is thus closed, fairly uniform in height, and canopy depth is seldom greater than 5 metres. The available plant biomass contained in the canopy stratum is considerably less than that available in equivalent East African forests (Table 2.5). The dimensions of the 3-dimensional spatial niche are smaller and the potential plant food biomass available per unit area is reduced for an arboreal animal. Per unit area the samango monkey at Cape Vidal therefore has less living space than its east African counterparts.

However, movement about the canopy for a primate is more easily accomplished at Cape Vidal than in forests such as Kibale or Kakamega. The almost uniform canopy height, the absence of emergents and the crown contouring effects of the coastal winds at Cape Vidal provide a continuous canopy stratum. The presence of emergents and the variation in canopy height tend to break up the canopy crown in other forests. In addition to making movement easier, the continuous canopy crown at Cape Vidal increases the accessibility of food held on terminal branches.

The dune forest differs in another important respect to lowland forests like Kibale and Kakamega, in the absence of figs (Ficus spp.). The extensive literature on the biology of members of the widespread moracean genus Ficus indicates these plants as focal species for a wide variety of frugivores (Tonin and Lawes, in prep., Janzen 1979, Breitwisch 1983, Jordano 1983, Ghiglieri 1984), by producing large crops of highly edible fruits. A noteworthy point regarding figs is that their obligate mutualism with pollinating agaonid wasps has largely released them from seasonal constraints on fruiting patterns, with a consequent potentially year-round supply of syconia from different trees. Janzen (1979) indicates that fruits of Ficus are relatively high in protein and low in toxins when ripe. The importance of Ficus as a food species for primates should not be underestimated. For instance Rudran (1978a) recorded a total percent frequency of use of figs by blue monkeys (Group II) at Kibale of 27.2 % of plant food observations. The seasonality of fruit production at Cape Vidal is further emphasized by the absence of figs whose sporadic fruiting patterns are used to good effect in other forests (Tonin and Lawes, unpub data).

Table 2.4. Characteristic features of the dune forest vegetation in the vicinity of Cape Vidal (28° 05'S 32° 33'E).

Canopy height	6 - 16 m
Emergent trees	uncommon, often absent, to 25 m tall
Leaves	simple, although compound leaves are common in secondary forest types ie: <u>Acacia</u> woodland. Trifoliate more common than the pinnate condition
Characteristic leaf size	nanophyll - microphyll <25 mm - 75 mm length
Buttresses	absent
Cauliflory	rare
Woody climbers	present, can be common
Vascular epiphytes	rare
Non-vascular epiphytes	rare

A latitudinal gradient in numbers of plant and mammal species in forest with increasing latitude is evident for those forests in which the <u>mitis</u> species group has been studied (Kibale - Kakamega - Zomba - Cape Vidal). Thus plant species diversity and richness is lower at Cape Vidal than at Kakamega, while Kakamega is in turn poorer in plant species than Kibale and so on (Hamilton 1974). Latitudinal gradients in species diversity are recognized for both faunal and floral elements (Dobzhansky 1950, Pianka 1966, Karr and Roth 1971, Fleming 1973, Hamilton 1974, Rohde 1978, Hubbell 1979, Deshmukh 1986) world-wide. Although most of the literature relates to the Americas it is clear that

Table 2.5. Comparative forest tree composition and structure for those forests where the <u>mitis</u> species group has been studied.

	Kibale[1]	Kibale[2]		Zomba[3]	Kakamega[4]	Budongo[5]	Kahuzi-Biega[6]	Cape Vidal
		Kanyawara	Ngogo					
Tree density (Ha^{-1})	328	268	404					278
Species richness (Ha^{-1})	35.7	4.54 per 0.025 ha	5.45		62 per 21.78 ha	55 per 1.45 ha		
Species diversity		2.77	2.79		3.45			
Basal cover (m^2/ha)		39	48					44
Canopy height	25-30 m			13 m	33 m	21-37 m		13 m
Emergent height	55 m				50 m	55 m		25 m
Altitude	1500 m	1500 m	1350 m	1830 m	1580 m	1005 m	2000 m	10 m
Rainfall/annum	1475 mm	1570 mm	1490 mm	2000 mm	2215 mm	1400 mm		1156 mm
Temperature range (°C)	13-26	16-23	17-24		11-29	max 24-32	13-24	13-28
Forest type	Lowland			Montane	Lowland	Lowland	Montane	Coastal

1. Struhsaker 1975, Rudran 1978a
2. Butynski 1990
3. Beeson 1987, Chapman and White 1970
4. Zimmerman 1972, Cords 1987
5. Langdale-Brown et al. 1964, Aldrich-Blake 1970
6. Schlichte 1975, Schlichte 1978

similar trends exist in Africa. This provides an interesting basis for comparison of the feeding ecology of these <u>mitis</u> populations. Gentry (1982) has shown that forest tree species richness in the neotropics declines from around 150 species at 3000 mm to 50 species at 1000 mm mean annual rainfall. At Kibale as many as 35 tree species ha^{-1} were recorded by Struhsaker (1975). This is more than were found in 48 PCQ plots over 15 ha at Cape Vidal (33 tree species total). A comparison of the species richness values in Table 2.5 emphasizes the relative paucity of tree species in southern African forests. A checklist for all the woody communities on the dunes of Maputaland by Weisser and Drews (1980) lists about 390 species. Breen and Jones (1971) list 147 woody plant species for the dune forest in the Sibaya area (90 km north of Cape Vidal), while 100 tree species (probably closer to 125 tree species) are positively identified from Kakamega forest alone (Zimmerman 1972).

The significance of latitudinal trends in plant species diversity are obvious for a widely distributed species such as the C. mitis species group. Towards the southern limits of its range the mitis species group is confronted with less variety in the plant component on which to base the diet. In addition, the plant biomass decreases with an increase in latitude. Thus not only do the monkeys have fewer food species to choose from but the available biomass of the foods is also lower. The dimensions of their spatial niche is also smaller per unit area. All of these have important consequences for the feeding and foraging behaviour of the samango monkeys at Cape Vidal.

The implications of the latter for food availability are discussed in the next Chapter.

CHAPTER 3: FOOD AVAILABILITY AND QUALITY

3.1 INTRODUCTION

Among the parameters that may affect the behaviour of a primate troop or individual, food availability is one of the more important. Both ranging patterns and dietary composition of primates have been shown to alter with fluctuations in food supply (Struhsaker 1978, Gautier-Hion 1980, Gautier-Hion et al. 1981, Boinski 1988, Harrison 1983, Richard 1985, Lawes et al. 1990). Butynski (1988) suggests that the abundance of guenon foods in the forest environment varies with the time of year in a predictable fashion in relation to rainfall, and has shown that the timing of mating and birth seasons in guenons is closely correlated with rainfall, and the seasonality of food availability and nutrition. There is therefore no doubt that the vagaries of food abundance and availability have important consequences for the social, reproductive and feeding behaviour of a primate population.

Long term studies (Struhsaker 1975, Milton 1982, Raemaekers et al. 1980, Ghiglieri 1984, Gautier-Hion 1985) have shown seasonal trends in the availability of food for primates in tropical forests. In east and central Africa, where rainfall is high and more evenly distributed throughout the year, climatic seasonality is reduced by the effect of the two short wet seasons (Jackson 1977). In southern Africa there is only one wet season and plant and insect species have, on average, shorter seasons and better defined seasonal peaks of abundance (cf. Rudran 1978a, pp. 25-28). This well defined seasonality of climate and in many cases seasonality of food abundance implies that there may be a season of food shortage.

Most authors measure guenon food availability based on indices of specific fruit abundance (Rudran 1978a, Gautier-Hion 1980, Gautier-Hion et al. 1981, Harrison 1983, Cords 1987, Lawes et al. 1990), since guenons are mainly frugivorous. This chapter shows that the fine variations in the phenological timing of all food items, including fruits, flowers, leaves and insects provides for a complex seasonal pattern of availability of food and nutrients at Cape Vidal and questions the validity of using fruit phenology alone as an indicator of the variation in the availability of essential nutrients for the monkeys over the annual cycle.

Any animal living at high latitudes must be able to survive food 'crunch periods', and a measure of an animals ability to survive is its fecundity under such conditions. Successful reproduction requires large amounts of protein for the growth and nourishment of the developing foetus, for lactation and for the development of the growing infant (Blaxter 1964, Pond 1977, Robbins 1983). Therefore the availability of protein sources, such as insects and young leaves, must be investigated in addition to fruit, which is a ready source of quick energy and carbohydrate. The critical nature of seasonal food shortage to the southern African samango monkey is examined here and referred to throughout the remaining chapters of this thesis. The extent to which the behaviour of the samango monkey is dependent on, and tracks the vagaries of, variable seasonal food supply, will determine the extent to which the socio-ecological debate in this thesis is representative of mitis at the limits of its ecological tolerance.

3.2 METHODS

3.2.1 PHYTOPHASE PHENOLOGY

3.2.1.1 Food availability

Fifteen individuals from each of eleven food species were examined systematically each month to determine the availability of food in the study area. These eleven species represented 60.8 % of the feeding scores for all plant species during the study period. Tree individuals of a species were selected over a wide area of the home range. The following vegetative components were assessed for each tree individual:

Flowers - bud, open, senescent
Leaves - bud, new, mature, old
Fruit - setting, unripe,ripe,old

These vegetative components were ranked on an increasing scale of 0 to 7 (Walker 1976):

RANK	0	1	2	3	4	5	6	7
% CLASS INTERVAL	0	1-10	11-25	26-50	51-75	76-90	91-99	100

The rank values were determined in terms of the estimated maximum possible abundance of each component. If there was no loss of any vegetative component from a tree, the sum of values for flowers, leaves and fruits would be 7 for each of these basic components. So if 60% of the estimated fruit crop was present and, of this, 40% was ripe and 20% unripe, the rank values for fruits would be; setting - 0, unripe - 2, ripe -3, and old - 0. To achieve the greatest degree of repeatability between monthly assessment of tree individuals, the rank value for any vegetative component was determined by answering the question " is the value more or less than half?". If judged to be less than a half, the decision was made as to whether it was more or less than a quarter, and so on.

For each month it was possible to calculate a mean rank value for a phytophase of a species from the formula (Walker 1976):

$$F_{pi} = \sum_{i=1}^{8} (n_i \ c_i)/N$$

where n_i = the number of tree individuals of a species in rank i

c_i = class mid-point of rank i

N = total number of individuals

A quantitative estimate of the availability of food phytophases was derived from a food availability index (FAI). The FAI for any phytophase for any month, was the sum of the availability indices for that phytophase for each plant species sampled during that month. The FAI for each species-specific phytophase was calculated using the equation:

$$FAI = D_{rel} \times F_{pot} \times F_{pl} \times N_{prop}$$

where;

D_{rel} - relative density of the tree species.

F_{pot} - maximum fruiting potential of the species. This value is a constant for each species. The constant is based on the maximum proportion of the canopy cover given to a

phytophase at the peak of the availability of that phytophase. Each plant species is ranked on a scale of 0.1 to 1 where 0.1 would represent exceptionally few items on a tree of that species when that items availability is at a maximum, and 1 would represent a typically laden canopy when that item is most available.
Lower rank limit Celtis africana=0.3
Upper rank limit Diospyros natalensis=0.9
For leaves the relative mean canopy volume of the tree species was substituted for F_{pot}.

F_{pi} - mean rank value for a phytophase for a species (see above).

N_{prop} - the proportion of individuals of a species with the phytophase present out of 15 individuals.

3.2.2 INSECT AVAILABILITY

It was important to establish whether the low proportion of insect in the diet was a function of dietary choice or insect phenology and abundance. Arthropods, mainly insects and spiders, were sampled by using malaise traps and by fogging the canopy crown with insecticide.

Two malaise traps were hung in the canopy about 250 m apart and were cleared each month. A mixture of glycol and 70% alcohol was present in the malaise bottles at all times. The contents of the malaise traps were stored in alcohol for later analysis.

Starting in October 1986 insects were fogged from selected trees every three months up to April 1987 (4 fogging samples). At the end of a month the feeding activity scores of the troop were examined and those specific tree individuals from which insects had been captured were noted. These specific tree individuals were divided into three groups depending on the frequency with which insects were captured from them (Most, Least and Moderately Successfully). The two easiest trees to fog were selected from each group. It was not clear whether or how the latter decisions might have biased the sample. Thus six trees were fogged every three months, an exercise which took between 4-6 days.

Two insecticides (Dedevap and Baythroid) were used. Dedevap is a dichlorvos fumigant particularly successful in control of flying insects, while Baythroid is a synthetic pyrethroid for the control of crawling and sedentary insects. For every 10 litres of water 10 ml of Dedevap and 1 ml of Baythroid were added. The two insecticides acted together to cover the range of insects eaten by the monkeys. The mixture was sprayed into the canopy crown from a point within the canopy using a hand pressure pump (Metabi) of the type used to spray vegetables. The amount of poison applied to a tree depended on the size of the canopy but never exceeded 20 litres.

Sheets of plastic were spread over the Isoglossa shrub layer beneath the full extent of the canopy crown. An hour after the fogging was completed the canopy branches were shaken briefly with a long pole to dislodge all insects. These insects were then retrieved from the plastic sheeting and stored in alcohol. The volume of the canopy was calculated from the product of the canopy width, length (measured at right angles), depth and the percent estimate of canopy volume (see Chapter 2).

No more than six trees were fogged at a time to prevent seriously influencing feeding activity on insects by the samangos. Fogging was always completed immediately after the last troop sample period and there was usually a gap of two weeks before the next troop behaviour sample period.

3.2.3 FOOD ITEM QUALITY-PROXIMATE ANALYSES

Throughout the study specific food items eaten by the monkeys were collected. The items were weighed fresh on a suitable scale, after which they were stored in paper packets and dried at 40°C. Where relevant each item (especially fleshy fruits) was separated into an edible (flesh) and non-edible (skin and seed) fraction, according to the monkeys preferences, and were treated separately in the final analysis.

Owing to the costs of the proximate analyses only those food items eaten by the monkeys and few controls (i.e. items not eaten by the monkeys) were collected. The interpretation of the proximate analyses results is limited to the nutritional content of the food items eaten by the monkeys.

The following proximate analyses and analysis methods were undertaken on each item:

1. Crude protein = total nitrogen x 6.25, AOAC Kjeldahl method
2. Crude fat - Soxhlet method
3. Crude fibre - pre-extraction in Soxhlet apparatus, followed by acid hydrolysis, alkali extraction, and ash determination and correction of sample to total weight of crude fibre.
4. Minerals and trace elements - Ca, P, Na, K, Mg, Fe, Cu, Zn.
   The concentrations of the minerals and trace elements were read on spectro-photometer in ppm based on standards of known concentration, and considering sample weight can be expressed either in ppm or %.
5. Energy - these values were obtained using bomb calorimetry.

3.3 RESULTS

3.3.1 PHYTOPHASE PHENOLOGY

Unripe and ripe fruit classes were grouped together to create an index of fruit availability for a plant species by month. A bimodal peak in the availability of fruit is evident from Figure 3.1a. Higher indices of availability were recorded during July to September and March to May, the two 'fruiting seasons'. Food availability was monitored for 15 months and the overlap of 3 months (over May to July) suggests that the fruiting rhythm may

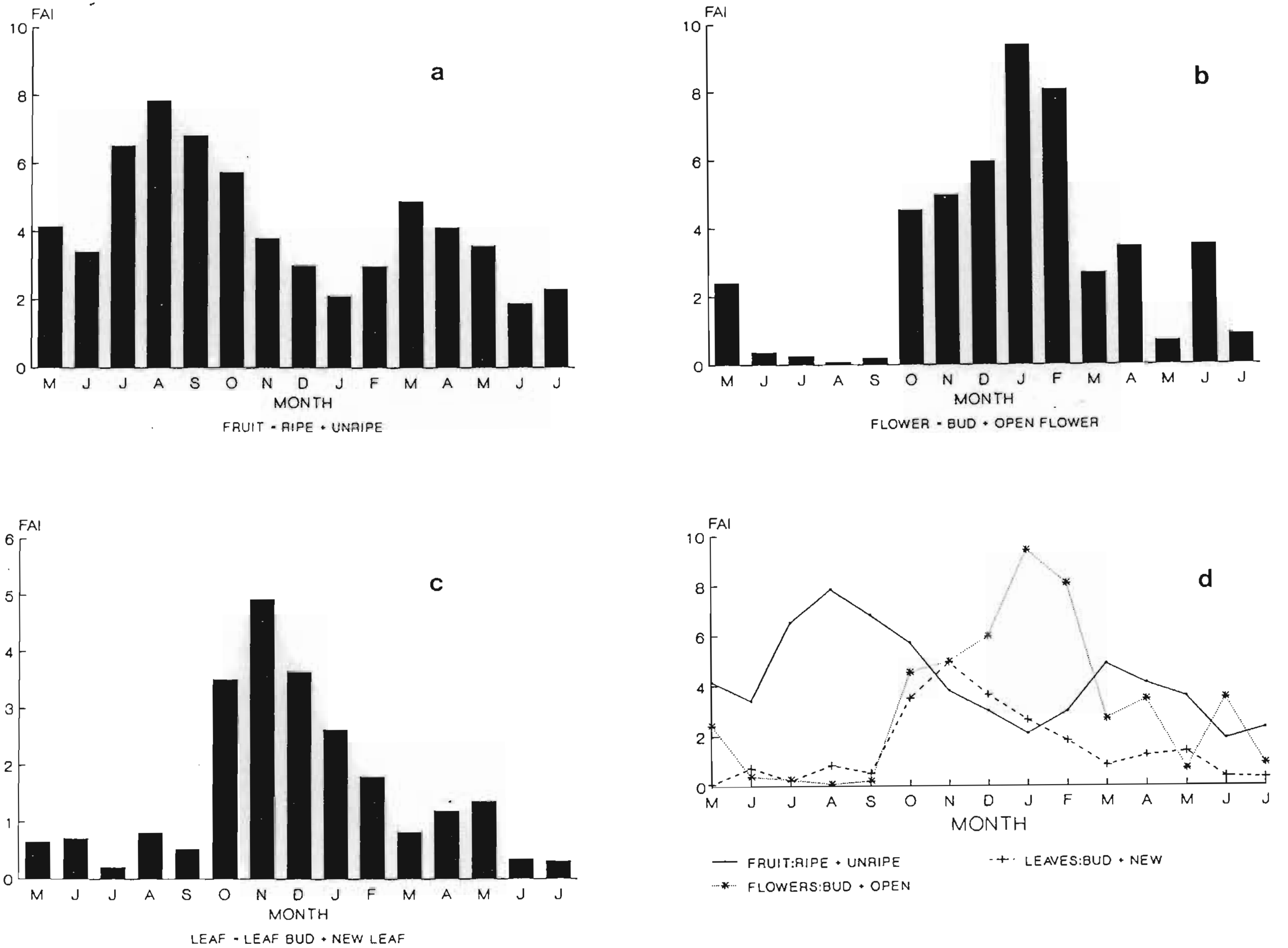

Figure 3.1. Food availability indices scored for the study area from May 1986 through July 1987. (a) Fruit indices; (b) Flower indices; (c) Leaf indices; (d) Relative timing of phytophase phenology (see text for methodology).

follow a consistent pattern in the short term. Fruit availability dropped to its lowest levels during January 1987.

The bimodal peak in fruit availability was preceded by a single flowering peak (Fig. 3.1b) of 6-7 months (October to April). A smaller peak in fruit availability appeared to run concurrently with the late stages of the flowering peak. The greater fruit availability peak followed the flowering peak by 1-1½ months.

Leaf bud and young leaf classes were grouped together to give an index of the availability of the most edible leaf phases. A unimodal peak in the availability of young leaf was evident (Fig.3.1c). A well developed peak during October 1986 to January 1987 was followed by a slight peak during April and May of 1987.

Fruit availability was at its greatest when flower and leaf availability was low (Fig.3.1d), from June to September. Young leaves and especially flowers were most available when fruit was least abundant during the mid-summer months of November 1986 through to February 1987.

3.3.2 INSECT PHENOLOGY

High insect/arthropod availability during the wet season is obvious from the data (cf. Fig. 3.2 and Fig. 3.3). The pattern of increase in dry-weight of winged arthropods caught in malaise traps coincided closely with the increase in rainfall at Cape Vidal (Fig. 3.2). This trend was confirmed by the fogging data (Fig.3.3). The dry mass of insects caught in malaise traps was greater in the earlier months of the rainy season (January), however the diversity of insect orders was low (H'=1.265) and most insects caught (61.8%) were beetles (Coleoptera). Diversity of insect orders caught was higher late in the rainy season and ranged from H'=0.703 in November 1986 to H'=1.626 in May 1987. These data are interpreted to represent a lower availability and diversity of insects in the early wet season with availability and diversity steadily increasing to March 1987 after which a decline was observed as the dry season approached.

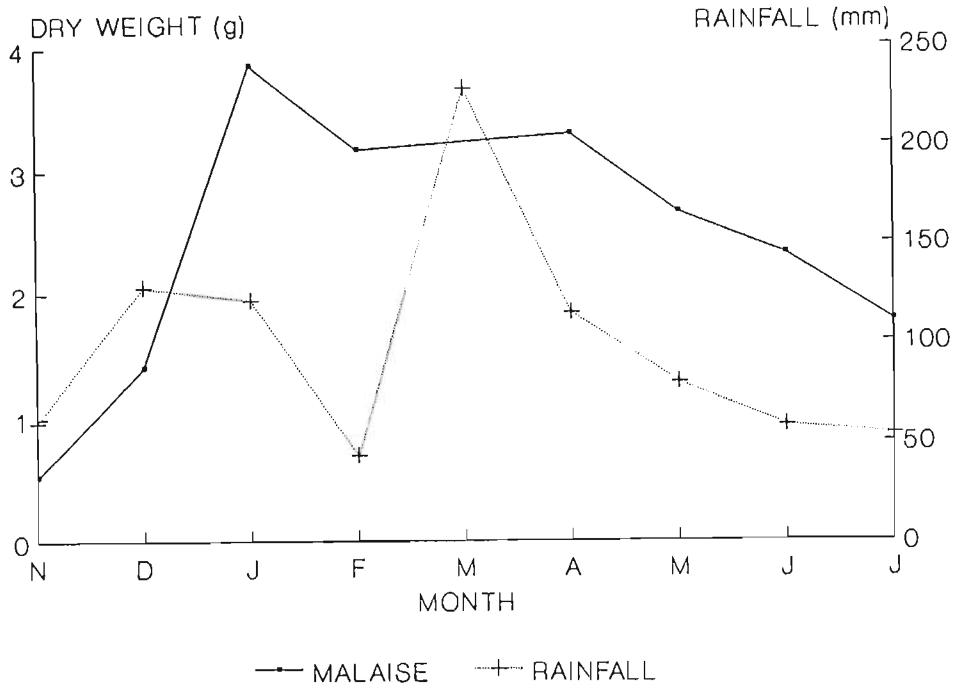

Figure 3.2. The dry weight of insects caught in two malaise traps from November 1986 through July 1987, and the relationship of insect dry weight to rainfall over the same period.

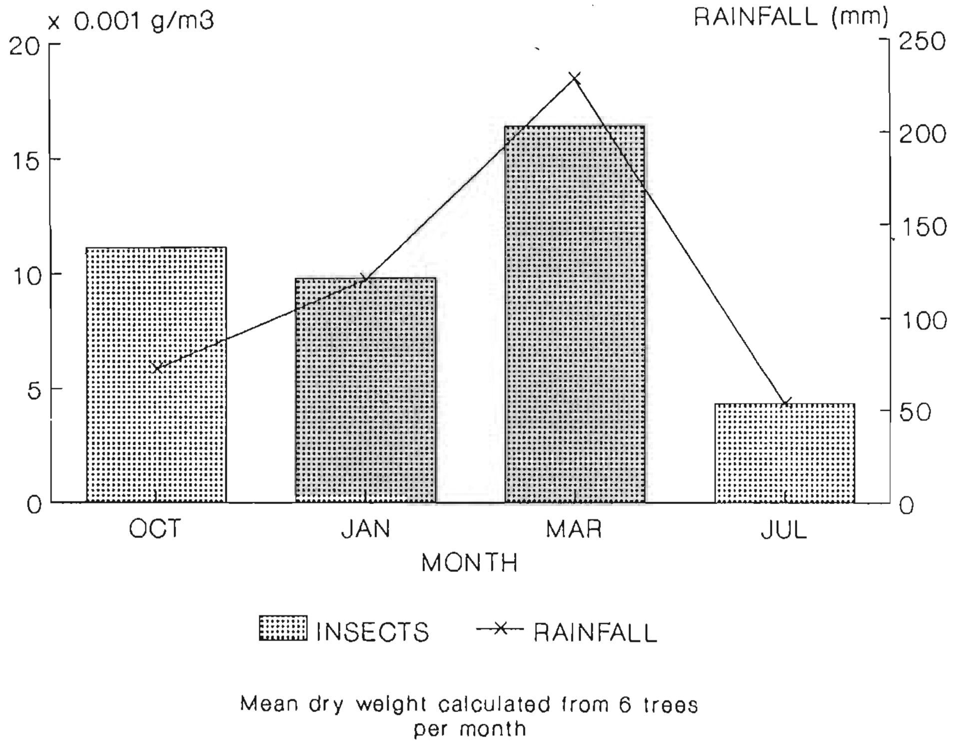

Figure 3.3. The dry weight of insects per unit canopy volume by season (determined from fogging methods), and the relationship of insect dry weight to rainfall over the same period

Fogging results support the above temporal pattern of insect abundance with a general increase, and peak in March, at the end of the wet season. However the biomass of caterpillars (a much favoured insect food of the monkeys) per unit canopy volume was 10x greater (4.7×10^{-3} g/m^3) in October 1986, at the beginning of the wet season, and 5x greater (1.9×10^{-3} g/m^3) in January 1987 than in the dry season of July 1987 (0.4×10^{-3} g/m^3). Much the same trend was shown for the caterpillar content of Acacia karroo trees fogged during October (2.2×10^{-3} g/m^3), January (3.3×10^{-3} g/m^3 and July (0.2×10^{-3} g/m^{-3}).

3.3.3 PROXIMATE ANALYSES

Whole fruits (skin, flesh) were lower in protein content, higher in fat and crude fiber content than flowers and leaves (Table 3.1). For some fruits the flesh was analysed separately to the skin and kernel. The flesh proved to have a lower protein, crude fibre and fat content than whole fruits, flowers or leaves. Notable exceptions were the arilated fruits (e.g. Apodytes dimidiata) where the fat content was exceptionally high (Table 3.1, and Appendix 3.1). Flowers and new leaves had high but similar protein levels, almost double that of fruit. Mature leaves had a slightly lower protein content than new leaves. Energy content differed marginally between fruit and leaves. Energy content of flowers was slightly lower than the energy content of either fruit or leaves.

Proximate analyses conducted in this study showed that plant food items differed most in their protein content and least in their energy content. Fruits are more palatable and digestible than flowers and leaves, because of the lower crude fibre levels (Davies et al. 1988) and lower levels of plant secondary compounds in the flesh of ripe fruit (Robbins 1983, p240). The nutrient content of food items analysed from dune forest south of Cape Vidal confirms the above findings (Frost 1980). Frost (1980) showed that fruits from tree species at Mtunzini (28° 58'S, 31° 45'E), and also found at Cape Vidal, had a high soluble carbohydrate content.

No proximate analyses of arthropod items were conducted. Arthropods provide a supply of high-quality protein, fats, and fluid (Redford and Dorea 1984 and references therein,

Table 3.1 Mean values for proximate analyses of protein, fat, crude fibre and energy of fruits, flowers and leaves, regardless of species, eaten by the monkeys.

ITEM		PROTEIN g/100g	FAT g/100g	CRUDE FIBRE g/100g	ENERGY kJ/g
FRUIT					
SETTING FRUIT (n=3)					
	mean	11.37	9.03	24.38	17.43
	s	3.39	11.53	16.24	4.32
UNRIPE FRUIT (n=11)					
	mean	11.40	5.39	29.05	16.41
	s	4.26	5.08	14.58	3.30
RIPE FRUIT (n=15)					
	mean	10.79	4.68	21.87	17.88
	s	6.19	2.71	8.58	1.41
FRUIT SKIN (n=9)					
	mean	10.80	2.63	24.06	17.31
	s	5.34	1.79	14.58	1.31
RIPE FRUIT (n=3) FLESH	mean	7.19	1.41	7.45	15.87
	s	3.83	0.57	4.85	0.64
ARIL (n=2) SKIN AND FLESH	range	5.95-16.55	31.58-33.32	13.47-16.08	22.08-23.28
SEED (n=2)	range	6.42-33.11	3.48-25.05	17.29-28.58	18.33-20.94
ISOGLOSSA SP FRUITING SPIKE		24.96	2.22	17.36	15.03
FLOWER (n=10)					
	mean	20.22	2.78	14.93	15.84
	s	6.51	1.06	4.92	1.42
LEAF					
NEW LEAF (n=7)					
	mean	20.14	2.48	15.04	16.77
	s	5.57	1.12	5.93	2.26
MATURE LEAF (n=7)					
	mean	17.55	3.65	16.97	17.25
	s	5.34	2.23	3.81	2.10

Richard 1985). Only magnesium, of the essential minerals, is not present in significant amounts (Richard 1985).

A full list of the minerals and trace elements found in the food items is given in Appendix 3.2. In general leaves contained more calcium, magnesium and iron than fruit. Flowers contained more iron than either fruit or leaves. Of the five minerals analysed calcium and potassium were most abundant in all plant food items while magnesium, sodium and phosphorous occurred in decreasing amounts. Iron and copper were more abundant trace elements in all food items than zinc.

3.4 DISCUSSION

By virtue of their large standing biomass and diversity of species tropical forests can give the impression of an environment in which there is a year round superabundance of food for primates. However, work on the patterns of leafing, flowering, and fruiting show that phytophase phenology can be exceptionally complex in rain forest (Leighton and Leighton 1983). It is this phenological complexity that can make it more difficult for primates to track the availability of foods at any one time, than one might expect. For instance, it is well known that while the timing of a phytophase (e.g. fruit) development may be synchronized across a few species, it is never synchronized across the whole community. Even individuals of the same species often show different phasic patterns (Oates 1987). It is this typically patchy distribution of food resources, over time and space, that makes the harvesting of food a particularly challenging prospect for primates, and often a challenge of greater difficulty than one would expect in an environment of apparent abundance (Bourliere 1979 pp. 33, Heideman 1989 pp. 1059).

Although phytophase production is never completely synchronized across a community, general peaks and troughs in abundance can be discerned. For instance, peaks of new leaf and flower production often occur in or at the end of a dry period and are followed by one or more fruiting peaks in the wet season (Frankie et al. 1974, Whitmore 1984, Butynski 1988) or visa versa (Janzen 1967, van Schaik and van Noordwijk 1985). An important feature of the peaks in food production is their relatively predictable and seasonal nature (Heideman 1989). Feeding and reproductive strategies are often based on the predictable nature of food production (Gautier-Hion 1988, Butynski 1988). Animals learn to rely on this seasonality in food availability to the extent that when the expected pattern is perturbed it can have catastrophic consequences. For example during 1970-71 a fruit famine on Barro Colorado Island (a result of a prolonged dry-season rainfall) caused heavy mortality and lowered reproductive rates in the animal community there (Foster 1982).

This relationship between phytophase productivity and rainfall has important consequences at Cape Vidal since rainfall is more seasonal there and, as a consequence, the seasonality of phytophase production is significantly seasonally controlled. In contrast to the findings of Butynski's (1988) review and my own work on phytophase seasonality in the Ngoye forest (Lawes et al. 1990), the fruiting season occurs during the late dry season or late winter months at Cape Vidal, while flower and new leaf production peaks strongly in the wet summer months. These seasonal phenological patterns at Cape Vidal are confirmed by Frost's (1980) work at Mtunzini, a mere 100 km south of Cape Vidal; he also showed a distinct fruiting peak during the dry season and a trough in the early wet season for dune forest. The phenology of dune forests in Natal would appear unique for their dry season fruiting peak (see also Tinley 1985, p156).

Of the three phases, fruit, leaf and flower, fruits are available year round at Cape Vidal, and the difference in amplitude in availability of fruits are not as prominent as those of leaves and flowers. The phenology of new leaves and flowers is such that there are times (July 1986-September 1987) when these phases are hardly available at all and a shift in the diet toward alternative protein sources is predicted (see Chapter 5).

At lower latitudes than Cape Vidal insects provide readily available alternative protein to leaves and flowers, as they are more abundant at low latitudes than high latitudes (Wolda 1978, Rautenbach et al. 1988) throughout the year. In addition seasonal variation is less marked and typically exceeds background levels during the wet season by 2-3x in East Africa (Lack 1986). This is in stark contrast to the 15x difference between seasons in southern Africa (Rautenbach et al. 1988). The shortfall in protein-rich plant foods during the dry season is made all the more critical by a predicted general absence of insects during July through September. It is therefore surprising to find that these months coincide with the early stages of pregnancy when protein demand in females is relatively high (Blaxter 1964, Pond 1977).

As the species with the most generalized food habits among the guenons and many other African primates (Struhsaker 1978, Gautier-Hion 1988, Butynski 1990), C. mitis should be least affected by temporary low levels of food (Butynski 1990). Yet all animals need relatively large amounts of protein for successful reproduction and offspring survival (Blaxter 1964, Pond 1977, Robbins 1983). The conspicuous seasonality in production of protein rich foods poses a number of questions regarding the socio-ecology of the samango monkey. For instance, (a) do the monkeys, and especially pregnant females, shift their use of food items when protein-rich items are less available? or, (b) conversely is the breeding season timed in some, as yet unseen, way to maximize the use of protein rich items? (c) Can this seasonal paucity of protein rich foods account in some way for the success of the mitis species group, above all other guenon species, in colonizing forests so far south? In other words, is it this ability to cope with lower levels of available protein that sets mitis apart from other guenons? (d) To what extent do the age-sex classes differ in their use of foods, and is female feeding behaviour (dependent as it is on protein for reproduction) the central most important strategy for survival in a female-bonded troop (Wrangham 1980)? In addition to these questions it is also necessary to establish unequivocally the extent to which the samango monkey population at Cape Vidal is food stressed. The answer to this question in particular, will provide the ecological context in which the data from this thesis can be best interpreted. In other words, does this thesis represent the ecology of mitis from a food-stressed population? In the chapters on the diet of the troop, the age-sex class differences in diet and especially the chapter on feeding and foraging behaviour, the above questions and their answers form the basis from which I will argue the socioecology of the samango monkey.

CHAPTER 4: DIET OF THE SAMANGO MONKEY

4.1 INTRODUCTION

Despite their wide distribution in equatorial Africa, the arboreal guenons tend to have grossly similar diets (Rudran 1978a, 1978b, Struhsaker 1978, Gautier-Hion 1980, Gautier-Hion 1983, Cords 1986a, Cords 1987, Gautier-Hion 1988, Butynski 1990). The diet is dominated by fruit but always includes some miscellaneous plant parts and insect/invertebrate material. The mitis species group in particular is noted for its broad diet (Schlichte 1978, Struhsaker 1978, Butynski 1990, Beeson 1989). It is this tolerance of a wide variety of food types that has enabled the mitis species group to use a broad spectrum of habitats from bamboo forest at 3300m altitude through lowland rain to dry coastal forests (Struhsaker 1978). However a broad based diet also has its disadvantages, and Struhsaker (1978) has shown that members of the mitis species group are more adversely affected by interspecific competition because its broad food habits overlap those of several species who are often specialists. Thus, one might predict that the diet of members of the mitis species group at any locality is moulded by habitat choice (including the food types available) and the sympatric competitors.

The dietary versatility of the mitis species group is unrivalled among the African guenons except perhaps by the more terrestrial Cercopithecus aethiops (Struhsaker 1967, Kavanagh 1978, Harrison 1984). While the diet may be largely based on fruit, members of the mitis species group from different localities may supplement the diet in different ways. Some mitis populations use larger proportions of leaves in diet (Beeson 1989), others more insects (Rudran 1978a, Butynski 1990) and, in some cases, more flowers (Schlichte 1978). Thus, the fundamental trophic niche of the species group, or the total range of trophic conditions under which a species can live (Hutchinson 1957), is very broad.

I will show in this chapter and those that follow, that on the whole, samango monkeys are relatively unaffected by the food limitations experienced at Cape Vidal and maintain a high quality diet throughout the year. In addition they are the only arboreal frugivorous primate in the region. In this chapter, I compare and contrast the breadth of the trophic niche of the Cape Vidal samangos with other mitis populations. The questions are: (a) to what extent do samangos at Cape Vidal experience competitive release, (b) and are they food stressed? Dependent on both answers it may be possible to draw conclusions on the extent to which the diet (realized niche) of the samango monkey at Cape Vidal describes the intrinsic (fundamental) trophic niche requirements of the mitis species group.

4.2 METHODS

Observations of feeding habits were collected during systematic follows of the troop from dawn to dusk for 3 to 5 days per month. Data presented are taken from sample days of duration longer than 10.5 hours in the dry (winter) season from April to August, or 11.5 hours in the wet (summer) season from September to March. Data collection from the study troop was conducted in the last week of each month. Analysis is restricted to data collected between July 1986 - July 1987. Although data exist for April - June 1986 they were collected while various methods were still being tested and may be subject to sampling irregularities.

Feeding activity was sampled during a 10 minute period centred on the hour and half hour. The troop was scanned and the feeding activity of each clearly visible individual recorded. Using a scan sampling procedure, the frequency method (Altmann 1974, Struhsaker 1975, Oates 1977, Rudran 1978a, Cords 1987, Butynski 1990), feeding observations were operationally distinguished from one another by the following criteria (Struhsaker 1975, Rudran 1978):

1. A different individual monkey feeding on the same item.
2. The same individual monkey feeding on a different item of the same food species.
3. The same individual monkey feeding on a different food species.
4. The same individual monkey feeding on the same food item of the same food species at least 30 minutes after any previous such observation.

Data points are independent of one another between scans, because feeding bouts on a single food source were never longer than 25 minutes (see Chapter 6). Thus feeding activities scored during a scan would not depend on those scored 25 minutes previously.

The frequency method of scan sampling permits a more sensitive measure of dietary diversity and monthly/seasonal variation in the diet than the commonly used scan sample procedure, the time-interval method (Clutton-Brock 1975a, Waser 1975, Chivers 1977, Dunbar 1977, Gautier-Hion et al. 1981). In the time-interval method each individual receives a maximum of one score per scan and no provision is made for the inclusion of those items eaten between scans, but not recorded during each scan period. Using the frequency method, the frequency of use of a food species may appear to be overestimated, especially for those species or items which the animal feeds on for short periods, since a score is given to each item category eaten by an individual although it may not have moved from the original food tree. This argument is counterbalanced by assuming that the action of choosing a separate food item on the same tree, or choosing a new food species, represents a change in feeding activity. In this way ingestion of different items from the same tree is interpreted as though the individual had chosen to feed on a separate species. By this method the use of the species in question is emphasized and hence the greater importance of that species to the monkeys is recognized.

Frequency scores of this nature cannot be used in activity budget calculations since they would overestimate the time spent feeding. Activity budgets were determined from from time-interval scans.

Three broad food categories were used; plant, exotic, and insect items. The distinction between plant food item categories was usually obvious. Ripeness of fruit was determined by colour and size as were the leaf classes. Young leaves were often of the same size as mature leaves, but lighter in colour and more supple. Exotic food items were rarely used and were those items taken from the periphery of the campsite (bread, exotic fruits and wastebin material).

The use of invertebrate food items was scored as either 'unsuccessful investigative behaviour' (sustained for at least 5 seconds) or as 'successful capture and ingestion of the prey'. In analyses of total dietary content, only successful ingestion of prey items was included. Unsuccessful foraging was considered only as an indication of the full potential of the invertebrate fraction of the diet. Since invertebrate prey was often difficult to identify, the substrate, and the speed and nature of the motor pattern used for prey capture were also recorded. The plant species used as sources of invertebrate prey were also recorded.

Indices of monthly dietary diversity were calculated using the Shannon-Wiener (H') diversity equation (Krebs, 1985). Dietary overlap was measured using the method of Holmes and Pitelka (1968).

4.3 DIET DURING AN ANNUAL CYCLE

4.3.1 Total dietary composition by item

A total of 5835 feeding records was obtained during the period July 1986 to July 1987. The item consumed was described for 5477 records. Fruit was the most abundant item (51.7 %) in the diet (Table 4.1). The second most used dietary component was leaves (25.8 %), followed by floral parts (13.4 %) and a small fraction of invertebrate prey (5.8 %). Over the study a small proportion of the diet (2.3 %) was derived from 'exotic' items taken within the campsite. No vertebrate prey items were recorded.

Table 4.1. The percent frequency of use of food items during the study period, July 1986 through July 1987 at Cape Vidal (n=5477 observations).

FOOD ITEM	%	FOOD ITEM	%
LEAF TOTAL	**25.8**	Unripe fruit	14.8
Leaf bud	2.5	Ripe fruit	32.8
New leaf	9.3	Old fruit	2.8
Mature leaf	13.9	**STEMS**	**0.4**
Dry leaf	0.07	**GALLS**	**0.1**
FLOWER TOTAL	**13.4**	**BARK**	**0.3**
Flower bud	2.6	**GUM**	**0.07**
Open flower	10.7	**BRACKET FUNGI**	**0.02**
Moribund flower	0.09	**INSECTS**	**5.8**
FRUIT TOTAL	**51.7**	**EXOTIC ITEMS**	**2.3**
Setting fruit	1.4		

Where food items were divided into the broad categories of fruit, flower and leaves, the use of 119 specific food items from 57 plant species was scored during the study period (Appendix 4.1). These 57 plant species represented at least 80% of the identified species within the home range (although no absolute count was done). A further subdivision of these categories (e.g. fruit = setting fruit, unripe, ripe and old fruit) yielded a total of 234 specific food items eaten by the monkeys.

4.3.2 Plant food species composition of the diet

Like other mitis populations (Aldrich-Blake 1970, Rudran 1978a; 1978b, Schlichte 1978, Beeson 1987, Cords 1987, Butynski 1990) the samangos concentrated their feeding on a small number of plant species, and 77.9 % (n=3934) of plant feeding observations were recorded from the top 10 plant food species and 94.1 % (n=4749) from the top 20 plant food species. Thus relatively few plant species (34.5 %) accounted for most (94.1 %) of the feeding records. Isoglossa woodii was the most used food plant with a 14.2 % frequency of use (Table 4.2).

Table 4.2. The rank order and cumulative percent frequency of use of the top 20 plant food species for the period July 1986 through July 1987.

RANK ORDER OF FOOD SPECIES	FREQ. USE	% CUMULATIVE FREQUENCY
1. Isoglossa woodii	719	14.2
2. Mimusop caffra	702	28.1
3. Acacia karroo	642	40.8
4. Grewia occidentalis	434	49.4
5. Diospyros natalensis	332	56.0
6. Diospyros inhacensis	294	61.8
7. Scolopia zeyheri	270	67.2
8. Dovyalis longispina	227	71.7
9. Olea woodiana	168	75.0
10. Strychnos madagascariensis	146	77.9
11. Apodytes dimidiata	122	80.3
12. Celtis africana	118	82.6
13. Sideroxylon inerme	116	84.9
14. Rhus natalensis	101	86.9
15. Euclea schimperi	87	88.6
16. Ziziphus mucronata	79	90.2
17. Adenia gummifera	54	91.3
18. Scutia myrtina	49	92.3
19. Allophyllus natalensis	47	93.2
20. Trema orientalis	42	94.0

When specific food items were considered, the 10 most used food items accounted for 47.7 % (n=2405) of feeding records (Table 4.3). The ripe fruits of Mimusops obovata were the most used food item at 10.6 % (n=535) of the total feeding records. It is apparent that while a few species are responsible for the majority of feeding records, their high rank is due to the diversity of items used from these species by the samangos. The top ranked food species were used for as many as three important food items i.e. the ripe fruits, open flowers, and the young leaves or mature leaves.

4.3.3 Inter-monthly variation in plant diet

While the presentation of results on a monthly basis is convenient because of the manner in which the data were collected, this temporal scale is essentially artificial and of little ecological significance. The division of the year into months does, however, allow for some comparison of the temporal variation in the diet with other studies

Table 4.3. The rank order and cumulative percent frequency of use of the top 20 specific food items for the period July 1986 to July 1987.

RANK ORDER OF SPECIFIC FOOD ITEM	FREQ. USE	% CUMULATIVE FREQUENCY
1. Mimusops caffra (ripe fruit)	535	10.6
2. Isoglossa woodii (ripe fruit)	354	17.6
3. Acacia karroo (mature leaf)	271	23.0
4. Grewia occidentalis (ripe fruit)	247	27.9
5. Diospyros natalensis (ripe fruit)	206	32.0
6. Isoglossa woodii (mature leaf)	183	35.6
7. Isoglossa woodii (open flower)	163	38.8
8. Dovyalis longispina (unripe fruit)	161	42.0
9. Acacia karroo (new leaf)	156	45.1
10. Diospyros inhacensis (mature leaf)	129	47.7
11. Scolopia zeyheri (open flower)	128	50.2
12. Mimusops caffra (open flower)	121	52.6
13. Grewia occidentalis (setting fruit)	89	54.4
14. Diospyros inhacensis (ripe fruit)	84	56.1
15. Scolopia zeyheri (unripe fruit)	83	57.7
16. Strychnos madagascariensis (unripe ft)	72	59.1
17. Acacia karroo (leaf bud)	71	60.5
18. Apodytes dimidiata (open flower)	69	61.9
19. Olea woodiana (unripe fruit)	62	63.1
20. Celtis africana (new leaf)	54	64.2

(although results must be treated with caution). In Chapter 8, I examine the more meaningful seasonal trends in the diet in relation to food availability.

A mean of 24.5 plant species was used in each month with a range of 18 (July 1986) to 30 species (May 1987). On the whole, there is moderate intermonthly variation in the frequency of use of plant species in the diet, and this is reflected by the coefficients of variation computed for the top 20 food plants (Table 4.4). The top ranking food plants have low coefficients of variation, indicating less variation in monthly use, but consistently heavy use throughout the year. The latter also emphasizes the dependence of the monkeys on few food species for the bulk of the diet and the high ranking position of these few species in the diet month by month. The high coefficients of variation for the other species indicate that the plant food "staples" are supplemented by a wide variety of plant species.

Comparison of the monthly frequency of use of the 5 top ranked food species and food items (for comparison with Rudran's (1978a) work) is shown in Appendix 4.2. The table shows that there is not a marked variation in monthly occupancy of the top ranked plant species. Mimusops obovata occupies the top rank in 5 consecutive months and Isoglossa woodii in 3 consecutive months.

The low intermonthly variability in the diet of samango monkeys is further illustrated by the rank orders of food items regardless of species (Appendix 4.3). Fruits were the top-ranking food items in all months of the study. Ripe fruit (mean=32.8%) was the most important item in all months except January (22.6%) and February (46.5%) of 1987 when unripe fruits of Diospyros natalensis and Grewia occidentalis, respectively, were more important. A moderate proportion of unripe fruit was included in the diet (setting+unripe; mean=16.2%). The range in the frequency of use of fruit was 29.7 % (January 1987) to 64.8 % (March 1987) (Fig. 4.1). Leaves or flowers usually ranked second, while exotic items and invertebrate prey occupied the lower ranked classes.

The main dietary distinction between months lies in the extent to which the samangos exploited leaves and flowers in relation to their consumption of fruit. Although no significant statistical relationship exists between the proportional consumption by month

Table 4.4. The mean, range, standard deviation, and coefficient of variation in the percentage frequency of use of the top 20 ranked food species (ranked by total frequency of use) over the 13 months of the study period.

SPECIES	MEAN	s	V	RANGE
1. *Isoglossa woodii*	11.4	12.6	110.4	2.3-40.7
2. *Mimusops caffra*	15.7	13.4	85.5	0-36.3
3. *Acacia karroo*	11.6	5.7	49.0	3.8-22.9
4. *Grewia occidentalis*	10.7	17.1	160.0	0-61.0
5. *Diospyros natalensis*	5.9	5.9	101.1	0-20.3
6. *Diospyros inhacensis*	6.2	7.3	117.1	0.8-24.3
7. *Scolopia mundii*	4.9	7.9	161.4	0-20.9
8. *Dovyalis longispina*	4.6	8.3	179.8	0-24.8
9. *Olea woodiana*	3.9	5.4	138.6	0.4-20.1
10. *Strychnos gerrardii*	2.7	3.6	133.8	0-12.5
11. *Apodytes dimidiata*	2.7	3.7	139.6	0-8.6
12. *Celtis africana*	2.4	3.0	124.6	0-8.2
13. *Sideroxylon inerme*	2.2	1.6	73.2	0.3-5.9
14. *Rhus natalensis*	2.4	5.1	210.5	0-17.2
15. *Euclea schimperi*	1.4	1.6	118.6	0-5.6
16. *Ziziphus mucronata*	1.8	2.4	131.8	0-8.1
17. *Adenia gummifera*	1.1	2.8	264.7	0-10.2
18. *Scutia myrtina*	0.7	1.7	248.1	0-5.8
19. *Allophyllus natalensis*	0.9	1.0	106.5	0-3.1
20. *Trema orientalis*	1.0	1.1	114.6	0-3.8

of fruit and that of leaves (r_s = -0.033, $P<0.91$, df = 11), the relationship between the proportion of fruit and the combined proportions of flowers and leaves in the diet for a month is significant (r_s = -0.637, $P<0.03$, df = 11). As expected, a negative correlation trend between the proportions of fruit and flowers in the diet by month is found (r_s = -0.522, $P<0.07$, df = 11), since flowers are the precursor phytophase to fruits and phenology is more seasonal at Cape Vidal, with fruiting following flowering in a more predictable fashion. This all suggests that a reduction in the amount of fruit in the diet is compensated for by the combined ingestion of alternative items. However, since the leaves and flowers eaten can never entirely compensate for the carbohydrate deficit caused by a drop in the consumption of fruit, and because of the physiological demands of shifting to leaves, the 'leaf and flower' category in the diet remains fairly constant unless fruit consumption drops or rises markedly (Fig. 4.2).

4.3.4 Inter-monthly plant diet overlap

The mean overlap in the percentage frequency of use of plant species between consecutive months was 58.2 % (n=13 months, range = 42.9-75.1 %). The least dietary overlap was observed during the months January 1987 through to May 1987 when fruit availability was comparatively low. Half the species used in a month were used in the following month. At the food species level this represents a considerable inter-monthly overlap in diet. Dietary overlap decreases to 44.8 % (n=12, range = 22.7-59.4), if the overlap in specific food items between consecutive months is considered. The separation of specific fruit items into ripe and unripe fruit, lowers the percent overlap to 38.9 % (n=12, range = 17.8%-56.2%).

4.3.5 Plant diet diversity

Diversity indices were calculated using the proportional frequency of use of the specific food items eaten each month, as opposed to the frequency of use of species <u>per se</u>. This produces a more sensitive measure of diversity. The mean monthly dietary diversity index (H) was 3.86 (n=13 months). Diet diversity indices ranged in value from 2.86

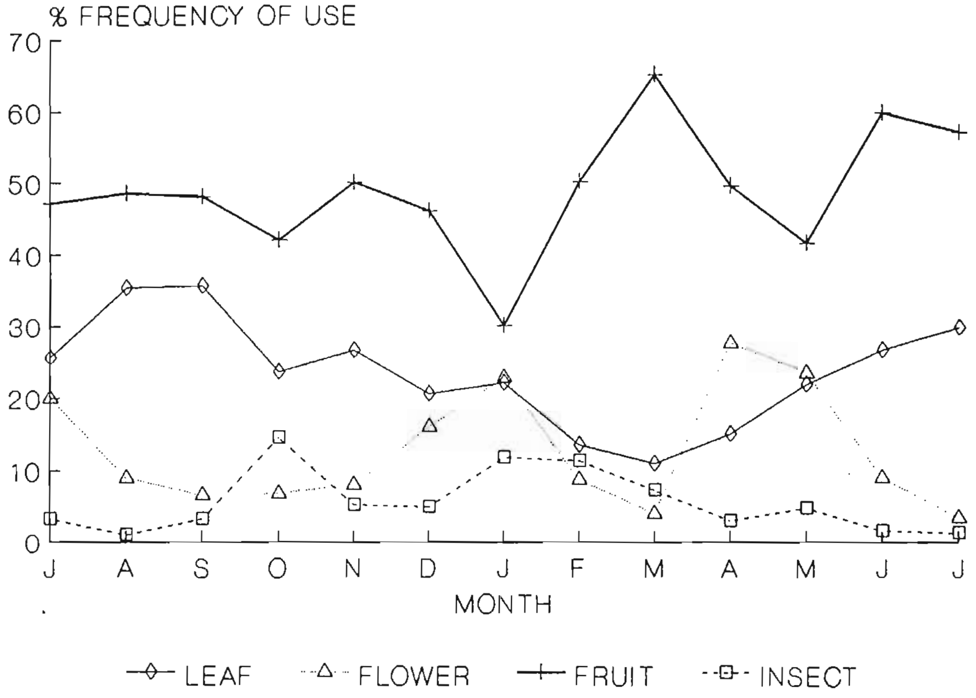

Figure 4.1. The monthly percent frequency of use of the major food types over the study period.

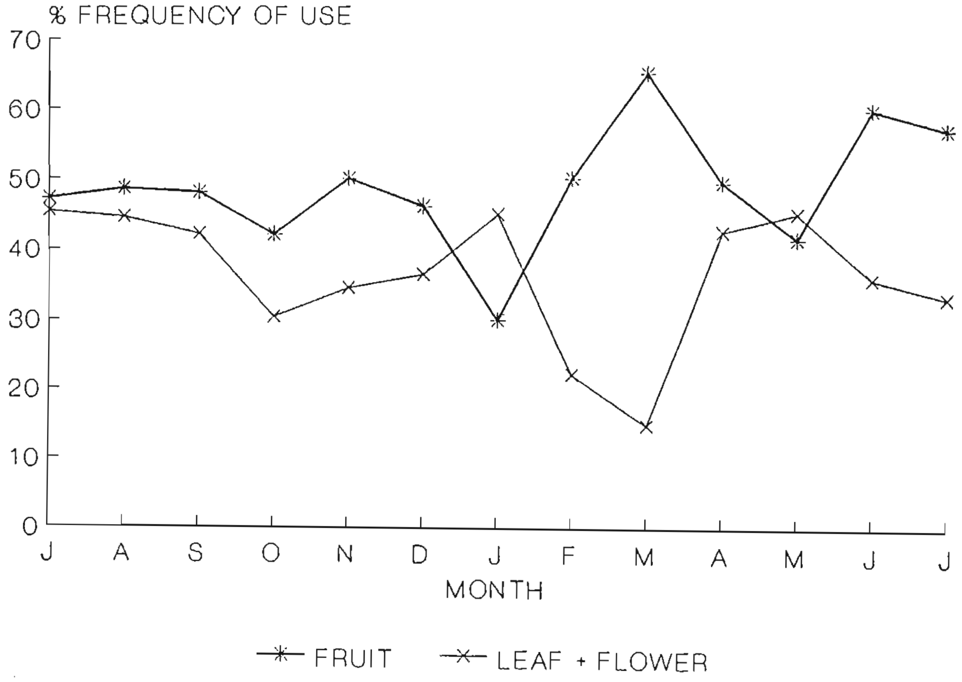

Figure 4.2. The monthly percent frequency of use of fruit compared to the use of leaf and flower items combined, over the study period.

(March 1987) to 4.82 (January 1987) (Fig. 4.3). Variation in the diversity of the diet was greatest during the summer months (January - May 1987) when fruit availability was low.

Although the diet during any month could consist largely of a few species or specific items, samangos, like other guenons, did sample other food items regularly but in small quantities. It is likely that this was a means of monitoring the locality and phenology of the food species available within the home range. Certainly the high intermonthly overlap in the diet is indicative in part of such investigative behaviour. Despite this, dietary diversity in guenons is not great because of the dominance of the highly ranked food items in the monthly diet (Rudran 1978a, Gautier-Hion 1980, Cords 1986a, Gautier-Hion 1988).

4.3.6 Invertebrate content of the diet

Invertebrates constituted a small fraction of the diet (5.8 %). This value does not include investigative behaviour and underestimates the effort involved in securing prey items. All feeding behaviour involving the search for invertebrate prey, as determined from the motor patterns employed, the microhabitats searched, and the item eaten, regardless of whether the action was successful or not, constituted some 7.6 % (n=426) of total "feeding" records. This figure must be regarded as the maximum potential frequency with which invertebrates may have been included in the diet. The frequency with which invertebrates were unsuccessfully sought, or not ingested, represented a further 2.0 % (n=111) of records. Using Rudran's (1978a) method whereby the frequency of ingestion scores is divided by the sum of the frequencies of investigations and ingestions, a relative measure of success in seeking out invertebrate prey was determined for the samangos at Cape Vidal. A total 71.5% of all investigations of microhabitats for invertebrates were successful.

Most insects were eaten during the hot months of higher summer rainfall (January through March 1987, Fig. 4.4). The samangos were also more successful at capturing insects during these months (Table 4.5), probably due to the peak in availability and hence greater abundance of insects.

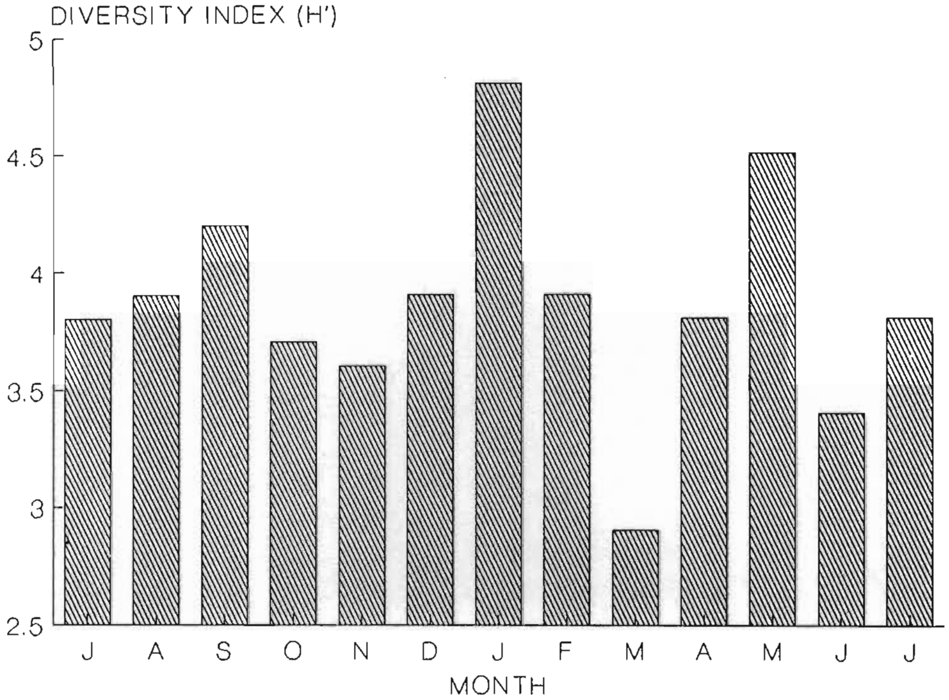

Figure 4.3. Specific food item diversity (Shannon-Wiener) for each monthly sample.

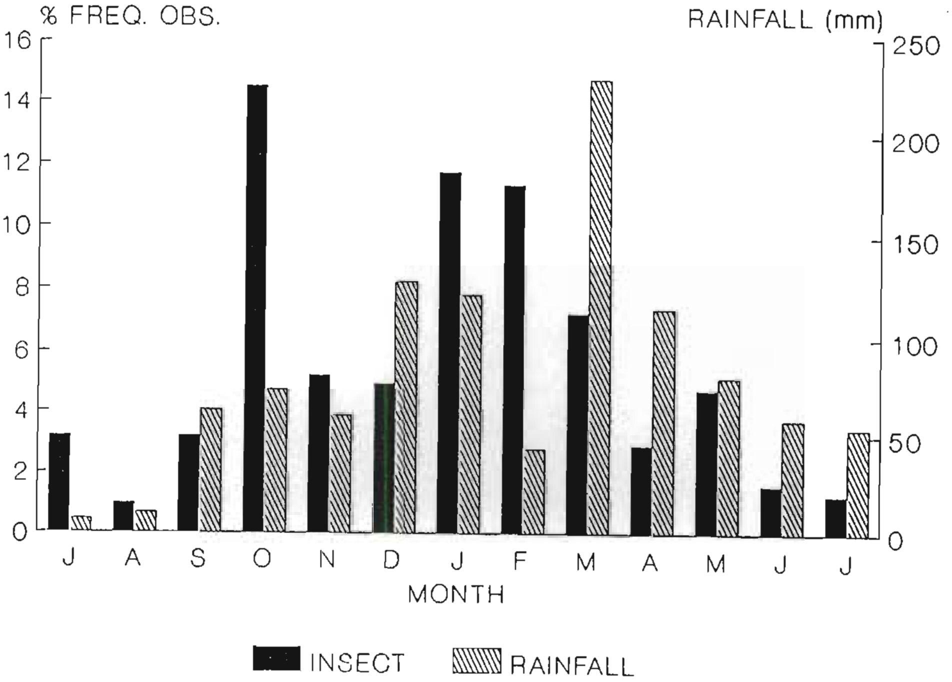

Figure 4.4. The relationship between the monthly percent frequency of of use of insects in the diet and rainfall.

The invertebrates could be identified at least to order in 129 of the 315 records of successful capture. With the exception of a millipede (class Diplopoda) all were insects. Of the nine orders of Insecta used by the monkeys (Table 4.6), the most used was the Lepidoptera (25.4%, n=79). These were mostly the caterpillar stages belonging to the Family Lasiocampidae (tent caterpillars), Family Geometridae (looper caterpillars) and Family Pyschidae (bagworms). Ants were the second most important prey items in terms of frequency of use (6.7%, n=21).

4.3.7 Plant species, microhabitats and motor patterns used in the capture of insect prey items

I identified 29 plant species from which invertebrate items were captured and ingested. The tree species from which invertebrates were most commonly captured (Table 4.7) were Acacia karroo (17.4%) and Euclea schimperi (14.6%). The frequency of use of the 10 top ranking tree species used for invertebrate capture was correlated with their frequency of use for vegetative components (r_s=0.406, df=8, P<0.22). Although not significant, the correlation trend does suggest that frequency of insect feeding by samangos in tree species at Cape Vidal is proportional to the time spent feeding on plant items in those tree species. This suggests that invertebrate feeding involved the opportunistic capture of prey during foraging for plant foods.

When all attempts at invertebrate prey capture were considered, ten different microhabitats constituting 89.2 % of all records were identified (Appendix 4.4). Regardless of whether an invertebrate feeding attempt was successful, any investigative activity indicated the importance of a microhabitat as a source of prey . The microhabitat most frequently involved in invertebrate prey capture was foliage (33.3%), although prey was also frequently taken from the bare surfaces of branches (27.7%). When specific microhabitats were considered, prey was most frequently taken from the bare branches of A. karroo (12.1%) and beneath rotten bark on E. schimperi (7.1%. Table 4.8).

Table 4.5. The frequency of investigation and ingestion, and the percentage success of capture of invertebrates for each month. (See text for explanation of calculation of % success of capture).

MONTH ACTIVITY	J	A	S	O	N	D	J	F	M	A	M	J	J
INVESTIGATION	-	5	15	15	11	7	8	15	10	4	14	3	4
INGESTION	9	4	18	64	21	15	57	47	22	12	29	10	7
SUCCESS	100	44	55	81	66	68	88	76	69	75	67	77	64

MEAN % CAPTURE SUCCESS = 72%

Table 4.6. The frequency of use of the invertebrate orders used by the monkeys over the study period, July 1986 through July 1987, and the percent frequency of use of each order.

MONTH	J	A	S	O	N	D	J	F	M	A	M	J	J	n	%
DESCRIPTION															
Investigation	-	5	15	15	11	7	8	15	10	4	14	3	4	111	/
Ingested item unidentified	5	3	5	23	15	12	33	31	15	9	20	7	6	184	58.8
Lepidoptera															
Geometridae															
Lasiocampidae	4	-	1	33	5	2	20	6	-	2	1	-	1	75	24.0
Pyschidae	-	-	-	-	-	1	-	-	-	-	-	-	-	1	0.3
Winged Adult	-	-	-	1	-	-	2	-	-	-	-	-	-	3	1.0
Cocoon	-	-	-	-	-	-	-	1	-	-	-	-	-	1	0.3
Hymenoptera															
Formicidae	-	-	-	1	-	-	-	2	7	1	7	3	-	21	6.7
Orthoptera															
Tettigonidae	-	-	-	-	-	-	-	1	-	-	1	-	-	2	0.6
Caelifera	-	-	-	-	-	-	1	-	-	-	-	-	-	1	0.3
Hemiptera															
Cicadoidea	-	-	-	-	-	-	-	1	-	-	-	-	-	1	0.3
Pentatomoidea	-	-	12	-	-	-	-	-	-	-	-	-	-	12	3.8
Coleoptera															
Carabidae	-	-	-	-	-	-	-	2	-	-	-	-	-	2	0.6
Neuroptera															
Myrmeleontidae	-	-	-	-	1	-	-	1	-	-	-	-	-	1	0.6
Mantodea	-	-	-	-	-	-	-	1	-	-	-	-	-	1	0.3
Phasmatodea	-	1	-	-	-	-	-	-	-	-	-	-	-	1	0.3
Isoptera															
Macrotermes sp.	-	-	-	-	-	-	-	6	-	-	-	-	-	6	1.9
Cl. Diplopoda															
pill millipede	-	-	-	-	-	-	1	-	-	-	-	-	-	1	0.3

Table 4.7. The percent frequency of use of the top 10 ranked tree species from which insects were taken.

SPECIES	FREQ. USE	% FREQ. USE
1. *Acacia karroo*	49	17.4
2. *Euclea schimperi*	41	14.6
3. *Mimusops caffra*	31	11.0
4. *Diospyros natalensis*	21	7.5
5. *Grewia occidentalis*	18	6.4
6. *Maytenus heterophylla*	14	5.0
7. *Dovyalis longispina*	13	4.6
8. *Sideroxylon inerme*	11	3.9
9. *Celtis africana*	8	2.9
10. *Olea woodiana*	7	2.5
	n 213	% 75.8

Table 4.8. The ranked percent frequency of use of the top 10 specific microhabitats from which insects were captured.

SPECIFIC MICROHABITAT	FREQ OF USE	% FREQ. OF USE
1. *Acacia karroo* (bare branch)	34	12.1
2. *Euclea schimperi* (beneath bark)	20	7.1
3. *Mimusops caffra* (bare branch)	14	5.0
Diospyros natalensis (foliage)		
4. *Maytenus haterophylla* (foliage)	12	4.3
5. *Euclea schimperi* (bare branch)	11	3.9
6. *Acacia karroo* (foliage)	10	3.6
Celtis africana (foliage)		
7. *Dovyalis longispina* (foliage)	9	3.2
8. *Euclea schimperi* (foliage)	8	2.9
9. *Mimusops caffra* (beneath bark)	7	2.5
Isoglossa woodii (foliage)		
10. *Mimusops caffra* (foliage)	6	2.1
TOTAL	n 162	% 57.7

Some 17 categories of motor pattern (n=414 records) were employed by the monkeys while investigating and capturing invertebrates. Slow motor patterns were most frequently employed (59.4%) (Appendix 4.5). This is in agreement with the fact that slow moving prey items such as caterpillars, formed a large fraction of the invertebrate diet.

4.4 DISCUSSION

While the diets of mitis species group populations are compared and contrasted, the diet of the samango is discussed without reference to the causal effects of age-sex class trophic requirements, or the effect of temporal change in food availability. These relationships are examined in later chapters (see Chapter 8). In addition to highlighting differences in gross diet between mitis populations, this account also provides confirmation that the samango, like other mitis subspecies, is a dietary generalist.

The mitis species group has been studied principally in lowland-type rain forest near the equator (e.g. Aldrich-Blake 1970, Schlichte 1978, Rudran 1978a, Cords 1986a, Butynski 1990) where climate and food availability are not notably seasonal. From these studies mitis has, in comparison with other arboreal guenons, the broadest diet. While it consumes the least fruit and the most leaves (Struhsaker 1978, Cords 1986a, Gautier-Hion 1988, Butynski, in press) it is generally regarded as a frugivore (Beeson 1989).

Perhaps the most important dietary problem faced by samangos is the seasonal fluctuation in protein rich food items (see Chapter 3), such as young leaves and insects. Insects are less abundant and more seasonally available in southern Africa than in equatorial Africa (Wolda 1978, Rautenbach et al. 1988). Insects are also an elusive food source and as such are not entirely suited to satisfying the energy/protein demands of the samango monkey at Cape Vidal. As a result Cape Vidal samangos, unlike blue monkeys (Rudran 1978, 19.83%; Schlichte 1978, 11%; Cords 1987, 16.8%; Butynski 1990, 35.4-45.4%), do not have a large proportion of invertebrates (5.8%) in their diet.

Although all mitis populations include invertebrates in the diet, all evidence points towards leaves as a more important protein source where food is seasonally available (Schlichte 1978, Struhsaker 1978, Beeson 1989). Recent work by Bruorton and Perrin (1989) shows that the gut of C. m. erythrarchus is well adapted to coping with a folivorous diet. Consequently, an ecological shift in the diet toward foliage is not as physiologically stressful an option as might be otherwise predicted. Indeed, Struhsaker (1978) found that blue monkeys did not increase the diversity of food species in their diet, or the length of their daily range, when they increased their leaf intake at Kibale. In fact, far from limiting or stressing the monkeys, the folivorous tendencies of blue monkeys may be especially important in causing substantial separation of their feeding niches from those of other cercopithecines (Rudran 1978b).

With the exception of those C. mitis populations where fruit was notably seasonal in abundance (e.g. Beeson 1989), or plant food diversity was low (e.g. Schlichte 1978), the Cape Vidal samangos and other samango populations (Breytenbach 1988) ate slightly more leaves and flowers combined, than did most other mitis populations (Table 4.9). The moderately high proportion of leaves and flowers in the diet at Cape Vidal, is attributed to: (a) the paucity of invertebrates in the diet (i.e. the only other major potential source of protein), (b) lower plant food diversity at Cape Vidal and, possibly, (c) the seasonality in the availability of fruit and hence the need to eat alternative items for both their carbohydrate and protein content.

A comparison of the diet and ecological correlates of the diet of the Kibale blue monkeys provides an opportunity to corroborate the cause of higher levels of folivory. The Kibale populations of mitis are not subject to either major seasonal changes in food availability or very low plant food diversity. However the Kanyawara blue monkeys of Kibale have a larger fraction of leaves (mean=31.4%, n=4 troops) in their diet (Butynski 1990), than do the Ngogo blues (22.8%, n=1 troop). Butynski (1990) points to a lower density of fruiting trees and a higher blue monkey population density at Kanyawara as the causal mechanisms of this difference in folivory. A similar situation exists at Cape Vidal where population density is extremely high (2.07 ind/ha; see also Chapter 10) and food availability is low (either due to lower plant species diversity, or seasonality of abundance). Like the Kanyawara blues this may necessitate a shift in the diet towards a greater leaf fraction.

Table 4.9. The percentage composition of the diets of *Cercopithecus mitis* populations.

Species and study site	Fruit	Leaf	Flower	Insect	Author
C. m. erythrarchus					
Entabeni, R.S.A	59.9	14.3	10.9	1.0	Breytenbach unpub.[1]
	42.8	36.4	6.5	0.8	
Cyprus, R.S.A	59.4	23.9	5.5	<5.0	Scorer 1980[2]
Cape Vidal, R.S.A	51.7	25.8	13.4	5.8	Lawes, this study
Karkloof, R.S.A	*	*	*	*	Mcmahon 1977
C. m. stuhlmanni					
Kanyawara, Kibale, Uganda	42.7	19.1	11.7	19.8	Rudran 1978 Struhsaker 1978
	22.1-28.9	22.4-35.4	2.9-7.8	35.1-45.4	Butynski 1990
Ngogo, Kibale, Uganda	30.1	22.8	9.8	35.9	Butynski 1990
Budongo, Uganda	60-70	*	*	*	Aldrich - Blake 1970
Lake Kivu, Zaire	45.8	16.3	24.5	13.4	Schlichte[3] 1978
Kakamega, Kenya	54.6	18.9	3.6	16.8	Cords 1987b
Diani beach, Kenya	*	*	*	*	Moreno-Black and Maples 1977
Muguga, Kenya	*	*	?	?	De Vos and Omar 1971
Zomba, Malawi	42.1	23.1	11.5	0.5	Beeson 1987

* = presence only of item recorded in the diet by author
? = no record of item mentioned by author
Unless otherwise stated the percent composition values of the diet are derived from the frequency of observation of an item in the diet.
1. Values taken from analysis of faeces.
2. The results of two five-day-follows, one each in Feb and Jun 1975, are meaned.
3. Calculated from Table 5c. pp. 513, Schlichte 1978;the total was corrected to 3253 records by the exclusion of ‘search time’ values in analysis of time spent feeding.

The ratio of mature to young leaf (13.9%:9.3%) at Cape Vidal is higher than at other sites (Rudran 1978a, mature:young 6.7:9.4; Cords 1986a, 2.3:16.6; Butynski unpub. data, Ngogo G33 7.4:19.1, Kanyawara G1 19.1:24.3). This is due to the combined absence of young leaf and alternative sources of protein (insects and flowers) at certain times of the year at Cape Vidal when mature leaf is eaten instead (see Chapter 8).

Unlike the Zomba (Beeson 1989) and, to some extent, the Kibale blue monkeys (Butynski 1990), where leaves and flowers ranked most highly in some months, fruits were the top-ranking food items in the diet of the samango in all months. Is fruit therefore as limiting a resource in the diet of the samango at Cape Vidal as in other populations? This can be examined by comparing the coefficients of variation in the monthly percentage frequency of use of fruit for different populations. Populations in which fruit is less limiting would be expected to show less variation in the use of fruit by month. Table 4.10 shows that the samango has a lower variation in the use of fruit by month than most populations but a high mean usage of fruit (51.7%), suggesting that fruit is not a limiting resource at any time during an annual cycle.

Although unripe fruit is infrequently eaten by other guenons (Gautier-Hion 1988), samangos include a sizable fraction of unripe fruits in their diet (16.2%). It is difficult to assess the use of unripe fruit by samangos because the comparative literature does not distinguish between ripe and unripe fruits. The inclusion of unripe fruits in the diet of the samango may be a consequence of three factors: (a) lower tree species diversity and hence less ripe fruit phytophase overlap in the timing of fruiting phenology at southern latitudes. In other words, there are gaps in ripe fruit availability such that unripe fruit is occasionally the only fruit phytophase available. (b) A small home range would contain fewer individuals of a food species and, as a result, lead to less variation in fruit phytophase production. Ripe fruits of a species may not always be available. (c) Lower levels of plant chemical defenses (such as tannins) occur in unripe fruits (Waterman 1984). Whatever the reason, samangos maintain a fairly high proportion of fruit items in the diet by including a high proportion of unripe fruits at times.

Since seasonality in fruit availability at Cape Vidal did not appear to drastically affect the proportion of fruit in the diet, one can only conclude that competitive pressure for fruits at

Cape Vidal must be exceptionally low, ensuring that even when fruit availability is at its lowest there is still sufficient fruit available, provided the monkeys eat unripe fruits.

Table 4.10. The coefficient of variation (V) in the percent frequency of use of fruit by month in the diet of C. mitis populations.

LOCALITY	V	MEAN %	MONTHS	AUTHOR
Kakamega	12.8	54.6	11	Cords 1986a[1]
Cape Vidal	17.9	51.7	13	This study
Ngogo, Kibale	42.8	47.0	20	Butynski unpub. data
Kanyawara, Kibale	62.4	42.7	16	Rudran 1978a
Kanyawara, Kibale	65.8	34.3	19	Butynski unpub. data
Zomba	77.3	24.2	9	Beeson 1987

1. Determined from Fig. 1, p817, Cords 1986.

The broad diet and dietary niche of mitis can result in interspecific competition. For instance Struhsaker (1978) found that mitis in the Kibale forest, Uganda, exhibited the greatest community overlap in food habits. Consequently he argued that the blue monkey was the species most likely to be affected by competition due, not to interaction with any one species, but to a combined dietary overlap with all of them. Although the samango has a very broad diet, and includes, in addition to the commonly shared items in mitis diet, more unripe fruit and mature leaf, the breadth of the trophic niche is made possible by the lack of congeneric competitors. This can be seen more clearly by comparing the variation in the composition of the diet in different mitis populations along a gradient of increasing competitive release. Thus in the Kibale forest, mitis lives in sympatry with at least four dominantly frugivorous primate species (Rudran 1978a, Ghiglieri 1984), and in the Kakamega forest with two frugivorous primate species (Cords 1987). Cords (1986a) suggests that mitis and ascanius are more frugiverous at Kakamega than at Kibale due to the absence of Cercocebus albigena and other frugivores at the former site (i.e. competitive release). At Cape Vidal and Ngoye (Lawes et al. 1990) there are essentially no competing congenerics. The samango monkeys at Cape Vidal and Ngoye, like blue monkeys at Kakamega, are more frugivorous in diet than the Kibale populations (cf. Rudran 1978, Butynski 1990). It would seem likely that the samango has expanded its trophic niche due to the combined effect of the absence of competitors and increased food seasonality.

The breadth of the trophic niche can be compared using diversity indices (Ludwig and Reynolds 1988). On average the samango monkey diet (specific food items) in any one month was more diverse than the blue monkey diet. For example the mean monthly specific plant food item diversity (H'=3.86) for samangos was substantially greater than the highest diversity index recorded for any month (H'=3.13) from blue monkeys (Rudran 1978a). Thus although fewer food species were used by samangos, the higher dietary diversity results from the regular use of more food items from the top ranking food species than was the case for blue monkeys. Once again, one can only conclude that this is made possible by the lack of competitive congenerics at Cape Vidal. Monthly dietary diversity was considerably lower for blue monkeys in the montane forests on the Zomba plateau (Beeson 1989) than that recorded for samangos despite the absence of competing congenerics at Zomba. However, food seasonality was pronounced at Zomba, and the frequent absence of fruit in the monthly diet necessitated the considerable use of leaves of a few species, resulting in a low dietary diversity.

In a single month Kibale blues concentrated more on a few specific food items than their Kakamega counterparts: the top five foods accounted for 76% (range 63-94%, n=7 months; Rudran 1978a) of the Kibale blue monkey diet, but only for 57% (range=44-69%, n=11 months, Cords, 1986) of the diet of Kakamega blues. Differences between Kakamega and Kibale may reflect the fact that the Kakamega forest is poorer in plant species richness than Kibale (Hamilton 1974), or that there are fewer competitors at Kakamega and, therefore the monkeys broaden their dietary niche (Cords 1986a). The use of the top 5 specific food items by the Cape Vidal samangos accounted for 64% (range=39-88%, n=13 months) of the diet. Although slightly higher than the Kakamega value, this may be due to the combined effects of lower plant species richness at Cape Vidal and a smaller home range area from which to choose food items.

Dietary overlap (Holmes and Pitelka 1968) of plant items is exceptionally high in guenons and most plant species are shared by sympatric Cercopithecus species (Gautier-Hion 1988). At Makokou, Gabon, the dietary overlap among three guenons, nictitans, cephus, and pogonias was 68% (Gautier-Hion 1980). Dietary overlap between mitis and ascanius at Kakamega, Kenya, from a year's data, was 77.0% for plant species, but less (70.4%) for species-specific items (Cords 1987). However, Cords (1986a) showed that overlap in the diet between age-sex classes of a species is lower than the overlap between the same age-sex classes of sympatric guenon species. The overlap in the use of specific food items by samangos in consecutive months (58.2%, range 42.9-75.1%) was higher than that recorded for blue monkeys by Rudran (1978a) in the Kibale forest (x=26.9 %, range = 7.1-55.9%; no distinction between ripe and unripe fruits) and by Beeson (1989) from Zomba (32.7%, range 1.6-54.6%). This once again reflects the greater use of food items from the highly ranked food species by samangos, and the lower variation in their use from month to month. It is clear that temporal changes in the diet of samango monkeys are not as frequent as in the feeding behaviour of the blue monkey.

Among the heavier guenons (mitis, nictitans, and neglectus), caterpillars and ants form the largest portion of the invertebrate diet while the smaller, more agile, guenons (ascanius, pogonias, and talapoin) concentrate on more mobile prey (Rudran 1978a, Struhsaker 1978, Gautier-Hion 1980, Cords 1987, Gautier-Hion 1988, Butynski 1990). Unlike the blue monkey which employs very few rapid motor patterns in prey capture (Rudran 1978a (8.25%); Cords 1987 (6.7%), rapid motor patterns constituted 35.0% of invertebrate capture by samangos. Cords (1987) shows that blue monkeys ingest more prey directly from the substrate while redtails (C. ascanius), with which they often form mixed groups, use more rapid motor patterns. In the absence of sympatric species, the samango fed over a wider range of prey types (i.e. incorporating slow and fast motor patterns) and may exhibit a potentially preferred pattern of invertebrate feeding behaviour for the mitis species group. Cape Vidal samangos were also more successful than Kibale forest blue monkeys in securing invertebrate prey. It would appear that in the absence of primate competitors, mitis is capable of exploiting both 'sedentary' and 'mobile' prey.

As expected, in the absence of congeneric competitors, samango monkeys make full use of the available food at Cape Vidal. Even potentially less palatable items such as unripe fruits and mature leaves are used. While insects are not abundant the monkeys eat all forms of insect prey. Dietary diversity each month is high, although the overlap between consecutive months is also high, suggesting that the monkeys maximize their use of food items between months. Under circumstances of low food plant diversity, low food species richness, seasonality in availability of food (especially the protein rich food items) and a lack of congeneric competitors, I suggest that the samangos at Cape Vidal have as broad a diet as possible and a comparatively broader dietary niche than the Kibale and Kakamega blues under the circumstances.

CHAPTER 5: ACTIVITY PATTERNS

5.1. INTRODUCTION

The fitness of an organism requires the maintenance of flexibility of response to environmental perturbation, and this flexibility must be achieved in the most economical manner possible (Slobodkin and Rapoport 1974). Within the context of the individual, initial response to environmental change would be expected to be behavioural, and only if this fails should a physiological response emerge. Richard (1985) summarized this by stating "behaviour is the individual attribute most quickly affected by an event in the environment". Activity patterns thus represent the most dependable and easily measurable response to change in environmental quality. Samango monkeys at the southern edge of the range of the <u>mitis</u> group are ideally suited to testing the effect of environmental seasonality on activity pattern.

In the functional analyses[1] of the chapters that follow I shall return time and again to cause and effect relationships whose basis of interpretation and comparison are the activity patterns of individuals, age-sex classes or the troop in general. For example, one could ask; how much effort does the troop put into feeding activity?; or alternatively, how does seasonality of food production affect the frequency of feeding activity? I shall not provide an intensive description of all conceivable activity patterns and their correlates in this analysis. It is my goal to present the basic temporal changes, and intraspecific differences, in activity patterns that will form the basis for subsequent comparison and discussion.

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[1] Functional analysis is concerned with the effect of an item of behaviour upon the performer's survival and reproductive success, that is upon its fitness (Chalmers 1979).

5.2 METHODS

Many of the problems associated with the collection of dietary data were common to the recording of activity. Methods of data collection were predicated by the poor observation conditions within the forest. It was usually not possible to keep all or even one member of the group under continuous observation for more than a few minutes. This prevented longitudinal sampling of individuals in the group. The data were therefore collected in a systematic manner regardless of the identity of an individual. An individual's activity within the group during predetermined moments in time was scored. This technique has been described by Altmann (1974) as the scan sampling procedure. The technique has been widely used in the determination of primate activity budgets; Colobus badius (Clutton-Brock 1975a), Cercocebus albigena (Waser 1975), Symphalangus syndactylus (Chivers 1977), Cercopithecus cephus (Gautier-Hion et al. 1981), Cercopithecus mitis stuhlmanni and Cercopithecus ascanius (Cords 1987). The activity scores were operationally distinguished from one another by the following criteria:

1. The activity of all individuals clearly visible in the group was recorded during a 10 minute period centred at the half hour.
2. Any activity of greater than 5 seconds duration by an individual was recorded. This prevented the observer from having to identify the animal's activity at a glance, leading to more accurate assessments.
3. Each individual received a maximum of one score per scan.

For the purposes of comparison five classes of activity were recognized:

FEEDING - the animal handled a food item (plant or animal) or manipulated the contents of its cheek pouch;

RESTING - the animal was sitting on a support. A category called 'sit scanning' was also included in this activity class. It described the attentive scanning of a potential food source with no manual disturbance of that food source. A monkey would frequently scan in this manner but without proceeding to feed and therefore this was regarded as a category of resting activity.

MOVING - this included climbing, walking, jumping, and 'move scan'. 'Move scan' described those animals moving very slowly and very attentive to a nearby potential food source (no manipulation of the food source);

Social behaviour included GROOMING and PLAY. Grooming included self-groomimg and allogrooming. Play was defined by boisterous chase and rough and tumble activities, almost exclusively confined to the immature age classes.

Other activities such as sexual behaviour and aggression occurred infrequently and hardly ever during the 10 minute scans. Although the latter behaviours were noted they could not be quantified by the time-interval method.

The 'time-interval' scan sampling method has an advantage over 'frequency' scan sampling (applied in Chapter 4 for the determination of trends in group dietary content). In 'time-interval' sampling, activity of troop individuals was scored during a ten minute sample period. Due to the time interval between each sample period the activity in one sample was independent of the activity in the next. Activity budgets could therefore be derived from these data. 'Frequency' sampling, subject to different sampling rules (see Chapter 4), was concentrated on feeding activity only, records of which could be obtained outside the 10 minute period. While neither interval scans nor frequency scans give an accurate estimate of time spent in an activity, Oates (1977) states that 'time-interval' scans give a closer estimate of the time spent feeding on different foods (as opposed to the frequency with which items were chosen) than the 'frequency' method. However, 'time-interval' scans have to be more frequently spaced to bring sample sizes up to that of 'frequency' sampling methods. 'Frequency' sampling was thus useful for determining temporal trends in the DIET of the troop and dietary diversity. The method was unsuitable for recording the comparative feeding activity budgets between the age/sex classes since it overestimated both the time spent feeding in general, and the use of any items which the animals fed on for short periods.

Scan samples were potentially affected both by overall visibility conditions and by the differential visibility of different individuals or activities. Scans were recorded as systematically as possible from one end of the troop's dispersion to the other. By this method the observer was less inclined to 'spot' activity records from the more conspicuous behaviours and hence bias the sample in their favour. During this systematic search of the troop every effort was made to observe clearly those individuals who at first sight were partially hidden, provided that in so doing the observer did not induce an active response to his presence.

5.3. RESULTS

5.3.1. TROOP ACTIVITY - ANNUAL AND SEASONAL PATTERNS

Overall, feeding behaviour was the most common, and social behaviour the least common, troop activity (Table 5.1). Play behaviour was exclusive to the immature age classes and is not included in the interpretation of troop activity. During certain months resting behaviour was more common than feeding behaviour (Fig. 5.1). It is significant that the latter months are months during which the day length was longest and therefore more time was available for resting ($r=0.87$, $df=11$, $P<0.001$).

The proportional frequency of feeding activities by the troop was not significantly correlated with daylength or the proportion of time spent resting, and did not vary much between months (mean=36.1%, $s=5.6$, $V=15.5\%$). The trend of the graph (Fig. 5.1) does suggest, however, that a slightly lower proportion of feeding scores were noted during the summer months when the days were longer and, surprisingly, fruit was less abundant.

Without accurate measurements of the time actually spent feeding, it is difficult to say whether this pattern represents a real decrease in feeding time by the troop. The drop in proportional frequency of feeding activity may also be a direct result of the increase in resting activity scores with an increase in daylength. Thus while the number of feeding scores may remain the same (i.e. no change in feeding activity budget), an increase in the number of resting scores in response to an increase in daylength would depress the proportional value of feeding activity, falsely suggesting that feeding activity decreased during the period under scrutiny. Of the troop activities, however, only resting behaviour was significantly correlated with daylength ($r=0.87$, $df=11$, $P<0.001$). By removing the resting activity scores from the sample set, one can effectively remove the most important effect of variation in photoperiod on activity pattern. In this manner a more biologically meaningful, although quantitatively exaggerated, trend in behaviours (other than resting) is achieved. A significant correlation between trend values and the actual proportional frequencies suggests that resting scores do not alter feeding or other activity trends. Thus for the purposes of simplicity I have completed all analyses that follow by using the original proportional frequencies.

Table 5.1. The mean, standard deviation, range and coefficient of variation of the percent proportion of each activity for the study period.

Activity	Mean	s	Range	C.V	n
FEED	35.8	5.4	27-45	15.1	3549
REST	29.4	5.5	21-39	18.7	2878
MOVE	22.6	2.8	17-26	12.3	2222
GROOM	8.0	3.2	2.4-13.3	40.0	787
PLAY	4.0	2.1	1.1-7.6	52.5	400

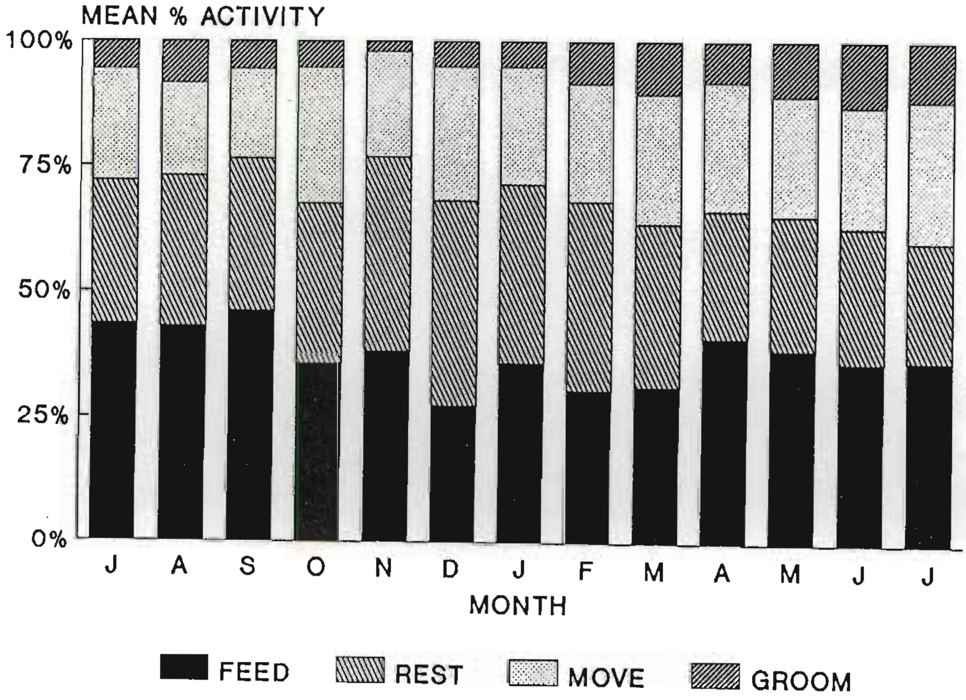


Figure 5.1. The monthly percent proportions of troop activities from scan samples, for the study period July 1986 through July 1987 (n=9836).

Feeding behaviour and locomotion (searching behaviour) are closely linked in primates. It was thus no surprise that a significant negative correlation between the frequency of feeding and moving patterns was recorded for the troop ($r=-0.71$, $df=11$, $P<0.01$). In addition the proportional frequency of locomotion scores also remained fairly constant (C.V.=12.3) over the months of the study (Table 5.1). The variation in locomotion scores which was noticeable was mostly confined to the months of June to October (Fig. 5.1). This period coincides with the breeding season when movement patterns were influenced by sexual (chase, harassment, avoidance) as well as feeding behaviour.

5.3.2. TROOP ACTIVITY - DIURNAL PATTERNS

The different activities were not equally likely to occur at different hours of the day. Feeding activity was most likely to occur in the morning and evening (Fig. 5.2). Resting activity and associated behaviours, such as grooming, were more common in the middle of the day. Variation in daylength tended to shift the timing of daily patterns of activity slightly, such that early morning and late evening activities remained spread over the same duration but the midday rest period varied to accommodate this. This shift in diurnal activity pattern tends to smooth the peaks and troughs in the activity curve for the whole study period. Examined by season the diurnal activity pattern shows that feeding behaviour is more specifically confined to an early and late morning, and late afternoon peak in both December and July (Fig. 5.3).

5.3.3. AGE-SEX CLASS DIFFERENCES IN ACTIVITY PATTERN

Age-sex classes differed significantly in the overall proportions of activities ($X^2=175.15$, $df=12$, $P<0.001$ Table 5.2). For further tests of significance, the proportional activity by month on age-sex class, was examined using the Kolmogorov-Smirnov two sample test (Roscoe 1969).

Males had a significantly lower proportion of feeding, and higher proportion of resting activity scores, than all other age-sex classes (in each case $D_N>0.615$, $n=13$, $P<0.02$). In addition, the male showed the greatest variation in amplitude of feeding activity

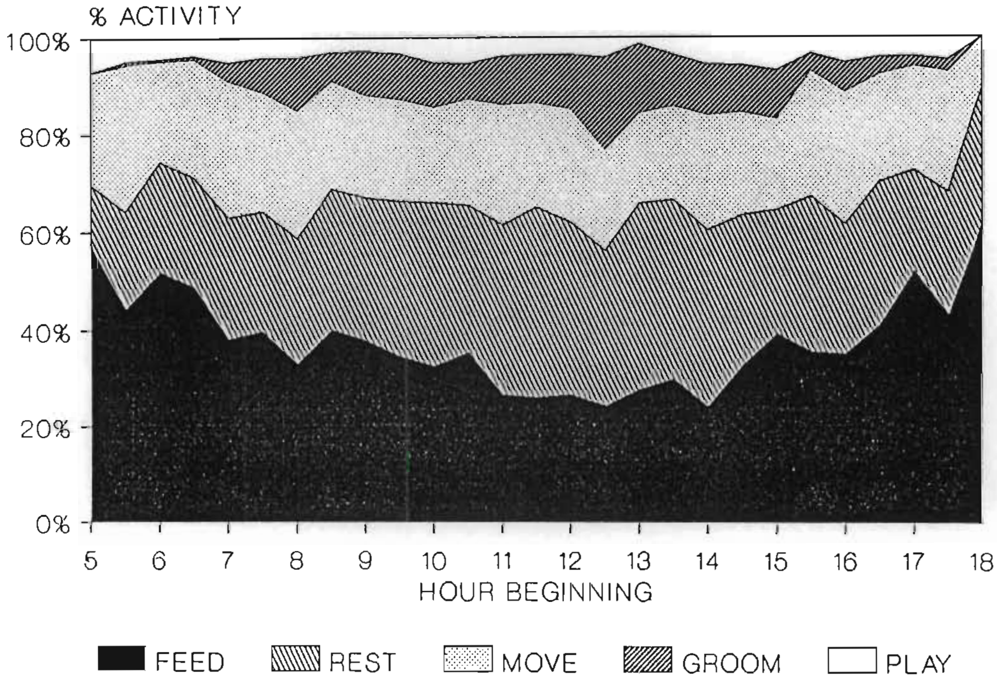


Figure 5.2. Diurnal troop activity - the hourly percent proportion of activities.

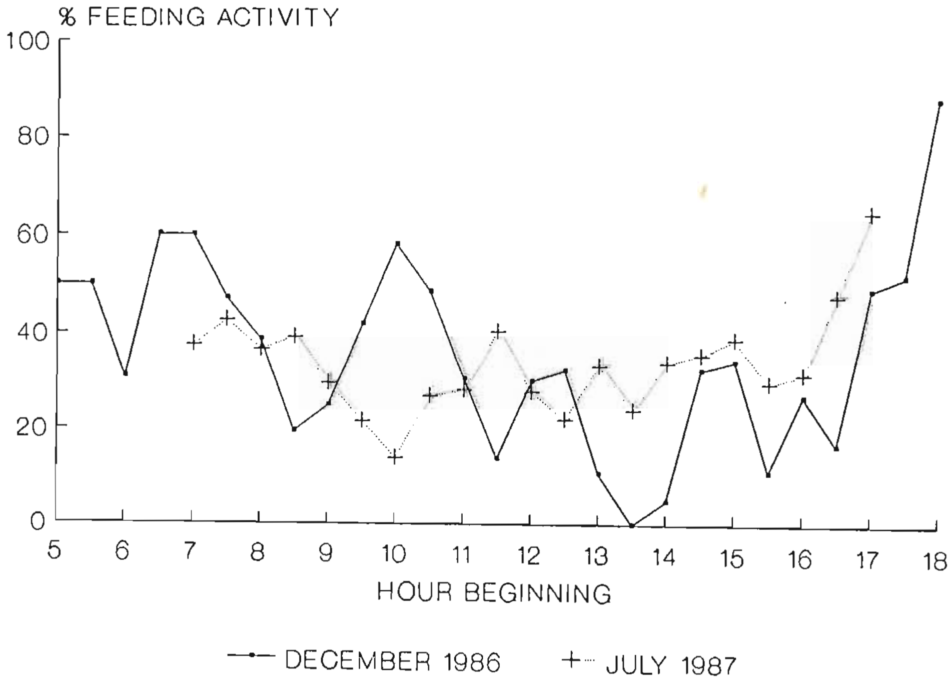


Figure 5.3. A comparison between December (summer) and July (winter) of the diurnal feeding patterns of the troop.

Table 5.2. The frequency and percent proportion of the activity types for each age-sex class over the study period, July 1986 to July 1987. Records collected using the time interval scan sampling method.

AGE-SEX		Feed	Rest	Move	Groom	Play	n
Male	%	24.9	46.8	22.9	5.2	-	428
Female	%	36.3	32.1	22.4	9.1	-	3395
Subadult	%	38.4	25.4	27.6	6.9	1.6	1536
Juvenile	%	36.1	27.5	21.5	7.9	7.2	4429

(mean=24.9%, s=8.3, V=33.2%) over the study period (Fig. 5.4), with a modal peak centred on April to July.

There was no difference in the distribution of feeding activity by month between the adult female, subadult and juvenile age-sex classes (Kolmogorov-Smirnov two sample test, all cases $P>0.9$). In contrast, adult females were observed to rest significantly more frequently than the subadults ($D_N = 0.62$, $n=13$, $P<0.02$), but not more than juveniles.

Although both the adult age-sex classes showed a significant negative correlation in their feeding and resting activity over the months of the study (male: $r=-0.89$, $df=12$, $P<0.001$; female: $r=-0.59$, $df=12$, $P<0.04$), no such relationship was recorded for juveniles or subadults (Pearsons correlation coefficient, $P>0.3$).

The activity of lactating females was scored over five months, October 1986 to February 1987. Despite the fact that the overall metabolic requirements of lactating females are presumed to be higher than other age-sex classes (Blaxter 1964, Pond 1977), there was no difference between the activity of adult females and females with infants ($X^2=5.24$, $df=3$, $P<0.15$) during this period.

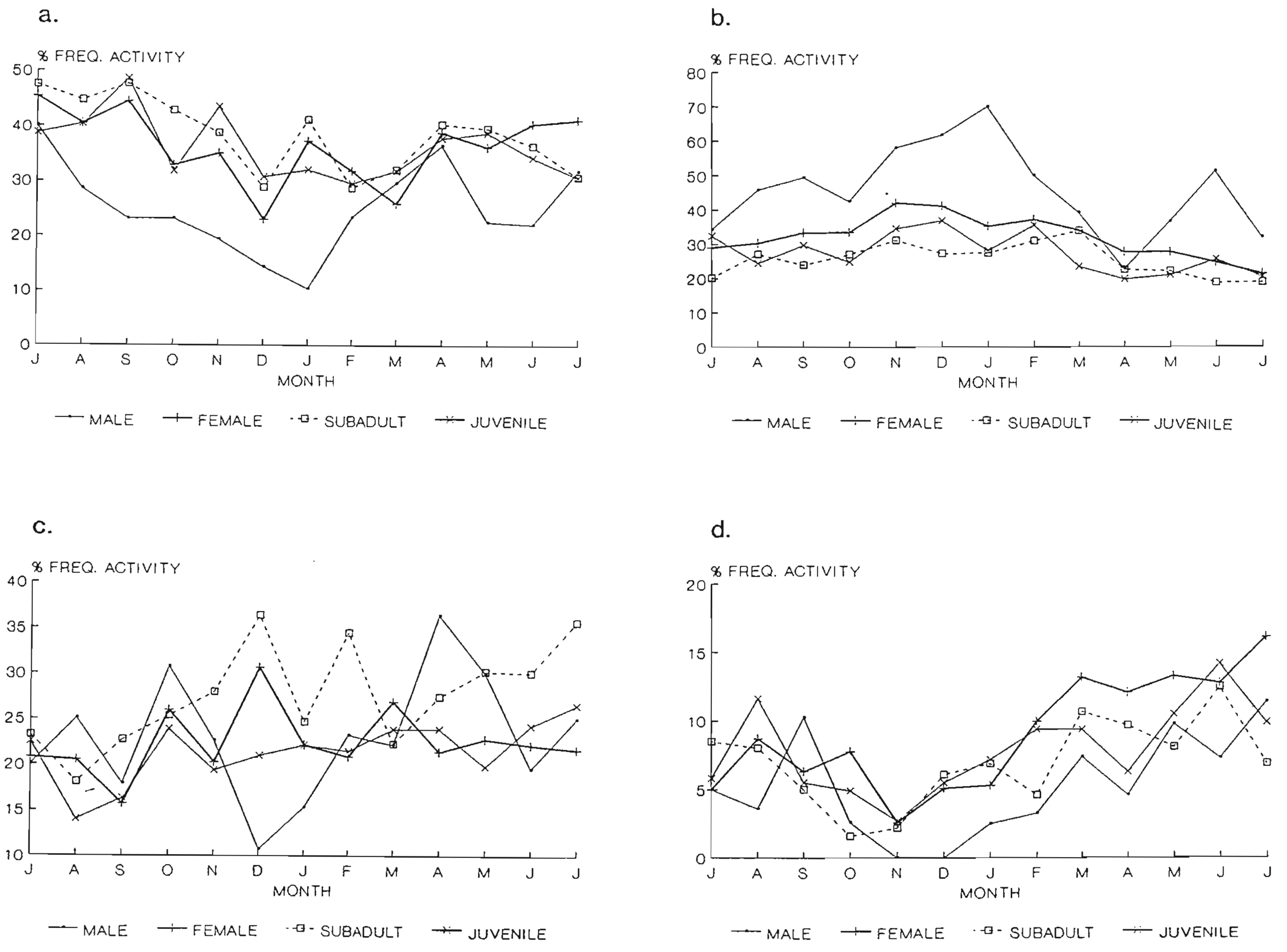


Figure 5.4. The monthly percent frequency of age-sex class activities over the study period. (a) Feeding activity; (b) Resting activity; (c) Locomotion; (d) Social activity /grooming/play.

Disregarding boisterous activities such as play, subadults moved significantly more than females and juveniles (in both instances $D_N=0.615$, $n=13$, $P<0.01$). If play activity is included (an activity exclusive to subadults and juveniles) in locomotion, then little difference in locomotion frequency existed between the two immature classes (subadults 29.1 %, juveniles 28.5 %).

Females were most and males least frequently involved in social activities such as grooming. Females groomed more frequently than males and subadults. There was no observable difference in grooming frequency between females and juveniles, primarily because these two classes were most often involved in mutual grooming activities. The social core of the troop's activity appears to centre on the females.

5.4 DISCUSSION

Feeding was the most common behaviour of the samango monkey at all temporal scales (i.e. annual, monthly, seasonal and daily). Since food is such a crucial resource, feeding activity is frequently the most common activity in primates. In fact the patterns of primate activity in space and time are often centred on the feeding activity of the individual or group. For example, resting may act as a catch-all category that absorbs whatever time is not required for feeding and socializing (see Dunbar 1988 and following references cited therein; macaques: Fa 1986, Seth and Seth 1986; vervets: Lee 1984). The negative correlation between feeding and resting in the adult sex classes suggests that resting behaviour may perform a similar function in samangos.

The amount of time spent feeding by a primate depends on (a) body size, (b) the habitat-specific costs of thermoregulation, (c) the animal's active metabolic requirement, (d) the reproductive metabolic requirement and (e) the nutritional quality of the available food (Dunbar 1988). For instance, larger arboreal dietary generalists, such as mangabeys, spend much longer searching for and eating their food than do either specialist folivores or smaller generalists like Cercopithecus monkeys (Homewood 1978). In addition, the amount of time available for feeding may also be constrained by the time needed for digestion of food (regardless of food quality). Thus, while resting may function mostly as a "catch-all" category, some resting may be essential for other purposes such as vigilance and in many cases as a period during which this digestion can take place. When samangos rest during mid-morning it is in all probability not due to fatigue, but permits digestion and assimilation after a heavy feeding session. In this instance resting can be seen to be more directly part of the feeding behaviour of the samango as opposed to the midday rest which primarily allows the monkeys to avoid heat and fatigue. However, the negative correlation between resting and feeding may also be a function of daylength. Thus, during months when daylength was longest the adult classes also rested for longer periods.

Before discussing activity patterns further, it is important to sound a cautionary note about using scan sampling techniques to determine activity patterns. Bearing in mind the increase in the frequency of activities other than feeding with an increase in day length, it is easy to see that even if the number of feeding scores remains constant each month (i.e. time spent feeding remains the same), if the proportion of scores for other activities increases the proportional value of feeding scores will drop. In this example it may be correct to assume that the monkeys rest more frequently, but totally fallacious to assume that the monkeys feed less frequently. Herein lies one of the major disadvantages of using scan-sampling for estimating activity budgets: frequency scores converted to proportions do not provide accurate information about time budgets. Thus, while the drop in feeding frequency during summer may be real (and a response to food availability and other correlates), it is also in part due to sampling peculiarities caused largely by the relationship between resting behaviour and daylength.

The use of resting time for digestion has been recorded from folivorous primates (Curtin and Chivers 1978, Bauchop 1978). In order to extract nutrients from plant structural elements, leaves have to be fermented for a prolonged period and this digestive activity is incompatible with other activities. Samangos have been shown to ferment and digest low quality foods such as leaves in their enlarged ceacum and colon (Bruorton and Perrin 1988). Fundamental to samango fitness at latitudes where food availability becomes more seasonal is this ability to accommodate a change in the quality of the diet as well as the shift in activity that goes with it.

It is important to recognize that behavioural mechanisms (i.e. altering activity patterns) are not the only possible means of response to environmental change (food availability) in the samango monkey. As predicted by Slobodkin and Rapoport (1974) physiological response is also important. The extent of physiological response may be greater for samangos than other mitis populations on account of the seasonality of climate and food resources in the sub-tropics, especially protein rich food sources. A corollary of the latter reasoning is that for physiological reaction to be necessary, the limits of behavioural response (activity patterns) must be reached. The question is, "Is the seasonality of food abundance, particularly protein rich foods, sufficiently severe for samango monkeys at Cape Vidal to reach the limits of behavioural response?" If this were the case, their activity patterns may well define the extent of the behavioural response capabilities of the mitis group.

It seems unlikely however that the latter is true for samangos at Cape Vidal. On the whole, they spent less time feeding and resting and more time moving and socializing than east African populations (Table 5.3). If the monkeys were forced to the limits of their ability to respond to shortage behaviourally, one would expect them to spend more time feeding and less time socializing. The activity patterns therefore confirm the conclusion made previously that the monkeys are not fruit-stressed, or, food limited at Cape Vidal. However, these conclusions aside, the differences in proportion of troop activity scores may simply be a function of the larger number of immature individuals in the troop at Cape Vidal (21.5 immature:10.5 adult). Juveniles and subadults certainly rest less and move more than adults (Table 5.2), and this could influence the total troop score. A comparison of adult female activity patterns from different populations tends to support the latter argument: adult females at Kibale and Cape Vidal do not differ in their activity

Table 5.3. Comparative activity budgets for the C. mitis group.

Study area		Feed	Rest	Move	Groom	Play	Other	n
Cape Vidal this study	%	35.8	29.4	22.6	8.0	4.0	-	9836
Kakamega [1] Cords 1987	%	46.5	36.1	14.4	1.4	-	1.6	2273
Kibale [2] Aldrich-Blake 1970	%	41.7	39.4	16.5	2.4	-	-	2696

1. Activity scores are derived from the combined values for the blue monkey group when in mixed-species associations and alone (see Cords 1987 p38).
2. Activity scores represent the combined values from each season represented in table on p115, Aldrich-Blake (1970).

patterns (Table 5.4). It is unlikely therefore that samango activity patterns are indicative of the extreme limits of behavioural response in the mitis group to latitudinal change in food abundance and seasonal availability.

Table 5.4. A comparison of adult female activity patterns from Cape Vidal (this study) and the Kibale forest (Butynski 1990[1]).

Study area	Feed	Rest	Move	Groom	n
Cape Vidal	36.3	32.1	22.4	9.1	3395
Kibale forest Kanyawara	36.2	35.7	19.7	8.3	9717
Ngogo	31.7	36.2	24.7	7.0	6079

1. Results from Table 9., pp.15. Values for feeding and foraging were combined under feeding, as were the values for scan, rest and self-clean under rest.

Given the number of variables on which the feeding activity pattern is dependent and the importance of feeding activity for survival and reproduction, it is remarkable that the estimated overall proportion of time spent feeding should be so consistent (35%-45%) among widespread populations of the mitis group (Table 5.3 and Table 5.4) and among other guenons in general (cf. Gautier-Hion 1980 Cercopithecus nictitans, C. pogonias and C. cephus p259, Gautier-Hion et al. 1981 Cercopithecus cephus, Cords 1987 C. ascanius). A number of hypotheses may account for this consistency: (a) there may be broadly similar food availability and feeding conditions in forests within the range of the mitis group, or (b) the guenons may be compelled by the energy demands of similar body size, and by the types and variety of resources available, to apportion their activity budget in a similar manner, or (c) guenons, and the members of the mitis species group in particular, may be energy maximizers. As such they would use the time available for feeding to eat as much as possible, maximizing their energy intake (Schoener 1971, Pyke et al. 1977). It may well be that in maximizing their energy intake the different mitis populations achieve similar overall proportional feeding times after the time essential for resting, socializing and moving is accounted for.

Locomotion or moving is the activity most likely to impinge upon feeding time since, in addition to time spent handling food, time must be spent searching for it. Time spent in movement is thus determined primarily by the dispersion of food in the habitat and by the size of the foraging group (van Schaik et al. 1983, Dunbar 1988). Although in some primates, for example baboons, time spent moving seems to be quite unrelated to time spent feeding (see Dunbar 1988 p91), this is not always the case (e.g. macaques: van Schaik et al. 1983). For samangos at Cape Vidal feeding and moving activities were negatively correlated, but the amplitude of variation in the proportional frequency of both feeding and moving was low (Table 5.1). These data suggest that the proportion of time available for feeding is sensitive to minor changes in searching time, or, conversely, that search conditions (i.e. food dispersion) were similar over the study period.

Robinson (1981) reported that behavioural traits varied with the age and sex of wedge-cap capuchin monkeys (Cebus nigrivittatus), such that juveniles spent more time playing than adults, subadult and adult females groomed and were groomed more frequently by the dominant male than were juvenile females, and adult males spent more time searching for food. Likewise, Caldecott (1986) found that adult male pig-tailed macaques (Macaca nemestrina nemestrina) had different movement and feeding activity patterns to females. This was also true for samangos at Cape Vidal. Juveniles played more, subadults spent more time feeding, females groomed more and males fed less and rested more frequently than other age-sex classes.

Differences in the time spent feeding and moving are often taken to indicate differences in foraging strategy between age-sex classes (Robinson 1981). The fact that the adult samango male spent less time feeding per unit of body weight (time minimizer: see Schoener 1971, Richard 1985) than any other age-sex class suggests the presence of an adaptive feeding strategy in this age-sex class. The marked variation in male mitis activity is purported to be an adaptive behaviour pattern by which, ultimately, the male maintains both his access to females and tenure as the troop male and in so doing improves his individual fitness (Tsingalia and Rowell 1984, Cords et al. 1987, Henzi and Lawes 1987, 1988). For example, the modal peak in feeding activity for the male is around April, just prior to the mating season, and some months after the major peak in fruiting activity. The male may, in fact, be accumulating nutritional reserves during this period in anticipation of the energetically expensive mating season activities. This is quite possible and has been recorded from squirrel monkeys who deposit fat reserves prior to mating (DuMond and Hutchinson 1967).

Great vigilance is required of a troop male if he is to succeed in maintaining his tenure and access to receptive females. Vigilant behaviour and feeding activities are incompatible and the male may need to spend more time than other age-sex classes observing troop activities and monitoring the proximity of other lone males. The male thus spends long periods sitting in the mid-canopy scanning the activities of individuals about himself. I scored this behaviour as a category of resting activity and the male is observed to "rest" more than any other age-sex class. A corollary of this argument is that the male must maintain a strictly defined diet both in quality and quantity (if he can afford less time than other age-sex classes for feeding); thus, being a time minimizer one would expect adult troop males to be greater dietary specialists. This is in contrast to the other age-sex classes who appear to be energy maximizers with broader dietary niches. The question of the comparative quality and quantity of food items ingested by the age-sex classes is discussed later (Chapters 6 and 8). Here, it is sufficient to state that age-sex class differences in activity suggest potential differences in feeding strategy.

In many ways this chapter provides the springboard from which the inductive arguments of later chapters will follow. It is meaningless to discuss activity patterns without considering the relationship between food availability, the diet and activity or the influence of the physical environment (daylength, rainfall etc.) on activity. Throughout the remaining chapters dealing with the diet, age-sex differences in the diet, ranging behaviour and foraging strategy, I shall return again to activity patterns and their specific significance as the vital first phase response to environmental change.

CHAPTER 6: AGE AND SEX DIFFERENCES IN DIET AND FEEDING BEHAVIOUR

6.1 INTRODUCTION

An investigation of the overall diet (Chapter 4) treats the troop as a single organism capable of making feeding and ranging decisions while, in reality, the 'diet' is the outcome of a complex set of interactions between the individuals within the troop and changes in environmental quality. It is clear that the discussion of the overall diet of the samango monkey is incomplete without considering the age-sex class differences in diet.

Guenons live in cohesive social units and, as such, group members use the same food resources over the same broad time and space dimensions. However, Cords (1986a) and Gautier-Hion (1980) have recently shown that dietary similarity of age-sex classes between guenon species is often higher than that within species. Intuitively one would expect age-sex differences in both diet and feeding behaviour within a troop, since a reduction in interindividual competition minimizes the competitive consequences of sociality (van Schaik et al. 1983, Wrangham 1986, Dunbar 1988).

Gautier-Hion (1980) attributed **sex** differences in the diet of adult guenons in Gabon to physiological and social constraints acting on adult females and males respectively. Thus differences in nutritional requirements between sexes result from disparate investments in reproduction, and could be partially responsible for sex differences in diet (Clutton-Brock 1977). **Age** class differences in diet are considered to be largely a consequence of the negative allometric relationship between body size and relative nutrient requirements (Schoener 1971, Pyke et al. 1977, Gaulin 1979). However the social implications of body size can lead to dominance hierarchies, based primarily on age and size, and could also cause further age differences in diet (Post et al. 1980, Janson 1988).

This account examines those age-sex class activities that function to reduce the spatial and/or temporal overlap in the use of food resources between age-sex classes.

6.2 METHODS

The scan sampling procedure used for determining age-sex differences in the relative frequency of use of food resources has been described (Chapter 4). However, time interval scan sampling of feeding activity on different items does not provide a reliable estimate of the amounts of different foods ingested, especially where feeding rate varies widely between foods (Altmann 1974, Hladik 1977). To correct for this deficiency, short focal samples of feeding behaviour of the type described by Post et al. (1980) were conducted between scan periods (see below). Focal samples provided information on the rate at which an item was ingested and the feeding bout duration for an item from a plant species used by that age/sex class.

The duration of all feeding bouts initiated during the sample were timed to completion. Feeding bouts were classified into three types, for analytical purposes, according to their mode of termination (Post et al. 1980). A bout was terminated:- i. 'spontaneously'- where the individual merely abandoned a food plant without obvious outside interference or did so to engage in some form of nonaggressive social interaction such as grooming or play; ii. 'interrupted' - here the feeding bout was abandoned due to the directed approach of another individual, or due to involvement in some form of aggressive interaction; iii. a 'time-out' situation where the focal animal disappeared from view.

The classification of bout termination permitted the inclusion of those observationally-censored bouts (i.e. type iii. above) in the analysis of bout durations. It could be argued that the observationally-censored bouts be discarded altogether thus avoiding the complications of further statistical analyses and the correct interpretation of the outcome. However, forest primates are notoriously difficult to observe and focal samples that are observationally-censored are the rule. A method of dealing with the censored samples, in this instance the statistical procedure of Kaplan and Meier (1958) and adapted by Post et al. (1980), was used to obtain product-limit estimates of mean feeding bout duration from the combined data set of feeding bouts terminated in all three of the ways listed above.

The Kaplan-Meier technique estimates the proportion of bouts whose duration would exceed some given length of time (t) in the absence of observational censoring of bouts or other uncontrollable forms of termination. The proportion, P(t), of all bouts whose duration exceeded some fixed length of time, t, regardless of the mode of termination of these bouts is calculated. A histogram of the density weights, P(t), attached to the failure times, t, is constructed from which the mean and standard deviation of the bout duration can easily be calculated. The mean is equal to the area under the corresponding survivorship histogram. The greater the number of intervals in the histogram the more accurate a value for the mean. As one increases the number of intervals the shape of the histogram approximates a curve more closely. The number of intervals was determined by the $\log_2 n$ rule, where n is the number of data points for the histogram. An adapted version of a minitab macro (Beder-Millar and McKenzie 1988) was used to calculate and construct the histogram.

The inter-individual distances between group members were used to illustrate the effect of feeding behaviour on social/spatial structure of samango monkeys. The method follows that of Rudran (1978a). The distances were obtained by successively considering each group member who was visible during a scan period as a focal animal and noting its neighbours. Neighbours were operationally defined as animals within 10 m of the focal animal for at least five seconds after the sample time. For any pair combination of age-sex class, a set of two inter-individual distances were obtained because an animal was considered as a focal animal as well as a neighbour to other focal animals. Although these two distances were not necessarily the same they did not differ greatly. Thus, the mean of these two distances was used to simplify results. Measures of proximity to infants were made only where the infant was moving independently.

The intragroup social structure can be further clarified by considering the frequencies with which each age-sex class was nearest neighbour to other classes. Observed frequencies were compared to frequencies expected from a random model (Rudran 1978a, Robinson 1981). When females were carrying their infant (lactating female) the spatial relationship between the female with infant and her nearest neighbour was considered more important than her relationship to her infant. As a consequence of these sampling procedures, the calculation of expected frequencies of nearest neighbours for infants were not independent and values for infants were discarded from frequency analyses only. Analyses which included lactating females in age-sex class pairwise comparisons were computed over the period October 1986 to February 1987 when these females were observed carrying their infants and could be operationally distinguished from other females.

By examining the age-sex class use of forest stratum and the proximity of nearest neighbours, I investigated the possibility that body size imposed mechanical limitations or advantages on the sampling efficiency of an age-sex class in relation to the distribution of food within the forest strata.

Predictions of age-sex differences in the diet from the data are subject to certain considerations: (a) Age-sex class size changed during the study period e.g. an adult female died, a subadult emigrated, and a number of infants were included in the juvenile class toward the end of the study. This explains why the distribution of observation scores between the age-sex classes is not quite proportional to the overall age-sex class composition of the study group given in Chapter 2. It was not possible to recognize all individuals and, as a result, (b) there is a possibility of sampling the same individual more than once in a sample period. Every effort was made to avoid this problem and the group was systematically and thoroughly scanned. (c) Since there was only a single male (outside breeding season), sample sizes for this class are small, causing considerable variation in results expressed as percentages for the male. Despite these considerations, I am confident that the observations are representative of age-sex class behaviour.

6.3 RESULTS

6.3.1 AGE-SEX DIFFERENCES IN THE DIET

6.3.1.1 USE OF PLANT SPECIES

a. Species richness

Of the total number of plant species (n=57) used by the troop, 36 plant species were shared by females, subadults and juveniles. For a large number of plant species (n=30) there were no records for the male, due in part to both the much lower sample sizes for the male and the fact that these plants were low usage species. These latter plant species were either understory shrubs (e.g. Tricalysia sonderiana) or small understory trees (e.g. Euclea natalensis, Ochna natalitia) with sparce fruit production or vines (e.g. Caesalpinia bonduc, Adenia gummifera). The mechanical problems of a heavy primate sampling the terminal fruits of the smaller plants or hanging vines may limit the species richness of the male's diet. Males used the fewest plant species (n=25), juveniles the most (n=53), and females (n=44) and subadults (n=40) an intermediate number of species. The age-sex classes differed most in their use of understory shrubs and trees, and vines. Like the male, adult females used vines species less frequently than did subadults and juveniles.

b. Frequency of use of plant species

Pairwise comparisons of the frequency of use of plant species regardless of the item eaten suggest that; (a) the relative frequency of use of plant species by the male and the juveniles differed significantly from other age-sex classes, while there was (b) no significant difference in the relative frequency of use of plant species between females and subadults (Table 6.1). In all comparisons the male used plant species in the diet significantly less frequently, and juveniles more frequently than expected (Table 6.1).

Table 6.1. Chi-squared statistic for comparisons between different age-sex class pair combinations of plant species composition of the diet (M=Adult male, F=Adult female, S=Subadult, J=Juvenile).

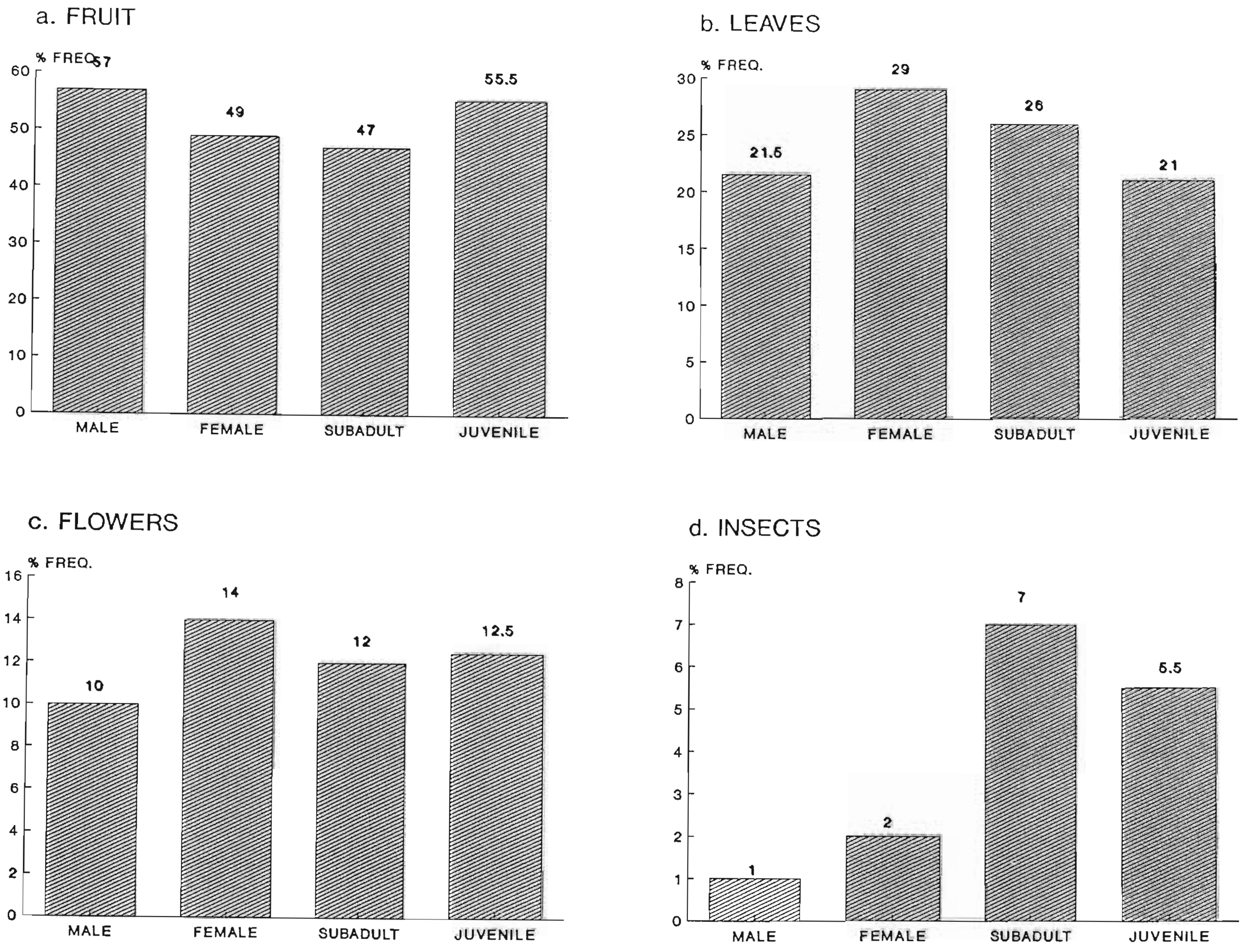
PAIR COMBINATION	M/F	M/S	M/J	F/S	F/J	S/J
X^2	73.8	32.3	146.4	23.6	42.5	76.4
df	21	21	21	26	26	25
P	0.001	0.05	0.001	0.6	0.02	0.001

The diversity of the diet based on the proportion of specific plant food items in the diet indicates that; (a) females with infants (H=4.914, 49 specific items) and the adult male (H=4.928, 60 specific items) have the lowest dietary diversity. However, (b) adult females without infants (H=5.909, 175 specific items) and juveniles (H=5.923, 206 specific items) have similar and the highest dietary diversity, while (c) subadults exhibit by comparison, relatively moderate diversity of the diet (H=5.345, 152 specific items).

The adult male was noted both for his use of fewer species than expected and a lower expected frequency of use of these species. This is not expected given that larger body size would ensure a higher absolute metabolic demand than the other age-sex classes. A larger body size and dominant status would, however, permit the male to dominate favoured food resources, especially fruit. For four important abundant fruiting species (Mimusops caffra, Grewia occidentalis, Diospyros inhacensis, Sideroxylon inerme) the male's use was greater than expected.

6.3.1.2 COMPOSITION OF THE DIET

The percentage composition of food items in the diet of the age-sex classes, for the study period, are illustrated in Figure 6.1. Pairwise comparisons of the frequencies of use of the food items (Table 6.2; see also Appendix 6.1) show that; (a) the adult male ate significantly more fruit and fewer leaves than females and subadults; (b) there was little difference in diet between the male and juveniles, and juveniles also had a high proportion of fruit in the diet; (c) females and subadults had very similar diets although



a. FRUIT

b. LEAVES

c. FLOWERS

d. INSECTS

Figure 6.1. Age-sex class variation in the total use of food item types.

subadults ate fewer leaves and slightly more insects (cf. Fig. 6.1); (d) flowers were used less overall by the male than by any other age-sex class (cf. Table 6.2).

Table 6.2. Chi-squared statistics for comparisons between age-sex class pair combinations of the plant food item composition of the diet, regardless of species (M=Adult male, F=Adult female, S=Subadult, J=Juvenile).

PAIR COMBINATION	M/F	M/S	M/J	F/S	F/J	S/J
X^2	18.6	21.4	11.9	16.5	33.6	32.3
df	8	8	8	11	11	12
P	0.01	0.01	0.16	0.12	0.001	0.001

Monthly overlap of specific plant food items in the diet were computed for pair combinations of the age-sex classes. The mean and range of monthly overlaps for each pair is given in Table 6.3. The adult male had the least (mean=50.0%) and juveniles the most (mean=61.2%) overlap in the plant diet with other age-sex classes. The mean age-sex class overlap for each month (Table 6.4) was positively correlated with the availability of fruit ($r=0.569$, $n=13$, $P<0.05$), and negatively correlated with the availability of flowers ($r=-0.613$, $n=13$, $P<0.03$). The mean percent monthly overlap in the plant diet for all age-sex classes was 58.1% (range=January 1987, 42.8% - April 1987, 64.6%).

6.3.2 AGE-SEX DIFFERENCES IN THE USE OF SPACE

6.3.2.1. Use of the forest strata

The use of the forest strata by the troop has been discussed (Chapter 7). No major difference in the age-sex class use of the forest strata was observed (Fig. 6.2a). In all cases thickets (range= male 7.16% - juvenile 11.65%), understory trees (range= female 10.68% - juvenile 14.03%) and the middle strata of the canopy (range= juvenile 11.83% - male 15.43%) were used most. The Isoglossa shrub layer was used the least (range= male 2.62% - juvenile 6.15%).

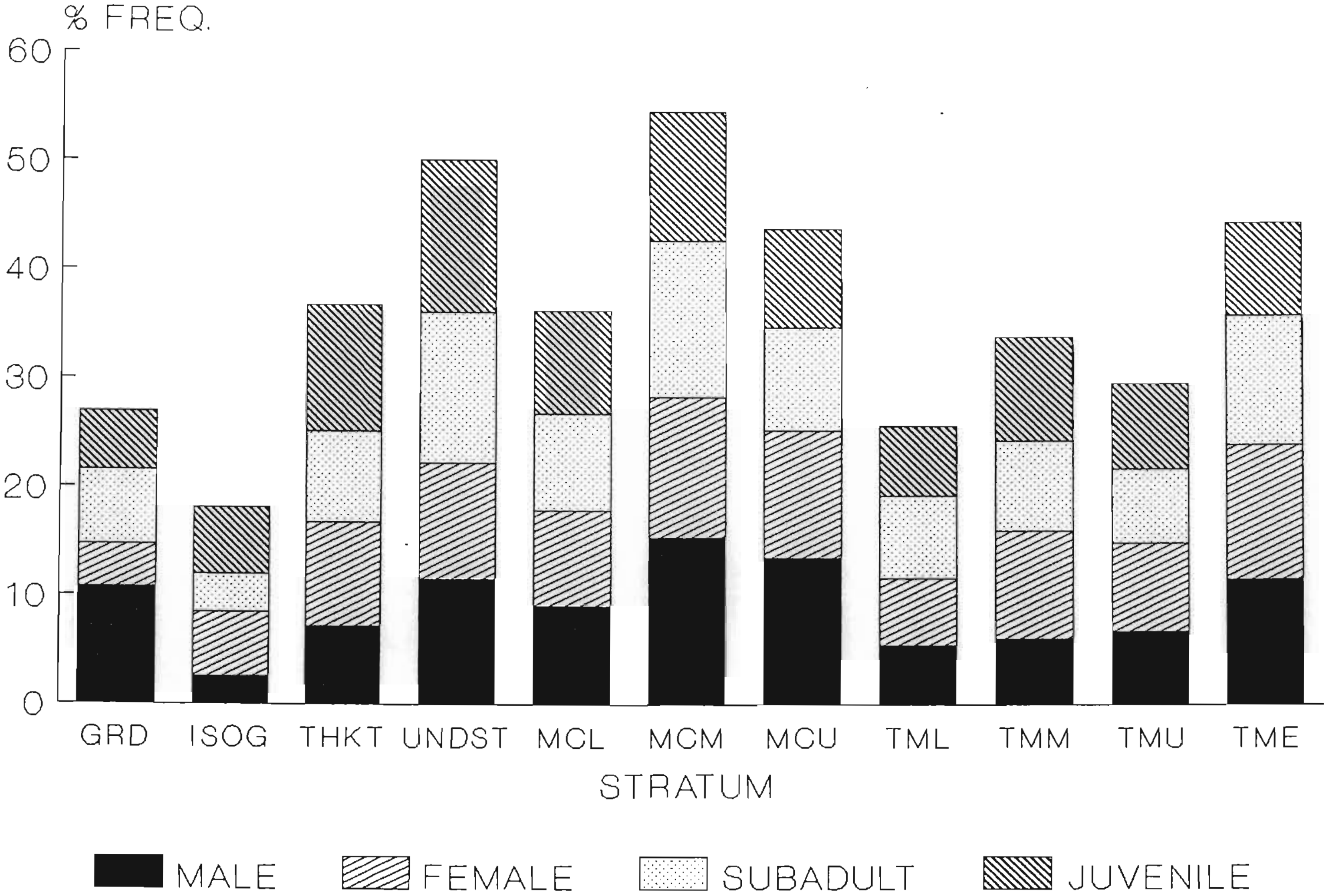


Figure 6.2a. The percent frequency of use of the forest strata by the age-sex classes over the study period (GRD ground, ISOG *Isoglossa* herb layer, UNDST understory tree, MCL lower branches mid-canopy, MCM mid-canopy middle branches, MCU mid-canopy terminal branches TML upper canopy lower branches, TMM upper canopy middle branches, TMU upper canopy terminal branches but not exposed, TME upper canopy terminal crown- exposed.

Table 6.3. Mean and range of percent overlap of species-specific items in the plant diets between different age-sex classes (n=13 months).

	Adult female	Subadult	Juvenile
Adult male	51.8 (29.2-66.2)	48.5 (30.5-71.6)	49.8 (30.5-61.9)
Adult female		64.1 (48.3-73.7)	70.3 (61.9-76.1)
Subadult			63.6 (54.7-75.6)

Table 6.4. The mean and range of monthly percent overlap of species-specific items in the plant diets over all age-sex classes for the study period.

MONTH	MEAN	RANGE
Jul 1986	60.9	49.2-74.5
Aug	63.6	54.0-70.5
Sep	61.7	45.4-75.6
Oct	63.4	50.8-71.5
Nov	55.7	40.6-70.8
Dec	49.7	30.5-65.1
Jan 1987	42.8	29.2-61.9
Feb	56.4	34.8-75.8
Mar	62.1	54.0-71.9
Apr	64.6	53.5-73.7
May	55.1	40.8-70.8
Jun	63.6	45.7-73.7
Jul	55.7	42.7-76.1
TOTAL	58.1	48.5-70.3

Males were slightly less inclined to use terminal branches, and more inclined to use middle canopy and forest floor than other age-sex classes (Fig. 6.2a). Subadults and juveniles were noted for their comparatively greater use of thicket and understory tree strata. Females differed little from other classes in their overall use of the forest strata, except in one respect; they used the terminal branches as frequently as did juveniles and more frequently than the male and subadults.

To determine whether use of the strata was a consequence of activity type, stratum use for feeding activity and other activities combined were plotted separately (Fig. 6.2b and 6.2c). Apart from a considerable increase in the use of the terminal, highly exposed branches of the canopy crown (range= juveniles 18,9% - male 32.9%), there was little variation in the use of the other strata among all age-sex classes (range= male, mid canopy 0.9% - male, upper canopy crown, not exposed 14.6%) while feeding (Fig. 6.2b). Males showed the greatest variation in the use of the remaining strata (mean= 6.7%, s=4.7, V=70.2%, n=10) and utilized all strata from the herb layer to the lower middle branches of the tree crown the least (range= 0.9%-3.8%). The male came to the ground (14.1%) more frequently than the other age-sex classes when feeding. This can be attributed to the fact that when the other age-sex classes were sitting in the Isoglossa herb layer, the male, because of his greater weight, had to sit on the ground to feed. The male utilized the upper-mid-canopy stratum (14.6%) where visibility is particularly good, more frequently than any other age-sex class (possibly to maintain his vigilance).

When not feeding there was little notable difference between the age-sex classes in the use of the forest strata. Although there was greater variation in the use of the forest strata in general (Fig. 6.2c). The thicket, understory tree and middle canopy strata were the most frequently used (mean=13.6%, s=2.8%, n=20, range= male, thicket 9.2% - male, mid canopy, central branches 19.1%). The ground, Isoglossa herb layer, and the terminal branches were the least used (mean=5.3%, s=2.2%, n=24, range= subadult, Isoglossa herb layer 1.9% - female, mid canopy, terminal branches 10.2%).

6.3.2.2 Age-sex class spatial relationships

The spatial relationships between different age-sex classes (Table 6.5a) were similar to those recorded by Rudran (1978a) for the blue monkey:

b.

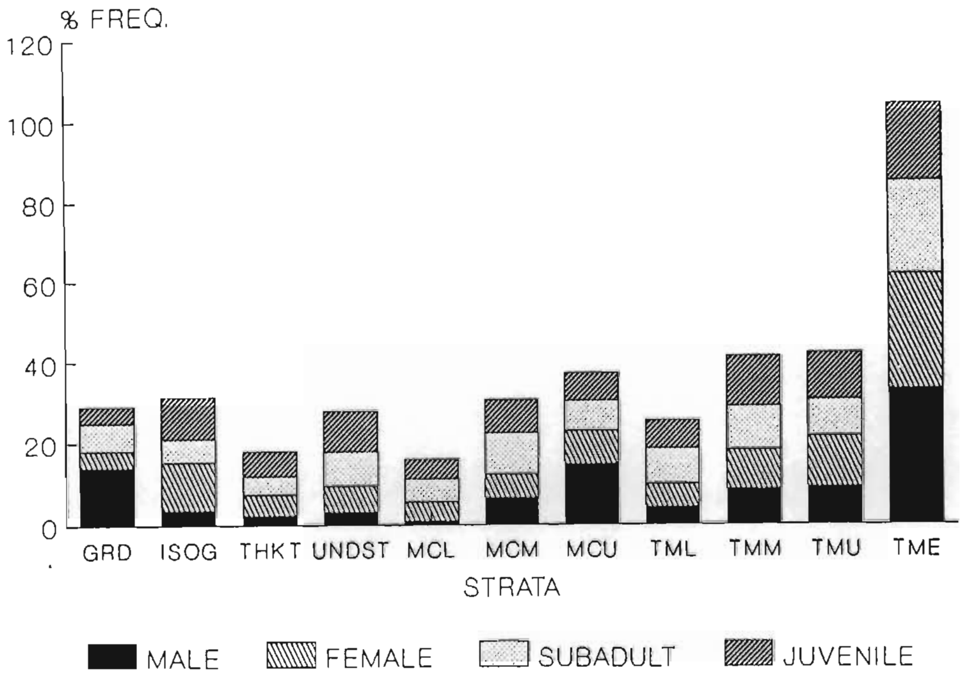


Figure 6.2b. The percent frequency of use of the forest strata by the troop while feeding (x-axis acronyms given in Fig. 6.2a).

c.

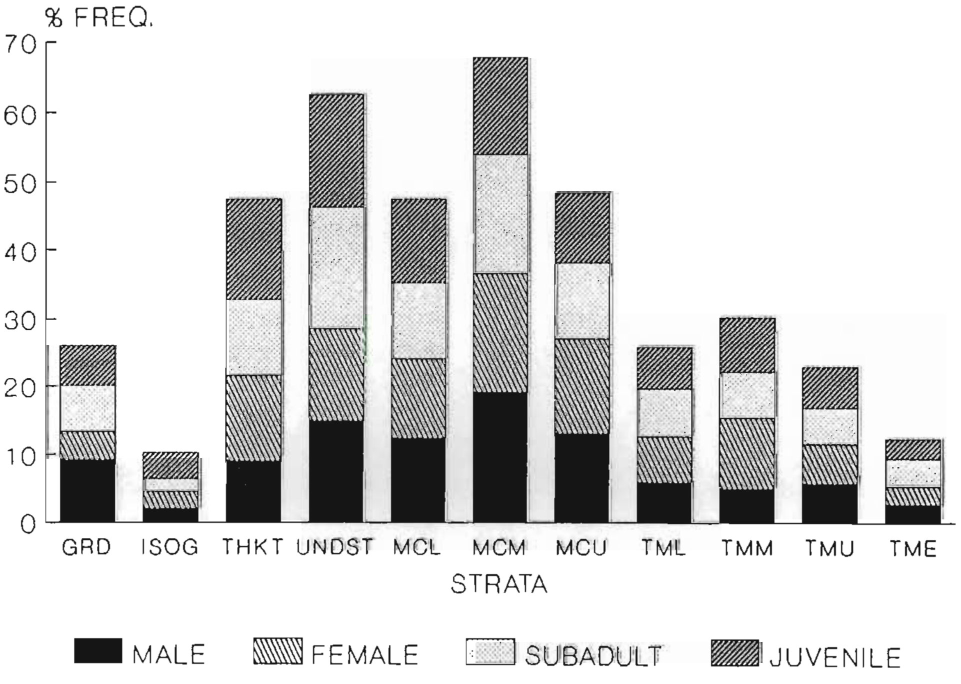


Figure 6.2c. The percent frequency of use of the forest strata by the troop while engaged in activities other than feeding.

(a) The inter-individual distances between the male and all age-sex classes (mean = 3.0 m) were the longest for any pair combination with that age-sex class. Thus on average the male had the greatest personal space.

(b) The adult male was closer to adult females than to other age-sex classes.

(c) Adult females were nearest to infants and, unlike blue monkeys (Rudran 1978a), the distance between adult females was shorter than that between adult females and the male.

(d) Subadults were closest to adult females and juveniles, and furthest from the adult male.

(e) Juveniles were closest to one another or active infants, and furthest from the adult male.

(f) Infants were active mostly during resting or social activity and were closer to one another than they were to their mothers.

The nearest neighbour relationships (given above) did not change in relation to the activity of the age-sex class (cf. Table 6.5b and 6.5c), although the mean distance between an age-sex class and its neighbour was significantly larger when feeding (paired t-test, $t=15.5$, $df=5$, $P<0.01$).

Subadults and females had slightly fewer than the expected number of nearest neighbours, while juveniles, and especially the adult male, had more than the expected number of nearest neighbours (Table 6.6). Males were more frequently neighbours of females than expected and vice versa. Females and subadults were least frequently associated.

In summary: (a) males were most often associated with females and least often with juveniles; (b) females were less frequently associated with subadults and juveniles than expected; (c) subadults were associated with males more often than expected and; (d) juveniles were nearest neighbours to their own age class more frequently than expected. Apart from the male and juveniles the age-sex classes were nearest neighbours to their own age-sex class as frequently as expected.

Table 6.5. Mean inter-individual distances (m) between different age-sex classes (a) regardless of activity, (b) when feeding and (c) for activities other than feeding, for the study period (n=2981 observations).

a. Over all activities

AGE-SEX CLASS	Female	Subadult	Juvenile	Infant
Male	2.7	3.8	3.1	-
Female	2.3	2.6	2.6	1.0
Subadult		2.9	2.5	1.2
Juvenile			2.1	1.1
Infant				0.7

b. Feeding

AGE-SEX CLASS	Female	Subadult	Juvenile	Infant
Male	3.0	4.0	3.5	-
Female	2.5	3.2	2.8	1.4
Subadult		3.4	2.9	1.5
Juvenile			3.0	1.4
Infant				1.3

c. Non-feeding

AGE-SEX CLASS	Female	Subadult	Juvenile	Infant
Male	2.5	3.7	2.9	-
Female	2.2	2.2	2.3	0.9
Subadult		2.5	2.2	1.1
Juvenile			1.8	1.0
Infant				0.7

Table 6.6. The observed and expected frequencies, and indices of association, of nearest neighbours of each age-sex class over all activities. (mean numbers of animals in each age-sex class is given within parentheses; focal animals in left vertical column, nearest neighbours in top row).

AGE-SEX CLASS/		Male (1)	Female (9.5)	Subadult (6.5)	Juvenile (15)	TOTAL
Male	obs.		253	103	178	534
	exp.		69.6	47.6	109.8	227.0
	ind.		**3.6**	**2.2**	**1.6**	**2.4**
Female	obs.	224	643	221	754	1842
	exp.	69.6	591.2	452.1	1043.3	2156.2
	ind.	**3.2**	**1.1**	**0.5**	**0.7**	**0.9**
Subadult	obs.	100	297	283	600	1280
	exp.	47.6	452.1	261.7	713.8	1475.2
	ind.	**2.1**	**0.7**	**1.1**	**0.8**	**0.9**
Juvenile	obs.	136	838	454	2179	3607
	exp.	109.8	1043.3	713.8	1537.5	3404.4
	ind.	**1.2**	**0.8**	**0.6**	**1.4**	**1.1**
TOTAL	obs.	460	2031	1061	3711	7263
	exp.	227.0	2156.2	1475.2	3404.4	7263
	ind.	**2.0**	**0.9**	**0.7**	**1.1**	

While indices of association between age-sex classes substantiate the points made earlier by inter-individual distances, they also show that associations between two age-sex classes were mostly, but not always, equally strong in both directions (e.g. male-juvenile pairs). Thus while the male was more frequently associated with juveniles than expected (index=1.6), this may have been related to the common use of food resources or canopy stratum. The association was less developed where juveniles were the focal animal (index=1.2) and suggests that juveniles may have avoided the male in certain situations, such as when feeding (see below).

The influence of the activity of the focal age-sex class on the frequencies and indices of association of nearest neighbours are given in Table 6.7 (focal age-sex class feeding) and Table 6.8 (focal age-sex class not feeding). The activity of the focal age-sex class had no effect on the identity of the nearest neighbour age-sex class. However the degree of association between the age-sex classes did vary according to the activity of the focal age-sex class.

Table 6.7. The observed and expected frequencies, and indices of association, of nearest neighbours of each age-sex class while feeding (mean number of animals in each age-sex class is given within parentheses, focal animals in left vertical column, nearest neighbours in top row).

AGE-SEX CLASS/		Male (1)	Female (9.5)	Subadult (6.5)	Juvenile (15)	TOTAL
Male	obs.		65	38	47	150
	exp.		25.5	17.5	40.3	83.3
	ind.		2.5	2.2	1.2	1.8
Female	obs.	79	245	127	378	829
	exp.	25.5	217.1	166.0	383.1	791.7
	ind.	3.1	1.1	0.8	1.0	1.0
Subadult	obs.	49	109	106	241	505
	exp.	17.5	166.0	96.1	262.1	541.7
	ind.	2.8	0.7	1.1	0.9	0.9
Juvenile	obs.	46	268	190	679	1183
	exp.	40.3	383.1	262.1	564.6	1250.1
	ind.	1.1	0.7	0.7	1.2	0.9
TOTAL	obs.	174	687	461	1345	2667
	exp.	83.3	791.7	541.7	1250.1	2667
	ind.	2.1	0.9	0.9	1.1	

Table 6.8. The observed and expected frequencies, and indices of association, of nearest neighbours of each age-sex class during social activities (mean number of animals in each age-sex class is given within parentheses, focal animals in left vertical column, nearest neighbours in top row).

AGE-SEX CLASS/		Male (1)	Female (9.5)	Subadult (6.5)	Juvenile (15)	TOTAL
Male	obs.		188	65	131	384
	exp.		48.0	32.8	75.8	156.6
	ind.		**3.9**	**2.0**	**1.7**	**2.5**
Female	obs.	145	398	183	707	1433
	exp.	48.0	408.3	312.2	720.5	1489
	ind.	**3.0**	**1.0**	**0.6**	**1.0**	**1.0**
Subadult	obs.	51	188	177	359	775
	exp.	32.8	312.2	180.7	493.0	1018.7
	ind.	**1.6**	**0.6**	**1.0**	**0.7**	**0.8**
Juvenile	obs.	90	570	264	1500	2424
	exp.	75.8	720.5	493.0	1061.8	2351
	ind.	**1.2**	**0.8**	**0.5**	**1.4**	**1.0**
TOTAL	obs.	286	1344	689	2697	5016
	exp.	156.6	1489	1018.7	2351.0	5016
	ind.	**1.8**	**0.9**	**0.7**	**1.1**	

The observed frequency of nearest neighbours and the degree of association of these nearest neighbours to the focal age-sex class suggest that (in each case the first mentioned age-sex class is the focal class): (a) The adult male was much less frequently associated with females and juveniles while feeding than he was when not feeding. (b) There was no change in the degree of association of females or juveniles with the other classes for all activities. (c) Subadults were more frequently associated with the male when feeding than with any other age-sex class.

In addition to satisfying the normal daily metabolic demand, adult females with infants are confronted with the energy costs of carrying the infant and lactation. The notion of mother-infant pairs having different age-sex class relationships to those of females without infants, is suggested by Rudran (1978a) to be a means of achieving greater exclusivity of food resource/patch use. This would allow them to cope with greater energy demands. It was found that (Table 6.9 and Table 6.10): (a) Mother-infant pairs associated with the adult male much less frequently than did females without infants, although there was no difference in the distance of either to the adult male when they were associated. (b) Females with infants were most frequently associated with either female class (Table 6.10a) but were usually in closer proximity to females without infants (Table 6.9). (3) Females with infants were less frequently associated than expected with both subadults and juveniles.

Table 6.9. The mean age-sex class nearest neighbour inter-individual distance (m) to adult females with and without infants for (a) all activities, (b) feeding activity, and (c) social activities, during the period October 1986 to February 1987. (F + I=Female with infant).

	Male	Female	Fem.+Inf.	Subadult	Juvenile
a. All activities					
Female	2.7	2.3	2.0	2.7	2.3
F + I	2.6	2.0	2.2	2.5	2.6
b. Feeding					
Female	3.3	2.5	2.7	3.3	2.7
F + I	3.2	2.7	2.8	2.4	2.6
c. Social					
Female	2.4	2.2	1.6	2.2	2.1
F + I	2.2	1.7	2.0	2.5	2.4

When feeding, mothers showed little difference in their spatial association with other age-sex classes, but had greater nearest neighbour distances to all age-sex classes except subadults. Within the group, females in general formed a subgroup (see point (b) above) and were closely associated at all times. These results are not entirely in agreement with Rudran's (1978a) findings that females with infants, as opposed to all females, formed subgroups; although mother-infant pairs were less frequently associated with all other age-sex classes than other females.

In conclusion samangos increased their distance from others when feeding, while nearest neighbour associations remained constant for all activity types.

Table 6.10. The observed and expected frequencies, and indices of association, of age-sex class nearest neighbours to females with and without infants, for (a) all activities, (b) feeding activity, and (c) social activities, during the period October 1986 to February 1987.

		Male	Fem.	F + I	Sub.	Juv.	TOTAL
a. All activities							
Female	obs.	45	167	138	75	377	802
	exp.	22.1	88.3	110.4	154.5	331.1	706.4
	ind.	2.0	1.9	1.3	0.5	1.1	1.1
F + I	obs.	14	136	106	57	196	509
	exp.	22.1	110.4	88.3	154.5	331.1	706.4
	ind.	0.6	1.2	1.2	0.4	0.6	0.7
b. Feeding							
Female	obs.	12	53	44	34	134	277
	exp.	7.3	29.3	36.6	51.3	109.8	234.3
	ind.	1.6	1.8	1.2	0.9	1.2	1.2
F + I	obs.	6	43	31	17	61	158
	exp.	7.3	36.6	29.3	51.3	109.8	234.3
	ind.	0.8	1.2	1.1	0.3	0.6	0.7
c. Social							
Female	obs.	33	114	94	41	243	525
	exp.	14.6	58.6	73.2	102.5	219.7	468.6
	ind.	2.2	1.9	1.3	0.4	1.1	1.1
F + I	obs.	8	93	75	34	135	345
	exp.	14.6	73.2	58.6	102.5	219.7	468.6
	ind.	0.5	1.3	1.3	0.3	0.6	0.7

6.3.3 AGE-SEX DIFFERENCES IN FEEDING BOUT DURATION AND INGESTION RATE

An age-sex class may differ in feeding behaviour from another in the relative frequency score of the composition, diversity and richness of the diet. The frequency sampling method is operationally defined so as to score an observed feeding bout regardless of its duration. The bout duration and ingestion rate together provide a quantitative assessment of the feeding efficiency of an age-sex class within a food patch or, alternatively, during a feeding score. It follows that if there is considerable difference in bout duration and ingestion rate for a food item among age-sex classes, then differences in the frequency of feeding activity scores between age-sex classes do not necessarily imply age-sex class differences in the proportion of time spent feeding. For instance, the male may have fewer feeding scores, implying that he spends less time feeding and therefore eats less food, but he may also have longer bout lengths and higher ingestion rates than other classes. The male would thus effectively achieve a higher nutritional intake per unit time, which would permit him to spend less time feeding.

6.3.3.1 Bout duration

A total of 1727 bouts was recorded of which 909 were spontaneously terminated. The mean feeding bout duration was calculated for each age-sex class using the product-limit estimate (Kaplan-Meier 1958) for all bouts regardless of termination type.

Bout durations calculated by product-limit (P-L) estimates were without exception longer than spontaneously terminated bouts (Fig. 6.3). The range in P-L estimates of bout duration was 62.7 seconds over all classes, and males had the shortest mean bout duration and females the longest (Table 6.11). The difference between estimates of the bout duration indicates that the longer a bout the greater the probability a time-out situation is recorded, and thus most time-out censored bouts were longer than average. Hence P-L estimates are inclined to increase the bout duration.

Table 6.11. The mean feeding bout duration (seconds) for the age-sex classes, calculated from spontaneously terminated bouts, and by the Kaplan-Meier (1958) method (i.e. including time-out bouts; see text for explanation).

	BOUT DURATION					
	Spontaneously terminated			Kaplan-Meier estimate		
AGE-SEX CLASS	Mean	s	n	Mean	s	n
Male	**133**	94	71	**156**	98	102
Female	**129**	100	292	**218**	139	580
Female+infant	**116**	160	61	**193**	196	104
Subadult	**113**	99	158	**166**	123	281
Juvenile	**111**	90	327	**180**	116	660

The mean bout duration, estimated by the P-L method and regardless of food item ingested, was significantly different ($F_{(7,1678)}=16.16$, $P<0.001$) for the age-sex classes (Fig. 6.3). The difference in mean feeding bout duration between age-sex class pairs (t-test for large unequal samples, $P<0.01$) showed that, (a) adult females had a significantly longer mean bout duration than all other age-sex classes except females with infants and, (b) no significant difference in the duration of the bout between other pairs of classes as found.

For data from observed spontaneously terminated bouts, only the adult females without infants showed a significant difference in mean feeding bout duration ($t_s=2.43$, df=617, $P<0.02$). Adult females had significantly longer bouts than juveniles and juveniles had the shortest bouts of any class (Table 6.11).

The mean bout durations for the major food items (fruit, flowers, leaves and insects) were significantly different ($F_{(4,1722)}=12.03$, $P<<0.001$; Table 6.12). Within each age-sex class longer bout durations were recorded for fruit and mature leaf feeding bouts. Shorter bout durations were noted for invertebrate, flower bud and new leaf feeding bouts. Presumably bout durations for the latter were constrained by the availability and harvesting difficulties associated with eating that item.

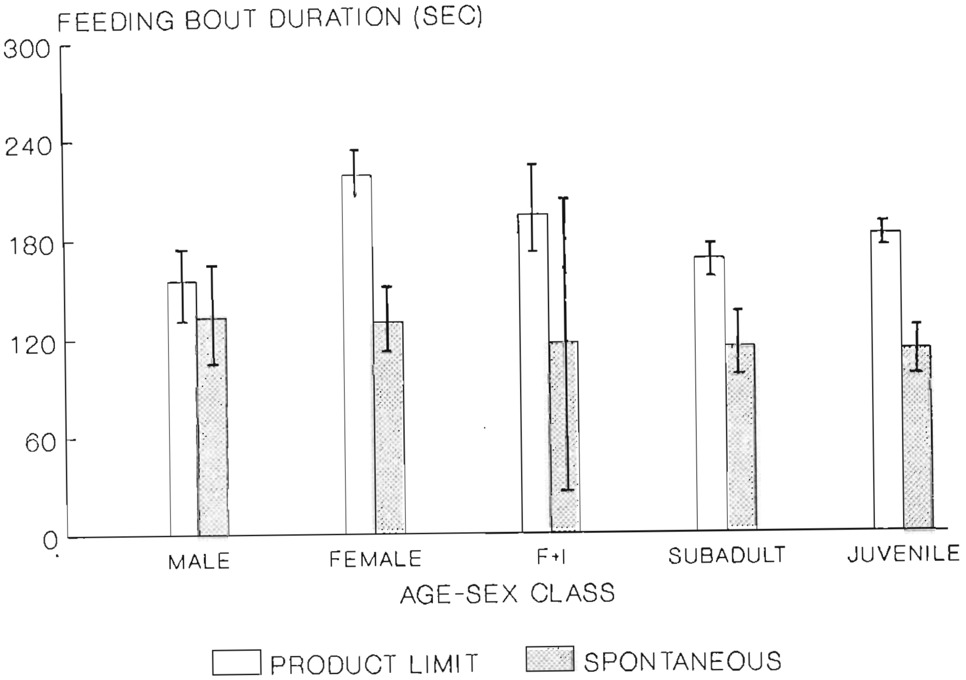


Figure 6.3. Mean age-sex class feeding bout duration (seconds, with 95% confidence limits), scored using either the product limit estimate or from records of spontaneously terminated bouts (see text for details).

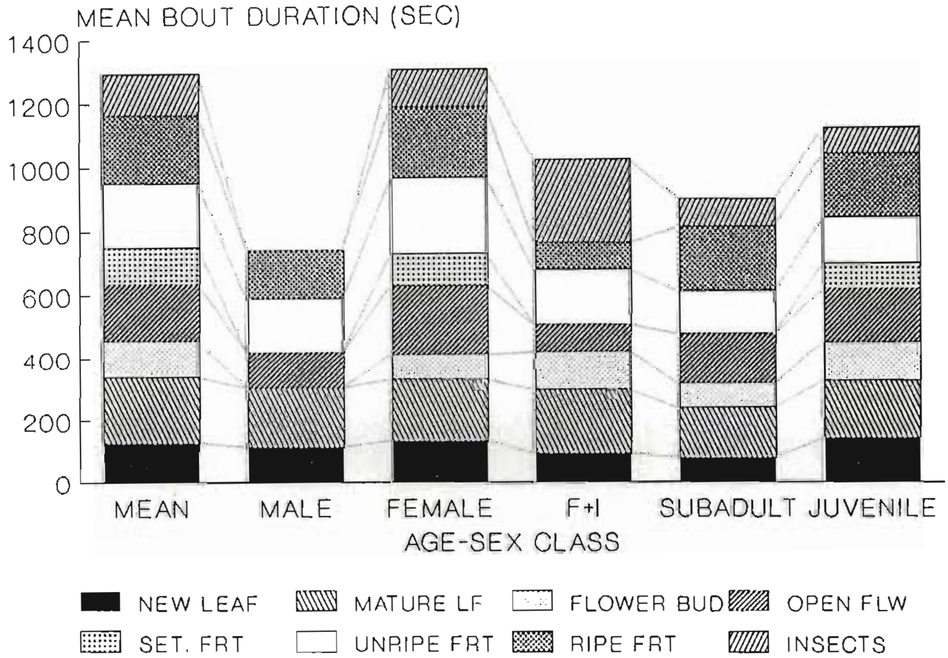


Figure 6.4. Mean age-sex class bout durations (Product-Limit estimates) for different food items

Table 6.12. The mean bout duration (seconds) estimated using the Kaplan-Meier method, for the food items, over all age-sex classes combined.

FOOD ITEM	Bout Duration	s	n
Young leaf	128	81	119
Mature leaf	213	127	217
Flower bud	116	86	86
Open flower	182	118	202
Setting fruit	113	84	29
Unripe fruit	200	177	307
Ripe fruit	214	119	666
Insects	128	120	60

Figure 6.4 suggests the following differences between feeding bout durations for food items for the age-sex classes, relative to the mean bout duration for a food item regardless of age-sex class: (a) Bout durations for all food items are shorter on average for the adult male and subadults. (b) Adult females without infants show above average bout durations for the ingestion of fruit items and open flowers. (c) Females with infants have shorter than average durations for fruit item bouts and greater than average for invertebrate feeding bouts. (d) Juveniles have average feeding bout durations for most food items.

6.3.3.2 Bout termination - Social implications

Intraspecific competition for food at the level of individuals within a troop, involves the displacement of an individual from, or prevention of access by an individual to, an otherwise exploitable food source. In this way members of a group are subject to socially imposed constraints on feeding behaviour (Dittus 1977, Post et al. 1980, Whitten 1983, Janson 1985, Mcfarland Symington 1988).

An analysis of the frequency of 'interrupted' bouts permits some interpretation of the extent to which social behaviour and competition for food influences the feeding behaviour of the different age-sex classes in the samango monkey. A total of 147 bouts (13.9%) were interrupted by one or other social interaction. The rate of bout interruption was very low and was highest for the younger age classes (subadults, 0.141 interuptions/bout; juveniles, 0.195 interuptions/bout) and lowest for for the adult sex classes (range 0.089-0.090 interruptions/bout).

The larger product-limit estimates (i.e. time-out) might suggest that bouts are longer if they are not socially interrupted (aggression, passive displacement by proximity, play or grooming behaviour). To test whether intra-group social interaction limited the bout duration the spontaneously terminated bouts for each age-sex class were divided randomly into two sample sets of equal size. To one set were added the social time-out durations. Estimates of mean bout duration were calculated for each sample separately. For the sample that included socially censored bouts P-L estimates were used, and for the sample that included only spontaneously terminated bouts, estimates were derived from the arithmetic mean. Within each age-sex class it was then possible to apply t-tests to test for significant difference between social and spontaneous terminations.

No significant difference (t-test, all $P > 0.05$) in the duration of socially and spontaneously terminated bouts for an age-sex class was found. That is, social interactions during a bout did not reduce the bout duration significantly.

The number of aggressive feeding bout interruptions was particularly low (36 or 3.4%) for the troop. The rate of aggressive feeding bout interruptions was low (mean=0.037 interruptions/bout, $s=0.014$). Adult females had lower rates of aggressive interruption than other age-sex classes (rate=0.013). Bouts involving fruit items were most frequently contested (1.52%) and leaf items least contested (0.28%). The level of intragroup aggression for food was therefore very low and it must be concluded that either age-sex class feeding strategies were sufficiently divergent to reduce direct competition for food to an insignificant level, or that food was not a limiting factor. Of course both conclusions could act in concert to reduce direct competition for food.

6.3.3.3 Ingestion rate

Bout durations can be used as one expression of the differences in feeding behaviour between age-sex classes. The choice of food item and ultimately the duration of a feeding bout is constrained largely by the difficulties of harvesting an item in relation to the nutritional gain per unit effort or time (Schoener 1971). The ingestion rate is a measure of handling time for a food item type. A high ingestion rate can only be achieved by access to a food resource that is immediately abundant and available to the individual, and requires little manipulative processing.

Access to a resource between age-sex classes has been shown here to be unrestricted by mechanical constraints of sampling the forest strata. Age-sex classes, however, increased their inter-individual distance while feeding, and access to food resources was likely to be based on individual dominance. A high ranking individual would be expected to dominate a locally abundant resource and would therefore exhibit higher ingestion rates. Indirectly, the ingestion rate would indicate the social status or competitive ability of the age-sex class or individual.

a. Ingestion rate

Estimates of the mean ingestion rate for any given age-sex class on any specific food type, were calculated only if a minimum sample of 5 hand-to-mouth movements had been obtained for each of at least two bouts from that age-sex class while feeding on the food item in question (Table 6.13). There was a significant difference ($F_{(8,1223)}=2.81$, $P<0.01$) in the mean ingestion rates of the major food items for all age-sex classes combined (Fig. 6.5). Leaf buds, flower buds and invertebrates, all items rich in protein (Gaulin 1979, Richard 1985, see this study), were all more rapidly ingested (range 0.184-0.244 items/second) than other food items (range 0.108-0.162 items/second). There was, however, no difference in the mean ingestion rate (items/second) of a food item type between age-sex classes ($F_{(4,1231)}=0.645$). All age-sex classes would appear, therefore, to alter ingestion rates to accommodate the use of a specific food item in a similar manner.

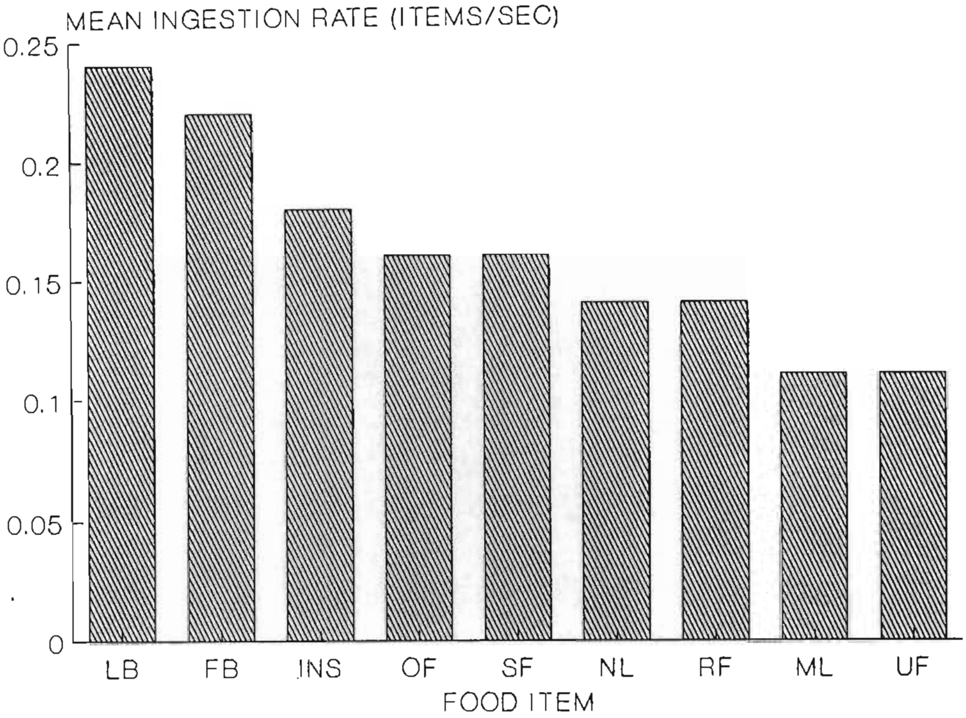


Figure 6.5. The mean age-sex class ingestion rates for the major food types. (LB leaf bud, FB flower bud, INS insect, OF open flower, SF setting fruit, NL new leaf, RF ripe fruit, ML mature leaf, UF unripe fruit)

b. Drop rate

The drop rate may indicate the extent to which an age-sex class encounters sub-optimal food items and may indicate the nutritional quality of a food patch.

In only 118 bouts or 6.8% of 1727 bouts were items dropped or rejected after selection by an age-sex class. Within bouts where items were dropped, the mean rate was very low (0.03 items/sec). No significant difference in either the age-sex class mean drop rate ($F_{(4,113)}=0.38$) or the rate at which a particular food item type ($F_{(7,110)}=0.25$) was dropped, was detected. It is concluded that for a food item no age-sex class feeds in patches of lower quality than other age-sex classes, or makes more unfavorable harvesting decisions than any other class. Optimal selection of specific food item patches would thus most likely be dependent on abundance within a patch.

Table 6.13. The ingestion rates (items/second), mean ingestion rates, and standard deviation, for the major food items regardless of species ingested by each age-sex class (n= 1235 bouts). (LB leaf bud, NL new leaf, ML mature leaf, FB flower bud, OF open flower, SF setting fruit, UF unripe fruit, RF ripe fruit, OL old fruit, IN insect).

ITEM	LB	NL	ML	FB	OF	SF	UF	RF	OL	INV	MEAN
MALE											
Rate	-	**0.15**	**0.11**	**0.14**	**0.23**	**0.32**	**0.10**	**0.13**	-	-	**0.15**
s	-	0.08	0.06	-	0.16	0.17	0.06	0.08	-	-	0.11
n	-	11	10	1	10	2	7	33	-	-	74
FEMALE											
Rate	**0.16**	**0.16**	**0.12**	**0.20**	**0.15**	**0.16**	**0.11**	**0.15**	**0.06**	**0.15**	**0.14**
s	0.04	0.11	0.05	0.08	0.10	0.16	0.06	0.41	0.01	0.05	0.27
n	3	27	73	11	60	5	75	180	2	9	445
FEMALE WITH INFANT											
Rate	-	**0.16**	**0.10**	**0.26**	**0.17**	-	**0.09**	**0.14**	-	**0.17**	**0.17**
s	-	0.06	0.07	0.11	0.06	-	0.04	0.09	-	0.17	0.11
n	-	6	12	18	9	-	7	8	-	3	63
SUBADULT											
Rate	**0.33**	**0.12**	**0.09**	**0.23**	**0.17**	**0.22**	**0.11**	**0.12**	-	**0.26**	**0.14**
s	0.14	0.07	0.03	0.07	0.12	0.06	0.06	0.07	-	0.10	0.10
n	3	10	22	11	27	2	35	68	-	7	185
JUVENILE											
Rate	**0.24**	**0.10**	**0.10**	**0.19**	**0.15**	**0.11**	**0.11**	**0.13**	**0.14**	**0.16**	**0.13**
s	0.07	0.07	0.05	0.08	0.09	0.05	0.07	0.08	-	0.18	0.08
n	2	20	45	20	58	7	69	237	1	9	468
MEAN											
Rate	**0.24**	**0.14**	**0.11**	**0.22**	**0.16**	**0.16**	**0.11**	**0.14**	**0.09**	**0.18**	**0.15**
s	0.11	0.09	0.05	0.09	0.10	0.12	0.07	0.25	0.05	0.13	0.01
n	8	74	162	61	164	16	193	526	3	28	1235

6.4 DISCUSSION

It is not always possible to distinguish the separate affects of age, sex and social constraints on the diet. For example the variation in the diet of a juvenile may either be a function of size or alternatively of low social status or a combination of both factors. At Cape Vidal fruit is not a limiting resource (see Chapter 4); although the availability of protein rich foods, important for successful reproduction and growth, can fluctuate significantly between seasons. Intra-group competition for food is therefore low and the influence of social hierarchies on dietary profiles is consequently minimal. There are also no congeneric diurnal frugivorous primate competitors. One can therefore largely ignore the issues of interspecific competition and food shortage in this investigation and expect that age-sex class differences in diet reflect intrinsic partitioning by virtue of size and physiological demand.

6.4.1 Age-sex differences in the diet

The negative allometric relationship between body weight and relative nutritional requirements (Kleiber 1961) has the following consequences (Bell 1971, Gaulin 1979, Temerin et al. 1984, Richard 1985): While larger animals will have (a) greater total metabolic requirements than small animals, they will actually (b) require less energy intake per unit of body weight. As a consequence (c) a larger animal is able to subsist on lower quality food (other things being equal), provided it can be obtained in quantity.

Females need more protein and energy than males because of the requirements of pregnancy and lactation (Hanwell and Peaker 1977, Robbins 1983) and thus have proportionally greater food requirements than would be suggested by body size alone. Smaller body size in females reduces the overall energy requirement but the demand for protein rich items is proportionally greater than those of the male (Pond 1977, Dunbar 1988). Cords (1986a) points out that most females are probably pregnant or lactating, or trying to get into breeding condition at any given time and Schoener (1971) predicted that most females should therefore be nutrient (protein) maximizers. In support of this argument adult females, throughout the range of the mitis group, feed significantly more frequently, and include a smaller proportion of fruit but a greater fraction of protein-rich food items (invertebrates, new leaf shoots, new leaves) in the diet, than do males (Rudran 1978a, Cords 1986a).

The rate of protein transfer from the female to her offspring is much higher during lactation than it is in utero (Blaxter 1964, Pond 1977). Female samangos thus utilize leaves, especially protein rich young leaves, more frequently than the male. The season of young leaf availability coincides with the timing of parturition and the period of lactation. The timing of the reproductive cycle must therefore be seen as a consequence of the availability of food (Lancaster and Lee 1965, Boinski 1988, Butynski 1988), and especially protein-rich foods at Cape Vidal. The greater demand for protein-rich items (young leaves) and proportionally less fruit by females, may reduce age-sex competition for essential food items like fruit between sex classes.

Although insects are richer in protein than young leaves (Gaulin 1979, Redford and Dorea 1984, Richard 1985), samango females had a lower proportion of insects in the diet than did juveniles and subadults. Females with infants, however, had much longer insect bout durations. This suggests that, unlike the younger age classes, females could not afford to search as long for insects (a more ephemeral food source than young leaves). However, if insects were found the female would feed for as long as possible thereby maximizing her use of the protein- rich food source. Subtleties of feeding strategy may thus also be able to reduce competition for resources between age-sex classes.

In contrast to females, males should minimize time spent feeding to allow maximum participation in other fitness-increasing activities (Schoener 1971). The male might be expected to feed for less time per unit body mass, and have a diet richer in energy (carbohydrate) than females (Clutton-Brock 1977), because (a) he does not incur the protein costs of pregnancy and lactation (and therefore can eat proportionally more fruit than leaf) and (b) his social dominance allows him priority of access to high quality foods. The male fed less frequently than any other age-sex class (see Chapter 5). Although large body size may suggest a greater tolerance of lower quality food items in the diet (Gaulin 1979), the male had the largest proportion of high quality fruit in the diet.

Clutton-Brock (1977) suggests that as part of the male feeding strategy the male has a faster ingestion rate than the female, allowing him to ingest required calories quickly and thus reduce feeding time. However, in one-male blue monkey groups, the male is highest ranking and can maintain priority of access to high quality fruits (Rudran 1978a). This permits him to be selective and maintain the highest quality of diet for the shortest bout duration (as opposed to the highest ingestion rate). At Cape Vidal the male included proportionally more ripe fruit (high quality item) in his diet (41%) than did females (31%). In addition, there was no difference in ingestion rate across the age-sex classes for a food item type. Males therefore did not have a comparatively faster ingestion rate than females. He did, however, have a significantly shorter feeding bout duration. The samango male may reduce feeding time by eating higher quality foods which allows him to ingest the required calories in a shorter bout duration.

Competition for mates is especially intense in the mitis one-male troop (Tsingalia and Rowell 1984, Cords 1986b, Butynski unpub.) and the samango is no exception (Henzi and Lawes 1987). The vigilance required to ensure that competitors do not gain access to receptive females is not easily compatible with foraging for and preying on insects (the alternative high energy food source to fruit). By reason of the energy demand of his large body size, the male must utilize fruit heavily as the only alternative means of obtaining sufficient food of suitable nutritional value to permit a reduction in foraging time. There is thus a very small proportion of invertebrates in the diet of the adult male samango (1%).

The adult mitis troop male is subject to similar social constraints (energy demand of maintaining group tenure) on the diet throughout the range of the species group (Tsingalia and Rowell 1984, Cords 1986b, Henzi and Lawes 1987, 1988, Butynski unpub.). It is not surprising, therefore, that there is little variation in the overall dietary profile of resident males from different populations (Rudran 1978a, Cords 1986a). Food, and especially fruit, would have to be especially limiting for the diet and feeding behaviour of a troop male to be affected, and it is highly unlikely that mitis would be present in a habitat at all under such conditions. If the adult male, a fruit "specialist", could not cope with a drop in the availability of fruit over an extended period, even in spite of his high ranking position and greater access to fruit, then it is unlikely that sufficient fruit would be available for other age-sex classes to survive conditions presented in this scenario.

The composition of the diets of the juvenile age-sex class and the adult male were remarkably similar at Cape Vidal. The difference in the proportions of fruit ingested by juveniles and the male were minimal at both Cape Vidal and Kakamega (Cords 1986a). In contrast, in the Kibale forest Rudran (1978a) found that juveniles ate 1.7 times less fruit than adult males. The major difference in dietary composition between males and juveniles across the mitis species group is tied to their use of invertebrates. Kibale juveniles used 5 times, Kakamega juveniles 2.6 times and Cape Vidal juveniles 1.5 times more invertebrates than adult males. At Cape Vidal the difference was smaller, with proportionally fewer invertebrates taken because of their lower and more variable abundance (Chapter 3).

Cords (1986a) proposed that the Kakamega blue monkeys may have undergone a competitive release in the absence of two larger primates (Colobus badius and Cercocebus albigena) with precedence at feeding sites shared with blue monkeys at Kibale (Struhsaker 1978). This is a situation very similar to that of the samango at Cape Vidal where there are no influential primate frugivore competitors although plant species richness is lower. At both Kakamega and Cape Vidal juveniles shifted their fruit consumption to approximate the proportions achieved by the male. At Kibale forest, juveniles had a notably depressed proportion of fruit in the diet (36.3 %) but a much greater invertebrate fraction (25.3 %). Juveniles, by virtue of their size and lower energy requirements, are able to utilize protein and energy-rich invertebrate resource at Kibale, where pressure on fruit as a food source is high. The high proportion of fruit in the diet of the juvenile samango supports the conclusion reached earlier (Chapter 4) that fruit is not a limiting resource at Cape Vidal, although it should also be remembered that invertebrates were less available at Cape Vidal as an alternative food.

The adult male had the lowest monthly overlap in the plant food diet with all age-sex classes. All other age-sex class combinations had very similar percent overlap values (63.6%-68.7%). Greater ecological separation in the plant diet of the samango age-sex classes may have been expected. However, this separation may be limited by the lower plant species richness at Cape Vidal.

6.4.2 Age-sex differences in the use of forest strata

The different use of the forest strata are clearly a consequence of the activity of the age-sex classes. Use of the canopy and especially the terminal branches were not limited by the body weight or size of the age-sex class (cf. Grand 1972). The male used the terminally exposed branches of the canopy more frequently than any other age-sex class. Any differences in the diet of the age-sex classes are thus unlikely to be a result of disparity in ability to utilize the canopy strata.

6.4.3 Intragroup spatial relationships

Overt aggression or displacement from food sources may lead to reduced food intake for some individuals in primates (Post et al. 1980). Aggressive interactions over food are widely observed in non-monogamous primates (e.g. Robinson 1981, Janson 1985, Mcfarland Symington 1988). As in this study Rudran (1978a) and Beeson (1987) both report relatively low levels of intra-group aggression for C. m. stuhlmanni at Kibale and Zomba respectively, despite greater intra-specific competition for food at these sites than at Cape Vidal. Interference competition for food may be more subtle in mitis, and reduced access to preferred foods may be a result of subordinates generally avoiding the dominant animals without having to be threatened by them (e.g. Macaca s. sinica, Dittus 1979).

Spatial relationships as an adaptive mechanism are measured in this study by (a) the proximity and (b) degree of association between age-sex classes. Females increased their distance from their nearest neighbours while feeding but did not change their degree of association with those age-sex classes. The male on the other hand had a greater inter-individual distance and lower level of association with the other age-sex classes when feeding, especially the females and juveniles. On the whole, however, the age-sex classes favoured an increase in inter-individual distance over a change in nearest neighbour age-sex class associations while feeding.

To avoid age-sex class competition for food individuals should forage near (i.e. associate with) animals whose resource exploitation is as dissimilar as possible. When feeding, the samango male-female association index was greater and their proximity closer, than for any other male-pair combination, and was undoubtably facilitated by their different feeding requirements. One would expect animals in the same age-sex classes (i.e. similar diets) to avoid one another while feeding. But no age-sex class avoided like-class members more when feeding, although longer inter-individual distances between the male and juveniles is probably due to the considerable similarity of their food type use.

Juveniles differed least from the male in their consumption of the major food items but most in their use of plant species. Smaller quantities of fruit are required by juveniles and they could thus use fruit from understory shrubs and trees that would not provide the male with sufficient nutritional return per unit effort, for example Euclea natalensis, Ochna natalitia, Tricalysia sonderana. This would account in part for the difference in the use of food species between the two classes. A juvenile would very often have to feed in a neighbouring tree (which in all probability would be a different species) or a least in a distal part of the canopy crown to accommodate a male-juvenile horizontal inter-individual distance of 3.5 - 4.0 m.

Specific food diversity would naturally be higher for juveniles than the male, as a result of greater juvenile-juvenile competition for food (the juveniles were the largest age-sex class), and because juveniles cannot afford to be as selective of food items as the male.

In conclusion these data show that an increase in inter-individual distance when feeding would be a more effective strategy for reducing interference competition, than altering age-sex class associations alone. This strategy is adopted by a number of frugivorous primates (Macaca s. sinica, Dittus 1979; Cebus nigrivittatus, Robinson 1981; Macaca fascicularis, van Schaik et al. 1983, because it (a) reduces the probability of energetically expensive agonistic interaction and the chances of losing the food resource (Dittis 1979). In addition (b), foraging efficiency decreases when other individuals are allowed at a feeding site since foraging success will be lower for an individual when it has to search in patches already covered by others (van Schaik et al. 1983) and (c), a more extensive troop spread increases the probability that some animals will encounter food items increasing the foraging efficiency of the troop (Robinson 1981).

Aggressive competition for fruit was negligible and largely avoided by the fact that there was sufficient food to go round and by the differing emphasis in age-sex class feeding strategy at Cape Vidal:

(a) Males, by virtue of their social status, dominated other classes and secured priority of access to high quality fruits (ripe fruits).

(b) The energy and protein demands of reproduction ensured that while females also utilized fruit they differed most importantly from other classes in their greater use of leaves.

(c) Subadults, larger than juveniles but subordinate to the females, appeared to have a mixed feeding response with a comparatively high proportion of insects (7%) and leaves (26%) but less fruit in the diet (47%) than juveniles.

(d) Small size and therefore smaller energy demands permitted juveniles to include a proportionally greater fraction of fruit (although a small quantity) and insects in the diet.

Considering (a) the much lower abundance of insects at Cape Vidal, and (b) greater competitive pressure of blue monkeys (e.g. Kibale, Rudran 1978a), the diets of adult samangos and blue monkeys are similar. Similarly, one can argue that even in populations where food availability is notably seasonal (e.g. Zomba, but no comparable data from Beeson 1987;1989) similar age-sex class feeding strategies would be adopted by mitis. Males would be time minimizers and quality maximizers, females would be energy and especially protein maximizers, and subadults and juveniles would be energy maximizers, but obtain a substantial part of their requirements from alternative items to those used dominantly by the male and females.

CHAPTER 7: USE OF THE HOME RANGE

7.1 INTRODUCTION

Home range has been defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). Although animals travel for a variety of reasons most authors (Altmann and Altmann 1970, Harvey and Clutton-Brock 1981, Marsh 1981, Mace et al. 1983, Fleagle 1985), agree with Mitani and Rodman's (1979) statement for primates, that "ranging patterns are primarily a function of feeding patterns". Until recently little attention has been given to those behavioural, and environmental correlates other than food, that might influence the pattern of range use. These include the position of night trees (Rasmussen 1979, Aldrich-Blake 1980) and waterholes (Altmann and Altmann 1970, Whitehead unpub. data), the weather (McKey and Waterman 1982), territory maintenance (Waser and Homewood 1979, Whitten 1982), the troop's movements on previous days (Fossey and Harcourt 1977, Schlichte 1978), intergroup interaction and avoidance (Struhsaker 1975, Waser 1976, Moreno-Black and Maples 1977, Harrison 1983, Isbell 1983), mixed species associations (Pook and Pook 1982, Cords 1987), and predation (McMahon 1977 p79).

While the influence of the availability and distribution of food resources on ranging behaviour cannot be ignored (and in this thesis is discussed in detail in Chapter 8), it is clear that ranging patterns may be affected by other parameters especially where the animals are not severely food stressed. I use this chapter to present and discuss those environmental and social correlates of ranging behaviour that best account for the gross (annual) pattern of range use. I show that this was largely affected by the distribution of preferred resting sites and I compare range use patterns defined by the resting, feeding and locomotory behaviour of the monkeys.

7.2 METHODS

Ranging data were recorded by methods allowing comparison with the results of Rudran (1978a) and Cords (1987). A grid system with 0.25 hectare (ha) quadrats was surveyed and marked out in the study area. This facilitated the accurate mapping of the troop's position and path movement on a 1:5 000 map. Since the mapped path of group progression did not take vertical movements into account and since individuals will move further than the central group mass, the results must be regarded as minimal distances moved by the troop. The actual time of entry of a quadrat by the centre of the group was recorded. The intensity of home range use was determined from the amount of time spent in, and the number of entries into, each specific quadrat.

Quantification of home range size was determined by the product of the total number of quadrats entered over the study period and the area of a quadrat (0.25 hectare). Struhsaker (1975) and Rudran (1978a) argue that the accuracy of such measurements are dependent on the size of the quadrat used. The method would be exact only in the case where the group occupied the entire area of each and every quadrat. This is seldom the case, and as a result the summation of the occupied quadrats will inevitably include small lacunae in most quadrats representing areas not used by the monkeys. In practice, the choice of quadrat size is dependent on the relationship between the cohesiveness of troop dispersion and the level of accuracy possible in the mapping analysis. In this study the 0.25 ha quadrat was judged as the smallest applicable area in which no sampling ambiguity, that is whether or not the greatest concentration of individuals was in one quadrat or another, would occur.

The straight line distance between the furthest individual on either side of the troop was estimated as an index of troop dispersion. Where troop dispersion was so great that it was difficult to assign the troop to a single quadrat, the time spent in each quadrat and the relative proportion of the whole troop in the each quadrat was recorded. These adjustments allowed for a more accurate assessment of the spatial and temporal use of a quadrat by the troop, and were used to determine patterns of range use.

It is possible to graphically represent and conveniently record the spatial pattern of range use by mapping either the time spent in or the number of visits to a quadrat. The difficulty, however, lies with the quantification of the spatial pattern, accounting for both the variation and grain of quadrat occupational density for a sample period, into a numerical index which can be compared between sample periods. As Pielou (1977) points out, spatial pattern has both intensity, the extent to which occupation density varies in space; and grain, the extent over which density is perceived to vary. An index that accounts for both would essentially be a measure of the intensity and extent of clumped patterns of range use. Indices of clumping are not uncommon in the literature. The Shannon-Wiener index of diversity (Krebs 1985) for example was used by Struhsaker (1975), Oates (1977), Rudran (1978a) and McKey and Waterman (1982) to assess variation in patterns of range use. Cords (1987) has used the coefficient of variation of ranging scores (quadrat use) in quadrats over time as an 'index of the evenness with which quadrats are used'. Other indices of clumping include the variance to mean ratio calculated on the distribution of discrete items in quadrats (Ludwig and Reynolds 1988) and Lloyd's (1967) index of patchiness (in Pielou, 1969).

Two problems are associated with these indices. First, results are greatly affected by the size of the quadrat used. More important are the effects of the second problem; these indices of clumping only measure variation in the intensity with which quadrats are used. No record of the location of quadrats is mathematically incorporated into the indices and they therefore do not assess grain. As has been seen, an examination of the grain of quadrat occupational density is imperative for an interpretation of spatial pattern. Rasmussen (1980) discusses various indices of range use and demonstrates the value of the Coefficient of Variation (CV) statistic as an index for the assessment of variation in occupational density of quadrats. Most importantly, the CV, unlike most other indices of clumping, is unaffected by multiplication or division of values in each quadrat by a constant and can thus be used for comparison between samples of different size.

By including a measure of distance between quadrats into the derivation of a range use index (RU) from the coefficient of variation statistic, an index that accounts for both intensity or variation and the grain of quadrat occupational density is achieved (Rasmussen 1980).

$$RU = \left[\Sigma_{i=1}^{P}(Xi - \overline{X})^2/P\right]^{\frac{1}{2}} \div \overline{X}$$

Where: Xi = the sum of the values in the ith pair of quadrats divided by the distance between their centres, and P = the total number of pairs of quadrats or N(N - 1)/2. If the RU index is zero then occupational density of all quadrats is the same. The variation and grain of occupational density increases with an increasing RU value or, in other words, use of the home range becomes more clumped. RU indices were calculated for the troop each month from the following quadrat values:

1. Time spent in a quadrat.
2. The number of visits to a quadrat.
3. The proportion of time spent in a quadrat engaged in one of three activities; feeding, moving, and resting or passive behaviour.

These RU indices were used to investigate the relationships between range use patterns and thirty-one behavioural and environmental factors by month.

Range overlap between sample months was determined using the method of Holmes and Pitelka (1968). By this method the sum of the shared percentages of mutually-used quadrats yielded the total overlap in monthly range. Thus, if the use of quadrats A, B, C, and D for a sample period was 40%, 30%, 20% and 10% respectively and the extent of use of the same quadrats for the consecutive sample period were 20%, 20%, 30% and 30%, the total overlap in range use between sample periods would be 70%.

Vertical use of the habitat was recorded from twelve height classes (Fig. 7.1) for all visible individuals during 10-minute scans every half-hour. The absolute location (expressed as metres height) of a monkey may be misleading if it is not expressed relative to the dimensions of the forest in which it is seen (for example, a monkey at 15m might be in the lower canopy of a high stature forest, or in the upper canopy of low stature forest). The height classes were thus defined as follows:

Class 1. Ground
- 2. *Isoglossa* sp. herb layer
- 3. Understory thicket
- 4. Understory tree
- 5. Lower canopy - central branches
- 6. Lower canopy - terminal branches
- 7. Middle canopy - central branches
- 8. Middle canopy - terminal branches
- 9. Upper canopy - central crown - not exposed
- 10. Upper canopy - terminal crown - not exposed
- 11. Upper canopy - central crown - exposed
- 12. Upper canopy - terminal crown - exposed

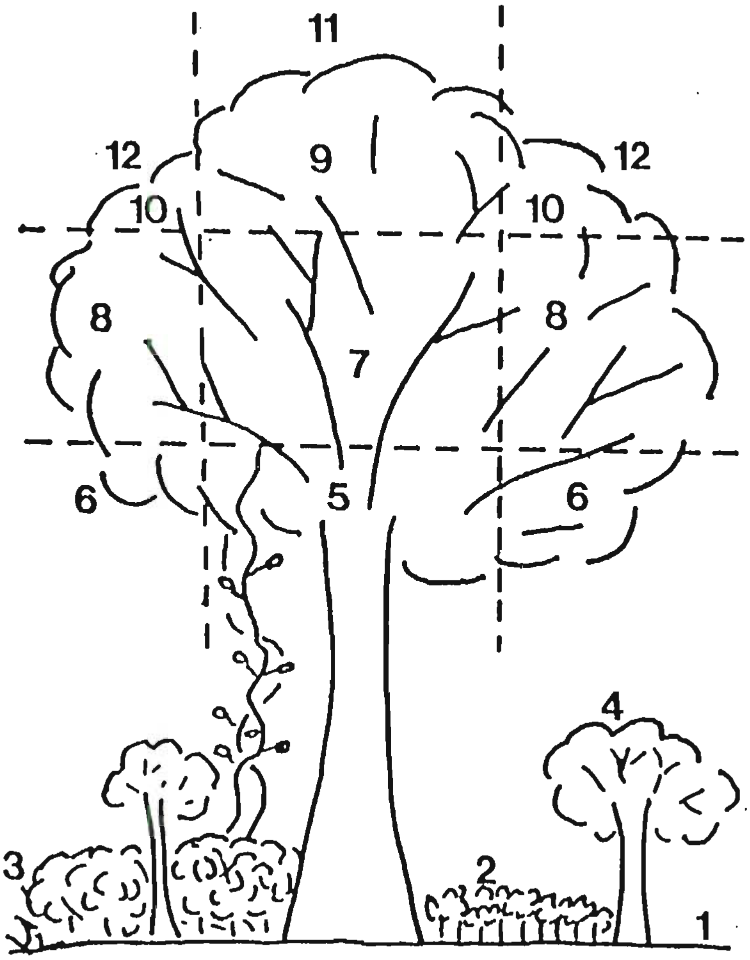


Figure 7.1. Diagram of the forest height classes used to describe the vertical position of the monkeys.

Understory thicket was found largely in the scrub thicket community and to a lesser extent, in the forest community (Tinley, 1985). The thicket comprised a tangle of climbers and creepers in a stratum usually above the herb layer but below the canopy of understory trees (1.5 - 3.0 m). Canopy use was related to activity type by further distinguishing between the use of central and terminal branches in the canopy. The question of predation as a factor limiting spatial use of the canopy crown was investigated by determining the degree to which individuals were prepared to become exposed on the canopy crown.

All statistical tests are two-tailed with the significance level set at $P<0.05$.

7.3 RESULTS

7.3.1 HOME RANGE AREA

Over the course of 13 months the study troop entered 60 quarter hectare quadrats, giving a home range of 15.0 ha. These figures were derived from the 45 days of observation for which there were more than eleven hours of observation. Home range size was not increased by including all observations of troop locality for the 17 additional part day follows. However, the home range estimate of 15 hectares must be considered an overestimation because group members were not mapped in every part of each quadrat they entered. The home range estimate decreased by 16.3% to 12.6 ha using the smaller quadrat size (1/16 ha).

Over the whole study period the number of days and months in which a quadrat was visited varied little between the 60 quadrats that comprised the home range (Fig. 7.2 and Fig. 7.3). In each case the use of quadrats was randomly distributed over time and the data sets typically conformed to a Poisson distribution (months $X^2 = 178.9$, $df = 11$, $P<0.001$; days $X^2 = 390.7$, $df = 15$, $P<0.001$; see Ludwig and Reynolds 1988). Green's index of evenness (GI;Ludwig and Reynolds 1988) also indicated a random pattern of use of quadrats over time (months $GI = 0.003$; days $GI = 0.007$). These data imply that, over the study period there was little or no concentration of use in any one quadrat.

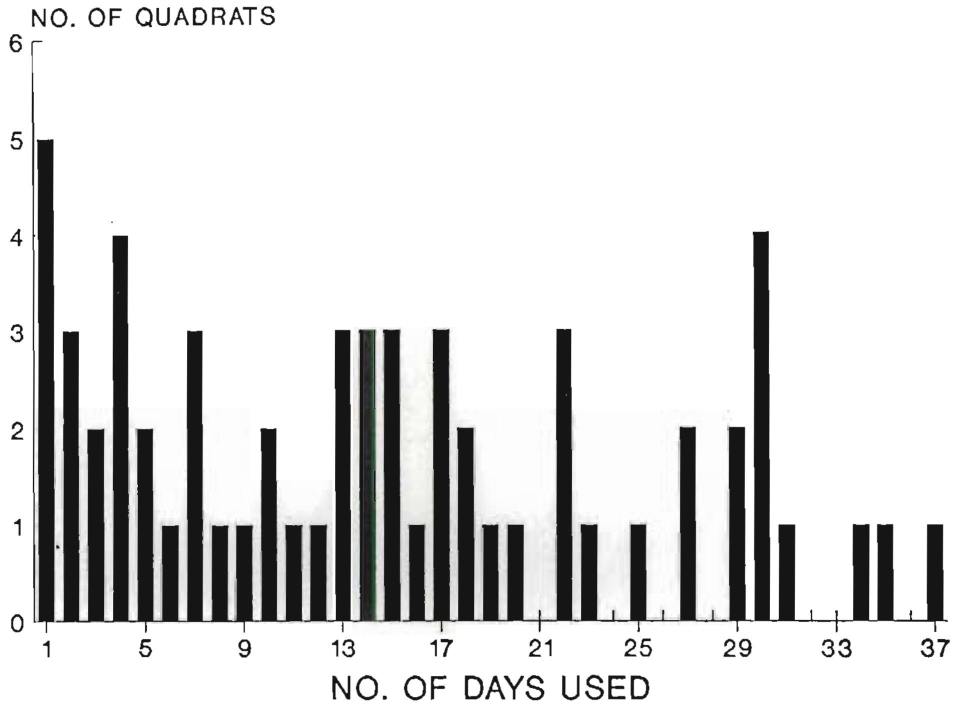


Figure 7.2. A frequency distribution illustrating the number of sample days quadrats were used by the troop.

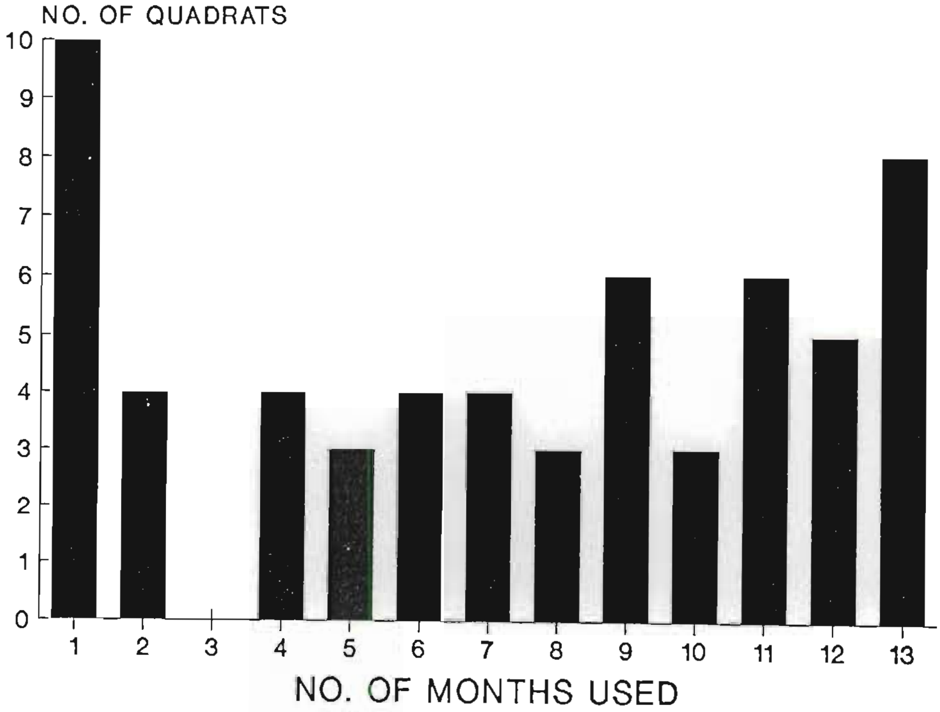


Figure 7.3. A frequency distribution illustrating the number of sample months quadrats were used by the troop.

The plot of cumulative increase in area used by the monkeys over the study period showed a very gradual increase in the size of the recorded home range, reaching a size of 12.5 ha by the fourth month which remained constant for the following six months (Fig. 7.4). The remaining three months, May, June and July of 1987 showed a further increase in the area used, and an area of 2.25 ha on the home range boundary not used previously was included. This suggests an expansion in home range area after a long period of stability.

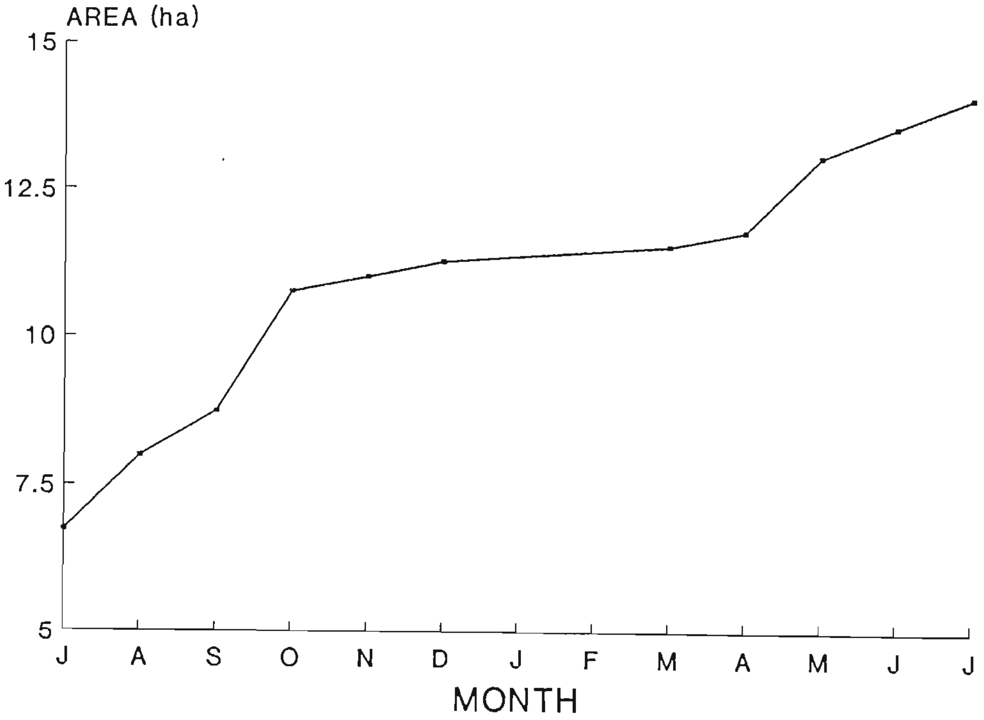


Figure 7.4. The cumulative increase in home range area over the study period, July 1986 through July 1987

A strong relationship between the number of visits to a quadrat and the time spent in that quadrat was recorded ($r=0.76$, $P<0.001$, $df=434$). Since the time spent in a quadrat was both a measure of the frequency of use and the duration of use of a quadrat it was considered a more sensitive index of occupational density than frequency of use alone (Fig. 7.5). On average the troop visited a quadrat 1.51 times a day ($s=0.78$, $n=907$ quadrat days) and spent 0.43 hours per visit (i.e. 25.8 minutes, $s=0.42$ hours, $n=1260$ day visits) in a quadrat (Table 7.1).

About half the quadrats (56.7%, $n=34$) comprising the home range were used on less than the average number of days (14.7 days), while 26 quadrats (43.3% of the home range) were used more frequently than the mean number of days. Quadrats were used a mean number of 7.3 months. Almost an equal number of quadrats were used more months than average ($n=29$) as were used less months than average ($n=31$). Only a single quadrat (H03) was used less than the average number of months but on greater than the average number of days. This quadrat was used as a midday rest site. Together, these data suggest that the gross use of space was random over time.

A few quadrats ($n=5$) were used on more days than average but were visited less than average (i.e. only visited once and for a short time on those days). All of the latter quadrats were located on the edge of the home range and it is tempting to assume that the single visit to a quadrat/day for a large number of days coincided with a need to patrol the range but where a short visit was adequate. These visits may have been related to monitoring food resources or maintaining territory boundaries.

7.3.2 DAY RANGE LENGTH

Group movements were co-ordinated and, like blue monkeys (Rudran 1978b), normally began with the directed movements of a few individuals who were then followed by the rest of the troop. Mean day range length for the thirteen month period was 1216.7 m ($s=255$, $n=45$, range 700m-1950m) (Table 7.2). The overall mean rate of travel of the

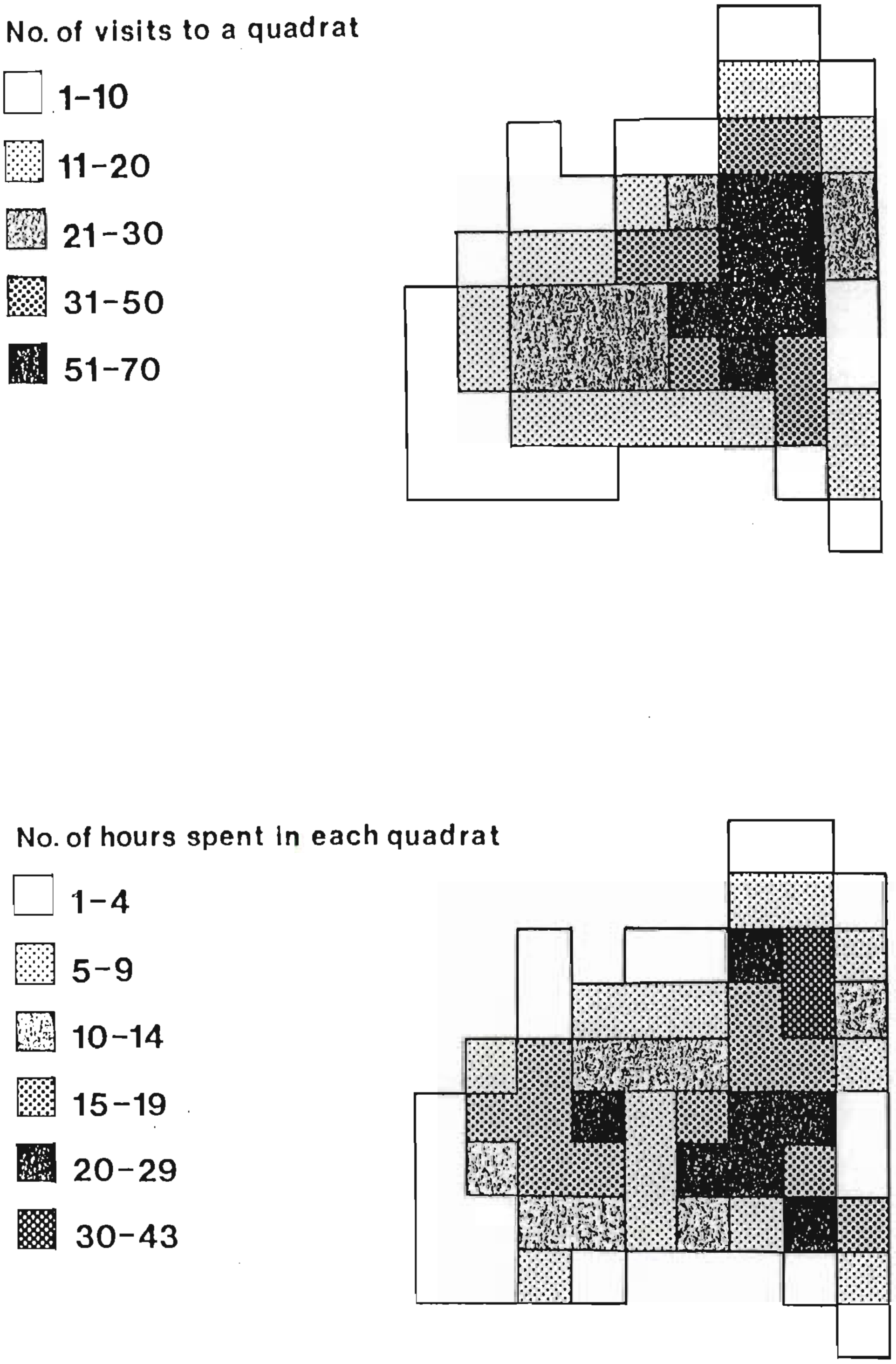


Figure 7.5. Maps of quadrat (50x50 m) use by the troop over the study period, measured as the number of observed visits to a quadrat and the number of observation hours spent in a quadrat.

Table 7.1. The mean number of visits and the mean duration of a visit (decimal hours) to a quadrat per day per month for the study period.

MONTH	VISITS	s	n	DURATION	s	n
July 1986	1.64	0.85	75	0.42	0.29	99
August	1.59	0.82	75	0.41	0.30	106
September	1.81	1.16	70	0.39	0.31	117
October	1.51	0.71	81	0.32	0.29	120
November	1.56	0.78	46	0.43	0.50	67
December	1.80	1.15	55	0.45	0.50	89
January 1987	1.37	0.72	86	0.56	0.87	107
February	1.27	0.57	64	0.47	0.52	85
March	1.40	0.72	65	0.43	0.33	83
April	1.35	0.61	60	0.45	0.43	76
May	1.49	0.72	97	0.34	0.27	133
June	1.35	0.71	59	0.49	0.43	77
July	1.44	0.67	74	0.42	0.37	101

Table 7.2. Mean day range length (m) and day range area (ha), and total area used during each monthly sample (3 consecutive days), for the study period.

MONTH	Day range length x	s	Day range area x	s	No. days n	Sample area (3 days)
J	1225	216	4.56	0.32	4	6.75
A	1178	92	4.63	0.83	4	7.00
S	1188	181	4.31	0.66	4	6.75
O	1678	243	6.75	1.56	3	11.00
N	1275	224	5.63	0.88	2	-
D	1256	173	4.58	1.18	3	8.00
J	1229	188	5.19	1.25	4	8.50
F	1078	270	5.25	1.25	3	9.00
M	1189	237	5.25	0.66	3	7.75
A	1139	241	5.08	1.53	3	8.25
M	1425	232	6.06	0.77	4	10.50
J	844	208	3.56	0.24	4	7.50
J	1104	211	4.63	1.09	4	7.25
TOTAL	1216	255	4.97	1.15	45 days	x=8.18

troop on days where the troop was observed for longer than eleven hours was 105.34 m/hr (s=22.79, n=43). The monkeys did not move at an equal rate throughout the day however, and a tendency toward a peak in the early morning and the late afternoon is clear. A greater distance was covered in the morning than in the afternoon (Fig. 7.6).

To interpret seasonal differences in diurnal variation in hourly travel rate some consideration of the seasonal variation in daylength must be made. Daylength at latitude 30° S for the last week of each month (centred on the 25 th) has a range of 10h13 for June to 14h05 for December (List, 1958). Months with daylight durations of less than 11.5 hours were termed winter months and included the months of April to August, while the remainder were termed summer months. There was no significant seasonal difference between summer and winter in the mean rate of movement per hour ($t=0.96$, df= 24, $P<0.4$). The monkeys therefore do not travel faster during winter to compensate for the shorter day.

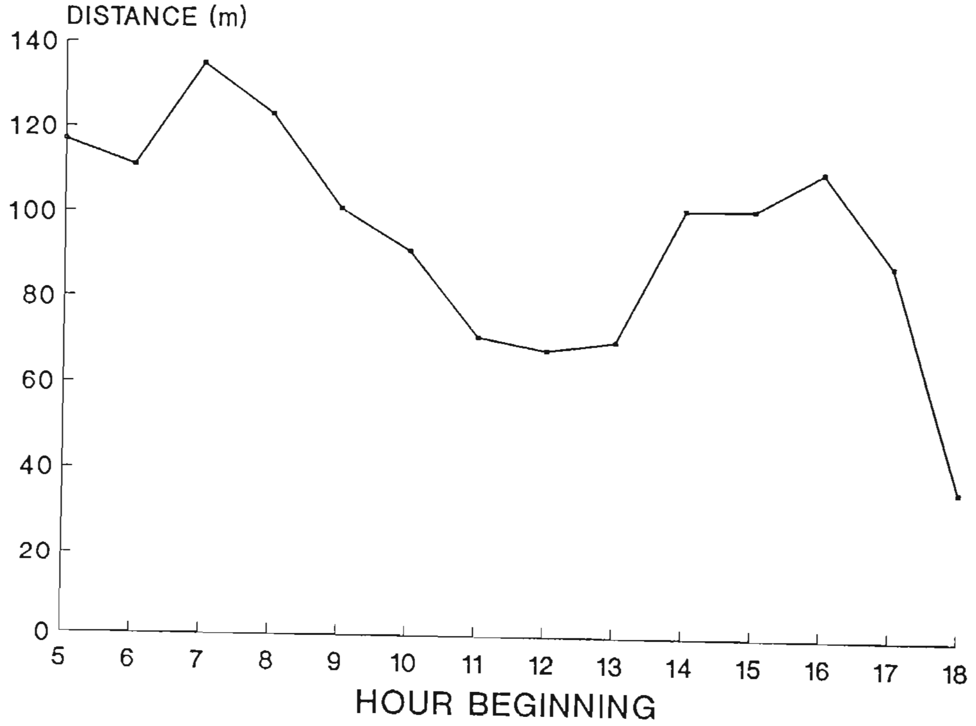


Figure 7.6. Mean distance moved during each hour of a day by the study troop.

There was a highly significant, although not surprising, relationship between distances covered during a day by the troop and the number of quadrats entered on that day (r = 0.734, df=41, P<0.001). On particularly hot days it was noted, although sample size is too small to permit verification, that day range was considerably reduced (16/2/87, 833m) and the monkeys would move into the dune scrub-thicket which was exposed to the cool breeze during the middle of the day.

The path route invariably crossed itself during the day, often as many as 4 to 5 times (Fig. 7.7).

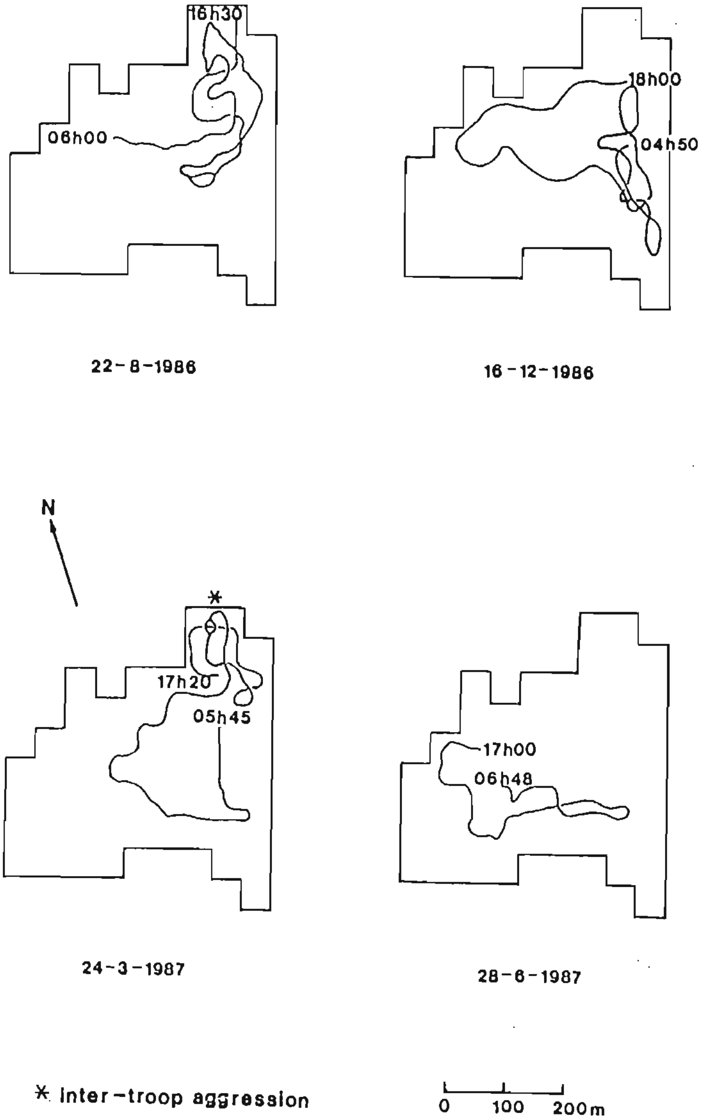


Figure 7.7. Maps of a typical day-path-route in each of four months (August 1986, December 1986, March 1987, June 1987).

7.3.3. DAY RANGE AREA

The mean area used per day was 4.97 hectares (s=1.15, n=45, range=3.25-8.50 ha) (Table 7.2). The proportion of total home range area covered by the mean day range area was 33.5%. On any one day the Cape Vidal samangos covered a third of their home range.

The mean percent overlap between consecutive daily ranges was 64.1% (s=17.0%, n=23). The high mean indicates that repeated use of quadrats on different days was frequent. In addition the troop was not found to use mutually exclusive areas of its home range during all other pair combinations of days over the study period.

7.3.4 MONTHLY SAMPLE RANGE AREA

The mean area used during three consecutive days of a month for the months of July 1986 through July 1987 was 8.38 ha (s=1.48, n=13). Thus over a three day period the troop would cover on average 55.87% (s=9.89%, n=13) of the total home range area. In only three of the months was less than half of the home range area covered by the troop (Fig. 7.8). In no instances were monthly sample ranges mutually exclusive, and because of its small size, the whole home range area was intensively used throughout its extent over the study period.

The mean percent overlap of monthly range areas (over 3 days) based on shared quadrat use between consecutive monthly samples was 80.1% (s=11.9). The mean percent overlap for all pair combinations of monthly sample range area overlap was 71.3% (s=12.7). Thus, a considerable portion of any month's range area was re-used during other months. The mean percent area of the total home range shared between consecutive months was 44.8% (s=3.6%) and 40.7% (s=8.2%) for all month-pair combinations.

The mean percentage overlap in monthly sample range use based on the percent frequency of use (number of visits to a quadrat) of a quadrat was 61.2% (s=11.1%).

Overlap between consecutive monthly samples was greater on average than for other pair combinations (x=52.8, s=11.4, n=78). While the troop might visit a quadrat equally

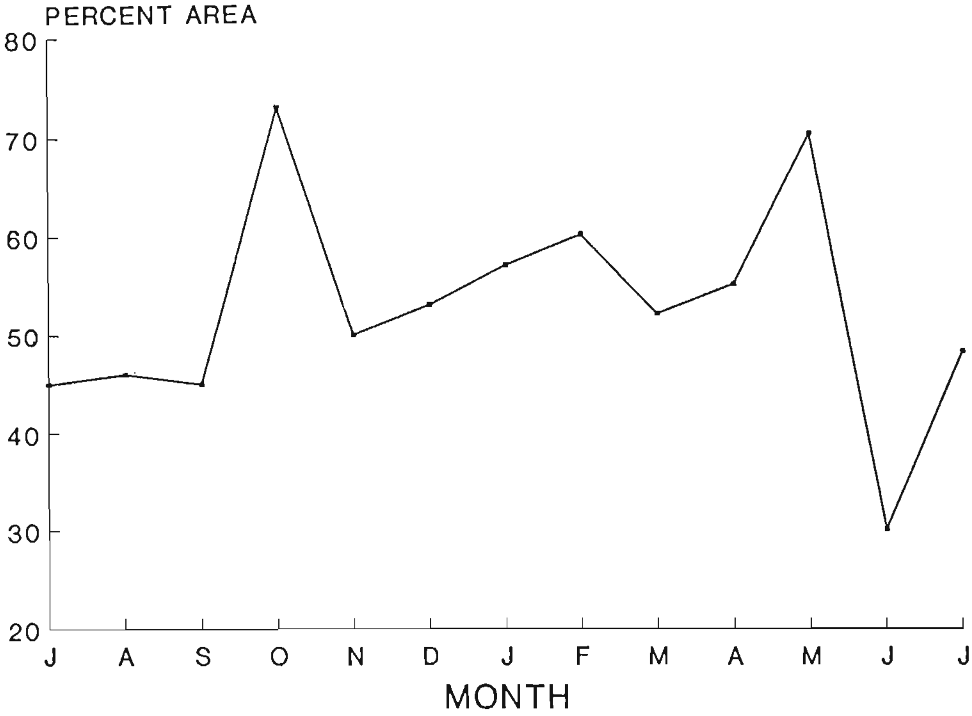


Figure 7.8. Percent of total home range area used over three days of a monthly sample period.

frequently between sample periods, the cumulative time spent in that quadrat might differ considerably. Thus, overlap statistics based on the percent time spent in a quadrat during consecutive monthly sample periods were also calculated. Overlap for all pair combinations showed a reduction in monthly range use overlap (55.8%) compared to statistics calculated from proportional number of visits, while the mean overlap between consecutive months was 48.3%. The troop thus consistently re-used large areas of the home range in consecutive sample periods.

7.3.5 HOME RANGE OVERLAP

The study troop's home range bordered on and overlapped in part with those of three other troops. Using 1/16 ha grids the overlap of camp troops (study troop) home range with that of caravan troop and hill troop was 2.5 ha and 3.3 ha or 16.7% and 22.0% of the home range respectively. A third troop, valley troop, overlapped on the western edge with 6.7% or 1 ha of the study troop's home range. Figure 7.9 shows the position of aggressive and passive intertroop encounters, and sightings of extra-troop position where only that troop was present. From Figure 7.9 it can be seen that the home range was defended mainly on the northern and southern boundaries. The western and eastern boundaries were clearly demarcated by an Acacia karroo belt and the sea respectively and were not seen to be disputed. While it was possible to determine the overlap in home ranges over the whole study period, the infrequency of observed intertroop encounters (x=0.064 encounters/hour, s=0.057, n=13) per month, including passive and aggressive interactions, made interpretation of seasonal variation in range overlap unreliable.

7.3.6 GROUP DISPERSION

The mean group dispersion for the study period was 80.3m (s=12.2, n=1136). The mean monthly group dispersion ranged from 62m (July 1986) to 100m (July 1987). The plot of group dispersion by month shows no obvious trend (Fig. 7.10). Correlations of dispersion values with nearest neighbour distances, food availability, activity and canopy use were insignificant although there is a possible relationship between the availability of new leaf parts and dispersion ($r = -0.491$, $df=11$, $P<0.08$).

7.3.7 USE OF THE FOREST STRATA

The percent frequencies of use of the twelve forest strata for the study period are given in Table 7.3. The least time was spent on the ground (5.27%), in the Isoglossa sp. herb layer (4.86%), and exposed on the central canopy crown (4.4%). For the most part the monkeys used the canopy strata (x=64.0%, s=4.89%, n=13) in favour of the subcanopy, and some 21.3% of the time was spent, if not on the ground, then very close to it. This is attributable to the use of the dune thicket as the favoured height class used for resting and other passive activities.

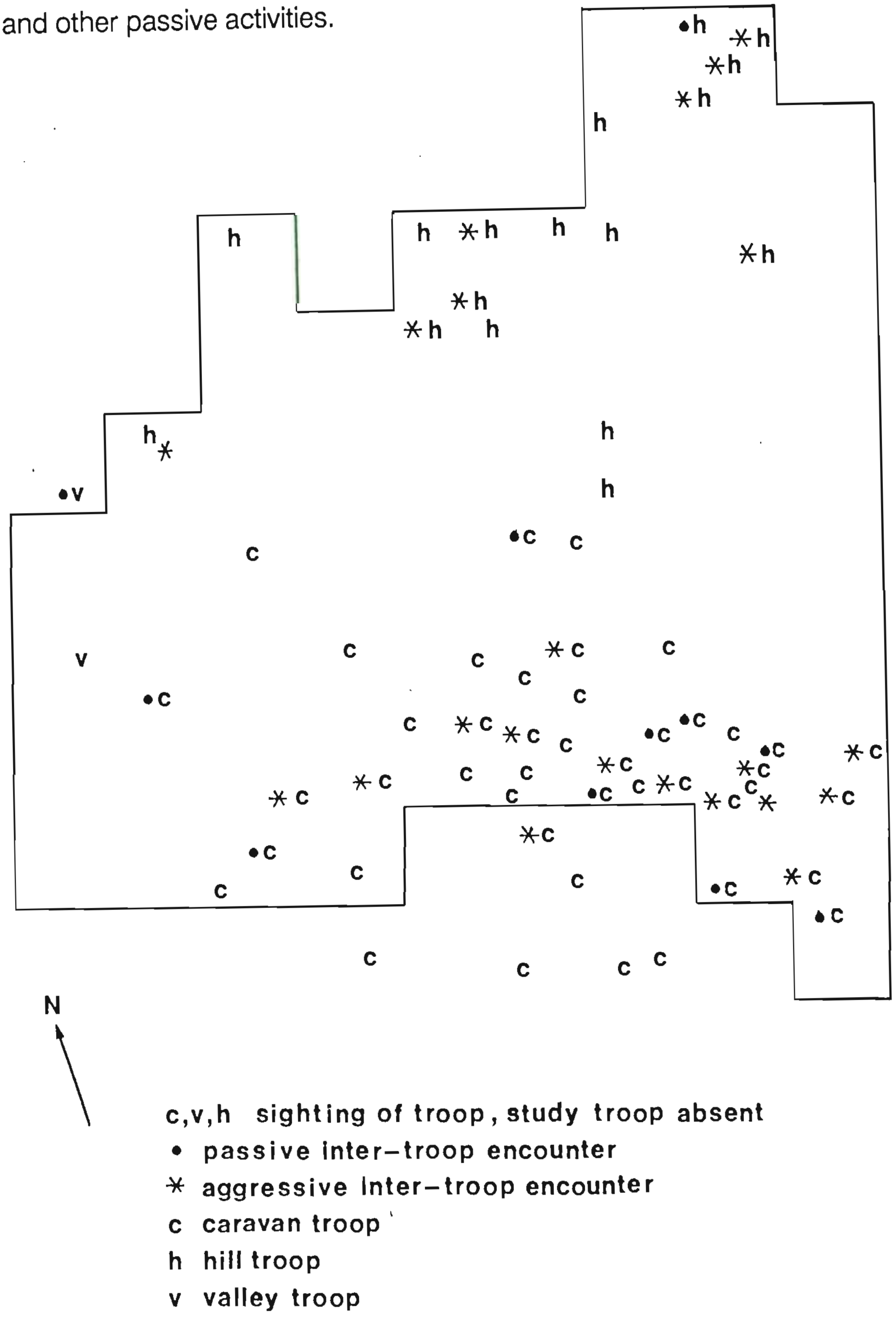


Figure 7.9. Map showing the extent to which neighbouring troops range area overlapped with the study troop. Also shown are the types of inter-troop encounter observed (passive or aggressive).

Table 7.3. The mean monthly percent frequency of use of the forest strata over the study period, July 1986 - July 1987.

FOREST STRATUM	% FREQ. USE	s
1. Ground	5.3	2.4
2. <u>Isoglossa</u> herb layer	4.9	3.7
3. Understory thicket	11.2	5.3
4. Understory tree	12.2	2.2
5. Lower canopy		
central branches	8.8	1.3
terminal branches	6.2	1.7
6. Middle canopy		
central branches	12.4	2.2
terminal branches	9.0	3.4
7. Upper canopy unexposed		
central crown	10.1	2.4
terminal crown	7.5	2.2
8. Upper canopy exposed		
central crown	4.4	2.2
terminal crown	5.6	3.3

n = 10 559 records

There was little difference in the diversity of use of height classes between months (Fig. 7.11). The thicket stratum was, however, used more during the summer months when the cool thickets provided a respite from the midday heat (Fig. 7.12). Toward the end of the study period during the months May 1987 to July 1987 the <u>Isoglossa</u> sp. herb layer began to flower and seed; in response the troop spent more time feeding in this stratum and this is reflected in the increased frequency of use of the stratum.

The daily use of the height classes confirms the above trends (Fig. 7.13). On the whole there was a very low incidence of use of the ground and <u>Isoglossa</u> sp. strata, although this increased gradually to a shallow peak from mid-morning to mid-afternoon. Use of the thicket stratum showed a strong peak in the middle of the day coinciding with the minimum use of the upper canopy. The understory and lower canopy layers were used more frequently than the latter but without considerable variation throughout the day. A

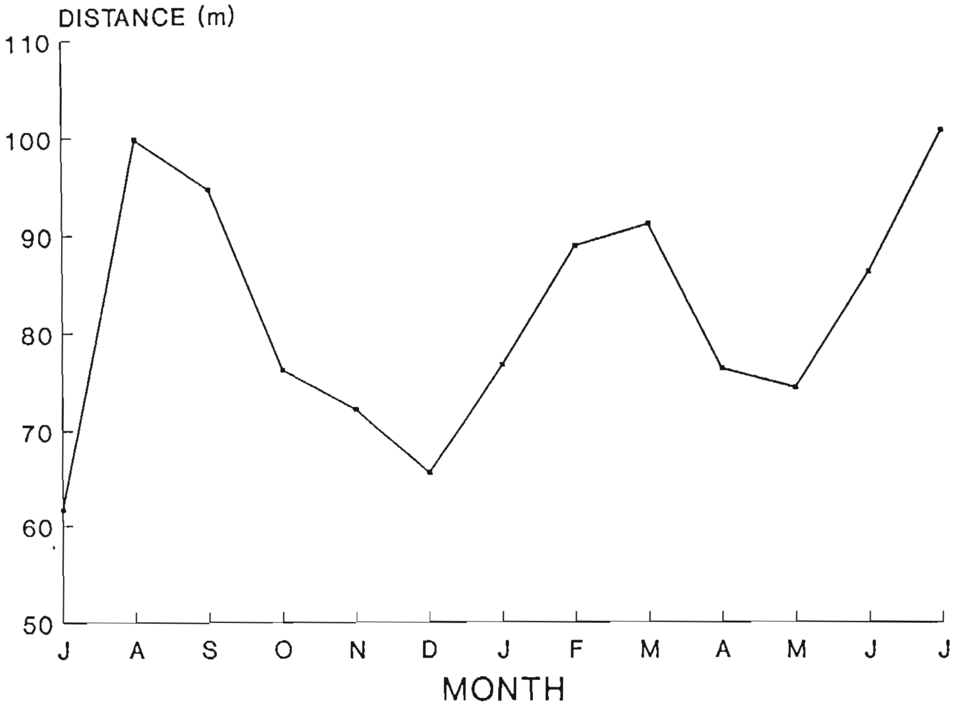


Figure 7.10. Mean monthly troop dispersion distance.

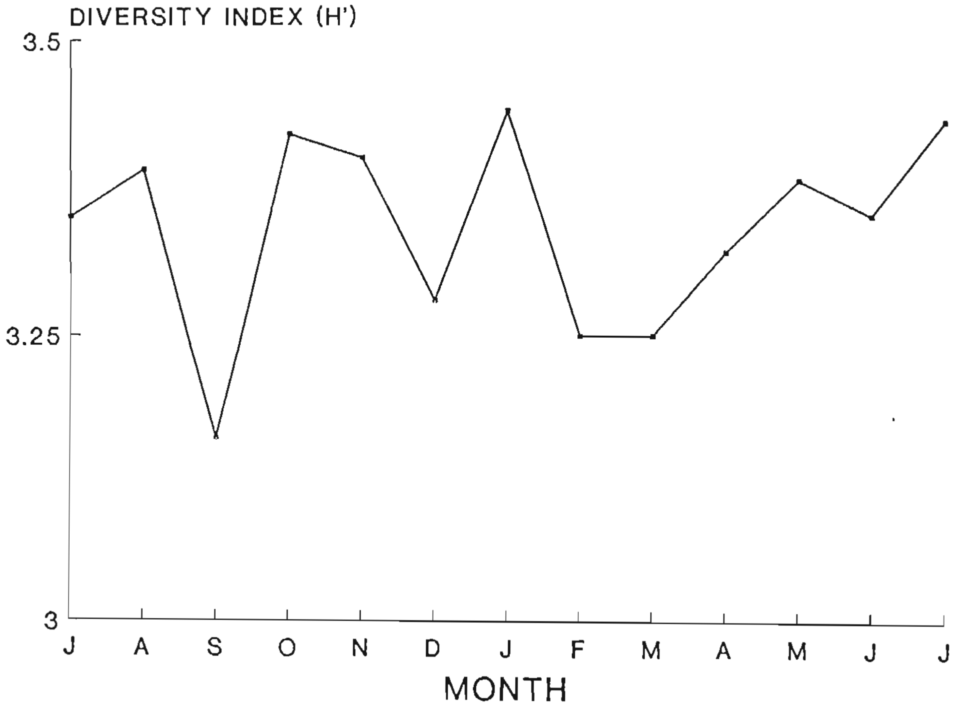


Figure 7.11. Monthly diversity of use (Shannon-Wiener) of forest height strata.

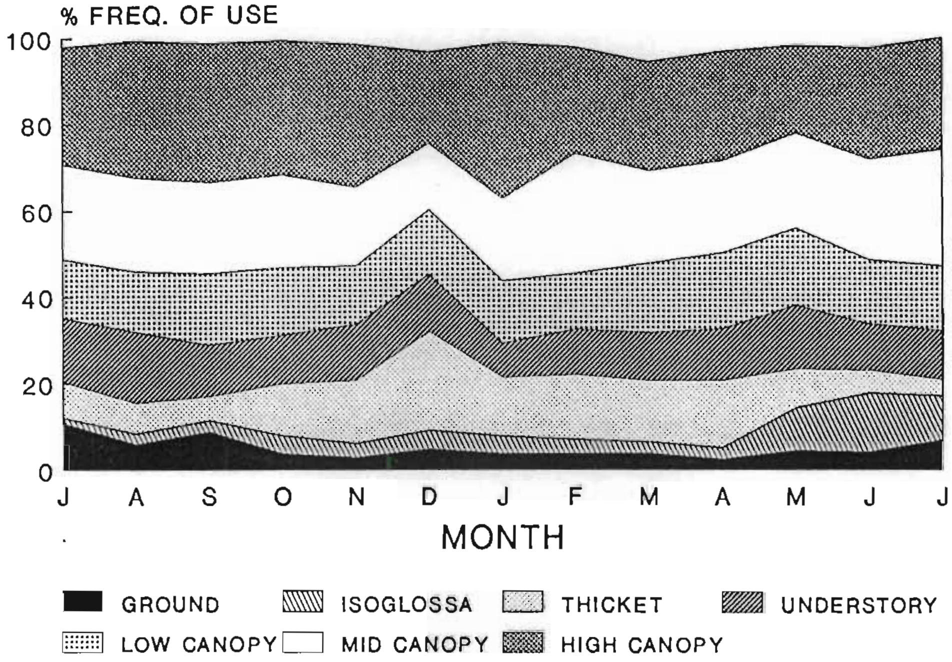


Figure 7.12. Monthly percent frequency of use of forest height classes.

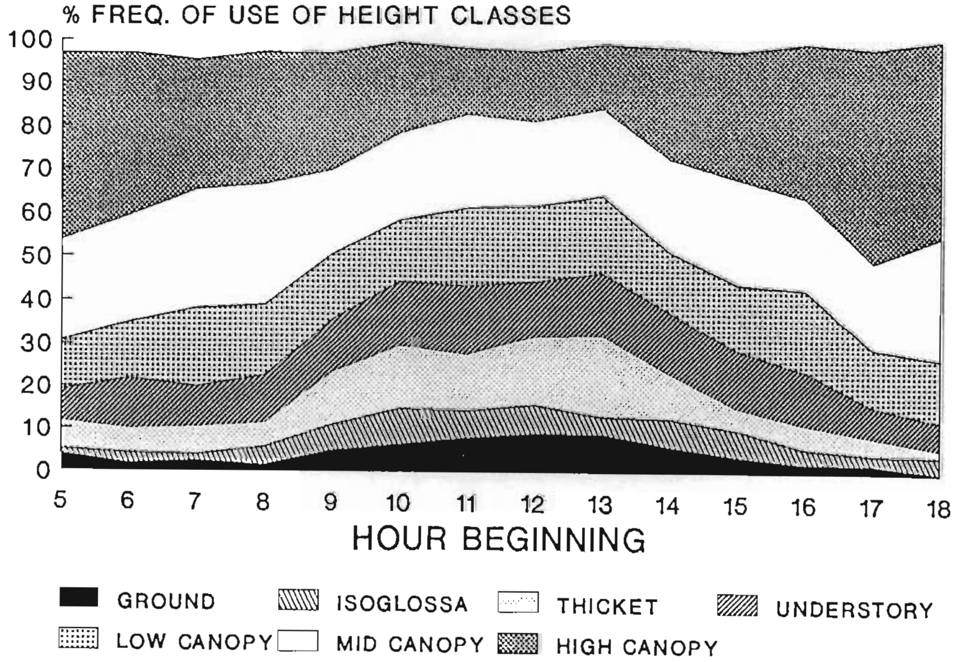


Figure 7.13. Diurnal percent frequency of use of forest height classes.

small peak in the frequency of use of the mid-canopy was evident for the early morning and late evening and this trend was more noticeably developed for the upper canopy stratum. In short the troop was inclined to use the canopy layers in the early morning while feeding, coming down to the lower strata to rest in the middle of the day.

7.3.8 CORRELATES OF RANGE USE

Range use indices (calculated by Rasmussen 1979; 1980 method) that examine the grain and intensity of range use for a sample month as measured by time spent in a grid, are given in Table 7.4.

Table 7.4. Range use indices (RU) for each month during the study period. RU_{total} is given for the ranging pattern based on the time spent in a quadrat, and the number of visits to a quadrat.

MONTH	RU_{total}		RU_{feed}	RU_{rest}	RU_{move}
	time/quadrat	visits/quadrat			
J	0.88	0.93	0.82	0.97	0.95
A	0.97	1.00	0.82	1.03	1.00
S	0.91	1.05	0.97	1.03	0.84
O	1.05	0.93	0.92	1.13	0.98
N	1.14	0.91	0.91	1.31	1.10
D	1.52	1.15	1.23	1.5	1.02
J	1.29	0.89	0.99	1.70	1.01
F	1.38	0.91	1.24	1.51	1.26
M	1.14	0.82	1.18	1.10	0.90
A	0.96	0.75	0.94	0.95	0.85
M	1.07	0.93	0.89	1.08	1.08
J	0.92	0.78	0.93	0.94	0.77
J	0.97	0.88	0.96	1.00	0.89

The gross range use pattern was more clumped during the summer months of November 1986 through to March 1987 (Fig. 7.14). When range use indices based on the proportion of time spent in a grid given to one of three activities were calculated

(RU_{rest}, RU_{feed}, RU_{move}), it was clear that the greatest variation in the pattern of use of the home range was displayed by the time spent resting in a quadrat (Fig. 7.15). The clumped pattern of range use in summer is thus a function of the clumped pattern of resting activities about the home range. This was corroborated by the significant positive correlation between the RU_{total} and the percent frequency of resting activities in a month ($r=0.79$, $df=12$, $P<0.001$).

RU_{total} or, in other words, the grain and intensity of quadrat occupational density as measured by the total time spent in a quadrat, was significantly and positively correlated to the monthly proportional frequencies in resting and grooming behaviour, the use of the thicket stratum, the number of daylight hours and the monthly maximum temperature (Table 7.5). These correlates can be explained as follows: as daylight hours increased the monthly maximum temperature increased, more time was available for resting and temperatures during midday were prohibitively high, discouraging activity. Thickets were used to rest in owing to their position close to the sea and the cool breeze often encountered there. Activities such as grooming were common during resting periods whilst feeding was uncommon hence the negative correlation of feeding activity with RU_{total} ($r=-0.792$, $df=13$, $P<0.001$). The pattern of range use was more clumped when the monkeys spent proportionally less time feeding.

RU_{total} was also correlated to the availability of flowers ($r=0.77$, $df=13$, $P<0.01$) and less so to the availability of young leaves ($r=0.61$, $df=13$, $P<0.05$).

Range use indices for a month calculated on the basis of the time spent resting in a quadrat (RU_{rest}), in addition to the above correlates, showed a significantly more clumped pattern of use of the range area as the proportion of mature leaf and ripe fruit declined in the diet, and as the proportion of unripe fruit in the diet of the troop increased for that month.

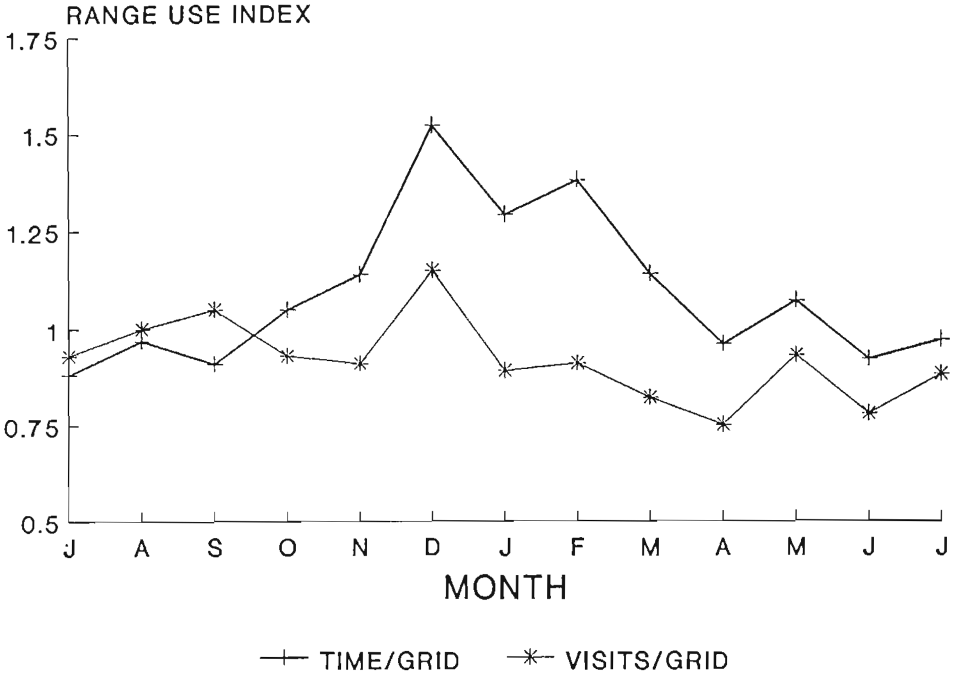


Figure 7.14. Monthly range use indices calculated separately, using Rasmussen's (1979) method, from both the time spent in a quadrat and the number of visits to a quadrat by the study troop.

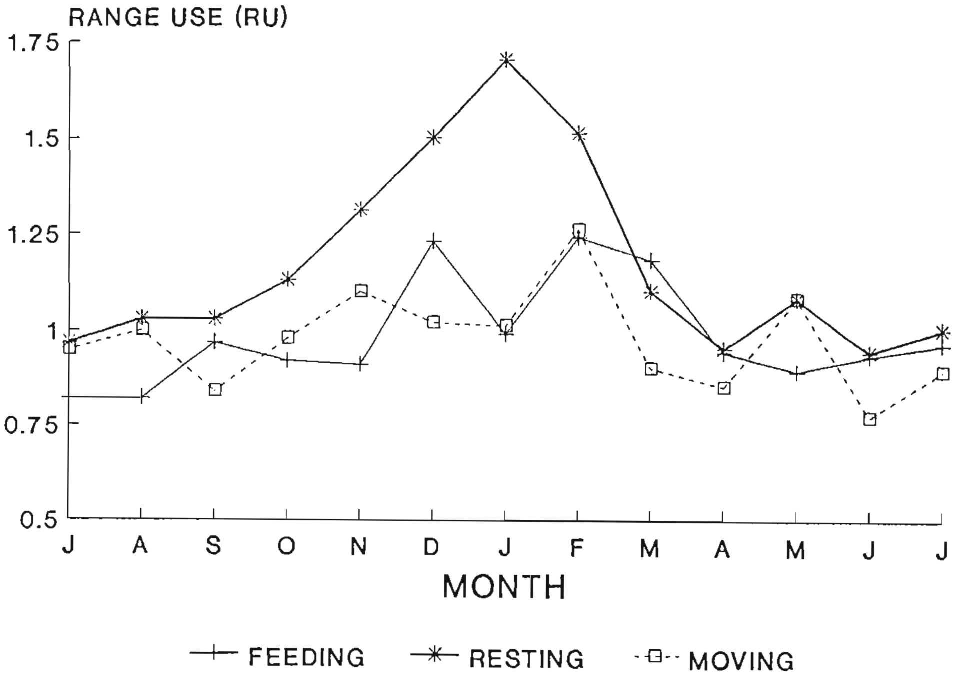


Figure 7.15. Monthly activity range use indices calculated from the time spent in a quadrat engaged in one of three activities (feeding, resting, moving).

Table 7.5. Partial correlation coefficients (r_{jk}) between values of RU and variables assessing nearest neighbour proximity, food availability, climate, activity, diet and height class use. Significant correlation are as follows: * P<0.05, ** P<0.01, *** P<0.001.

ECOLOGICAL CORRELATE	RU_{TOTAL}	RU_{REST}	RU_{FEED}	RU_{MOVE}
N-N TRP	-0.134	0.004	-0.323	0.141
N-N M	0.421	0.478	0.535	0.404
N-N F	0.208	0.347	0.177	0.496
FEED	-0.792***	No correlation values, since these values were used in the computation of RU_{REST}, RU_{FEED}, and RU_{MOVE}		
REST	0.793***			
MOVE	0.285			
GROOM	-0.021			
PASSIVE	0.810***			
NEW LEAF	-0.547	0.365	-0.046	0.190
MAT LEAF	0.129	-0.567*	-0.487	-0.351
FLOWER	0.129	0.200	-0.169	0.102
UNR FRT	0.441	0.562*	0.511	0.512
RP FRT	-0.293	-0.566*	-0.103	-0.516
INVERT	0.066	0.235	-0.130	0.188
EXOTIC	0.322	0.252	0.137	0.233
FAI FRT	-0.456	-0.430	-0.412	-0.102
FAI FLW	0.767**	0.869***	0.553*	0.473
FAI LEAF	0.611*	0.634*	0.217	0.519
DIET H	0.172	0.456	-0.128	0.345
DEFEND	-0.003	0.009	-0.297	0.119
ISOGLO	-0.167	-0.240	-0.123	-0.277
THKT	0.816***	0.649**	0.643**	0.437
UDST	-0.303	-0.459	-0.443	0.108
CNPY	-0.494	-0.139	-0.431	-0.148
GRD	-0.445	-0.355	-0.329	-0.255
HGHT H	-0.115	0.053	-0.540 [1]	0.092
DAY HR	0.769**	0.810***	0.493	0.393
RAINFALL	0.253	0.258	0.503	-0.360
TP X	0.821***	0.784***	0.757**	0.489
TP MAX	0.828***	0.780***	0.772**	0.487
AGGRO	0.097	-0.015	0.151	-0.025

---

[1] The significance level is 0.056. The trend suggested by this correlation is a less clumped ranging pattern with greater diversity of use of the height classes. Thus when the troop is using the thicket heavily one would expect the

range use pattern to be clumped.

Table 7.5. Continued/ Acronyms used for the 31 range use variables in Table 7.5.

Mean proximity of nearest neighbour

N-N TRP	for all individuals regardless of age/sex class
N-N M	to adult male
N-N F	to adult female

Percent frequency of observation of activity type

FEED	feeding activity
REST	resting (sitting) activity, excluding all other passive activities
MOVE	locomotive activity
GROOM	grooming activity
PASSIVE	all passive activities, including resting and grooming

Percentage observed proportion of food item in the diet

NEW LEAF	leaf bud and new leaf items
MAT LEAF	mature leaf items
FLOWER	flower buds and open flowers
UNR FRT	unripe fruit (does not include setting fruit)
RP FRT	ripe fruit
INVERT	invertebrate items ingested
EXOTIC	alien or exotic food items taken from camp site

Food availability indices

FAI FRT	for fruit, ripe and unripe
FAI FLW	for all floral phenotypes
FAI LEAF	for leaf phenotypes

DIET H	Diet diversity indices
DEFEND	Defendability indices (Mitani and Rodman, 1979)

Percent observed frequency of use of height classes

ISOGL	use of *Isoglossa sp.* herb stratum
THKT	use of thicket
UDST	use of understory stratum
CNPY	use of all canopy classes
GRD	use of the ground

HGHT H	Height class use diversity indices

Table 7.5. Continued/ Acronyms used for the 31 range use variables in Table 7.5.

Climate

DAY HR	daylight hours
RAINFALL	rainfall
TP X	monthly mean daily temperature
TP MAX	monthly maximum temperature
AGGRO	intertroop aggression, occurrence/hour

7.4 DISCUSSION

To a large extent the spatial and temporal use of the home range by the Cape Vidal samangos was a function of the small size of the home range area. The following section examines some of the probable determinants of home range size and compares the patterns of range use of samangos at Cape Vidal with other mitis populations.

7.4.1 Home range size

Variation in home range size among primate species has been attributed to the relationship between body weight and metabolic requirements, and the nature of the diet (Milton and May 1976, Clutton-Brock and Harvey 1977, Harvey and Clutton-Brock 1981, Mace et al. 1983), and the degree to which a primate is terrestrial or arboreal (Clutton-Brock and Harvey, 1977). Intraspecific variation in home range size has been attributed to habitat quality (Butynski 1990, Takasaki 1981), distribution and abundance of food resources in time and space (Clutton-Brock 1977, Ghiglieri 1984, Bennett 1986), troop size (Struhsaker 1975, Clutton-Brock and Harvey 1977, Takasaki 1981), population density (Freeland 1979, McKey and Waterman 1982), and interspecific competition (Clutton-Brock and Harvey 1977), or a combination of these parameters.

Although there is considerable variation in troop home range size within C. mitis (Table 7.6), five studies have recorded similar home range sizes to those of the Cape Vidal population (Aldrich-Blake 1970, De Vos and Omar 1971, Moreno-Black and Maples 1977, Scorer 1980, Beeson 1987). In contrast to the Cape Vidal population, however, troop size was relatively small (range 13.6-20) in all these studies. Takasaki (1981) concluded for macaques that intraspecific variations in troop size and home range area were related to habitat quality such that there was a negative correlation between home range area and habitat quality, and a positive correlation between troop size and home range area. If Takasaki's (1981) reasoning is accepted, then the large troop size at Cape Vidal (30-35 individuals) and small home range (15 ha) can only mean that habitat quality at Cape Vidal is very high. This corroborates observed feeding behaviour at Cape Vidal.

Habitat quality is an important determinant of home range size (cf. Dunbar 1988) in mitis. Habitat degradation has been noted to affect home range size in the mitis species group and both De Vos and Omar 1971 and Beeson 1987 attribute small home range size to the encroachment of commercial forest plantations on forests with high mitis population densities. The blue monkeys of Budongo forest (Aldrich-Blake 1970) also have exceptionally small home ranges (5.2 ha-11.7 ha) and troop sizes (mean=13.3 individuals). In this case extensive logging programmes (Aldrich-Blake 1970) may have caused the displacement and compression of home ranges (Rudran 1978a) so that even troops in relatively pristine forest nearby are affected.

The effect of sympatric primate competitors on home range size may further compound the effects of habitat destruction and may cause troop size to be lowered (cf. Aldrich-Blake 1970) as home range area decreases due to human interference. However, samangos have few frugivore competitors and certainly no arboreal primate competitors in most southern African forests. Yet Scorer (1980) and Van der Zee and Viljoen (unpub. report) show that the home range and troop size of eastern Transvaal samangos is, on average, small. Cape Vidal samangos would appear to be fortunate in that while they too are without primate competitors, they also have abundant fruit resources, thus large troop sizes are associated with relatively small home range areas.

Since most animals cannot obtain their food without moving, it is often assumed that the home range area defines that area needed to ensure a steady supply of food sufficient for reproduction. Competitors are part of the interpretation since they influence the 'supply of food'. This implies that provided an animal can reproduce successfully, it will not use more area than is necessary to obtain food. This notion of a finely-balanced relationship between troop size and home range area should be challenged:

Table 7.6. Comparative troop sizes, home range areas (ha) and population densities (individuals/ha) for the *Cercoptihecus mitis* troop.

Troop Size	Home range Area	Population Density	Author
C. m. labiatus			
18.5	34.0 [1]	0.49	Lawes et al. 1990
35.0 [2]	24.0	–	McMahon, 1977
C. m. erythrarchus			
13.6	19.7	1.45	Scorer, 1980[3]
34.0	15.0	2.02	Lawes, this study
9.5	11.4	0.78 [4]	van der Zee and Viljoen, unpub. report
C. m. stuhlmanni			
13.3	8.0	1.66	Aldrich-Blake, 1970
12.0	25.0	0.48	Schlichte, 1978
20.0	72.5	0.35	Rudran, 1978
15.0	17.5	1.21	Beeson, 1987
32.6	23.9	1.69	Cords, 1987
18.7	50.6	0.42	in Cords, 1987 [5]
18.5	33.0	0.65	Butynski 1990
12.0	253.0	0.05	Butynski 1990
C. m. kolbi			
16.0	13.7	1.20	De Vos and Omar, 1971
20.0	18.0	-	Moreno-Black and Maples, 1977

1. Home range area estimated from personal observation.
2. Value estimated by McMahon (1977).
3. Mean values from Scorer (1980) pp 205,212,213. n=5 troops.
4. Calculated from the following values given by the authors - 156 troops, mean troop size = 9.5 individuals, and indigenous forest available to samangos = 1500 ha.
5. Compiled by Cords (1987) from Rudran (1978), Struhsaker (1978) and unpub., and Butynski (1982) and unpub., Kanyawara area

First, one could only expect such a relationship to exist in troops or populations where the animals are limited in such a way that they are forced to optimize their use of space in this manner. For example, although they would appear not to be food stressed, the high population density of samangos at Cape Vidal may well have compressed the home range down to the minimum size that can support the troop. A high degree of range overlap (6.8 ha, 45 %) and the low incidence of aggressive defence of the range boundary, imply that samangos at Cape Vidal are less territorial than would be expected if a minimum home range size had been reached. It is unlikely therefore that the small home range size represents the minimum size that can support the troop, although I would suggest that home range size at Cape Vidal must be regarded as close to the minimum area that contains all necessary resources (leading to a superabundance of some, such as fruit), for high density populations in Indian Ocean coastal belt forest.

Second, troop size and home range area may vary in response to a number of factors besides food availability (although this may be the most important correlate) such as predation pressure, disease, and interspecific competition, the histories of which are largely unknown in most studies. Butynski (1990) warns of the danger of seeking solutions to observed ecological relationships in the "here and now". After considering numerous ecological correlates, Butynski (1990) accounted for a 10 fold difference in home range area between subpopulations of mitis 10 km apart in the Kibale forest, as the probable outcome of disease at Ngogo. In this instance, blue monkey troops at Ngogo troops have expanded their home ranges accordingly to be able to make the best use of food resources available to them, hence the large home range size (253 ha). Home range size is therefore not always indicative of the minimum area required for food resources by a monkey troop. In addition to the influence of high food availability and the lack of primate competitors, the size of the study troop and the high densities of samango monkeys at Cape Vidal, may also be attributed to the low levels of predation and disease. At least 3 neighbouring troops are of similar size and also have small home range sizes. The troops all appear to have a high proportion of young immature individuals and this (since there is no evidence for high levels of juvenile mortality) might suggest that the population is growing rapidly and that the population numbers have yet to stabilize at Cape Vidal.

Given the number of factors that may influence troop size (predation, disease, interference competition) and the ability of the mitis species group to live in a variety of habitats and use a wide range of foods, it is hardly surprising that the relationship between troop size and home range area for the mitis species group is not significant ($r=-0.198$, $df=11$, $P<0.517$). Home range size of different populations was negatively correlated with population density ($r=-0.741$, $df=12$, $P<0.01$) although the relationship is best described by a curve (Fig. 7.16);

$$\text{Home range area} = e^{4.341-1.09\ \text{population density}}$$

where home range is measured in ha and population density as individuals per ha. Population density is thus a better indicator than troop size of the influence of a number of ecological determinants on the space requirements of different mitis troops. Population density represents the result of the combined effects of food resource availability, competition, disease and predation over the whole population. While a troop's size may be the outcome of only one of the latter parameters and may not be significantly correlated with home range area predictions.

The fact that home range size is significantly negatively related to population density within the mitis species group, and this includes the samango populations who have no arboreal competitors, implies that home range area is determined dominantly by intraspecific interaction within a population as opposed to interspecific competition. Interspecific competition would, however, limit the availability of food which would indirectly lead to home range area/size adjustments within species populations. In conclusion, Cape Vidal samangos are at high densities and have small home ranges because of the relative abundance of food resources, intraspecific competition for space, the lack of primate competitors, low predation rates and a low incidence of disease or accident related deaths.

7.4.2 Correlates of ranging behaviour

The ranging pattern of Cape Vidal samangos is characterised by: (a) long daily range distances (mean = 1217 m), (b) use of a large proportion of the home range during daily

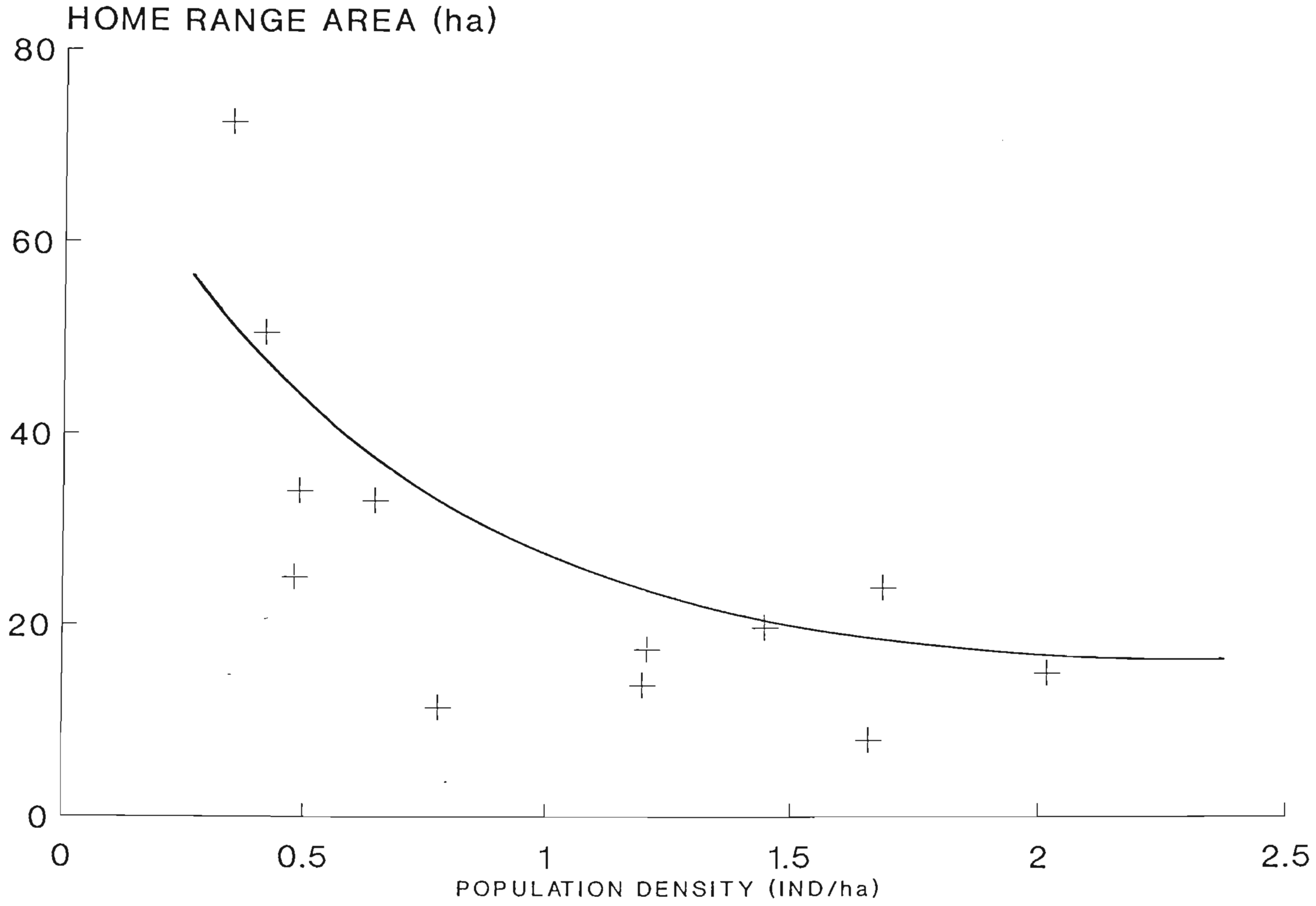


Figure 7.16. The relationship between population density (ind/ha) and troop home range area for the mitis species group (Home range area = $e^{4.341 - 1.09 \text{ population density}}$).

movements, (c) intensive use of at least half the home range over a few days (3 days) during each monthly sample, (d) a more clumped pattern of range use during the summer months (November - March), (e) an annual pattern of range use is largely determined by the amount of time spent resting (passive activity) in quadrats at different time of the year, and (f) considerable home range overlap with other samango troops although the study troop was occasionally observed to actively defend the boundaries of the home range.

Data for mitis indicates some intraspecific variation in overall mean day range lengths. Butynski (1990) gives figures of 1216 m and 1406 m for two different troops 10 km apart in the Kibale forest. Also in the Kibale forest Rudran (1978) gives a mean path length of 1290 m. Cords (1987) records a similar value in the Kakamega forest of 1136 m. There is no significant relationship between these home range sizes and day range lengths for the C. mitis superspecies (r = 0.44, df = 6), however populations with smaller home ranges tend to have shorter day range lengths (Table 7.7). For example, Aldrich-Blake (1970) states "the greatest movement recorded in a day was 1000 yards (914.4 m)" in the Budongo forest where mean home range size was 8 ha. Beeson (1987) cites mean day range lengths of 500 m and 539 m for two troops of 11 and 19 individuals respectively with a mean home range area of 17.5 ha. Schlichte records a distance of 594 m/day within a home range of 25 ha. The Cape Vidal samangos are an exception to this trend, they have a long day range length of 1216 m and a small home range (15 ha).

van Schaik's et al. (1983) work on Macaca fascicularis shows a positive relationship between day range length and troop size in another forest omnivore. It is assumed that animals in larger troops have to expend more energy to obtain food since dispersed food sources are rapidly depleted by a large troop. Although there is no relationship between troop size and day range length for mitis in general (r=0.33, df=8), it is possible that the long day range length at Cape Vidal is a result of the large troop size, small home range size, lower food species diversity and the need to maintain as diverse a diet as possible.

On the whole the East African mitis used a relatively small area of the home range on any day such that these daily ranges were often mutually exclusive and between 25 and 50 percent of the area was used on one day alone in a sample period (Rudran, 1978;

Table 7.7. Mean day range length and day range area for populations of *mitis*.

FOREST	DAY RANGE LENGTH	DAY RANGE AREA	TROOP SIZE	AUTHORS
Budongo	914 m [1]	-	13.5	Aldrich -Blake 1970
Kibale	-	3.5-10.5 ha	20.0	Rudran 1978a
Kibale				
Kanyawara	1216 m	5.25 ha	12.0	
Ngogo	1406 m	6.25 ha	18.5	Butynski 1990
Lake Kivu	594 m	-	12.0	Schlichte 1978
Kakamega	1136 m	12.83 ha	32.6	Cords 1987
Zomba Group 2	500 m			
Group 5	539 m		15.0	Beeson 1987

1. Aldrich-Blake (1970) records day range as "1000 yards"

Schlichte, 1978; Butynski, unpub. data; Cords, 1987). Schlichte (1978) suggests that the latter ranging pattern is partly due to active avoidance of areas used on the previous day, and in this way the troop avoids resampling an area from food has already been taken. Cords (1987) seldom recorded a troop re-entering a quadrat on a day and positively correlated the number of quadrats used with the number of hours the troop spent in association with redtails (*C. ascanius*). Both Schlichte (1978) and Cords (1987) imply that such patterns of movement are intended to expose the troop to as wide a variety of food sources as possible without re-using a food source. Cape Vidal samangos on the other hand frequently recrossed their path route on any one day either in moving toward favoured resting sites or by returning to feed selectively on a food item. This was especially notable where the troop used young leaves. They would use these leaves toward late morning often returning in the evening to feed on them again (e.g. *Acacia karroo*, *Diospyros inhacensis*).

Some *mitis* populations showed a tendency to split into smaller satellite groups of 4-5 individuals during daily movement (Aldrich-Blake, 1970; Moreno-Black and Maples, 1977). McMahon (1977) and van der Zee and Viljoen (1984) recorded that a troop (*C. mitis labiatus*) would sometimes split, however, this behaviour was not noted in the Cape Vidal population. The advantages of such behaviour are presumably to maximize the use of widely dispersed food sources en route.

Although the Cape Vidal samangos did not split one may have expected them to have a relatively wide troop dispersion pattern because of the large troop size. This was not the case, however, and in general there does not appear to be any relationship between troop size and mean troop dispersion (Table 7.8), with small troops showing varied mean dispersion distances (Aldrich-Blake, 1970: 14.5 individuals, +- 137 m dispersion; Rudran, 1978: 20 individuals, 50 m). At Cape Vidal the troop was less dispersed when there was more new leaf available. This was a response in many instances to the concentration of a high protein resource on a single tree. Furthermore, although wide troop dispersion prevented continuous visual contact between troop members, the degree of troop dispersion did not change during the breeding season when vigilance was of greater importance for both male and female. Troop dispersion is therefore unlikely to be a function of troop size alone but is more probably influenced by the social behaviour of the troop, or the patchiness of food dispersal.

Rudran (1978) ascribed differential quadrat use to the temporal variation of food abundance in them and found that blue monkeys ranged less diversely when food was concentrated than when food was more widely distributed. Butynski (1990) found that in areas where food was less available (Kanyawara), the blue monkeys had shorter day ranges and foraged over smaller areas each day. For the Cape Vidal population, using the accumulative area used on three consecutive days in each monthly sample as an indication of monthly range area, no difference in monthly sample range area between

Table 7.8. Troop size and troop dispersion for populations of the C. mitis superspecies.

Subspecies	Mean Troop Dispersion	Troop Size	Author
C. m. labiatus			
	58.2	18.5	Lawes et al., 1990
C. m. erythrarchus			
	80.3	34.0	This study
C. m. stuhlmanni			
	+-137.2	13.5	Aldrich-Blake, 1970
	50.0	20.0	Rudran, 1978
	108.7	45.0	Cords, 1987

summer and winter (t = -0.63, df = 11), or between periods of food availability (t = -0.53, df = 11) was found. Samangos did not use a smaller area of the home range in response to fewer daylight hours or reduced food availability. While they did not use a smaller area of the home range between food seasons the pattern of home range use was more clumped. This implies a more selective use of food patches and resting sites as food availability began to decline. The small size of the home range with its clearly delimited array of available resources at any one time does, however, ensure that while the monkeys might clump their activity in certain areas they still need to cover a large proportion of the small home range each month to obtain sufficient food or sufficient variety.

The gross pattern of home range use in terms of time spent in different quadrats, is determined largely by the resting behaviour of the troop. Patterns of resting range use are more clumped, and the proportion of time spent resting by the troop increases (Chapter 5) during the summer months. This is particularly interesting because food (fruit) availability declines during these months. If the monkeys were food-stressed, one would expect feeding time to increase and resting time to decrease (and therefore resting range use patterns to be less clumped) as food became less available. Clearly, in this instance the samangos increase their resting time during summer not because they have to (i.e. because they are thermally stressed) but rather because they are not food stressed even when food availability drops, and there is more time available for resting during summer months since daylight length is longer. Daylight length is almost 4 hours shorter in the middle of winter than in the middle of summer. The fact that patterns of range use defined by resting behaviour are considerably less clumped in winter is thus a function of the shorter daylength, when there is less time available for resting even though food is abundant. Patterns of range use defined by feeding and foraging activities achieve a relatively greater degree of importance during winter although indices of clumping are still slightly greater for resting activities. This is not to say that ranging patterns related to feeding and foraging behaviour are entirely of secondary importance to those defined by resting behaviour but serves to emphasize the fact that patterns of range use are based on more than just feeding behaviour alone. The movement of the troop about the home range specifically in response to the variation in food distribution and abundance is discussed in the next chapter.

CHAPTER 8: FEEDING AND FORAGING BEHAVIOUR

8.1. INTRODUCTION

Why should the samango monkey, one of many dietary generalists among the guenons, be the only arboreal guenon in southern Africa? This is the fundamental issue of this thesis. Standard theory proposes that climatic seasonality, and the associated seasonal control of food availability, provide seasonal shortfalls in food availability (Leighton and Leighton 1983, Oates 1987), such that, southern African forests cannot support a large variety of arboreal frugivores, and, certainly no more than one guenon species (Lawes et al. 1990). Lower forest plant biomass per unit area at southern latitudes provides additional support for this argument. While the overall abundance and variation in availability of food may account for the presence of only one arboreal guenon species, it does not explain why C. mitis alone radiated into southern Africa. To investigate this we need to understand what is common to the foraging strategies of C. mitis populations in widely differing habitats. Here I re-examine the seasonality of food production and its consequences for diet acquisition by the Cape Vidal samango, and compare the findings to both C. mitis and other guenons from other study sites.

Many studies have demonstrated relationships between seasonal differences in feeding/ranging behaviour and seasonal variation in food availability and food distribution for primates in general (Clutton-Brock 1975b, Chivers 1974, Dunbar 1977, Richard 1978, Terborgh 1983, Caldecott 1986) and guenons specifically (Struhsaker 1978, Rudran 1978a, Kavanagh 1978, Gautier-Hion 1980, Gautier-Hion et al. 1981, Harrison 1984, Cords 1986, Butynski 1990). Oates (1986) states that species relying heavily on foliage tend to decrease their level of activity at times of the year when high-quality food is scarce, while species that rely heavily on fruits or insects (guenons) increase the amount of time spent looking for and processing food. Gautier-Hion (1988) in her review of guenon diet and dietary habits, described guenons as selective rangers. She showed that the ability of guenons to maintain optimal or near-optimal diets depended on an excellent knowledge of the timing and distribution of fruit production about their home ranges. No single strategy, however, could describe the seasonal foraging behaviour of all guenons.

At Ngoye forest I showed that greater climatic seasonality and lower plant diversity at southern latitudes combined to produce marked seasonality of food resources (Lawes et al. 1990). Using a limited data set I developed a hypothesis to show that the samangos at Ngoye had feeding strategies that were contingent on the availability of food in a season (Lawes et al. 1990). The basic tenet of my feeding strategy hypothesis stemmed from the theory of optimal diet. Data from the Ngoye population showed that when food was abundant, the troop fed selectively, choosing items on the basis of availability and energy content so as to yield the best 'profit'. However, when food was less abundant, and fruit was in all likelihood a limiting resource, the monkeys were much less selective and used food items in proportion to their availability. It was my intention to investigate these apparent feeding strategies at Cape Vidal. Here a habituated samango troop provided more detailed information not only on feeding behaviour but also on the foraging behaviour of the samango, and further insight to the versatility of mitis feeding behaviour.

Evidence provided in this chapter confirms an early conviction that samango monkeys at Cape Vidal, unlike those at Ngoye, are not food limited. The monkeys were able to make considerable use of fruit year-round. Where dietary shifts are noted, these are largely due to temporary shortages of protein-rich food items, like insects and young leaves. Unlike equatorial forests there is not a readily available year-round abundance of insects at Cape Vidal. Samangos obtain their protein mainly from leaves. While this may be physiologically more difficult than obtaining protein from insects, the abundance of suitable and available leaf items does not cause any additional food stress for the samango at Cape Vidal.

In the absence of any serious food limitations or major frugivore competitors, the feeding ecology of samango monkeys at Cape Vidal raises three interesting possibilities. First, the Cape Vidal samangos represent a C. mitis population which is largely free to make preferred food choices. Therefore, these samangos provide a natural experiment, although under conditions of low insect abundance, in which intrinsic food choices characteristic of the mitis species group can be identified. Second, the ability of the mitis species group to use large quantities of leaves (cf. Beeson 1989) with no apparent decline in fitness (samangos at Cape Vidal possess the highest density of any *mitis* population), must clearly be responsible for their successful southward radiation. Third, despite some seasonal variation in food abundance and availability, samangos at Cape Vidal are highly successful. This brings into question the relative importance of food seasonality *per se* (seasonality with respect to temporal fluctuations in food biomass only) as a hypothetical mechanism limiting primate distribution and abundance. The importance of food diversity and the extent of competition for food resources may, in fact, be more important.

8.2 METHODS

This account covers a number of data sets already discussed and the reader is referred to the methods sections of the relevant chapters: food availability and food quality, diet, and ranging behaviour. One method not yet discussed, is concerned with determining the relationship between the spatial and temporal distribution of food across the home range and the foraging behaviour of the troop.

In addition to the actual availability of specific food items on a tree, the use of food plants by monkeys may be affected by differences in the densities of food trees and their canopy size. The food availability index (FAI) summarizes these parameters. A food selection ratio (FSR) was calculated from the frequency of use of a food species divided by the fruit FAI of that species (since fruit was the most important nutritional item in the diet).

$$\text{FSR} = \frac{\text{Freq. use of food item during a sample}}{(\text{FAI of food item during sample} \times 100)}$$

FSR's were calculated for each of the top ranking food species for which FAI's were available (11 species). These species contributed 61% (n=3066) to the observed diet. No FAI was scored in the field for 3 important species in the diet, *Isoglossa woodii* (n=719), *Grewia occidentalis* (n=434) and *Strychnos madagascariensis* (n=146). With the inclusion of these three species 86% of the observed diet would have been accounted for. The measurement of the density and canopy size for the former two species was impractical since I. woodii is a widespread herb that covered 60-70% of the ground while G. occidentalis is a thicket species and also difficult to assess in a comparable manner to the tree species. FAI values for the latter two species were "guesstimated" retrospectively at the end of each sample period on the basis of (a) their abundance in the study area, and (b) my intuitive feeling as to their relative importance as food species on a monthly basis. In the case of S. madagascariensis, the relative importance of the species as a food plant was not recognized until it was too late to include it in phenological assessments. I did not estimate FAI's for this species and it is excluded from analyses.

The food available in each of the demarcated 50x50 m quadrats of the home range (used by the troop during a monthly observation period) was recorded three times over the study period (December 1986, March 1987, June 1987). For the other months of the study period I adopted Gautier-Hion's (1981) approach and selected 6 quadrats from among those used by the troop in that month. Two quadrats were selected among the least used, two among the most used, and two others were intermediate. In all cases, the number and phenological state of all tree species in fruit, flowering or with a prominent new leaf flush, were recorded for each quadrat. These sampling procedures were chosen to test the hypothesis that time spent in one quadrat is related to food item availability and/or quality in the same quadrat.

8.3 RESULTS

Here I examine the temporal and spatial changes in food supply and quality and their relation to food selection by the monkeys. It should be remembered that there are difficulties in interpreting the quality of a food item. For instance protein values measured as crude protein may not faithfully represent the amount of protein **available** or **extractable** by the monkey. Food items may be apparently nutritious, but the presence of plant secondary compounds can confound the measured values. Thus the level of "noise" is high when considering the biological significance of proximate analyses. Without sophisticated biochemical analysis whereby the "extractability" of the nutrients required by the primate are determined for each specific item, the real significance of the proximate food values determined in this study remain hidden. Thus, if relationships between use of a food item and its quality are expected but not found, this does not necessarily mean that such a relationship is invalid. I would suggest that in many instances one's intuitive feelings about relationships between the quality of an item and other feeding correlates (i.e. frequency of use and time of use) should be respected. I have frequently argued such cases in the absence of specific corroborative data, in the hope that the salient biological interpretations are at least expressed.

8.3.1 FOOD AVAILABILITY, FOOD QUALITY AND TEMPORAL VARIATION IN THE DIET AND FEEDING

8.3.1.1. Food selection ratios

The selection ratios (Table 8.1) show that the frequency of use of food species was affected by their density and canopy size. For example, the frequent use of Mimusops caffra was apparently due to its very high density in the home range. Another example of the latter is the high frequency of use (n=719) of the widely dispersed herb Isoglossa woodii. The selection ratios also show that there were less abundant species more preferred than M. caffra. Dovyalis longispina was the most preferred food species. Both Scolopia zeyheri and Celtis africana were also more preferred than indicated by their frequency of use.

From the above it is evident that many food species were not selected on the basis of their abundance alone. Food selection ratios for the specific item in the diet by month (Appendix 8.1) (where the denominator of the ratio is the FAI of the specific food item for that month) show that the monkeys were more selective of specific food items from July to October 1986, and April 1987 (Table 8.2). This coincides with the months of greatest fruit availability and suggests a seasonal shift in feeding strategy.

Table 8.1. Selection ratios of the food plants most used during the study period.

Species	Frequency of use	Density / ha	Canopy volume	FAI	Selection ratio I	Selection ratio II
I. woodii[1]	719	-	-	25.00	-	0.29
M. caffra	702	59.45	550.04	27.98	0.21	0.25
A. karroo	638	36.25	84.65	4.25	2.08	1.50
G. occidentalis [1]	434	-	-	18.00	-	0.24
D. natalensis	332	21.75	131.23	4.13	1.16	0.80
D. inhacensis	294	21.75	176.97	4.14	0.76	0.71
S. zeyheri	270	7.25	332.50	1.33	1.12	2.03
D. longispina	227	4.35	216.85	0.74	2.41	3.07
O. capensis	168	21.75	217.11	0.67	0.36	0.67
S. madagascariensis	146	8.70	304.50		0.55	
A. dimidiata	122	10.15	304.47	1.23	0.39	0.98
C. africana	118	7.25	281.48	0.91	0.58	1.30
S. inerme	116	24.65	399.35	7.41	0.12	0.16
Z. mucronata	79	10.15	288.60	0.90	0.27	0.87

Selection ratio I = (Freq. use / (density x canopy volume)) x 10 (see Rudran 1978).
Selection ratio II = Freq. use / (FAI x 100)

[1] FAI values were guesstimated in the field for these species (see text).

Table 8.2. The mean food selection ratio (FSR) and coefficient of variation for all months of the study period.

	J	A	S	O	N	D	J	F	M	A	M	J	J
Mean FSR	40.7	10.4	24.9	2.3	2.5	0.8	4.2	2.1	1.4	8.2	2.1	3.5	10.6
s	96.5	25.2	47.6	6.6	4.8	0.7	8.9	3.0	2.3	23.9	2.8	4.1	24.4
V	237	243	191	287	192	106	212	143	162	291	133	117	230
	█	█	█	█	▒	▒	▒	▒	█	█	█	▒	▒

█ Fruit abundant ▒ Fruit less abundant

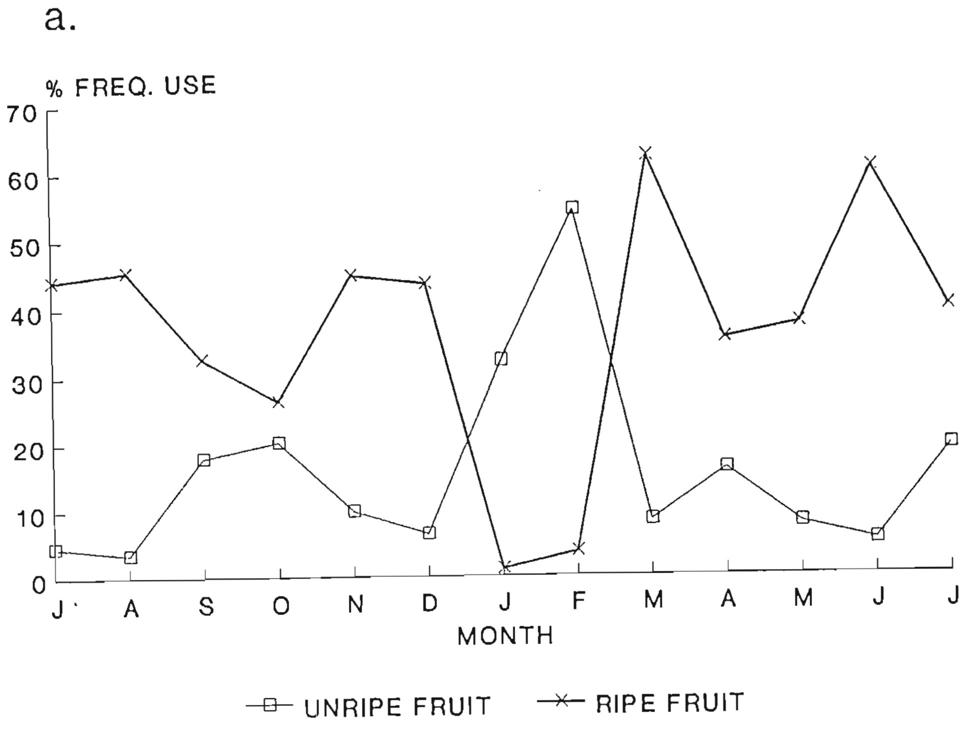
8.3.1.2 Seasonal variation in the diet

a. Fruit

Food availability varied between rainfall seasons and fruit was the most available item in the latter part of the dry season (i.e. late winter). In the dry season ripe fruit was eaten consistently more frequently than unripe fruit. During the wet season, when fruit was less available, considerably more unripe fruit was eaten and, in some of these months (e.g. January 1987, February 1987), unripe fruit was used almost exclusively (Fig. 8.1a). It is clear that ripe fruit was preferred over unripe fruit but when fruit became less available the monkeys shifted the diet towards unripe fruits. There was a strong negative correlation between the use of ripe and unripe fruit by the troop ($r=-0.86$, $df=12$, $P<0.001$). Fruit was the most important dietary item in both seasons.

There was no seasonal correlation between the frequency of use of specific fruit items and their FAI (Table 8.3; Spearman rank correlations). More important is the absence of a correlation between the frequency of use of a food item, and its availability, during months when fruit was less available (Table 8.3). To expect a positive correlation between use and availability, when fruit is least abundant, one must assume that the monkeys are fruit-stressed. The lack of correlation suggests that the monkeys were not. Even when food was least plentiful, it was never so scarce as to prevent a certain degree of selectivity of food items.

Furthermore, the frequency of use of the top-ranked specific fruit items, when fruit was least available, was not correlated to the nutritional content of the food items (energy, protein or fat content). In two months (March 1987, May 1987) of comparative food abundance the mean selection ratios dropped to their lowest levels, and the use of fruit items showed a strong trend towards a positive correlation with the fibre content of the item (in both months $df=8$, $r_s=0.63$, $P<0.09$). This is in contrast to other months where correlation values were mostly negative. From this it can be inferred that at times the monkeys were unable to routinely avoid eating certain unpalatable (i.e. fibre rich) fruit items.



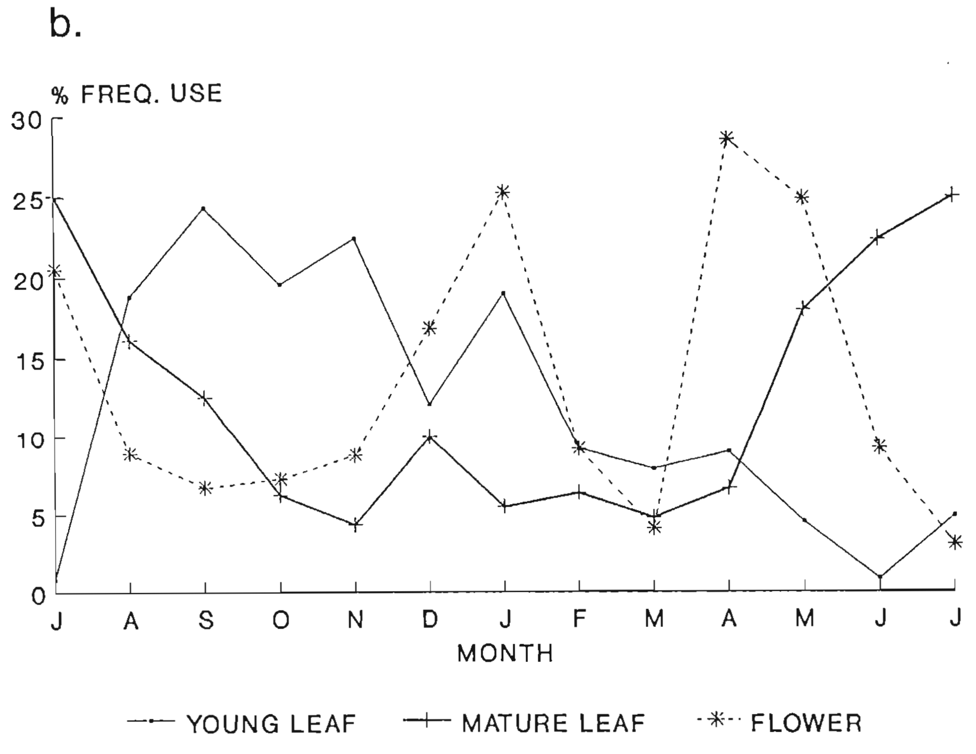


Figure 8.1. Monthly percent frequency of use of plant food items by the troop. (a) unripe and ripe fruit, (b) young and mature leaf, and flowers.

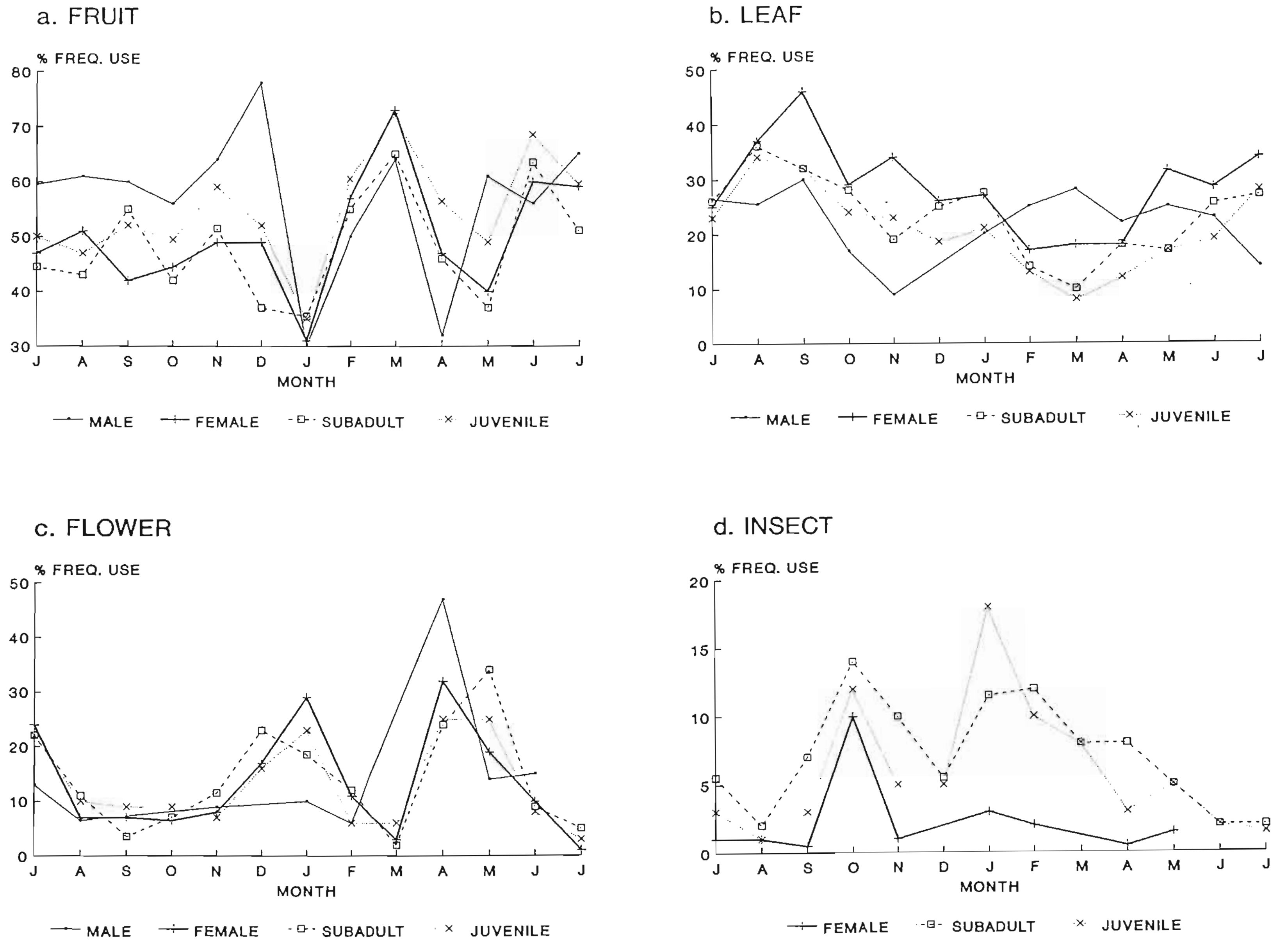
Table 8.3. Spearman rank correlation of the frequency of use of the top ranked fruit items in a month against the availability of those items.

	J	A	S	O	N	D	J	F	M	A	M	J	J
r_s	0.12	0.89	0.47	0.71	0.46	0.92	-0.1	0.38	0.06	0.57	0.81	0.57	0.75
n	6	7	10	7	5	8	11	8	8	8	8	7	7
P	0.79	**0.03**	0.16	**0.08**	0.36	**0.02**	0.75	0.31	0.87	0.13	**0.04**	0.16	**0.06**
	■	■	■	■	▒	▒	▒	▒	■	■	■	▒	▒

■ Fruit abundant ▒ Fruit less abundant

The percent frequency of use of fruit each month (regardless of fruit phytophase sub-category), was similar for all age-sex classes, except the adult male (Fig 8.2a). The male showed a sharp peak in the frequency of use of fruit during December 1986. This peak in use of fruit by males is important since it coincides with (a) a decrease in the use of fruit by other age-sex classes, (b) a decline in the observed frequency of feeding activity by the male, (c) low fruit abundance levels and (d) the end of the period of fruit abundance. This suggests that as the period of fruit abundance draws to a close the adult male is able to maintain priority of access to fruit resources and does so as long as possible. By January 1987, all age-sex classes had reduced their frequency of use of fruit considerably, in accordance with the decline in fruit availability. This month must be considered the fruit "crunch" period.

Of all the age-sex classes, only the male's frequency of feeding activity showed signs of following fruit availability ($r=0.461$, $df=12$, $P<0.11$). The monthly proportion of feeding activity by the adult male would be expected to be correlated most to the availability of fruit, since the diet of the male is dominated by fruit. Excluding the months immediately prior to and including the mating season (April to July), feeding activity of the male was significantly correlated with fruit availability ($r=0.714$, $df=8$, $P<0.03$). The time spent feeding by the male increased from 10.3% in January to 36.4% in April (the start of breeding) and then declined to 22.5%. Fruit availability was comparatively low over this period but lowest in January. These results suggest two possibilities for male feeding strategy: (a) for most of the year the male optimizes/maximizes his feeding effort by apportioning his use of fruit in relation to fruit availability (in this scenario the male therefore cannot be fruit stressed during this time), or, (b) in anticipation of the oncoming


a. FRUIT

b. LEAF

c. FLOWER

d. INSECT

Figure 8.2. The age-sex class differences in the percent frequency of use of food items over the study period.

mating period, and the strong probability that a concomitant increase in vigilance will reduce available feeding time, the male increases his feeding time (inverse relationship between feeding time and fruit availability) so as to improve his physical condition in preparedness. The latter is not unheard of in primates and sexually- active male squirrel monkeys deposit extensive fat reserves prior to the mating season (DuMond and Hutchinson 1967)

b. Leaf

Leaf buds and new leaves, especially during the dry season, were not always available. Mature leaves were eaten more than young leaves for this reason. However a strong negative correlation between the use of mature leaves and the availability of young leaves ($r=-0.66$, $df=12$, $P<0.02$) shows that mature leaves were only eaten when young leaves were not as available. Thus, in the wet season, especially from September 1986 through January 1987, a shift towards the use of leaf buds and young leaves is noted in accordance with increased abundance ($r=0.55$, $df=12$, $P<0.05$), although leaves in general were less frequently eaten during these months (Fig 8.1b).

When young leaves were most available, the specific leaf items most eaten by the troop in a month for the months of October 1986 through January 1987, were also the most abundant leaf items (Table 8.4). However, when young leaves were less available, the use of specific leaf items (including mature and new leaf) by the troop correlated closely with the protein content of those specific items (August 1986 through October 1986, and January 1987 through April 1987; Table 8.5).

Although all age-sex classes showed a peak in the use of young leaf from August 1986 through November 1986 (Fig. 8.2b), the adult female class showed a greater frequency of use of leaves for the months of May through to November than any other class. This period coincided with the timing of the gestation period when the demand for protein (from leaves) was steadily increasing in pregnant females. Significantly, by the end of October when parturition was complete and protein demands of lactation were at their greatest (Hanwell and Peaker 1977), a dramatic increase in the amount of available young leaf took place. A shift in female use of leaf, from mature to the more easily

Table 8.4. Spearman rank correlation of the frequency of use of the top ranked leaf items in a month against the availability of those items.

	J	A	S	O	N	D	J	F	M	A	M	J	J
r_s	-0.6	0.51	-0.02	0.8	0.47	0.65	0.7	0.48	0.33	0.87	0.48	-0.2	0.21
n	4	8	8	9	10	9	8	7	6	9	8	4	9
P	0.27	0.18	0.94	**0.03**	0.16	**0.06**	**0.06**	0.23	0.46	**0.02**	0.21	0.73	0.54
	▨	▨	▨	█	█	█	█	▨	▨	█	█	▨	▨

█ Young leaf abundant ▨ Young leaf scarce

Table 8.5. Spearman rank correlation of the frequency of use of the top ranked leaf items in a month against the protein content of those items.

	J	A	S	O	N	D	J	F	M	A	M	J	J
rs	0.21	0.75	0.71	0.74	0.11	0.30	0.68	0.84	0.82	0.59	0.17	0.40	0.56
n	4	8	8	9	10	9	8	7	6	9	8	4	9
P	0.72	**0.05**	**0.06**	**0.04**	0.73	0.39	**0.07**	**0.04**	**0.07**	**0.09**	0.65	0.48	0.12
	▨	▨	▨	█	█	█	█	▨	▨	█	█	▨	▨
		▒	▒	▒	▒	▦	▦	▦	▦				

█ Young leaf abundant ▨ Young leaf scarce

▒ Gestation period ▦ Lactation period

digestible and protein rich young leaves, was observed at this time and the percent proportion of young leaf in the monthly diet of females was significantly correlated to its availability over the study period ($r=0.69$, $df=12$, $P<0.01$; cf. Gautier-Hion 1980). The timing of these events permitted lactating females, for whom protein demands were greatest, access to a more abundant protein rich resource.

Although the use of a leaf item by females and its protein content only approached significance during the 'breeding' season (all cases Spearman ranked correlations $P<0.13$ in breeding season, as opposed to $0.16>P<0.80$ in other months), females did eat more leaf than the other age-sex classes during this period, implying that their protein requirements were greater than other age-sex classes.

Of all the age-sex classes only the adult male's use of new leaves was not significantly correlated to its availability (male: r=-0.057, df=12, P<0.85; female: r=0.69, df=12, P<0.01, subadult: r=0.61, df=12, P<0.03; Juvenile: r=0.55, df=12, P<0.05), and the male used fewer leaf items in the diet than other age-sex classes. Unlike the other age-sex classes, the adult male does not require as proportionally large amounts of protein for either reproduction (cf. females) or growth (cf. juveniles) and, therefore eats less leaf.

c. Flowers

Flowers were most abundant and were eaten frequently during the wet season. However, despite a much lower availability of flowers during the early part of the dry season, flowers were also heavily used during July 1986, April 1987 and May 1987. As a result, the use of flowers by the troop was not correlated with availability (r=0.19, df=12, P>0.53). The high frequency of use of flowers in the dry season resulted from the use of the flowers of a single species in those months, and was most probably due to both the absence of an alternative abundant protein source and the ready availability of flowers from those species. Although insects, a good protein source, were available at this time their use in the diet was largely confined to the immature monkey age classes (see below). In July 1986 the use of Scolopia zeyheri flowers contributed 21% to the diet, and the use of the abundant Mimusops caffra flowers during April 1987 and Isoglossa woodii flowers during May 1987 contributed 25% and 41% to the diet respectively. In contrast, fewer flowers were eaten (<15% of diet) from a wider number of species with a more even division of usage in other months.

This use of flowers illustrates the ability of the monkeys to respond dynamically to changes in food availability and nutrition within the home range. This is all the more interesting when one considers that I. woodii is a sufrutescent that flowers every 6-7 years, meaning that the monkeys have to recognize the value of this food source after a long period of disassociation from the food item.

There was little difference between age-sex classes in the use of floral items (Fig 8.2c), although the male showed a considerable increase in the use of flowers during April 1987.

A highly significant negative correlation between the proportions of fruit and flowers in the diet was noted for all age-sex classes (male $r=-0.642$, $P<0.02$; female $r=-0.605$, $P<0.03$; subadult $r=-0.695$, $P<0.01$; juvenile $r=-0.675$, $P<0.01$; all $df=12$). Further, a significant inverse relationship existed between the availability of fruit and flowers ($r=-0.591$, $df=12$, $P<0.04$). As the precursor phytophase to fruit, flowers were available at a time when fruit was generally not. Thus, the dietary relationship between fruit and flowers is an artifact of phytophase succession, and is not solely due to the selective feeding habits of the monkeys.

d. Insects

Insects were the most seasonally variable of all food types, being abundantly available only during the wet season. It is no surprise to find that the use of insects is almost entirely confined to this time of the year (Fig. 8.2d), although the monthly correlation of availability on use of insects is not significant ($r=0.55$, $df=8$, $P<0.12$). Like their feeding response to the flowers of certain species, the monkeys also showed a prompt response to the presence of a concentration of caterpillars in the Acacia karroo stand during October 1986. The use of insects in this month comprised 14.5% of the diet.

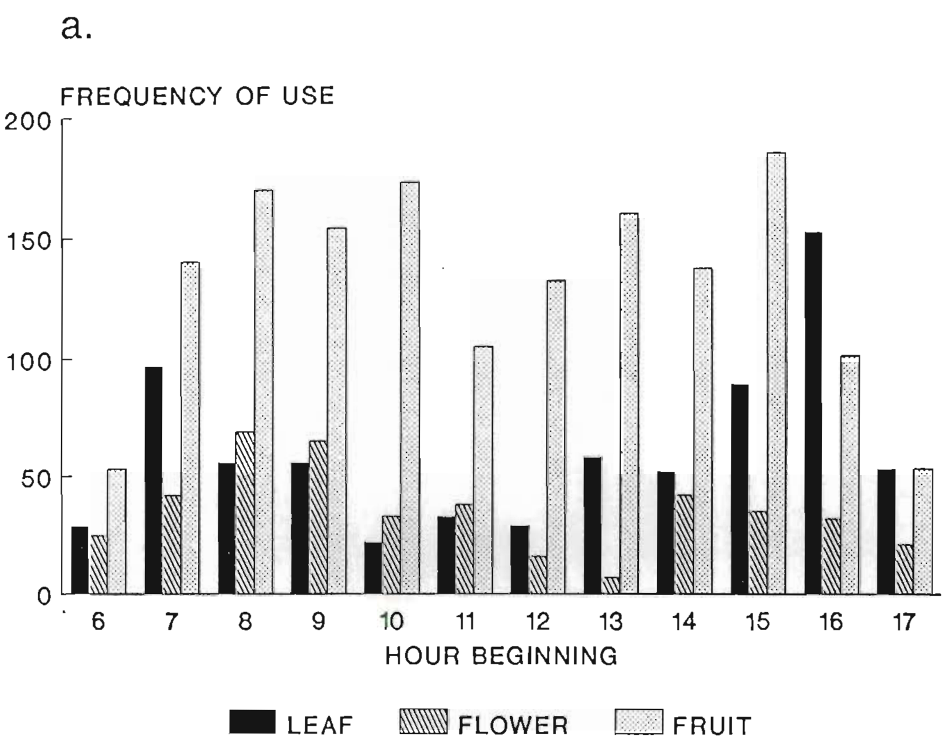
Since insects were only seasonally available and insufficiently abundant to permit all-year- round use as an alternative protein source, only those age-sex classes of small body size (juveniles) could afford to seek out insects throughout the year, and reap nutritional benefits despite the energy cost of prey capture. In a habitat where insects are generally not abundant, for a larger monkey age-sex class, an insect does not provide sufficient nutritional return for the effort of capture and the cost of time that could be spent eating something else. This explains why females only used insects when they were abundant, and why the males seldom ate insects. It is a general rule that small primates tend to have a large proportion of insect in the diet (Gaulin 1979, Richard 1985, Gautier-Hion 1988). Cords (1986a) data, from another mitis population, supports my suggestion that the use of insects is more favoured by smaller age-sex classes. It was, therefore, not surprising to find that only the small immature age classes showed an increase in the use of invertebrates when the proportion of fruit in the diet decreased (albeit not significantly correlated cf. Fig. 8.2a and 8.2d) at Cape Vidal. Juveniles, and to a lesser extent subadults, managed to use insects year-round (Fig. 8.2d).

8.3.1.3. Diurnal variation in the diet

The food requirements of a typical day may provide a good insight into the reasons for the partitioning of the gross diet among the different food item categories. For instance, it may well be that the gross diet is fundamentally a result of the daily response to specific short-term energy and nutrient demands built up during the night resting period. To determine whether the monkeys sequenced the ingestion of items during the day, the frequency of use of food items in each hour of the day was examined.

A bimodal peak in a day's use of all food item types, whether they were plant (Fig. 8.3) or invertebrate items (Fig. 8.4), was evident. The peaks in use of items were concentrated in the early-morning and late-evening. There were no major deviations in the diurnal use, or sequence of use of items between seasons, except for a slight temporal shift in the peaks in accordance with the number of daylight hours. More fruits than leaves were eaten in the early morning but this trend tended to be reversed in the evening during both seasons. In the mid-afternoon the frequency of use of fruit exceeded that of leaves, however, in the last hour before sunset the monkeys concentrated their feeding effort on leaf items. The monkeys use of leaves showed the greatest hourly variation (summer V=65.7%; winter V=60.86%) in the use of a plant item category during a daily cycle in both seasons. Fruit showed the least variation in use throughout the day (summer V=39.9%; winter V=33.9%), but, the highest frequency of use in each hour except late evening. This further emphasizes the importance of fruit in the diet of the samango.

Given the opportunistic manner in which insects were sought out, their use could be expected to follow the diurnal feeding pattern in both seasons. Thus in winter, when insect abundance was low, the frequency of use of insects was concentrated during the peak feeding periods of the day when the animals were known to be actively searching for food (Fig. 8.4a); the coefficient of variation in the use of insects is relatively high (V=67.1%). There was less variation in the use of invertebrates during the day in summer (V=52.4%), presumably because insects were more abundant and easier to find (Figure 8.4).



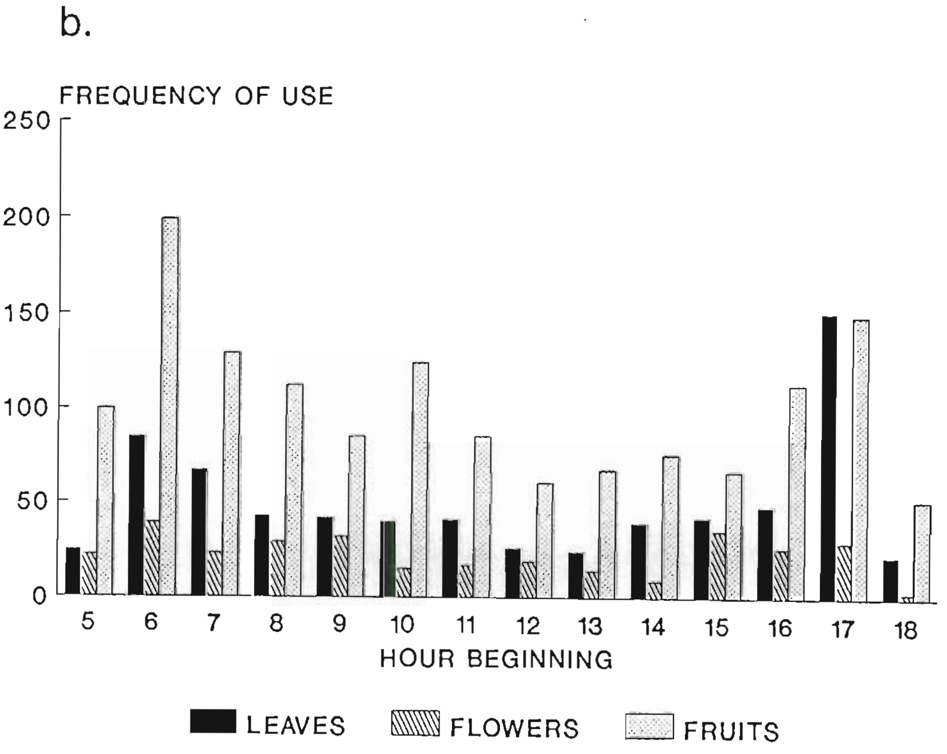
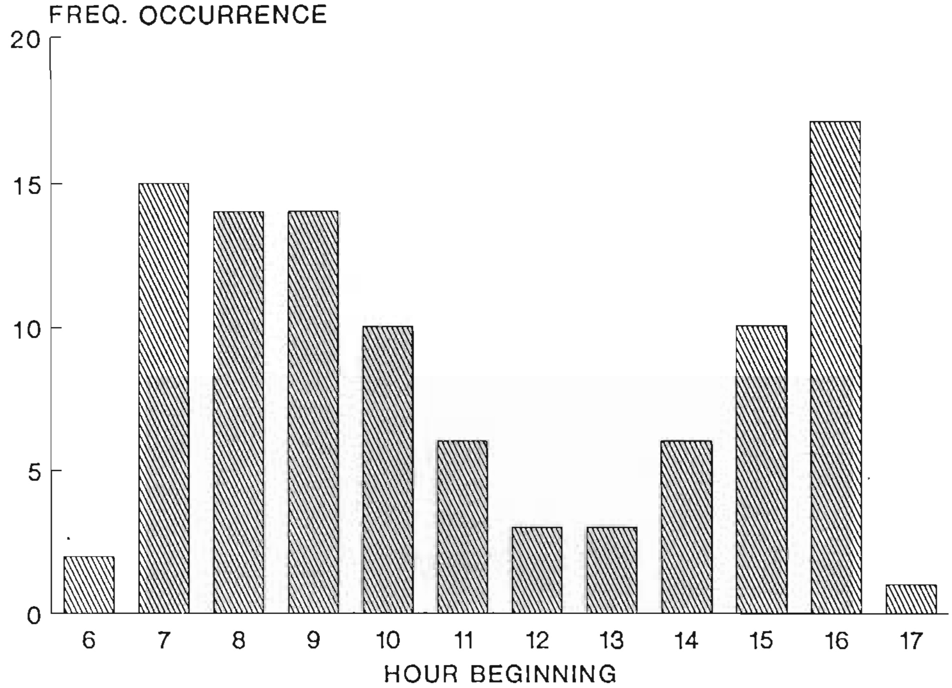


Figure 8.3. Diurnal hourly frequency of use of plant food items in (a) winter: Jul-Aug 1986, Apr-July 1987, and (b) summer: Sep 1986-Mar 1987.

a.



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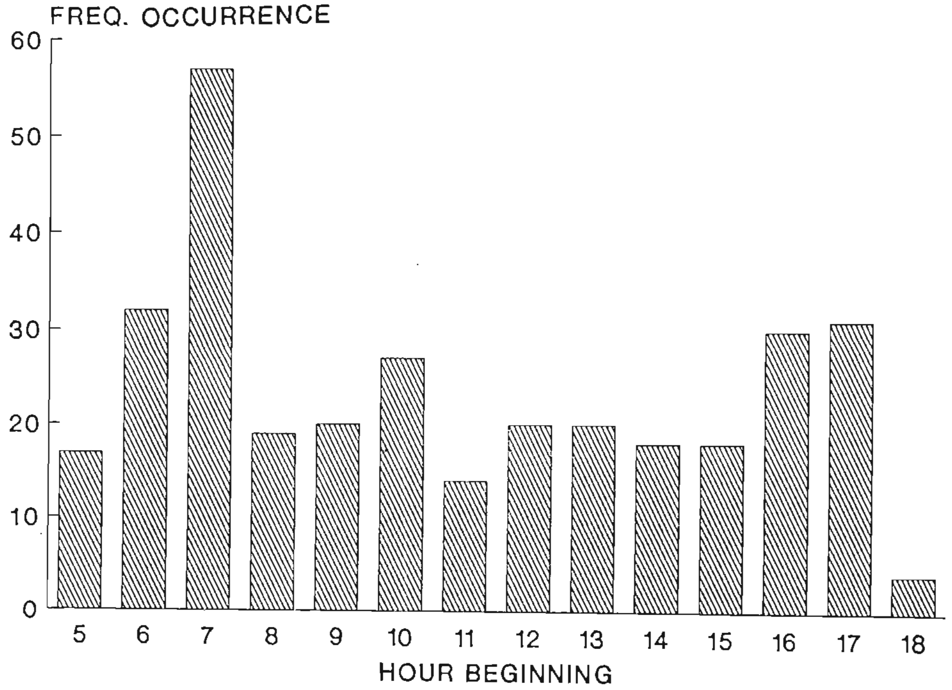


Figure 8.4. Diurnal hourly frequency of occurrence of troop foraging activity for insects in (a) winter: Jul-Aug 1986, Apr-July 1987, and (b) summer: Sep 1986-Mar 1987.

8.3.1.4. Food availability and social structure

There was a significant correlation between mean inter-individual distances (for all feeding focal age-sex classes combined) and fruit availability by month (Fig. 8.5, r=0.664, df=12, P<0.01). The same correlation with leaf (r=0.089, df=12, P<0.8) and flower (r=0.007, df=12, P<0.9) items was not significant. This supports the hypothesis that fruit may have been the most contested food item, and thus the availability of fruit segregates the food seasons.

As food availability and the choice of food patches declines, the age-sex classes were presumably forced into closer association in order to feed on the reduced fruit resources. Although inter-individual distance exhibits a positive linear relationship with food availability, even when food is at its least abundant, inter-individual distances are still longer for feeding animals than for non-feeding animals (Fig. 8.6).

8.3.1.5. Food availability and feeding activity

In general, for all age-sex classes, feeding activity increased slightly when fruit was abundant. More important was the effect on feeding activity of seasonal reduction in the availability and diversity of protein-rich food sources. For example, females did not alter their proportion of feeding activity relative to the availability of fruit (r=0.302, df=12, P<0.15), but did show a trend towards an increase in feeding effort when availability of new leaf declined (r=-0.549, df=12, P<0.06). In the same way, the adult male showed an increase in feeding activity as the availability of new leaf declined (r=-0.639, df=12, P<0.01), and there was a significant correlation between the proportion of male feeding activity and fruit availability for those months outside of the 3 month mating season (r=0.714, df=12, P<0.03). Notwithstanding the above correlations, the actual differences in the proportional duration of feeding activity between the seasons of food abundance were not significant (percentages in range 30%-70%, therefore no arcsine transformation of data required; see Alder and Roessler (1977, p347)) either for males (t=2.18, df=11) or females (t=0.79, df=11).

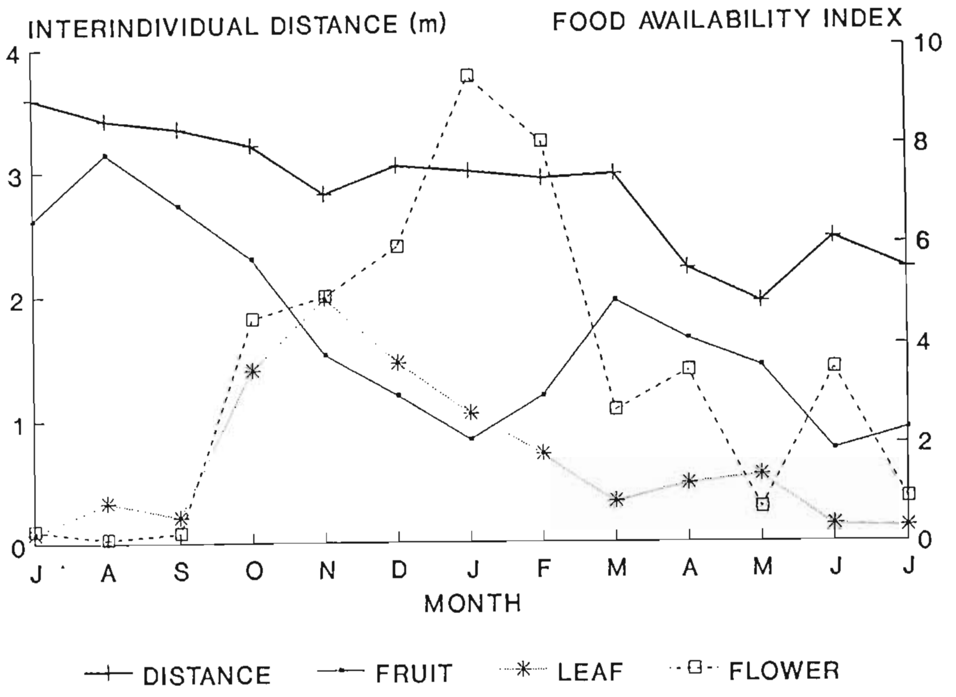


Figure 8.5. The relationship between mean monthly interindividual distance and food item availability over the study period.

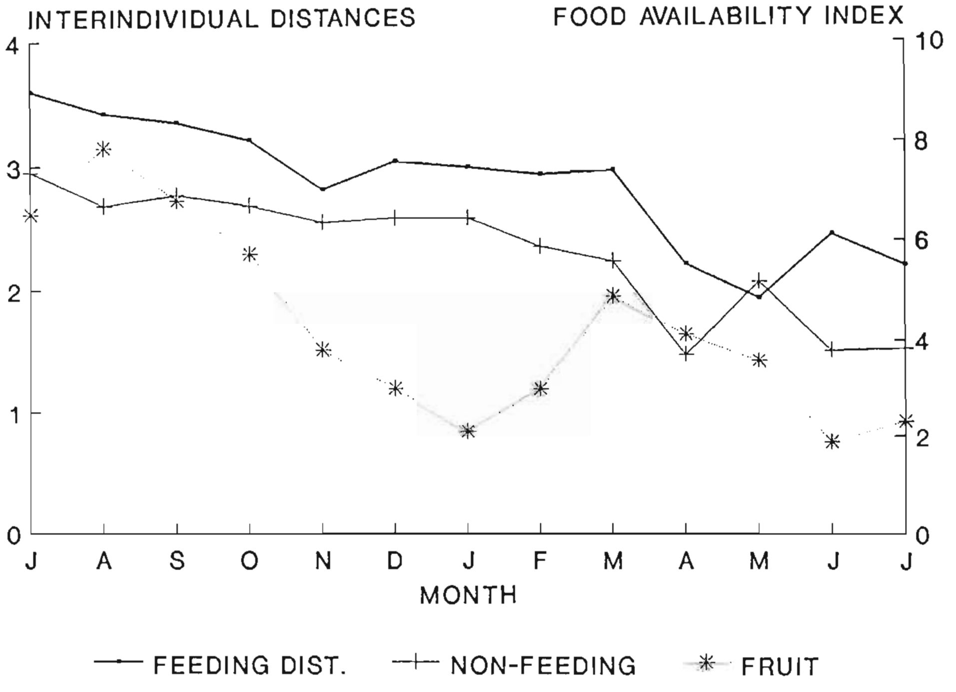


Figure 8.6. The relationship between mean monthly interindividual distances during feeding and non-feeding activity, and the availability of fruit.

Although the availability of new leaf and fruit were not correlated over the study period ($r=-0.21$, $df=12$, $P>0.5$), new leaf was least available when fruit was most abundant. Consequently, the significant negative correlation between new leaf availability and feeding activity by the adult age classes, may suggest that although feeding effort increases at a time when fruit is more available, feeding activity is more likely to be increasing as a consequence of the greater feeding effort required to compensate for the deficit in protein- rich leaves.

While the troop does not increase feeding time in winter, ($t=1.43$, $df=11$) it has to spend less time resting ($t=-3.78$, $df=11$, $p<0.01$) to accommodate shorter daylength. From this it appears that the monkeys expend no more energy in obtaining their food in winter than they do in summer.

8.3.2. FOOD AVAILABILITY AND USE OF SPACE

In Chapter 7 (Use of the home range), I showed that the gross pattern of use of the home range by the troop, measured in terms of the time spent in a grid, was strongly correlated to the resting behaviour of the troop. Here I am concerned with those patterns of range use that relate directly to feeding behaviour. Therefore, I will discuss range use indices, day range length, and rates of movement again, but specifically with the aim of elucidating patterns of feeding behaviour. (The methods and data from which these analyses are taken are reviewed in Chapter 7).

Range-use while feeding was more dispersed when fruit was abundant ($r_s=-0.44$, $df=12$, $P<0.13$), but became more clumped as the proportion of unripe fruit in the diet, and the availability of flowers in the home range, increased (Table 8.6). There was, however, no significant relationship between range use pattern and either the availability of young leaf, or, the use of young leaf in the diet. Range use patterns did, however, appear to become more dispersed as the proportion of leaf in the diet increased ($r_s=-0.506$, $df=12$, $P<0.08$).

The mean number of visits to quadrats was strongly correlated with the use of leaves in the diet ($r_s=0.633$, $df=12$, $P<0.03$), but not to the availability of young leaves over the

Table 8.6. Spearman rank correlations between feeding range use pattern over the study period (n=13 months), the availability of food items in the home range and the use of food items in the diet by the troop.

CORRELATES	Range use index	Mean No. visits/quadrat
Availability of item		
Fruit	-0.440	0.785***
Flower	0.577*	-0.730***
Leaf	0.244	-0.386
Proportional use of item		
All fruit	0.372	-0.046
Unripe fruit	0.569*	-0.319
Ripe fruit	-0.331	0.267
All leaf	-0.506	0.633**
Young leaf	0.180	0.218
Mature leaf	-0.402	0.309
Flowers	-0.118	-0.546

* P<0.05 ** P<0.02 *** P<0.01

study period. In addition, the mean number of visits to a quadrat in a month was also positively correlated to the availability of fruit, and inversely correlated to the availability of flowers (Table 8.6). These data show that a quadrat might be visited more frequently when fruit was abundant, or when the proportion of leaf in the diet increases (and the feeding range use pattern was more dispersed). It is argued that the monkeys range more systematically to select the most profitable protein-rich leaf items, since there is more unpalatable mature leaf available than young leaf at this time. This selective ranging behaviour is made possible by the wider and greater abundance of fruit.

The mean time spent in locomotion (climbing, searching activities) in a quadrat increased with the availability of young leaves ($r_s=0.71$, df=12, $P<0.02$).

Monthly mean day-range-length was negatively correlated with the proportion of fruit in the diet (r_s=-0.65, df=12, P<0.03) and positively correlated with the availability of new leaf in the home range (r_s=0.59, df=12, P<0.04). Despite the significance of the correlation, there was very little difference in the actual day-range-length between fruit abundant (August and September 1986) and fruit scarce (December 1986 and January 1987) periods (t=-0.7, df=7, P>0.5). Thus, while day-range-length tended to increase as the monkeys used less fruit in their diet, and as new leaf became more available, the actual increase was minimal and approximated 100m. The total area used on three consecutive days in each monthly sample was no different between summer and winter (t=-0.63, df=11), or between periods of different food availability (t=-0.53, df=11). Thus, samangos did not use a smaller area of the home range in response to fewer daylight hours or reduced food availability. Although there was no difference in the size of the area of the home range used between food seasons, the troop did attempt to use more of the home range when fruit was least abundant. This is shown by the percent overlap in the frequency of use of quadrats between consecutive months, which declined from a mean of 68.8% (fruit abundant, s=4.8%) to a mean of 50.5% (s=7.8%) when fruit availability was generally low, and to a value of 42% (during December 1986 and January 1987) when fruit was most scarce. Further, the percent overlap in the frequency of use of quadrats between consecutive days in a sample period, decreased by 6% from September 1986 to 48% in January 1987 when food was less abundant. This suggests that day ranges were more likely to be different on consecutive days in months when food was scarce.

Day-range-lengths are two-dimensional path route measures and do not account for the variation in use of the forest levels. Further confirmation of the trend toward a greater use of the home range as food availability declines, is found in the use of the forest height classes. During September, when fruit was abundant, the troop used the canopy strata more frequently than in January when fruit abundance was at its lowest. The diversity of use of height classes was accordingly lower in September (H'=3.16) than in January (H'=3.44). These differences in canopy stratum use were only evident for periods when extremes of food abundance were noted.

8.3.3. FOOD DISTRIBUTION AND USE OF SPACE

This section attempts to answer the question of whether the foraging behaviour of the troop was a consequence of the distribution of food in the home range? That is, did the troop concentrate their feeding effort more in those quadrats of greater food potential? The time spent in each of six selected quadrats from each month (see methods) was correlated with the number of food species and individuals in the quadrat. As for the time spent in a quadrat, the number of food species and number of food bearing individuals, were ranked on a three point scale of low, moderate or high. The degree of association between quadrat-use and potential food availability in a quadrat was tested using 3x3 contingency tables.

The use of a quadrat over the whole study period was not influenced by the number of species in a quadrat ($X^2 = 7.69$, df=4, $P<0.11$), but was strongly influenced by the number of trees with food items in a quadrat ($X^2 = 22.26$, df=4, $P<0.001$), to the extent that quadrats with more food trees were used more frequently. This implies that (a) patch size may be of considerable importance to the monkeys in a habitat that is not food limited, and, (b) within limits, patch size may be more important than the quality of food in the patch under these conditions (food abundant). In other words, if two patches of different size contained food items of the same nutritional quality at Cape Vidal, the monkeys would favour the larger food patch over the smaller.

In three months of the study (December 1986, March 1987, June 1987), a total count of food bearing tree species and individuals was made over the whole area used during the monthly sample. Unfortunately none of these months represent a period when fruit was exceptionally abundant although fruit was moderately abundant during March 1987. In both December 1986 and June 1987 fruit was less abundant than in most other months. Thus a comparison of quadrat-use by the troop between the fruit scarce months (either December 1986 or June 1987), and the month of moderate fruit abundance provided added information on seasonal changes in feeding strategy.

Compared to March 1987, there were significantly fewer fruit-bearing species ($t=3.06$, df=51, $P<0.01$) and individuals ($t=2.57$, df=51, $P<0.02$) in a quadrat than during December 1986 (Fig. 8.7). Neither the time spent in, nor the number of visits to, a

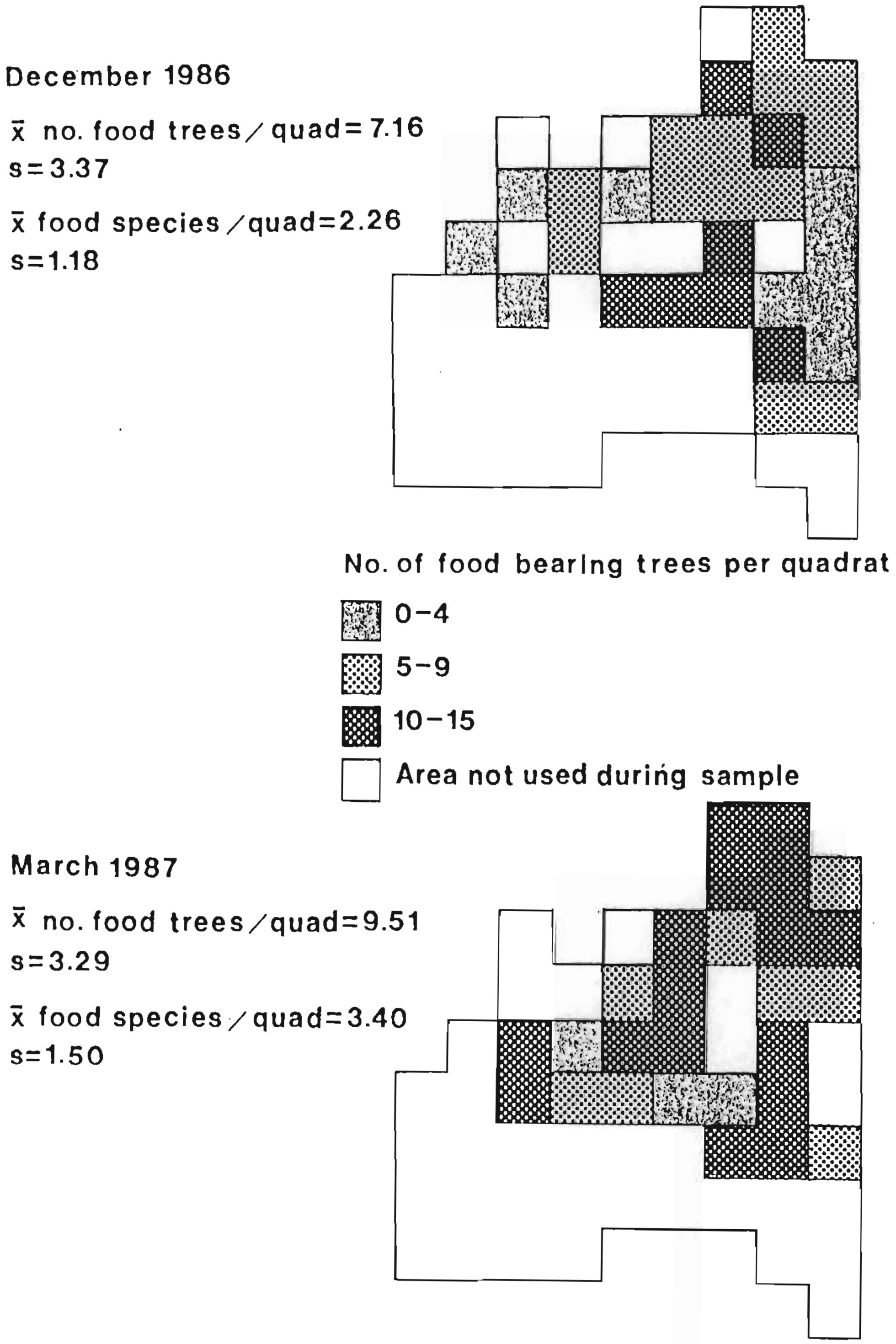


Figure 8.7. The distribution of food bearing trees in quadrats over the monthly range area for two months: December 1986 when fruit was relatively scarce and, March 1987 when fruit was relatively abundant.

quadrat were correlated with the number of species or individuals in a quadrat during December. The time spent in a quadrat during December 1986 was, however, correlated with the availability of flowers in the quadrat (Table 8.7). In contrast, during March 1987, the troop spent more time in quadrats with more food-bearing trees and visited these quadrats more frequently. The food trees in quadrats were mostly fruit-bearing trees. Thus both the time spent in a quadrat and the number of times the troop visited a quadrat, were correlated with the availability of fruit in those quadrats, and the potential energy content of a quadrat (see Table 8.7 for explanation of calculation of energy content of quadrat).

Table 8.7. Spearman rank correlations between the time spent in, or the number of visits to a quadrat, and food availability and quality in a quadrat (N_{Dec}=30 quadrats, N_{Mar}=28 quadrats). * P<0.05, ** P<0.01, *** P<0.001.

	Fruit shortage DECEMBER 1986		Abundant fruit MARCH 1987	
Quadrat use:	Time	Visits	Time	Visits
No. food species/quadrat	NS	NS	NS	NS
No. food trees/quadrat	NS	NS	0.489**	0.493**
Fruit availability/quadrat [1]	NS	NS	0.582***	0.543***
Flower availability/quadrat [2]	0.489**	0.385*	NS	NS
Potential energy/quadrat [3]	NS	NS	0.557***	0.550***

1. Fruit availability/quadrat = sum of FAI's for fruiting species, calculated from the number of fruiting individuals of a species present.
2. Flower availability/quadrat = sum of FAI's for flowering species, calculated from the number of flowering individuals of a species present.
3. Potential energy/quadrat = sum of the product of the energy value and FAI for fruit items from species present.

See FAI index for explanation of use of FAI.

The frequency of use of the top-ranking food plant species was significantly correlated to their dispersion about the home range when food was moderately abundant (March 1987; r_s=0.75, df=12, P<0.01). When food was less abundant (during both December 1986 and June 1987) there was no correlation between the frequency of use of the top-ranking food plant species and their dispersion.

8.4. DISCUSSION

8.4.1. SAMANGO DIET

Within the guenons, the amplitude of seasonal variations of gross food type intake is larger for the heavier species such as mitis and nictitans (Gautier-Hion 1988). The bimodal pattern of seasonal consumption of fruit noted for the guenons in general (Rudran 1978a, Gautier-Hion 1980, Cords 1986) is a consequence of the bimodal peak in fruit production in equatorial forests (Gautier-Hion 1980). The diets of different species differ the most when fruit production is lowest. From this it is assumed that fruit can be a limiting resource, and is the prime factor leading to dietary shifts by season. Just how limiting fruit is in the diet over the mitis range, can be determined by examining coefficients of variation (V) of the frequency of use of the fruit throughout the year (see Table 4.10). One would expect populations in which fruit is less limiting to have less variation in the use of fruit by month. The value of V is low for the Cape Vidal population (n=13 months, V=17.88), suggesting that fruit is a less limiting resource there, than for those populations at Kibale or on Zomba Plateau. While values of V are similar for the Cape Vidal and Kakamega populations, samangos spent proportionally less time feeding at Cape Vidal (35.4%) than blue monkeys at Kakamega (43.8%). From this crude analysis, it appears that samango monkeys at Cape Vidal are able to obtain more fruit in less time (from a very small home range), and show less variation in their use of fruit, than do most blue monkey populations.

A model of interspecific competition between four sympatric primates, including mitis, in the Kibale forest suggests that while dependent on fruit to satisfy energy demands, they are not limited by the quantity of fruit available (Skorupa 1983). If this is the case for a population with high V values (cf. Table 4.10) it can only mean samangos experience an abundance of fruit at Cape Vidal. Skorupa (1983) does, however, point out that the model parameters may have been assessed during a period of environmental relaxation, and that fruit availability may still be a limiting factor during environmental bottlenecks. I also add that the coefficient of variation of the use of fruit may not always be an indicator of the fluctuation in fruit availability over a study period, but may result from the preferential use of alternative high energy foods (such as insects) at certain times of the year. Despite this, the exercise illustrates the point that samangos are able to rely on fruit year round for energy, in the relative absence of insects.

It is important to recognize at the outset of this discussion that the samangos at Cape Vidal are not fruit limited, nor, in general, food limited. This important conclusion is confirmed, as we have seen, by (a) a high proportion of fruit in the diet throughout the year (51.7%) with a low coefficient of variation of the use of fruit (V=17.9%), but also by (b) no increase in the diversity of the diet as fruit availability (r=-0.12, P>0.7) or the availability of leaves or flowers declined, (c) nor did the proportion of time spent feeding differ significantly between seasons of fruit abundance, and (d) there was an exceptionally low incidence of aggressive encounters over fruit items (see Chapter 6).

The important corollary is that if the Cape Vidal samangos are not food stressed (i.e. fruit is abundant), the diet should therefore represent intrinsic food choices, within the constraints of the food types available. The most significant constraint is the absence of an abundant and easily digestible protein-rich (insect) food source. However, even this constraint is not as serious as one might expect, since, given the constant supply of fruit there is always ample time for animals to obtain protein, when insects decline in abundance, by switching to leaves which need more processing time (see activity budget). Thus, at any time of the year one could expect that the observed diet of the monkeys is a consequence of intrinsic preferences and is not, to a marked degree, the product of serious dietary compromise.

In addition the diet of the samango monkey at Cape Vidal likely represents the broad food choices that are intrinsic to the members of the mitis species group when insects are not abundant.

What, then, are these food choices? Hladik (1977) has shown that fruits are the most profitable food items when compared to leaves and insects in terms of easily assimilated energy. This is corroborated by data in Chapter 3 where fruits eaten by the samangos are shown to be high in energy and fats. The samangos therefore maximized their intake of readily available energy by selecting fruit as a primary component of the diet throughout the year. In addition, they were more selective when fruit was more available (see Table 8.2), and did not only eat those fruits that were most available.

The samangos also achieved a high level of dietary mix often optimizing the use of flowers, leaves and insects as sources of protein without jeopardizing the time needed to maintain the supply of energy from fruits. For example, some flowers, in addition to being a more concentrated source of soluble carbohydrates (because of their low fibre content), contain substantial amounts of protein (cf. Gaulin 1979, Richard 1985, Chapter 3). The flowers of 10 species eaten by samangos at Cape Vidal had a high mean protein content (20.2% of dry mass, s=6.5%). It is possible that the flowers eaten, when flowers in general were not abundant (July 1986, April 1987 and May 1987), provided sufficient protein for a balanced diet. In general, however, samangos showed a significant inverse relationship between the proportion of fruit and flowers in the diet by month. Given the seasonality of flower production at Cape Vidal, it is unlikely that this relationship is indicative of any thing more than the use of flowers as the precursor phytophase to fruit. Both flowers and insects were highly preferred although temporally most unavailable, and their overall proportions in the diet is consequently low (flowers 13.4%; insects 5.8%).

The use of insects by the troop also illustrated the ability of the monkeys to respond dynamically to fleeting changes in food availability, and in so doing, optimizing their use of available resources.

Where dietary mix was imperative, but alternative protein sources limited, the monkeys were forced to eat mature leaf. However, the monkeys practically ignored this less 'profitable' source of protein when young leaf was available and used young leaf almost exclusively.

Despite the fact that young leaf was preferred, more mature leaf was included in the diet than young leaf. The use of mature leaf was related to the absence of young leaf, and a lack of suitable alternative protein sources for most of the dry season. The greater proportional use of mature leaf in the diet during dry season months (a greater proportion of leaf even when compared to the use of new leaf at the height of new leaf abundance) can be explained by the fact that considerably more mature leaf would have to be eaten to provide the same nutritional return of young leaf. Mature leaf has a higher structural carbohydrate and fibre content (not to mention secondary plant compound content) making digestion and assimilation of nutrients difficult (Hladik 1978). Thus, an apparent increase in feeding effort on mature leaf when young leaf is scarce does not necessarily reflect greater nutritional requirements (i.e. protein) but merely the extra effort required to maintain the degree of nutritional balance in the diet.

Although leaves are primarily eaten for their protein content, studies of blue monkey feeding behaviour suggest that leaves are also used to supplement the carbohydrate content of the diet. Thus, in many studies blue monkeys have a high proportion of leaves in the diet at times when the proportion of fruit is low (Aldrich-Blake 1970, DeVos and Omar 1971, Rudran 1978a, Struhsaker 1978, Cords 1986, Butynski 1990). While no such relationship was observed at Cape Vidal, this may be a consequence of the low amplitude of variation in the use of fruit in the diet, and is further evidence that samangos are not fruit stressed.

A further illustration of the importance of an ability to include leaves in the diet is found in the timing and seasonality of reproduction. Pyke (1983) argues that animals forage in ways that maximize their Darwinian fitness. Wrangham (1980) argued that in female-bonded troops such as those typified by the mitis species group, Darwinian fitness is primarily dependent on the feeding strategy of adult females. Butynski (1988) suggests that the guenon breeding season (gestation and lactation) is timed to occur when fruit is most abundant and thus, by inference, adult female feeding strategy combines the demands of the breeding season with the period of greatest food availability.

I suggest that this study shows that fruit is not the critical food correlate determining the timing of the breeding season in C. mitis or other guenons (cf. Beeson 1989). The timing of the samango breeding season at Cape Vidal corresponds with maximum availability of young leaves (protein) and emphasizes the importance of protein for growth of the embryo and lactation. Gautier-Hion (1980) also noted a significant shift in the diets of female guenons of three species to foods with a high- protein content (young leaves, insects) when females were pregnant or lactating.

Most of the guenon populations reviewed by Butynski (1988) were from study sites at low latitudes where seasonality of food resource availability was not pronounced, and protein in the form of insects was abundant. Under these conditions, guenons may synchronize the breeding season with high rainfall and fruit availability. I propose that where peaks in protein availability are not synchronous with fruit availability, the timing of the breeding season will be more closely correlated to the availability of protein-rich items.

Since male breeding behaviour is in many ways linked to the reproductive activity of receptive females (Henzi and Lawes 1987, 1988), the male changes his foraging activity to accommodate the energy cost of reproduction. I have shown above that the male shows an unexpected increase in feeding time prior to the breeding season. Since mitis troops are female-bonded and females form the social core, the feeding requirements of adult females are, therefore, central to the foraging and feeding behaviour of a troop. It is likely, therefore, that reproduction and the consequences for the female feeding strategy, will ultimately have a domino effect on the diets and feeding behaviour of the other age-sex classes. Thus the timing of the use of young leaves by female samangos represents the single most important directly-fitness-related feeding strategy adopted by samango monkeys.

8.4.2. DIURNAL FEEDING ACTIVITY AND DIET

The gross composition of the diet is a reflection of the day to day demand for an adequate mix of nutrients in the diet. After all the monkeys live from day to day, not month to month, and as such the optimal mix of nutritional requirements have to be approximated on a daily basis. The diurnal use of food items in guenons has a typically bimodal pattern (Gautier-Hion, 1980; 1988; Cords, 1987b). Primates wake up in the morning with empty stomachs and a major feeding bout usually occurs early in their active period. Highly digestible and energy-rich fruits, and some leaves, are eaten in the morning reducing the energy deficit. The midday rest period that follows is important since an early feeding bout that fills the stomach must be followed by a period of digestion. In the feeding bouts that follow the rest period, the monkeys again turn their attention mostly to fruit and small amounts of leaves, with the use of fruit peaking 1-2 hours before the end of daylight.

Unlike other populations of mitis, samangos follow the late afternoon peak in the use of fruit with an intensive feeding session on leaves (in both summer and winter). This facilitates subsequent digestion. Leaves are more difficult to digest than fruits, and take longer to pass through the gut (Bauchop 1978, Milton 1981). Despite this the protein gained from leaves is essential to survival and many leaves have to be eaten for a small gain in nutrients. Since the monkeys are not fruit-stressed, they are able to obtain sufficient fruit by early evening, and can take advantage of the night, when foraging is impossible, to slowly digest the large volume of protein-rich leaf material. The monkeys optimize their use of feeding time and food items by sequencing their use of fruit and leaves to achieve the best mix of foods for the most efficient digestion. The fact that this sequencing is consistent for both the wet and dry season indicates that the pattern is not determined by food availability.

There are few records of diurnal fluctuation in use of food items in C. mitis. In contrast to my work, Cords (1987b) found an increase in the frequency of use of fruit in the late evening. Leaf consumption in the blue monkey (Cords, 1987b) peaks in the late morning (1100-1200 hours), which coincides with the beginning of the resting period of the day during which digestion of the leaf material is possible.

8.4.3. RANGING AND FORAGING BEHAVIOUR

Optimal foraging theory (see Schoener 1971, Pyke et al. 1977, Pyke 1983) suggests that when food availability is reduced (i.e. search effort exceeds the energy return from a preferred food and the energy per time or the benefit/cost ratio drops) a foraging primate can adopt one of two strategies dependent on just how scarce food is at the time. It can either (a) decrease foraging time and become less selective but maximize the use of the higher quality foods that are available as they are encountered, or, if food abundance is very low, (b) increase foraging time to maintain as high a quality diet as possible but at increased energetic costs (Schoener 1971, Harrison 1984, Butynski 1990). The essential point to be made is that it is possible to decrease food selectivity only if there is sufficient food available to allow a relative decrease in foraging effort. This permits the monkeys to maintain their nutritional profit from their food although food availability has decreased.

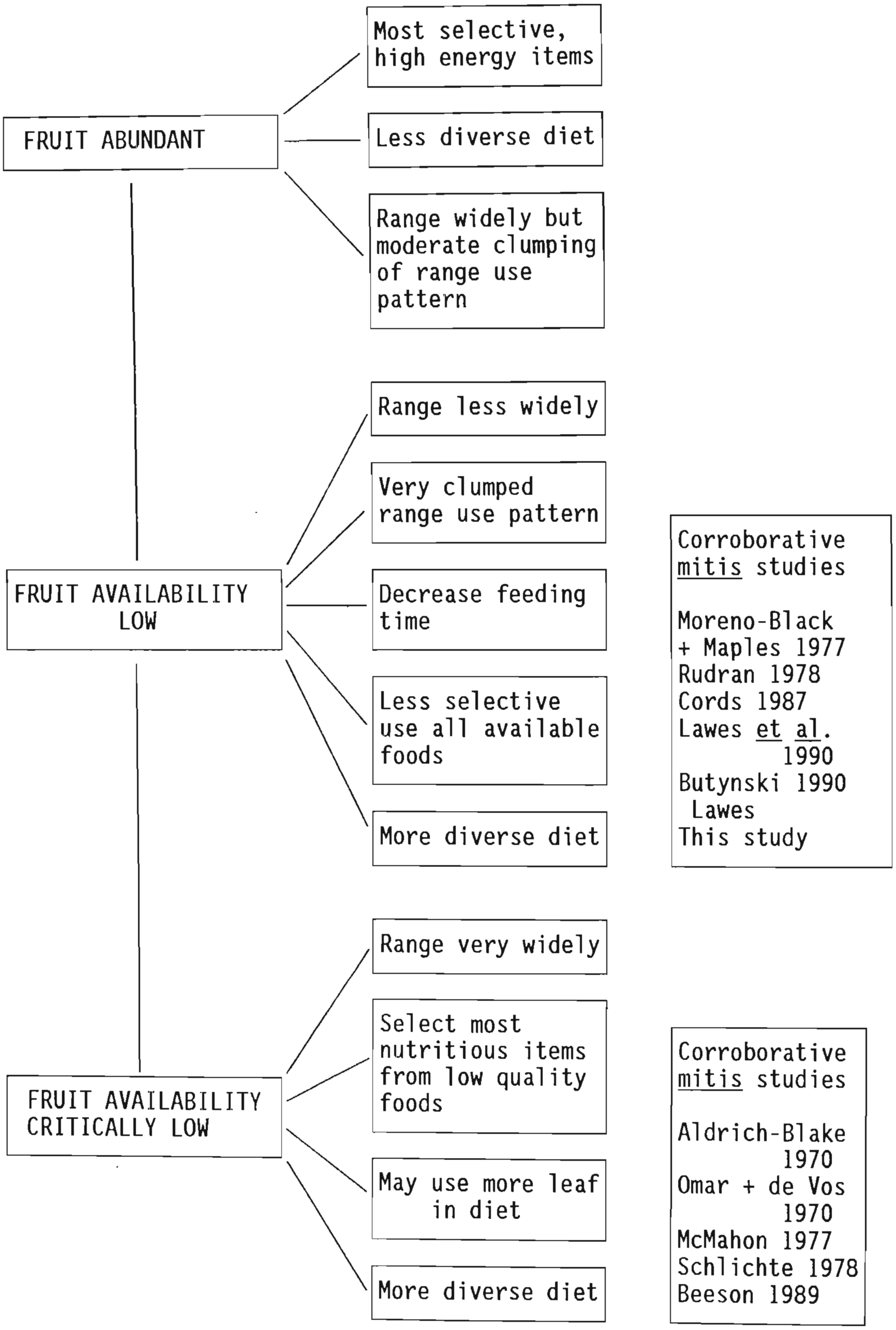
For example, Homewood (1978) found that the Tana River mangabey (Cercocebus galeritus galeritus) avoided the energetically expensive costs of ranging widely for preferred foods by adopting an opportunistic approach to the detection and consumption of less preferred foods as food availability declined. As food availability declines further, the monkeys have to search more thoroughly for food, often by ranging more widely (cf. baboons: Anderson 1981, Dunbar 1988; colobus, Clutton-Brock 1975, Marsh 1981, Mckey and Waterman 1982; C. mitis: Schlichte 1978, Beeson 1989) and being as selective as possible to maintain the highest nutritional return to counter the greater costs of searching. Because there is usually a lack of fruits at this time, often the items chosen are leaves (Beeson 1989), and it is in these forests that the importance of the gut adaptations in the mitis species group are highlighted. The difference between the two strategies can then be seen as the difference between maintenance and survival diets.

A review of available C. mitis literature indicates that different populations adopt one or other of the alternative strategies in the food scarce season. Figure 8.8 illustrates the effect of diminishing food availability on feeding and foraging behaviour in the mitis species group. Although Figure 8.8 categorizes feeding strategies, matching them to periods of differing food availability, the distinction between the strategies is not absolute. Rather the two strategies, associated with food abundance and extreme scarcity, represent two ends of a continuum.

a. Foraging behaviour during considerable food shortage

It has been suggested for periods of **considerable** food shortage that C. mitis shows a tendency to move more systematically about the home range (Schlichte 1978, Scorer 1980, Beeson 1989), or range use patterns are less clumped. The monkeys range widely selecting the most nutritious items from a broader spectrum of lower quality foods such as mature leaves (Beeson 1989), and travelling longer distances to reach pockets of food often outside the usual range area (Schlichte 1978, Scorer 1980). At the same time the monkeys sample all profitable food items. In this way greater diversity of the diet

Figure 8.8. This diagram illustrates different foraging strategies adopted by _C_. _mitis_ populations as food becomes less available.



becomes a consequence of the declining availability of preferred foods. At Kahuzi-Biega in Zaire, food diversity, in addition to the actual availability of foods, was a further confounding factor determining the feeding behaviour of the blue monkey. Unlike Kibale blues, those at Kahuzi-Biega were unable to increase dietary species diversity while reducing food quality. Kahuzi-Biega blue monkeys had to maximize their use of all food species. They achieved this by a "systematic" ranging pattern, and by making extensive use of most or all food items from plant species seldom used.

Scorer (1980) found that the samangos (C. m. erythrarchus) in the forests of the Transvaal escarpment doubled their day-journey-length in winter (1869m, as opposed to summer 829m), when food was less abundant. He also found that the monkeys were prepared to move some distance to feed on the leaves and seeds of Acacia karroo and A. ataxacantha. The diet (in terms of the variety of different items eaten) was more diverse in winter and the monkeys made more use of leaves, especially young leaves, than in summer when fruit dominated the diet. McMahon (1977) recorded similar ranging behaviour for samangos (C. m. labiatus) in the Karkloof range. In response to lower fruit availability in winter (July to September), the monkeys ranged very widely, and used leaves and seeds from nearby black wattle plantations.

Omar and de Vos (1970) in the Aberdare forest reserves found that Sykes monkey (C. m. kolbi) also ranged widely in the dry months when food was less abundant, and moved into exotic pine plantations to supplement their diet with cambium from young trees. This use of pine has also been recorded from the Zomba plateau in Malawi (Beeson 1987) and the Entabeni forests in the Eastern Transvaal, R.S.A. (Von dem Bussche and Van der Zee 1985). The fact that exotic plantations represent an assured food source during food scarcity may warrant the long distances covered in some instances to obtain food from wattles or pines.

Aldrich-Blake (1970) and McMahon (1977) both recorded troop fission in C. mitis troops when food was least available and widely scattered. However Aldrich-Blake found that fission also occurred when food was abundant but widely distributed. Clearly troop fission is a function of the dispersion of food and patch size, and may not be solely related to lower levels of food availability. Troop fission was not observed at Cape Vidal.

Thus a number of C. mitis studies confirm a wide ranging foraging pattern and less selectivity of food items when food is particularly scarce (or food diversity is low).

b. Foraging behaviour during moderate food shortage

Where food is available and moderately abundant during the lean period, a different foraging strategy has been noted in C. mitis (Rudran 1978a, 1978b, Lawes et al. 1990, Butynski 1990). For example, Rudran (1978) found that when food was concentrated in patches and not widely distributed, blue monkeys ranged less. Butynski (1990) confirmed Rudran's (1978a) findings and found that in areas where food was less available but clumped, the same blue monkey population had shorter day ranges and foraged over smaller areas each day.

Seasonal foraging patterns are not always clearcut and different species will have different strategies. For example, Kavanagh (1978) found that two Cameroon populations of the West African vervet monkey (Cercopithecus aethiops tantalus) responded to a dry season decline of fruit in different ways. At one site, Buffle Noir, total feeding time increased, diet diversity decreased, and invertebrates accounted for more than 50% of feeding records. At Kalamaloue, a drier site, total feeding time decreased, diet diversity increased, and flowers and invertebrates together accounted for more than 65% of the diet. If one can take drier to mean less productive, then the strategies adopted in Cameroon are invoked in the opposite order to that proposed for mitis as fruit availability declines.

c. Foraging behaviour during food abundance

The above foraging scenarios for C. mitis are in contrast to foraging strategies observed during periods of food (fruit) abundance. At sites where there is a **marked seasonal difference in food availability**, C. mitis appears to range less widely when food is most available (Schlichte 1978, Beeson 1989) and day-range-area decreases (Schlichte 1978, Beeson 1989). It is possible in the latter studies that food abundance is low year round (although never critical), and the seasonal feeding strategies change between the two food-scarce scenarios given in Figure 8.8. In forests where **food availability does not differ markedly between seasons and food is generally abundant**, blue monkeys ranged more widely when food was relatively more abundant (Rudran 1978a, Cords 1987, Butynski 1990). Day-journey-length increased (Cords 1987) but activity was concentrated in fewer quadrats, and thus a smaller area of the home range was used more intensely when fruit was more abundant in the diet. Kakamega blue monkeys used different parts of the home range on consecutive days when the proportion of fruit in the diet was high (Cords 1987). The combined area used over the food abundant period was larger, and troop ranging behaviour more extensive, although daily range was smaller. The diversity of the blue monkey diet may also decline when fruit is more abundant (Moreno-Black and Maples 1977, Rudran 1978a), presumably as a consequence of a more selective diet. For samangos at Ngoye, when dietary diversity declined, preferred species were high in energy, and there was no correlation between the frequency of use of foods and their availability (Lawes et al. 1990).

d. Foraging behaviour of the samango monkey at Cape Vidal

It is obvious from the above that to compare and contrast C. mitis feeding strategies, the extent to which food becomes seasonally limited is critical. As regards the Cape Vidal samangos, it is clear that periods of apparent fruit paucity were not as severe as those encountered by the Zomba or Lake Kivu populations. Foraging strategy at Cape Vidal thus compares most directly to those strategies used by other mitis populations in habitats where food is abundant and the amplitude of seasonal fluctuations in food availability is low.

In so far as I was able to divide the year into seasons of food abundance, data from this study suggest that when food is abundant the troop (a) ranges over a smaller area (albeit an insignificant seasonal difference in area) per day by travelling over slightly shorter distances, (b) revisits quadrats more frequently, but (c) distributes the time spent feeding more evenly over the area of the home range. Home range use is therefore more dispersed when fruit is abundant. In contrast, when fruit is less abundant, (a) more unripe fruit and new leaf, and less mature leaf was included in the diet. (b) Although less time overall was spent in a quadrat per visit, the monkeys showed a more clumped foraging pattern since they spent more time feeding in certain quadrats over a sample period. (c) Both day-range-length and area showed a slight increase (statistically insignificant) as the availability of fruit declined. In addition (d) the lower percent overlap in the use of quadrats between consecutive months when fruit was less abundant shows that the monkeys ranged more widely about the home range area over the months of food shortage. In any one month, however, use of the home range was more concentrated). Finally (e) an increase in diversity of use of the canopy strata does indicate a more thorough search of all potential food sources when food is less abundant.

It is important to note that the home range was comparatively small at Cape Vidal (cf. Table 7.6, Chapter 7) probably as a function of high food availability, since the monkeys did not have to range over a large area to obtain sufficient food. However, it is precisely the small size of the home range that ensures that the monkeys use a large part of the home range on a daily basis throughout the year. Therefore, the use of the home range was not exclusive between days, months or seasons. Although the greater diversity of use of canopy strata, and the slightly longer day-range-lengths might suggest a marginally wider ranging pattern when food declines, this cannot be compared to the wide ranging survival strategies of some C. mitis troops (e.g. Schlichte 1978, Beeson 1989).

An interesting and informative comparison between the seasonal use of food patches by samango monkeys (in this case defined by quadrat use) and that of seed eating birds under experimental conditions (Caraco et al. 1980), suggests that samango monkeys are risk-sensitive feeders (see Stephens and Krebs 1986). Risk sensitive foragers may either be 'risk-prone' or 'risk-averse'. Caraco et al. (1980) found that yellow eyed juncos (Junco phaenotus), that were provided with less food than required to meet their daily energy requirements, were more prepared to select food trays where there was a probability of greater reward, rather than those trays where reward was a certainty. In this way these birds were categorized as risk-prone. In contrast birds with positive energy budgets chose trays where food reward was certain and were thus risk-averse. Samangos showed a switch from risk-proneness to risk-aversion in association with changes in food availability.

During the month of December, when fruit availability declined at Cape Vidal (although there were food-bearing trees in all quadrats used in that month), the distribution of food-bearing trees was more clumped than in March when food was more abundant (see Fig. 8.7). Although the monkeys concentrated their feeding effort in certain quadrats during December, these quadrats were not the quadrats of greatest food availability (measured by numbers of food bearing individuals). Patches were not selected for their fruit content, even though fruit was still available (albeit unripe fruit), but rather for flowers. Because of the small size of the home range, the distribution of food was easily monitored and all potentially profitable food patches were reached with little effort. The monkeys therefore reduced their feeding time slightly, foraged over a marginally wider area, but concentrated their feeding effort in certain quadrats, using more flowers and new leaves to balance the large amount of unripe fruit in the diet. In this way they maximized the use of profitable foods in patches for the minimum of foraging effort. During this month of lower food abundance the monkeys were prepared to risk selecting those food patches of potentially greater nutritional return rather than use patches of greater food abundance. When food was less abundant the samangos therefore had a risk-prone feeding strategy

Observations made in Gabon by Gautier-Hion et al. (1981) show that during the dry-season when fruit was less abundant, the guenon Cercopithecus cephus, unlike the samangos at Cape Vidal, relied on the most abundant fruiting species, and spent more time in quadrats with more fruiting individuals of a species and were thus risk-aversive.

When food is abundant patches are selected on the basis of their size and quality. During March 1987 fruit was widely available and the monkeys had sufficient food to maintain a positive energy budget. Since fruit was abundant the effect of specific food quality on patch choice was minimal. Patch size, however, was important. More time was spent more frequently in quadrats with large numbers of food-bearing trees. By virtue of their size these large patches had more fruiting individuals and therefore higher food quality. This explains the correlation between quadrat use and both the number of food-bearing trees and the number of fruiting trees (i.e. higher quality food items). This is in contrast to seasons of lower food abundance where food quality in a patch is more important since the monkeys need profitable food items most.

Thus when food was abundant, samangos adopted a risk-aversive foraging strategy, whereby they sought out patches of greater food availability and selected foods of high quality from within patches. Patches of greater food availability provide greater potential for mixing the diet without significantly reducing the quality of food available, thus providing a balanced diet for minimal effort.

This risk-aversive feeding behaviour was also recorded from samango monkeys at Ngoye (Lawes et al. 1990), where a high proportion of visits by the monkeys to areas of greater food availability also suggested that samangos first foraged for large food patches and then selected higher quality foods in the patches. Clearly it is the availability of food patches and the combination of foods present within the patches that determine the diet of samangos when food is abundant. Thus a high quality food item in a small patch or patches may not be used as frequently as one might expect under risk-aversive foraging. I hope to cover the issue of patch size and food content in later papers on foraging strategy.

From the above it is clear that samango monkeys are able to switch their diet (feeding behaviour) and foraging behaviour freely, in response to changes in food availability and abundance. Gut adaptation that allows the samango to switch the diet between protein resources is instrumental in permitting a risk-sensitive foraging strategy. This is especially relevant when food availability declines and the animal has to make critical food choices. Under the latter conditions the monkeys can afford to be more risk-prone than expected, safe in the knowledge that should preferential foods (e.g. flowers) become unavailable, they can always fall back on supplementing the diet with leaves.

8.4.4. WHY IS THE SAMANGO MONKEY THE ONLY ARBOREAL GUENON IN SOUTHERN AFRICA?

Although the samango monkeys at Cape Vidal provide further evidence of the remarkable opportunism and dietary flexibility of the mitis species group, it does not explain why they alone, of the arboreal guenons radiated into southern Africa. Other guenons show dietary versatility and take food items from a wide variety of categories (e.g. C. ascanius, C. cephus), and yet they did not radiate into southern Africa. That there are no other arboreal guenons in southern Africa is is further exacerbated by the fact that, despite food seasonality, the Cape Vidal samangos are not food limited, and furthermore, occur at the highest densities of any mitis population.

Here I suggest that the important dietary issue limiting the radiation of the African guenons is their relative ability to obtain and assimilate protein. In equatorial Africa guenon protein requirements are largely satisfied by eating insects from an abundant insect fauna all year. This animal protein is easily assimilated and can form a large part of the diet. For instance, insects accounted for 25% of C. ascanius, and 16.8% of C. mitis, feeding scores in the Kakamega forest (Cords 1987). In the Kibale forest (Uganda) insects accounted for as much as 45.4% of feeding scores of blue monkeys (Butynski 1990).

The situation changes as one moves southward away from the equator. Insect abundance becomes more seasonal and declines overall (Wolda 1978) and fewer insects are included in the diet (e.g. Zomba, Malawi 0.3%; Beeson 1987). In southern Africa, forest insects are only available during the wet season (see Chapter 3), and even then insects are not abundant. The time and effort required to capture insects may be energetically prohibitive and the proportion of insects in the diet drops accordingly (this study 5.8%). Under these conditions the guenon whose feeding behaviour is sufficiently flexible to enable it to substitute one source of protein for another will be most likely to survive. A corollary of this is that the monkey must be able to easily assimilate the protein-rich food item. The most abundant alternative protein source is young and palatable mature leaves. Leaves are high in fibre and structural carbohydrates and are therefore difficult to digest without special digestive ‘equipment’.

Gut morphology and specialized symbiotic gut microflora, permitting a high degree of folivory in the diet of the mitis group (cf. Beeson 1989), must be seen as the strategic trophic adaptation held by the mitis species group. The competitive advantage that folivory confers on an essentially frugivorous primate, has allowed the mitis species group to become almost exempt from the effects of climatic seasonality and food restriction. A frugivorous-folivore or frugivore-neofolivore (Ripley 1970) like the blue monkey, has a competitive edge over frugivore-insectivores (like the redtail monkey) because it can easily shift the diet to leaves when necessary and forage in a manner that best utilizes these resources. The importance of the foliverous tendencies of blue monkeys has been noted by other authors too and is cited as important in causing substantial separation of their feeding niches from those of other cercopithecines (Struhsaker 1978, Rudran 1978b). Cords (1987) found that blue monkeys at Kakamega had proportionally twice as much leaf in the diet than cohabiting redtails (blues 22.7%; redtails 9.7%). At least one study has found that blue monkeys can survive on little or no fruit for months at a time by using a high proportion of leaf (52%) in the diet (Beeson 1989).

Cercopithecus ascanius, (perhaps the only other arboreal guenon species most likely to have radiated into southern Africa) is a frugivore-insectivore and cannot easily use a predictable and superabundant food source, such as leaves, when food availabilities fluctuate. Redtail monkeys, for the latter reason, must therefore live in an environment with high trophic diversity, high food densities, temporal overlap in the production of food sources and an abundant source of protein in the form of insects (Struhsaker 1978).

Although the samango is the only arboreal guenon in the southern African subregion it is not the only guenon species in the region. The vervet monkey (Cercopithecus aethiops pygerythrus) is also found within the range of the samango monkey. Its extensive distribution throughout sub-Saharan Africa, similar body size and phylogenetic affinities provide an obvious comparison to the samango monkey. Given the success of the vervet in the subregion one could expect to confirm the same flexibility of diet, the ability to shift the diet between protein sources, and an ability to switch foraging strategies. The vervet does not, however, exhibit gut adaptations similar to the samango (Bruorton 1989) and there is no evidence to suggest that it is capable of using inordinately large amounts of leaves. Therefore the vervet is unlikely to be able to shift the diet in an advantageous manner between protein sources. The vervet is, however, semi-terrestrial, and the clue to its success must relate to this.

Fedigan and Fedigan (1988) in their review of aethiops field studies, concluded that vervets were habitat and dietary generalists. In addition, their demographic characteristics (see Fedigan and Fedigan 1988, p411) allowed vervets to adjust group and population size rapidly. They suggested that this, coupled with the fact that vervets are neither forest nor savanna specialists, provided vervets with greater ecological maneuverability, and advantage in ecotonal habitats, than their congenerics. While the issue is more complex than I am able to go into here, it would seem that vervets survive by virtue of their environmental tolerance and behavioural flexibility. Like samangos, vervets are able to respond facultatively to changes in food abundance and availability and thus are ideally suited to coping with seasonal habitats. In the case of vervets the nature of the response, and their success, is largely initiated by behavioural adaptation and reproductive strategy. In samangos it is physiological (gut) adaptation that provides the flexibility in diet, that in turn, provides the samango with ecological maneuverability (risk-sensitive foraging) and superior fitness capabilities in the forest environment.

The folivorous tendencies of the *mitis* species group, exemplified by the samangos' ability to digest mature leaves, has provided *mitis* with a capability for exceptional dietary versatility. This in turn has reduced the intensity of competition for food with other primate species, permitting *mitis* to be sympatric with other cercopithecine species. Dietary versatility has also permitted *mitis* to invade a variety of forest types from high altitude bamboo through to dry coastal forests (the sand-veld forest/thicket of Maputaland), and even the thicket/grassland mosaic found on islands off the Mozambique coast (P. Dutton pers. comm.). In this way *mitis* has become the most widespread arboreal guenon.

The problems facing the radiation of other guenons (besides *mitis*) do not account for the absence of colobines in southern Africa. The vagaries of fruit production and insect availability in southern Africa would not be expected to seriously affect colobines. The factors limiting colobines may well relate to lower forest leaf biomass and diversity in the southern African subregion. This is an interesting problem that I will leave at this point.

It is clear from this study that seasonality of food resources *per se*, (i.e. seasonality with respect to temporal fluctuations in overall food biomass only) is not the crucial limiting factor influencing guenon distribution and abundance. This is made evident by the success of samango monkeys in a seasonal environment. It is the seasonality of abundance of specific nutrients and food types that are important. Here I have shown how seasonal abundance of insects leads to potential protein shortage which causes samango monkeys to shift their diet to leaves. Despite this shortage of protein, 'food' is abundant year round at Cape Vidal. I would suggest that studies of guenons in equatorial Africa should, therefore, avoid the trap of overemphasizing food biomass abundance per se as the critical determinant of feeding strategies. Rather these studies should concentrate on determining the seasonal importance of specific nutrients. While at Cape Vidal the seasonal importance of protein is clear by virtue of the seasonal absence of insects, a similar nutrient 'bottleneck' may arise, in other more northern populations of guenons. There nutrient 'bottlenecks' may be more a response to the concurrent effects of fluctuations in food diversity and the greater competition for food resources, than due to the absence of a specific nutrient source altogether.

In conclusion, the feeding and foraging behaviour of samangos appear to conform in many respects to those east African populations of mitis that do not experience marked seasonal food stress. Further, samango monkeys do not having to compete for their food either with other frugivorous primates or with with large numbers of other frugivorous taxa (birds, bats, squirrels, rodents). It may be useful, therefore, to regard the feeding and foraging behaviour of samangos, unconstrained as they are, as most representative of the intrinsic behavioural choices favoured by mitis under conditions of general food abundance.

CHAPTER 9: SUMMARY TO SECTION-A

9.1 SUMMARY

Members of the C. mitis species group have been studied in a number of forests mostly at low latitudes. This study represents the first detailed socio-ecological study of the southern-most representative of the C. mitis group, the samango monkey (Cercopithecus mitis erythrarchus). Part of the value of this study, therefore, lies in the ecological comparisons or contrasts that can be drawn with other C. mitis studies. The correct interpretation of the differences and similarities between the results of this study and those of other C. mitis populations rests heavily on the appropriate assessment of the ecological conditions under which the samango monkeys at Cape Vidal exist. I have presented several lines of evidence to suggest that the samango monkeys at Cape Vidal are not food stressed. This evidence is summarized below:

(a) Samangos at Cape Vidal live at very high densities (2.02 ind/ha, highest recorded for the mitis group) with small home range areas (± 15 ha). High levels of food productivity and availability would permit such high densities. There is considerable inter-troop home range overlap (mean=4.2ha or 28%). The ratio of passive to aggressive inter-troop encounters (1:2) represents a large fraction (33%) accounted for by neutral encounters. The incidence of food-related intra-troop aggression at Cape Vidal was exceptionally low. The high population density and comparatively low levels of aggressive food-related intra- and inter-troop interference competition (due to both the lack of frugivorous competitor species and low levels of intra-troop competition) suggests a general abundance of food for the monkeys in the dune forest at Cape Vidal.

(b) The samangos at Cape Vidal maintain a high proportion of fruit in the diet year round (51.7%, V=17.9%, n=13 months). Clearly the season of low fruit abundance is not a critical 'crunch' period and fruit is generally abundant in the habitat and the diet.

(c) Although protein-rich food sources such as insects are present at much lower densities at Cape Vidal than in tropical lowland forests (Wolda 1978, Rautenbach et al. 1988), adaptations of the gastrointestinal tract, and the symbiotic gut microflora, permit the samango to maximize use of young and mature leaves to circumvent the problem of obtaining sufficient protein for reproduction and growth (Bruorton and Perrin 1988, Bruorton 1989, Davies, Bruorton and Perrin in press). The monkeys are therefore less stressed by the relative scarcity of protein-rich insect resources at Cape Vidal than one might predict.

(d) Samangos have a higher overlap in the use of specific food items between consecutive months (44.8%) at Cape Vidal than do blue monkeys at Kibale (Rudran 1978a; 26.9%) and Zomba (Beeson 1989; 32.7%), from which comparative data are available. Lower plant species richness, and broad temporal peaks in the availability and phenological state of food items, probably accounts for the high inter-monthly dietary overlap at Cape Vidal. However the absence of arboreal (primate) competitors at Cape Vidal (especially the potential impact that food competitors would have on food availability) suggest that samangos have more opportunity to select favoured foods, while at the same time sampling other potential food items. A high degree of dietary overlap between months may be indicative of food choice by the monkeys, whereby preferred foods are consistently selected for long periods. This corroborates the hypothesis that samangos are not food stressed at Cape Vidal, and the availability of foods is fairly predictable from month to month (as reflected in the high degree of monthly dietary overlap).

(e) Despite lower plant species richness at Cape Vidal, the diversity of specific food items in the diet of samangos was higher in any month (mean H'=3.86) than the mean food item diversity of blue monkeys at Kibale (Rudran 1978a; highest diversity index for a month=3.13) or at Kakamega (Cords 1986; H'=3.32). This was achieved by the use of all available food items from a food species by samangos. Lower plant species richness necessitates the use of leaves and flowers as protein sources, from food plant species, in addition to the use of the energy rich fruits from these species. The samangos at Cape Vidal maintained a more diverse diet (also rich in fruit) with less change in the content of the diet from month to month than did blue monkey troops living in habitats where food was relatively abundant (e.g. Kibale and Kakamega populations). Food abundance and food item diversity at Cape Vidal were therefore sufficient to provide a diverse diet, high in energy and essential nutrients.

(f) Further evidence that the monkeys were not seasonally food stressed is shown by the insignificant change in the proportion of time spent feeding between seasons. In fact the monkeys spent proportionally more time resting than feeding when high quality fruit items were less available. Considering the feeding behaviour and content of the diet over this period, I conclude that the monkeys were not resting more frequently because they were food stressed (and therefore saving energy by reducing the time spent moving), but were able to rest more because the days were longer, and because they were able to obtain sufficient food to permit long resting bouts.

(g) The grain and the intensity of the patterns of home range use reflect the absence of food stress at Cape Vidal. Clumped patterns of range use, indicating selection of parts of the home range for certain activities, are more significantly related to resting than feeding activities. Although the samangos did show some clumping in range use pattern while feeding, especially when food abundance declined, the degree of clumping while foraging did not match that caused by choice of resting sites.

(h) The absence of food stress at Cape Vidal enabled the monkeys to obtain food over a relatively small area despite their large troop size. The mean day range area approximated 33% of the home range area, while over three consecutive days the troop used 56% of the home range area. This extensive use of the home range in the short-term, is undoubtably a function of the small home range size, but may also be attributed to the systematic foraging behaviour of a troop which is committed to maintaining high dietary diversity from a small area. A notable feature of samango daily routes is the frequency with which they double back. This is mostly indicative of the repeated use of favoured resting sites, to which the troop moved after major feeding bouts. It is because the monkeys are not food stressed that they are able to use energy seeking out favoured resting sites, even when food abundance is low.

(i) At Cape Vidal samango foraging behaviour was most similar (in many respects) to foraging behaviour exhibited by C. mitis groups, such as the Kibale (Rudran 1978a; 1978b, Butynski 1990) and Kakamega (Cords 1986; 1987) blue monkeys, which are less food stressed during seasonal food shortages, than they were to other mitis populations, such as the Lake Kivu (Schlichte 1978) and Zomba (Beeson 1987; 1989) populations. The samangos at Cape Vidal had a clumped feeding pattern, and displayed less overlap in home range use between monthly samples when food was less abundant. This implies that the troop used an area of the home range intensively, before moving to sample another part of the home range. As part of this intensive search of small parts of the home range, the troop showed an increase in the diversity of use of the canopy strata when food abundance declined. Dietary diversity also increased as a consequence of the need to become less selective and sample all potential foods. Becoming less selective, however, did not prevent the monkeys from including a large proportion of fruit in the diet but required that they use more unripe fruit. In contrast mitis troops on Zomba plateau (Beeson 1989) and at Lake Kivu (Schlichte 1978) were severely fruit limited at times, more so since the diversity of fruiting species was low at these sites. Under these circumstances, although eaten (food items represented the most nutritious available) they were mostly of low quality. Due to the lack of fruits these troops were obliged to maintain diverse diets consisting of moderate to low quality items (leaves and flowers). The Zomba blues for example, used leaves extensively during the period of food paucity (Beeson 1989).

(j) There is some evidence that samango monkeys might be risk-sensitive foragers, with a tendency to be more risk-aversive than risk-prone in their strategies. Although the monkeys were generally less selective in most months when food was less available, they did respond to increases in the availability of preferred food items. This is shown by the greater use of quadrats with more flowering trees during December 1986. They used these quadrats more than those that had a higher general food content. In this way they might be considered risk-prone foragers (Stephens and Krebs 1986) during part of the season of lower food abundance. On the whole, however, samangos were more inclined to be risk-aversive foragers. They generally selected quadrats that contained higher food abundance over those that might have had less abundant but higher quality foods.

From the above it is clear that the present study is important because it represents the ecology of a subspecies of the C. mitis species group, firstly, in the absence of sympatric congeneric arboreal frugivorous competitors, and secondly, under conditions of moderate to high food abundance. The results of the study increase our understanding of the fundamental niche dimensions of the C. mitis species group. For example, it shows that C. mitis is able to derive the majority of its protein requirements from low quality foods (leaves), can use a wide variety of insect prey types in the absence of competitors, and survive and reproduce at high densities in an environment subject to seasonal change in climate, day length and most importantly, changes in food abundance, which are of longer duration than in tropical latitudes. This study thus confirms the ecological versatility of a primate species already known to have broad trophic niche capabilities and exceptional habitat tolerance (Struhsaker 1978, Beeson 1989).

Gut morphology and specialized symbiotic gut microflora, permitting a high degree of folivory in the diet of the C. mitis group, must be seen as the strategic trophic adaptation held by the C. mitis species group. Studies of the gut of C. m. erythrarchus specimens taken from the Cape Vidal population indicate the importance of hindgut fermentation as an alternative means of obtaining both protein and energy from leaves (Bruorton and Perrin 1988). The competitive advantage that folivory confers on an essentially frugivorous primate, has allowed the mitis species group to become almost exempt from the effects of climatic seasonality and food restriction. Within southern Africa, the ability of samangos to use mature leaf has undoubtably led to their success as the only arboreal guenon in the region.

9.2 FURTHER RESEARCH

No study can be complete without suggestions for further research. The issues arising from this study that need particular attention are:

(a) A review of techniques for describing forest productivity and food availability as it pertains to primates. It is extremely difficult to compare different forest habitats without simple standardized information on aspects of forest structure and floristics such as (i) tree density per unit area (preferably per ha.), (ii) species richness per unit area, (iii) forest height and division of strata, including estimates of stratum biomass, (iv) fruit, flower, and leaf phenology.

(b) Studies of the gut morphology, microbial fauna and digestive physiology of different African guenons. Bruorton (1989) shows that morphological and physiological parameters of the gut of both samango and vervet monkeys are subject to environmental influences, and may not be constant over large geographical areas. It would therefore be interesting and significant for the interpretation of C. mitis feeding ecology to investigate the properties of "the gut" from different populations of C. mitis in central and east Africa. Investigations of this nature should, however, not be restricted to C. mitis alone among the guenons. Other interesting species would be (i) C. nictitans, on account of its ecological similarities to C. mitis and extensive distribution in west Africa, (ii) C. ascanius, since redtails are the species most closely associated with C. mitis in east African forests (Struhsaker 1978, Cords 1986; 1987), and (iii) C. nigroviridis whose stomach shows signs of "incipient" sacculation (Hill 1966).

(c) The role of secondary plant compounds in determining the strategic response, especially of those primates with strong folivorous tendencies, to changes in dietary diversity and the choice of foods, must be further investigated. Although I merely touch on this topic in this thesis, the importance of secondary compounds as a further mediating factor in determining dietary composition in the samango monkey should not be ignored. A study of the role of secondary plant compounds could parallel further work on gut morphology, its microflora and physiology, of the *C. mitis* species group.

(d) This study describes the socio-ecology of *C. mitis* in the absence of sympatric arboreal primate competitors and under conditions of moderate food abundance. The logical progression would be to investigate the socio-ecology of the species in the absence of competitors but under considerable food stress. Some of the islands of the Mozambique coast (e.g. Bazaruto Island) lend themselves to such an investigation. The scrubby vegetation on these islands (P. Dutton pers. comm.) must be regarded as representative of marginal habitat conditions for *C. mitis*. In addition there are no other primates on the islands apart from the lesser bushbaby (*Galago moholi*). I hope to initiate a study of the Bazaruto samangos which would define the minimum habitat requirements of the *mitis* group, their minimum dietary requirements, and feeding and foraging strategies in the face of adverse conditions.

(e) Wrangham (1980) emphasized the importance of the adult females' feeding strategy in female-bonded troops. The means by which females obtain sufficient protein for reproduction, and the timing of these events, is of particular interest in southern Africa where there is a seasonal absence of insects and young leaves. The Hogsback Forests of the eastern Cape would be ideal for such a study. These forests are more southernly located than Cape Vidal and experience colder winters and, as such, insect numbers are expected to be more seasonally controlled and the issue of protein availability is more likely a critical one.

SECTION B:

THE STATUS OF THE SAMANGO MONKEY IN NATAL AND CONSERVATION MANAGEMENT PROPOSALS.

CHAPTER 10: STATUS OF THE SAMANGO MONKEY IN NATAL

10.1 INTRODUCTION

In recent years much attention has been focused on the plight of forest dwelling African primates (Struhsaker 1972, Bermant and Lindberg 1975, Asibey 1978, Rodgers 1981, Struhsaker 1981b, Rodgers and Homewood 1982, Bernirschke 1986 (and references therein), Oates 1986b, Johns and Skorupa 1987, Marsh and Mittermeier 1987 (and references therein), Fay 1988). The consensus of opinion is that the conservation of forest primates essentially deals with the conservation of their habitat which, in turn, relies on the management of human populations (Struhsaker 1981b). Throughout the world and in southern Africa, tropical forest is being destroyed. Estimates of the rate of destruction vary (Diamond 1985), the World Wildlife Fund (1989) statement suggests it might be as much as eight million hectares per annum. At this rate even widely distributed species, such as C. mitis, will suffer irreparable habitat loss unless forest conservation measures are enforced effectively now and in the future.

The task of conserving forest habitat in South Africa, and in the province of Natal specifically, is made very difficult by the fact that most forests are small and isolated. In addition, more than one forest type is represented by Natal's forests. Fragmentation of a population increases the probability of local extinctions in several ways (Terborgh and Winter 1980). First, insofar as habitat is rarely uniform in quality, some population fragments may have become isolated in areas of poor habitat from which they cannot move. Second, the area of the habitat island might be insufficient to provide food all year round. Third, there may be imbalances in the food web created by extinctions of other species due to the above causes. For example, frugivorous primates including the samango depend on fruit trees, which may rely on frugivorous birds/bats for the dispersal of their seeds. Thus, the extinction of disperser and pollinator species can have multiplier effects on other animals (Marsh et al. 1987). Fourth, and perhaps most important, with small populations sizes, levels of inbreeding rise, leading to progressive loss of phenotypic fitness and hence a decline in the population (Soule' 1980). Primates that naturally live at low densities will be particularly at risk from such habitat fragmentation. To ensure the survival of the samango, both the monkey and its habitat will need to be actively managed.

The objectives of this study were to:
(a) Find a method of censusing samango monkey populations that had acceptable levels of precision, accuracy and repeatability. For this reason the census methodology is discussed in some detail.
(b) Determine the distribution of the samango in Natal, and evaluate the validity of the rare status (Smithers 1986) assignation for the samango.
(c) Investigate the possible causes of variation in density of samango monkeys between forests of Natal, with a view to developing sound management proposals.
(d) Develop management proposals for the samango that would fit within the framework of a much larger effort to conserve indigenous forest within southern Africa.

10.2 METHODS

10.2.1 ESTIMATING SAMANGO DENSITY

A modified strip transect sampling technique, King's method (Robinette et al. 1974, Burnham et al. 1980, Collinson 1985), was used to estimate samango monkey density. Strip transect methods have been used extensively in east Africa on primates such as the black and white colobus (Oates 1974), the red colobus (Struhsaker 1975), chimpanzee (Ghiglieri 1984), the blue monkey (Butynski, in press), in west Africa (Whitesides et al. 1988) and elsewhere (Wilson and Wilson 1975, Defler and Pintor 1985). Strip transect sampling is based on the concept of plot sampling. All plot sampling methods involve enumeration, or at least determining by some means, the number of objects occurring within two dimensional sampling plots of given dimensions (Burnham et al. 1980, Collinson 1985). The dimensions of the sampling plot are generally defined by the length and width of the transect. The aim of a modified strip transect method is to provide a compromise between the desirability of (a) including as many animals as possible in the sample (improving an estimates's precision), and (b) reducing bias arising from observers failing to detect animals within the boundary of the sampling strip (Collinson 1985).

Strip transect methods employ a variety of assumptions which include the following (Burnham et al. 1980, Franzreb 1981, Collinson 1985):
(a) animals are uniformly and randomly distributed; (b) the probability of observing individuals decreases with distance from the transect, or remains constant to a given distance and then declines rapidly; (c) the behaviour of animals in one portion of the transect width does not influence those in another, and thus sightings of troops are independent events; (d) animals directly on the path would never be overlooked; (e) animals do not move in response to the observer's presence prior to being detected; (f) the response behaviour of the animals/animal groups does not change appreciably throughout the sampling period; (g) the response behaviour is similar despite sex and age of the animals; (h) no group or individual is counted more than once; (i) there is no difference in the observers ability to detect the study animal during the sample period; (j) there are no measurement errors. These assumptions are seldom all realized.

The disadvantages of modified strip transect methods are that they are based on models that are statistically invalid (Burnham et al. 1980), and their underlying assumptions are easily violated when the animals of interest are highly mobile and visibility is relatively restricted and/or heterogeneous (Collinson 1985). However modified strip transect methods provide a greater precision of the estimate for a given amount of sampling effort than other transect methods (Collinson 1985). Although King's method does not provide absolute values of density, with a large number of replicates a census can give reasonably accurate estimates (Robinette et al. 1974, Struhsaker 1981b).

10.2.1.1 King's modified strip transect method

An estimate of the abundance of lone individuals and individuals within troops was calculated separately from the equation:

$$D = \frac{n}{2 \times w \times L} \times 10\,000 = \text{individuals/ha}$$

where:

D = the number of individuals per unit area (in individuals per hectare)

n = the total number of individuals seen directly on and on either side of the sampling line while travelling along the line from start to finish

w = the estimated width (m) of the strip effectively sampled on each side of the sampling line (effective strip width), measured between the observer and the nearest individual

L = is the total length of the transect (m)

In most strip transect methods a straight line transect is a prerequisite. A straight line transect reduces the chances of counting the same troop or individual twice. During the provincial survey I walked in forests where straight line transects had not been prepared. I had to make use of existing animal and foot paths and in some cases make my own. King's method was more flexible than the popular strictly straight line transect Kelker method (in that one did not need to measure angles), and with simple precautions most of the assumptions of strip transect sampling were satisfied. Robinette et al. (1974) recommend King's method above Kelker's, and Anderson and Posphala's methods, for rough terrain where compass-line courses are difficult if not impossible to follow.

The length of the transect was measured with a 'Pinion' pedometer, and the distance verified on a map where a known path route had been used. I moved slowly and quietly and at a speed of 1-2 kmh^{-1} along the transect (path route), stopping periodically to watch and listen for primates. If I detected signs of samangos, especially loud vocalizations, I did not leave the the survey route (defined by the path I was following) in search of them (Wilson and Wilson 1975). Upon detecting the monkeys, I spent no more than 10 min with any single individual or troop. The time limit spent with the monkeys was a compromise between the information gained in remaining with a group (e.g. troop age/sex class structure, number of individuals), and the possibility of otherwise unsampled monkeys moving into the area of the transect. Most transects covered short distances of 5-7 km, taking 3-4 hours to complete. Where a route was repeated on a separate day, I walked, if possible, in the opposite direction from the previous sample. This reduced potential biases resulting from differential habitat use by the samangos and from the direction of travel by the observer.

For all sightings the pedometer distance, time, and habitat (common tree species) were recorded. The distance from myself to the centre of the troop was estimated retrospectively once I had established the extent of troop dispersion. All distances were estimated by eye. I tested my estimates of distance regularly and found them to be consistently accurate to within 2-3 m. The position of the sightings was plotted on a map (if obtainable at reasonable scale).

To avoid underestimating monkey density no survey was conducted during the middle of the day when the monkeys would be inactive (Wilson and Wilson 1975). Walks were completed by late morning (up to 11.30 am) and begun by early afternoon (from 3.00 pm).

10.2.1.2 Reducing the sampling error

A problem with generating estimates of density, from any strip transect technique (and the major source of error) is the determination of the real width of the transect strip sampled (Ghiglieri 1984, Defler and Pintor 1984). Defler and Pintor (1985) discuss the choice of either the observer-to-animal distance or the path-to-animal (in this case shortest distance from path-to-animal) distance, and conclude in favour of the path-to-animal distance. Struhsaker (1975) argues against the use of the path-to-animal distance on the basis that animals of a species directly over the census trail receive a value of zero for the detection distance, and as a result he felt that the observer-to-animal distance was more representative of the true area sampled. Almost all primate surveys measure distance only to the first individual of each species sighted in a group (Struhsaker 1975, Defler and Pintor 1985). Whitesides et al. (1988) point out that without an accurate estimate of the distance to the centre of the group, rather than to the nearest or first individual sighted, such density estimates may be biased. In this study the observer-to-animal distance was in reality the best estimate of distance from the observer to the middle of the troop.

Occasionally during a transect walk I would sight a troop some considerable distance away; for instance, through a gap in the trees, one might see a troop on the opposite valley slope. The inclusion of these sighting distances would greatly bias the sample, and would increase the value for the mean sighting distance (causing density to be underestimated) to a distance within which, it was probable that all individuals were not seen. These sightings were discarded.

Walking in small forests (<500 ha), I found that it was frequently necessary to walk along the forest edge, the bank of a wide riverbed, or along a cliff base within the forest, and thus only half the potential transect width could be surveyed. Under these conditions a record of the distance covered was kept and the sample area corrected accordingly in the analysis.

The probability of sighting increases as a function of the size of the troop (Quinn 1981). Thus smaller troop sizes in a forest could result in an underestimate of primate density (Wilson and Wilson 1975, Defler and Pintor 1985, Whitesides et al. 1988). This was not considered a problem during this study. Samango troops always gave alarm calls which minimized the probability of failing to see a troop. In effect the observer-to-animal distance was really a flushing distance. At first I attempted to record whether the monkeys had been detected by alarm calls or observer vigilance, to allow a later correction for observer vigilance in the sample. I soon discarded this because the monkeys invariably saw me before I saw them, and I assumed the observer-to-animal distance was a measure based on mutual detection. Robinette et al. (1974) state that the initial sighting distance or flushing distances would establish the effective width of the transect accurately.

Sighting a troop did not necessarily mean that all of the monkeys comprising it were seen and counted by the observer. Troop size estimates could have a considerable influence on the density estimate. A mean troop size for a local population was determined from my own estimates and combined with local records or field staff observations where available.

10.2.1.3 Calculating the estimate of transect width

Three methods for calculating the best estimate of transect width were considered (Collinson 1985, Defler and Pintor 1985):

(a) The mean of the strip width estimates (Robinette et al. 1974). Usually the arithmetic mean is applied where the data are normally distributed. However, where the distribution is skewed a geometric mean may be applicable. The log-normal distribution may be more symmetrical and therefore the geometric mean may be a better measure of its centre.

(b) The distance at which a notable drop in frequency of detection was observed, determined from a frequency distribution of sighting/strip width distances (maximum reliable sighting distance) (Defler and Pintor, 1985; p257). The criterion for this distance is the first interval at which the number of detections of troops drops significantly (50%) below that of the immediately previous interval (Whitesides et al. 1988).

(c) The maximum distance of detection of animals, or the maximum sighting distance.

The basis of choice would appear to be whether the species surveyed is a cryptic or noncryptic species (Defler and Pintor 1985). For cryptic species, option (b) is favoured while option (a) is more appropriate for noncryptic species. In view of the vocalization cues that accompany sightings of samangos, they are regarded for the purposes of censusing as a noncryptic species. For this study the arithmetic mean value of the strip widths was favoured and is compared in the 'Results' with the other estimates.

10.2.1.4 The precision and accuracy of King's method

At Cape Vidal the census technique was most rigorously applied because more census walks were completed. The estimate of density achieved by King's method could be compared to an estimate derived from known home range areas from two troops. In this way two important practical considerations could be investigated: (a) what is the appropriate sample size (transect length, or number of troops observed) and, (b) how accurate is the census technique?

Ultimately the sample size will depend on the precision required. In general, the larger the sample size, the more precise the results. However a point is eventually reached where more samples will not reduce variability significantly. Since this point cannot be determined before the study has begun, one must analyze the data as the study progresses so that the results and estimates of precision can be monitored. The precision of an estimate is the 95 % confidence limits expressed as the percentage of the estimate mean (Struhsaker 1981b). The lower this percentage, the more precise the estimated mean. One then plots this estimate of precision against the cumulative number of censuses completed. The point on the curve where any further increase in effort is not repaid by a proportional increase in precision can either be calculated exactly or found where the curve begins to reach an asymptote.

10.2.2 PROVINCIAL CENSUS SURVEY OF SAMANGO POPULATIONS

A broad survey attempts to cover large geographical areas in a relatively short period of time. When dealing with forest habitats the most one can hope for in this kind of survey is data on geographic distribution, relative abundance in different areas, and limited information on age and sex composition of the populations (Struhsaker 1981b).

There are two major types of forest within the southern African subregion (White 1978, Moll 1978, Cooper 1985): (a) Afromontane forest, (b) and Indian Ocean coastal belt forest. Samango monkeys are found in forest of both types. Both forest types were censused using King's method. Within each forest type, forest subtypes (Cooper 1985) and within subtypes, forest that had a history of abuse, and forests that had been well protected, (Table 10.1) were selected. The survey was thus stratified with respect to forest type, subtype, history of the forest, and along the altitudinal gradient (coastal-montane). A total of 17 forests were visited and 14 of these were censused.

The present distribution of the samango monkey in Natal was derived from Pringle (1974), Scorer (1980), Bourquin (1988) and sighting records of my own and others (K. Cooper, M. Ward, P. la Hausse, D. Ward, R. Nuttall, R. Nanni, I. Gordon).

Table 10.1. Illustrates the division of those forests in Natal that were censused, into forest type, subtype (Cooper 1985) and historical disturbance classes.

AFROMONTANE		
	Undisturbed	Disturbed forest
Mist Belt Mixed _Podocarpus_ forest	Ngome (F) Nkandla (K)	Overbury (P) Karkloof (N,P)
Montane _Podocarpus_ Forest		Pongola Bush (N)
INDIAN OCEAN COAST BELT FOREST		
Dune Forest	Cape Vidal (F)	
Coast Lowlands Forest	Duku Duku (F)	Manguzi (K)
Coast Scarp Forest*	Mtamvuna (N) Ngoye (K)	Oribi Gorge (N) Hluhluwe (N)
Swamp Forest	Kosi Bay (K) Eastern Shores (N)	
Sand Forest	Sihangwane (K)	
Riverine Forest	Mkuze (N)	Ndumu (N)

* MacDevette _et al._ (in press) show that the coastal scarp forests of Natal are synonymous with mist belt mixed _Podocarpus_ forests in terms of their floristics.

F Owned by Forestry Department
K Kwazulu
N Natal Parks Board
P Privately owned

A questionnaire was sent to 23 institutions where specimens might have been housed, and would give an insight to the past distribution of the species in Natal.

10.3 RESULTS

10.3.1 PAST DISTRIBUTION OF THE SAMANGO IN NATAL

The only references to the distribution of animal species before scientific explorations lies in the books and journals of early travelers. Hunting journals from the late nineteenth century were not useful in this regard since monkeys were not considered game species nor food species. Wahlberg (1844 cited in Ellerman et al. 1953) did, however, record the species Cercopithecus samango "inland of 'Port Natal'", but did not give a more accurate place name. Early references to samangos can be found in Sclater (1900), Thunberg (1793 or 1795), Roberts (1913; 1931; 1954 and references cited therein).

The name samango derives from the local Zulu word 'insimango' and has no other meaning (A. Koopman pers. comm.). The origin of the common name in the literature goes back as far as 1844 (Wahlberg 1844 cited in Ellerman et al. 1953). It is interesting that Sclater (1900) specifically refers to the samango being rare in Natal, although this may have been related more to the difficulties associated with finding the species in forest than the actual status 'per se'. The samango has thus probably always been a difficult species to observe.

The destruction of indigenous forest in Natal has undoubtably resulted in the extinction of local populations of samangos. However, from questionnaire returns only a single distributional anomaly was detected. A male and female C. m. erythrarchus were collected at Tete pan on the Pongola flood plain in 1955. Outside of the Ndumu Game Reserve, samangos are no longer found on the flood plain today (Pers. obs.).

10.3.2 THE PRESENT DISTRIBUTION OF THE SAMANGO IN NATAL

Within Natal the samango subspecies occupy different forest types (Fig. 10.1). C. m. labiatus is found in Afromontane forests and the coastal scarp forests of the Indian coastal belt forests, and C. m. erythrarchus occurs in the Indian Ocean coastal belt forests, other than the coastal scarp forests.

There is some debate about the floristics of Natal forests and their Afromontane and coastal affinities. MacDevette et al. (1989) include the coastal scarp forests, defined by Moll and White (1978) and used by Cooper (1985), in a category called 'inland forest'. Their classification would suggest that coastal scarp forests are more closely allied to Afromontane forest, especially mist-belt mixed Podocarpus forests, than coastal forests. This would agree with the proposed radiation history of C. m. labiatus in Natal (Lawes 1990). However, until this issue is resolved I have used the classification proposed by Moll and White (1978) and used by Cooper (1985) to distinguish between the forest types (and subtypes) used by samango monkeys in Natal.

In all instances I have followed Cooper's (1985) convention and have used both the forest names and areas assigned by him to the forests of Natal. Samango monkeys are found in fifty-three indigenous forest patches totaling 51 647 ha or 56.6 % of Natal's indigenous forest area (Appendix 10.1.). The actual area of forest known to be occupied by each subspecies is given in Table 10.2. Less of the **present** extent of all Afromontane forest (54.8 %) is occupied by samangos than Indian Ocean coastal belt forest (59.2 %). These estimates do not, however, account for the extent of a forest type actually available to samangos. A more meaningful biological estimate of the utilization of forest in Natal by the samango monkey is given in Table 10.3. This estimate takes into account the effects on the present distribution of the samango, of the constraints of climate and altitude, and the probable radiation history of the samango subspecies in southern Africa (Lawes 1990).

Within the Afromontane forest subtypes, mountain Podocarpus forest is found at altitudes where the climate is too severe for samango monkeys to survive, thus C. m. labiatus is almost completely confined to mist-belt mixed Podocarpus forest in Natal (except for the Pongola Bush Forests (867 ha) which are Mountain Podocarpus forests,

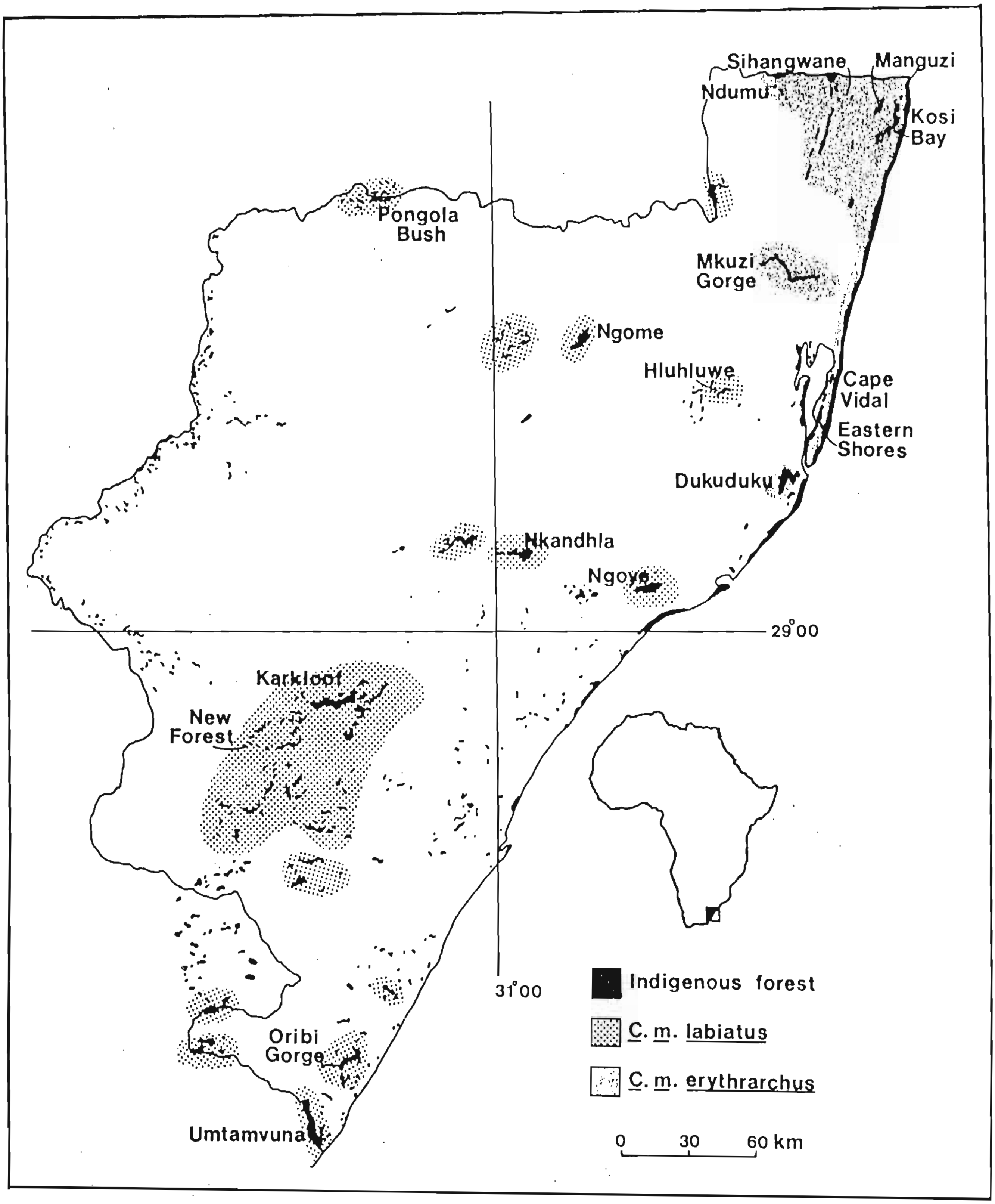


Figure 10.1. The distribution of the samango monkey subspecies in Natal. Note that C. m. erythrarchus is confined to the coastal and coastal plain forests of northern Natal while C. m. labiatus is distributed over the interior in Afromontane forests.

Table 10.2. The area (ha) of a forest category (Cooper 1985) occupied by samango monkeys in Natal.

	Area of forest type inhabited by samangos	Total area of forest type in Natal	% Total area inhabited
INDIAN OCEAN COASTAL FOREST BELT (*C. m. erythrarchus*)			
DUNE	9721	14491	67.1
COAST LOWLAND	3989	8777	45.5
COAST SCARP	9268	15076	61.5
RIVERINE	465	1887	24.6
SWAMP	3652	4843	76.0
SAND	3542	5986	59.2
TOTAL	30637	51060	60.0
AFROMONTANE FOREST (*C. m. labiatus*)			
MIST BELT MIXED *Podocarpus*	20143	30868	65.3
MOUNTAIN *Podocarpus*	867	9273	9.4
TOTAL	21010	40141	52.3
GRAND TOTAL	51647 ha	91201 ha	56.6

Table 10.3. Forest area utilization in relation to corrected estimates of available forest area as determined from climate constraints on the distibution of, and the radiation history of samango monkeys in Natal.

TOTAL FOREST AREA UTILIZED BY SAMANGOS AT PRESENT	51 647 ha
TOTAL FOREST AREA IN NATAL	91 201 ha

TOTAL AVAILABLE FOREST AREA = T - C - H

where: T = Total forest area in Natal

C = Area of forest climatically unsuited to samango occupation i.e. Mountain *Podocarpus* forest.

H = Area of forest in which it is unlikely samangos have ever existed i.e. dune forest (3970 ha), coastal lowland forest (4688 ha) and swamp forest (654 ha) south of the Umfolozi swamp.

TOTAL AVAILABLE FOREST AREA = 91 201 - 8406 - 9312
= **73 483 ha**

PROPORTION OF AVAILABLE FOREST OCCUPIED BY SAMANGO MONKEYS:
AREA OCCUPIED/AREA AVAILABLE

Afromontane forest = 21 010 ha/31 735 ha x 100 = 66.2%

Indian Ocean coastal forest = 30 637 ha/41 748 ha x 100 = 73.4%

Total = 51 647 ha/73 483 ha x 100 = 70.3%

and the coastal scarp forests). Thus, of Afromontane forest available for *C. m. labiatus* occupation, 66.2 % is utilized. On the other hand the use of Indian Ocean Coastal Belt forests by *C. m. erythrarchus* is suggested to have been limited by the spread of coastal forest in the past. Elsewhere I propose that the southward extent of the radiation of *C. m. erythrarchus* was stabilized by the Umfolozi swamp barrier to the south and by the presence of *C. m. labiatus* in forest to the west during the last 6000 years (Lawes 1990). It is therefore unlikely that coastal dune forest and coastal lowland forest to the south of the Umfolozi swamp ever contained samangos. Thus, 73.4% of potentially available

Indian Ocean coastal belt forest is utilized, mainly by C. m. erythrarchus. Overall, samangos utilize 70.3 % of potentially available forest in Natal.

10.3.3 PRESENT CONSERVATION STATUS OF FORESTS OCCUPIED BY SAMANGO MONKEYS IN NATAL

Some 80.0 % of the forests (41 314 ha) utilized by samangos in Natal are either controlled by the Department of Environment Affairs, the Natal Parks Board or the KwaZulu Bureau of Natural Resources (Table 10.4). Although a large fraction of the habitat occupied by samangos in Natal is therefore protected by a conservation body, this represents only 56.2 % of potentially available samango habitat.

10.3.4 ESTIMATES OF DENSITY FOR SAMANGO POPULATIONS IN NATAL

By testing the precision and accuracy of King's method at Cape Vidal a more meaningful interpretation of density estimates from other forests was obtained.

10.3.4.1 King's census method at Cape Vidal

Results from Cape Vidal using King's method were compared to estimates calculated from known troop sizes and home range areas. Two troops at Cape Vidal had home range areas of 15 ha (This study) and 18 ha (A. Terblanche, pers. comm.), and the troop size was 34 (30-37)and 28 (26-30) individuals respectively. Observation has shown that the troops had an average 3 ha overlap with an average of three neighbouring troops. An estimate of density from home range area is calculated:

$$\text{Density (HRE)} = n/(HR - (HO/(t + 1)) = \text{individuals/ha}$$

where:

n = mean number of individuals per troop
HR = mean home range area per troop
HO = mean home range overlap per troop
t = mean number of neighbouring troops

Table 10.4. The ownership of forests (after Cooper 1985) occupied by samango monkeys in Natal.

	State	NPB	KwaZulu	Private
INDIAN OCEAN COASTAL BELT FOREST				
DUNE	6200	110	3411	-
COASTAL LOWLAND	3500	-	489	-
COASTAL SCARP	-	3408	5470	390
RIVERINE	-	285	-	180
SWAMP	410	-	3242	-
SAND	-	-	3542	-
AFROMONTANE FOREST				
MIST BELT MIXED *Podocarpus*	4129	688	5898	9428
MOUNTAIN *Podocarpus*	-	532	-	335
TOTAL AREA (ha)	14239	5023	22052	10333
% of total area (51647 ha) occupied by samangos, in each ownership class	27.6	9.7	42.7	20.0

For Cape Vidal the estimate of density from home range (HRE) is:

$$\text{HRE} = 33.5/(16.5 - 3/4) = 1.96 \text{ ind/ha}$$

It is assumed that the HRE is a more accurate estimate of density than any transect method. From Table 10.5 it can be seen by comparison that the accuracy of King's method improves where: (a) the arithmetic sighting distance is used in the density calculation and, (b) the sample size (length) or number of transects is increased. The maximum reliable sighting distance may be a convenient calculation where the number of sightings are large. For small samples the frequency distribution of sighting distances does not permit the confident selection of a maximum reliable sighting distance. This constraint is prevalent among the censuses done during the provincial survey. The arithmetic mean sighting distance offers the best option (Table 10.5).

In general King's method (arithmetic mean sighting distance) overestimates density under forest conditions, and more so for smaller sample sizes (Table 10.5). Even where high precision (large sample size) is achieved the method overestimates by 5-10 % (cf. Robinette et al. 1974). For a typical provincial survey census, where sample size may not be high, the overestimate can be as high as 8-15 % (Table 10.5) and is probably closer to 15-20 % in reality. Robinette et al. (1974) corroborate these overestimate values. In this study all coefficients of variation of sighting distances for the censused populations were below 45% (mean=24.4%, s=10.4%, n=14). According to Robinette et al. (1974) and based on the coefficient of variation, an overestimation of actual population density of 10-15% is probable ($Y=123.52 - 0.529X$; where $Y=$ % of actual population size, and $X=$ coefficient of variation of sighting distances; Robinette et al. 1974).

How many transects are sufficient? The precision of estimated mean number of social groups per census as a function of number of censuses completed (Struhsaker 1981b) provides part of the answer (Fig. 10.2). The graph clearly shows that after the first 18 censuses, precision shows low gains. In this case 18-25 transects should be sufficient to achieve an acceptable level of precision. A greater number of censuses does not reduce variability significantly. Since transects were 4.8 km long, 18 transects would represent 86.4 km of transect. This is an unrealistic distance to cover for most forests. The limitations of time and forest size precluded such distances in forests visited during the provincial survey.

Rather than ask how many transects are sufficient for acceptable levels of precision, it may be more applicable to know how many transects are required to make comparisons with other areas or with the same transect in different time periods? Janson and Terborgh (unpub. manuscript, cited in Struhsaker 1981b) suggest that the minimum sample (i.e. number of troops = N) necessary to distinguish with 95 % confidence a given degree of difference between two means is roughly approximated by:

Table 10.5. Comparison of the estimates of Cape Vidal samango population density (individuals/ha) using different sighting distance calculations, with the estimate of density derived from home range area, troop size and range overlap (for explanation see text).

HOME RANGE AREA METHOD

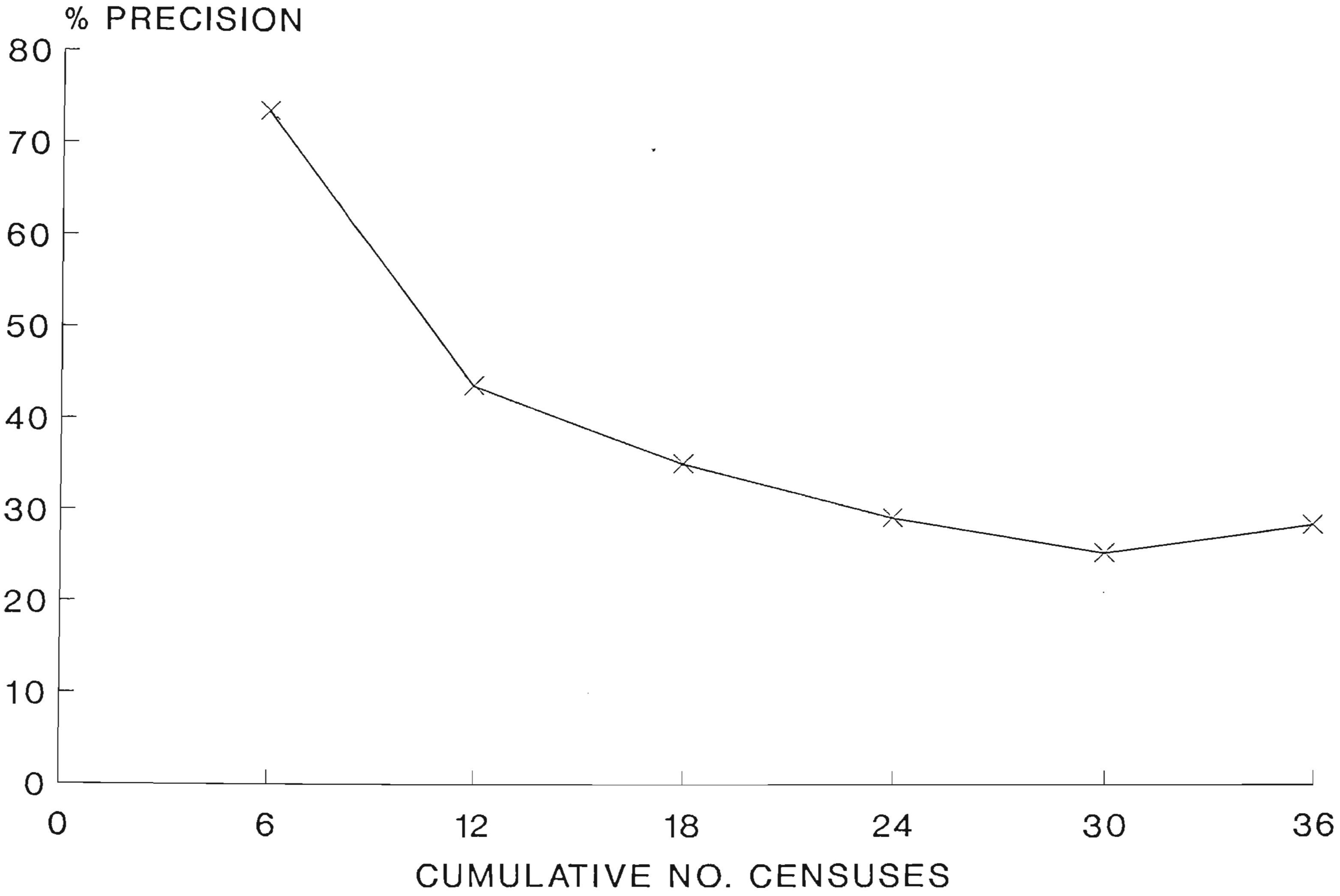
n = Mean troop size = 31 individuals
HR = Mean home range area = 16.5 ha
HO = Mean home range overlap = 3 ha
t = Mean number of neighbouring troops = 3 troops

HRE = n/(HR - (HO/t + 1)) = 1.96 individuals/ha

KING'S METHOD (density in individuals/ha from using different methods of calculating sighting distance)

	Geometric M.S.D.^{1}	Arithmetic M.S.D.	Maximum R.S.D.^{2}	Maximum S.D.^{3}
5-Day Census 1985	2.18	2.07	1.73	1.33
16 Month Census 1986 - 1987	2.15	2.02	1.90	1.38

1. M.S.D. = mean sighting distance
2. R.S.D. = reliable sighting distance
3. S.D. = sighting distance



% PRECISION = 95% CONFIDENCE LIMITS/ x
NO. OF GRPS x 100

Figure 10.2. Precision of estimated mean number of social groups per census as a function of number of censuses completed.

$$N = ((4 \times C.V.)/(\text{degree of difference between means}))^2 + 1$$

where C.V. = coefficient of variation of the mean number of troops seen per transect. If one wanted to be able to detect at least a 25 % change in the samango monkey population at Cape Vidal, then the minimum sample size required would be:

$$N = ((4 \times 0.63)/(0.25))^2 + 1 = 103 \text{ troops}$$

which would indicate 40 transects or a distance of 197 km. In addition, Jansen and Terborgh (unpub. manuscript cited in Struhsaker 1981b) suggest that because the data are not normally distributed, the samples should be at least 10-20% larger than predicted from their formulae. Thus considerable effort must be expended to determine detectable changes in population size over time. The minimum number of transects will obviously change with changes in either C.V. or the degree of difference between the means demanded, and thus the requirements will be different for each population. In this study, time did not permit the observation of the large values of N required.

Where sample sizes are small (i.e. length of strips and number of troops), the census system must, at best, be regarded as an index of comparative abundance within different forests. In some cases where sample sizes are large, reasonably accurate estimates of density were made.

10.3.4.2 Estimates of density - Provincial survey

Since estimates of mean troop size are difficult to obtain it is recommended that troops/km^2, for purposes of comparison of population estimates over time, be used. Thus field staff do not have to get accurate counts of troop size immediately, although these would be useful later. Fourteen forests were censused and the range in density estimates across forest types is considerable. Coastal dune and lowland forests, which are exclusive to C. m. erythrarchus, have particularly high densities of samangos, as much as 2-3 times higher than most other forest types. Coastal scarp and riverine forest have notably lower densities of samangos than most others. In general, C. m. labiatus populations exist at lower densities than C. m. erythrarchus (Table 10.6).

Table 10.6. Estimated densities (individuals/ha) of samango monkey populations in 14 forests in Natal.

FOREST	km's walked	Troop Size	No. T	Arithmetic M.S.D.	Density ind/ha	grps/km²
AFROMONTANE						
Mist Belt Mixed Podocarpus Forest						
Ngome	34.10	±24 (4)	8	33.75	0.83	3.46
Karkloof	21.10	±20 (4)	7	50.0	0.66	3.30
New Forest	17.90	±12 (1)	3	51.66	0.19	1.58
Nkandla	54.20	heard	-	-	<0.05[1]	?
Mountain Podocarpus Forest						
Pongola Bush	44.60	±19 (1)	9	43.33	0.44	2.32
INDIAN OCEAN COAST BELT FOREST						
Coastal Dune Forest						
Cape Vidal 5-day census	50.20	31 (2)	28	41.9	2.07	6.66
Cape Vidal 16 month census	177.15	34 (2)	87	37.8	2.02	5.94
Coastal Lowlands Forest						
Manguzi	24.70	±15 (3)	9	32.20	0.85	5.66
Duku Duku	30.40	±15 (7)	14	37.50	0.92	6.13
Coastal Scarp Forest						
Hluhluwe	57.80	13 (2)[2]	8	45.00	0.20	1.54
Umtamvuna	41.00	±13 (3)	10	55.00	0.29	2.23
Oribi Gorge	28.90	26 (3)[3]	5	56.00	0.40	1.54
Ngoye	52.80	16 (2)	18	56.30	0.48	3.00
Swamp Forest						
Kosi Bay	38.00	±17 (4)	8	44.38	0.40	2.35
E. Shores	8.00	heard	-	-	?	?
Sand Forest						
Sihangwane	43.85	±13 (2)	8	40.00	0.30	2.31
Riverine Forest						
Ndumu	51.64	±15 (3)	11	58.64	0.27	1.80
Mkuzi Gorge	6.50	6-8?	2	>200	-	-

± = estimates of troop size based on rough counts
() number of troops on which troop size value is based

1. At Nkandla a troop was heard on two occassions, but despite a considerable distance covered no troops were seen.
2. Troop size derived from my count of a troop and a count provided by Dr. J. Venter, Hluhluwe Game Reserve.
3. Bruorton (unpub. report)

All other troop sizes derived from my confirmed counts.

Without correction for overestimation, estimates of mean density per population are 0.59 ±0.28 individuals/ha (s=0.48, n=14, 95% confidence limits) and 3.13 ±0.99 troops/km² (s=1.73, n=14, 95% confidence limits). These values yield total estimates in the region of 30 471 ±14 461 individuals or 1617 ±511 troops of samango monkeys in Natal. Less 15% (overestimation value) samango numbers would be 25 900 individuals or 1374 troops.

10.3.5 ENVIRONMENTAL CORRELATES OF SAMANGO DENSITY IN NATAL

10.3.5.1 Forest structure

From the census work it was clear that the samango tolerates a wide variety of physiognomic and floristic forest types. They were found in swamp forest with a very open canopy, sand forest with a high deciduous plant species component (Lawson 1986), through to relatively high altitude mountain Podocarpus forest. The ability of the C. mitis species group to live in a variety of forest types is corroborated by Gartlan and Brain (1968), Schlichte (1978), Struhsaker (1978) and Aveling (1984).

Although I put considerable effort into determining habitat structure preference at two sites, Ngoye and Cape Vidal, results were inconclusive. For instance monkeys at Ngoye seldom used scrub forest (see definition in Geldenhuys et al. 1988) and appeared to avoid it (Table 10.7). Yet the Cape Vidal population used thicket intensively for resting, moving, and social behaviour. In fact a habitat preference index based on:

$$\text{Preference index} = \frac{\%\ \text{observed use}}{\%\ \text{area of habitat}}$$

showed a greater preference for dune thicket, among Cape Vidal samangos, than the dune forest itself (Table 10.7). Schlichte (1978) found that a blue monkey troop in Zaire preferred the shrub layer for non-feeding activities but looked for food in the canopy. This suggests a partitioning of behaviour between habitat structural types.

Table 10.7. Habitat structure preference ratios for the samango monkey from Ngoye forest and the Cape Vidal dune forest.

HABITAT	% AREA	% OBSERVED USE	% PREFERENCE RATIO
NGOYE			
A+B	17.6	40.1	2.3
C	12.1	23.9	2.0
D	30.9	20.8	0.7
E	14.5	2.6	0.2
F	17.1	9.1	0.5
G	4.1	2.2	0.5
H	1.8	0.9	0.5
I	2.0	0.2	0.1
TOTAL	45 ha	451 troop sightings	
CAPE VIDAL			
Acacia karoo woodland	11.6	3.9	0.3
Coastal thicket	14.2	18.0	1.3
Dune forest	74.2	78.1	1.1
TOTAL	15 ha	10528 individual sightings	

A+B	Tall canopy (18-25 m), moderate understory, visibility on ground good >50 m
C	Tall canopy, dense understory, visibility poor <25 m
D	Low canopy (12-18 m), dense understory tree and shrub strata, visibility poor
E	Scrub forest (10-15 m), dense understory and shrub strata, lianes and scandent shrubs abundant
F	Draped forest, areas of tree fall where vines have almost completely covered clearing and adjacent tree crowns
G	Swamp forest, standing in water logged low lying regions, low canopy cover
H	Open glade forest, clearings with no canopy component, some shrubs and mostly grasses
I	Rocky outcrops

See text for calculation of preference ratio

The monkeys also entered the Acacia woodland at Cape Vidal for short, intensive feeding bouts. It is not unknown for samangos to enter monospecific stands of 'forest' as is indicated by their use of commercial pine (Omar and De Vos 1970, von dem Bussche and van der Zee 1985, Beeson 1987) and black wattle plantation (McMahon 1977). This again points to the wide-ranging habitat tolerances of the species.

The forest structural differences and habitat preferences of the monkeys between the Ngoye and Cape Vidal study sites were marked (Table 10.8). The canopy height, mean canopy volume and canopy species diversity was lower, but stem density was higher at Cape Vidal than Ngoye. I conclude that while samangos spend a large proportion of their time in tall forest they will frequently use other structural types in response to food requirements and/or social activity. I very much doubt that the samango has any specific habitat structure preference. The term forest can be used in its broadest structural sense to apply to the samango and C. mitis in general (cf. Skorupa 1986).

Table 10.8. Habitat types and measures of their structure from Ngoye and Cape Vidal forest. For an explanation of forest structure types see Table 10.7.

HABITAT DESCRIPTION (Canopy trees only)	NGOYE				
Forest type	A+B	C	D	E	Dune forest
MEAN VALUES					
NPFS (m)	11	12	7	11	4
INT IND DIST (m)	8	10	7	9	6
HEIGHT (m)	19	21	16	12	13
STEM DENSITY (ind/ha)	165	106	196	214	278
CANOPY VOL. (m^3)	404	551	222	160	209
CBH (cm)	189	212	142	123	95
% COVER	79	60	73	80	83
SHRUB DENSITY (ind/m^2)	0.12	0.43	0.43	0.46	0.14*
SPECIES DIVERSITY H'	3.49	3.00	4.30	4.63	2.63
Hmax	4.70	3.90	4.85	5.25	4.52

* excludes counts of Isoglossa woodii stems
NPFS nearest potential food species
INT IND DIST inter-individual distance

10.3.5.2 Plant species diversity

In the previous section I suggest the possibility that use of forest structure types is dependent on food requirements and not habitat structure per se. The samango is more likely to respond to a sufficient supply of fleshy fruits (carbohydrates/energy) and protein-rich food sources (young leaves and insects) than habitat structure (Bourliere 1979). Without phenological data it is difficult to know what food is available when. However, estimates of plant species richness and diversity can be used to provide a rough index of the potentially available food species in a forest.

The estimated density (troops/km^2) of samango populations was plotted against the plant species richness and species diversity of all of 9 censused forests (plant diversity data for 9 of the 14 censused forests was available (D.K. MacDevette, unpub. data)). There was no significant correlation between the above values; however, inspection of the graphs showed the presence of an outlier represented in both correlations by the coastal scarp forest (Fig. 10.3a and 10.3b). Removal of this outlier resulted in significant correlations (Fig. 10.3c and 10.3d) for both species richness ($r=0.73$, $df=7$, $P<0.05$) and species diversity ($r=0.81$, $df=7$, $P<0.02$). This suggests that samango population density is related in some way to the effects of species richness and species diversity which is discussed in detail latter.

10.3.5.3 Forest history

Even forests of considerable size do not necessarily contain large numbers of samangos. The Nkandla forest (2787 ha) for instance, has exceptionally low population numbers in comparison to other forests of this type. What has caused this probable decline in numbers? Of the many factors, the most probable are human disturbance elements such as wood cutting and hunting. How one decides whether a forest has been recently disturbed or not, is very subjective. For my purposes I took signs of recent wood-cutting, debarking, the presence of cattle and fire- damaged forest edges as my major indicators (Appendix 10.2).

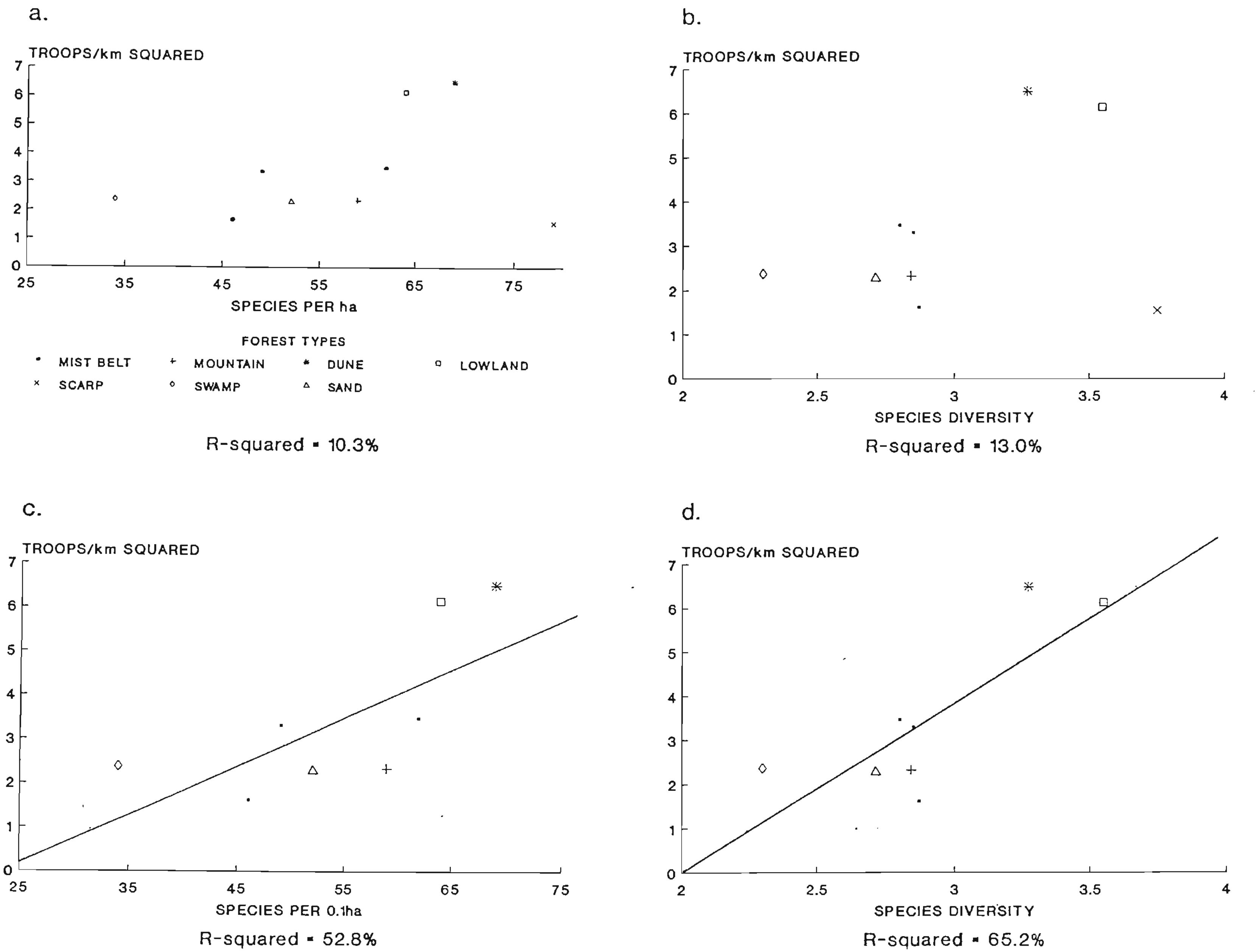


Figure 10.3. The relationship between the number of troops per km-squared and plant species richness and diversity for different forest types in Natal. (a.+ b.) Illustrate the affect of the coastal scarp forest outlier (labelled x) on the scatter of points. (c.+d.) Show significant regressions (high R-squared values) once outlier has been removed from plots.

Comparison between forests within a single subtype that had a history of abuse and those that had been well protected was possible for mistbelt, coastal scarp and coastal lowland forests (Fig. 10.4). By my subjective ranking the graph clearly shows that estimates of monkey density are lower for forests with high levels of disturbance. Disturbances of the type described above act together to cause between 8% to 56% decrease in the number of groups per kilometre squared (x=34.8, s=21.8, n=4). This conclusion is supported by other studies of forest primates (Johns 1985, Johns and Skorupa 1987).

10.3.5.4 Forest size

The size of the forest blocks occupied by samangos varies considerably (Cooper 1985, Fig. 10.5). The largest, Duku Duku forest, covers 3500 ha while one of the smaller forests, the Fort Nottingham forest, is only 131 ha in area. Samangos are also found in the coastal dune forests north of St Lucia estuary. Although Cooper (1985) lists the coastal dune forests of northern Natal as separate forests, they do in fact form one long belt, some 9721 ha in extent. Other forests, especially mist belt mixed Podocarpus forests, such as the Karkloof forests (4826 ha) and the Fort Nottingham forest (131 ha) are in reality comprised of small forest blocks. These forest patches are, however, closely spaced (0.5-2.0 km), and are separated by grasslands or commercial softwood plantations, into units as small as 40-70 ha in some cases.

The mean size of the forests known to be inhabited by samangos (incorporating Cooper's (1985) subdivision of the coastal dune forests into smaller areas) is 947.5 ha (s=1093.9, n=53). However, the strongly skewed frequency distribution of forest size occupied by samangos (Fig. 10.5a) results in a large sample variation and the median (450 ha) is a more representative value of forest size. The median size of forest occupied varies between forest type and therefore between the subspecies. Forests occupied by C. m. labiatus (Fig. 10.5b; median=397 ha) appear to be smaller than those occupied by C. m. erythrarchus (Fig. 10.5c median=700 ha). Mean forest size is 723.1 (s=877.4, n=38) for C. m. labiatus and 1424.6 (s=1314.1, n=15) for C. m. erythrarchus.

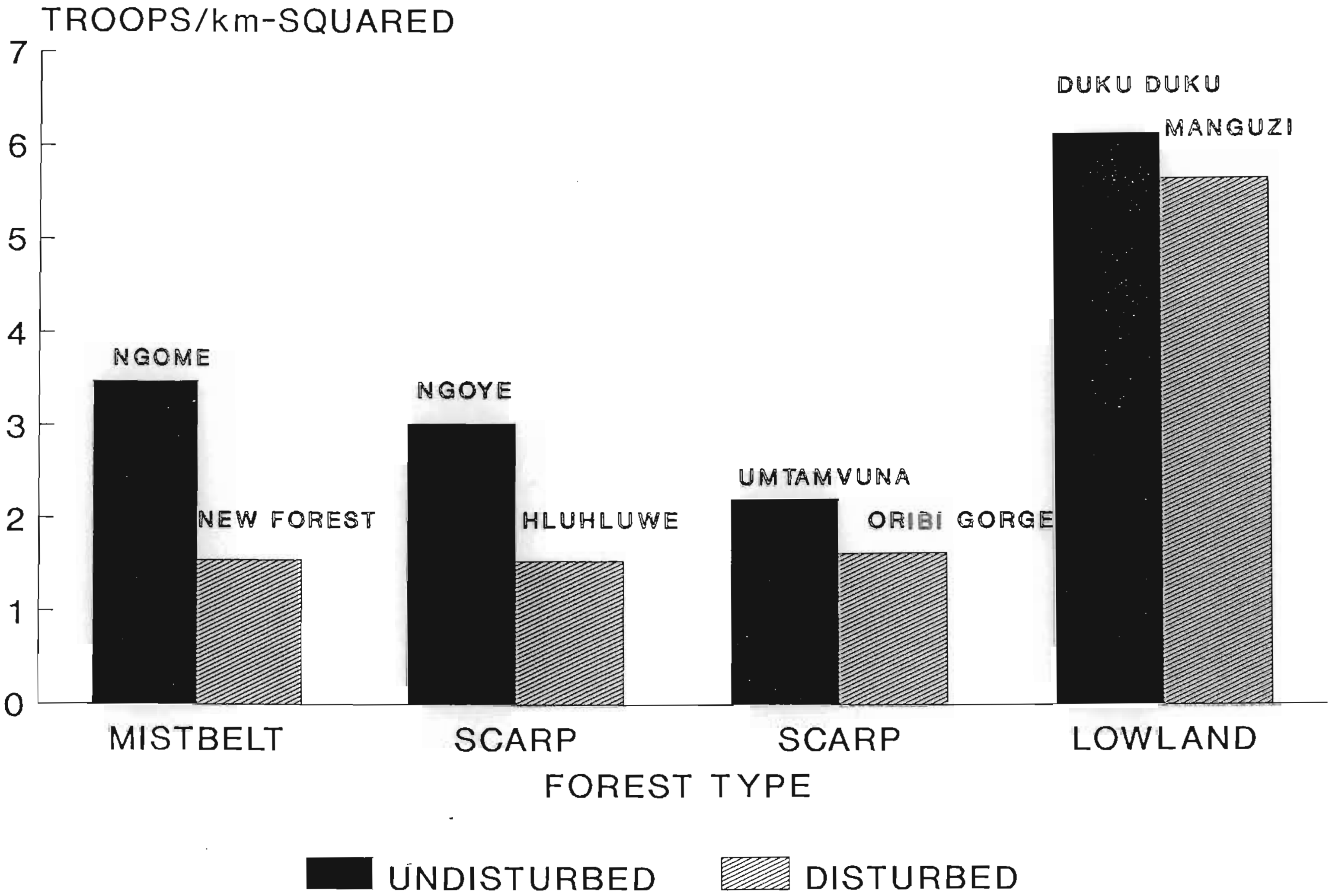


Figure 10.4. The difference in relative abundance of samango monkeys (Troops/km-squared) between disturbed and undisturbed forest.

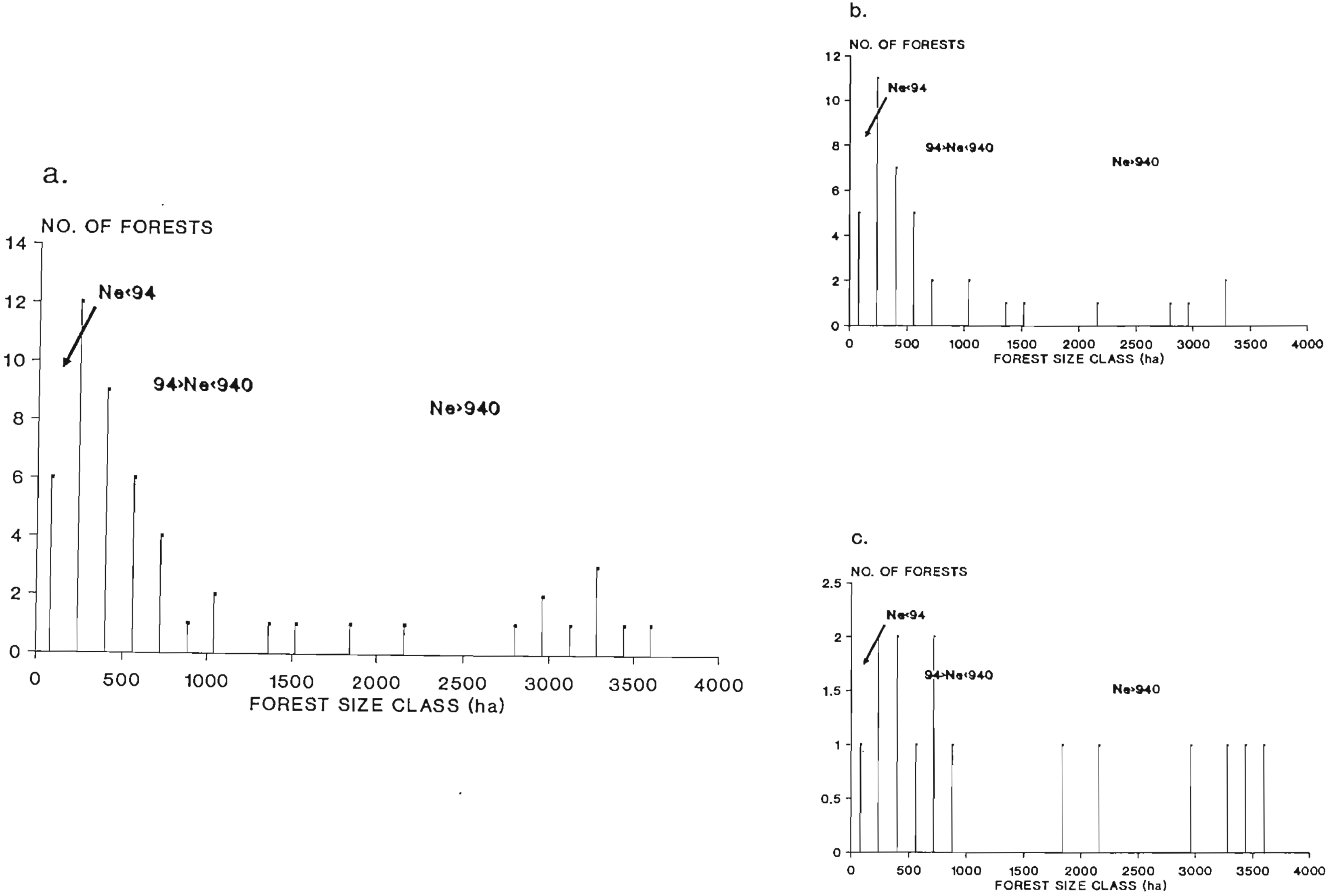


Figure 10.5. Frequency distributions of forest areas occupied by samango monkeys in Natal. (a) Frequency distribution for all forests in Natal. (b) Frequency distribution of those forests occupied by *C. m. labiatus*. (c) Frequency distribution of those forests occupied by *C. m. erythrarchus*. See chapter 11 for an explanation of Ne values on graphs.

There was no correlation between forest size and samango population density measured either as troops/km^2 (r=0.27, df=13) or individuals/ha (r=0.20, df=13).

10.4. DISCUSSION

The distribution and status of the samango monkey within Natal, is constrained by the availability of suitable forest habitat. Like many other forest mammals, the samango monkey owes its precarious status primarily to the gradual, and hence largely ignored, removal of indigenous forest. The results of the census programme show that samango numbers in Natal are fairly high (N>25 000). Included in this total are at least 10 large populations and most forests occupied by samangos support population numbers capable of maintaining short- term fitness. However, in view of the fragmented and threatened nature of Natal's indigenous forest (Bartholomew 1989), the apparent large numbers of samangos in Natal are no cause for complacency. The current rare status ascribed to the samango (Smithers 1986, S.A. Red Data Book) must be regarded as valid given the definition "a species with small populations which are not at present endangered or vulnerable, but which are at risk". Conservation of the species must be achieved indirectly through the 'coarse filter approach' (Hunter et al. 1988) of preservation of its habitat.

It is suggested that samango distribution in terms of regional presence and absence, excluding the Maputaland riverine forests, is much the same today as it has ever been. However the abundance of the samango has declined drastically in the last 100 years. For example, the Karkloof forest has decreased in area from an estimated 32 376 ha in 1880 (Fourcade 1889 cited in Taylor 1961), through 6000-8000 ha in 1944 (Rycroft 1944) to 4826 ha (Cooper 1985, includes forests listed as Karkloof, Benvie, Holbeck, Blinkwater) in the 1980s. Even if the 1880 estimate is high, there may have been an 80 % reduction of forest area in the last 100 years. A similar reduction in area is highly probable for most forest types in Natal (Marwick 1973, Brink and Van der Zel 1980). Further there has been considerable destruction of forest in northern Maputaland since the 1950s (Moll

1980). The Manguzi coastal lowland forest, in particular, has been reduced from estimates of 5600 ha at proclamation (Ward, M. pers. comm. cited by Bartholomew 1989) to 489 ha (Cooper 1985). Consequently, it is highly probable that the area of forests, and therefore the status of the samango monkey in Natal, have been reduced by as much as 60 to 70 % over the last 100 years.

Recently, Siegfried (1983;1984) has reviewed the need for developing species-conservation priorities for species in Red Data books. The samango as a member of the widely distributed polytypic C. mitis species group cannot be said to have a high conservation priority in Africa. However, Siegried (1984) advocates a pragmatic ranking system for species in need of conservation attention, based primarily on their known or suspected roles in ecological processes which are essential for the functioning of ecosystems. Eisenberg (1980) states that large mammals and birds, in an ecosystem, are usually sensitive indicators of ecological integrity by virtue of their high position on the trophic pyramid. The samango is the largest arboreal mammal and the dominant mammalian frugivore in the forests of Natal. Where human interference factors (primarily hunting) and disease can be safely excluded, changes in demography of samango monkey populations could provide useful corroborative evidence of forest condition.

10.4.1 Plant species diversity and samango population density

From the results it appears that samango population density is related to the richness and diversity of plant species in a forest. Why do coastal scarp forest populations not fit the trend? Coastal scarp forests have high plant species diversity but low samango population numbers.

Is it possible that high plant species diversity can become a factor limiting population size (troops/km^2)? This seems unlikely at first because central African forests have a substantially higher plant species richness and diversity than southern African forests, and support 6-7 sympatric diurnal primates and a greater primate biomass (Struhsaker 1981b). However, high plant species diversity does have an effect on food availability for the arboreal frugivore, which in turn can influence the carrying capacity of a forest. A high plant species diversity can result in; (a) a greater number of plant reproductive strategies (in terms of fruit types) the monkey has to contend with, (b) a lower overall phenological synchrony of food item type (i.e. fruiting seasons become less well defined), (c) and most importantly specific food items become more widely dispersed. The combined effects of these factors may be compounded by lower levels of productivity in southern Africa than equatorial Africa.

In southern Africa, climatic seasonality forces the majority of forest plant species into reproductive strategies cued by seasonal rainfall. Very definite periods of food abundance and shortage can exist (Lawes et al. 1990). The availability of fruit may greatly exceed the consumptive capacity of the frugivore community during periods of abundance, but these periods alternate with times of scarcity when many frugivores are obliged to feed on substitute resources of presumably inferior quality. In the samango these substitute resources are mainly young leaves and those mature leaves that are palatable. Terborgh (1986) states that regardless of their quality, the "keystone" resources that sustain frugivores during times of general scarcity are of great ecological significance, because they appear to set the carrying capacity of the community.

I suggest that within southern African forests there is a threshold point in plant species diversity (Fig. 10.6), above which specific "keystone plant resources" referred to by Terborgh (1986), become too widely dispersed during periods of food shortage to maintain a large primate population. Although a higher plant species richness and diversity may mean that food is probably always available, it is widely dispersed, and the troop has to maintain a larger home range to obtain sufficient nutrients and thus population density is lower in forests with high plant diversity and species richness.

The regression of troops/km^2 on plant species richness predicts that samango monkeys would not be able to exist in forest where the plant species richness over a relatively small area (0.1 ha) drops below 33 (Fig. 10.3c; $Y = -2.87 + 0.117x$). Presumably because below these plant species richness levels too few keystone food species are present to tide over the seasonal food bottleneck. The theoretical curve (Fig. 10.6) indicates that above a plant species richness of 65-70 species, population density will begin to decline in response to the wider dispersion of food species. However, the forest will continue to support samango

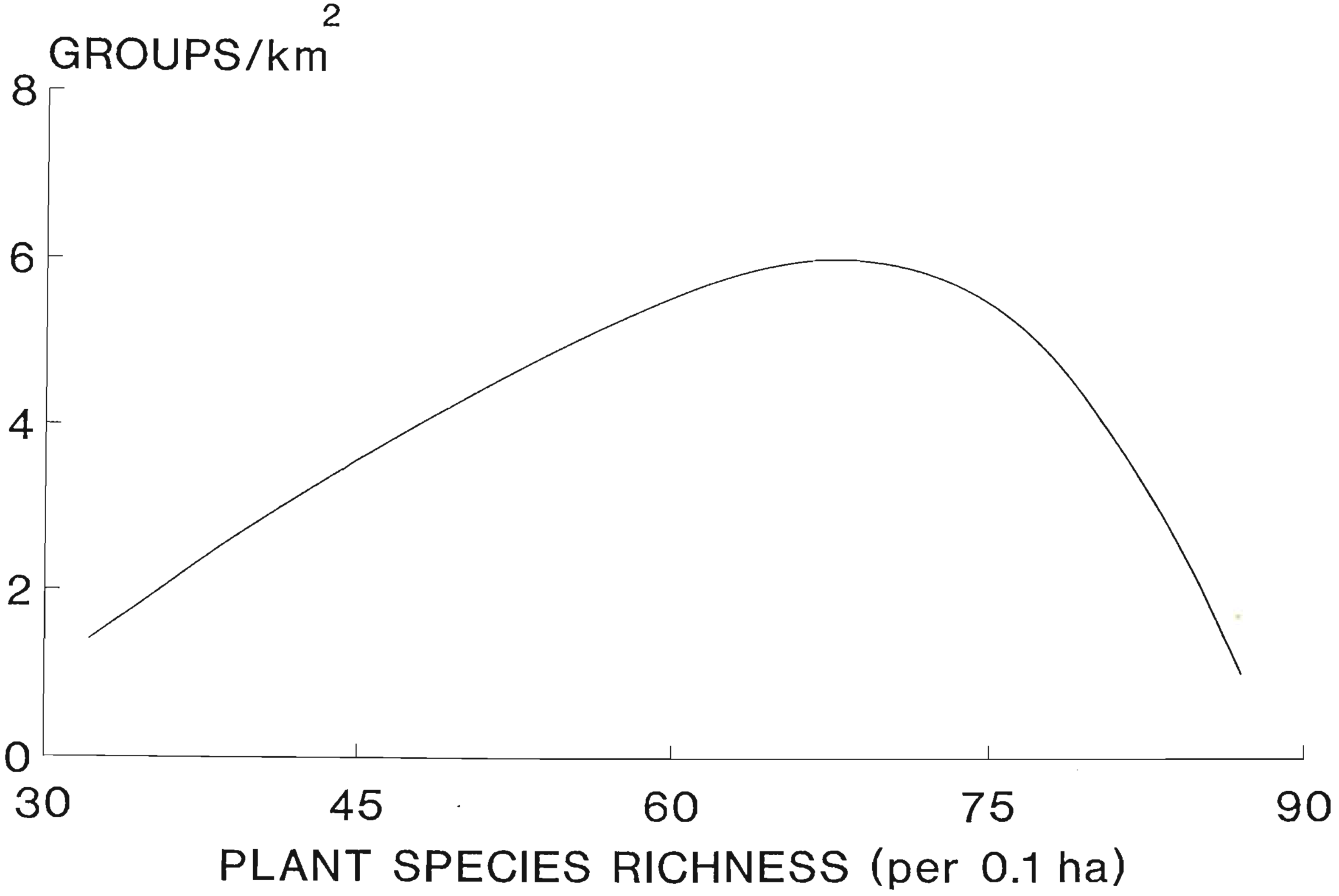


Figure 10.6. A heuristic curve illustrating the probable relationship between social group density and plant species richness (per unit small area 0.1 ha) for forests in Natal. Based on actual values the curve shows that high plant species richness does not necessarily permit high monkey densities.

monkeys at lower densities because the higher plant species diversity means that there are always food resources available, albeit widely dispersed.

For example at Ngoye samango density is lower, and the plant diversity is greater than at Cape Vidal and the distance to the nearest potential food tree from a random point is almost three times greater at Ngoye (see Table 10.8). This distance may increase dramatically with even minor changes in food abundance (Lawes et al. 1990). In so far as the primate carrying capacity of a forest is primarily related to the abundance and availability (energy required to obtain food) of food resources, it would seem reasonable to assume that plant species diversity and richness provide a rough index of expected samango density in Natal's forests.

While this study illustrates that a species population density can be influenced by plant species diversity, studies in Cameroun, the Kibale forest of Uganda (Gartlan and Strusaker 1972, Struhsaker 1975, Struhsaker 1981b), and the Amazon (Schwarzkopf and Rylands 1989), clearly demonstrate that species diversity among anthropoids is directly related to tree-species diversity. Here high plant species diversity may limit the carrying capacity of a primate species in a forest, while at the same time providing a wider range of food resources and trophic niches, enabling more than one primate species to live sympatrically.

The generally lower densities of the coastal scarp populations are ascribed to the interplay between high plant diversity, seasonality of plant food production, and the dispersion of food resources. The important conclusion is that high plant species diversity does not necessarily imply high samango population carrying capacities. Where climax forests are concerned population numbers may stabilize at a carrying capacity way below the carrying capacities of the dynamic, younger dune and lowland forests. If one uses Ngoye forest as one of the finest examples of climax coastal scarp forest in Natal (Huntley 1965, Axelrod and Raven 1978), then samango densities in a stable forest community with high plant species diversity, approximate one individual per two hectares.

CHAPTER 11 MANAGEMENT PROPOSALS

11.1 INTRODUCTION

The conservation strategy for the samango monkey must take into account the fact that the survival of the species is most threatened by forest destruction. The success of a management plan for a forest mammal will, therefore, depend on the effective application of sound forest management principles. A management plan for Natals indigenous forests is a high priority. I have avoided discussing forest management options except where they are specifically pertinent to the monkeys and would refer the reader to Geldenhuys (1983), Scheepers (1983), van Dijk (1987), McKenzie (1988) and MacDevette et al. (1989) for the most recent summary and review of indigenous forest management policy in South Africa.

Monkey numbers in Natal are reasonably high and if the protection of forests could be guaranteed, the samango could be removed from Red Data Book status. Despite the latter it would be expedient to manage the samango monkey in Natal in a manner that would maximize its genetic potential. One of the major concerns of conservation biology is the maintenance of genetic diversity within a population (Kimura and Crow 1963, Soule 1980, Lande and Barrowclough 1987). This, in practice, is accomplished by conserving as large a population as possible which in turn requires a large area of habitat. Lande and Barrowclough (1987) show that it is the genetical effective population size that is the primary variable of importance to biologists concerned with monitoring or managing the genetic variation present in a population. While determination of the actual effective population size is difficult in the case of the samango, most of the management proposals presented here are based on methods of improving the genetic variation within a population. As a result the theory behind the conservation proposals presented here, is derived mainly from the concept of, and the debate that has been generated by, the efforts to determine effective population size for various organisms.

I have divided the management action into two plans, the long-term and short-term plan. Long-term plans are concerned with managing genetically viable populations, the preservation of all major forest blocks that contain samangos at present, and developing research priorities regarding the samango monkeys in these large (>1600 ha) forests. The short term plan accepts the limitations of small population size and habitat fragmentation, but acts to improve genetic variation within existing small populations.

11.2 EFFECTIVE POPULATION SIZE (N_e)

Effective population size (N_e) is that optimal number which would maintain genetic diversity and the long term survival of a species (Frankel and Soule' 1981). Put another way, the effective size of a population is the number of individuals in an ideal population that would have the same genetic properties (in terms of genetic drift) as an actual population with its own complicated pattern of demographies, sex ratio, and so on. A wide variety of factors influence the effective population size (Li 1976, Soule' 1980, Frankel and Soule' 1981), for example, the survival to adulthood of progeny, the age of maturity and the number of offspring per adult female per annum, the level of genetic variation in the population, the frequency distribution of progeny among families, and these factors are not easily measurable in wild populations. Lande and Barrowclough (1987) and Harris and Allendorf (1989) provide the most useful review of methods for calculating N_e, however even their simplified equations cannot be used without accurate data on population sex ratio and the number of progeny produced by an individual during its lifetime. Short term studies, such as the present study, do not provide adequate information of this nature.

While the concept of N_e provides a useful theoretical background for maintaining genetic diversity, the actual value of N_e, while useful, is not essential for managing a population in such a way that maximum genetic variability under the circumstances is maintained. Any action taken to increase the population size or its rate of increase will result in a reduction in the rate of loss of genetic variability. The practical management decisions necessary for managing samango monkey populations for maximum genetic variability, depend on our knowledge of: (a) the sex ratio in the adult population, (b) the emigration of the progeny, (c) and the degree and consequences of population size fluctuation.

11.2.1 Adult sex ratio

For the maintenance of genetic diversity a population with a skewed sex ratio need be considerably larger than one where the sex ratio is equal (Kimura and Crow 1963). Samangos live in fairly stable groups where there is a single male to as many as 10-12 females. Fortunately this skewed sex ratio does not hold true for reproductive activity (Henzi and Lawes 1987; 1988). Large numbers of lone males (25 identifiable males at Cape Vidal in the 1986 breeding season alone) may move through the troop and copulate successfully. Maximum genetic diversity is maintained in a population in this way, and effective population size can be somewhat smaller than would be predicted by Kimura and Crow (1963) on the basis of troop structure alone. In addition, genetic diversity within a population can be easily bolstered by artificially moving adult males to and from different populations.

11.2.2 Emigration of progeny

As young males begin to reach sexual maturity they are evicted from the troop by the resident adult male or may leave of their own accord. During my study a young male (white-tip) left the troop and joined a bachelor group that remained in the near vicinity. From the numbers of males that visit a troop during the breeding season it is likely that at least some males cover a fairly large area and visit more than one troop in a population (Henzi and Lawes 1987, 1988). Even the identity of the troop male does not stay constant for long periods. The identity of the resident troop male at Cape Vidal changed from 'pinky' in 1986 to 'yellow eartag' in 1987 who has maintained his tenure into the 1989 breeding season. Adult males will also cover open ground between forest patches, and have been observed 0.5-1.5 km from the closest forest boundaries in the Karkloof (P. Lowry, pers comm.) and in the Fort Nottingham area (R. Nanni, pers comm.). Thus the male progeny become widely distributed with time and do not return to the parent troop when they become reproductively active. In addition to the eviction of males the emigration of a young individual (round yellow eartag) of unknown sex to a neighbouring troop was recorded at Cape Vidal. The emigration and reproductive behaviour of adult males, must result in an almost random mating pattern between male and female, and substantially reduce the chances of high levels of inbreeding within a population.

11.2.3 Population fluctuations

Populations of vertebrates can fluctuate markedly in size. Changes in food abundance, climate and pathogens often account for large fluctuations in numbers. Foster (1982) described widespread starvation of frugivores following climatically-induced fruit crop failures on Barro Colorado Island, Panama, in 1970. Butynski (in press) attributes low blue monkey densities at Ngogo in the Kibale forest to the effects of disease or hunting pressure. In the case of the isolated samango populations, when population 'crashes' occur, the survivors are the progenitors of all future generations and if they contain but a sample of the genes that existed in the original population, future generations will have a corresponding deficit in genetic diversity. Effective population size must be such that it can cope with population declines without drastic loss of alleles and permit a rapid recovery of population numbers.

In the absence of accurate N_e estimates for most vertebrates, Frankel and Soule' (1981) provide a **minimum** effective population size consistent with short-term preservation of fitness at 50 **breeding adult** individuals (my own emphasis). They base this number on calculations that allow for no more than a 1% change in the levels of inbreeding per generation (i.e. loss of heterozygosity will not surpass 1%). These values must be used with caution since they are only crude rules of thumb (see Lande and Barrowclough 1987, for criteria needed to provide reasonable estimates of N_e). In addition they state that where the sex ratio is unequal, the minimum number for the least numerous sex is fifteen. This minimum effective population size is not intended to prevent a loss of genetic variation - only a loss of immediate fitness; i.e. vigour, disease resistance, viability and fecundity (Frankel and Soule' 1981). A hypothetical troop composition (based on my observations) of a single male, eight females, and eleven immature individuals, would require a minimum of four troops (32 adult females and 4 adult males) and 14 bachelor males to satisfy the minimum $N_e=50$ yielding a minimum population size of 94 individuals. The requirement of 32 adult females equates well with Quinn and Hastings' (198) suggestion that local populations contain no fewer than 20 breeding females.

If one examines the frequency distribution of forest size occupied by samangos in Natal (Fig. 11.1), it is clear that the larger proportion of forests (79.2%) do not meet N_e requirements of 940 individuals or 1600 ha for long term survival of the species. The forests that do meet the requirements are: (a) Mist belt mixed Podocarpus forests -

Ngome (3309 ha), Qudeni (3111 ha), Nkandla (2787 ha), Karkloof (2899 ha); (b) Coastal dune forest - coastal forest complex of Maputaland (9721 ha); (c) Coastal lowland forest - Duku Duku (3500 ha); (d) Coast scarp forest - Ngoye (3229 ha); (e) Sand forest - Sihangwane 3542 ha); (f) Swamp forest - Kosi bay area complex (3242 ha). Most forests (87.5%) are large enough to ensure the short term fitness of their populations (i.e. >160 ha but <1600 ha). Those forests that fall below minimum size of 160 ha are smaller forest patches (e.g. Fort Nottingham and Pongola Bush forests) that belong to forest complexes. There are few forests below the potential 160 ha size limit that contain samangos.

Advances in the theory of island biogeography (MacArthur and Wilson 1967, Wilcox 1980, McCoy 1983) suggest that when the total area of an ecosystem is reduced species diversity will decline until it reaches a new equilibrium for the size of the ecosystem. No reduced area, no matter how well protected, can retain all its original species when it becomes an "island" of forest surrounded by other forms of land use. Below 160 ha most Natal forests appear to have undergone this faunal species equilibration with the loss of the samango monkey.

11.4 LONG-TERM MANAGEMENT PLAN REQUIREMENTS

11.4.1 Determine the genetic makeup of existing populations

This is particularly important in view of the small, fragmented, widely separated populations (Mittermeier 1986). The goal of such studies would be to develop an effective management plan for the entire population. Protein electrophoresis, a simple and relatively cheap method, may be an appropriate means of determining the validity of the subspecific division of the samango monkey in Natal. Large sample sizes

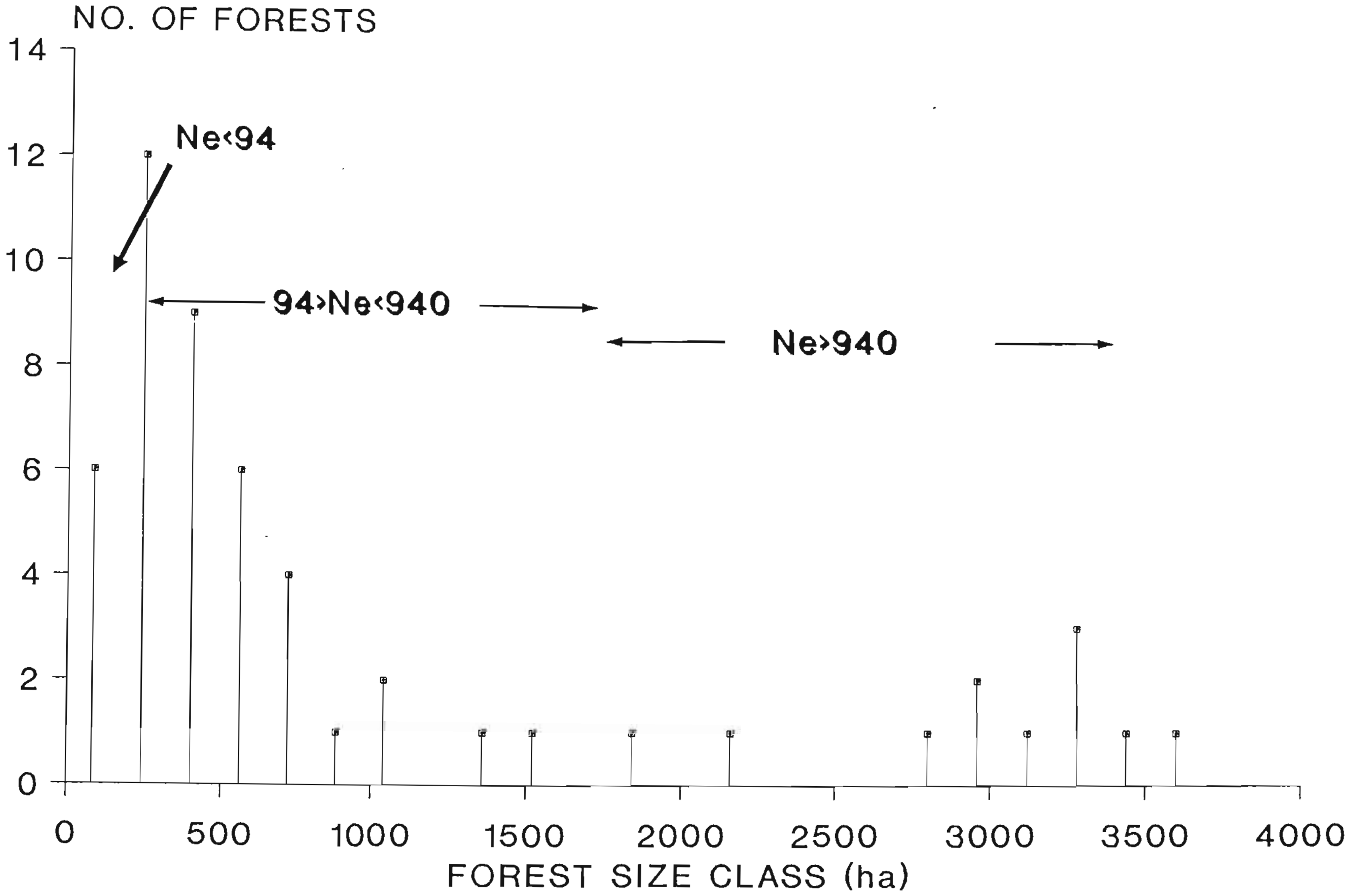


Figure 11.1. Frequency distribution of forest area occupied by samango monkeys in Natal. Graph also shows the frequency distribution of forests of effective size (see text for explanation of Ne).

(individuals) are required of fresh material (blood plasma) from each subspecies and populations within subspecies. The advantage of the method is that one does not have to kill the animal.

A better technique for determining the validity of subspecific status particularly among mammals, has been pioneered in this country by Prof. E.H. Harley (pers. comm.) and co-workers at the University of Cape Town. The technique, which involves the examination of mitochondrial DNA, does however require the sacrifice of the animal.

11.4.2 Maintain the present subspecies as separate entities

In the absence of adequate electrophoretic data, the present subspecies of the samango must be managed separately. Comrie Greig (1979), playing the devil's advocate, provides the argument that subspecies rarely do more than hint at the true extent of genotypic variation within species, and are often merely convenient and subjective labels attached to readily recognizable populations. However, the value of maintaining the genetic integrity of subspecies is supported by many authors (Simon 1966, Lovari 1975, MacFarland and Reeder 1975, Tudge 1976, Comrie Greig 1979). Comrie Greig (1979 p74) goes on to support the latter in "that the conservation of genetic variability within each species is best accomplished by maintaining subspecies and ecotypes as far as possible in their historical, geographical or topographical locations, and not by combining genotypes in one panmictic population through translocation". Tudge (1976) also makes the point that one should not 'blend' subspecies as, apart from other reasons, the subtle differences between subspecies "provide the closest view of evolution at work".

As long as sufficiently large areas of suitable habitat exist, and thus ensure the long-term survival of each subspecies, there is no plausible reason for mixing the subspecies of the samango in translocation procedures. The mixing of subspecies must be seen as a last resort in the event that a catastrophic event, such as an epidemic, critically reduces the chances of short-term survival of a subspecies. This is very unlikely for samangos given the independent nature of more than one large population of each subspecies within Natal.

11.4.3 Manage forest subtypes separately

Conservation and management plans for forest subtypes (i.e. Afromontane forest type, Mountain _Podocarpus_ forest subtype) should be reviewed independently. The floristics of each forest subtype are unique and thus different keystone plant species will be important to the samangos in each subtype. Monkeys moved from one forest to the next must be able to recognize and rapidly respond to changes in food species and food availability. If individuals are moved from one forest subtype to another, they are subjected to a new environment and there may be insufficient time for the individual to recognize and find food resources before starvation results. Samango genotypes will have adapted to specific environments over time, thus where translocations are deemed necessary, and to improve the chances of survival of the animals involved, translocation should take place within forest subtypes.

11.4.4 Conserve all forests with N>940, or area>1600 ha

For all forest subtypes in Natal an effort should be made to conserve at least one forest of a size that provides the potential for long-term survival of the species. The importance of this proposal is emphasized by the fact that for most forest subtypes there is only one forest of suitable size. Forest subtypes and recommended forests are:

Mountain _Podocarpus_ forest
(a) Pongola Bush complex (867 ha)

Mist Belt Mixed _Podocarpus_ forest
(a) Ngome (3309 ha)
(b) Karkloof complex (4826 ha)
(c) Qudeni (3111 ha)

Coastal Dune forest
(a) Coastal dune forest complex of Maputaland north of St Lucia estuary (9721 ha)

Coastal Lowland forest
(a) Duku Duku (3500 ha)

Coast Scarp forest
(a) Ngoye (3229 ha)

Sand forest
(a) Sihangwane (3542 ha)

Swamp forest
(a) Kosi Bay complex (3242 ha)

Notable exceptions from the list are the riverine forests which are all too small to contain populations of N>940.

These large forests should not be linked in any way nor should translocation be permitted between them. This policy takes cognizance of intraspecific variation in genotype, and the need to conserve as much of this intraspecific variation, in its separate populations, as possible (Comrie Greig 1979, Lande and Barrowclough 1987).

11.4.5 Develop long-term samango/forest mammal research programmes

High priority research includes:

(a) The continued monitoring of samango population dynamics in all of the major forest blocks.
(b) Plant phenological studies for determining keystone plant species in each forest subtype.
(c) Radio-tracking adult lone males to determine the extent of their range and therefore the potential level of gene flow in a population.
(d) Determine genetic makeup of populations.
(e) Establish trapping stations for the provision of monkeys for reintroduction programmes.

(f) Determine the causes of low samango density in forests of area > 1600 ha (e.g. Nkandla forest).

An intensive research presence not only serves to gather longitudinal data on the biology of the animals and their habitat, but also functions as a very effective deterrent against poaching and habitat encroachment.

11.4.6 Prevent further habitat encroachment and abuse, and encourage applicable plantation management

Perhaps the most dangerous threat to Natal's indigenous forests is the development of soft wood plantations in the Natal midlands and coastal areas. The exotic trees are often planted up to the edge of indigenous forest. This results in the destruction of the forest boundary during felling operations when trees fall into the indigenous forest. In addition access roads are often run up the edges of plantations alongside the indigenous forest effectively destroying the forest ecotone and chances of forest expansion. The exotic trees often seed into the indigenous forest.

For the monkeys, interaction with the exotic trees eventually leads to disaster. The immediately adjacent pine trees provide new avenues for exploration and a potential food resource to the samangos. The monkeys will eventually investigate the new habitat and can cause considerable damage to a plantation (Omar and De Vos 1970, Von dem Bussche and Van der Zee 1985, Beeson 1987). Unfortunately the only successful method of completely preventing further damage once its has begun, is to systematically shoot all samangos found in plantations. I strongly recommend that conservation bodies liaize with the forestry industry to prevent such action and to provide for a buffer zone of no agricultural/commercial activity around existing forests. Further recommendations for the management of commercial softwood plantations so as to avoid samango damage are (Omar and De Vos 1970, Beeson 1987):

(a) In addition to the natural exploratory tendencies of the monkey, disturbance of any sort is likely to make the monkey excurse into adjacent plantations once they have been so sited. Foresters should resist any temptation to encroach too closely on the existing boundary of indigenous forest. Small pockets of indigenous forest, especially where they contain samangos already, should never be surrounded and isolated by exotic plantation. One can be sure that once samangos begin to use a plantation, a critical threshold of natural habitat disturbance has been reached. It may be worthwhile researching the nature of these disturbances, more so than say the exact nature of the damage to softwoods. For example, Beeson (1987) estimates that for more than 70 years blue monkeys on Zomba tolerated the gradual destruction of their habitat without causing any trouble to the foresters, and then, in 1976, after large areas of indigenous forest were cleared (1973-74), they began using the pine trees as an alternative food source.

(b) Less palatable exotic tree species could be planted in plantations in areas containing high densities of samangos that are already known to use pine trees. Omar and De Vos (1970) found that of the three commonly planted pine species, the less palatable to Sykes monkey (C. m. kolbi) were Pinus patula and P. radiata. There is, however, no evidence to suggest that samango monkeys show the same preferences for these pine species elsewhere, and it is quite likely that these preferences will have to be determined for each site (and only after some loss to the plantation). Planting of apparently less palatable pine species is often discarded as an alternative by foresters because of the lower yields of these species. In addition, I do not recommend this as a viable management option since I believe that the monkeys are versatile enough to be able shift the diet to accommodate these pine species.

(c) Plantation boundaries in areas particularly hard-hit (usually trees between 7-21 years of age (von dem Bussche and van der Zee 1985)) could be patrolled in the early morning and evening when the monkeys are known to feed heavily, and also at those times of the year when damage is most prevalent (e.g. summer months; von dem Bussche and van der Zee 1985).

(d) Plantation owners should be encouraged to maintain a wide strip of open grassland (at least 50m wide) around plantations. While it is known that samangos will cross open grasslands for some distance, if this corridor were also patrolled, it could act as an effective deterrent to regular movements into the pine by the monkeys.

(e) As far as possible plantations should be consolidated, theoretically reducing the boundary area exposed to samango damage. Small patches of plantation should never be planted in clearings within indigenous forest blocks, as this invites discovery and realization by the monkeys that pine is an alternative food species.

(f) Other methods of limiting samango movement into pine plantations have been used with limited success (von dem Bussche and van der Zee 1985), for example electric fencing, scarecrows and noise devices and shooting programmes.

The commonly held belief that samango monkeys take to pine bark because of a lack of natural food or deficiencies in certain nutrients has been dismissed by von dem Bussche and van der Zee (1985), on the grounds that most pine damage takes place at a time when natural fruits are most available (Geldenhuys et al. 1984) in those forests (Entabeni). I would challenge this conclusion. My work at Cape Vidal has shown that protein- rich resources (young leaves and insects) were much less available when fruit was most abundant. The fact that fruit is abundant does not mean that the monkeys are not experiencing a shortage of one or other essential nutrients, in this case protein. Furthermore, the decline in the availability of that nutrient need not be excessive to cause samangos to shift their diet to an alternative source of the same nutrient. Put simply, once samangos recognize the food potential of pines they will continue to use them whenever possible and more so when 'nutrient shortage' occurs.

Even if each pine tree or item is not laden with a particular critical nutrient, because of the size and monospecific nature of pine stands, they represent to the samango a dependable, unvarying, and abundant source of food or nutrients which can be used with relative ease. Once the samangos begin to sample exotic softwoods the damage is done and the resulting commercial losses will have to take their place in the budgets of pulp and paper companies alongside the costs of preventative management. It is important to realize that prevention is easier than cure and those companies in areas where damage to plantations could become a potential problem must be made aware of the importance of applying preventative management polices despite their cost.

Further threats to indigenous habitat take the form of exotic aliens which vigorously outcompete indigenous seedlings to produce large monospecific stands in indigenous forest, for example Solanum mauritianum (e.g. Karkloof) and ginger (e.g. Enon). Grazing cattle in forest is extensively practiced and can have a major impact of forest succession (Cameron and Swart 1988). Wood-cutting operations either for firewood or building materials cause further extensive damage to forest succession and regeneration by the removal of reproductively immature trees.

A further problem is the effect of fires on forest margins. Constant hot burns have for example shrunk the once extensive Nkandla forest (Cooper 1985). I agree with Cooper's (1985) recommendation that firebreaks be burned some distance (30-40 m) from the forest edge.

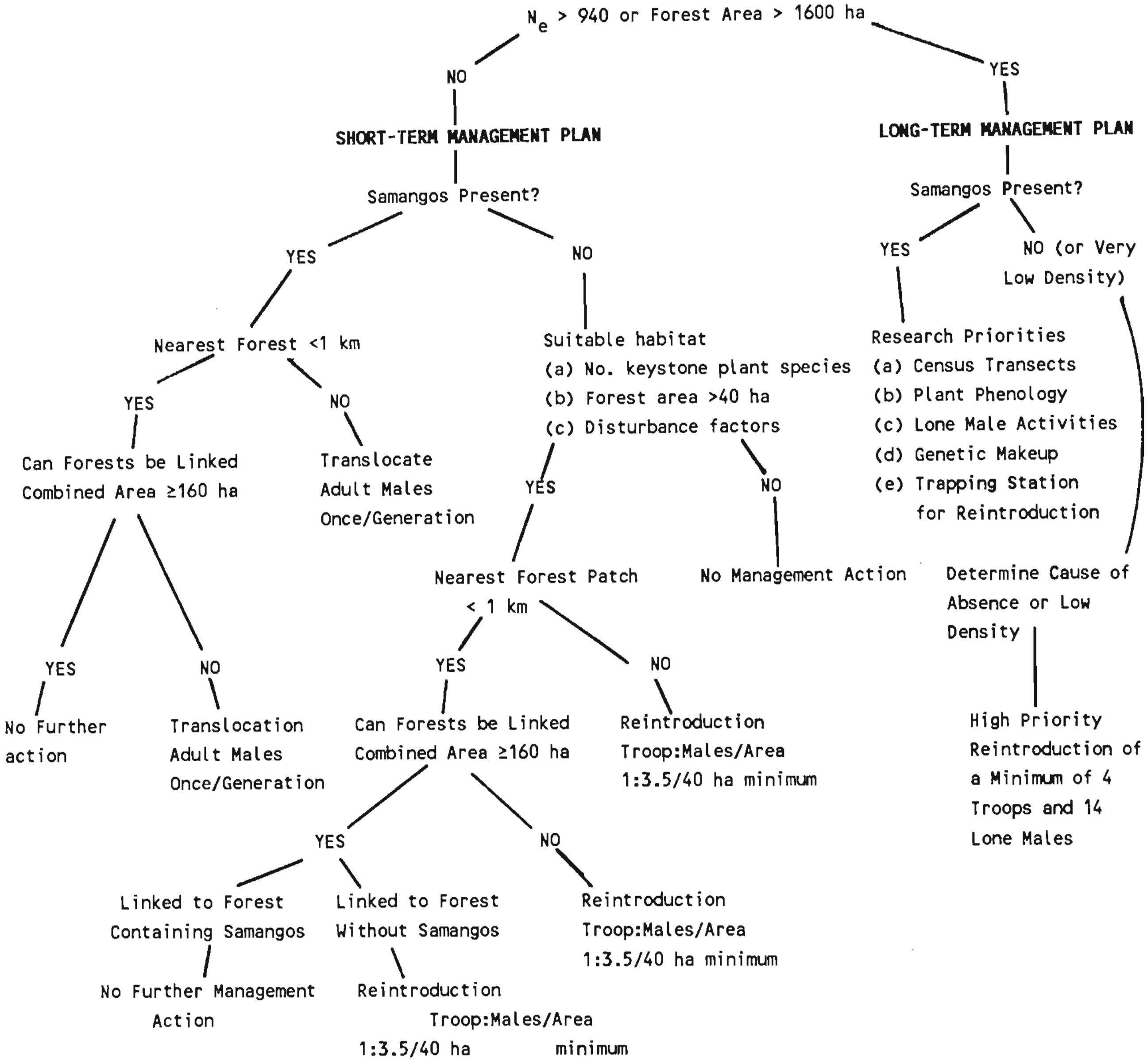
11.4.7 Education

It is my experience that most people have no knowledge of the existence of the samango monkey. Awareness of the samango monkey could be included within the framework of a broader plea for Natal's forests. Education programmes and public awareness campaigns should focus first on people in the immediate vicinity of the protected areas in which the species occurs, and second on government officials who are responsible for making and implementing government policy. Mittermeier (1986) notes the success of using primates as so called "flagship" species in forest conservation awareness programmes.

11.5 SHORT-TERM MANAGEMENT PLAN REQUIREMENTS

Forest size, the distance to the nearest forest patch, and the presence of samango monkeys, will ultimately determine the type of short-term management action applicable for a samango population (Fig. 11.2). Short-term management plans will be concerned with managing those forests between 160 and 1600 ha in area.

Figure 11.2. DECISION FLOW CHART FOR MANAGEMENT OF SAMANGO MONKEYS IN NATAL



NOTES:

Translocation	- implies the removal of samangos to and from (bidirectional) a forest
Reintroduction	- implies the removal of samangos from one forest to another forest of the same subtype, in the near vicinity, and known to have been occupied in the past by samangos.
Linking forests	- implies the provision of corridors via which adult samangos can move between indigenous forest blocks, thus increasing the size of the interbreeding population. Corridors need only provide adequate cover for movement.

Reintroduction ratios are based on requirements for $N_e=50$:

50 adult individuals = 4 troops + 14 lone males

= 32 females + 4 troop males + 14 lone males

Management priorities are to:

(a) Develop some successful means of providing corridors of cover between closely spaced forests.

(b) Establish a set of translocation and reintroduction procedures to act as guidelines for management staff.

(c) Divide the small forests in Natal into 3 categories

  i. Forests that contain samangos
  ii. Forests without samangos, but where they were probably present in the past
  iii. Forests from (i) and, (i) and (ii) that can be linked by corridors.

(d) Determine the conservation priority of a small forest by summing the rank values for conservation criteria.

11.5.1 Corridors

The need for movement corridors as a successful means of conservation management has been extensively discussed by Harris (1985, 1988) and Harris and Gallagher (1989). The prime objective of a corridor is to provide sufficient cover to permit the movement of samango monkeys between two forests, and thus improve the gene flow between otherwise isolated populations. It may be possible to plant gaps between forests with indigenous species (Geldenhuys 1975). However, there are often local climatological and edaphic reasons for gaps and it may be necessary to use hardy exotics to provide cover and protection for indigenous seedlings that are planted. In the southern Cape where indigenous forest has been removed from an area in the recent past, it has recuperated well under the fast growing canopy of exotic species (Geldenhuys 1983, Geldenhuys et al. 1986). Blackwood (Acacia melanoxylon) has proved a most successful nurse species for indigenous forest recuperation in the eastern Cape (Knight et al. 1987).

Allan-Rowlandson (1986) found that bushbuck and duiker could survive entirely within plantations where 'even-aged' management of the plantation had been pursued. Under these conditions intensive activities such as pruning, thinning and felling were limited both temporally and spatially. As a result the diversity of cover and forage within the plantation for these antelope was high. I suggest a similar 'even-aged' policy be used to create and maintain corridors. However, the exotic tree species should not be planted to form a closed canopy since this will alter the light regime, lead to edaphic changes (large amounts of fallen leaf and twigs of the exotic), and ultimately prevent the establishment of indigenous tree and shrub seedlings (Shimizu and Tabata 1985) that may be planted.

Corridors need not be particularly wide to meet the needs of samangos and a minimum width of 100 m should suffice. Corridor width should however consider the requirements of all animals likely to benefit from being able to move between two forest patches. A problem with establishing corridors will be the attitude of the land owner. This may be overcome by recommending that the exotic trees be made available in time as woodlots. Concentrating the planting of exotics on the margins of the corridor will facilitate easy removal with the minimum of damage. Alternatively corridors could be initiated as windbreaks or established in riparian environments, helping to stabilize river banks, and improve the quality of a drainage system.

An advantage of corridors over translocation and reintroduction of animals is that it allows the gradual assimilation of additional genetic variation between populations without the gene pool becoming swamped. In addition corridors promote genetic interchange in two directions and serve to maintain full and balanced plant and animal communities in both interconnected areas.

11.5.2 Translocation and reintroduction

The decision to translocate or reintroduce monkeys should be made with caution. Ideally one must know the size of the forest, the suitability of the habitat, the possible reasons for an absence or low densities of samangos in the forest to which animals are to be moved, and the donor and recipient population densities before considering genetic conservation. Persons trained to comprehend the genetic implications of such translocations must be consulted.

I regard translocation to mean the artificial movement of monkeys to and from existing populations. Reintroduction on the other hand, implies the artificial movement of monkeys to forest where they once occurred but are no longer present. Population genetics models hold that approximately one migrant per generation is sufficient to maintain genetic variability in local populations (Ewens 1979, Lacy 1987). Once the decision to translocate or reintroduce has been made the following guidelines are suggested:

a. Consult the decision flow chart (Fig. 11.2) to determine whether one should move adult males or troop/s.

b. It is recommended that troops are only reintroduced and not translocated.

c. Troops should not be moved into areas that already have a large ($N > 940$) healthy resident population (Strum and Southwick 1986).

d. Troops should also not be reintroduced to forests of less than 160 ha unless the forest can be effectively linked with other forest patches.

e. Reintroduction of troops should involve intact social units as far as possible, to avoid the consequences of fighting due to a lack of kinship relationships.

f. Troops should be stocked at 1 troop/32-40 ha, derived from the mean value of 3.13 troops/km^2 or 1 troop/32 ha (estimated mean troop size = 20 individuals). Stocking levels can be changed according to the different troop densities for each forest subtype.

g. Troop:Lone male ratio for reintroductions should be 1:3.5 per 32-40 ha The ratio is based on a requirement for a minimum of 15 males in an $N_e = 50$ (Frankel and Soule' 1981).

$N_e = 50$ = 4 troops + 14 lone males
= 32 females + 4 troop males + 14 lone males
Ratio Troop:Lone male = 4:14 = 1:3.5

h. From the calculation in (f) lone males should be translocated at 3.5 individuals per 32-40 ha. Although the necessity to follow this stocking level is alleviated if translocation is bidirectional between forests. So an equal number are taken from each forest and translocated to the other.

i. Every effort should be taken to ensure that trapped males are not troop males. Captured males should be marked with a leather punch by making a hole in the cartilage of the ear. This will prevent a recently translocated male being translocated back to his original forest.

j. Translocations are made from the nearest natural population, and not from the most readily 'available' (Comrie Greig 1979). This ensures the highest survival rate of translocated animals by moving animals from floristically similar forest. Thus as far as possible animals should be translocated within forest subtype.

11.5.3 Forests that require management of the resident samango monkey population

Of all the forest subtypes in Natal only the Mist Belt Mixed Podocarus forests provide any opportunity for active management of the samango. These forests tend to be more fragmented and smaller than most (Fig. 11.3), but still collectively account for a large proportion of the total forest area occupied by samango monkeys in Natal (38%). In addition they also form the majority of privately-owned forests (14 573 ha) in Natal, and are the most poorly managed forests. A total of 8114 ha of privately owned 'Mist Belt' forest, or 16% of the total occupied forest area in Natal, are used by samangos. The sum of all privately-owned (or unprotected) forests, occupied by samangos, for all other forest subtypes together amounts to 905 ha or 2% of the total area of forest occupied by samangos in Natal (refer Table 10.4). Mist Belt Mixed Podocarpus forests thus represent

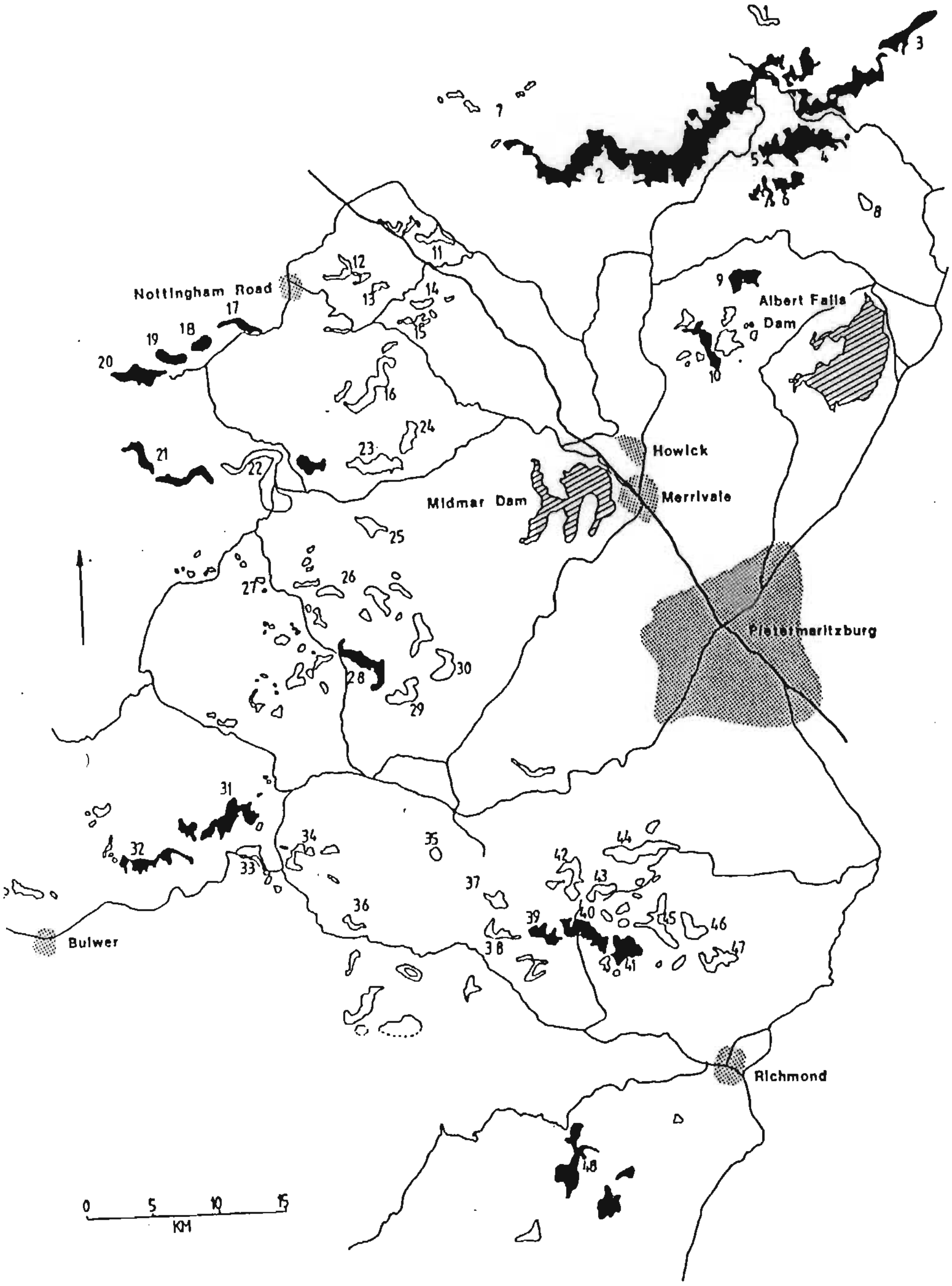


Figure 11.3. The geographical distribution and relative areas of Afromontane Podocarpus mist belt forests in the Natal midlands. Shaded areas represent those forest in which samangos are known to occur. Forests are numbered and their respective names are given below:

1. Kildare 2. Karkloof 3. Blinkwater 4. Holbeck 5. Mbona 6. Amberley 7. Sherwood 8. Newington 9. Hawkstone 10. The Start 11. Boschhoek (north) 12. Willowstream Park 13. Glen Airum 14. Boschfontein North 15. Boschfontein South 16. Linwood 17. Onverwacht/The Grange 18. Lion's Bush 19. Fort Nottingham 20. Overbury 21. Umgeni Poort 22. Dargle Complex 23. Maritzdal 24. Carlisle 25. Hopedale 26. Boschhoek (south) 27. Nhlosane Complex 28. Elandshoek 29. Pinewoods? 30. Vaalhoek 31. Mt. Shannon 32. Camden 33. Lundy's Hill 34. New Forncett Complex 35. Elandskop 36. Nooitgedacht 37. Hamilton 38. Collingham 39. Keerom 40. Newborough Grange 41. Enon 42. Recovery 43. Trewirge 44. Rockeby Park 45. Onrust ? 46. Onrust ? 47.

extremely important samango populations which, due to their small size, will need active management to ensure their genetic viability and short-term survival.

Cooper (1985) proposed the grouping of these small- to medium-sized forests in private ownership into 'conservancies'. It is doubtful whether concervancy management of forests is intensive enough for successful samango conservation. Although 15 possible groupings were proposed (see Cooper 1985, p52-54), not all are practical for samango management because of the large distance between patches and as samangos are not present in some groupings. While I do not dismiss the need to include reasonably closely spaced forests (1-3 km) into unified conservation areas, to provide practical management options one has to fine-tune Cooper's (1985) divisions to provide subcomplexes where forests are in close proximity and could be joined by corridors. Illustrated in Figure 11.3 is the major portion of the northward trending arc of fragmented Mist Belt Mixed Podocarpus forests around Pietermaritzburg. Time did not permit me to establish the full extent of samango distribution in the area. Questionnaires and conservation zone officers could be used to fill the gaps in the distribution.

Mist Belt Mixed Podocarpus forests where active short-term management strategies are recommended:

(a) Corridors or translocations (if corridors are not feasible)

i. Dargle forest (194 ha)
ii. Byrne Group - includes Newborough Grange (602 ha) and Enon (281 ha) forests, although it may be necessary to translocate males to Osgodsby (150 ha)
iii. New Forncett forests (110 ha), if monkeys are present.
iv. Umgeni Poort forests (233 ha)
v. Fort Nottingham area forests (± 175 ha)
vi. Mbona forests - Holbeck (745 ha) and Amberley (254 ha)
vii. The Start forests (552 ha)

(b) Reintroductions

Survey work needs be completed to provide a full list of forests not occupied by samangos in the Natal midlands area. The Boschhoek (near N3), Willowstream Park, Boschfontein North complex and Boschfontein South complex are to the best of my knowledge unoccupied by samango monkeys and may make suitable sites for reintroduction.

Reintroduction of the C. m. erythrarchus subspecies, as a conservation proposal is complicated by the ethics of moving individuals into areas that may not ever have been populated by samangos. The causes of the absence of samangos (C. m. erythrarchus) from the coastal dune and lowland forest south of the Umfolozi river are debatable (Lawes 1989) and are discussed briefly elsewhere in this chapter. The range of the C. m. erythrarchus subspecies is extensive, from northern Natal, through the eastern Transvaal and into Zimbabwe. There is no apparent need to extend the range of the subspecies further southward in Natal by reintroduction.

11.5.4 Conservation priority indices for forests

A conservation priority rating, based on features of habitat quality, and plant species and faunal diversity, could be assigned to each forest. This would permit the best application of time and money for indigenous forest management and would ensure that conservation efforts are coordinated to include as many features of the forest and its inhabitants as possible.

A conservation priority rating for forests will of necessity be based on a number of criteria. Guidelines for selecting forest habitat for protection are discussed in McNeely et al. (1987). A tendency to overemphasize ecological criteria in determining conservation priorities should be balanced with scientific, educational, social, economic and pragmatic criteria (Kellert 1985, McNeely et al. 1987).

For the indigenous forests of Natal I suggest that forests be ranked in order of conservation priority according to the summed scores for the following criteria (Adamus and Clough 1978, Kellert 1985, Oates 1986b, McNeely et al. 1987, Bartholomew 1989):

a. Forest size
b. Forest disturbance
    i. Hunting/poaching
    ii. Traditional utilization/medicine
    iii. Firewood and pole removal
    iv. Cattle grazing
    v. Fire
    vi. Agricultural encroachment
    vii. Strip mining/industrial threat
c. Ownership and availability
d. Floral endemics
e. Faunal endemics
f. Endangered species
g. Rare and vulnerable species
h. Plant species diversity
i. Long-term economic benefit
    i. Watershed protection
    ii. Tourism
j. Social acceptance
k. Urgency of conservation action i.e. immediate action required to avert serious threat.
l. Management feasibility.

The short-term and long-term survival of the samango monkey in Natal depends, almost entirely, on sound forest management policies. This point cannot be emphasized enough. Because forest destruction is often a gradual process, occurring over many human generations, the effects are not obvious or are ignored as unimportant at the present time. There is a very real danger of many of the indigenous forests of Natal being reduced to below acceptable size while we wait and watch. The samango monkey is entirely confined to forest of one type or another. The relationship between population density and forest area, and the same relationship with plant species richness and plant diversity per unit area (see Chapter 10), imply that samango monkey population density is sensitive to the condition of different forest types. The samango monkey can, therefore, act as a good indicator species for determining the condition and faunal carrying capacity of our forests. This study has provided evidence for the need for cautious management of both forest flora and forest fauna, and emphasizes the role that monitoring samango monkey populations can play in aiding this process.

APPENDICES

The appendices have been arranged and numbered according to their order of appearance in each chapter. Thus Appendix 5.2. refers to an appendix cited in Chapter 5 and is the second appendix cited in that chapter. This should make the use of appendices and the task of cross referencing data easier.

C. pygerythrus

C.m. labiatus

C.m.erythrarchus

Appendix 1.1. Non-denaturing polyacrylamide gel electrophoresis (7.5%) of liver extract from the vervet monkey and both samango subspecies. In each case only a single individual was used and sample size is thus very small. The arrows show bands of difference between the

Appendix 1.2. Body measurements and physical description of samangos monkeys from the southern African subregion.

Table 1.2.1. Body measurements (mm) from adult male and female samango monkeys (_C_. _m_. _erythrarchus_).

Measurement	Adult Male (n=5)	Range
Mass (kg)	7.16	6.2-7.8
Chest circumference	383	355-405
Waist circumference	330	292-365
Upper arm circumference	150	136-166
Trunk height	368	335-385
Foot length	153	147-156
Tail length	707	680-730
Head and body over curves	595	564-616
Sitting height	491	425-530

Measurement	Adult Female (n=2)
Mass (kg)	4.45
Chest circumference	296
Waist circumference	287
Upper arm circumference	102
Trunk height	299
Foot length	123
Tail length	591
Head and body over curves	468
Sitting height	382

Table 1.2.2. Mass of adult samangos _C. m. labiatus_ from the Karkloof forest (McMahon 1977).

	Mass	Range
Adult male (n=3)	7.13 kg	6.82-7.73
Adult female (n=9)	4.62 kg	3.64-5.69

Appendix 3.1. Proximate analyses of food items of dune forest tree species (g/100g) on a moisture free basis in order of energy content (kJ/g).

SPECIES	PROTEIN	FAT	CRUDEFIBRE	ENERGY
NEW LEAF				
Isoglossa woodii	25.18	1.57	16.49	13.40
Mimusops caffra	25.29	3.46	10.61	14.16
Celtis africana	20.84	1.96	9.46	16.42
Scolopia zeyheri	15.59	1.59	7.79	17.03
Olea woodiana	18.61	4.38	18.39	18.64
Diospyros natalensis	10.69	1.53	24.13	18.79
Acacia karroo	24.79	2.88	18.41	18.97
MATURE LEAF				
Isoglossa woodii	23.30	2.42	15.64	13.42
Scolopia zeyheri	9.16	3.26	11.48	16.42
Strychnos madagascariensis	13.59	2.97	23.98	17.07
Sideroxylon inerme	16.27	2.66	18.37	17.46
Secamone filiformis	16.51	3.65	16.91	17.64
Mimiusops caffra	19.87	2.02	14.99	18.40
Adenia gummifera	24.16	8.56	17.44	20.34
PETIOLE				
Scolopia zeyheri	18.45	2.39	9.78	18.29
FLOWER BUD				
Dovyalis longispina	26.65	1.61	21.45	15.03
Ziziphus mucronata	25.77	2.40	13.91	15.21
Diospyros natalensis	25.91	4.24	13.07	17.36
OPEN FLOWER				
Mimusops caffra	6.03	2.03	7.49	13.04
Isoglossa woodii	24.19	1.99	15.97	15.21
Strychnos madagascariensis	14.60	1.29	20.14	15.55
Grewia occidentalis	17.07	3.68	17.83	15.61
Acacia karroo	17.87	3.40	18.96	16.16
Diospyros inhacensis	23.76	4.16	13.30	17.29
Scolopia zeyheri	20.35	3.04	7.21	17.91

Appendix 3.1. continued

SPECIES	PROTEIN	FAT	CRUDEFIBRE	ENERGY
SETTING FRUIT				
Celtis africana	14.91	1.01	18.88	12.67
Olea woodiana	11.04	3.85	42.66	18.51
Dovyalis longispina	8.16	22.24	11.60	21.11
UNRIPE FRUIT (flesh and skin)				
Celtis africana	15.18	6.97	15.34	8.96
Mimusops caffra	7.35	6.01	7.63	13.04
Acacia karroo	19.17	2.08	38.20	16.25
Rhus natalensis	11.58	3.49	30.64	16.34
Scolopia zeyheri	15.77	1.10	12.49	16.51
Euclea schimperi	7.16	1.87	39.70	16.60
Grewia occidentalis	12.54	3.18	57.34	16.77
Schutia myrtina	7.98	3.02	33.75	16.86
Diospyros natalensis	5.97	1.66	21.73	17.64
Olea woodiana	9.05	14.17	39.09	19.63
Sideroxylon inerme	13.69	15.79	23.66	21.89
FLESH + SEED - unripe fruit				
Diospyros natalensis	7.29	3.41	11.41	17.03
Grewia occidentalis	17.16	23.66	37.41	21.72
SKIN - unripe fruit				
Dovyalis longispina	19.77	4.43	15.56	16.07
Diospyros natalensis	4.89	1.40	29.26	16.94
Adenia gummifera	10.37	2.10	53.63	18.25
RIPE FRUIT (flesh and skin)				
Dovyalis longispina	15.80	3.21	13.71	15.12
Euclea natalensis	4.45	1.79	19.25	16.12
Grewia occidentalis	14.65	4.44	33.71	16.86
Diospyros natalensis	2.73	2.07	16.71	17.16
Rhus natalensis	8.38	5.93	14.80	17.29
Schutia myrtina	6.97	4.92	24.12	17.50
Tricalysia sonderiana	9.66	2.82	16.56	17.64
Strychnos madagascariensis	9.21	0.78	14.41	17.73
Sideroxylon inerme	10.35	9.83	14.86	17.85
Scolopia zeyheri	7.81	4.89	32.72	17.90
Acacia karroo	28.10	7.20	25.34	18.33
Olea woodiana	9.45	3.33	19.48	19.01
Diospyros inhacensis	10.86	2.60	32.70	19.29
Mimusops caffra	6.56	7.19	11.97	19.49
Isoglossa woodiana	16.96	9.20	37.76	20.86

Appendix 3.1. continued.

SPECIES	PROTEIN	FAT	CRUDEFIBRE	ENERGY
FLESH - ripe fruit				
Mimusops caffra	3.72	1.60	2.19	15.38
Ziziphus mucronata	6.55	0.77	8.42	15.63
Diospyros inhacensis	11.30	1.87	11.75	16.60
SKIN - ripe fruit				
Ziziphus mucronata	4.35	1.49	15.98	15.55
Dovyalis longispina	15.40	2.03	12.87	16.89
Strychnos madagascariensis	14.66	0.63	14.10	17.12
Acacia karroo	13.49	1.77	35.99	17.24
Mimusops caffra	6.63	3.55	8.29	17.64
Diospyros inhacensis	7.65	6.28	30.83	20.07
ARIL				
Apodytes dimidiata	5.95	31.58	16.08	22.08
Ochna natalitia	16.55	33.32	13.47	23.28
SEED				
Acacia karroo	33.11	3.48	17.29	18.33
Apodytes dimidiata	6.42	25.05	28.58	20.94
FRUITING SPIKE				
Isoglossa woodii	24.96	2.22	17.36	15.03

Appendix 3.2. Minerals and trace elements in food items from dune forest tree species, expressed as percent content and parts per million respectively.

	Ca	P	Na	K	Mg	Fe	Cu	Zn
SPECIES	%	%	%	%	%	ppm	ppm	ppm
NEW LEAF								
Isoglossa woodii	3.56	0.18	1.09	2.16	2.00	155	0	28
Mimusops caffra	3.36	0.14	1.17	1.56	1.56	200	6	86
Celtis africana	2.79	0.19	0.14	1.13	0.47	175	3	20
Scolopia zeyheri	0.52	0.14	0.25	1.46	0.15	248	4	32
Olea woodiana	0.41	0.15	0.43	1.52	0.11	72	32	14
Diopsyros natalensis	0.52	0.15	0.35	0.79	0.27	35	0	5
Acacia karroo	1.50	0.18	0.36	0.96	0.25	224	0	8
MATURE LEAF								
Isoglossa woodii	4.11	0.16	1.47	1.87	2.40	188	1	25
Scolopia zeyheri	2.09	0.05	0.39	0.61	0.29	269	10	16
Strychnos madagascariensis	1.36	0.17	0.36	1.95	0.53	150	2	13
Sideroxylon inerme	1.56	0.13	0.48	1.19	0.40	278	3	10
Secamone filiformis	0.94	0.16	1.09	1.41	0.40	268	0	23
Mimusops caffra	1.03	0.20	0.50	1.28	0.27	480	12	90
Adenia gummifera	1.45	0.21	0.10	2.96	0.33	210	2	16
PETIOLE								
Scolopia zeyheri	0.66	0.19	0.24	1.50	0.17	110	4	40
FLOWER BUD								
Dovyalis longispina	0.73	0.36	0.54	3.20	0.29	646	6	76
Ziziphus mucronata	1.63	0.35	0.17	2.60	0.38	425	10	35
Diospyros natalensis	0.74	0.31	0.09	1.68	0.16	2520	34	32
OPEN FLOWER								
Mimusops caffra	1.05	0.08	0.07	0.82	0.13	1440	4	236
Isoglossa woodii	2.01	0.28	0.16	2.84	1.36	300	5	48
Strychnos madagascariensis	1.42	0.24	0.13	2.70	0.39	405	7	53
Grewia occidentalis	2.54	0.15	0.21	1.39	0.46	135	4	33
Acacia karroo	0.86	0.19	0.29	1.55	0.17	2190	0	200
Diospyros inhacensis	0.63	0.28	0.12	1.68	0.41	4260	8	28
Scolopia zeyheri	0.51	0.27	0.23	2.25	0.19	224	10	42

Appendix 3.2. continued.

	Ca	P	Na	K	Mg	Fe	Cu	Zn
SPECIES	%	%	%	%	%	ppm	ppm	ppm
SETTING FRUIT								
Celtis africana	8.87	0.22	0.13	1.09	1.30	103	5	23
Olea woodiana	0.38	0.12	0.41	1.30	0.09	60	44	2
Dovyalis longispina	0.19	0.16	0.14	1.77	0.13	75	3	23
UNRIPE FRUIT (flesh and skin)								
Celtis africana	17.55	0.30	0.19	1.14	1.20	128	8	28
Mimusops caffra	0.25	0.07	0.19	1.00	0.12	114	6	86
Acacia karroo	1.22	0.22	0.17	1.33	0.26	60	3	20
Rhus natalensis	0.34	0.17	0.17	2.02	0.20	70	0	10
Scolopia zeyheri	0.62	0.16	0.20	1.83	0.16	96	2	16
Euclea schimperi	0.52	0.11	0.14	0.90	0.24	53	2	10
Grewia occidentalis	0.98	0.14	0.05	1.59	0.25	23	3	23
Schutia myrtina	0.86	0.10	0.14	0.94	0.18	28	0	8
Diospyros natalensis	0.41	0.84	0.26	0.98	0.13	28	16	0
Olea woodiana	0.40	0.13	0.70	0.94	0.08	162	142	8
Sideroxylon inerme	0.41	0.11	0.27	1.37	0.18	173	0	18
FLESH + SEED - unripe fruit								
Diospyros natalensis	0.17	0.19	0.08	0.57	0.12	53	40	28
Grewia occidentalis	0.06	0.33	0.01	1.11	0.22	93	43	50
SKIN - unripe fruit								
Dovyalis longispina	0.21	0.18	0.31	1.55	0.16	205	28	125
Diospyros natalensis	0.46	0.06	0.22	0.70	0.10	46	4	32
Adenia gummifera	0.37	0.13	0.11	2.57	0.19	82	2	18
RIPE FRUIT (flesh and skin)								
Dovyalis longispina	0.21	0.21	0.53	3.20	0.30	124	2	24
Euclea natalensis	0.70	0.95	0.34	0.89	0.31	50	3	11
Grewia occidentalis	0.86	0.16	0.14	1.77	0.30	80	768	33
Diospyros natalensis	0.41	0.05	0.30	0.80	0.08	109	0	64
Rhus natalensis	0.21	0.14	0.11	1.44	0.14	45	0	8
Schutia myrtina	0.77	0.11	0.16	0.84	0.17	120	65	8
Tricalysia sonderiana	0.39	0.21	1.24	1.65	0.48	38	2	13
Strychnos madagascariensis	0.14	0.14	0.13	1.24	0.24	112	4	19
Sideroxylon inerme	0.35	0.11	0.29	1.18	0.15	307	0	19
Scolopia zeyheri	1.12	0.12	0.22	1.01	0.22	62	3	12
Acacia karroo	0.61	0.28	0.11	1.00	0.33	34	2	32
Olea woodiana	0.36	0.18	0.40	2.06	0.12	112	2	16
Diospyros inhacensis	0.31	0.12	0.10	1.21	0.10	80	2	8
Mimusops caffra	0.44	0.05	0.22	0.93	0.11	80	4	118
Isoglossa woodii	0.63	0.21	0.04	1.42	0.51	203	5	30

Appendix 3.2. continued.

SPECIES	Ca %	P %	Na %	K %	Mg %	Fe ppm	Cu ppm	Zn ppm
FLESH - ripe fruit								
Mimusops caffra	0.16	0.01	0.39	0.68	0.10	72	2	106
Ziziphus mucronata	0.27	0.14	0.28	2.30	0.11	28	5	8
Diospyros inhacensis	0.12	0.18	0.13	2.17	0.11	86	147	39
SKIN - ripe fruit								
Ziziphus mucronata	0.50	0.06	0.04	1.50	0.24	50	3	5
Dovyalis longispina	0.18	0.21	0.14	2.50	0.20	150	3	43
Strychnos madagascariensis	0.17	0.13	0.08	1.64	0.36	43	0	28
Acacia karroo	1.16	0.13	0.40	1.52	0.16	122	0	12
Mimusops caffra	0.48	0.04	0.47	1.18	0.12	110	0	112
Diospyros inhacensis	0.22	0.08	0.13	2.00	0.06	96	52	0
ARIL								
Apodytes dimidiata	0.39	0.15	0.51	1.75	0.20	184	11	13
Ochna natalitia	0.17	0.30	0.08	0.70	0.25	50	8	20
SEED								
Acacia karroo	0.44	0.38	0.07	1.17	0.35	58	4	120
Apodytes dimidiata	0.39	0.16	0.19	0.99	0.19	60	15	13
FRUITING SPIKE								
Isoglossa woodii	1.95	0.28	0.34	2.44	1.10	318	3	43

Appendix 4.1. List of the food plants exploited by samango monkeys at Cape Vidal during July 1986 to July 1987. (LB leaf bud, NL new leaf, ML mature leaf, DL dry leaf, FB flower bud, OF open flower, MF moribund flower, SF setting fruit, UF unripe fruit, RF ripe fruit, OL old fruit, ST stems, GA galls, BK bark, GM gum).

SPECIES USED BY MONKEYS	LB	NL	ML	DL	FB	OF	MF	SF	UN	RP	OL	ST	GA	BK	GM
LORANTHACEAE															
Tieghemia quinquenervius						x									
COMMELINACEAE															
Commelina benghalensis			x												
ULMACEAE															
Celtis africana	x	x	x		x	x		x	x	x				x	
FABACEAE															
Acacia karroo	x	x	x	x	x	x	x	x	x	x	x				x
Caesalpinia bonduc		x	x						x	x	x				
Albizia adianthifolia			x												
ERYTHROXYLACEAE															
Erythroxylum emarginatum						x									
RUTACEAE															
Vepris lanceolata		x								x					
Teclea gerrardii									x						
MELIACEAE															
Trichelia emetica										x					
EUPHORBIACEAE															
Drypetes natalensis						x									
ANACARDIACEAE															
Rhus natalensis			x		x	x			x	x		x			
CELASTRACEAE															
Maytenus heterophyla		x				x	x								
Allocasine laurifolia										x					
Cassine aethiopica			x												
ICACINACEAE															
Apodytes dimidiata	x	x			x	x			x	x	x				
Trema orientalis			x		x			x	x	x					
SAPINDACEAE															
Allophylus natalensis	x	x	x		x	x			x	x	x	x		x	
Deinbollia oblongifolia			x												
RHAMNACEAE															
Ziziphus mucronata	x	x	x		x	x		x	x	x		x			
Scutia myrtina									x	x					

Appendix 4.1. /Continued.

SPECIES USED BY MONKEYS	LB	NL	ML	DL	FB	OF	MF	SF	UN	RP	OL	ST	GA	BK	GM
VITACEAE															
Rhoicissus digitata			x												
Rhoicissus revoilii		x				x									
TILIACEAE															
Grewia occidentalis	x	x	x		x	x		x	x	x	x	x		x	
OCHNACEAE															
Ochna natalitia		x	x			x	x			x	x				
FLACOURTIACEAE															
Scolopia zeyheri (mundii?)	x	x	x			x		x	x	x					
Dovyalis longispina	x	x	x			x		x	x	x					
PASSIFLORACEAE															
Adenia gummifera		x	x			x			x						
Passiflora edulis						x									
ARALIACEAE															
Cussonia sphaerocephala						x									
SAPOTACEAE															
Mimusops caffra		x			x	x		x	x	x	x	x			
Sideroxylon inerme	x	x			x	x		x	x	x	x		x	x	
EBENACEAE															
Diospyros natalensis		x	x		x			x	x	x				x	
Diospyros inhacensis	x	x	x		x	x		x	x	x					
Euclea schimperi	x	x			x	x		x	x	x					
Euclea natalensis									x	x					
OLEACEAE															
Olea woodiana		x	x		x	x	x	x	x						
LOGANIACEAE															
Strychnos madgascariensis	x	x	x		x				x	x	x				
ASCLEPIADACEAE															
Secamone filifolius		x	x							x		x			
Sarcostemma viminale			x												
BORAGINACEAE															
Cordia caffra		x													
VERBENACEAE															
Priva meyeri						x									
Clerodendrum glabrum		x													

Appendix 4.1. /continued.

SPECIES USED BY MONKEYS	LB	NL	ML	DL	FB	OF	MF	SF	UN	RP	OL	ST	GA	BK	GM
URTICACEAE															
Laportia peduncularis		x													
Clausena anisata		x													
ACANTHACEAE															
Isoglossa woodii	x	x	x	x	x	x		x	x	x		x	x		
RUBIACEAE															
Kraussia floribunda			x						x	x					
Tricalysia sonderiana	x	x			x				x	x					
Psychotria capensis										x					
Pavetta revoluta						x									
Catuneragam spinosa			x												
ASTERACEAE															
Brachylaena discolor									x						
Tragia durbanensis			x												
UNIDENTIFIED															
Vine 1 to Vine 3		x													
Bracket fungi															

Appendix 4.2. The rank order (1-5) and percent frequency of use of the top five food species for each month.

RANK MONTH	1	2	3	4	5	
J	D. in	S. mu	A. ka	A. di/M. ca	S. in	
	24	21	12	11	6	n=255
A	M. ca	A. ka	D. in	C. af	R. na	
	31	18	17	8	7	n=363
S	M. ca	A. ka	D. lo	D. in	C. af	
	18	18	16	12	8	n=515
O	M. ca	D. lo	A. ka	I. wo	D. na	
	29	25	10	7	4	n=323
N	M. ca	D. lo	Z. mu	O. na	O. wo	
	36	15	8	6	5	n=347
D	M. ca	R. na	I. wo	A. ka	O. wo	
	31	17	10	8	6	n=250
J	D. na	A. ka	A. gu	S. mu/D. in	A. di	
	12	11	10	9	9	n=374
F	G. oc	O. wo	S. ge	M. ca	D. na	
	25	20	13	11	7	n=304
M	G. oc	C. af	I. wo	M. ca	D. in/O. wo	
	61	4	3	3	2	n=236
A	M. ca	G. oc	A. ka	D.na	I. wo	
	25	23	12	12	9	n=378
M	I. wo	D. na	A. ka	G. oc	S. my	
	31	20	13	7	6	n=557
J	I. wo	A. ka	S. mu	D. na	E. sc	
	41	13	10	9	6	n=588
J	I. wo	A. ka	S. mu	S. ge	S. in	
	25	23	21	7	4	n=542

A. di = Apodytes dimidiata, A. ka = Acacia karoo, A. gu = Adenia gummifera, C. af = Celtis africana, D. in = Diospyros inhacensis, D. na = Diospyros natalensis, D. lo = Dovyalis longispina, E. sc = Euclea schimperi, G. oc = Grewia occidentalis, I. wo = Isoglossa woodii, M. ca = Mimusops caffra, O. na = Ochna natalitia, O. wo = Olea woodiana, R. na = Rhus natalensis, S. in = Sideroxylon inerme, S. ge = Strychnos gerrardii, S. mu = Scolopia mundii, S. my = Scutia myrtina, Z. mu = Ziziphus mucronata.

Appendix 4.3. The rank order (1-5) and percent frequency of use of specific food items for each month. (Species, item, percent frequency of use).

RANK MONTH	1	2	3	4	5
J	S. mu open fl 21	D. in ripe ft 12	A. di ripe ft 11	A. ka mature lf + M. ca ripe ft 10	D. in mature lf 9 n=255
A	M. ca ripe ft 31	D. in ripe ft 10	A. ka leaf bud 9	R. na open fl 5	D. in mature lf 4 n=363
S	M. ca ripe ft 17	D. lo unripe ft 11	A. ka new lf 10	A. di old ft 7	A. ka leaf bud + D. in mature lf 5 n=515
O	M. ca ripe ft 29	D. lo unripe ft 10	A. ka new lf 8	I. wo mature lf 6	D. na fl bud 5 n=323
N	M. ca ripe ft 23	D. lo unripe ft 10	Z. mu new lf 8	O. na ripe ft 6	O. wo fl bud 5 n=347
D	M. ca ripe ft 32	R. na ripe ft 16	I. wo mature lf 10	O. wo open fl 4	D. in new lf 3 n=250
J	A. gu unripe ft 10	A. ka open fl 8	D. na unripe ft + S. mu new leaf 7	A. di open fl 6	D. in fl bud 5 n=374
F	G. oc unripe ft 24	O. wo unripe ft 18	S. ge unripe ft 12	M. ca open fl 7	D. na unripe ft 6 n=304
M	G. oc ripe ft 59	T. or ripe ft 4	C. af ripe ft + A. ka new lf 3	I. wo mature lf + O. wo new lf 2	D. in mature lf 1 n=236

Appendix 4.3. continued.

RANK MONTH	1	2	3	4	5
A	M. ca open fl 25	G. oc ripe ft 22	D. na ripe ft 9	A. ka unripe ft 7	I. wo open fl 4 n=378
M	I. wo open fl 26	D. na ripe ft 19	A. ka mature lf 7	S. my ripe ft + I. wo mature lf 5	A. ka unripe ft 4 n=551
J	I. wo ripe ft 40	A. ka mature lf 13	S. mu open fl 10	D. na ripe ft 9	S. in old ft 4 n=558
J	I. wo ripe ft 24	A. ka mature lf 19	S. mu unripe ft 15	S. ge ripe ft 6	S. in ripe ft 3 n=542

ft = fruit, lf = leaf, fl = flower
A. di = *Apodytes dimidiata*, A. ka = *Acacia karoo*, A. gu = *Adenia gummifera*, C. af = *Celtis africana*, D. in = *Diospyros inhacensis*, D. na = *Diospyros natalensis*, D. lo = *Dovyalis longispina*, E. sc = *Euclea schimperi*, G. oc = *Grewia occidentalis*, I. wo = *Isoglossa woodii*, M. ca = *Mimusops caffra*, O. na = *Ochna natalitia*, O. wo = *Olea woodiana*, R. na = *Rhus natalensis*, S. in = *Sideroxylon inerme*, S. ge = *Strychnos gerrardii*, S. mu = *Scolopia mundii*, S. my = *Scutia myrtina*, T. or = *Trema orientalis*, Z. mu = *Ziziphus mucronata*.

Appendix 4.4. The ranked frequency of use of microhabitats from which insects were taken, and their mean percent of frequency of use for the period July 1986 to July 1987.

MONTH MICROHABITAT	J	A	S	O	N	D	J	F	M	A	M	J	J	n	%
1. Foliage	-	-	11	37	20	7	17	23	5	4	8	2	4	138	33.3
2. Bare branch	-	-	3	16	3	5	29	24	5	6	19	3	2	115	27.7
3. Beneath bark	3	-	9	5	7	3	8	7	6	1	6	1	4	60	14.5
4. Dead twigs	-	-	1	4	-	2	2	2	-	-	-	1	1	13	3.1
5. Dry leaf	2	-	3	1	-	1	1	-	2	-	1	-	-	11	2.7
6. Rotten terminal branch	-	-	-	2	-	1	4	-	1	2	-	1	-	11	2.7
7. Leaf litter	-	-	4	4	-	-	1	1	-	-	-	-	-	10	2.4
8. Spiders web	-	-	1	3	-	-	-	2	1	1	2	-	-	10	2.4
9. Humus in bole	-	-	-	-	-	-	-	-	1	-	-	-	-	1	0.2
10. Rotten log (ground)	-	-	-	-	-	-	-	-	1	-	-	-	-	1	0.2
11. Unknown	3	4	1	7	2	3	3	3	5	2	7	5	-	45	10.8

n=415

Appendix 4.5. The percent of frequency of use of the motor patterns employed to capture invertebrate prey.

MOTOR PATTERN	FREQ. OF USE	% FREQ. OF USE
RAPID MOVEMENTS		
Run first, grab, both hands to mouth	17	4.1
One hand grab, hand to mouth	87	21.0
Two hand grab both hands to mouth	39	9.4
Repeated one hand pick, hand to mouth	2	0.5
TOTAL	145	35.0
SLOW MOVEMENTS		
ONE HAND REACH FOR FOOD ITEM		
Rub on branch, hand to mouth	15	3.6
No rub, hand to mouth, unrepeated	70	16.9
No rub, hand to mouth, repeated	16	3.9
ONE HAND REACH FOR SUBSTRATE		
Mouth to substrate	22	5.3
Item picked, hand to mouth	26	6.3
TWO HAND REACH FOR SUBSTRATE		
Licking food item	2	0.5
Picking with lips	17	4.1
Uncurl, manually examine	11	2.7
MOUTH TO SUBSTRATE, NO HOLDING		
Lick	3	0.7
Mouth applied	64	15.5
TOTAL	246	59.4
INITIAL MOVEMENT NOT SEEN		
Rub, place in mouth	3	0.7
Rub between hands, into mouth	4	1.0
Hold with hands, into mouth	16	3.9
TOTAL	23	5.6

Appendix 5.1. The mean percent proportion of activity types during the periods of fruit abundance and fruit scarcity in each age-sex class. Fruit abundant; July 1986 -October 1986, March 1987-May 1987. Fruit scarce; November 1986-February 1987, June 1987-July 1987.

FRUIT AVAILABILITY AGE-SEX CLASS		Abundant	Scarce	t-Test
MALE				
Feed	mean	29.0	20.2	t=2.18 df=11 N/S
	s	6.9	7.5	
Rest	mean	38.7	56.3	t=2.44 df=11 P<0.05
	s	8.3	15.9	
Move	mean	26.0	19.4	t=1.97 df=11 N/S
	s	6.6	5.4	
Groom	mean	6.2	4.1	t=0.97 df=11 N/S
	s	3.0	4.5	
FEMALE				
Feed	mean	37.7	34.8	t=0.79 df=11 N/S
	s	6.8	6.7	
Rest	mean	30.8	33.6	t=0.73 df=11 N/S
	s	2.8	8.7	
Move	mean	22.0	22.9	t=0.43 df=11 N/S
	s	3.8	3.8	
Groom	mean	9.5	8.7	t=0.36 df=11 N/S
	s	3.4	5.2	
SUBADULT				
Feed	mean	42.1	34.0	t=2.69 df=11 P<0.05
	s	5.5	5.4	
Rest	mean	25.3	25.8	t=0.17 df=11 N/S
	s	4.6	5.6	
Move	mean	24.2	31.5	t=3.01 df=11 P<0.02
	s	3.9	4.7	
Groom	mean	7.4	6.5	t=0.49 df=11 N/S
	s	3.1	3.4	
JUVENILE				
Feed	mean	38.4	33.5	t=1.58 df=11 N/S
	s	5.8	5.2	
Rest	mean	25.1	30.2	t=1.61 df=11 N/S
	s	4.6	6.5	
Move	mean	18.8	22.5	t=4.92 df=11 P<0.001
	s	8.3	2.5	
Groom	mean	7.7	8.2	t=0.26 df=11 N/S
	s	2.7	4.0	

Appendix 5.2. The significant age-sex class activity correlates (Pearsons correlation coeffecient) of fruit, leaf and flower availability over the study period (n=13 months).

ACTIVITY	Feed	Rest	Move	Groom
FRUIT AVAILABILITY				
Male	-	-	-	-
Female	-	-	-0.577	-
			$P<0.03$	
Subadult	0.693	-	-0.591	-
	$P<0.01$	-	$P<0.05$	-
Juvenile	0.578	-0.555	-0.679	-
	$P<0.05$	$P<0.05$	$P<0.02$	-
LEAF AVAILABILITY				
Male	-0.639	-	-	-0.772
	$P<0.01$	-	-	$P<0.002$
Female	-0.549	0.718	-	-
	$P<0.06$	$P<0.01$	-	-
Subadult	-	-	-	-0.709
	-	-	-	$P<0.02$
Juvenile	-	-	-	-0.638
	-	-	-	$P<0.02$
FLOWER AVAILABILITY				
Male	-0.665	0.652	-	-0.642
	$P<0.01$	$P<0.02$	-	$P<0.05$
Female	-0.518	0.675	0.569	-
	$P<0.06$	$P<0.02$	$P<0.05$	-
Subadult	-	-	-0.528	-
	-	-	$P<0.07$	-
Juvenile	-0.535	-	-	-
	$P<0.06$	-	-	-

Appendix 6.1. The monthly frequency and percent proportion of the food items, regardless of species, in the diet for each age-sex class during the study period, July 1986 to July 1987. Food item records collected using the frequency sampling method (see Rudran 1978a).(LB leaf bud, NL new leaf, ML mature leaf, FB flower bud, OF open flower, SF setting fruit, UF unripe fruit, RF ripe fruit, OL old fruit, **Bold face=%**).

a. Male

MONTH	J	A	S	O	N	D	J	F	M	A	M	J	J	TOT
ITEM														
LEAF														
LB	-	2	1	-	1	-	-	-	-	-	-	-	-	4
	-	**6½**	**5**	**-**	**9**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**1½**
NL	-	1	2	2	-	-	1	3	2	2	-	1	-	14
	-	**3**	**10**	**11**	**-**	**-**	**10**	**19**	**14**	**11**	**-**	**4**	**-**	**5½**
ML	4	5	3	1	-	-	1	1	2	2	7	5	4	35
	26½	**16**	**15**	**6**	**-**	**-**	**10**	**6**	**14**	**11**	**25**	**19**	**14**	**14**
TOTAL														
	8	8	9	3	1	-	2	4	4	4	7	6	4	53
	26½	**25½**	**30**	**17**	**9**	**-**	**20**	**25**	**28**	**22**	**25**	**23**	**14**	**21½**
FLOWER														
FB	-	-	-	-	1	-	-	1	-	-	-	-	-	2
	-	**-**	**-**	**-**		**-**	**-**		**-**	**-**	**-**	**-**	**-**	**1**
OF	2	2	-	-	-	-	1	-	-	9	4	4	-	22
	13	**6½**	**-**	**-**	**-**	**-**	**10**	**-**	**-**	**47**	**14**	**15**	**-**	**9**
TOTAL														
	2	2	-	-	1	-	1	1	-	9	4	4	-	24
	13	**6½**	**-**	**-**	**9**	**-**	**10**	**6**	**-**	**47**	**14**	**15**	**-**	**10**
FRUIT														
SF	-	-	2	-	-	-	1	-	-	-	-	-	-	3
	-	**-**	**10**	**-**	**-**	**-**	**6**	**-**	**-**	**-**	**-**	**-**	**-**	**1**
UF	1	5	4	3	-	-	2	8	-	3	3	-	3	32
	6½	**16**	**20**	**17**	**-**	**-**	**20**	**50**	**-**	**16**	**11**	**-**	**10**	**13**
RF	5	14	5	7	7	7	-	-	9	3	14	15	16	102
	33	**45**	**25**	**39**	**64**	**78**	**-**	**-**	**64**	**16**	**50**	**56**	**55**	**41**
OL	3	-	1	-	-	-	-	-	-	-	-	-	-	4
	20	**-**	**5**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**1½**
TOTAL														
	9	19	12	10	7	7	3	8	9	6	17	15	19	141
	59½	**61**	**60**	**56**	**64**	**78**	**30**	**50**	**64**	**32**	**61**	**56**	**65**	**57**
INVERTEBRATES														
	-	-	-	-	-	-	1	1	1	-	-	-	-	3
	-	**-**	**-**	**-**	**-**	**-**	**10**	**6**	**7**	**-**	**-**	**-**	**-**	**1**
EXOTIC														
	-	2	1	1	2	2	3	2	-	-	-	2	6	21
	-	**6½**	**5**	**6**	**18**	**22**	**30**	**13**	**-**	**-**	**-**	**7**	**21**	**8½**
OTHER														
	-	-	1	4	-	-	-	-	-	-	-	-	-	5
	-	**-**	**5**	**21**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**2**
TOTAL FREQUENCY														
	15	31	20	18	11	9	10	16	14	19	28	27	29	247

APPENDIX 6.1. CONT/

b. Female

MONTH ITEM	J	A	S	O	N	D	J	F	M	A	M	J	J	TOT
LEAF														
LB	-	9	13	2	6	2	4	1	-	-	1	-	-	38
	-	**9**	**8**	**1**	**4**	**2**	**2**	**1**	**-**	**-**	**½**	**-**	**-**	**2**
NL	-	6	36	32	36	12	38	14	8	14	10	1	7	214
	-	**6**	**22**	**21**	**25**	**11**	**18**	**9**	**12**	**10**	**5**	**½**	**3**	**11**
ML	17	22	28	10	7	14	14	10	4	11	49	65	67	318
	25	**22**	**17**	**7**	**5**	**13**	**7**	**7**	**6**	**8**	**25½**	**28**	**31**	**16**
TOTAL	17	37	77	44	49	28	56	25	12	25	60	66	74	570
	25	**37**	**46**	**29**	**34**	**26**	**27**	**17**	**18**	**18**	**31½**	**28½**	**34**	**29**
FLOWER														
FB	-	2	-	9	13	11	17	3	1	-	1	-	-	57
	-	**2**	**-**	**6**	**9**	**11**	**8**	**2**	**2**	**1½**	**½**	**-**	**-**	**3**
OF	16	5	12	1	-	7	44	13	1	45	36	23	3	206
	24	**5**	**7**	**½**	**-**	**7**	**21**	**9**	**1½**	**32**	**18½**	**10**	**1**	**11**
TOTAL	16	7	12	10	13	18	61	16	2	45	37	23	3	263
	24	**7**	**7**	**6½**	**9**	**17**	**29**	**11**	**3**	**32**	**19**	**10**	**1**	**14**
FRUIT														
SF	-	-	2	-	-	2	12	1	-	2	1	-	1	21
	-	**-**	**1**	**-**	**-**	**2**	**6**	**1**	**-**	**1½**	**½**	**-**	**½**	**1**
UF	2	1	13	27	18	4	53	79	7	17	15	14	43	293
	3	**1**	**8**	**17½**	**13**	**4**	**25**	**53**	**10**	**12**	**8**	**6**	**20**	**15**
RF	22	47	34	42	52	45	-	3	43	46	57	125	80	596
	32	**47**	**21**	**27**	**36**	**43**	**-**	**2**	**63**	**33**	**29**	**53**	**37**	**31**
OL	8	4	21	-	-	-	-	-	-	1	5	2	4	45
	12	**4**	**13**	**-**	**-**	**-**	**-**	**-**	**-**	**½**	**2½**	**1**	**2**	**2**
TOTAL	32	52	70	69	70	51	65	83	50	66	78	141	128	955
	47	**51**	**42**	**44½**	**49**	**49**	**31**	**57**	**73**	**47**	**40**	**60**	**59**	**49**
INVERTEBRATES	1	1	1	15	1	-	7	3	-	1	3	-	-	33
	1	**1**	**½**	**10**	**1**	**-**	**3**	**2**	**-**	**½**	**1½**	**-**	**-**	**2**
EXOTIC	-	3	1	4	1	1	4	4	-	1	-	1	8	28
	-	**3**	**½**	**2½**	**1**	**1**	**2**	**3**	**-**	**½**	**-**	**½**	**4**	**1**
OTHER	2	1	5	12	9	6	16	15	4	3	15	3	3	94
	3	**1**	**3**	**8**	**6**	**6**	**8**	**10**	**6**	**2**	**8**	**1¼**	**1**	**5**
TOTAL FREQUENCY	68	101	166	154	143	106	209	146	68	139	193	234	216	1943

APPENDIX 6.1. CONT/

c. Subadult

MONTH	J	A	S	O	N	D	J	F	M	A	M	J	J	TOT
ITEM														
LEAF														
LB	-	20	9	2	1	2	1	1	-	-	-	-	-	36
	-	**16**	**7**	**3**	**2**	**6**	**2½**	**2**	**-**	**-**	**-**	**-**	**-**	**4**
NL	1	5	21	11	8	3	7	2	2	5	3	-	3	71
	1	**4**	**15**	**15**	**15**	**8**	**16**	**4**	**4**	**13**	**5**	**-**	**5**	**9**
ML	18	20	14	7	1	4	4	4	3	2	7	14	13	111
	25	**16**	**10**	**10**	**2**	**11**	**9**	**8**	**6**	**5**	**12**	**25½**	**22**	**13**
TOTAL														
	19	45	44	20	10	9	12	7	5	7	10	14	16	218
	26	**36**	**32**	**28**	**19**	**25**	**27½**	**14**	**10**	**18**	**17**	**25½**	**27**	**26**
FLOWER														
FB	-	5	2	5	6	6	1	-	1	-	1	-	-	27
	-	**4**	**1½**	**7**	**11½**	**17**	**2½**	**-**	**2**	**-**	**2**	**-**	**-**	**3**
OF	16	8	3	-	-	2	7	6	-	9	18	5	3	77
	22	**7**	**2**	**-**	**-**	**6**	**16**	**12**	**-**	**24**	**32**	**9**	**5**	**9**
TOTAL														
	16	13	5	5	6	8	8	6	1	9	19	5	3	104
	22	**11**	**3½**	**7**	**11½**	**23**	**18½**	**12**	**2**	**24**	**34**	**9**	**5**	**12**
FRUIT														
SF	1	1	10	-	-	-	3	-	-	-	-	-	-	15
	1	**1**	**7**	**-**	**-**	**-**	**7**	**-**	**-**	**-**	**-**	**-**	**-**	**2**
UF	2	4	19	14	4	2	11	26	7	4	4	3	10	90
	3	**3**	**14**	**19**	**7½ ½**	**6**	**26**	**53**	**14**	**11**	**7**	**5½**	**17**	**11**
RF	22	42	33	17	23	11	1	1	25	13	13	31	18	250
	31	**34**	**24**	**23**	**44**	**31**	**2½**	**2**	**51**	**34**	**23**	**56**	**31**	**30**
OL	7	6	14	-	-	-	-	-	-	-	4	1	2	34
	10	**5**	**10**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**7**	**2**	**3**	**4**
TOTAL														
	32	53	76	31	27	13	15	27	32	17	20	35	30	408
	44½	**43**	**55**	**42**	**51½**	**37**	**35½**	**55**	**65**	**46**	**37**	**63½**	**51**	**47**
INVERTEBRATES														
	4	3	10	10	5	2	5	6	4	3	3	1	1	57
	5½	**2**	**7**	**14**	**10**	**5½**	**11½**	**12**	**8**	**8**	**5**	**2**	**2**	**7**
EXOTIC														
	1	6	1	4	1	3	1	-	3	-	-	-	3	23
	1	**5**	**1**	**5**	**2**	**8**	**2½**	**-**	**6**	**-**	**-**	**-**	**5**	**3**
OTHER														
	-	3	2	3	3	1	2	3	4	2	4	-	5	31
	-	**2**	**1½**	**4**	**6**	**1½**	**4½**	**6**	**8**	**5**	**7**	**-**	**9**	**4**
TOTAL FREQUENCY														
	72	123	138	73	52	36	43	49	49	38	56	55	58	842

APPENDIX 6.1. CONT/

d. Juvenile

MONTH	J	A	S	O	N	D	J	F	M	A	M	J	J	TOT
ITEM														
LEAF														
LB	-	18	12	4	10	-	4	3	-	-	-	-	-	51
	-	17	6	3	6	-	2	2	-	-	-	-	-	2
NL	1	8	35	25	20	15	29	9	8	11	10	3	18	192
	2	7½	17	16	12	11	16	6	7	6	4	1	7	8½
ML	13	10	19	7	8	10	5	8	1	11	34	56	57	239
	21	9½	9	5	5	7½	3	5	1	6	13	18	21	10½
TOTAL														
	14	35	66	36	38	25	38	20	9	22	44	59	75	482
	23	34	32	24	23	18½	21	13	8	12	17	19	28	21
FLOWER														
FB	-	4	-	11	12	12	9	2	3	-	-	-	-	53
	-	4	-	7	7	9	5	1	3	-	-	-	-	2
OF	13	6	19	3	-	9	32	8	3	45	64	26	9	237
	22	6	9	2	-	7	18	5	3	25	25	8	3	10½
TOTAL														
	13	10	19	14	12	21	41	10	6	45	64	26	9	290
	22	10	9	9	7	16	23	6	6	25	25	8	3	12½
FRUIT														
SF	-	-	15	-	-	2	14	1	1	1	-	1	1	36
	-	-	7	-	-	2	8	½	1	½	-	½	½	1½
UF	4	2	26	37	14	8	46	80	5	31	18	14	53	338
	7	2	13	24	8½	6	25	54	5	17	7	4	19	15
RF	19	39	42	39	82	59	4	9	72	72	100	201	103	841
	32	37½	21	25	50½	44	2	6	66	39	40	64	38	37
OL	7	8	23	1	-	-	-	-	-	-	6	-	5	50
	11	7½	11	½	-	-	-	-	-	-	2	-	2	2
TOTAL														
	30	49	106	77	96	69	64	90	78	104	124	216	162	1265
	50	47	52	49½	59	52	35	60½	72	56½	49	68½	59½	55½
INVERTEBRATES														
	2	1	6	19	8	6	32	15	9	6	13	7	4	128
	3	1	3	12	5	5	18	10	8	3	5	2	1½	5½
EXOTIC														
	1	5	1	4	4	6	-	6	2	2	-	3	18	52
	2	5	½	3	3	5	-	5	2	1	-	1	7	2
OTHER														
	-	3	5	5	4	5	4	8	5	4	7	4	3	57
	-	3	2½	3	3	4	2	5	5	2	3	1	1	2½
TOTAL FREQUENCY														
	60	104	203	155	162	132	179	149	109	183	252	315	271	2274

Appendix 8.1. Selection ratios (FSR) for the most commonly eaten specific food items in a month. (Selection ratio = frequency of use of item/(FAI of item x 100)).

Specific food item		MONTH												
		J	A	S	O	N	D	J	F	M	A	M	J	J
A. karroo	lf	-	4.7	37.0	0.2	0.7	0.9	1.1	0.5	0.6	1.7	0.5	-	3.9
	fl	-	-	-	-	-	0.5	2.3	-	-	-	-	-	-
	fr	1.5	5.4	3.1	1.5	-	-	-	-	0.6	3.5	1.8	0.8	4.4
A. dimidiata	lf	-	-	-	-	0.1	0.6	0.1	-	-	-	-	-	-
	fl	-	-	-	-	-	-	2.2	4.4	0.4	-	-	-	-
	fr	311.1	7.5	185.0	-	-	-	-	-	0.4	-	6.0	-	-
C. africana	lf	0.9	0.5	1.1	0.3	-	0.4	-	1.3	-	-	1.3	-	-
	fl	-	6.0	30.0	-	-	-	-	-	-	-	-	-	-
	fr	-	-	100.0	3.7	-	1.4	-	-	8.2	15.0	-	-	-
D. inhacenis	lf	24.0	18.9	38.9	0.1	5.3	0.2	0.2	0.1	0.6	3.0	2.6	7.9	14.0
	fl	-	-	-	-	-	0.2	3.2	-	-	-	-	-	-
	fr	3.0	4.0	1.9	-	-	-	5.0	-	-	-	-	-	-
D. natalensis	lf	0.7	-	0.1	0.03	1.3	0.3	1.1	1.4	0.2	0.4	0.1	0.2	0.2
	fl	-	-	-	0.3	0.01	-	-	-	-	-	-	-	-
	fr	-	-	-	-	-	1.5	12.3	2.7	0.5	6.0	10.6	12.8	4.0
D. longispina	lf	-	3.3	0.2	0.2	2.0	1.3	0.9	-	3.3	1.1	3.3	-	5.0
	fl	-	-	-	0.7	-	-	-	-	-	-	-	-	-
	fr	-	-	41.6	26.6	18.9	-	-	-	-	-	-	-	-
G. occidentalis	fr	-	-	-	-	-	-	-	1.9	3.6	2.2	0.8	1.4	-
I. woodii	lf	-	0.1	0.1	0.1	0.1	0.1	0.1	0.04	0.03	0.1	0.2	0.1	0.02
	fl	-	-	-	-	-	-	-	-	-	0.3	2.8	-	-
	fr	-	-	-	-	-	-	-	-	-	-	-	4.5	2.6
M. caffra	lf	-	-	-	-	-	-	-	-	-	0.3	0.04	-	-
	fl	-	-	-	-	-	-	0.2	0.5	0.3	2.7	0.2	-	-
	fr	0.6	2.0	1.8	2.3	3.9	2.9	38.0	7.7	0.1	-	-	-	2.0
O. woodiana	lf	0.4	0.3	0.5	0.1	0.5	0.2	0.2	0.2	0.2	0.1	0.3	0.1	0.3
	fl	-	-	-	0.4	1.0	0.6	-	-	-	-	-	-	-
	fr	-	-	-	-	-	0.8	1.1	10.0	-	-	-	-	-
S. zeyheri	lf	-	-	-	-	0.04	-	0.9	-	-	-	-	-	3.0
	fl	54.0	-	2.0	-	-	-	-	-	-	-	-	6.2	8.8
	fr	-	1.2	-	-	-	-	-	-	-	-	-	1.1	18.0
S. inerme	lf	-	0.4	-	0.1	0.02	0.02	-	0.05	-	0.4	-	-	0.4
	fl	-	-	2.5	-	2.5	-	0.1	0.2	-	-	-	-	-
	fr	-	2.0	2.2	-	-	-	-	-	-	0.6	1.1	3.8	2.2
Z. mucronata	lf	-	100.0	0.7	0.1	0.3	-	-	-	-	100.0	-	-	100.0
	fl	-	-	-	-	-	1.0	1.2	0.3	-	-	-	-	-
	fr	11.4	-	-	-	-	-	14.3	-	-	1.2	2.5	-	-
Mean FSR		**40.7**	**10.4**	**24.9**	**2.3**	**2.5**	**0.8**	**4.2**	**2.1**	**1.4**	**8.2**	**2.1**	**3.5**	**10.6**
s		**96.5**	**25.2**	**47.6**	**6.6**	**4.8**	**0.7**	**8.9**	**3.0**	**2.3**	**23.9**	**2.8**	**4.1**	**24.4**
V		**237**	**243**	**191**	**287**	**192**	**106**	**212**	**143**	**162**	**291**	**133**	**117**	**230**

Appendix 8.2. The percent proportion of the major food items in the diet by season for the age-sex classes.

		FRUIT ABUNDANT	FRUIT SCARCE	t-Test
MALE				
Leaves	mean	24.9	15.7	t=2.44 df=11 P<0.04
	s	4.3	10.2	
Flowers	mean	11.5	6.7	t=0.66 df=11 N/S
	s	16.8	5.9	
Fruit	mean	56.2	57.2	t=0.12 df=11 N/S
		10.9	16.3	
FEMALE				
Leaves	mean	29.2	27.8	t=0.31 df=11 N/S
	s	10.1	6.3	
Flowers	mean	14.1	12.8	t=0.22 df=11 N/S
	s	11.0	9.4	
Fruit	mean	49.2	50.8	t=0.26 df=11 N/S
		11.1	10.9	
Insects	mean	2.1	1.0	t=0.7 df=11 N/S
	s	3.5	1.8	
SUBADULT				
Leaves	mean	23.9	23.0	t=0.20 df=11 N/S
	s	9.2	5.4	
Flowers	mean	14.8	13.2	t=0.29 df=11 N/S
	s	12.1	6.5	
Fruit	mean	47.5	48.9	t=0.25 df=11 N/S
		9.4	10.8	
Insects	mean	7.1	7.2	t=0.04 df=11 N/S
	s	3.7	4.6	
JUVENILE				
Leaves	mean	21.4	20.4	t=0.23 df=11 N/S
	s	9.7	5.0	
Flowers	mean	15.1	10.5	t=1.04 df=11 N/S
	s	8.4	10.5	
Fruit	mean	53.7	55.8	t=0.36 df=11 N/S
		8.6	11.4	
Insects	mean	5.0	6.9	t=0.68 df=11 N/S
	s	3.8	6.2	

Appendix 10.1. Samango monkey distribution in the indigenous forests of Natal. The superscript * denotes forests in which the presence of samango monkeys requires confirmation.

AFROMONTANE FOREST

MIST BELT MIXED Podocarpus FORESTS	Area	Total Area
State (Forestry) owned		
Ngome	3309	3309
Fort Nottingham	68	68
Ingeli	752	752
Mpeshini*	872	
Lovedale Forest Complex*	600	
		4129
Natal Parks Board (NPB)		
Karkloof	450	450
Soada	238	238
		688
KwaZulu		
Qudeni	3111	3111
Nkandla	2787	2787
Bazini* (near Mpeshini)	250	
Mpeshini*	60	
		5898
Private		
Fort Nottingham	63	63
Overbury	124	124
Umgeni Poort	233	233
Blinkwater	1081	1081
Karkloof	2899	2899
Benvie	101	101
Holbeck	745	745
The Start	552	552
Hawkstone	178	178
Qunu Falls	441	441
Moyeni	258	258
Pateni	362	362
Enon	281	281
Newborough Grange	602	602
Dargle Complex	194	194
Mt. Shannon	569	569
Camden	320	320
Elandshoek	212	212
Kia Ora	213	213
Rensberg Forest Complex*	450	
Kwa Ceza*	235	
Maritzdal*	258	
Boschhoek*	237	
Trewirgie*	283	
Pondwana/Mnyati Complex	212	
		9428
	GRAND TOTAL	21143 ha

Appendix 10.1. continued

MOUNTAIN Podocarpus FOREST	Area	Total Area
State owned		
Incandu*	527	
Normandien*	552	
NPB		
Pongola Bush	532	532
Private		
Pongola Bush (Beneke)	206	206
Pongola Bush (Ekombela)	129	129
Normandien*	76	
		335
Defence Force Area		
Hlatikulu (Biggarsberg)*	252	
	GRAND TOTAL	867 ha

INDIAN OCEAN COAST BELT FOREST

DUNE FOREST		
State owned		
North Bhangazi	700	700
St. Mary's Hill	3000	3000
Cape Vidal	1850	1850
Perriers Rocks	650	650
		6200
NPB		
Sodwana Bay	110	110
KwaZulu		
Kosi Bay	360	360
Lake Sibayi	2100	2100
Black Rock	951	951
		3411
	GRAND TOTAL	9721

Appendix 10.1. continued.

COAST LOWLANDS FOREST		
State owned		
Duku Duku	3500	3500
KwaZulu		
Manguzi	489	489
GRAND TOTAL		3989

COAST SCARP FOREST		
State owned		
Mehlomnyama Forest Complex*	250	
NPB		
Hluhluwe	441	441
Oribi Gorge	1450	1450
Krantzkloof	404	404
Mtamvuna	1113	1113
Dhlinza*	170	
Ngoje*	325	
		3408
KwaZulu		
Gwaliweni	1306	1306
Ngoye	3229	3229
Mfumbe Complex	550	550
Rosslers Gorge	385	385
Ntimbankulu*	495	
Hlabisa*	385	
		5470
Privately-owned		
Rosslers Gorge	390	390
Entumeni*	623	
		390
GRAND TOTAL		9268

RIVERINE FORESTS		
NPB		
Ndumu Reserve area	285	285
Mkuzi Reserve area*	1282	
Privately-owned		
Mkuzi River area	180	180
GRAND TOTAL		465

Appendix 10.2. Disturbance factors noted in forests censused in Natal.

AFROMONTANE FOREST

MIST BELT MIXED *Podocarpus* FOREST

Ngome - Well conserved - State, Forestry Dept. Signs of very old saw pits.

Karkloof - Some areas protected - Natal Parks Board area well conserved. Outside of NPB area wood cutting and bark removal, cattle and poaching snares abundant. Old saw pits abundant. Forest boundaries often fire damaged

Overbury (New Forest) - Private ownership - Mr Ross. Cattle are grazed in the forest, some pole cutting activity and old saw pits are present. No snares were found.

Nkandla - Conserved area - KwaZulu Forestry. Current pole and wood cutting activities obvious. Poles (15-20) found bundled and hidden nexted to the road in two places. Bark removal and snares were also noted in the bottom of valleys on the south-eastern side.

MOUNTAIN *Podocarpus* FOREST

Pongola Bush - Conserved area - Natal Parks Board. Until recently (60 years ago) wood was removed for use by cabinet makers in the area. Old saw pits are abundant. Cattle are grazed in the forest. Major thorough fares cut through the forest. Forest boundaries clearly affected by fire.

INDIAN OCEAN COASTAL BELT FOREST

DUNE FOREST

Cape Vidal - Conserved area - State/NPB. *Acacia karoo* woodlands indicate signs of recent human habitation. No further disturbance factors

COAST LOWLAND FOREST

Duku Duku - Conserved area - State Forestry Dept. Wood removal in the past but little disturbance recently

Appendix 10.2. /continued.

Manguzi	-	Conserved area - KwaZulu Bureau of Natural Resources. The Manguzi forest has been drastically reduced in size in recent years. The forest patch that remains enjoys protection is in good condition and well patrolled but unfortunately very small.

COAST SCARP FOREST

Mtamvuna	-	Conserved area - Natal Parks Board. Well protected on the Natal side of the Umtamvuna River where the census was conducted.
Oribi Gorge	-	Conserved area - Natal Parks Board. Forest located in small patches. The area has a history of logging and this must have had an effect on both the extent of the forest and tree species diversity. From a samango point of view the gorge does not appear to be a prime habitat area.
Ngoye	-	Conserved area - KwaZulu Bureau of Natural Resources. Logging activities were present until as recently as 1924 (NAKOR unpub. rep.). The forest continues to be exploited by local inhabitants. Hugh piles of felled saplings (20-30, 3m lengths) were regularly encountered during my two year stay. Stumps of saplings are present everywhere throughout the forest. Gun shots were heard by myself but I did not find any snares. Cattle graze deep into the forest. Despite the high levels of human activity the Ngoye forest remains as one of the finest examples of its forest type and of indigenous forest in Natal.
Hluhluwe	-	Conserved area -Natal Parks Board. The forest area is relatively small (440 ha) and of poor floristic quality (cf. Whately and Porter 1983) when compared to the Ngoye forest to the south. Fire has been an important factor contributing to the patchy distribution of forest in the area (Berry and Macdonald 1979).

Appendix 10.2. /continued.

SWAMP FOREST

Kosi Bay -	Conserved area - KwaZulu Bureau of Natural Resources. Well conserved remnants of considerable size. There is some encroachment on the forest boundaries by subsistence agriculture and cattle, especially in the region of the upper Sihadla River
Eastern Shores-	Conserved area - State/NPB. Narrow 80 -150 m wide belt which suffers little disturbance.

SAND FOREST

Sihangwane -	Conserved area - KwaZulu Bureau of Natural Resources. Recently proclaimed area.

RIVERINE FOREST

Mkuze Gorge -	Privately owned/NPB. Forest is fairly inaccessible (high up on gorge sides) and on a steep gradient. I was only able to view the forest from 200-300 m distance. Cooper (1985) claims that serious destruction of forest has occurred and the incidence of disturbance must be regarded as high
Ndumu -	Conserved area - Natal Parks Board. Small area of riverine forest that contains a high density of exotic fruit trees such as the guava and mango. The forest is well patrolled and their is certainly no poaching of any sort (wood or animal).

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