428

THE BEHAVIOURAL ECOLOGY OF GREEN MONKEYS (CERCOPITHECUS SABAEUS), AT MT.ASSIRIK, SENEGAL.

by

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Many members of S.A.P.P. helped in the collection of climatological data, and sampling the vegetation. In particular, Sarah Harrison helped with the endless task of recording the vegetation in 2,854 quadrats, as well as gathering much useful information on groups of green monkeys neighbouring the study group. Many people replaced me for lunchbreaks during my all-day follows, and in my absence kept track (mostly!) of the green monkeys. And most importantly, many shared their lives in our very small, isolated community, which made the experience of Mt.Assirik so memorable and formative. Byron Alexander, Jim Anderson, Pam Baldwin, Dick Byrne, Sue Chambers, Steph Hall, Sal Harrison, Cliff Henty, Norman McBeath, Bill McGrew, Martin Sharman, Caroline Tutin, thank you all.

In several ways, life in Senegal would have been less refreshing and far more difficult without the great practical assistance and hospitality shown by Stella Brewer, Bruno Bessanine, Rene Bonang, Michel Fernandez, Claude Lucazau, Patrice Marty, and Nigel Orbell.

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ABSTRACT.

The aims of this study were to provide detailed information on the ecology of green monkeys in Senegal, to examine adaptive behavioural variation by comparing their behaviour with that of other populations of this widespread species-group (C.aethiops), and to use field-data to test hypotheses about adaptive strategies, particularly those concerned with how their foraging patterns changed with the seasonally variable availability and distribution of resources.

Field-work was carried out at Mt.Assirik, in the Parc National du Niokolo-Koba, Senegal. The climate, vegetation, and fauna of the region were described. On most criteria, Mt.Assirik is vegetationally richer in density and diversity of species than two study-sites compared in Cameroon, and one in Kenya, where other populations of C.aethiops have been studied. The demographic structure of the population of green monkeys at Mt.Assirik was assessed. The mean size of groups was 19 monkeys, who lived at a comparatively low overall density of 4.4 per km2. This, the lowest density recorded for C.aethiops, is ascribed to the extensive areas of sparse, unsuitable habitat that constitute a large part of the vegetational mosaic of the region.

A single group of green monkeys was studied in detail, over one complete annual cycle. Aspects of their feeding, ranging, activity-budgets, and territorial behaviour were recorded during 5-day sample-periods each month, in parallel with close monitoring of the changing composition, density, and distribution of important resources.

The green monkeys' diet was omnivorous and diverse, including over 65 species of plants, many invertebrates, and some eggs and meat. Preference was given to fruits and flowers, although particular species were not selected; rather, these foods were eaten in proportion to their availability. Leaves, gum, seeds, and fungi were secondary choice foods. There was little overlap in the composition of the diet from month to month, indicating the strong seasonality of the environment. There was a fairly consistent intake of invertebrates each month.

The monkeys spent between 35% and 55% of their time feeding. Diurnal rhythms of activity were strongly influenced by temperature: the monkeys stopped feeding and travelling when it was either too hot or too cold. On a finer time-scale, feeding was more closely synchronized between the monkeys when they fed on less common species. Several age and sex differences in feeding were found. In particular, females with very young infants fed less than other adults. No particular height-niche was occupied by the monkeys.

The study group ranged over an area of 1.78 km2, the largest range recorded for any *C.aethiops* group. Their ranging patterns differed from month to month, and were significantly influenced by the availability and distribution of food, water, sleeping sites, and habitat-types, and by patterns of intergroup relations. Territorial behaviour itself was strongly influenced by the availability and distribution of key food sources, and the intensity of intergroup encounters varied accordingly.

Many differences in patterns of feeding and ranging between populations of *C.aethiops* are related to the floristic composition of the vegetation, but comparisons were limited by lack of appropriate data on the availability and distribution of food at other sites.

Data on the seasonally varied patterns of feeding, ranging, and activity-budgets, and changing patterns of resource availability, were drawn together to examine the adaptive strategies underlying the monkeys' behaviour. Several models in optimal foraging theory were tested. Time and energy spent in feeding and travelling increased as food-availability increased. Their choice of diet was optimal in that they were more selective when profitable food-items were common: higher proportions of the diet were given over to fruit and flowers when food-availability was high. In parallel with these strategies, a nutritive balance was maintained by consistent inclusion of at least some foliage and invertebrates in the diet, however much fruit was eaten.

CONTENTS.

CHAPTER 1. INTRODUCTION.

CHAPTER 2. STUDY SITE.

CHAPTER 3. METHODS.

CHAPTER 4. VEGETATION.

CHAPTER 5. GREEN MONKEY POPULATION:
DEMOGRAPHY, DENSITY, DISTRIBUTION.

CHAPTER 6. FEEDING.

CHAPTER 7. ACTIVITY-BUDGETS.

CHAPTER 8. RANGING.

CHAPTER 9. TERRITORIALITY.

CHAPTER 10. OPTIMAL FORAGING.

CHAPTER 11. CONCLUSION.

CHAPTER 1.

INTRODUCTION.

1.1 AIMS.

The aims of this study were:

i) to provide detailed knowledge of the far West African form of *C.aethiops*, for comparison with other subspecies, to investigate adaptive variation in the behaviour of this widespread species-group; and for comparison with other selected species of primates, to contribute to a wider understanding of the relationship between social organization and ecology.

ii) to provide quantitative data on the behavioural ecology of *C.sabaeus*. Data on the seasonality of many behaviours are used for testing specific hypotheses concerning adaptive strategies used by the monkeys, including some hypotheses modelled in the framework of optimal foraging theory.

iii) to contribute to a long-term study of the ethology and ecology of four sympatric primate species, *Pan troglodytes verus*, *Papio papio*, *Cercopithecus sabaeus*, and *Erythrocebus patas*, in Senegal.

1.2 INTRODUCTION.

Many species of primates differ widely in their patterns of social behaviour. One of the most likely reasons for this is that species have evolved in response to different environmental pressures. A major approach to understanding this variation in behaviour has been to investigate the relationship between social organization and ecology using the comparative method pioneered by Crook (1964). Comparisons between the ecology of different species are at the heart of understanding the adaptive significance of variation in social organization.

Initial attempts to relate behavioural and environmental differences were made at a general level. Crook and Gartlan (1966) classified species of primates into five grades according to the nature of their diets, habitats, and social organization. These grades represented levels of adaptation in forest, forest-fringe, tree savannah, and arid environments. This classification was revised by several authors (Crook, 1970; Denham, 1971; Eisenberg et al., 1972; Jolly, 1972), although all have assumed ´types´ of social organization and environment, and looked for ways in which these types covaried.

This approach stimulated much research, but had its shortcomings. One problem with broad categorising was that as more data on different populations became available, exceptions to the rule were found, and revision was necessary.

There were examples of more variation in social structure between species allocated to the same ecological grade than between species in different grades (e.g. Clutton-Brock, 1974). Struhsaker (1969) stressed that not all variation in social behaviour can be accounted for in ecological terms, for "each species brings a different phylogenetic heritage into a particular ecological scene". Critiques of the classification schemes pointed out that since social behaviour varies widely between species allocated to the same ecological category, interspecific differences could not be expected to relate closely to ecological variables at such a general level (S.Altmann, 1974; Clutton-Brock, 1974). Both authors pointed out that there are many ways in which different species can react to a similar environment, depending partly on the species' genetic background and partly on the particular environmental variables through which selective pressures operate. As a result, different behaviour patterns can evolve which serve similar functions.

Perhaps the most important reason why correlations were poor is that the ecological variables considered were too broad. For example, the density, dispersion, or seasonality of different resources within a particular habitat can vary greatly, so that one might expect social organization to vary according to the ways in which different species deal with these finer ecological variables. Similarly, the aspects of social organization considered may have been too simplistic (see, for example, Wrangham, 1979).

These problems stimulated a move away from typological comparisons, and led to a more detailed level of research into feeding, ranging, grouping, and anti-predator behaviour as aspects of primate ecology that were most likely to reveal the adaptive significance of differences in social organization. Field studies either looking at one species in several areas of its distribution, or comparing closely related species in a similar habitat, have provided information of the kind used in more detailed comparative analyses by Clutton-Brock and Harvey (1977a, b) and Milton and May (1976). The importance of this approach is that different aspects of social organization and ecology are treated as continuous variables, and the use of multivariate statistics can provide quantified correlations and tease out confounding variables. Although this approach does not elucidate any causality in the relationships between social organization and ecology, the correlations shown do provide a useful basis for hypothesis-testing. Clutton-Brock and Harvey overcame another criticism of earlier work and emphasised phylogenetic influences by showing trends of relationships for genera rather than species.

The work cited above is concerned with ´species averages´. Comparative studies of different populations of a single species have the important advantage of controlling for phylogenetic variation. Some of the more obvious aspects of social organization are very stable across different populations of any species: for example, hamadryas baboons (Papio hamadryas) form harem-groups both in the wild and in zoos (Kummer and Kurt, 1965), and savanna baboons (P.anubis, P.cynocephalus, and P.ursinus) live in multi-male groups throughout Africa (e.g. Hall and deVore, 1965; Altmann and Altmann, 1970). However, important differences in many aspects of the social behaviour of one species in different populations have been shown (e.g. Gartlan and Brain, 1968; Kavanagh, 1978, 1981; Tutin et al., 1981; Yoshiba, 1968). It is constructive to build up a knowledge of the behavioural flexibility of a species, and use this information to examine the important ecological influences on social behaviour. Some species, such as C.aethiops, have successfully adapted to a wide range of habitats, with a very wide distribution, and thus are particularly amenable to research into populational differences in behaviour, while other more specialist species, such as the terrestrial, vegetarian, mountain gorilla (Gorilla gorilla beringei: Schaller, 1963), or the forest-living Cercopithecus monkeys of West Africa (Gautier and Gautier-Hion, 1969; Gartlan and Struhsaker, 1972), are restricted to a narrow range of habitats.

The comparative approach has produced broad conclusions about trends in the evolution of social organization, and generated many testable hypotheses. However, a different approach is needed to understand the details of why animals adopt the particular strategies they do in response to environmental pressures. The emphasis of this approach lies on the behaviour of individuals of a species, analysing their behaviour in terms of costs and benefits. This approach is particularly amenable to modelling based on optimality principles, where sets of alternative behavioural strategies and their consequences can be precisely defined, and behaviour predicted according to optimal strategies. Optimality models seek to predict which trade-off between the various costs and benefits of particular behaviours will give the maximum net benefit to the individual. This has been most fruitfully applied to feeding strategies, under the umbrella of optimal foraging theory (for review, see Pyke *et al.*, 1977). In the case of a single group of monkeys living in a highly seasonal environment, responses to the changing distribution and density of resources can be examined in terms of predicted optimal foraging strategies.

The comparative method and optimality principles are two powerful tools in behavioural ecology that are used to understand how ecological forces shape animal behaviour.

1.3 TAXONOMY AND DISTRIBUTION OF *C.AETHIOPS*.

The species-group *Cercopithecus aethiops* is one of the most successful of the African monkeys, in terms of its wide distribution and abundance. Its geographical range covers most of sub-saharan Africa, with the notable exception of the rain-forests of West and Central Africa (Tappen, 1960).

According to the classification system of Dandelot (1959), (see also Hill, 1966; Napier and Napier, 1967), there are five species within the super-species *C.aethiops*:

C.(a.) sabaeus.......the green monkey.

C.(a.) tantalus......the tantalus monkey.

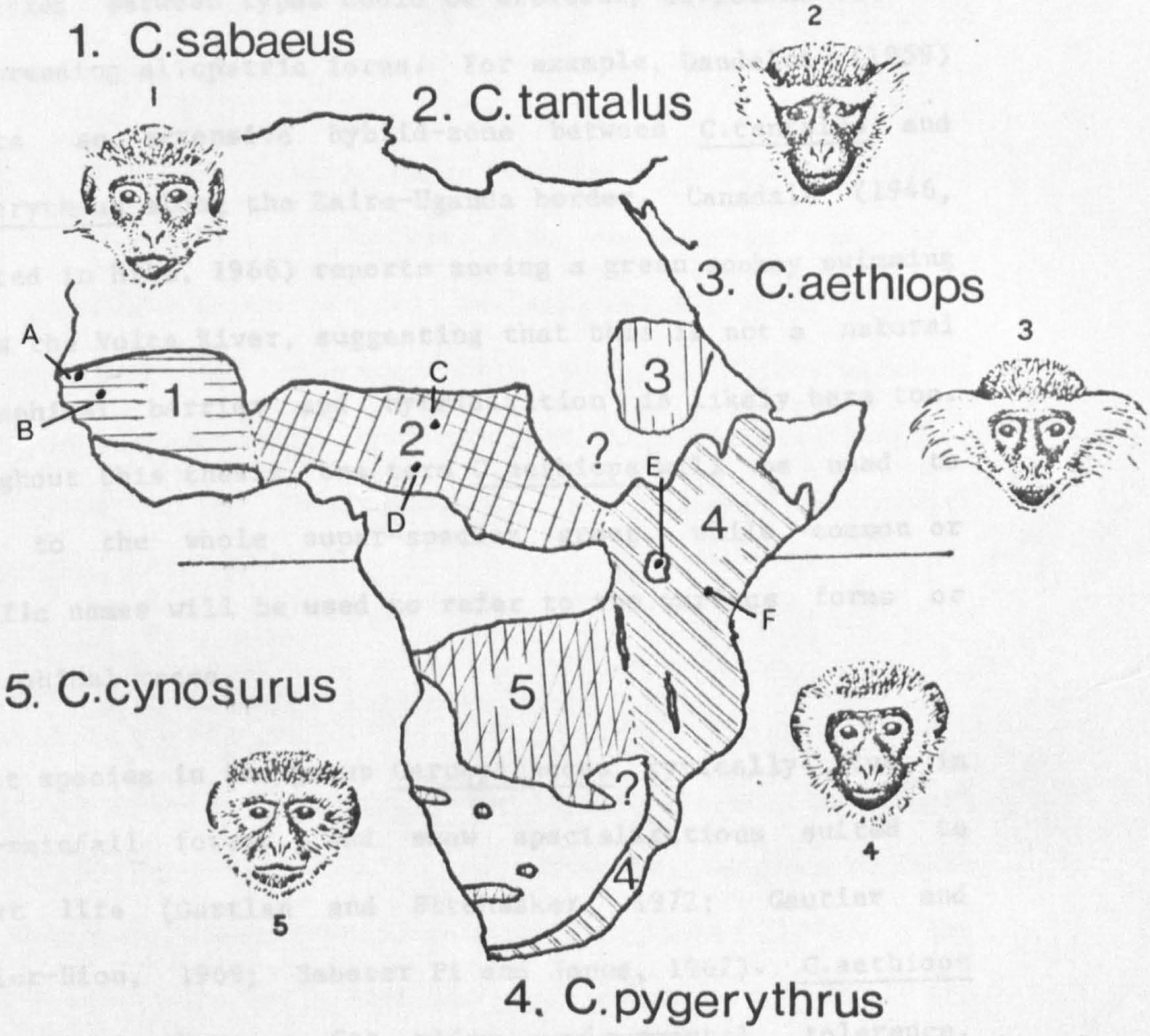
C.(a.) aethiops......the grivet monkey.

C.(a.) pygerythrus...the vervet monkey.

C.(a.) cynosurus.....the malbrouck monkey.

While the aethiops-tantalus groups have 7 subspecies, and the pygerythrus-cynosurus groups have 13 subspecies, sabaeus stands alone as a species without further subdivision.

The geographical distribution of C.sabaeus is restricted to the area west of the Volta and White Volta rivers, and north of the West African forest-zone (Booth, 1956), although Tahiri-Zagret (1976) reports the distribution much further south into the forest-zone in Ivory Coast. C.tantalus extends eastwards between the Sahara and the Central African forest-zone, to northeastern Zaire and western Uganda (Dandelot, 1965). To the east of this border, C.pygerythrus extends from East Africa into South Africa. C.(a.) aethiops occurs in Sudan and Ethiopia, while C.cynosurus is centred on Angola (see Figure 1.1) In addition, the West Indian islands of St.Kitts and Nevis have exotic populations of C.sabaeus descended from monkeys brought from West Africa by 17th century slave traders (Sade and Hildreth, 1965).



A River Senegal.
B Mt.Assirik.
C Kalamaloue.
D Buffle Noir.
E Lolui Island.
F Amboseli.

Figure 1.1. A map showing the distribution of 5 "species" of C.aethiops across Africa. Six major study-sites are also shown.

The allocation of specific status to these various forms is necessary to account for their morphological differences, particularly in pelage and facial hair patterns, but the boundaries between types could be arbitrary divisions between interbreeding allopatric forms. For example, Dandelot (1959) reports an extensive hybrid-zone between *C.tantalus* and *C.pygerythrus* along the Zaire-Uganda border. Cansdale (1946, reported in Hill, 1966) reports seeing a green monkey swimming across the Volta River, suggesting that this is not a natural geographical barrier and hybridization is likely here too. Throughout this thesis, the term *C.aethiops* will be used to refer to the whole super-species group, while common or specific names will be used to refer to the various forms or geographical races.

Most species in the genus *Cercopithecus* typically live in high-rainfall forest, and show specializations suited to forest life (Gartlan and Struhsaker, 1972; Gautier and Gautier-Hion, 1969; Sabater Pi and Jones, 1967). *C.aethiops* in contrast shows a far wider environmental tolerance. Firstly, it is found commonly in riverine vegetation and a variety of savanna woodlands, and also inhabits temperate grasslands, the fringe of evergreen and tropical rainforests, and mangrove and papyrus swamps. Considerable climatic variation is found between these vegetation-types, both in rainfall and in temperature. Secondly, the diet of *C.aethiops* is omnivorous and diverse, including fruit, flowers, foliage, insects, and occasionally meat. And thirdly, Jolly (1964, quoted in Gartlan and Brain, 1968) gives anatomical evidence that arm length increases with increasing terrestriality in *Cercopithecus* monkeys and *Erythrocebus patas*. In this respect, the semi-terrestrial *C.aethiops* is intermediate between the terrestrial *E.patas* and the arboreal *Cercopithecus* species.

The combination of these three factors, the comparative lack of specialization in habitat, diet, and anatomy, suggests a very adaptable animal suited to considerable environmental variability. And evidence built up from field-studies of *C.aethiops* is beginning to show that this adaptability is correlated with flexibility in many aspects of social behaviour.

1.4 FIELD-STUDIES OF *C.AETHIOPS*.

Field studies of *C.aethiops* have varied greatly in length and quality. The problems of observing monkeys in dense vegetation have been described by Aldrich-Blake (1970). Not only can limited visibility and contact-time bias the collection of data, but variability in the approach and methods used by investigators can also limit the level at which comparisons between studies can be made. Some studies have been too short to collect the quantified data needed for a socio-ecological analysis (Baskin and Krige, 1973; Dunbar, 1974; Dunbar and Dunbar, 1974; Krige and Lucas, 1974, 1975; Moreno-Black and Maples, 1977; Poirier, 1972). Other studies have been longer, but have specialised in one aspect of behaviour (deMoor and Steffens, 1972 - radio-tracking of ranging patterns; Lancaster, 1972 - social development of infants; Rose, 1977 - interspecific play). Six long-term field-studies with broader scope and data on various aspects of behaviour and ecology have been done (see Figure 1.1):

- in Senegal: Galat and Galat-Luong, 1976, 1977; 740 hours of observation over 18 months.
- in Uganda: Gartlan, 1966; Gartlan and Brain, 1968; Gartlan, 1969; 1470 hours, 13 months.
- in Cameroon: Kavanagh, 1977, 1978, 1980, 1981; 1090 hours, 14 months.
- in St.Kitts: McGuire, 1974; 7500 hours, 54 months.
- in Kenya: Struhsaker, 1967a, b, c, e, 1971; 2250 hours, 12 months.
- in Kenya: Wrangham, 1981, and Wrangham and Waterman, 1981; three periods totalling 9 months.

The number of hours of observation does not necessarily reflect the quality or quantity of data, as conditions of observation varied greatly between sites. The Galats visited a group of green monkeys in northern Senegal over a period of 18 months, and systemmatically studied their feeding. Gartlan studied an unusual population of vervets on Lolui Island in Lake Victoria, where there were no predators or competitors, but he provided limited quantified data on behavioural ecology. Kavanagh studied three populations of tantalus monkeys in Cameroon, living in different types of habitat. Kavanagh's work is rich in comparative data, but limited to 4-month periods of observation at each site. The work of McGuire and his colleagues on St.Kitts suffered from poor observation conditions, which greatly limited their data, despite many hours spent in the field. Struhsaker carried out a pioneering study of vervet monkeys in Amboseli, Kenya, providing useful data on many aspects of social behaviour, but only few quantified data on ecology. Wrangham also worked in Amboseli, providing a very detailed account of drinking by the vervets, and their feeding in relation to the ecology of two species of *Acacia* tree, the major items in their diet. Recently, other long-term research on vervet monkeys has been completed in Amboseli, focussing mostly on details of social behaviour that fall outside the scope of this thesis (Cheney, 1981; Cheney and Seyfarth, 1980a, b; Cheney *et al.*, 1981; Lee, 1981; Seyfarth, 1980; Seyfarth *et al.*, 1980).

The present study provides detailed, quantified data on many aspects of the behavioural ecology of a well-known group of green monkeys, observed continuously and systemmatically for over a year.

1.5 RATIONALE.

In order to achieve the aims set out above, and as a member of the Stirling African Primate Project (SAPP), this study was carried out at Mt.Assirik in the Parc National du Niokolo-Koba, Senegal. Although basic demographic data were collected on all groups of green monkeys encountered in the study area, I chose a single group as the focus of intensive study, for several reasons: firstly, in order to record the seasonal variations in climate and vegetation, and the monkeys' responses to these changes, observations on the same individuals were needed over a complete annual cycle; secondly, the emphasis of the study was on fine behavioural and ecological detail, which may have been jeopardized had observation time been spread too thinly over several groups. The risk of choosing a group that was atypical of the population was assessed before systemmatic observations began. A third major advantage to following the same group of monkeys over three consecutive years as a member of SAPP was the knowledge of kinship in the group that I built up. Such information is vital for a sociobiological interpretation of many patterns of behaviour.

CHAPTER 2.

STUDY SITE.

2.1 PARC NATIONAL DU NIOKOLO-KOBA.

This study was carried out in the Parc National du Niokolo-Koba, a large park of 8130 km2 situated in south-eastern Senegal (see Fig.2.1). The area was a hunting reserve until the creation of the PNNK in 1954 (Dupuy, 1971). Vegetationally it lies at the border of the Sudan and Guinea savanna zones (McGrew *et al.*, 1981). Two major rivers, the Gambia and one of its tributaries, the Niokolo, cross the park, which is surrounded by subsistence farming communities, but contains no resident human population. The park is open to tourists from December to May, and most visitors remain in the vicinity of the hotel (Simint1) at the mid-western end of the park, leaving the eastern end relatively undisturbed. Mt.Assirik was officially closed to tourists during SAPP´s tenure.

2.2 MT.ASSIRIK.

The Stirling African Primate Project had a research camp near Mt.Assirik, in the south-eastern part of the park (12o53´N, 12o46´W). The main study area covered over 50 km2 around Mt.Assirik, and was chosen for the sympatric occurrence of chimpanzees (*Pan troglodytes verus*), guinea baboons (*Papio papio*), green monkeys (*Cercopithecus sabaeus*), and patas monkeys (*Erythrocebus patas*), which formed the subjects of

Figure 2.1. A map of the Parc National du Niokolo-Koba. The study-site is circled.

Avec l'autorisation de l'I.G.N., document établi d'après la carte au 1/200.000e

SAPP's broad aim, a synecological study of four sympatric anthropoid species in Senegal.

Mt.Assirik, the highest point in the park (altitude 311m), is a low, flat-topped hill, and from its summit plateau, wooded ridges and gullies radiate on all sides (Fig.2.2). About 100m below the summit, the ground levels out into extensive grasslands, woodlands, and treeless laterite plateaux. In several places, erosion has cut deep gorges into the laterite, forming steep-sided valleys between two expanses of plateau. These valleys support narrow ribbons of isolated gallery forest, and a few provide the only permanent streams in the study area. It was one of these, Lion Valley, that formed the core ranging area of the study group of green monkeys.

2.3 FLORA AND FAUNA.

Apart from an average of 4 members of the research team (1976-1979), and 3 members of a small chimpanzee rehabilitation project 7km away (1975-1979), there were no residents near Mt.Assirik. There was no overlap in the areas used by the chimpanzees at the rehabilitation camp and the green monkeys under study. The base stones of a few huts indicated that there had been tiny villages in the region, but reports from local inhabitants surrounding the park suggest that these had been vacated at least 15 years previously. We found no discernable differences in the vegetation at these sites, and no domestic plants. Tourists were extremely rare in this section of the park, owing to its inaccessability.

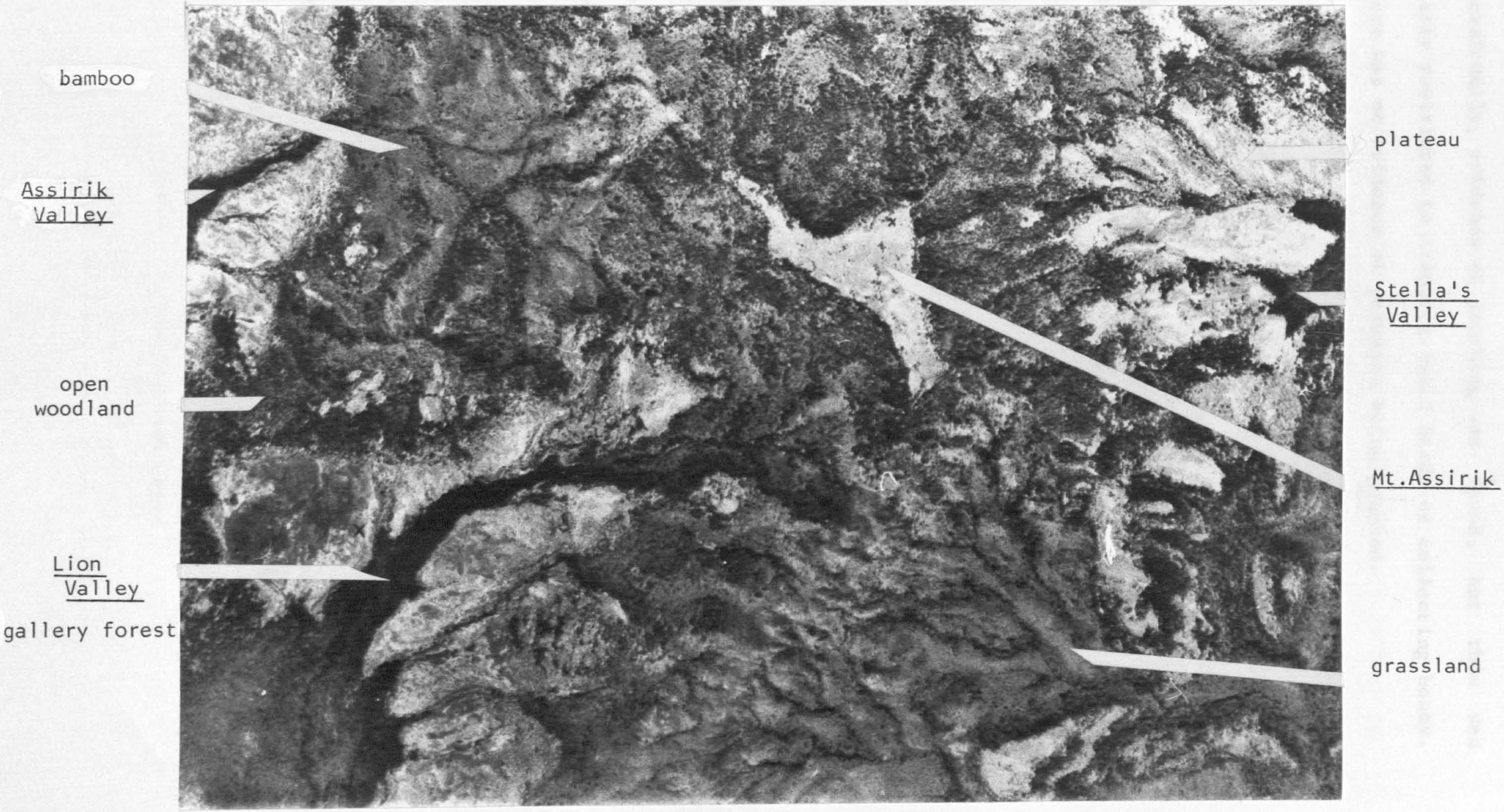


Figure 2.2. Aerial photograph showing the summit plateau of Mt.Assirik, and part of 3 major valleys (including Lion Valley, the core of the study group's home-range). Note the large expanses of treeless, laterite plateaux (white), and bamboo/grassland, compared with the small strips of gallery forest (black), (see chapter 4).

Occasionally, evidence of poaching was found, but this was mostly restricted to trapping small birds or collecting honey. There was no evidence of primates being poached.

This suggests an intact flora and fauna, suffering little human interference in recent years (although some species have become extinct in historical times, e.g. giraffe (*Giraffa camelopardalis peralta*) and topi (*Damaliscus k. korrigum*), see Dupuy, 1971). One notable exception to this is the annual burning of grass that occurs at the beginning of the dry season, in December, as a matter of park policy. In areas particularly susceptible to burning, several species of fire-resistant plants (e.g. *Combretum* sp.) predominate.

A complete list of the fauna of the PNNK appears in Dupuy (1971). Some species that prefer low-lying, wetter habitat in the park were absent from Mt.Assirik, e.g. cob (*Adenata k. kob*) and waterbuck (*Kobus defassa unctuosus*). Table 2.1 lists the wide range of potential predators on green monkeys that occur around Mt.Assirik.

2.4 CLIMATE.

Members of the research team collected climatological data daily for four years. In this section, I shall present only data pertinent to the year of systemmatic study of the green monkeys, from November 1978 to October 1979, unless otherwise stated.

There are two sharply defined seasons which characterize the climate: a dry season from November to May, generally without rainfall, and a wet season from June to October. The dry season starts with gradually decreasing humidity and relatively cold mornings, and with most grasses seeded and drying out, and the leaves on most trees senescing. Annual grass-burning generally occurs in December, after which the landscape changes dramatically, visibility increases greatly, and daily temperatures rise while humidity falls. February is marked by the persistent and desiccating Harmattan, the wind that blows off the Sahara from the north-east. This is the driest time of the year in terms of humidity, and consquently probably the time with the highest demand for drinking water. Although standing water continues to dry up, the humidity rises again in the late dry season, until the build-up of

Table 2.1 A list of the potential predators on green monkeys.

Carnivores:	
Panthera leo	lion
Panthera pardus	leopard
Crocuta crocuta	spotted hyaena
Lycaon pictus	african hunting dog
Canis adustus	side-striped jackal
Primates:	
Pan t.verus	chimpanzee
Papio papio	guinea baboon
Snakes:	
Bitis bitis	puff adder
Naja nigricollis	black cobra
Naja haje	egyptian cobra
Python sebae	python
Large birds of prey:	
Hieraetus spilogaster	Bonelli's eagle
Polemaetus bellicosus	martial eagle

thunderclouds brings the first storms of the rainy season. After this, the new growth of vegetation is very rapid, drinking water is freely available, and air temperatures decrease.

Figures 2.3, 2.4, and 2.5 show the data for rainfall, temperature, and humidity respectively, collected from the woodland site (camp: see methods). Figure 2.6 presents data for maximum and minimum air temperatures at each of three sites, plateau, woodland, and forest, showing microclimatic differences.

There were only small differences in minimum air temperature across the three habitat types, the lowest values (around 18oC) occurring in December. However, there were important differences in maximum air temperatures: April was the hottest month of the year, with maxima on the plateau of around 45oC, and yet maxima in the forest of only 34oC. The annual mean difference in temperature between forest and plateau was 9oC, which has important implications for the behaviour of most animals, especially during the hot months.

Figure 2.7 shows mean monthly humidities at noon for each site, for comparison. Again, there were important microclimatic differences: the forest remained more humid than woodland or plateau throughout the year. The onset of the rains each year was predictable to within several weeks (see also Stern _et al._, 1981), with thunderstorms occurring generally from mid- to late May. Rain usually fell every few days, in downpours of approximately 10 mm. Over 4 years

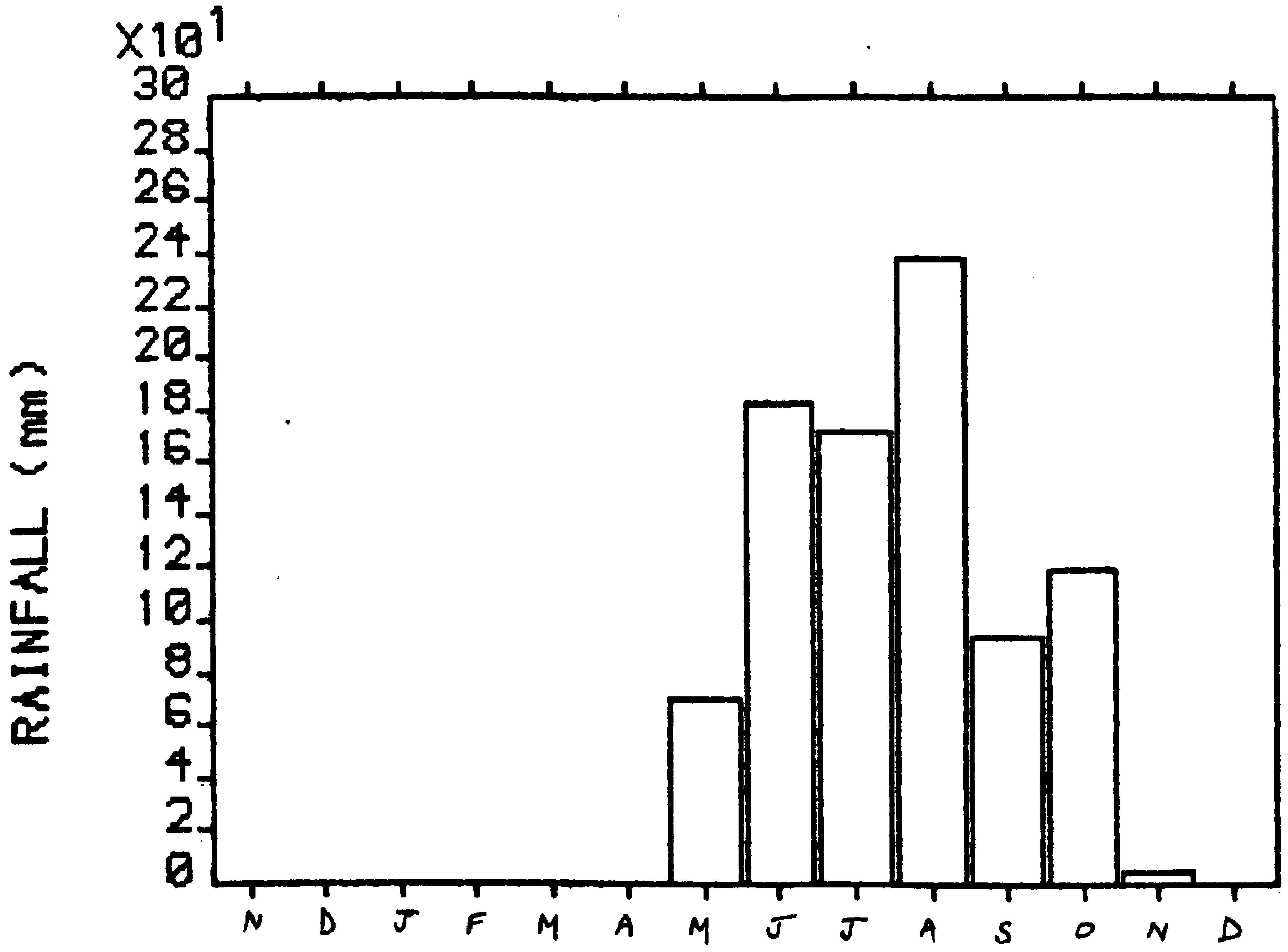


Figure 2.3. Monthly rainfall at Mt.Assirik, Nov 1978-Nov 1979.

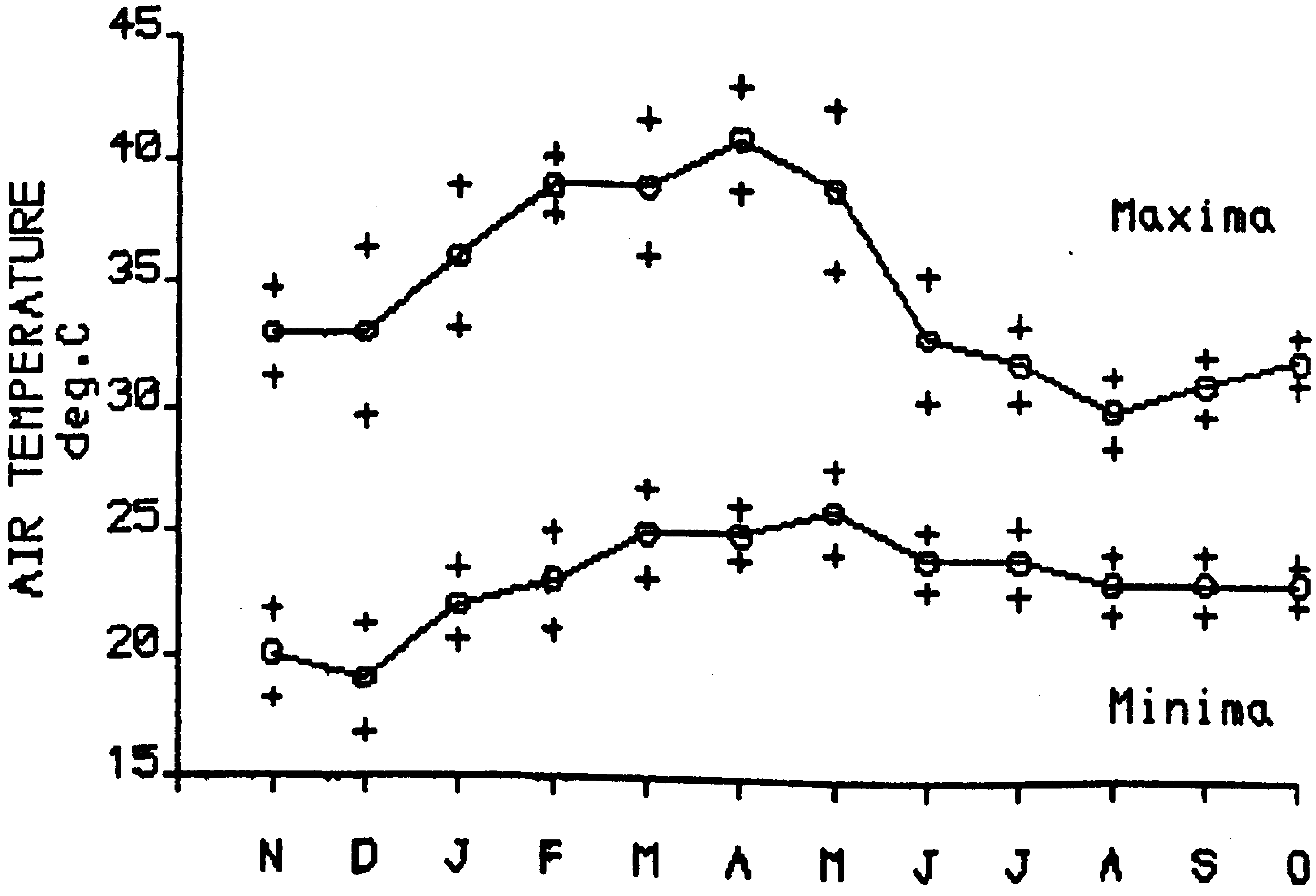


Figure 2.4. Mean monthly maximum and minimum air temperatures (0), and their standard deviations (+), in woodland.

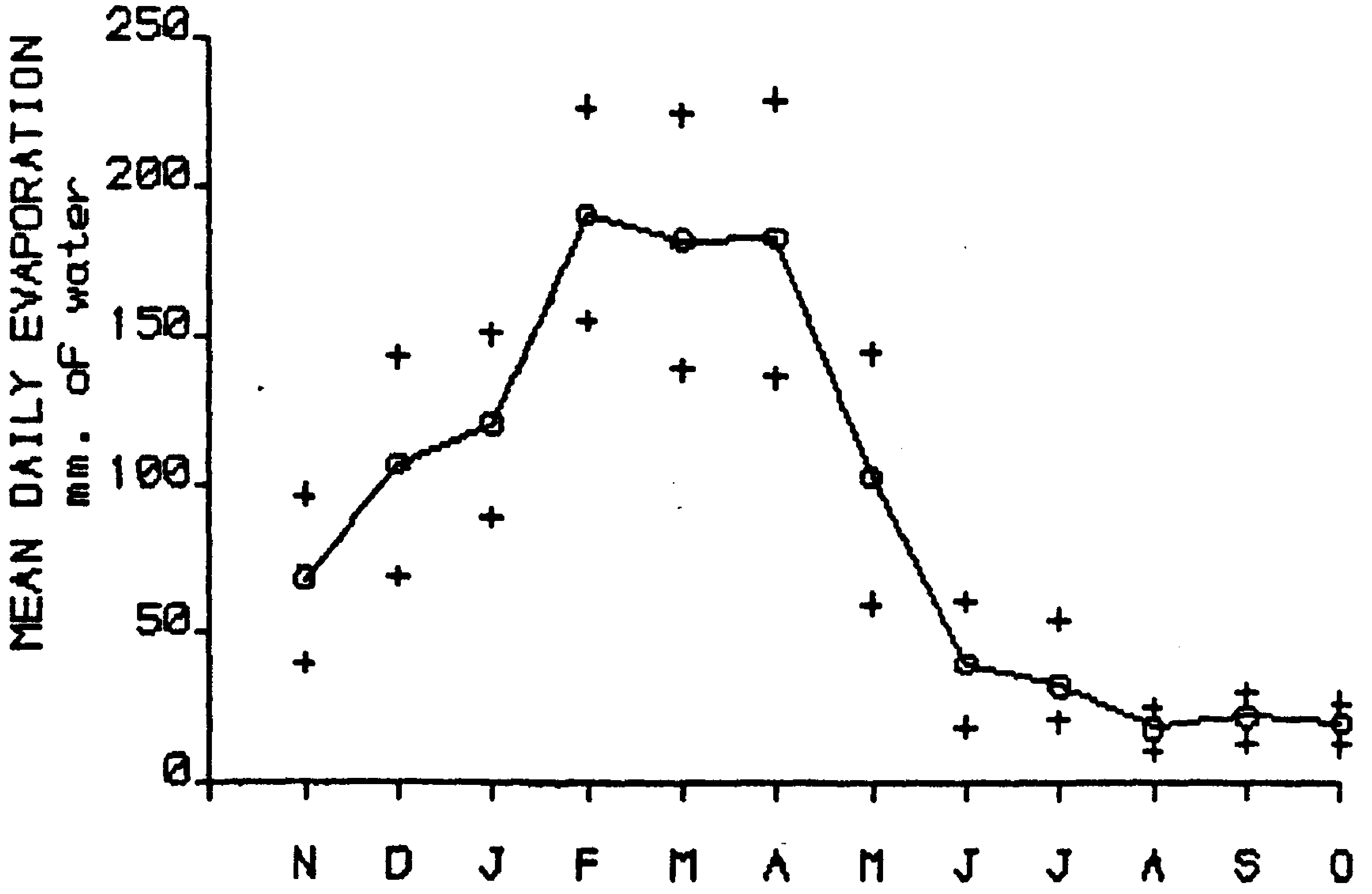


Figure 2.5. Mean daily evaporation (mm. of water) from a Piche Evaporometer, for each month of the year.

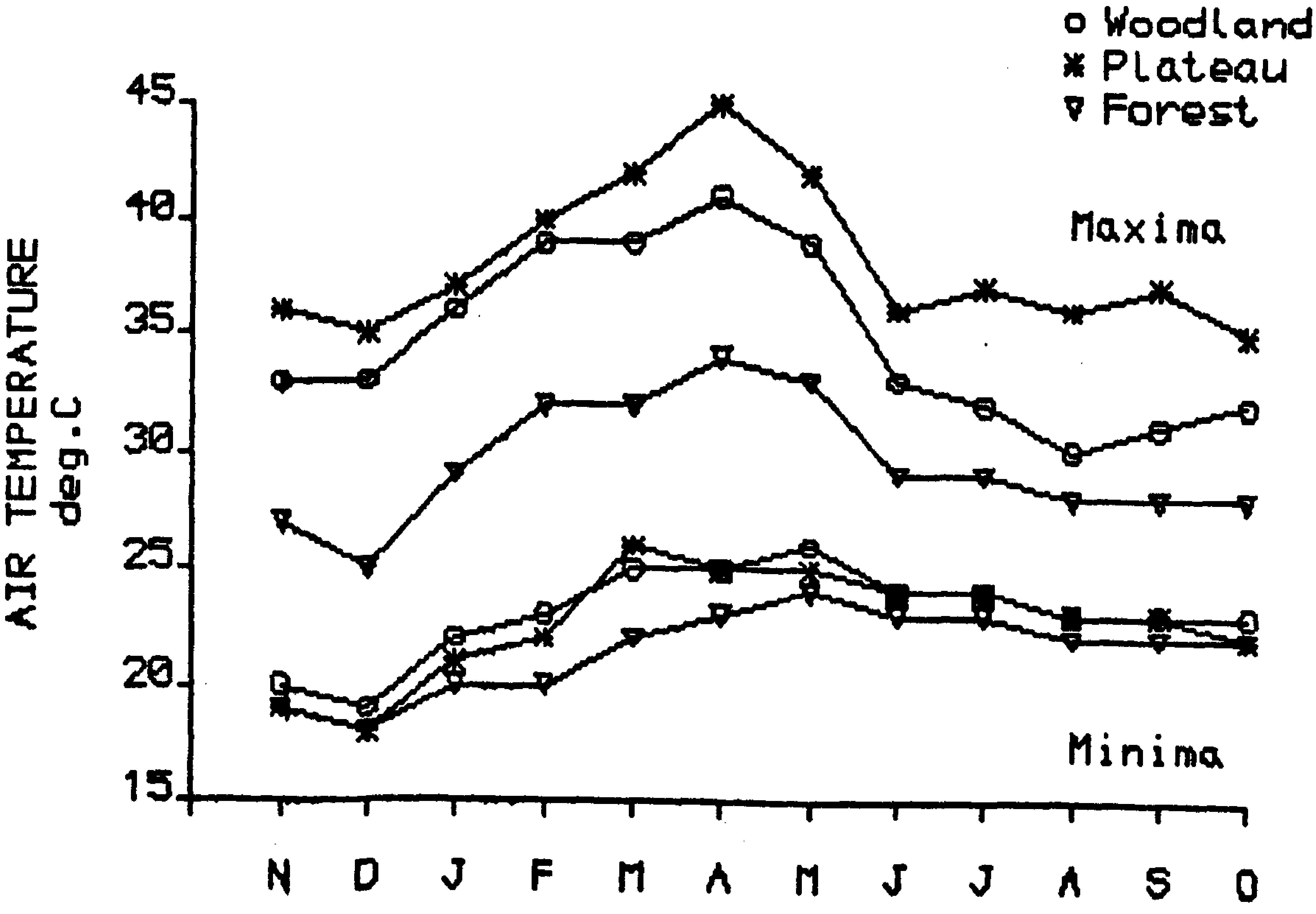


Figure 2.6. Comparison of mean monthly maximum and minimum air temperatures between plateau, woodland, and forest.

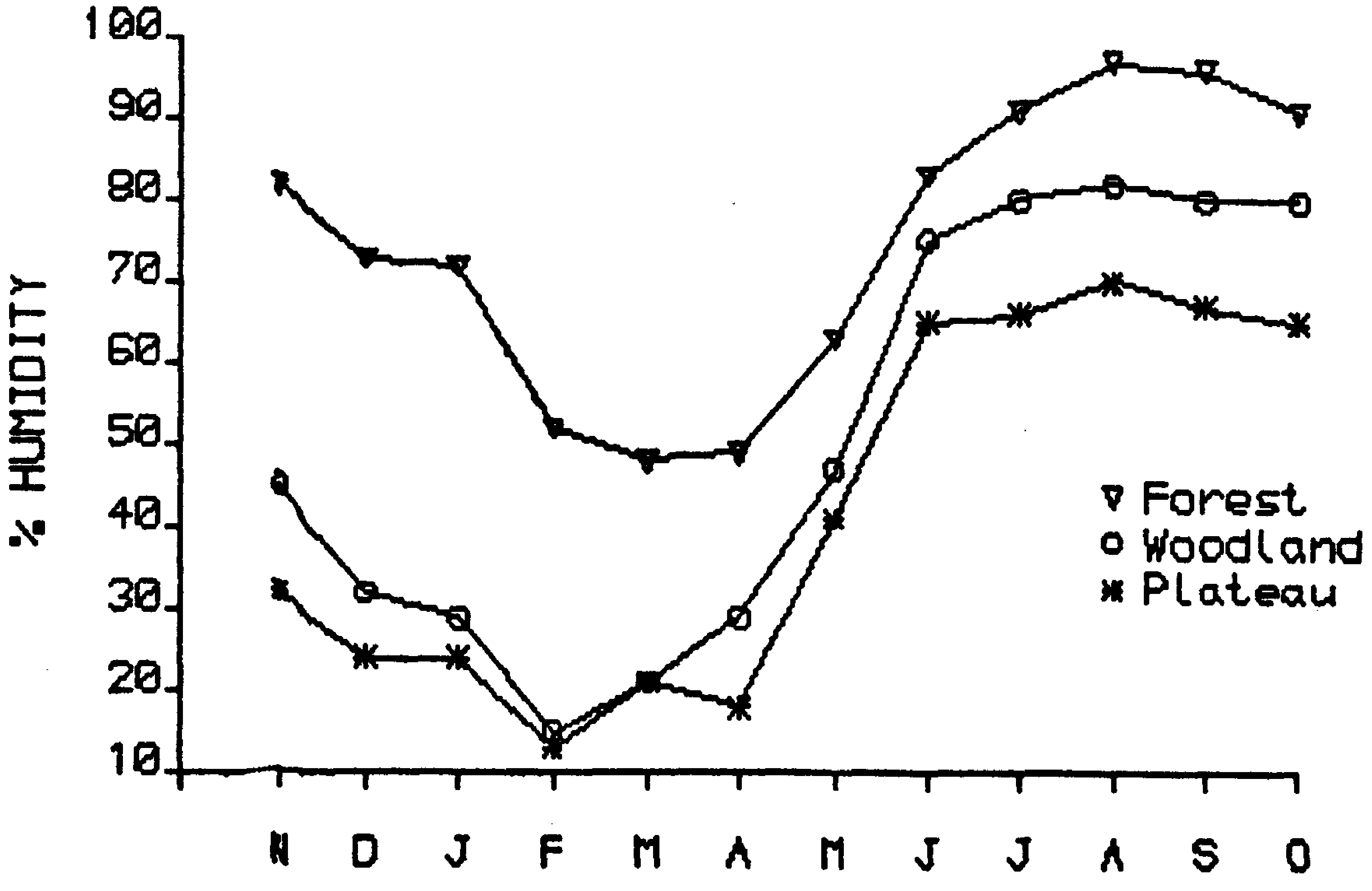


Figure 2.7. Comparison of mean monthly relative humidity at noon, between plateau, woodland, and forest.

(1976-1979 inclusive), annual rainfall figures were 891, 824, 1224, and 879 mm. The mean annual rainfall over a 35-year period at Tambacounda, 140 km. to the northwest, was 872 mm. (Griffiths, 1972). Towards the end of the dry season of 1977-1978, the flow of water stopped in Lion Valley, although some standing pools of water remained. It is not known how often, if at all, drinking water in this valley completely dries up.

CHAPTER 3.

METHODS.

3.1 INTRODUCTION.

In this chapter I shall describe the methods used in this study, and the schedule of data collection and analysis. Owing to the ´unspoilt´ nature of Mt.Assirik as a field-site, purely observational methods were used, which were as unobtrusive as possible to the fauna and flora in the area. I spent an initial period from June 1977 to January 1978 at Mt.Assirik; this served as a pilot-study of green monkeys in the general area and of one group in particular. I habituated this group to the presence of a human observer at close range, such that my presence had no apparent effect on the behaviour of the monkeys. I also sought to identify its members. I tried several methods of sampling the monkeys´ behaviour in order to assess which methods were most suitable for the conditions of observation (visibility, habitat-type, topography, and tolerance of the monkeys). I familiarized myself with this group´s home-range, with the presence and locations of neighbouring groups, and with most of the important species of plants in the region. Finally, I drew a detailed, large-scale map of the area for plotting both the vegetation and the monkeys´ daily movements.

[*] This was easiest when monkeys of different ages were seen side by side, for comparison. In practice, my sense of the relative sizes of strange monkeys developed over time, especially with reference to the study group, whose members I could reliably age,up to adulthood, by comparison amongst siblings. The transition in males from subadulthood to full sexual and physical maturity was less clear cut, and there was more individual variation, than in younger monkeys. Later analyses of age/sex differences in behaviour rely exclusively on data from the study group, and thus no misjudgement of age classes could bias results. More care should be taken, however, over conclusions based on comparisons with other studies, where alternative ageing criteria may have been used.

This pilot-work was followed by preparation at Stirling from April to September 1978, formulating a detailed research proposal in the light of the first observations. This focussed on methods of data collection that were compatible with the computer facilities at Stirling. This practical preparation led to little time being lost on my return to Mt.Assirik in September 1978, and I began detailed, systematic observations without difficulty.

3.2 SURVEY OF THE GREEN MONKEY POPULATION.

A standardized checksheet was printed on 6" x 8" card and carried in the field by SAPP researchers. Each time green monkeys were encountered, a record was made of the location, habitat, and details of group size and composition. Sightings and movements were marked on a large map of the area surrounding Mt.Assirik. The nature of the vegetation and the shyness of most green monkeys encountered meant that it was a slow, fragmentary process to build up a picture of all the groups and their ranges. Censuses were taken whenever possible, and as green monkeys breed seasonally, their ages were classified into yearly classes based on physical size and maturation.* The following categories were used:

Infant:	1st year of life, noting presence or absence of black natal coat, or if clinging to mother.
Yearling:	2nd year.
Juvenile:	3rd year, bigger than yearling.
Subadult male:	4th year, can be same size as adult, but

without fully matured physique.

female: 4th year, button-shaped nipples apparent.

Adult male: 5th year or older, fully developed musculature and canines, and pendulous scrotum (indicating descended testes).

female: 5th year and older, reproductive age. Parous females have elongated nipples. *

* Although Lancaster (1972) gives 4 years as the reproductive age for vervet monkeys along the Zambezi River, no 4 year-old females in any group at Mt.Assirik were seen with infants, or pregnant.

Groups neighbouring the study group became better known than more distant groups, but were nevertheless repeatedly censused when the opportunity arose, to try to monitor demographic changes. All details of demographic changes (births, deaths, immigrations, emigrations, maturation) were kept for the study group. Matrilineal kinship in the group was known for 3 years (1977-1979), and there was strong circumstantial evidence of the mothers of infants born in 1976.

3.3 THE STUDY GROUP.

3.3.1 Research Schedule.

To quantify the behavioural ecology of this group, a schedule of monthly 5-day samples was adopted. This meant following the group from dawn to dusk on five consecutive days during the middle of each month. The group was located during an afternoon, followed to the sleeping site that night, and picked up the following dawn to start a 5-day sample. A day´s follow began and ended when monkeys were settled in their sleeping trees. Observations were made through 10 x 40 binoculars, and typical observational distances were between 5 and 25 meters. I was relieved for an hour´s lunchbreak each day by a SAPP researcher, who maintained contact with the group. This break was timed differently each day, so as not to bias any particular hour by the break in data-collection. I took the 5-day periods to be representative samples of the monkeys´ behaviour during each month. (In November, data from one day were lost, due to malfunction of the tape-recorder, leaving only four days). I chose five days as the length of the sample because I estimated that this would be long enough for typical patterns of feeding and ranging to emerge, and yet not too long to preclude other aspects of research for this study (see below), as well as domestic duties in camp. Also, 5-day samples are comparable with other studies (e.g. Kavanagh, 1977; Rudran, 1978; Struhsaker, 1975).

The remaining period each month was spent transcribing data, mapping and monitoring the vegetation, and for seven months, carrying out a detailed study of infant development using focal-animal sampling (J.Altmann, 1974). Domestic duties accounted for part of one day in every three or four, except during 5-day samples.

3.3.2 Five-day Samples.

During each monthly 5-day sample, three types of behavioural data were collected: i) range-use was mapped; ii) maintenance activities were sampled; and iii) social interactions, vocalizations, intergroup encounters, etc. were recorded. The methods of collecting and analysing these data were as follows:

3.3.2.1 Ranging. -

The location of the group was mapped every 30 minutes, i.e. by instantaneous scan-sampling (J.Altmann, 1974). This was done by encircling, on a large-scale map, the area occupied at that moment by the monkeys. Each circle was labelled with the time, and the type of habitat. In the analysis, each map was superimposed with a transparent grid, each cell of which represented a quadrat 25m square. Quadrats measuring 50m square (0.25 hectare) would have been more compatable with other ecological studies (e.g. see Clutton-Brock, 1977), but the vegetation and topography at Mt.Assirik was so heterogeneous that in many cases 0.25 ha.-quadrats would have overlapped several types of habitat, and obscured much detail.

For this reason, the finer measurement of 0.0625 ha.-quadrats was more suitable. Since not all of every quadrat was visited, smaller quadrats gave a more accurate measure of area occupied when summed. In general, the smaller the quadrat, the better the discrimination between different patterns, be it ranging or vegetational composition (within the limits of the accuracy of measurement possible in the field). Each quadrat had a co-ordinate reference, for computer analysis.

i) Length of day-range: the distance travelled each day by the monkeys was calculated as the sum of the straight line distances between the centre points of each circle on the map. This represents a minimal measure since it takes no account of vertical movement, nor of sloping terrain; further, it is a gross estimate of the group's movement, and not the distance travelled by any individual in the group, who may move about within the 'circle'.

ii) Speed of movement: from the distance moved in each 1/2-hour interval, the speed of the group's movement at any time of the day can be calculated.

iii) Size of home-range: the monthly 'home-range' was calculated as the total number of quadrats used during a 5-day sample. The criterion for a quadrat being 'used' was that at least 20% of it should be occupied. Thus the total area used is slightly overestimated, since only part of any quadrat need be used for it to be scored. Quadrats which the monkeys passed through, in a straight line from one 1/2-hour location to the next, were included in the home-range total. However, these quadrats are excluded in any analysis involving time spent in quadrats.

iv) Range-use: the differential usage of quadrats was calculated from the number of times (i.e. the number of 1/2-hour intervals) that any quadrat was used. Where the group's location covered several quadrats, each of those quadrats was scored for one 1/2-hour interval.

v) Sleeping sites: locations were mapped at the end of each day's records, and in analysis these were represented by locations in particular quadrats.

3.3.2.2 Maintenance Activities. -

The monkeys' feeding patterns and activity-budgets were systematically sampled using the method of instantaneous scan sampling (J.Altmann, 1974). Every 15 minutes throughout each day, I scanned the monkeys in view, and for each monkey, recorded a set of data into a cassette tape-recorder strapped to my waist. Due to generally poor observational conditions, I allowed a 5 minute period, starting at each 15 minute interval, in which to walk around and maximise the number of monkeys that were recorded in each scan. To reduce any bias towards eye-catching activities, after spotting a monkey I would pause for a count of five, then record the relevant information. The activity recorded was the 'instantaneous activity', as opposed to the first activity to last for 5 seconds, the 'sustained activity', used by some workers (see discussion in Marsh, 1981). No monkey was noted more than once in any scan. The following data were recorded for each monkey seen:

Date.....day and month.

Time.....time beginning each 15 minute interval.

Subject..indentity of monkey.

Height...monkey's height above the ground, within 5m bands:

0= on the ground; 5= 0-5m; 10= 5-10m etc.

Activity..one of the following mutually exclusive categories:

- Resting: sitting, lying, standing, or otherwise inactive.
- Feeding: foraging, picking, manipulating, chewing.
  - food-species (each species was assigned a number, for purposes of computer analysis).
  - food part (bud, flush leaf, flower, fruit, gum, seed, fungus, stem).
  - if invertebrate, substrate from which it was collected (leaf litter, earth, foliage, bark, grass).
- Socializing:
  - grooming (partners identified under nearest neighbour)
  - playing (ditto)
  - clinging (infants)*

Nearest neighbours...identity of any monkey in contact (C) with the subject, or within one meter (N).

*It was hard to distinguish a suckling from a resting infant when it was wrapped up in its mother's arms. All such instances were scored as clinging, until August, when the distinction between resting and suckling could reliably be made.

Initially, there was a fourth category of activity, ´moving´. However, in practice it proved difficult to make a quick and clear judgement between moving and resting, since much of the obviously non-foraging movement involved moving short distances, resting, then moving again for a short time, etc. Apart from the time spent in social activity, I decided that for a study with the emphasis on feeding ecology, the important distinction within the time-budget was between feeding and not-feeding, so that moving was not used as a mutually exclusive category; foraging movements were recorded as ´feeding´, while ´resting´ became a broader category readily defined as not feeding or socializing. Using range-maps to calculate distances travelled provides an unambiguous and independent measure of energy expended in ´moving´.

Under the category of ´socializing´, aggressive and sexual interactions were not recorded. They occurred too quickly to be meaningful in a time-budget analysis, and they were strongly attractive to my attention, and thus open to bias. Both activities were recorded opportunistically (see below).

Sampling behaviour at set intervals gives an overall estimate of the amount of time spent in any given activity. Likewise, the proportion of feeding time that is spent on a particular food species is taken to represent the proportion of that species in the diet. This way of measuring the composition of the diet may not give an accurate estimate of the amount of food ingested, because feeding rates may vary among food-items. Hladik (1977b) measured both the time spent feeding by chimpanzees and the weight of food this represented, and found large discrepancies: 14% of time spent feeding on fruits produced 63% of the fresh weight of food in the diet, a ratio of 1:4.5; 49% of time eating leaves produced 33% of the weight of the diet (1.5:1), while 37% of time spent on insects produced only 4% of the weight of the diet (9:1). However, no sampling of feeding rates or weights of food was done to quantify this in the green monkeys, and so time records are used in all analyses of diet. Analysis of heights used by the monkeys and age and sex differences in activity-patterns were also based on data from the scan-sampling. This method is useful for comparison with other studies of feeding ecology in primates (see e.g. Clutton-Brock, 1977).

All data from scans were transcribed from tapes onto checksheets prepared in a format for punching onto computer cards. A total of 16,342 records were made. The number of scans made was 2090, giving an overall mean of 7.8 records per scan. Most analyses were carried out using SPSS (Statistical Package for the Social Sciences) computer programs (Nie _et al._, 1975).

To avoid bias towards ´visible´ activities, and thus their excessive representation in scans, the number of monkeys engaged in each activity in each scan was expressed as a proportion of the total number of individuals in the scan. Thus, each record has a weighting, and all weightings in each scan add up to one. Weighted and unweighted data on activity-budgets were compared to see whether any particular activity was over-represented in scans due to an observation bias. Feeding and socializing both showed significantly higher percentages in weighted than in unweighted data (Wilcoxon matched-pairs comparison, $p<.05$), while resting showed lower percentages (Wilcoxon, $p<.01$). This implies that feeding and social behaviour were consistently over-sampled (boosted in the raw data), and resting under-sampled, suggesting that my attention was attracted more to the former activities. However, in all three activities, the mean percentage differences between the weighted and unweighted data were so small relative to the percentages themselves (feeding: -1.1%; resting: +1.8%; socializing: -0.8%) that raw, unweighted data were used throughout subsequent analyses. The disadvantage of using weighted data is that the sample size is considerably reduced, an option to be avoided if at all possible.

Weighted and unweighted data on the proportions of important types of food in the diet were also compared, to check for observational bias towards certain food-species. Some species of tree are more open and thus make it easier to observe feeding monkeys, while other species may only reveal one or two feeders with other monkeys remaining unseen. Feeding records for the latter kinds of trees may thus be under-represented. Important species of food are defined as those which accounted for more than 5% of the monkeys' feeding time per month, based on unweighted data. In all months except November, there were no significant differences between weighted and unweighted data (Wilcoxon, $p>.05$); in November, unweighted data were significantly over-estimated, but only by an average of 1.4%. For all species throughout the year, over- or under-estimation of the precentages of time spent feeding, in unweighted data, is slight (mean discrepancy = 1.2%). Once again, raw unweighted data were used throughout the analysis of feeding.

These two analyses show that my efforts to be random in sampling the monkeys' behaviour during scans were successful, and that any biases towards 'eye-catching' activities or food-species were minimised.

3.3.3 Vegetation.

A total of 174 specimens of plants were collected by SAPP researchers, then pressed, dried, and sent to the Royal Botanic Gardens at Kew for identification. A number of different techniques were used to sample various aspects of the habitat. The aims were to describe the composition and structure of the different types of vegetation, and to quantify the density, distribution, and availability of food-species that were important to the green monkeys. The following methods were used:

3.3.3.1 Transects. -

Having classified the vegetation into 5 habitat types (see chapter 4), each type was sampled using line-transects (Chapman, 1976, Eberhardt, 1978). This proved a quick method of providing data on dominant species and structure, and for use in drawing profile diagrams to represent the stratification in each vegetation type. This transect sampling was carried out by the SAPP research team (see Baldwin, 1979, for full details).

Briefly, the method involved recording the species, girth (at 1m above the ground), amd estimated height of all trees over 2m high that crossed the vertical plane above the transect line. Transects ran north-south from starting points chosen for convenience, and a total of 500m of transects was carried out in each vegetation type.

This method is not appropriate for measuring relative frequencies of species within or between samples. Large trees will be over-estimated, as their larger horizontal area increases their chances of crossing the transect-plane, compared with small trees. Estimates of species density are best derived using quadrats and counting trees within specified areas (see below).

3.3.3.2 Distribution Maps. -

I could not assume that the dominant species of plants characteristic of a particular vegetation type were evenly distributed throughout that type. The habitat is sufficiently heterogeneous, and the vegetation sufficiently varied within each type, that sampling small areas by transect lines would be inaccurate for rare or clumped species. This is true even if more time-consuming but more effective quadrat-sampling techniques were used. It is exactly these rare or clumped species that are often crucial in their effects on the feeding and ranging patterns of animals, and it was important to take account of such species, even if they were not dominant species in the habitat. In addition, more accurate data on the overall pattern of distribution of all important food-species throughout the monkeys' home-range were necessary, in order for the details of ranging behaviour to be interpreted.

The following method was used to derive distribution maps of the important vegetation. The home-range area of the study group was divided up into 25m square quadrats, by superimposing a transparent grid onto a large-scale map (see also methods for ranging analysis). Thirty-six species of plants were chosen in the field, on the basis of their assumed importance in the annual diet of the green monkeys. (In later analysis, plants were defined as important according to specific criteria, and 21 species were selected). I then visited each quadrat in the home range, and recorded the presence or absence of each plant species. The habitat type of each quadrat was noted, and each quadrat had a coordinate reference for use in computer analysis. A total of 2,854 quadrats were visited. From this information, a map for each species was drawn, giving the distribution of all quadrats containing that species. A distribution map of the vegetation types was also drawn.

The pattern of distribution of each species was quantified using these maps. A plant may be randomly or evenly distributed, or scattered in widely separated clumps. I calculated an index of the degree of clumping as follows: for every quadrat that contained a particular species, I counted the number of the surrounding 8 quadrats that also contained that species. The "index of clumpedness" was the mean number of surrounding quadrats that contained the focal species. A low number suggested that the species occurred in isolated groups of quadrats, and thus had a clumped distribution pattern; whereas a high number suggested a more continuous, even distribution.

The size of quadrat is obviously important for the calculation of this index. Different sized quadrats, represented by blocks of 16, 36, and 64 of the initial quadrats, were used on a sample of species to compare the indices derived. All indices were similar, suggesting that the proposed index is not only a measure of local clumpedness (based on blocks of 9 quadrats), but also a measure of clumpedness over wider areas.

3.3.3.3 Plant Density, Size, And Phenology. -

To estimate the local density of each important plant-species (i.e. for each species, the mean number of trees per quadrat in which that species occurs), a sample of 30 quadrats containing a species were chosen at random, and all trees of that species over 2m high were counted. Eleven of the 36 chosen species occurred in fewer than 30 quadrats, so sample size was smaller for these.

Data on tree size were also collected: a sample of 15 trees of each species was randomly chosen, and estimated measurements were taken of tree height, average crown-diameter, and maximum crown-depth. I intended to derive estimates of the food-producing areas of trees, but because most crown shapes are irregular, computing surface area or volume from the above measures would be inaccurate, so I chose a compromise that did not involve as many assumptions about crown-shape, and used the area of ground below the tree that was covered by the crown as my estimate of food-producing area. This is not an absolute measure, but rather a relative measure that would discriminate between different tree species. (Struhsaker (1975) used the sum of the maximum crown depth and the maximum crown diameter as an index of crown size: this method produced estimates that are highly correlated with the above method, r= .98, p<.001).

The phenology of these important species were regularly monitored. For each species, a monthly checksheet was filled in, recording the presence or absence of:

Leaves - buds or flush, mature, senescing, or no leaves.
Flowers- abundant, common, rare, absent.
Fruit - abundant, common, rare, absent
(and ripe or unripe).

In addition to these largely descriptive measures, if the fruit or flowers of any species were a major item in that month's diet, I sampled a randomly chosen 50 trees of that species, recording whether or not each contained fruit/flowers, thus quantifying the percentage of trees that had fruit or flowers available to the monkeys that month. The phenological monitoring and sampling took place immediately before each month´s 5-day sample, so that the data were directly relevant to the monkeys´ feeding and ranging patterns for that month.

Data on plant distribution, density, size, and phenology were used to test specific hypotheses concerning feeding and ranging. Measures of the overall availability of each food during each month were derived from the above data as follows:

N x LD x m2 x AV = total area of tree canopy that contains food available to the monkeys, throughout their range.

where N= number of quadrats containing a species (from distribution maps).

LD= local density; trees per quadrat in which that species occurs.

m2= mean crown area of each tree of that species.

AV= percentage of trees of a species that have food available (from phenological samples).

For all sections of analysis that involve measures of the availability of a food-resource, the invertebrate part of the diet is omitted since it is difficult to arrive at a measure of invertebrate availability comparable with data on vegetational availability. Sweep-netting could have been used, but measuring insects in tree-canopies, in leaf-litter, or in rotten branches would have been difficult.

3.3.3.4 Vegetational Cover And Visibility. -

At six-monthly intervals, in February (mid-dry season) and August (mid-wet season), the transect lines marked out during vegetational sampling were revisited. Using a method desribed by Aldrich-Blake *et al.*(1971), estimates of the percentage of vegetational cover at three different height levels were made, at 15m intervals along the transects in each of the five vegetation types. Cover was measured as the percentage of one square metre on the ground that was covered by vegetation at ground, shrub, and tree level. Shrubs were woody plants with trunks or stems less than 20cm. in diameter, trees were greater than 20cm. in diameter. These data were collected collaboratively by SAPP researchers over two years.

Visibility was measured in each habitat by Sharman (1981), following a method used by McArthur and McArthur (1961). The method involved recording the distance at which half, and all, of the squares on a 50cm x 50cm chequered board disappeared from view. The target board was always placed with one edge on the ground, and observations were made from 60cm. and 170cm. above the ground (roughly, a primate on and off the ground). However, these measures of visibility were collected with terrestrial baboons in mind, and are thus most susceptible to the presence or absence of ground cover. Visibility through and within the tree canopy would be as important to the green monkeys as ground visibility. I measured arboreal visibility in a sample vegetation type, to compare with ground cover measures: in the gallery forest, I estimated the distance, within 5m bands, to the first "wall of vegetation" through which I could not see clearly, looking horizontally, vertically, and at an angle of 45°. Such measures were taken in the four cardinal directions, from each of 30 sample points, randomly chosen in the forest.

Photography was also used for a record of seasonal change in each vegetation type. Photographs were taken from the same spot at three-monthly interval throughout the year (using an Olympus OM1 with standard 50mm. lens, and colour print film).

3.4 CLIMATOLOGICAL DATA.

Rainfall was collected daily in a rain-guage situated on an open plateau.. Temperature and humidity were measured at three sites, plateau, woodland (camp), and forest (valley streambed), so that differences in microclimate between sites could be monitored. At each site, maximum and minimum air temperatures were recorded daily, and temperatures and humidities were recorded hourly from 0700-2000 hours (opportunistically at the forest site). In addition, evaporation rate was measured daily in camp: this provided a standardized measure of daily evaporation, without reference to hourly levels of humidity.

All thermometers were placed in well-ventilated positions, 1m from the ground, in the shade. Standard wet-and-dry-bulb thermometers were used for hourly records of temperature and humidity, and resettable thermometers were used to measure maxima and minima. A Piche Evaporometer was used for measuring rates of evaporation: this involved a measured amount of water in an inverted glass tube being allowed to evaporate via a paper filter.

All data were collected collaboratively by SAPP researchers.

3.5 STATISTICS.

A mixture of parametric and non-parametric statistics were used, according to the suitability of the data (Siegel, 1956; Sokal and Rohlf, 1969). Unless specified, all tests were two-tailed. Only .05, .01, and .001 levels of significance are given.

CHAPTER 4.

VEGETATION.

4.1 INTRODUCTION.

Knowledge of the structure, composition, and distribution of vegetation is important for the explanation of many aspects of the behaviour of wild primates, in particular, their feeding and ranging patterns, time-budgets, and intergroup relations. In this thesis, consistent reference is made to various measures of the vegetation at Mt.Assirik, and its influence on the behaviour of the green monkeys. In this chapter, I present data on the details of the structure and species-composition of the different habitat-types, and on the availability and distribution of foods eaten by the green monkeys.

4.2 HABITAT-TYPES.

Habitat-types can be defined in at least two ways: in terms of species-composition, or in terms of structure. The former is self-explanatory, and the latter makes use of variables such as heights of trees, continuity of the canopy, visibility, degree of vegetational cover, and density of plants. Both Baldwin (1979) and Sharman (1981) have discussed the vegetation at Mt.Assirik, defining habitat-types and mapping these over areas of 50 km2 and 100 km2 respectively, using aerial photographs.

I shall briefly describe the habitat divisions used by S.A.P.P. (Baldwin, 1979), which were classified according to Ellenberg and Mueller-Dombois (1967). Their system of physiognomic description was designed to accommodate all types of vegetation on a global scale, and thus is suitable for comparative analyses. The following five habitats were recognised:

i) Gallery forest: classified by Ellenberg and Mueller-Dombois (1967) as Tropical (or subtropical) semi-deciduous lowland forest (I.A.3a). This habitat is restricted to areas of permanent or long-standing water, mainly in the steep-sided valleys. The cover of the canopy is generally continuous, but the stratification is not uniform throughout the forest, with some emergent trees reaching up to 40m (e.g. Ceiba pentandra). Most trees are evergreen. An herbaceous understory occurs in areas where the tree canopy is discontinuous.

ii) Woodland: classified as Drought-deciduous lowland woodland (II.B.1a). This habitat occurs on gently sloping, well-drained soil, and the tree canopy is discontinuous. The trees shed their leaves in the dry season. The understory consists mainly of grasses.

iii) Bamboo: classified as Flat-leaved tree savanna with isolated palms and deciduous trees (V.A.1b(2) and (3)). This habitat occurs in large depressions of clayey soil, where bamboo (Oxytenanthera abyssinica) is very much the predominant species, with some tall trees scattered throughout.

iv) Grassland: classified as Narrow-leaved savanna with isolated deciduous trees (V.A.2a(2)). This habitat covers the

Table 4.1. The mean density, heights and girths of woody plants, and the number of species, within each type of vegetation.

Type of vegetation	Woody vegetation > 2m high		Heights estimated		Girths measured		Species N in top	
	N	Density	N	mean	N	mean	N	ranking 50%
Forest	231	1: 2.2m	221	10.2m	115	105cm	49	7
Woodland	138	1: 3.4m	132	6.9m	76	87cm	33	5
Bamboo	50	1: 10.2m	49	9.3m	30	129cm	21	4
Grassland	48	1: 10.7m	48	3.5m	24	31cm	16	3
Plateau	9	1: 63.7m	9	2.6m	-	-	1	1

Table 4.2. A list of dominant species (i.e. those in top-ranking 50%) in each type of vegetation.

Forest:

1. *Sorindeia juglandifolia*
2. *Saba senegalensis*
3. *Combretum tomentosum*
4. Sapotaceae
5. *Oncoba spinosa*
   Ficus umbellata
   Diospyros mespiliformis

Woodland:

1. *Hexolobus monopetalus*
2. *Pterocarpus erinaceus*
3. *Afzelia africana*
4. *Combretum* sp. (A)
5. *Vitex madiensis*

Bamboo:

1. *Combretum* sp. (A)
2. *Pterocarpus erinaceus*
3. *Acacia macrostachya*
4. *Piliostigma thonningii*
5. *Diospyros mespiliformis*

Grassland:

1. *Crossopteryx febrifuga*
   Combretum collinum
   Combretum sp. (A)
2. *Annona senegalensis*
   Piliostigma thonningii

Plateau:

1. *Combretum collinum*

same type of terrain as bamboo, and also slightly raised, undulating hills. Few trees are scattered throughout the continuous grass covering.

v) Plateau: classified as Narrow-leaved savanna with isolated deciduous shrubs (V.A.2b(2)). The plateaux are solid sheets of laterite covered with poor, thin soils, which support only short grasses during the rains, and very few shrubs (almost exclusively Combretum collinum).

In some places, adjacent habitats merge gradually, notably in basins or depressions where soil type and drainage only differ slightly; for example, between grassland and bamboo there is often a transitional zone. In other cases, the vegetation changes abruptly and without transitional stages, as for example between plateau with its poor, thin soil, and gallery forest growing from the rich, moist soil in the gorges that cut through these plateaux.

Details of the structure and predominant species-composition of these habitats, as measured from line-transects, are given in Tables 4.1 and 4.2, and Figure 4.1.

Table 4.3 Habitat composition of SAPP study area.
p= the proportion of sampled area made up by each habitat.

Baldwin (50 km2)	----p----		Sharman (100 km2)
Gallery forest	3%	0.4%	Riverine gallery forest
Woodland	37%	48.6%	{Open woodland : 27.3%
			{Dry forest : 21.3%
Grassland/Bamboo	32%	30.3%	{Scrub grassland: 7.7%
			{Scrub : 22.6%
Plateau	28%	20.6%	{Grassland : 6.2%
			{Combretum scrub: 14.4%

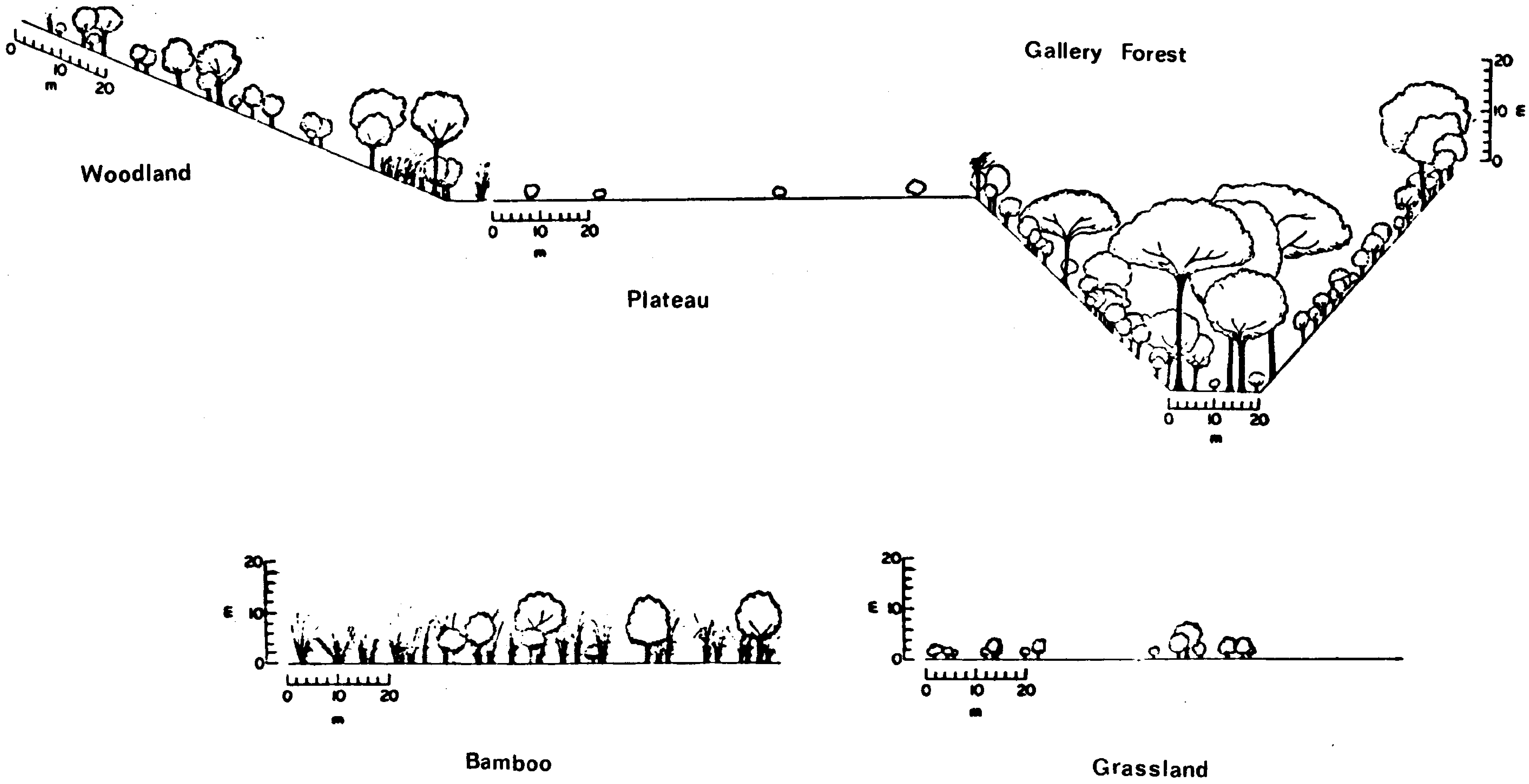


Figure 4.1. Schematic, cross-sectional diagrams of the 5 major habitat-types in the S.A.P.P. study-area (from Baldwin, 1979).

Table 4.3 summarizes the results of the aerial photograph surveys by Baldwin (1979) and Sharman (1981).

While Baldwin sampled the area within a 4 km radius of Mt.Assirik, Sharman also covered areas further away to include the home range of baboons that he studied. Table 4.3 shows a slightly higher concentration of bare laterite plateaux and gallery forest in the more immediate surrounds of Mt.Assirik (Baldwin′s data), where the valleys radiate from the summit, cutting through the sloping laterite, whereas there is more woodland covering flatter areas further from this centre (Sharman′s data). In either case, the proportion of gallery forest is extremely small, given its importance in the dry season in providing sleeping areas, relatively cool refuges with shade, and drinking water for the chimpanzees (Baldwin, 1979), baboons (Sharman, 1981) and green monkeys (this study, chapter 8). The area used by my study group was 1.78 km2, and its habitat composition is shown in Table 4.4.

I made several finer distinctions of habitat-type, based on gross structural differences that may have been important to the green monkeys: woodland was subdivided into closed woodland, where tree canopies were continuous and often

---

Table 4.4. Habitat-composition of study group′s home-range.

Gallery forest: 6.5%
Woodland : 38.5% {35.8% Open woodland
{ 1.9% Closed woodland
{ 0.8% Scrub
Bamboo : 4.0%
Grassland : -
Plateau : 51.0%

---

threaded with evergreen lianas; open woodland, where trees were less dense and the canopy discontinuous; and scrub, which sometimes occurred just off the plateaux, under the rims of valleys, where the vegetation consisted of low, dense bushes and vines, with scattered tall trees. Figure 4.2 shows a map of the vegetation in the green monkeys' home-range.

Table 4.4 shows that the area of gallery forest used by the green monkeys was greater than expected from its availability in the whole SAPP study area. There was very little bamboo and no grassland. Woodland was used in proportion to its overall availability. The proportion of plateau was very high, but this habitat was rarely used (see chapter 8).

4.3 COVER, VISIBILITY, AND SEASONAL CHANGE.

The highly seasonal climate at Mt.Assirik means that the vegetation undergoes dramatic changes at different times of the year. Adam (1971) gives a free and vivid description of the seasonality in the park (translated by M.Sharman): "The dry season is the season of implacable sun, white skies, colourless, indistinct horizons, the savanna scorched by fire, soil black with ash, skeletal trees, whirlwinds that lift dust high into the atmosphere, the overheated soil radiating like a furnace.... The vegetation awakens with the rains. The grass grows 2m tall, hiding everything....the dirt roads disappear beneath the grass, the animals vanish, the dry gullies become torrents, the baked mudflats become mires, the forests which had been shadeless are now a vault through which the sun barely glitters....everything disappears beneath the exuberant

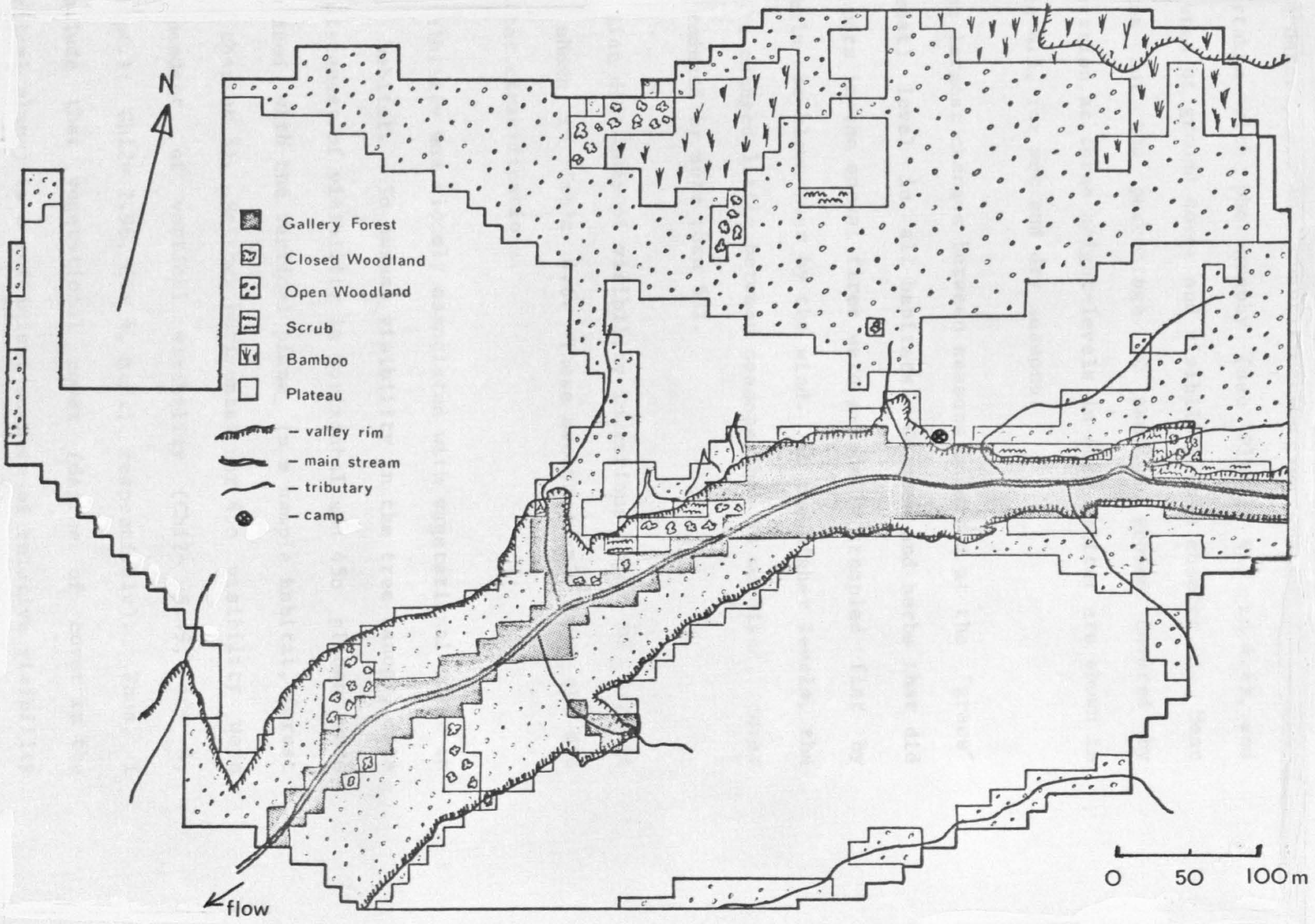


Figure 4.2. A map of the vegetation in Camp Group's home-range, showing also the tributaries and main stream running down Lion Valley.

vegetation".

The description and quantification of these changes was undertaken with photography (see Plates 4.1 to 4.4), and measures of ground cover and visibility (see chapter 3). Mean scores for the percentage of sampled ground covered by vegetation at three height-levels in each habitat are shown in Table 4.5, for wet and dry seasons.

The largest changes between seasons occurred at the ´grass´ (lowest) level in all habitats. Grasses and herbs that did not burn in the annual fires were generally trampled flat by animals or blown over by the wind. At the higher levels, the forest changed little between seasons, but in woodland, cover was reduced by more than 50%.

Median distances of visibility in various types of habitat are shown in Table 4.6. These are Sharman´s data, and his habitat classifications.

Visibility was closely associated with vegetational cover in each habitat. To assess visibility in the tree canopy, data on distances of visibility in horizontal and 45o planes were compared with the vertical plane, in a sample habitat, forest (see chapter 3). Neither horizontal nor 45o visibility were independent of vertical visibility (Chi2= 8.49, df= 4, .05<p<.1; Chi2= 2.96, df= 4, n.s.; respectively). Thus, I conclude that vegetational cover (degree of cover in the vertical plane) is a sufficient measure of relative visibility at various heights, in all habitats.

Plate 4.1. Identical locations pictured in January (top), August (mid), and November (bottom). Note the narrow strip of forest in Lion Valley, which cuts deeply through two expanses of plateau.

Plate 4.2. As for Plate 4.1., but showing the seasonal changes in open woodland.

Plate 4.3. 'Inside' view of the gallery forest, taken through the gap left by a large fallen tree. Note the plateau edge at bottom right of the picture.

Plate 4.4. View of gallery forest from above. Note several emergent kapok trees (Ceiba pentandra).

4.4 GREEN MONKEY FOODS.

In addition to the more general data collected by SAPP on the habitat structure and composition of the vegetation at Mt.Assirik, I collected specific data on the availability and distribution of foods eaten by green monkeys within the study group's home range (see chapter 3). Summary data on the frequency (of occurrence in quadrats throughout the range), size, density, and distribution of 23 species are given in Table 4.7. Figure 4.3 shows distribution maps of

Table 4.5. Summary of vegetational cover surveys.
(figures are percentage cover)

Habitat	Season	height-level		
		Grass	Shrub	Tree
Forest:	wet	21%	20	84
	dry	4	17	76
Woodland:	wet	55	12	50
	dry	9	5	24
Bamboo:	wet	38	76	31
	dry	3	24	22
Grassland :	wet	67	13	4
	dry	17	6	6
Plateau:	wet	47	3	0
	dry	5	4	0

Table 4.6. Visibility of chequer-board: median distances (in metres) at two heights (60 and 170 cm.).

Type of habitat	Season	Half-visible		Invisible	
		60cm	170cm	60cm	170cm
Gallery:	wet	12	13	11	12
	dry	7	10	16	24
Open wood:	wet	3	3	5	6
	dry	21	22	56	68
Closed wood:	wet	9	10	9	12
	dry	24	21	46	59
Plateau:	wet	3	4	7	8
	dry	54	54	88	83

Table 4.7. Measures of the frequency, relative abundance, size, density, and distribution of the 23 major species of fruit and flowers in the green monkeys' diet.

N = Number of quadrats in which species occurs
%Tot = N as percentage of total (2,854) quadrats
Area = Mean area of individual tree canopy, m2 (for spreading vines, area calculated from proportion of a quadrat covered)
LD = Local density, number of trees per quadrat (not given for spreading vines)
CI = "Clumpedness index", mean number of surrounding quadrats also containing species.

Species	N	%Tot	Area	LD	CI
Adansonia digitata	37	1.3	48	1.1	0.43
Cassia sp	72	2.5	10	1.7	1.42
Ceiba pentandra	57	2.0	155	1.2	1.82
Cissus populnea	156	5.5	6	vine	2.26
Cyanotis lanata	120	4.2	31	as vine	3.83
Daniellia oliveri	22	0.8	25	1.6	1.00
Diospyros mespiliformis	38	1.3	26	2.6	1.37
Ficus umbellata	46	1.6	95	1.8	2.70
Ficus lecardii	22	0.8	24	1.1	0.36
Ficus sp	8	0.3	45	1.0	0.25
Landolphia heudelotii	142	5.0	88	vine	2.92
Lannea acida	304	10.7	11	1.4	2.92
Lannea microcarpa	188	6.6	23	1.3	1.39
Nauclea latifolia	38	1.3	40	1.3	1.58
Pterocarpus erinaceus	995	34.9	22	3.6	5.50
Pterocarpus lucens	20	0.7	22	1.5	0.90
Pseudospondias microcarpa	50	1.8	78	1.9	2.20
Saba senegalensis	275	9.6	81	vine	3.90
Sorindeia juglandifolia	190	6.7	7	3.0	4.90
Spondias mombin	50	1.8	56	1.2	0.96
Vitex madiensis	867	30.4	4	4.2	5.60
Ziziphus mauritiana	180	6.3	15	1.4	2.64
Ziziphus mucronata	8	0.3	23	1.5	3.50

´species-quadrats´ for a sample of 4 of these species. Species were chosen out of 36 species sampled, on the basis of their importance in the diet (i.e. constituting over 5% of the diet during any month). These data concern fruit and flowers only, since the availability of invertebrates, grasses, and species within the herbaceous understory were difficult to measure. Justification for including only fruiting and flowering species in analyses involving food availability is given in chapter 6. In terms of the energy content of these foods, they are important in framing predictive hypotheses concerning energetic strategies. Data on the availability of these species each month are given in Table 4.8.

The total amount of fruit and flowers available each month was calculated by summing the amounts of each important species for that month. These results are presented in Table 4.9.

4.5 COMPARISONS WITH OTHER SITES.

Only one other study of C.aethiops provides detailed data on

Table 4.9. Total amount of food available each month (area of fruiting/flowering canopy, m2).

Nov:	2,766	May:	12,717
Dec:	5,080	Jun:	31,849
Jan:	44,844	Jul:	11,028
Feb:	4,549	Aug:	7,520
Mar:	14,184	Sep:	4,396
Apr:	8,418	Oct:	3,238

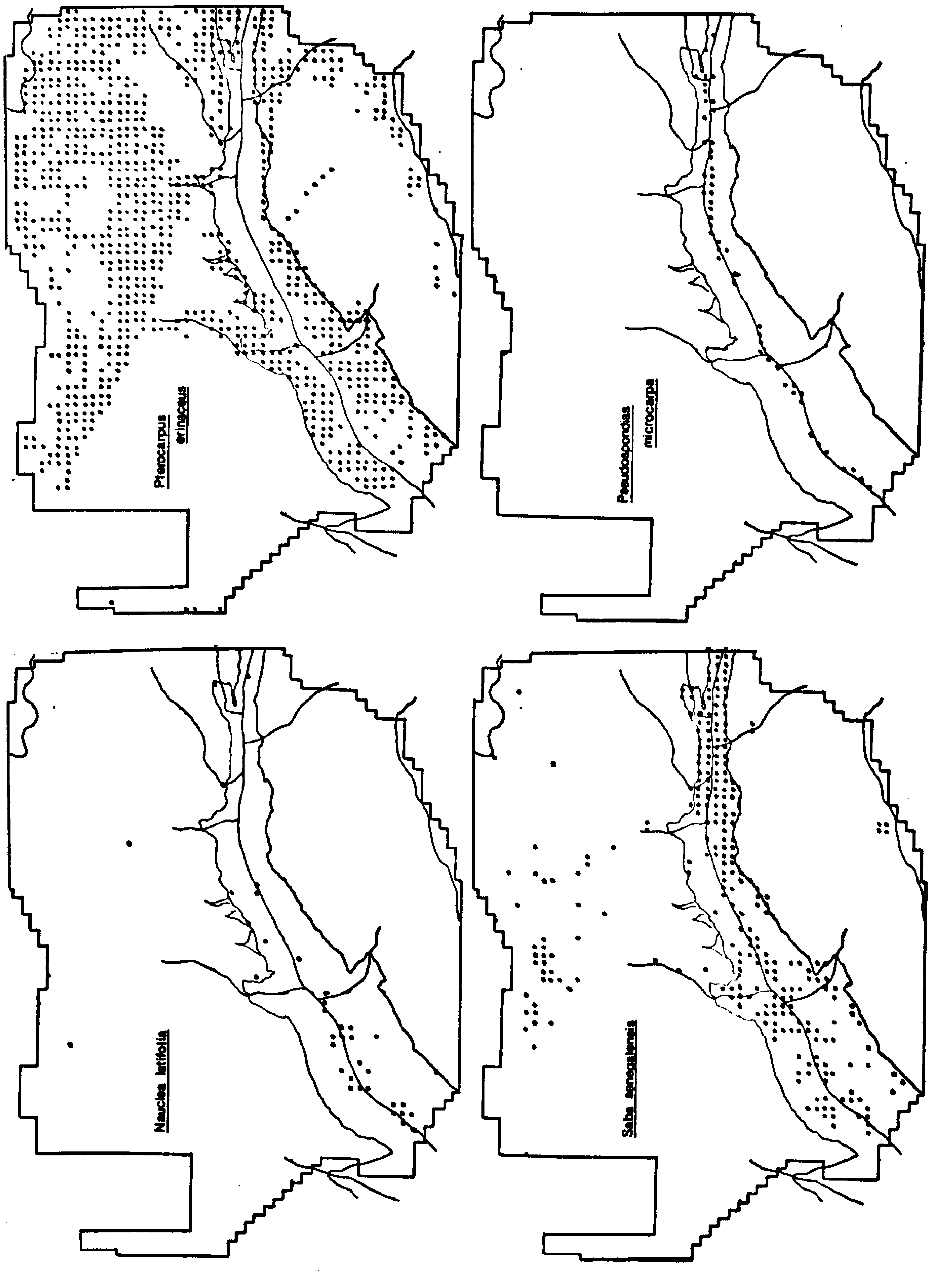


Figure 4.3. A sample of distribution maps of major food-species. Dots show the location of every quadrat containing the relevant species.

Table 4.8. Availability of major food species each month.

Key: % = % of trees in phenological sample that were fruiting or flowering
Av = area of canopy, per quadrat, containing fruit or flowers (Av= Area x LD x %)
T = total area of canopy containing fruit or flowers available to the green monkeys, throughout their range (T= Av x N)

Species:		Zma	Fle	Cpe	Dme	Per	Zmu	Dol	Fum	Pmi	Lac	Csp	Fsp	Siu	Sse	Lmi	Lhe	Plu	Cla	Nla	Adi	Smo	Yma	Cso
Nov	% :	70	10																					
	Av:	15	3																					
	T :	2700	66																					
Dec	% :			25	55	1																		
	Av:			47	37	1																		
	T :			2679	1406	995																		
Jan	% :				24	56	100	20																
	Av:				16	44	35	8																
	T :				608	43780	280	176																
Feb	% :				20	4			20															
	Av:				14	3			34															
	T :				532	2985			1564															
Mar	% :								62	58	86	75	33											
	Av:								106	86	13	13	15											
	T :								4876	4300	3952	936	120											
Apr	% :								39	35	28			40										
	Av:								67	52	4			8										
	T :								3082	2600	1216			1520										
May	% :								52						21	70								
	Av:								89						17	21								
	T :								4094						4675	3948								
Jun	% :								37						83		83	25						
	Av:								63						67		73	8						
	T :								2898						18425		10366	160						
Jul	% :								21								75							
	Av:								36								66							
	T :								1656								9372							
Aug	% :																		100	89	88	10		
	Av:																		31	46	46	7		
	T :																		3720	1748	1702	350		
Sep	% :																			80		83		
	Av:																			42		56		
	T :																			1596		2800		
Oct	% :								5											35		7	10	12
	Av:								9											18		5	2	1
	T :								414											684		250	1734	156

the vegetational composition of the monkeys´ habitat: Kavanagh (1977) surveyed a sahelian site (Kalamaloue) and a Guinea savanna site (Buffle Noir) in Cameroon. Limited data on Amboseli in Kenya are also available, from Wrangham and Waterman (1981) and Western and van Praet (1973). Since I shall be referring to these works in a number of comparisons of the behavioural ecology of C.aethiops, I present a detailed comparison of the vegetation at these sites in Table 4.10.

The vegetation at Mt.Assirik contains a higher number and diversity of species than the other sites in this comparison. The density of trees is difficult to compare, as only the quadrat-sampling (by Kavanagh, and Western and van Praet) gives true estimates of density. Both sites in Cameroon are more densely wooded than Amboseli, although they seem similar to Mt.Assirik. The woodland at Amboseli has declined drastically (by 90%) in the past few decades, as a result of high levels of salinity in the rising water-table (Western and van Praet, 1973). Mt.Assirik has much more tree cover than either site in Cameroon, although woodland at Kalamaloue is similar to that at Mt.Assirik. The difference is particularly noticeable in the gallery forest, and is further demonstrated by the higher proportions of understory cover, at ´grass´ level, at the Cameroonian sites - presumably because more light penetrates the tree canopy. Finally, there are more taller trees at Mt.Assirik than at either site in Cameroon: although Kavanagh does not present data on tree heights, his cover data show virtually no tree cover over the 10m height, in any habitat (maximum 3% and 4%, for BN and Kal

Table 4.10. Vegetational comparison between study sites.

1. Species: number of species, and diversity = number of species in the top-ranking 50% of vegetation sample. (diversity (number))

	Mt.Assirik	Kalamaloue	Buffle Noir	Amboseli
Gallery forest:	7 (49)	1 (5)	3 (14)	
Transition :			6 (23)	no data but only 9 food-species eaten by vervets
Woodland :	5 (33)	3 (12)	6 (31)	
Bamboo :	5 (21)			
Grassland :	6 (16)			
Plateau :	1 (1)			
Floodplain :		1 (2)		
"Open area" :		3 (6)		

2. Density of trees: at Mt.Assirik, number of trunks per metre of transect; other sites, number of trees per hectare

	Mt.Assirik	Kalamaloue	Buffle Noir	Amboseli
Gallery forest:	1:2.2	650/ha	750/ha	
Woodland :	1:3.4	365/ha	295/ha	0.4-4.4/ha

3. Cover: % vegetational cover at grass and tree level, wet
and dry season. Kavanagh(1977) ground= grass
" 1m-20m= tree

		Grass			Tree		
		MtA	Kal	BN	MtA	Kal	BN
Gallery forest:	wet:	21	100	80	84	40	50
	dry:	4	25	60	76	15	30
Woodland:	wet:	55	74	27	31	32	11
	dry:	9	9	9	22	21	6

respectively). At Mt.Assirik, 31% of all trees sampled on transects were over 10m tall.

Thus, on nearly all criteria the vegetation at Mt.Assirik is much richer than at Kalamaloue, Buffle Noir, or Amboseli, in terms of the number and diversity of species, the density of vegetational cover, and the size of trees.

Some descriptions of habitat are available from other study-sites, but comparisons with Mt.Assirik are difficult. The River Senegal (Galat and Galat-Luong, 1977) has lower rainfall (see chapter 5), more extreme temperature variation, a shorter wet season (June to September), and a sahelian vegetation with poor gallery forest and extensive *Acacia* woodlands; in general, a harsher environment than Mt.Assirik. Sine-Saloum in Senegal (Galat and Galat-Luong, 1976) consists predominantly of species-poor mangroves, but these, together with abundant crabs, provided very rich food sources for the green monkeys. Bole Valley in Ethiopia (Dunbar and Dunbar, 1974) has higher rainfall than Mt.Assirik, and extensive gallery forest. Lolui Island in Uganda (Jackson and Gartlan, 1965) also has higher rainfall, and a very rich forest fringing the island. Such descriptions may be of limited comparative use, but they demonstrate the wide variety of habitats to which *C.aethiops* can adapt.

CHAPTER 5.

GREEN MONKEY POPULATION: DEMOGRAPHY, DENSITY, DISTRIBUTION.

5.1 INTRODUCTION.

This chapter attempts to quantify some of the characteristics of the population of green monkeys around Mt.Assirik, for several reasons: to compare with other populations of C.aethiops, for an assessment of the gross influence of habitat on group-size and population density; and to assess whether my study group was typical of the wider local population in its demographic structure, size, and habitat-occupancy, so that conclusions from the study could be generalised.

5.2 GROUP STRUCTURE.

Complete counts were made of nine groups. The size of any one group varied considerably throughout the year (see below), so data from single counts do not represent mean group-size, but reflect the most recent demographic changes that have occurred in the counted group. The nine groups listed below were counted at different times of the year, so that although the figures are not annual means for each group, they are not biased in one particular direction. Results are presented in Table 5.1.

Only four groups were censussed completely. One of these was atypically small (Crazy Man), and because data are so few, I omitted this group from calculations of mean age/sex composition, to avoid undue bias. Results of the demographic breakdown are shown in Table 5.2.

5.3 DEMOGRAPHIC CHANGE.

I monitored the demographic changes that occurred in the study group over 2.5 years. During this time, the size of the group ranged from 18 to 28 members. These changes are shown

Table 5.1. Sample of group-sizes around Mt.Assirik.

Group	Size
Camp (study group)	25.5 (annual mean)
Downstream	20
Crazy Man	8
Stella's Waterfall	25
3rd Trib	20 *
New Valley	18 *
Assirik Valley	18
Cross Valley	21 *
Siminti	16 (60km from Mt.Assirik)
Mean =	19.2 (n=9)

* possibly several missed

Table 5.2. Age/sex composition of sample groups from Mt.Assirik.

Group	Age/sex class													
	AM	SM	AF	SF	JM	?	JF	YM	?	YF	IM	?	IF	Total
Camp (means)	4.7	2	7	1.2	2		0.8	2		1.2	3.2		1.4	25.5
Downstream	4	1	6	2					1	2		4		20
Siminti	4	3	4	0					...........5.............					16
(Crazy Man	1		2			1	1		1			2		8)
Mean:	4.2	2	5.7	1.1					..........8.5............					

AM:AF = 1:1.4
Adult:Immature = 1:1.2

in Table 5.3.

5.3.1 Birth.

Like other species of C.aethiops, green monkeys have a restricted birth season, which occurs at Mt.Assirik during February, March, and April each year. Over two seasons, 11 infants were born into the study group, representing just under 80% reproductive success for 7 adult females. During the 1979 birth season, all 7 females were pregnant, but two lost their infants at, or prior to, birth. Data from three other local groups give the same rate of reproductive success (3/4, 2/2, 4/6: mean = 81%).

5.3.2 Mortality.

During 30 months, 6 young monkeys disappeared from the study group and were presumed dead. All were younger than three years old. Several causes of death are possible. Malnutrition seems unlikely, as no signs of this were shown during the study, even during the period of most scarcity of food; nor was there any evidence of disease. Accidental death and predation seem the most likely causes.

The monkeys faced a considerable variety of danger from aerial, arboreal, and terrestrial predators. Table 2.1 showed a list of the fauna to which the green monkeys showed responses indicating they were potential prey.

* For example, between July and October 1977, an adult male (called 'Lo') left the group, reducing the number of adult males from 4 to 3. Numbers within rows of dots indicate that no further division of age/sex classes was possible.

Only one death was witnessed in the field, when a nine month old infant was killed by another group-member, probably an adult male. Full details were not observed, but the infant suffered a canine slash across his back which broke two ribs and punctured the pleural cavity. Two adult males stayed with the infant, threatening me if I made any movement towards it, but after one hour they left to join the rest of the group that had moved off. The infant died four hours later, having crawled 20m to water. There were no signs of the infant´s mother during this episode. The reason for this infanticide

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Table 5.3. Demographic changes in Camp group over 30 months. First in each pair of rows shows census, second shows change. *

Key to changes:
- left group
+ joined group
* new-born
> into older age class
$ infanticide
? missing, presumed dead

Date	Age/sex class										Total	
	AM	AF	SM	SF	JM	JF	YM	YF	IM	IF	no.of monkeys	Change
Jul 1977	4	7	0	0	......10......				3	0	24	
	Lo-				.......2?.....							1- 2?
Oct 1977	3	7	0	0	.......8......				3	0	21	
					.......2?.....				1$			2? 1$
Jan 1978	3	7	0	0	2	0	2	2	2	0	18	
					2>		2>	2>	2>		6*	6*
Mar 1978	3	7	2	0	2	2	2	0	...6..		24	
	Fl+Ol+								...1?.			2+ 1?
Oct 1978	5	7	2	0	2	2	2	0	...5..		25	
	Zu+								...1?.			1+ 1?
Dec 1978	6	7	2	0	2	2	2	0	2	2	25	
	Ro-											1-
Jan 1979	5	7	2	0	2	2	2	0	2	2	24	
			Ca-1>		2>	2>	2>		2>	2>	5*	1- 5*
Apr 1979	6	7	2	2	2	0	2	2	4	1	28	
	Pt-											1-
Dec 1979	5	7	2	2	2	0	2	2	4	1	27	

Summary: 4- 3+ 11* 6? 1$

is unclear: the infant screamed as he was wounded, and at the scene a violent chase erupted between two adults, an adult male chasing and grappling with another adult, probably male. The chase may have been in response to a deliberate attempt by the ′killer′ to wound the infant, or the wound may have been the result of displaced aggression by an adult, or simply an accident during a fight between two adult males. Several days before this event, the same infant had received a bite through the left thigh, which had severed several muscles, resulting in a marked limp. Thus the infant may have been slow to avoid a quarrel between males.

Deliberate infanticide may be explained in species living in one-male groups in terms of the killer, usually a new male usurping the resident group male, increasing his reproductive success by bringing females quickly into oestrous as a result of killing their existing young infants (see review by Hrdy, 1979). This argument does not hold for species with seasonal breeding cycles. However, even in multi-male groups newly transferred males may increase their chances of fathering successfully reared offspring if they kill the older (and unrelated) half-siblings of their offspring-to-be, thus freeing the mother′s parental investment. Busse and Hamilton (1981) provide convincing evidence in Papio anubis of paternal care of offspring against such attack from newly transferred males. In the present case, the following may be argued: the infant in question was extremely slow in maturing (the infantile white facial markings were still present, several months later than normal), and possibly a newly transferred male had recently impregnated this infant's mother; the risk of this unrelated, late maturing, previous offspring making extra demands on the mother could be eliminated by infanticide, thus increasing the new male's chances of reproductive success. The evidence to confirm or refute this is not available. Whatever the case, infanticide is likely to make only a minor contribution to overall mortality in green monkeys.

A third cause of mortality that may well be important is accidental falls by young infants. Several times I saw infants falling after slipping from branches or misjudging a jump, and being saved only by a vine that chanced to be in the path of fall. On one occasion, an infant fell approximately 10m and landed on a soft pile of leaf litter between two rocks, where he lay stunned and rigid for 10 seconds before getting up: had the fall landed a few inches either way, the infant would almost certainly have been killed on the rocks. The same infant, on another occasion, dislocated his left leg so badly that it remained locked over his back for three weeks before he recovered. During this period his movements and ability to cling to his mother were severely limited.

5.3.3 Male Migrations.

The third major factor in demographic change is the migration of adult males. Over 30 months, three strange males joined the study group, and five males left, two of whom were certainly born in the group and had just reached adulthood when they left. The immigration and emigration of adult males did have a significant effect on the demographic structure of the group: the ratio of adult males to females ranged from 1:2.3 to 1:1.3 over 30 months, i.e. between 3 and 6 males to a constant 7 adult females. Both the lowest and highest ratios occurred at some stage during the mating season.

5.4 POPULATION DENSITY.

There are two ways of calculating the density of monkeys in any population. One method is to divide group-size into home-range-size, to give the density of monkeys in the areas they are known to use. This takes no account of the distribution of groups over a wider area: ranges may overlap to various degrees, or certain areas may not be used at all. Hence the second method is to count all the groups (and their members) in a region and divide the total membership into the area of the region sampled. The first method provides a figure of the local density, which represents the number of monkeys that are living in a particular area and competing with each other for its resources. The second method provides a density figure for the use of a wide area by the population as a whole, and more closely reflects the carrying capacity of the habitat. In areas where the vegetation is relatively homogeneous, the two methods will produce similar results, but in areas like Mt.Assirik, where the habitat is composed of a heterogeneous mosaic of very different vegetation-types, the results will differ.

*There are several potential problems with using mean group-sizes in calculations of density. In the case of local density, using the smallest and largest group-size that made up Camp Group over the year (18-28) gives densities ranging from 10 to 16 per km2. Similarly, the range of population densities was from 3.7 to 5.8 monkeys per km2. Similar error may arise from varying estimate s of home-range-size. Such error may be important in comparisons with other populations of <u>C.aethiops</u>, where similar error may be present. For example (see Table 5.4), it would not be safe to assume a real difference in the density of monkeys at Mt.Assirik (14.3 per km2), Chobi (22 per km2), and Buffle Noir (18 per km2). However, differences in estimates of density at Mt.Assirik and, say, Kalamaloue (149 per km2) or Amboseli (104 per km2) are large enough to be highly important, despite potential errors in their estimation.

5.4.1 Local Density.

I have details of the home-range-size of the study group only:

$$\text{Density} = \frac{\text{mean group-size}}{\text{home-range-size}} = \frac{25.5}{1.78} = 14.3 \text{ per km2.} \qquad *$$

5.4.2 Population Density.

I chose the SAPP study area of 50 km2 around Mt.Assirik as the sample region for the local population. Information on the groups of green monkeys around Mt.Assirik was not systemmatically gathered (see chapter 3); rather, a picture of the likely number of groups and the extent of their ranges was built up over several years through circumstantial evidence from opportunistic sightings. Thus, I estimate that 11 or 12 groups inhabited the 50 km2 area within a 4 km radius of Mt.Assirik:

$$\text{Density} = \frac{\text{n. of groups x mean size of group}}{\text{50 km2}}$$

$$= \frac{11.5 \times 19.2}{50} = 4.4 \text{ per km2.} \qquad *$$

The discrepancy between the two estimates is due, in the second estimate, to the large areas of plateau, bamboo, and grassland (making up 60% of the sample area) which are of little use to the green monkeys, or never used at all. Chapter 8 gives full details of the use of these different vegetation-types by the study group. These details are also likely to apply to other groups around Mt.Assirik.

If 11 or 12 groups inhabited 50 km2, each group had an average of 4.3 km2 available to it. However, the study group ranged over 1.78 km2, which suggests that more than the same area again is unsuitable habitat for the monkeys. A home range of 1.78 km2 is the biggest yet recorded for any C.aethiops group (see chapter 8), and yet circumstantial evidence suggests that other groups at Mt.Assirik used even larger areas. It is important to note, however, that there was very strong differential usage of each vegetation-type, and there were large areas of the mosaic habitat which were unsuitable for green monkeys. Common to each group was access to some gallery forest, and water at the end of the dry season. Given that gallery forest was important for both sleeping trees and water at the same time during the year, I suggest that forest is the limiting factor on the distribution of green monkeys in this region. Since only 3% of the sampled region was forest, such a low overall density of monkeys (4.4 per km2) is to be expected.

5.5 DISCUSSION.

5.5.1 How Typical Was The Study Group?

Camp group was the largest of the nine groups counted, but its variation in size from 18 to 28 over the course of several years encompasses the sizes of six of the other eight groups. Only three groups were used to calculate a normal group's make-up. These are too few cases to assess confidently the typicality of Camp group. Nevertheless, Camp group closely resembled the small sample available: the ratio of adult males to females was 1:1.5 (Camp) vs. 1:1.4 (local mean), and the ratio of adults to immatures was 1:1.2 (Camp) vs. 1:1.2 (local mean).

Each group around Mt.Assirik had access to a certain amount of forest, which may be an essential resource that limits the distribution of green monkeys because of its supply of water and evergreen sleeping sites in the late dry season. Certainly, some food resources were not available to all groups: for example, Pseudospondias microcarpa was largely confined to the two major valleys around Mt.Assirik, and its fruits were a prized food for all primates which had access to them; Tamarindus indica was also a prized food source, but there was only one tree of this species in Camp group's range. However, such resources were unlikely to have been vital, since alternatives were available; nor were they likely to contribute to the vegetational composition of a home-range so that it was very different from others.

At Mt.Assirik there were only two major tracts of gallery forest, in valleys with 'permanently' flowing water, one of which was Lion Valley. Camp group occupied a major portion of this valley, with two other groups having access to smaller areas, one upstream and one downstream. In this respect, the study group probably used a higher proportion of the gallery forest in the area, compared with most other groups. Lion Valley also had the advantage that in dry years it was less likely to suffer a serious water-shortage than other, lesser valleys.

In conclusion, in terms of its size, composition, and access to important, limited resources, the study group was not atypical. There is no reason to suppose that the behaviour of this group cannot be generalized to the local population.

5.5.2 Other C.aethiops Populations.

The C.aethiops species-group shows much variation in the size of groups and in population-density throughout its distribution. Table 5.4 gives a summary of published data.

Groups range in size from under 10 members to one remarkable count of 174 in northern Senegal (Galat and Galat-Luong, 1978). This group might have been a drought-created congregation, but the authors give no details. Densities range from 14 monkeys per km2 to as high as 250 per km2. The adult sex ratio, however, is consistant across populations, showing one to two adult females for every adult male in a group. This suggests a relatively fixed phylogenetic trait throughout the species-group.

Gartlan (1973) observed that group-size was inversely related to annual rainfall, based on data from five African locations. As the number of data points has increased, exceptions to this pattern have emerged, but the relationship still holds: the correlation between mean group size and mean annual rainfall from 18 sites is significant and negative ($r= -.46$, $p<.05$; logarithmic transformation of both variables gives $r= -.61$, $p<.01$). A similar relationship exists among

Table 5.4 Statistics on demography, density, and distribution in 18 populations of C.aethiops, ranked from largest to smallest in group-size. Approximate annual rainfall is also given.

Location		Race *	Mean grp size	(n)	Rain (mm)	Ratios AM/AF	A/I	Density /km2	Home range (ha)	Source
Kalamaloue	Cameroon	T	76	(1)	650	1.8	1.6	149.0	56	Kavanagh (1977)
River Senegal	Senegal	S	61.5	(11)	200	1.5	0.9			Galat & G-Luong (1978)
Livingstone	Zambia	P	55	(1)	660	2.1	1.5			Lancaster (1971)
Sine Saloum	Senegal	S	33	(1)	1050	1.4	1.1	23.6	138	Galat & G-Luong (1978)
Bole Valley	Ethiopia	A	29	(1)	2000					Dunbar & Dunber (1974)
Amboseli(1963)	Kenya	P	24	(9)	380	2.1	1.2	104	41	Struhsaker (1967c,e)
Waza	Cameroon	T	23	(2)	650					Gartlan (1973)
St.Kitts:savan	W.Indes	S	21	(17)	500	1.0	1.3	135	19	McGuire (1974)
Mt.Assirik	Senegal	S	19.2	(9)	940	1.4	1.2	14.3	178	this study
Chobi	Uganda	T	18	(3)	1140			22.0		Gartlan (1973)
Buffle Noir	Cameroon	T	18	(1)	1450	2.0	1.1	18.0	103	Kavanagh (1977)
Amboseli(1971)	Kenya	P	17.9	(9)	380	1.5	1.3			Struhsaker (1973)
Bakossi	Cameroon	T	14.5	(2)	3580	1.8	1.1	112.6	28	Kavanagh (1977)
St.Kitts:forest	W.Indes	S	13	(14)	1120	1.0	1.6	255	6	McGuire (1974)
Lolui	Uganda	P	12	(46)	1590	1.4	0.8	88.8	15	Gartlan (1973)
Badi	Senegal	S	11.8	(5)	1500	1.2	0.6	60	20	Dunbar (1974)
Casamance	Senegal	S	10	(1)	1500	2.0	2.3			Galat & G-Luong (1978)
Kak	Cameroon	T	8	(3)	2690					Gartlan (1973)

* S = sabaeus; T = tantalus; P = pygerythrus; A = aethiops

grey langurs (Presbytis entellus) in India, where bigger groups are found in drier areas (Hrdy, 1977). The correlation with rainfall is most likely to be a reflection of the effect of different amounts of rainfall on the vegetation: areas of low rainfall (or highly seasonal rainfall) generally have more clumped resources which are unpredictable in space and time, whereas wetter areas have more evenly distributed, predictable and consistent resources (such as water, sleeping trees, and certain major foods). Comparative examples can be made of North Senegal (200 mm rainfall) vs. Sine-Saloum (1050 mm) (Galat and Galat-Luong, 1976, 1977); Chobi (1140 mm) vs. Lolui Island (1590 mm) (Gartlan and Brain, 1968); Buffle Noir (1450 mm) vs. Bakossi (3580 mm) (Kavanagh, 1977).

Large sized groups would be predicted at sites with unpredictable, clumped resources (low rainfall), based on the proposition that each monkey must cover a wide area to find the necessary resources, but that the total area can support a large number of monkeys. Forming large groups may be advantageous for several reasons: scarce resources (e.g. water, sleeping trees, certain foods) can be shared rather than wasting time and energy living in small groups and searching for undepleted resources, or contesting them with conspecifics by defending territories. Monitoring large areas and communicating about resources is more efficient in large groups, as is detection and defense from predators.

This analysis applies also to sizes of groups in other species, based on how they use the habitat according to dietary specializations. For example, certain primates that feed on a wide variety of fruits, or have a diverse diet and pattern of range-use (i.e. using clumped resources) form big groups, while others that eat mainly leaves (i.e. uniform distribution of resources) form small groups: *Presbytis entellus* (group-size = 25) vs. *P.senex* (9), (Hladik and Hladik, 1972); *Colobus badius* 40+ (20) vs. *C.guereza* 5-10 (12), Clutton-Brock, 1974a (Struhsaker and Oates, 1975); *Lemur catta* (18) vs. *L.fulvus* (9), (Sussman, 1977). In these examples, the habitats exploited are similar for each of the pair of compared species, and thus rainfall is not a pertinent variable.

The important variable is feeding strategy, which in turn affects ranging patterns. This emphasises the point made in the above analysis of *C.aethiops*: particular habitats may require specific strategies of feeding and ranging. Thus, size of group may be adapted to the composition of the habitat, which in turn is affected by the amount of rainfall.

A similar example is found in the polyspecific associations of some forest-living species of *Cercopithecus* monkeys. Gautier-Hion and Gautier (1979) report that 80% of sightings of *C.nictitans*, *C.pogonias*, and *C.cephus* in north-east Gabon are comprised of polyspecific groups. The dispersed distribution of fruit trees necessitates exploiting a wide area of forest by any one monkey, but the whole area can support many monkeys. In other words, the resources are as well exploited by large groups as small groups: but if large groups have increased vigilance and knowledge of the habitat, associations of different species in large polyspecific groups are advantageous. Polyspecific groups may be selected in preference to very large monospecific groups because in dense forest, a large group may have difficulty in maintaining internal social cohesion (e.g., visual communication between all group-members; structure of mating patterns), a disadvantage that does not apply to several, small, social units that join in foraging associations in order to optimize the use of resources.

However, from the proposition that in regions of low rainfall, individuals must cover large areas to include the necessary resources, one might predict larger home-ranges for large groups than for small groups. This is the case for each of the pairs of species compared above (Presbytis, Colobus, and Lemur), but the relationship does not hold for C.aethiops groups (correlation between group-size and home-range-size: r= .15, n= 11, n.s.). This is perhaps not surprising, for several reasons: first, authors of comparative studies often mention the problems of comparing results across field-sites, since different methods, definitions, degrees of estimation, and field conditions may introduce bias es. Secondly, and perhaps more importantly here, home-range-size is too simple a measure to use without reference to details of range-use and habitat quality. Struhsaker (1967e) found no correlation between group-size and home-range-size within the population of vervet monkeys at Amboseli, but did find a strong relationship between group-size and the amount of optimal habitat defended.

There is another set of evidence concerning ecological correlates with group-size in primates, which focusses on the density of food resources rather than their distribution. Group-size increases with increasing food density: Gaulin *et al.*(1980) showed that bigger groups of *Alouatta palliata* were associated with higher densities of *Ficus* trees on Barro Colorado Island, where *Ficus* species are the major food-item for the howler monkeys. Struhsaker (1975) noted smaller groups of *Colobus badius* in marginal habitats, which have lower densities of important foods. Hamilton *et al.*(1976) reported groups of *Papio ursinus* in the food-rich Okavango Swamps that were 2 to 4 times larger than groups living in the impoverished Namib Desert. Struhsaker's (1973, 1976) recensuses of *C.aethiops* in Amboseli showed a decline in group-size associated with a natural reduction in food resources.

However, an alternative strategy for dealing with high-density food resources is shown in *Cercocebus albigena*. Freeland (1979) compared populations of mangabeys from two sites in the Kibale Forest, and found that at the site where food trees occurred at higher density, there was no change in group-size, but there were more groups per unit area. The higher density of mangabeys was accommodated by groups having smaller home-ranges.

[*] In this discussion, several terms have been used which have strictly defined definitions to a sociobiologist, but which have been used in a looser sense here. Several points should be clarified. 'Strategy' has not been used in the strict sense of the word, namely a genetically programmed 'evolutionarily stable strategy', but rather in the sense of a set of rules for an efficient feeder that may have been learned, and that often involve decisions in response to environmental variables. Statements about small or large groups being selected in areas of high or low rainfall are not intended to imply group-selection arguments, but are simply shorthand for "individuals living in small or large groups..." : the selection works through individuals, based on the advantages of living in small or large groups. 'Adaptation' is a consequence of natural selection, although it is most often an assumption. A behaviour is adaptive if it increases individual or inclusive fitness, but rarely can this be directly tested. However, adaptive behaviours can often be recognised by showing a close fit with a problem in an animal's environment, and thereby lies the assumption.

All this suggests that primates have evolved several means of coping with variations in the density and distribution of food. In the case of C.aethiops, the problem may be solved by differing combinations of group-size, population-density, and home-range-size, according to local environmental pressures. The negative correlation between group-size and rainfall may be confounding several factors. In areas with very low rainfall, the predominant environmental pressure may be towards big groups because monkeys must aggregate around water, which is seasonally the scarcest resource. The density and home-range-sizes of these large groups may then be determined by the density and distribution of food, which are pressures of secondary importance in this case (e.g., large groups at Kalamaloue, where reliably available water was scarce in the dry season, but food-availability was not limiting, allowing a high density of monkeys) In areas where scarcity of water is not the main environmental pressure, group-sizes, like density and home-range-sizes, are more likely to be determined by variations in the density and distribution of food resources: in areas of higher rainfall, or where the habitat is fairly uniform, with food more evenly distributed in space and time, small groups with small ranges are selected, living at high density (e.g. Lolui Island, St.Kitts, Bakossi); in drier areas, where foods are more clumped and unpredictable, larger groups living at lower densities are selected (e.g. Mt.Assirik, Chobi, Buffle Noir). *

CHAPTER 6.

FEEDING.

6.1 INTRODUCTION.

It is only from recent, detailed studies of primate ecology that we are starting to appreciate the extent to which feeding behaviour varies within and between species: in terms of selectivity, dietary diversity, age and sex differences, diurnal patterns of feeding and use of vegetation, and the influence of food seasonality on ranging behaviour (e.g. Clutton-Brock, 1977; Montgomery, 1978).

The emphasis in these studies has been on detail, in response to the shortcomings of early attempts to relate ecology and social structure using gross ecological and behavioural variables (e.g. Crook and Gartlan, 1966). Until recently, much of the detail has been behavioural, and generally insufficient attention has been paid to measurements of environmental detail, such as vegetational composition of the habitat, distribution and density of resources, and the phenology of plants. Recent examples of studies with closer attention to fine ecological detail include work in the Kibale Forest, Uganda (e.g. Struhsaker, 1975, 1978; Oates, 1977; Rudran, 1978); in the Krau Game Reserve, Malaysia (e.g. Chivers, 1977 ; Raemaekers, 1980); Hladik's work in Panama, Sri Lanka and Gabon (e.g. Hladik, 1977a, 1977b, 1978); and other studies in Gabon (e.g. Gautier-Hion, 1980; Gautier-Hion *et al*., 1981).

Although intraspecific variation in feeding behaviour has been demonstrated in a number of primates (e.g. *Pan troglodytes*, Hladik, 1977b; *Colobus badius*, Marsh, 1981; *Propithecus verreauxi*, Richard, 1977; *Colobus badius*, Struhsaker, 1975; *Cercocebus galeritus*, Waser, 1977), long-term, quantitative data on the feeding behaviour of different populations of *C.aethiops* are still limited, despite its being one of the most common African primates. Some such data are provided for green, tantalus, and vervet monkeys, by Galat and Galat-Luong (1977), Kavanagh (1977, 1978), and Wrangham and Waterman (1981), respectively. Other studies have been very brief, or qualitative in their information on diet and feeding behaviour (Dunbar, 1974; Dunbar and Dunbar, 1974; Gartlan and Brain, 1968; Hall and Gartlan, 1965; Struhsaker, 1967a). These studies show that *C.aethiops* is a dietary opportunist, eating a wide variety of types of food, including fruits and berries, seeds and nuts, leaves, buds, shoots, flowers, fungus, grasses, gum, bark, meat, eggs and invertebrates. In a survey of the diets of 131 species of primates, Harding and Teleki (1981) found that *C.aethiops*, with *Pan* and *Papio*, have the most omnivorous diet - they eat all of the types of food that any primate is known to eat.

Apart from suggesting a lack of specialization in the diet of *C.aethiops*, the poor detail of many of the above-cited studies does little to clarify the degree of selectivity or diversity in the diet, in particular as this relates to seasonally variable food availability, and to the nutritive values or toxic components of different foods. Recent feeding studies have shown that dietary variation between populations often results from differences in food availability (e.g. Hladik, 1977b; Kavanagh, 1978; Struhsaker, 1975), and models of feeding behaviour in optimal foraging theory (Pyke _et al._, 1977; Schoener, 1971) provide testable hypotheses regarding dietary changes in response to changes in food density. There is a growing body of evidence that demonstrates a relationship between phytochemistry and food selection in some primates (e.g. Gartlan _et al._, 1978; Glander, 1981; Hladik, 1977b, 1978; Milton, 1980; Oates _et al._, 1980; Wrangham and Waterman, 1981). Sex differences in diet are also emerging (e.g. Clutton-Brock, 1977; Galdikas and Teleki, 1981; Waser, 1977), differences which may have important evolutionary implications (see Clutton-Brock, 1977; McGrew, 1979).

This study of feeding ecology had the following aims:

i)to provide a detailed, quantified record of green monkey feeding patterns, in parallel with detailed monitoring of food plants, and details of the density and distribution of those resources.

ii)to provide comparative data for an examination of both intraspecific and interspecific variation in feeding behaviour - a record that is essential for surveys of primate characteristics, such as that of Clutton-Brock and Harvey (1977).

iii)to test some of the predictions of optimal foraging theory, in an examination of the adaptive significance of the monkeys' feeding behaviour in relation to changes in their environment. This requires both behavioural and environmental detail, and at least one annual cycle of study in order to cover any variation in feeding behaviour due to seasonal variation in the environment. The year can conveniently be divided into monthly samples, to provide 12 data-points on many ecological and behavioural variables that can be used to test predictions from optimal foraging theory.

This chapter will be presented as follows: data and discussion will be presented in sections on the content of the diet, selection of food, diversity of the diet, dietary overlap between months, animal foods, and age/sex differences in the diet. No data will be presented on the techniques and postures of feeding, which resemble those of Cercopithecus aethiops tantalus, and are well described by Kavanagh (1978). Results will then be discussed in relation to several other studies of primate feeding behaviour, for intra- and interspecific comparison. Tests of optimal foraging predictions will be carried out in chapter 10, incorporating data on ranging patterns and activity budgets.

6.2 ANNUAL DIET.

Throughout the annual cycle of monthly 5-day samples, the monkeys were recorded as feeding on a minimum of 65 species of plants (Table 6.1), as well as on many invertebrates, and some eggs and vertebrates (Table 6.4, below). However, together with invertebrates and herbs, only the top-ranking 5 species made up over 50% of the annual diet. Fruit was eaten from 47 of the species (e.g. see Plates 6.1 and 6.2), while flowers

Table 6.1. Species and parts of plant-foods eaten by green monkeys from Camp group, during 5-day samples throughout the year. Also, proportions of the annual diet accounted for by each species (%). Parts: Fr.= fruit; Fl.= flower; Lf.= leaf; Sd.= seed; Gu.= gum.

Species	Parts					Rank	%
	Fr.	Fl.	Lf.	Sd.	Gu.		
Pterocarpus erinaceus		*	*	*		1	7.2
Ficus umbellata	*		*			2	7.2
Spondias mombin	*				*	3	5.6
Pseudospondias microcarpa	*	*	*			4	5.1
Landolphia heudelotii	*					5	4.7
Saba senegalensis	*					6	4.5
Nauclea latifolia	*		*			7	4.1
Diospyros mespiliformis	*		*			8	3.4
Cyanotis lanata		*				9	2.7
Lannea acida	*		*		*	10	2.2
Lannea microcarpa	*				*	11	2.0
Ceiba pentandra		*			*	12	1.9
Sorindeia juglandifolia	*					13	1.3
Olyra latifolia			*	*		14	1.3
Zyziphus mauritiana	*		*			15	1.3
Ficus lecardii	*		*			16	1.1
Ficus sp.	*					17=	.8
Adansonia digitata	*					17=	.8
Cassia sp.	*					19	.8
Combretum tormentosum			*		*	20	.8
Treculia africana	*					21	.7
Vitex madiensis	*					22	.7
Parkia biglobosa	*	*			*	23	.7
Cola cordifolia	*				*	24=	.6
unknown A.		*	*			24=	.6
Daniellia oliveri		*	*			26	.6
Pterocarpus lucens		*				27	.5
Zyziphus mucronata	*					28	.5
Cissus populnea	*					29	.5
Grewia lasiodiscus	*					30	.4
Ficus vogelii	*					31	.4
Lophira alata					*	32	.3
Afzelia africana	*				*	33	.3
Boscia angustifolia	*	*				34=	.3
Icacina senegalensis	*					34=	.3
Bombax costatum	*	*				36	.3
Morinda geminata	*					37=	.3
Cassia sieberiana		*				37=	.3
Khaya senegalensis		*			*	39	.2
Oxytenanthera abyssinica		*				40	.2
Raphia sudanica					*	41	.2
Opilia celtidifolia	*					42=	.1
Cordyla pinnata	*	*				42=	.1
Paullinia pinnata	*					44	.1

Plate 6.1. A 2-year old eating fruits of Spondias mombin.

Plate 6.2. A 1-year old male eats a Landolphia heudelotii fruit.

were eaten from 19 species, leaves from 13 species, and gum from 13 species (although the array of species included in the categories of "herbs" and "grasses", the herbaceous and graminaceous forest and woodland understory, were not individually identified). Most fruits were easily obtained and processed: thin skins were eaten but thicker shells were discarded, and pips or stones were sometimes consumed too, with the pericarp. Some species of fruit had extremely hard shells (for example, *Adansonia digitata*, *Afzelia africana*, *Oncoba spinosa*, *Strychnos spinosa*), and were inaccessible to the green monkeys, except in cases when they found such fruits opened but discarded half-eaten by baboons. On occasion, the green monkeys waited near groves of baobab trees (*A.digitata*) that were full of feeding baboons, and then moved in to search under the trees after the baboons had left.

Generally only large flowers were consumed - species that produced many hundreds of tiny inflorescences were often ignored, perhaps because of little return on time invested in harvesting such small flowers. Medium sized flowers were consumed whole, in handfuls, and from larger flowers, petals and sepals were mostly discarded, and the stamen, stigma, or flower base was consumed.

From trees, mature leaves were never seen to be eaten; the monkeys chose young, flushing leaves or shoots. From grasses, the succulent bases of stems were eaten, as well as seeds later in the year, and from the herbaceous understory in closed canopy vegetation, the monkeys ate handfuls of young leaves, and many soft seeds and pods later in the year. Gum was generally eaten in a thick viscous state, or as it hardened into crystals. This was picked from the branches of a variety of tree species, but generally those that grew in drier areas, such as <u>Combretum</u> spp. on the plateau edges. Fungi grew in damp areas of the valley, from decaying wood or leaf-litter, but in the early wet season, the monkeys ate a species of ´puffball´ mushroom (sp. ?) that grew out on the open plateaux.

Apart from exploiting trees, shrubs, and ground cover, some monkeys rarely dredged and ate algae from ponds, and licked the earth or rocks in certain caves. It is possible that this was done to acquire specific minerals that were deficient in the diet (e.g. see Oates, 1978), but occurrences were so few that they were probably not of great importance.

There is considerable interannual variation in the importance of many food-species, since the abundance of many fruit crops at Mt.Assirik varies from year to year, and several species sometimes fail completely. <u>Pseudospondias microcarpa</u>, ranked as the 4th most important species in the annual diet during November 1978 - October 1979, failed completely the previous year (March 1978). <u>Hexolobus monopetalus</u> is a species which constituted less than 0.1% of the sampled diet for the year of this study, since the fruit crop failed that year. Yet in August-September 1977 this very widespread species produced an abundant crop of fruit, on which the monkeys spent much time feeding. For this reason, and because some species produce a very brief crop of fruit or flowers that may not coincide with a monthly 5-day sample, some species may be misrepresented in the sampled diet, or perhaps may not appear at all, although they are eaten.

Figure 6.1 shows percentages of the annual diet made up by different food-parts. Fruit formed the largest part of the diet (50.2% of feeding time), with invertebrates (13.1%), flowers (13%), and seeds (12.8%) making up a further 38.9%. Foliage, gum, fungus and stems made up the small remainder, in addition to the rare vertebrate prey and eggs.

6.3 MONTHLY DIET.

Table 6.2 shows the proportions of the diet (= % of feeding records) made up by each major food-species during each month of the year. Figure 6.2 shows a similar summary for food-parts. The following sections will investigate the monthly differences and similarities in the monkeys' feeding patterns, in food selection, diversity of the diet, and extent of change of diet between months.

6.3.1 Selection Of Food-species.

To see whether the monkeys were feeding on various species in proportion to their availability, or if they were selecting certain species on some other basis, selection ratios were calculated for each major food-species (i.e. species accounting for 5% or more of feeding records) for each month. For the moment, this analysis will be restricted to fruit and flowers only (see below). A selection ratio is the ratio between the observed proportion of the diet made up by any one

Table 6.2. Proportions of the monthly diet made up by each major food-species (% of feeding records), and the respective selection ratios (see text).

Species	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Herbs	36.0	8.5						6.4	10.5	6.3	40.0	
Zyziphus mauritiana	14.3 (.53)											
Invertebrates	14.3	26.4		13.6	12.8	14.3	12.3	22.1	21.3		8.9	7.9
Grasses	9.9			17.8					11.6			
Ficus lecardii	5.9 (8.94)											
Ceiba pentandra		22.2 (.83)										
Diospyros mespiliformis		16.4 (1.17)	11.2 (1.84)	12.0 (2.26)								
Pterocarpus erinaceus		9.8 (.98)	53.3 (.12)	14.5 (.49)								
Zyziphus mucronata			6.2 (2.21)									
Daniellia oliveri			6.1 (3.47)									
Ficus umbellata				16.3 (1.04)	9.9 (.20)	7.9 (.26)	10.9 (.27)	5.1 (.18)	21.0 (1.27)			13.1 (3.16)
Pseudospondias microcarpa					27.2 (.63)	26.3 (1.01)						
Lannea acida					12.8 (.32)	7.6 (.63)						
Cassia sp.					9.2 (.98)							
Ficus sp.					8.0 (6.67)							
Sorindeia juglandifolia						15.3 (1.01)						
Saba senegalensis							22.8 (.49)	31.1 (.17)				
Lannea microcarpa							22.3 (.56)					
Landolphia heudelotii								18.5 (.18)	35.5 (.38)			
Pterocarpus lucens								6.4 (4.00)				
Cyanotis lanata										32.3 (.87)		
Nauclea latifolia										18.5 (1.06)	18.8 (1.18)	6.6 (.96)
Adansonia digitata										5.5 (.32)		
Spondias mombin										5.4 (1.54)	52.1 (1.86)	9.6 (3.84)
Vitex madiensis												6.8 (.39)
Cissus populnea												5.0 (3.21)

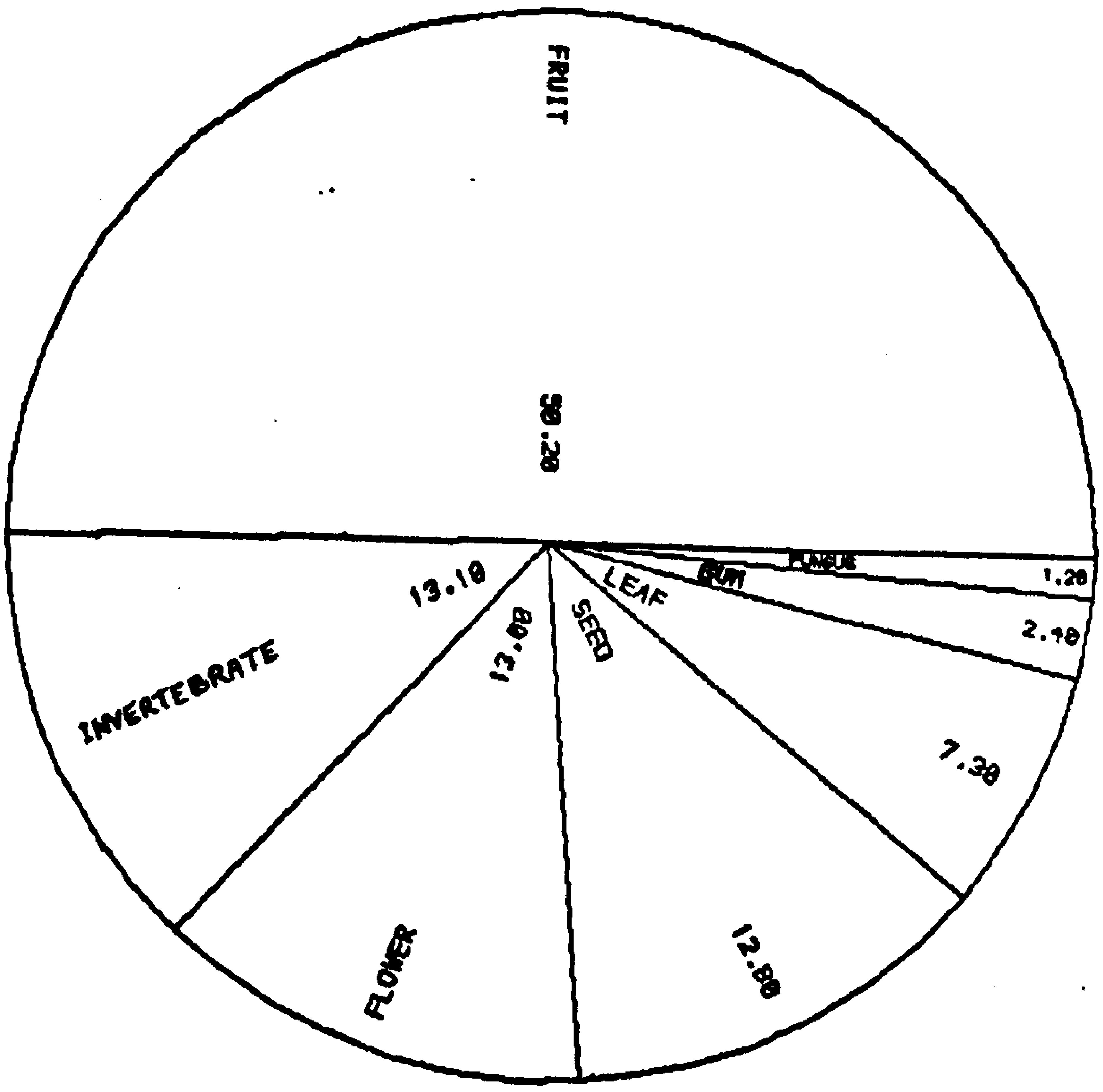


Figure 6.1. Proportions of the annual diet made up by each food-part.

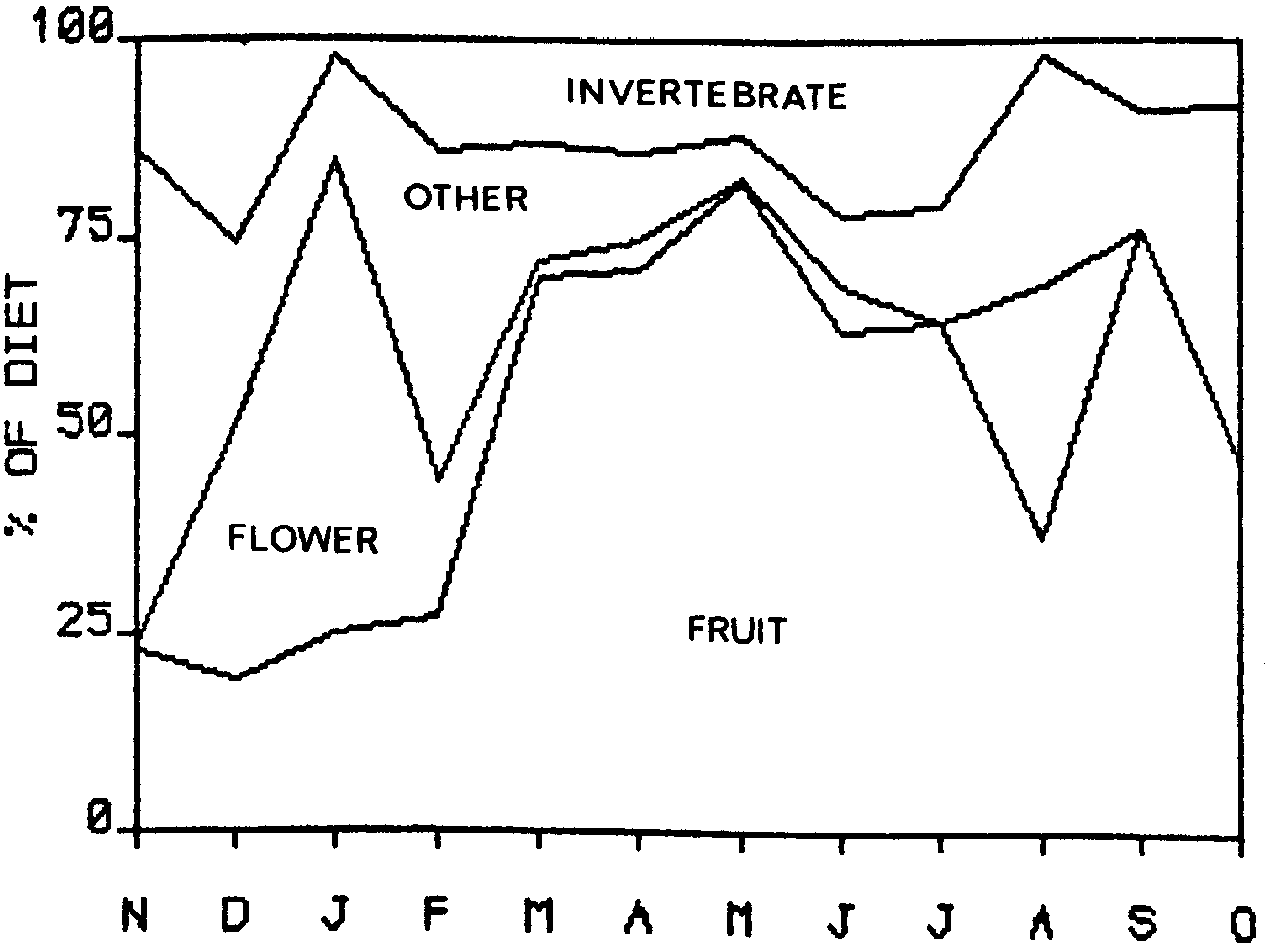


Figure 6.2. Proportions of the monthly diet made up by fruit, flowers, "other" (foliage, gum, seeds, fungus), and invertebrates.

species, and the proportion expected on the basis of its relative availability; thus a species which forms a high proportion of the diet, but which has a low relative availability, will have a high selection ratio. Here, the observed proportion is the percentage of feeding time accounted for by a species, and for the expected proportion, the total available canopy area of the species is used. (For the calculation of this area, see chapter 3). It is important to incorporate phenological measures, as well as canopy-sizes and tree-densities, in any measure of availability, since simply using the percentage of trees of a species in the vegetation sample (e.g. Clutton-Brock, 1975) takes no account of these important variables. Using ´canopy area available´ as an expected value not only provides ratios that are comparable within any month (i.e. the available canopy area of each food-species will represent its proportional availability within the month when other ratios from that month are compared); but it also provides ratios that are comparable between months, since the available canopy area of a species is an absolute value, and thus comparable to any other ratio calculated. The formula, then, is:

$$\text{s.r. for species A} = \frac{\text{\% of feeding records on species A} \times 100}{\text{total species A canopy area available.}}$$

Selection here refers only to the monkeys´ use of a species relative to its availability, and makes no reference to preferences for taste, accessibility, ease of processing, or nutritional value. Grasses and species from the herbaceous understory are lumped into broad categories (grass and herbs) since species identification during feeding was impractical. Since it proved difficult to provide reliable estimates of the availability of herbs and grass, and of invertebrates, these foods are omitted from this analysis: in addition, they are special cases, and will be discussed separately.

Table 6.2 includes the food selection ratios. As can be seen, the ratios range from 0.12 to 8.94, a 75-fold difference, indicating a vast range of selectivity for different species. However, I have doubts about the selection ratio as a meaningful value, since the value is determined to a large extent by the availability of the species concerned, and very little is contributed by its proportion in the diet; for example, due to the rarity of *Ficus lecardii* trees, the selection ratio for this species in November was extremely high (despite it making up only 5.9% of the November diet), whereas *Pterocarpus erinaceus* is extremely common, and its flowers formed 53.3% of the January diet, yet because these flowers were so common, its selection ratio was about 75 times lower than for the *Ficus*. These selection ratios would thus seem to have little biological significance, since they support the argument that *P.erinaceus* is not selected nearly as much as *F.lecardii* because the former is so common, and the latter is so rare. It seems more likely that the monkeys do choose *P.erinaceus* flowers precisely because they *are* so common. (An important proviso should be added to this statement: that is, given that the monkeys do eat flowers, *P.erinaceus* flowers form a big part of the January diet because they are so common. I shall return to this later.)

To check on this influence of availability, selection ratios were plotted against availability . A log-log transformation revealed a very strong negative correlation ($r= -.90$, $p<.0001$, omitting grasses and herbs from the analysis). In other words, over 80% of the variation in selection ratios is accounted for by availability. Thus, selection ratios indicate little selectivity except in proportion to the availability of each species. The residual 20% of variation in selection ratios may be related to qualitative differences between food-species: for example, variation in specific nutrients, secondary compounds, digestability, or simply taste. These factors in food choice will be discussed in chapter 10.

If the proportion of the diet made up by each species is plotted against its availability (Figure 6.3), the result expected from the previous analysis is clear: the correlation between the proportion of a species in the diet and its availability is strong and positive (after log-log transformation, $r= .70$, $p<.0001$).

[This finding may have important implications for conclusions that are based on selection ratios in other studies: for example, I calculate from Struhsaker (1975; p275,table 42) - the correlation between his "cover index" (amount available) and species selection ratios (with log-log transformation) is $r= -.86$, $n=13$, $p<.001$; Rudran (1978; p20,table 19) - the (log-log) correlation between availability and selection ratio is $r= -.86$, $n=12$, $p<.001$; Oates (1977; p293,table VI) - the same correlation is $r= -.70$, $n=15$,

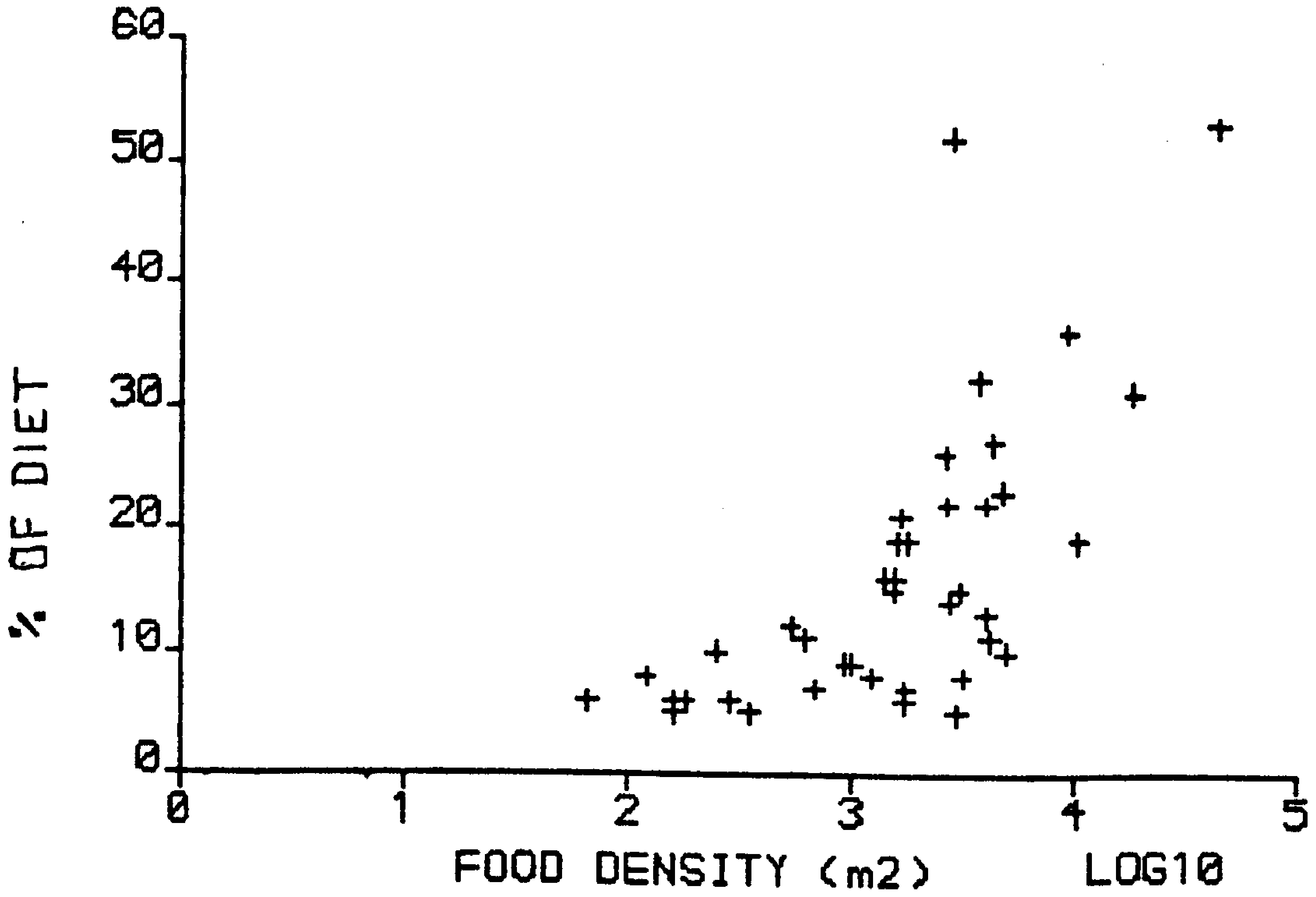


Figure 6.3. The proportion of the diet (=% of feeding time) made up by each species, plotted against its ($\log_{10}$) current overall availability.

$p<.01$.]

However, the monkeys were selecting certain foods, since some plant species in their range were not eaten at all (see below). The key point is that amongst the species that were eaten, the monkeys did not select some more than others, but fed from each species in proportion to its availability. This analysis of species-selection according to food-availability provides a quantified demonstration of the opportunistic nature of the feeding strategy used by the green monkeys.

This statement needs to be refined, since all species concerned in the previous analysis involved only fruit and flowers. No account has yet been made of herbs and grasses, or of the several species of leaves, gum and fungus. For these foods, no single major species were involved, so they are analysed in terms of food-parts rather than species.

6.3.2 Selection Of Food-parts.

If the monkeys were not selecting particular species of food (at least, of fruit and flowers), then were they selecting particular food-parts? Figure 6.2 showed a strikingly high proportion of fruit in the diet, fruit being the top-ranking food-part in 9 months of the year. As availability measures were only taken for important food-species (as previously defined), I have too few quantitative data to plot food-part proportions of the diet against their availability (except for fruit and flowers, see Figure 6.3). Instead, for a qualitative analysis, I used other S.A.P.P. researchers as knowledgeable observers to obtain independent estimates of the relative availability of certain food parts. Observers were asked to estimate on histograms the monthly availability of specified food-parts. These are not absolute values of availability; the height of any histogram bar is used only to distinguish one month's availability from other months. There was close agreement between observers.

In Figure 6.4 these monthly estimates of the availability of each food-part are plotted together with the proportions of the monthly diet made up by the relevant food-parts. For all food-parts except leaves, their proportions in the diet closely relate to their availability. Figure 6.4 provides some evidence, then, that as with fruit and flowers, other food-parts were eaten in relation to their availability from month to month.

Feeding on flush leaves was an exception to this, and may have depended on the availability of other foods present at the same time; for example, during the months of peak leaf-flushing (March, April, May), there was very little leaf-feeding, possibly because fruit was so abundant during these months and over 70% of feeding time was devoted to fruit; and vice versa, the month with the highest intake of leaves (February) produced very little, poor quality fruit. In parallel to this, leaves may be important in regular small quantities irrespective of availability, to provide essential nutrients, such as specific amino acids (see Chapter 10).

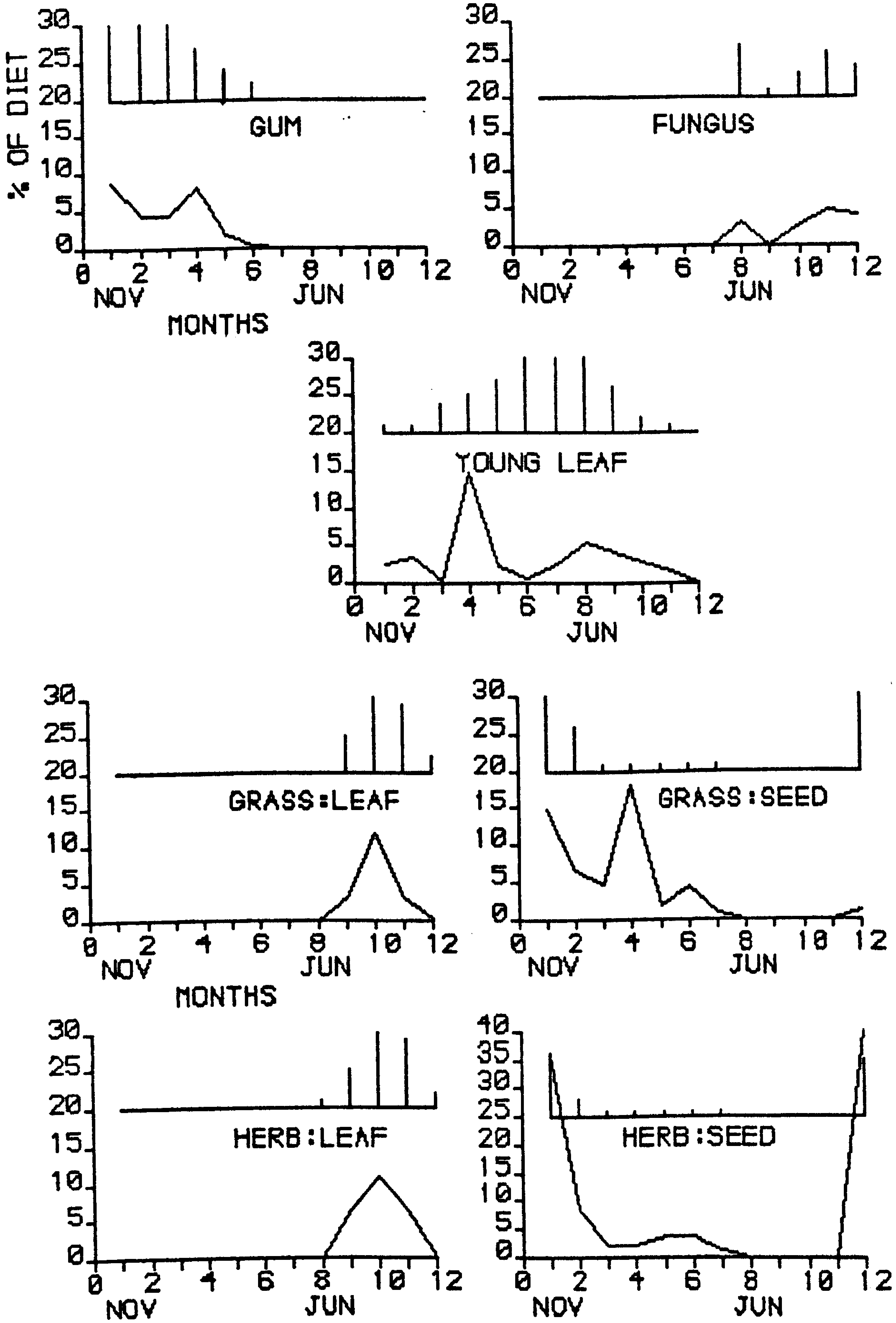


Figure 6.4. Proportions of the monthly diet made up by food-parts other than fruit or flowers. Above each are plotted independent estimates of the relative availability of that food-part (see text).

The diet in February stands out as an exception in general: the proportions of gum, young leaves, and grass seeds in the diet were higher than expected on the basis of availability. February was the most difficult month for the monkeys, if not for overall availability of food, then for its quality: although during November and December there was less fruit than in February, there was an abundant supply of herb seeds and pods; in February, in mid dry season, there was no ´backstop´ supply of green herbs and grasses, and the quality of the fruit was low, consisting largely of dried and shrivelled fruit and fruit skins discarded from the previous month´s feeding, while much of the next crops of fruit was still unripe. The low quality of fruit in February may have been responsible for the monkeys´ increased dependence on grass seeds, gum, and leaves in the diet. I shall return to the idea of certain food-parts as ´backstops´ in the diet, in the following section, although it should be remembered at this point that fruit and leaves provide very different elements in a diet and are not simply interchangeable.

To try and get at the question of selective preferences for different food-parts, S.A.P.P. researchers were once again used as independent observers to estimate the absolute availability of grass and herbs. The following conclusions are based on these estimates: for any quadrat in which herbs occurred, on average 50% of the quadrat was covered by herbs; and for grass (prior to burning), the estimate was 75%. The areas from these figures were multiplied by the number of quadrats containing herbs and grasses respectively, to give estimates of the overall areas of availability. These are comparable to other estimates of fruit and flower availability, except that no phenological data are incorporated, and that estimates are concerned with a two-dimensional carpet of herbs and grasses rather than three-dimensional tree canopies. The figures derived for total availability are:

Herbs: 111,700 m2.
Grasses: 484,370 m2.

The figures take no account of monthly differences in quality, which varied greatly, with lush green foliage in the wet season, drying out in the early dry season, the soft seeds in October and November becoming hard and dry as the dry season progressed. Burning drastically reduced the availability of grasses, leaving only rare patches unburnt, although grass seeds were often picked from the earth after fires had swept through and burnt the dry foliage.

When compared to the mean monthly availability of fruit and flowers, which was 12,595 m2 (range: 2,766 - 44,850 m2), it is obvious that, even if overestimated, the availability of grasses and herbs far exceeded that of fruit and flowers. And yet their proportion in the diet did not, except in the case of herb seeds in October and November. From this, I conclude that fruit and flowers were selected more than herbs and grasses.

I made no attempt to estimate the availability of fungus, gum, or flushing leaves. Although fungi were not common, gum and young leaves were abundant at certain times of year. These food-parts rarely accounted for more than 5% of the diet, and are thus not considered major food-items, although they may play an important part in the diversity of the diet and its nutrient-balance.

In conclusion, in their vegetable diet the monkeys were primarily selecting fruit and flowers, and eating these in proportion to their availability. Secondary to fruit and flowers, the monkeys selected the leaves and seeds of various grasses and herbs, as well as gum, fungi, young tree leaves and leaf shoots, stems, and seeds. These food-parts too (excluding leaves) were eaten in proportion to their relative availability from month to month, but not in proportion to their absolute availability when compared to fruits and flowers in the same month.

This analysis has been concerned only with the selection of vegetable foods. Animal foods are also important in the diet, and will be discussed in a later section. The question of whether the monkeys are selecting an optimal diet will be discussed in Chapter 10, within the framework of optimal foraging theory.

6.3.3 Diversity Of The Diet.

Although Table 6.1 shows a minimum of 65 species of plants to be included in the annual diet, these are by no means equally exploited - over 50% of the diet was made up only from invertebrates, herbs, and the top-ranking 5 plant-species. To examine monthly differences in the extent of exploitation of different plant species, indices of diversity were calculated for each month's diet, and are shown in Figure 6.5. These indices were calculated using the Shannon-Weaver equation (as quoted in Struhsaker, 1974, 1975), as for the indices of diversity in monthly ranging patterns. Indices for monthly diversity of food-parts eaten are also shown. The two sets of indices follow each other closely, except for the months of March, April, and May, where the indices for food-parts show much less diversity, due mainly to the very high proportion of fruit in the diet. Overall, the figures for species-diversity are higher than those for diversity of food-parts because of the greater variety of species available compared to food-parts available.

6.3.3.1 Diversity Of Species. -

To test the hypothesis that diversity in the diet is related to food availability, both measures of diversity were plotted against availability. In the case of species diversity, there was no correlation (H:species with availability: m2, r= -.17, p=.30; H:species with log-availability:ln m2, r= .02, p=.47). It seemed that the calculation of species diversity for any month was influenced more by the number of species eaten than

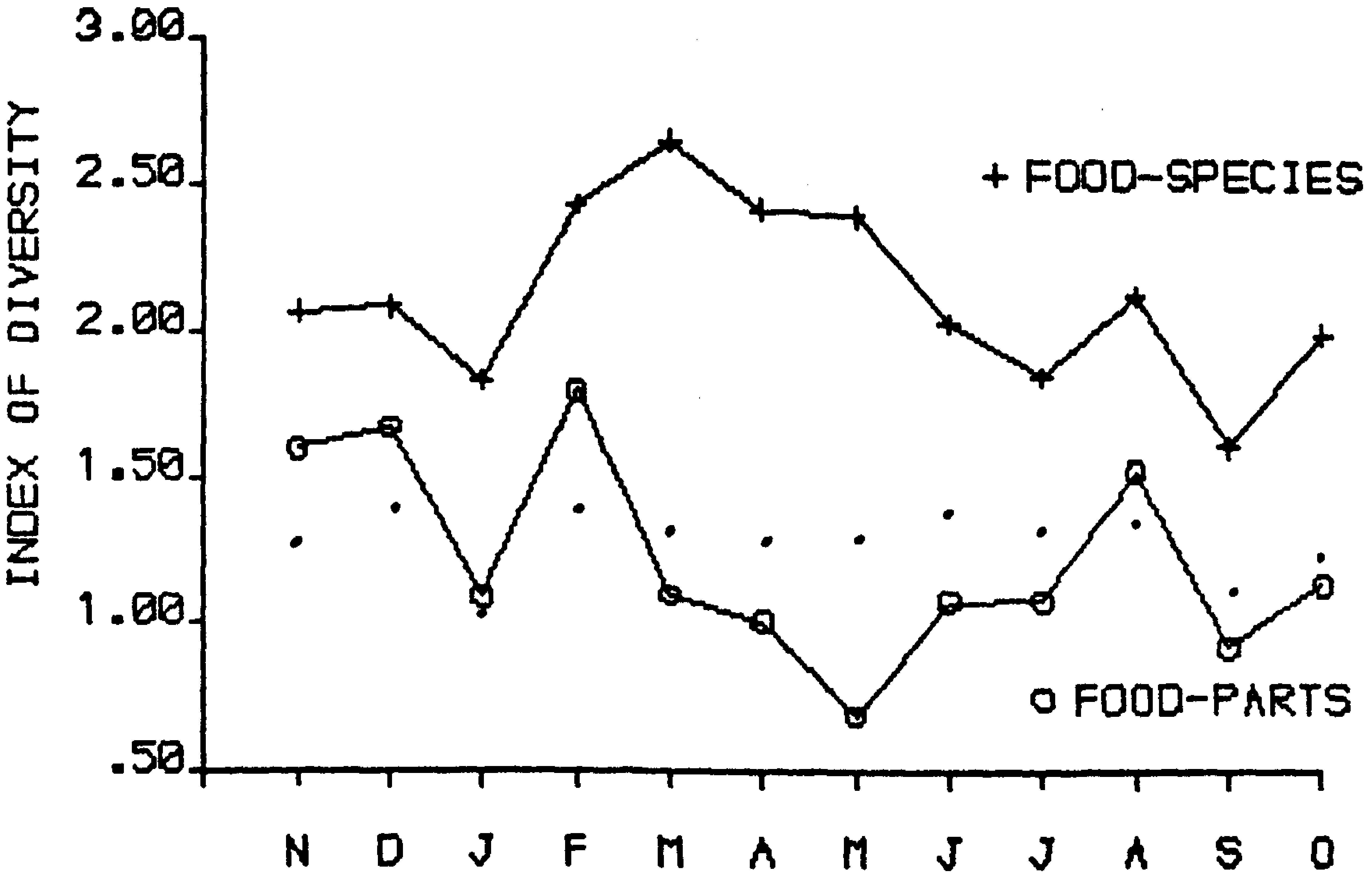


Figure 6.5. Monthly indices of diversity for food-species (+), and food-parts (0). Dots show indices for the top-ranking 5 food-species each month.

the distribution of time spent feeding on those species: a correlation shows this to be the case (H:species with number of species, r= .64, p<.02). Rasmussen (1980) too points out that the Shannon index is sensitive to the number of items used in its calculation, as well as diversity. In other words, in months when more species are eaten, the diet is more diverse. However, one aspect of feeding patterns that an index of dietary diversity attempts to measure is how evenly time is spent on various foods. By definition, a highly diverse diet is one in which feeding time is spent evenly over many foods, whereas a diet with a low index of diversity is one in which much time is spent on very few foods, and little time spent on the rest. Since the above measures of species-diversity are correlated with the number of species in the diet (see above), monthly differences and similarities in the distribution of feeding time across important food-species are being obscured. This effect can be controlled by calculating diversity indices for the top-ranking 5 species each month (i.e. controlling the number of species contributing to the index). The top-ranking 5 species were chosen because they generally cover the month's important foods, but the figure is arbitrary. These new diversity indices, measuring the evenness of the distribution of time across the 5 most important species each month, show much less monthly variation than the previously calculated indices (Figure 6.5). This confirms that the number of species in any month's diet is a major factor contributing to the month's index of diversity, and that without this effect, much of the monthly variation in diversity disappears. The months of

January and September stand out as having lower diversity of species in the diet, due to over 50% of the diet being made up by one species only. In the other months, there is much the same spread of feeding time over the top-ranking 5 species.

6.3.3.2 Diversity Of Food-parts. -

This finding fits the prediction from the previous analysis, as follows: since there was no selection of food-species, but rather the monkeys fed in proportion to availability (except foliage, and invertebrates - see later), diversity too should be determined mainly by the number of species there were available to eat, and not restricted by any "choice" from the monkeys. This implies that the green monkeys ate as wide a range of species as was available. This holds true only if it is shown that in months when fewer species were eaten, there were indeed fewer species available, and that the monkeys were not choosing to eat fewer species for some other reason. Conclusions about species diversity should also be refined to meet the expectations of selectivity of food-parts; namely, given that fruit and flowers were the primary choice of food-part, species diversity might be expected to be maximised for these food-parts in preference to other parts.

To this end, a table was drawn up from general phenological records, indicating the presence or absence of food-parts on all major food species, throughout the year. This represents as nearly as was practical, a complete list of the fruiting species found in Camp group's range, but species producing flushing leaves are under-represented. For some species, a complete record of the cycle of each food-part was not available; in some cases the choice of species to be included in the phenological monitoring was made as the year's study progressed; in other cases, the flowering stage of the cycle passed too quickly to be relevant to this analysis, or in the case of some non-deciduous species there was no distinct phase of leaf flushing. It is important to emphasise that for this analysis no account was taken of the quantity of food or its quality (e.g. ripeness of fruit, presence of secondary compounds), but simply its presence or absence. From this table, the percentage of occasions on which a species could have been eaten (i.e. was available), and was eaten, was calculated for fruits, flowers, leaves, seeds, and gum.

The results clearly showed that the monkeys were maximising the number of fruit species in each month's diet: on 93% of occassions when fruit species were available they were eaten. Thus, in months when fewer species of fruit were eaten, it was indeed because fewer species were available. However, this maximisation of species did not apply to flowers, leaves, seeds, and gum, which were eaten on 40%, 33%, 40%, and 47% (respectively) of occasions on which they were available. The figure for flowers may be misleading because certain species produced very tiny flowers that were probably not worth harvesting (in terms of time invested) - certainly most of the species with larger flowers were exploited, and thus perhaps 'substantial' flowers rank closer to fruit in this analysis.

These results too are consistent with the prediction from the analysis of food-part selection, i.e. that the choice of leaves, seeds, and gum was secondary to fruit and flowers, and so too their contribution to the species-diversity of the monthly diet was less than that of fruit and flowers. The reasons for these choices will be discussed in Chapter 10, considering energetic and nutritive components of the diet, and avoidance of secondary compounds.

At this point, I shall return to the relationship being questioned at the beginning of this section, i.e. that between diversity and availability. The correlation between monthly diversity of food-parts in the diet and (log) availability was r= -.44 (p=.07), which although not statistically significant, is suggestive of the predicted trend: as the availability of fruit and flowers increased, the diversity in food-parts decreased, since higher proportions of the diet were given over to fruit and flowers.

In the analysis of food-selection, I suggested a relationship between fruit/flower feeding and time spent feeding on other food-parts, such that the amount of leaves, for example, in the diet depended not only on the availability of leaves, but also on the availability of fruit and flowers. Thus some secondary choice food-parts may become 'backstop' foods, exploited in case of short supply of fruit/flowers. The correlation between the proportion of non-fruit/flower vegetable food-parts (i.e. excluding invertebrates) and the proportion of fruit in the diet was strong and negative (r= -.93, p<.001): the more fruit and flowers in the diet, the less of other vegetable foods were included. This relationship might seem self-evident, but may be viewed differently when considering that the amount of animal food in the diet was not correlated with the proportion of fruit and flowers (see section on animal foods, below). However, although non-fruit/flower food-parts may be included in the diet relative to the amount of fruit or flowers, this does not affect the absolute presence or absence of these food-parts: the monkeys did tend to sample a diverse range of food-parts where possible, so that even in months with abundant fruit or flowers, they still included some of the other available food-parts in their diet, most likely for the maintenance of a nutritive balance.

From a nutritive point of view, fruit and leaves are not interchangeable, as fruits are a concentrated source of ready energy (soluble carbohydrates), and leaves provide mainly protein. However, since leaves do contain small amounts of soluble carbohydrates (e.g. Milton, 1980) it is possible that in times of shortage of fruit or flowers (such as during February), leaves may provide a ´backstop´ source of ready energy, above a certain minimum required for protein. Since leaves are less patchily distributed than fruit or flowers, they can generally be found with less search, and thus less expenditure of energy. This will be discussed further in Chapter 10, together with the question of whether or not the monkeys are optimising dietary diversity.

No mention has yet been made of invertebrate foods with reference to dietary diversity. This will be discussed in the section on animal foods (see below).

6.3.4 Overlap Of Diet Between Months.

The extent of change of the diet between months provides a good measure of the degree of seasonality in the diet. Dietary overlap is calculated as the sum of the shared percentages of feeding times on each specific food-item. (For example, the diet of month A has fruit of species X (20%), and species Y (15%), while month B has species X (10%) and species Y (50%): the shared percentages are 10% for species X and 15% for species Y = 25% overlap.) For this analysis, invertebrates have again been excluded in calculations, since the species of invertebrate and their locations (substrates) were likely to differ from month to month (see next section). Results are shown in Table 6.3.

Table 6.3. Overlap in the diet between months: percentage of overlap of all parts of major species (excluding invertebrates, as species and substrate may differ from month to month).

	N	D	J	F	M	A	M	J	J	A	S	O
N		20	9	14	7	10	4	1	5	1	1	38
D			28	23	7	9	4	0	0	0	0	10
J				39	8	9	4	2	3	0	1	4
F					17	11	15	6	16	1	0	15
M						54	18	7	11	1	2	10
A							24	9	13	3	1	8
M								31	14	0	0	12
J									27	1	1	5
J										15	11	13
A											37	15
S												29
O												

In most cases (63 out of 66 pair-combinations) the overlap between neighbouring months was higher than for other months - as would be expected in a seasonal environment: the mean overlap between neighbouring months was 29.9% (range:14.6 - 54.4%), whereas the mean overlap between non-neighbouring months was 6.5% (range: 0.0 - 23.4%). These low figures show the strong seasonal variation in the availability of food from month to month. Some foods span several months, but in general the monkeys have a very different set of foods to deal with each month throughout the year, and must consistently monitor the phenological cycles of potential incoming foods as existing foods go out of season.

6.3.5 Animal Foods.

The feeding analysis has until now been concerned only with vegetable foods, although animal foods did form a consistently important part of the monkeys´ diet. Items such as birds´ eggs, several species of small vertebrates, and scorpions were eaten only rarely, and generally by adults (Table 6.4). A variety of birds regularly mobbed the green monkeys, suggesting that the eggs and perhaps fledglings of these species were also prey to the monkeys. Reference to Table 6.4, which lists all sightings during 15 months, shows the rarity of green monkey depredation on these small vertebrates and eggs.

Invertebrates, however, were eaten regularly throughout the year, making up 13.1% of the annual diet (Table 6.1 and Figure 6.1). In ten months they were important foods (constituting over 5% of the diet), and in three of those months invertebrates formed over 20% of the diet (Figure 6.6).

It was difficult to identify invertebrates as they were eaten, but it was obvious that they came from a wide variety of species and developmental stages, and were subject to great seasonal variation in availability and distribution. The invertebrates identified were nearly all arthropods (earthworms, *Lumbricus* sp., were an exception), and the monkeys ate the eggs, larvae, pupae or adult forms from several orders of insects (listed in Table 6.5), according to

Table 6.4. Vertebrate prey eaten by the green monkeys. (Scorpion is included here because of its size, the technique used to capture it, and its substantial amount of 'meat').

Species	Captured by
Reptiles:	
Agama agama - rainbow lizard.	SP, adult male.
Agama agama - rainbow lizard.	SP, adult male.
Chamaeleo senegalensis - chameleon.	VG, adult female.
Mabuya perroteti - skink.	?
unknown sp. snake skin	OJ, subadult male.
Eggs:	
Centropus senegalensis - coucal	SP, adult male.
Francolinus bicalcaratus - francolin	FL, adult male.
unknown sp.	RO, adult male.
Birds' nests searched, no eggs or fledglings found:	OL, adult male.
	FL, adult male.
	? , adult male.
	? , juvenile.
	?
Scorpion:	
Pandinus gambiensis - blue scorpion	SP, adult male.

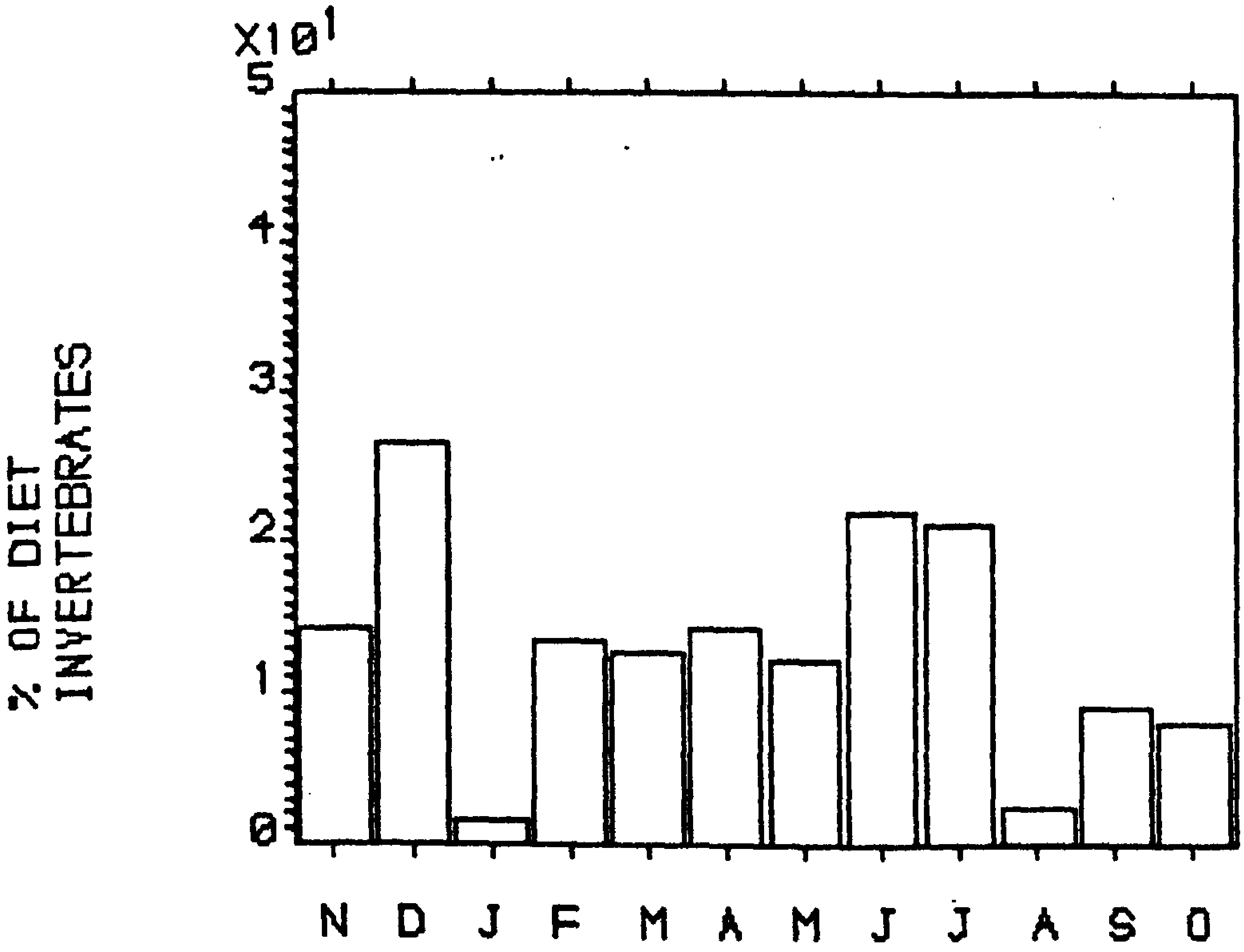


Figure 6.6. Proportions of the monthly diet made up by invertebrates.

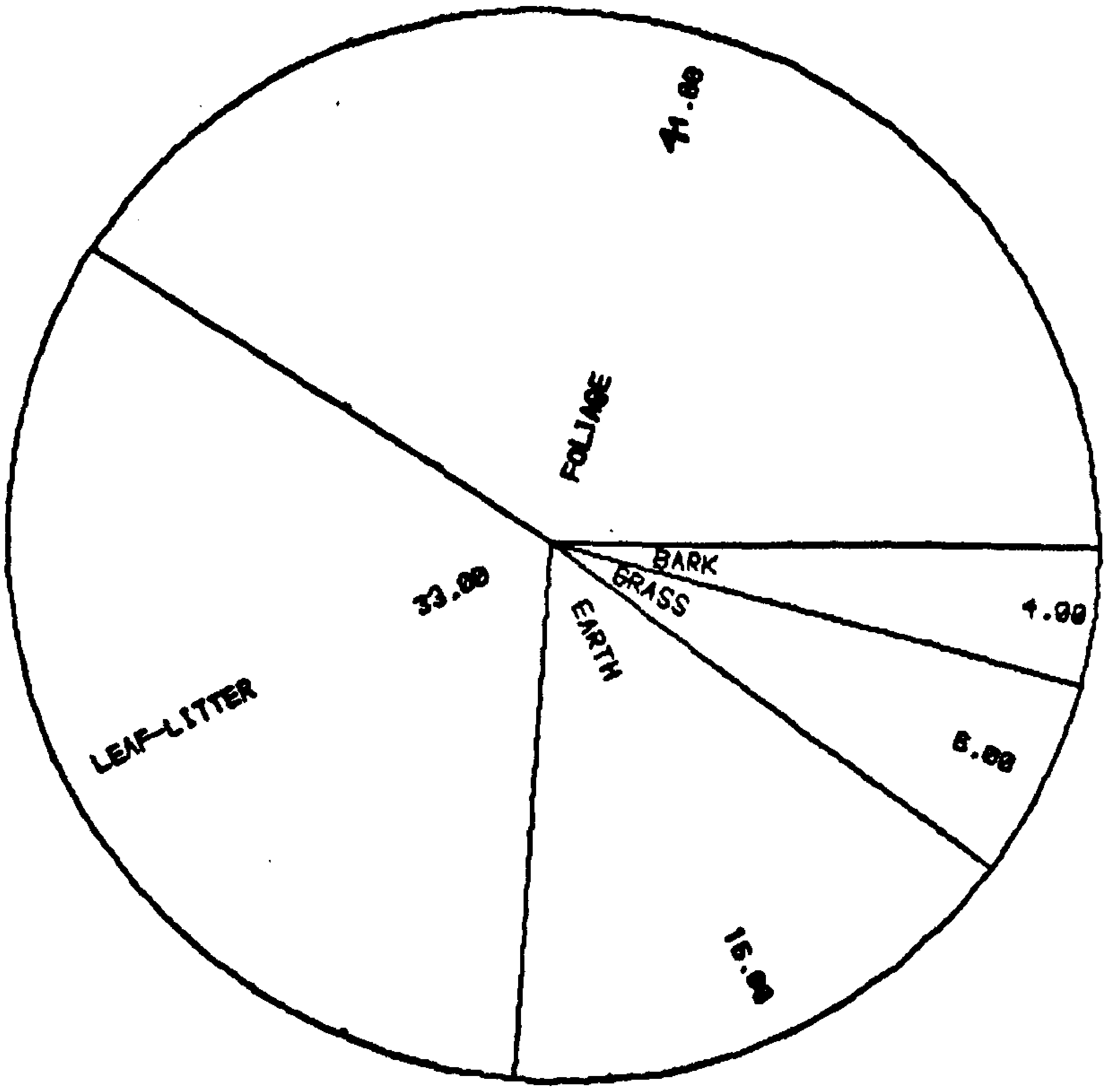


Figure 6.7. The relative annual use of different substrates in the search for invertebrate prey.

seasonal availability.

The movements used by the monkeys to capture invertebrate prey gave some indication of the variety of species and developmental forms eaten: these ranged from unhurriedly picking, mouthing, and scraping through dry leaf-litter, or breaking open dead twigs and bark, through snatching or trapping slightly more mobile prey in the foliage or under cool rock overhangs, to the extremes of pouncing, leaping into the air, or running at full gallop to catch flying grasshoppers or moths; earthworms were pulled from the mud after the first rains of the season (see Plate 8.2); safari ants were rapidly stuffed into the mouth, followed by urgent retreats to pull off those that were biting; baked insects were picked from plateau and woodland areas immediately after the annual fires had passed through (see Plate 8.1); and occasionally laterite rocks were turned over in search of invertebrate prey beneath - one such rock weighed over 7 kg, and was pushed over by a subadult male of probably half that weight, with much effort.

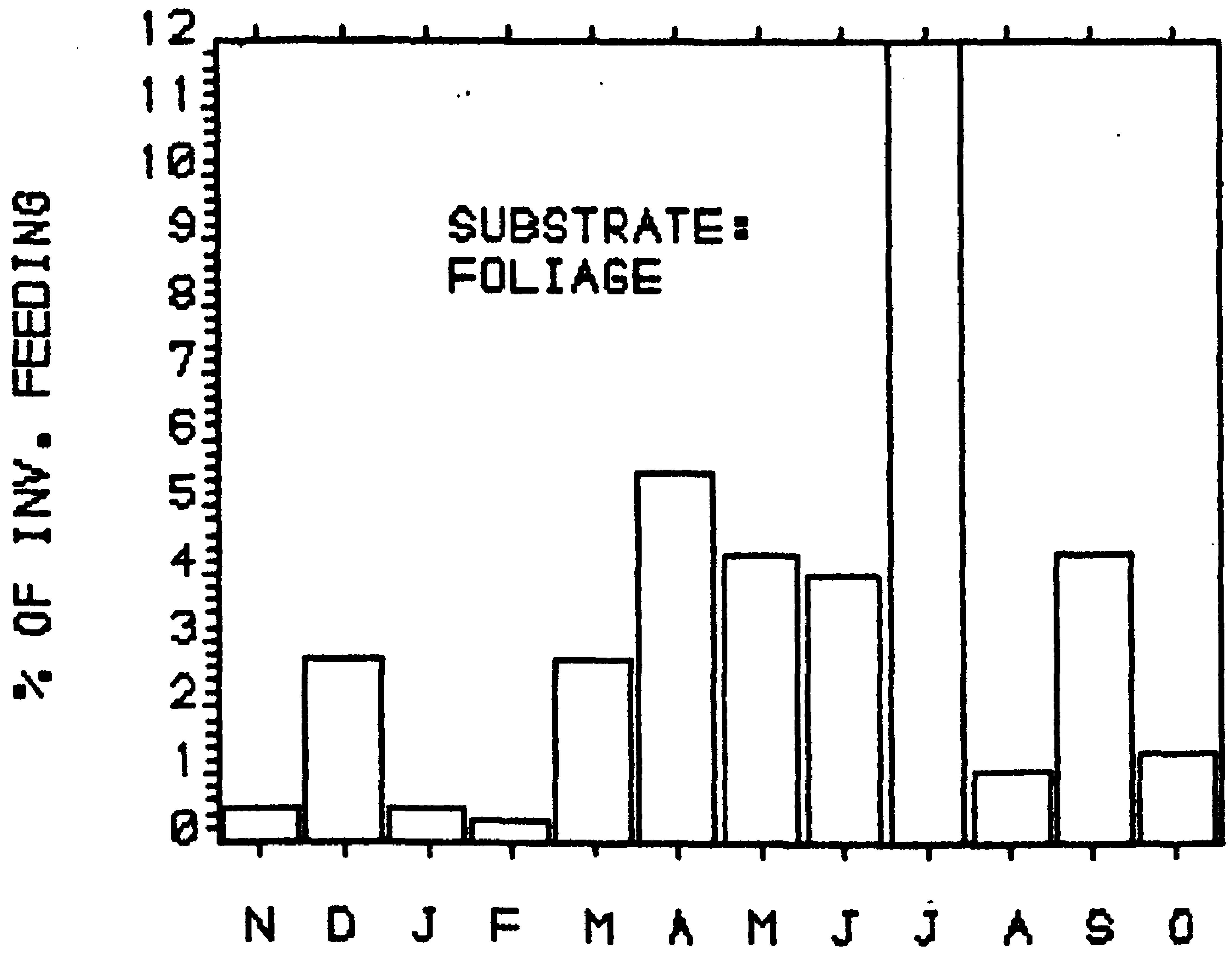
It is known that insect abundance and diversity varies seasonally (Janzen and Schoener, 1968; Fogden, 1972;

Table 6.5. Orders of invertebrates identified as being eaten by the green monkeys.

Coleoptera (beetles)
Diptera (flies)
Hymenoptera (wasp galls, ants)
Isoptera (termites)
Lepidoptera (caterpillars, moths)
Orthoptera (locusts)
Several species of centipedes and spiders.

Sinclair, 1978; Wolda, 1978). Insect abundance is often related to leaf production, which is closely tied to rainfall in the tropics; in addition, superabundances of certain windborne insects arrive with the storms that end the dry season (Sinclair, 1978); even in one region within the same season, insects are more abundant in wetter areas (Janzen and Schoener, 1968). The implications of this for Mt.Assirik are that the wet season sees a continuous abundance of potential invertebrate prey for the green monkeys, and in the dry season the availability of this prey is reduced, and its distribution restricted to cooler, wetter areas such as the forest in the valleys. In any case, the supply of invertebrates remaining in open woodland or on the plateaux was drastically reduced in the early dry season by the annual fires.

Without independent data on the availability and distribution of invertebrate prey, the next best compromise was to examine the substrates used by the monkeys in their search for insects. These data were collected during scan sampling, and provides a picture of the changing distribution of invertebrates, and the changing species or developmental stages of prey available. While Figure 6.7 shows the relative use of different substrates in search of invertebrates over the whole year, Figure 6.8 shows the monthly use of each substrate. Neither the undersurfaces of bark, nor clumps or blades of grass, were commonly used as a source of invertebrates. The use of earth as a source was limited to June and July, after the early rains had softened the earth to mud, and many insects had lain eggs in pools or damp earth



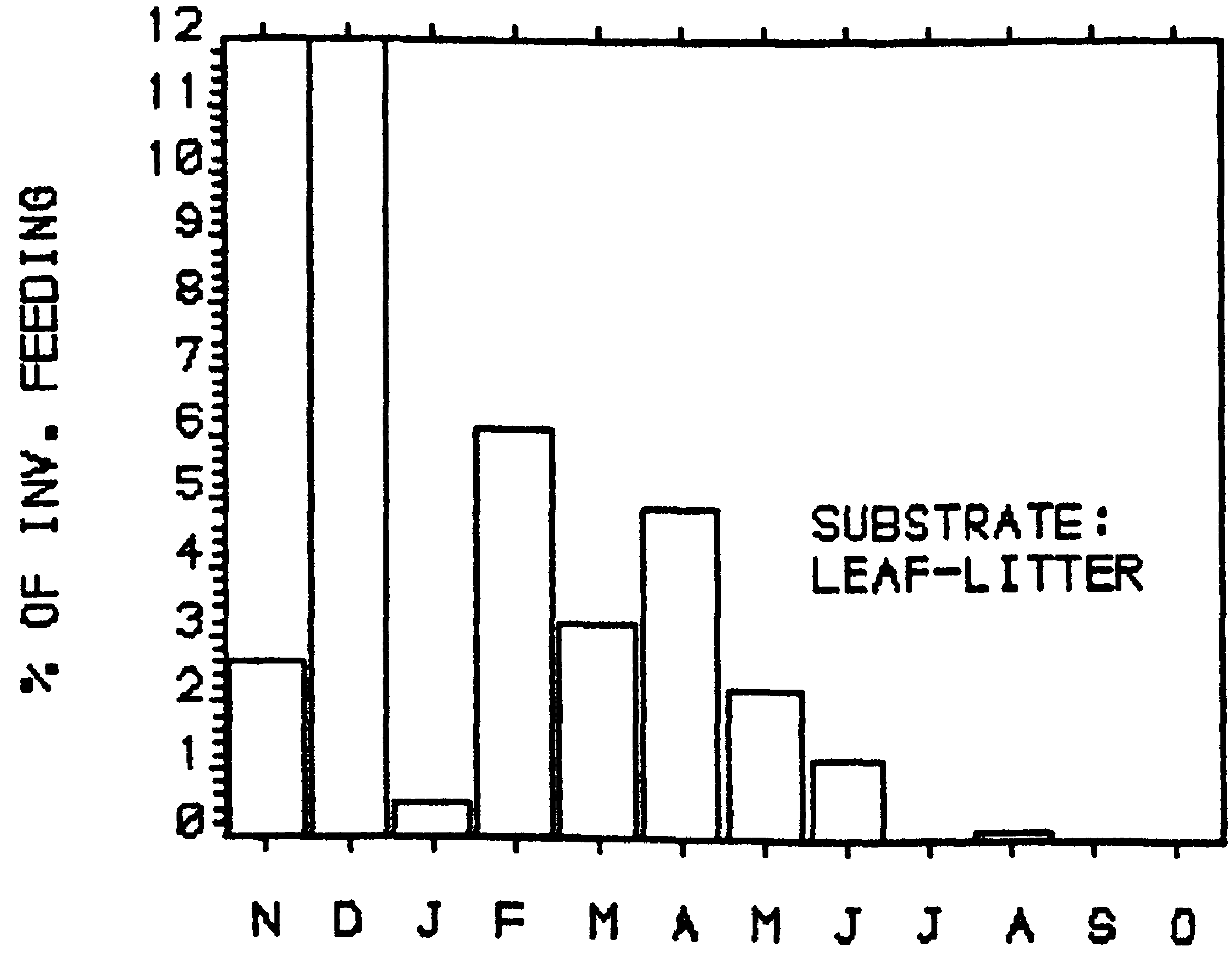


Figure 6.8. The monthly use of each substrate in the search for invertebrate prey.

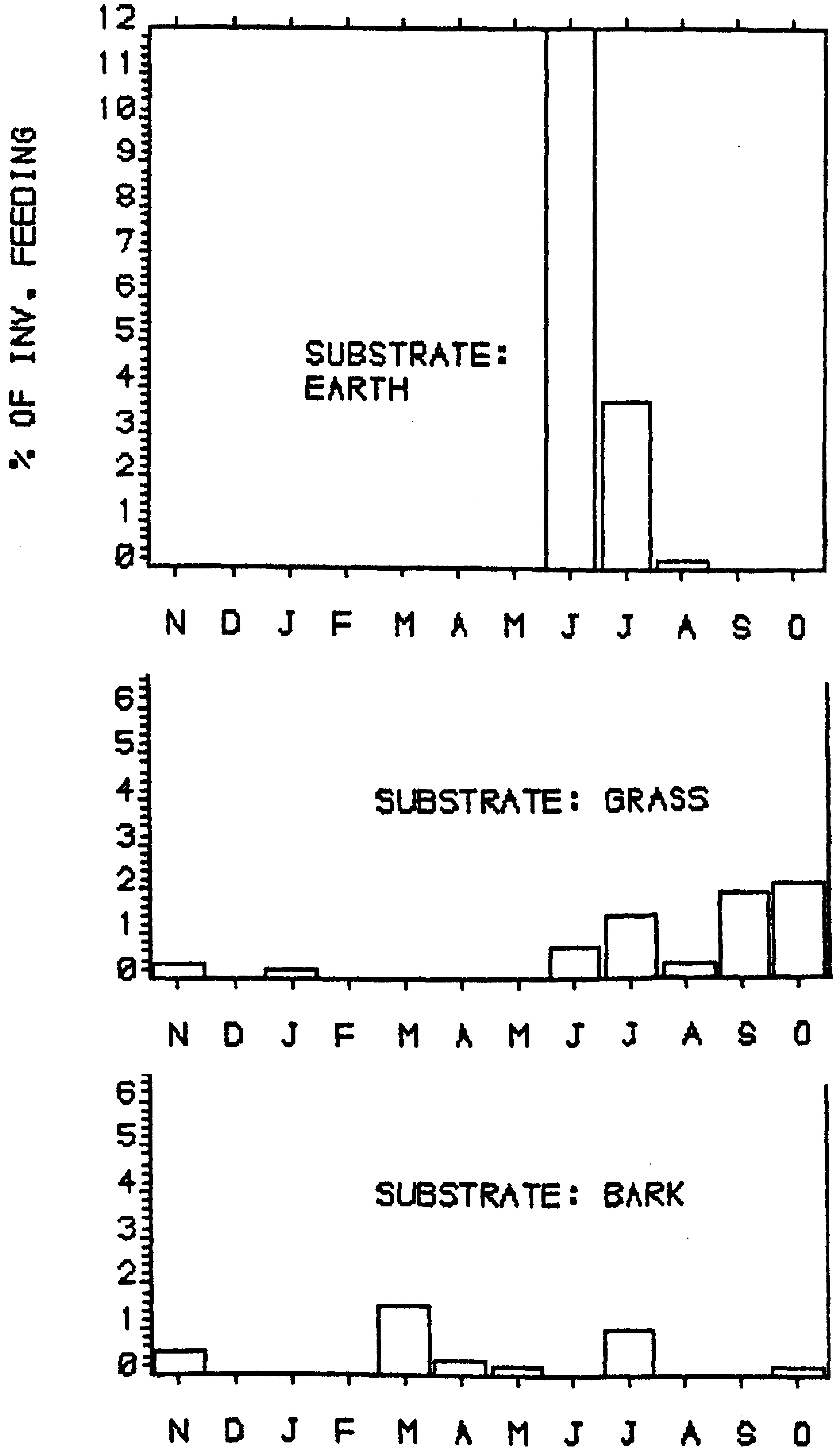


Figure 6.8. (cont.)

(Sinclair, 1978). Bare or sparsely covered earth was intensively scraped for worms and eggs/larvae during this period.

Tree foliage and leaf-litter were the other two major sources of invertebrates; certain caterpillars and pupae lived under mature leaves in the forest trees towards the end of the dry season, and the continued use of foliage throughout the wet season presumably reflects the exploitation of different invertebrates or developmental stages that are associated with leaf production during the wet season (Fogden, 1972). In July in particular, certain species of trees (*Khaya senegalensis* and *Pterocarpus erinaceus*) produced flush leaves that rapidly became host to innumerable galls, upon which the monkeys fed.

The use of leaf-litter as a source of invertebrates was restricted to the dry season: during the rains, most leaf-litter decayed rapidly, and after the annual fires in the early dry season, much leaf-litter was burnt off in the woodlands. Thus, the forest in the dry season was the primary location for a build-up of leaf-litter, and in any case was probably a preferable site for insects, as the forest floor remained relatively cool and moist.

Earlier in this Chapter I discussed food selection and diversity of the diet with reference to vegetable foods. Since no quantitative measures of invertebrate availability were taken, similar analyses cannot be carried out for animal foods. Nevertheless, some descriptive evidence is suggestive:

in terms of selection of particular species of invertebrate, it is highly likely that the monkeys chose some and not others, since many invertebrates have defensive mechanisms against predators, such as venom, stings, noxious taste etc. In terms of selection of invertebrates as a food-part, one can estimate whether they were selected irrespective of abundance, or eaten according to availability: if the wet season produces a far greater abundance than the dry season, then Figure 6.6 suggests that there was positive selection, and invertebrates were not eaten simply according to their availability (i.e. there was no difference between wet and dry season in the monthly proportion of invertebrates in the diet: Mann-Whitney U=16, n.s.). Although in June and July, the first months of the rains, the monkeys obviously were making use of a sudden superabundance of invertebrates, in general their intake was fairly consistent between months. This suggests that the green monkeys allotted a consistent amount of time to foraging for invertebrates, and thus selected on some basis other than availability. Furthermore, invertebrate intake was independent of the amount of fruit or flowers in the diet: this was not the case for other food-parts, whose inclusion in the diet tended to depend on the availability of fruit or flowers, since these were selected in preference to the former (regression of %non-fruit/flower parts (excluding invertebrates) on %fruit/flowers in the diet, $r= -.93$, $p<.001$; regression of %invertebrates on %fruit/flowers, $r= -.35$, n.s.: i.e. invertebrate feeding was independent of fruit/ flower feeding). This consistent inclusion of a certain amount of animal food in the diet each month will be discussed further in Chapter 10, with reference to protein-intake and the balance of nutrients. I shall also try and account for the two exceptional months, January and August, that had a very low intake of invertebrates (see Figure 6.6), in terms of alternative sources of protein in those months.

6.4 AGE AND SEX DIFFERENCES IN FOOD-PARTS EATEN.

The 4-year-long period of immaturity in green monkeys makes feasible feeding specialisation and niche differentiation among age/sex classes. Although sexual dimorphism in green monkeys is slight, differences in the diet may arise from differing nutritional requirements as well as intraspecific competition.

An analysis was carried out to test for differences between age/sex classes in the proportions of time they spent feeding on fruit, flowers, invertebrates, and ´other´ food-parts (leaves, grasses, herbs, seeds, gum, stems, and fungi), and the proportions of the diet made up by these foods. The following age/sex classes were used: adult/subadult males and females, immature males and females (excluding infants), and infants. Means for each age/sex class in each food-part category are shown in Figure 6.9 (proportions in the diet), and Figure 6.10 (proportions of total time spent on the various food-parts - i.e. to account for age/sex differences in proportions of time spent feeding - see chapter 7). Significant age/sex differences were found in the proportions of fruit and flowers in the diet (Anova: proportions of fruit

- F=12.3, p<.0001; flowers - F=6.90, p<.0001; invertebrates - F=2.05, n.s.; 'other' - F=1.41, n.s.), and in time spent feeding on all food-parts (Anova: time spent feeding on fruits - F=50.85, p<.0001; flowers - F=5.72, p<.01; invertebrates - F=9.56, p<.0001; 'other' - F=11.05, p<.0001). Subsets of means that are significantly different (using the LSD test for post-hoc comparison of means, at p<.05) are marked with symbols.

Looking first at proportions of total time spent on each food-part, infants had the lowest scores. Young infants got most of their food from suckling their mothers, only moving onto solid foods after several months. Given certain sampling difficulties (that a resting infant was difficult to distinguish from a suckling infant when wrapped up in its mother's arms), suckling was not quantified for the first 3-4 months after birth. At this age, when suckling was scored separately in scan sampling (for the last three months of the study; i.e. infants from 4-8 months old), the amount of suckling was still high: infants were spending on average 42.2% of their feeding time suckling, the other 47.8% feeding on solids. However, during this time the 4-8 month old infants were still only spending 27.2% of their total time in feeding activities, which is far below the figure for the older monkeys (49%). This suggests either that their food demands remain low in late infancy, or that they suckle at night in the sleeping trees, when no sampling took place. It seems very likely that suckling did continue during the night.

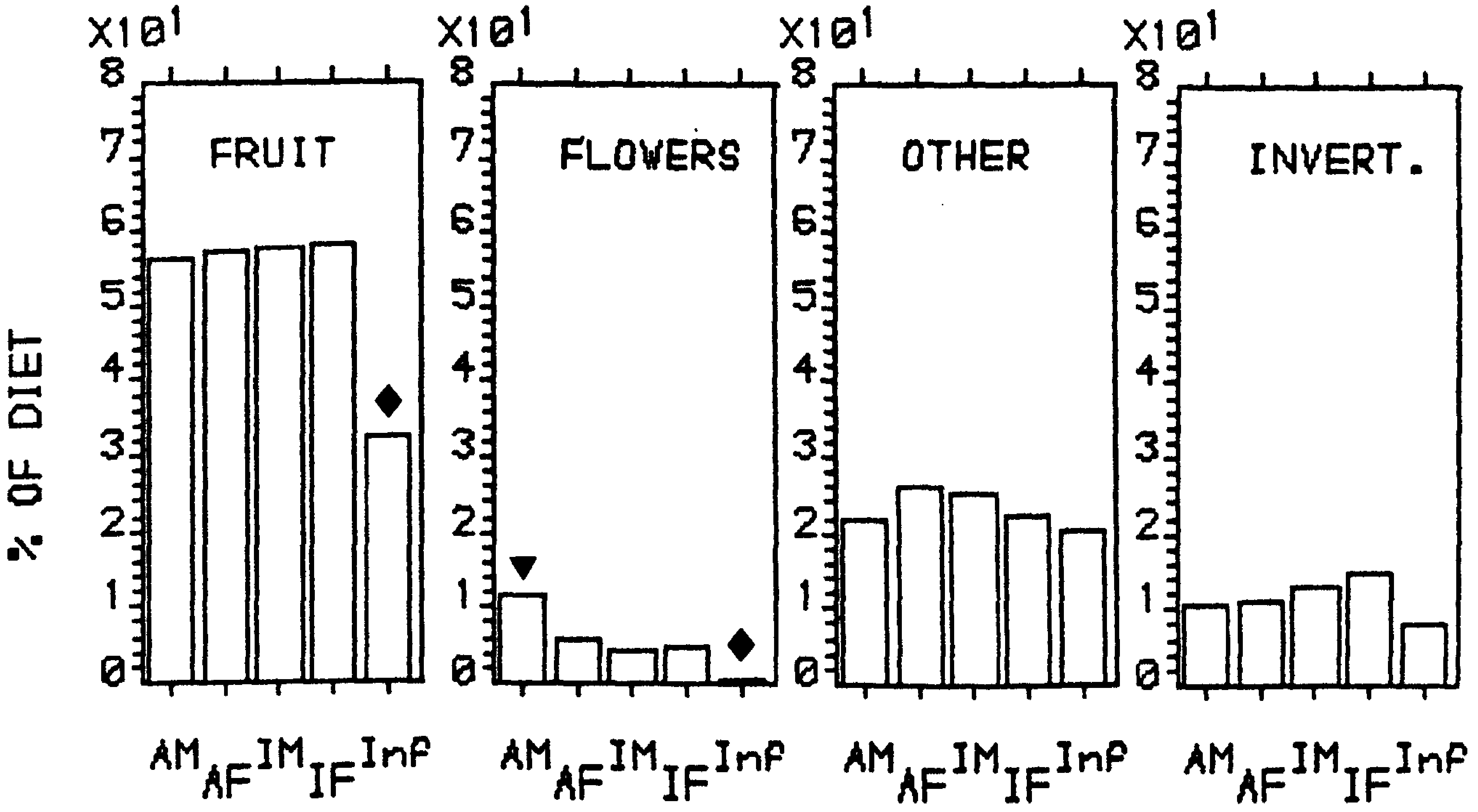


Figure 6.9. Mean proportions of the annual diet of each age/sex class made up by each food-part. Adult males (AM), adult females (AF), immature males (IM), immature females (IF), infants (Inf). Symbols are used to separate subsets of means that are statistically different (p<.05).

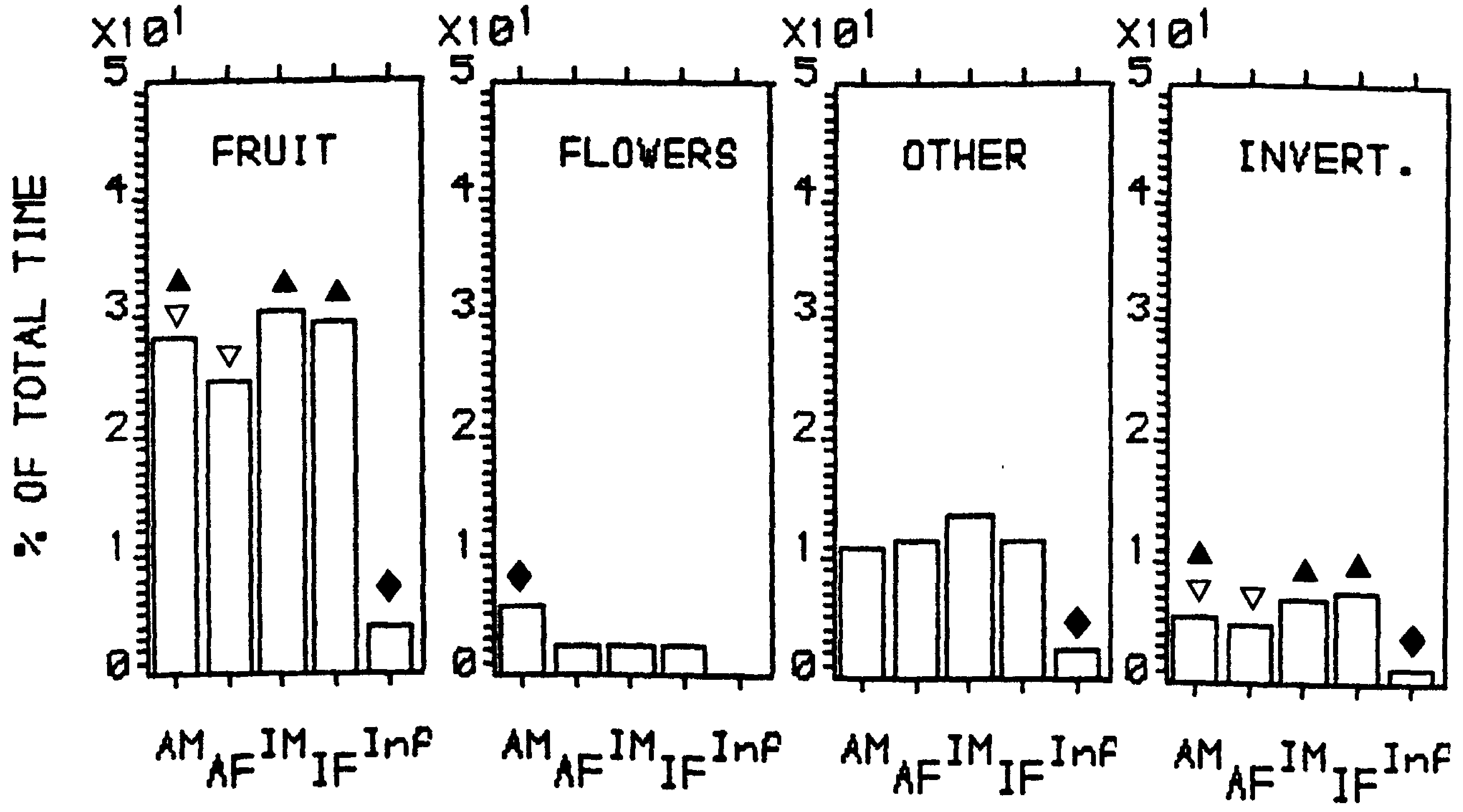


Figure 6.10. As for Figure 6.9., but showing the proportions of total time spent feeding on each food-part.

Leaving aside infants, the feeding time spent on fruit, invertebrates, and ´other´food-parts is similar for each age/sex class. The post-hoc LSD tests show no _exclusive_ subsets of means, but these means do suggest that immatures spent slightly more time than adults feeding on fruits and invertebrates. This may reflect a lack of experience in the ability of younger monkeys to process fruit fast, or capture insects efficiently. There is also a suggestion of lower levels of fruit feeding by adult females - this is investigated fully in chapter 7.

The case for flowers is different: adult males spent more time than others eating flowers. This probably reflects the priority of access that adult males had over females and immatures at food sources that are both highly prized and limited in availability (separate study, in prep.). The major species of flower in the annual diet was _Pterocarpus erinaceus_: when widely available, there seemed to be little competition between the monkeys over the flowers (see Plate 6.3). But at isolated trees, or when overall availability was lower, feeding competition became more intense. Adult males generally arrived before others at such feeding sites (separate study, in prep.), and often maintained exclusive access to patches within the tree canopy. The advantage to males in increased feeding time on flowers may be marked because individual flowers are so short-lived (a _P.erinaceus_ flower typically lasts one or two days), in addition to which flower sources are quickly depleted.

Plate 6.3. An adult female feeds on Pterocarpus erinaceus flowers.

Looking at proportions of the diet, no age/sex differences were seen for invertebrates, or foliage ('other'). Infants had low proportions of fruit in their diet, which probably reflects the unsuitability of fruits as weaning foods, as opposed to soft, easily processed and digestable young leaves, flowers, and insects. Again, adult males had higher proportions of flowers in their diet than other monkeys.

It should be noted that these analyses were carried out using data for the whole year lumped together, which could be obscuring important seasonal differences. Strong seasonality in feeding and diet has already been demonstrated (this chapter, chapter 7). Seasonal variation in age/sex differences in the diet are examined in detail in chapter 7.

6.5 DISCUSSION.

As in other chapters, results have been discussed within each section. Further consideration of the nature of the diet in terms of optimal foraging theory will be given in chapter 10.

6.5.1 Comparative Discussion.

A number of features of the diet of green monkeys at Mt.Assirik have been raised, and these provide scope for comparison with the diet of other populations of C.aethiops. Data on the composition of the diet are available from five other populations (Dunbar and Dunbar, 1974; Galat and Galat-Luong, 1977; Kavanagh, 1978; Wrangham and Waterman, 1981), but once again, comparisons may be limited by methodological inconsistencies: in this case, it should be noted that Wrangham and Waterman present data only on the diet of adult female vervets, and the Dunbar's study may have been too brief to have a fully representative sample of a seasonally varied diet. Indeed, Galat and Galat-Luong, Wrangham and Waterman, and the present study all provide evidence of considerable interannual variation in the composition of the diet, indicating the care with which comparisons should be made, even from long-term studies.

The composition of the diets of six populations of C.aethiops are summarized in Table 6.6. The same food-parts were eaten by all groups of C.aethiops, but in very different proportions in each of the six populations. There are large differences in the number of plant species eaten (which is associated with the number of species available, see comparisons in chapter 4), and this may relate to the changes in dietary focus. At four sites fruit and flowers were the major element in the diet. Monkeys at the two sites with a low diversity of species (River Senegal and Amboseli) showed the most dramatic shift in focus, eating predominantly leaves, and gum, respectively. At Amboseli, over 50% of the diet came from two species of Acacia. In the species-poor mangroves of Sine-Saloum, Galat and Galat-Luong (1976) showed (in a short study) the green monkeys to eat a rich but monotonous diet formed predominantly by fiddler crabs (Uca tangeri) and two species of mangrove (Rhizophora sp.). The ability of C.aethiops to dramatically shift its dietary emphasis may be

Table 6.6. Composition of the diet in six different populations of *C.aethiops*, as measured by the time spent feeding on various food-parts. The table includes the number of species eaten.

Site	Fruit	Flower	Leaf	Insect	Seed	Gum	No. species	Author
Mt.Assirik :	50	13	7	13	13	2	65	this study
River Senegal:	27	3	42	8	(fruit)	11	17	Galat
Buffle Noir :	27	34	5	29	1	2	26	Kavanagh
Kalamaloue :	61	11	17	7	2	1	41	Kavanagh
Amboseli :	12	16	23	8	8	26	9	Wrangham
Bole Valley :	51	18	19	7	(fruit)	-	23+	Dunbar

the key to its successful adaptation to many different habitats throughout Africa.

At all sites except River Senegal, a higher proportion of fruit was consumed in the wet season than in the dry season: data from Mt.Assirik showed an average of 57% of the wet season diet as fruit, as opposed to 45% of the dry season diet, although the dry season months showed a much greater variation (19-82%) compared to the wet season (37-75%). This suggests that despite intermittent superabundant fruit resources in the dry season, the wet season may be more consistent in its supply of fruit, a major source of ready energy for populations whose feeding strategies are based mainly around fruit. Seasonal variation in the consistency of food supply may be important in the evolution of some aspects of the social organization of C.aethiops, particularly those aspects related to reproduction and birth seasonality (separate study, in prep). However, such seasonal effects may not be consistent in all populations: for example, Wrangham and Waterman (1981) give no indication of seasonal variation in the availability of A.xanthophloea gum, a major food-item which, like most fruit, is high in soluble carbohydrates.

Meat-eating is widespread among C.aethiops populations. Known prey include birds, rats, a hare, crabs, and eggs, to which this study adds a chameleon, a scorpion, and several species of lizard (Galat and Galat-Luong, 1978b; Kavanagh, 1977; McGrew et al., 1978; McGuire, 1974; Skinner and Skinner, 1974; Struhsaker, 1967e). (Crabs and scorpions are included in this list, although not vertebrates, as they contain substantial amounts of 'meat' compared to insects).

Unfortunately, comparative data on age/sex differences in diet are not available: Wrangham and Waterman (1981) collected data on adult females only, and Kavanagh's (1977) data are inconclusive, as his samples were small and he had no individual recognition of monkeys, so that individual variation in diets could not be assessed independently from variation between age/sex classes. If differential nutritional requirements were the major influence on sex differences in diet, one would expect consistencies between populations. If such consistency is absent, differences in diet may be related to competition between individuals, which would differ according to the availability and distribution of food at different sites. These two variables can be expected to interact: Wrangham and Waterman (1981) reported that dominant female vervets had access to the best food-parts; the present study showed superior competition from adult males as a class, over fruit and flowers in the dry season, but not in the wet season. However, new mothers tended to eat more foliage than others in the wet season, not through competitive exclusion from fruits, but perhaps from increased needs for protein after the nutritional stress of lactation.

Among other Cercopithecus monkeys, Gautier-Hion (1980) has shown similar sex-related differences to the above: male C.nictitans, C.pogonias, and C.cephus eat more fruit than do females, who eat more leaves and animal matter, especially when these are abundant. Such abundance in Gabon coincides with the end of pregnancy in the females, and Gautier-Hion too infers physiological regulation of feeding at this time, in response to an increase in protein requirements (see chapter 7).

CHAPTER 7.

ACTIVITY-BUDGET.

7.1 INTRODUCTION

The proportions of time that are spent in different activities are an important aspect of the ecology of any organism. The variation in activity-budgets seen in a wide range of species of primate has been shown to suit particular physical characteristics and environmental conditions: the proportion of the day spent feeding is positively related to body weight, and negatively related to the proportion of foliage in the diet (Clutton-Brock and Harvey, 1977b). Intraspecific comparisons between different populations have also revealed differences in activity budgets (e.g. Kavanagh, 1978; Marsh, 1981; Oates, 1977), but the adaptive significance of these differences remains unclear. In particular, details of food availability and reference to energetic models of feeding behaviour have not been considered.

Monthly variation in activity-budgets, particularly in time spent feeding, has been demonstrated within species (e.g. Clutton-Brock, 1974; Homewood, 1978; Kavanagh, 1978; Oates, 1977; Waser, 1977), but although variation in several measures of food-availability is implicated, again no conclusive relationship has been stated. Oliver and Lee (1978) showed that reduced food-availability was associated with a decrease in the time young baboons spent playing. It seems that, allowing for differences in body-weights and broad dietary characteristics, primates may balance their activity-budgets to suit environmental conditions, and precise relationships between these variables should be stated.

There are other parameters in which activity-budgets vary: many field-studies have demonstrated diurnal rhythms of activity (see Clutton-Brock, 1977b), but as yet no conclusive statement has been made regarding the functional significance of these rhythms, which may vary between populations of a species or seasonally within a group (e.g. Chalmers, 1968b; Clutton-Brock, 1974b; Struhsaker, 1975; Waser, 1977). The commonly found morning and evening feeding peaks, and midday resting period, may represent an adaptation to changes of temperature throughout the day, but similar patterns in nocturnal monkeys (Charles-Dominique, 1971; Doyle, 1974) suggest that digestive factors may also be involved: if feeding is limited by digestion-time, early and late feeding peaks may maximize food-intake.

Social facilitation may act to synchronize feeding and drinking amongst members of a group (Kummer, 1971). Whatever the mechanism, synchronous feeding and drinking while members of a group are at a feeding-site or waterhole may be adaptive in a habitat with clumped and widely distributed resources, since an individual leaving the group for food or water at other times might risk being preyed upon.

In many species of primates, activity-budgets vary between age or sex classes. In most cases, adult females and young spend more time feeding than do adult males (e.g. Clutton-Brock, 1974b; Dunbar, 1977; Kavanagh, 1977; Marsh, 1981; Smith, 1977; Waser, 1977); two exceptions are *Pongo* and *Gorilla* (Rodman, 1977; Fossey and Harcourt, 1977), where the reverse is true. Males might feed for less time per unit-body-weight than females, if the latter have greater nutritional and energetic demands during pregnancy and lactation. Other factors may include access to high quality foods by more dominant individuals, or higher rates of feeding; extreme sexual dimorphism in body-weight may account for the reverse trend in *Pongo* and *Gorilla*.

The distribution of heights at which various activities occur is an important measure of niche-separation, either between species or between individuals of different age or sex within a species (e.g. Clutton-Brock, 1973; Kavanagh, 1978; Waser, 1977). The amount of time spent in various activities on the ground indicates the degree of terrestriality of a species: certain forest-living monkeys show characteristic heights for particular activities, and are never seen to come to ground (e.g. Gartlan and Struhsaker, 1972; Gautier-Hion and Gautier, 1979), while most baboons (*Papio* sp. and *Theropithecus gelada*) and *Erythrocebus patas* rarely spend time in trees (e.g. Dunbar, 1977; Hall, 1965; Sharman, 1981).

Thus, an analysis of how the green monkeys allotted their time to different activities was carried out, with the following aims:

i) to provide basic data on the activity-budgets of the green monkeys at Mt.Assirik. By looking at the distribution of activities throughout each day, one can examine the effects of immediate environmental changes (temperature, humidity, rainfall, sunlight) on diurnal rhythms of activity; age and sex differences in activity patterns, variation in heights used, and the degree of synchrony of activities, may provide insights into the habitat-use and social organization of green monkeys.

ii) to investigate seasonal variation in time-budgeting, with reference to variation in available resources. This permits testing models of optimal foraging that involve constraints of time in the balancing of energetic costs and benefits.

iii) to draw comparisons with other populations of C.aethiops, to investigate adaptive differences in time-budgeting that are related to ecological variables.

In this chapter, I shall present data on seasonal, diurnal, and age/sex differences in the activity-budgets of the green monkeys, together with an analysis of feeding synchrony, and the vertical distribution of activities. Findings will be related to other studies. Tests of optimal foraging theory will be carried out in chapter 10.

7.2 ANNUAL TIME-BUDGET, AND MONTHLY VARIATION.

Of the annual total of 16,342 scan records, 44.8% were of feeding, 46.7% were of resting, and 8.5% were of socializing (5.0% grooming, 3.2% playing, 0.2% nursery activities). The proportions of time allotted to different activities varied each month (Figure 7.1). Analyses of variance were computed to test whether the variation between months in the proportions of any of these activities was greater than the variation over 5 days within months. There was significant variation in time-budgets between months (Feeding: $F=3.35$, $p<.002$; Resting (see below); Socializing: $F=3.88$, $p<.001$). Despite significant monthly variation, social activities took up relatively little time compared to feeding and resting. There was a high negative correlation between time spent feeding and time spent resting ($r= -.83$, $p<.001$), implying that time not devoted to feeding was mostly spent resting, and not necessarily to socializing. In other words, an explanation of intermonthly variation need only be found for one of these two variables: monthly variation in time spent feeding is explained within the framework of optimal foraging theory in chapter 10. To anticipate, an increase in time spent feeding was associated with increased food-availability.

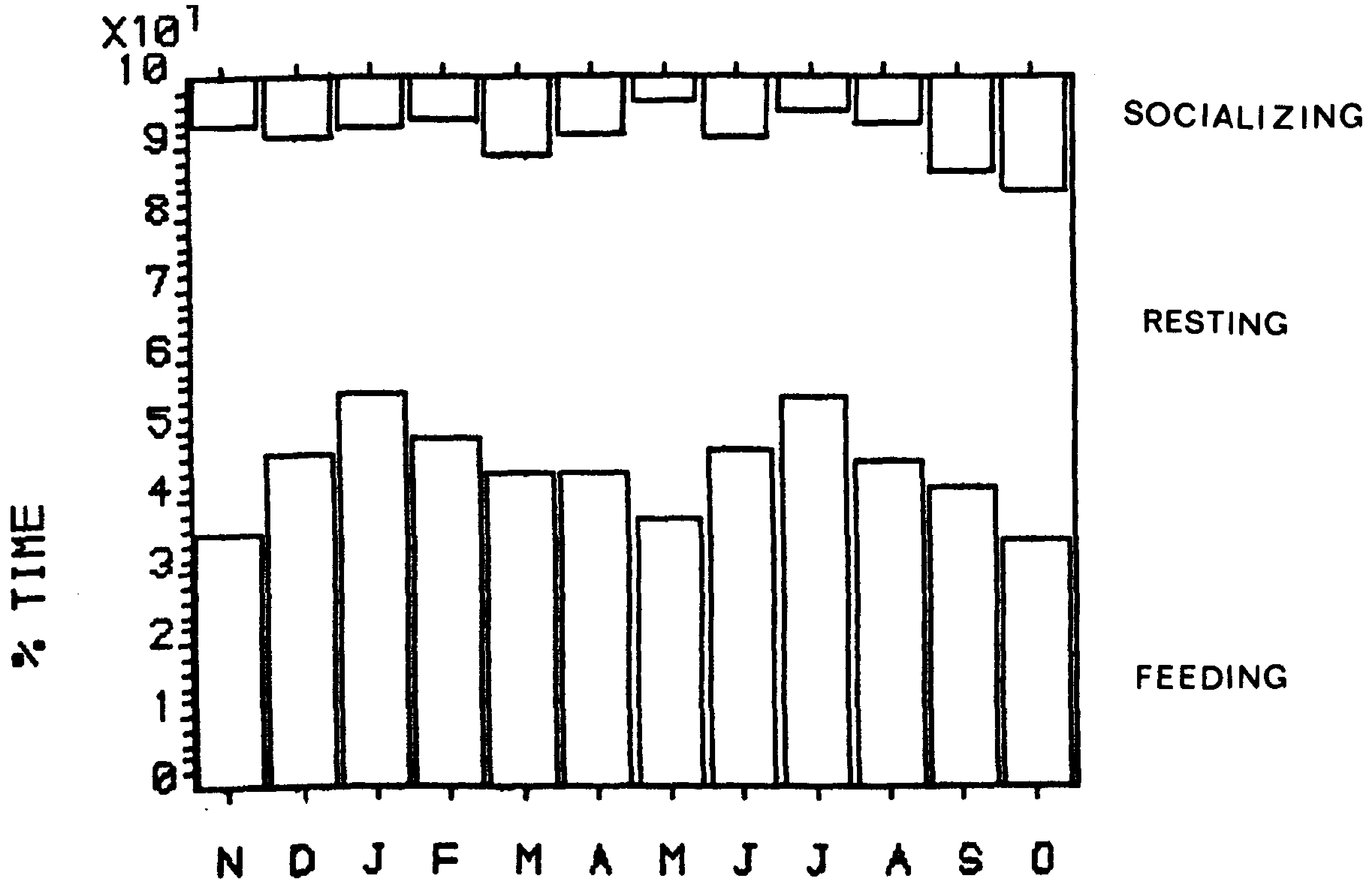


Figure 7.1. The proportions of time allotted to feeding, resting, and socializing each month.

7.3 DIURNAL RHYTHMS.

In this section I shall examine diurnal variation in activity patterns, both within each monthly sample of 5 days, and between months, in an anlysis of seasonal influences on daily rhythms. Given that feeding and ranging are the major maintenance activities, this analysis will concern only feeding rhythms and associated ranging patterns. To make the feeding data manageable, I have lumped each hour´s four consecutive 15-min. scan records into one record for the hour: thus, scan records from 0800, 0815, 0830, and 0845 are combined to form one record for 0800.

7.3.1 Diurnal Feeding Patterns.

The first hypothesis tested is that feeding activity is broadly related to temperature changes throughout the day. This leads to a prediction about seasonal influences on diurnal feeding rhythms, such that monthly changes in temperature will differentially affect diurnal rhythms. To test this hypothesis, I calculated, for each month´s 5-day sample, the mean percentage of time spent feeding for each hour of the day. Then, for each month, these hourly figures were correlated with the corresponding mean hourly temperatures, and the following coefficients were obtained:

Nov: r= .70
Dec: r= .69
Jan: r= -.30
Feb: r= -.07
Mar: r= -.42
Apr: r= -.46
May: r= -.61
Jun: r= -.36
Jul: r= .52
Aug: r= -.03

Sep: r= .03
Oct: r= .49

These coefficients range from high and positive in November to high and negative in May, and are related to the overall mean monthly temperature as follows: the correlation between these monthly coefficients and mean monthly temperatures is r= -.68 (p<.01). In other words, in the hottest months hourly feeding activity was inversely related to temperature, and as months got cooler, the strength of this inverse relationship weakened; and in the coldest months, diurnal changes in feeding and temperature became positively related. These relationships are represented schematically in Figure 7.2.

However, fluctuation in mean temperature from month to month occurred mainly in the late dry season, from January to May (29.4 - 34.9 oC). During the wet and early dry seasons (June to December), there was little monthly variation in mean temperature (26.4 - 27.6 oC), and yet still considerable variation in the diurnal feeding/temperature coefficients. Furthermore, examination of each month's diurnal temperature cycle (Figure 7.3 : a sample of three months) shows that although November and December (early dry season) had mean monthly temperatures equivalent to the wet season, their cycle of temperatures through the day was different: they had cold mornings and evenings, colder than during the wet season, and midday temperatures higher than during the wet season. November and December probably had this distinct temperature pattern for the following reason: although the rains usually stop by October, and November/December midday temperatures

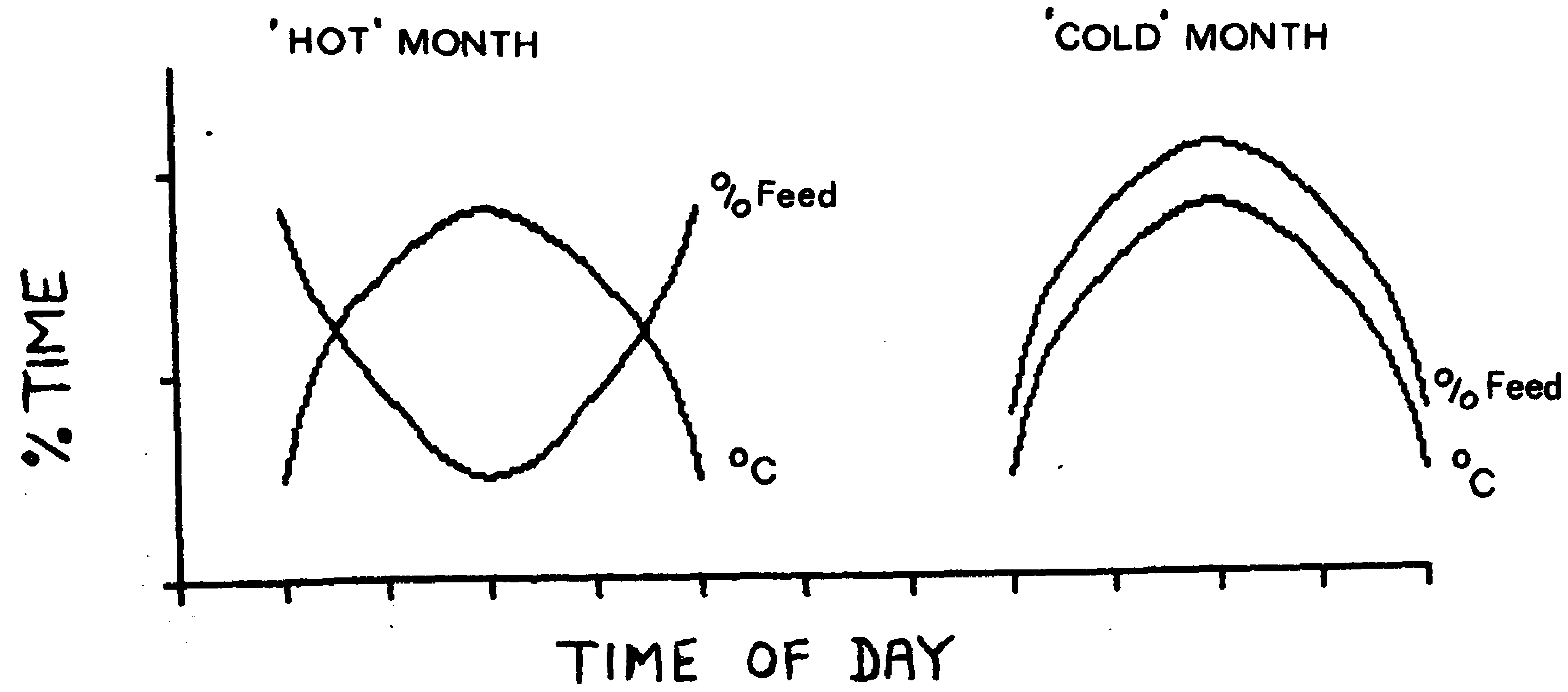


Figure 7.2. Schematic diagram to illustrate the relationship between diurnal feeding rhythms and temperature, during a 'hot' and a 'cold' month (see text).

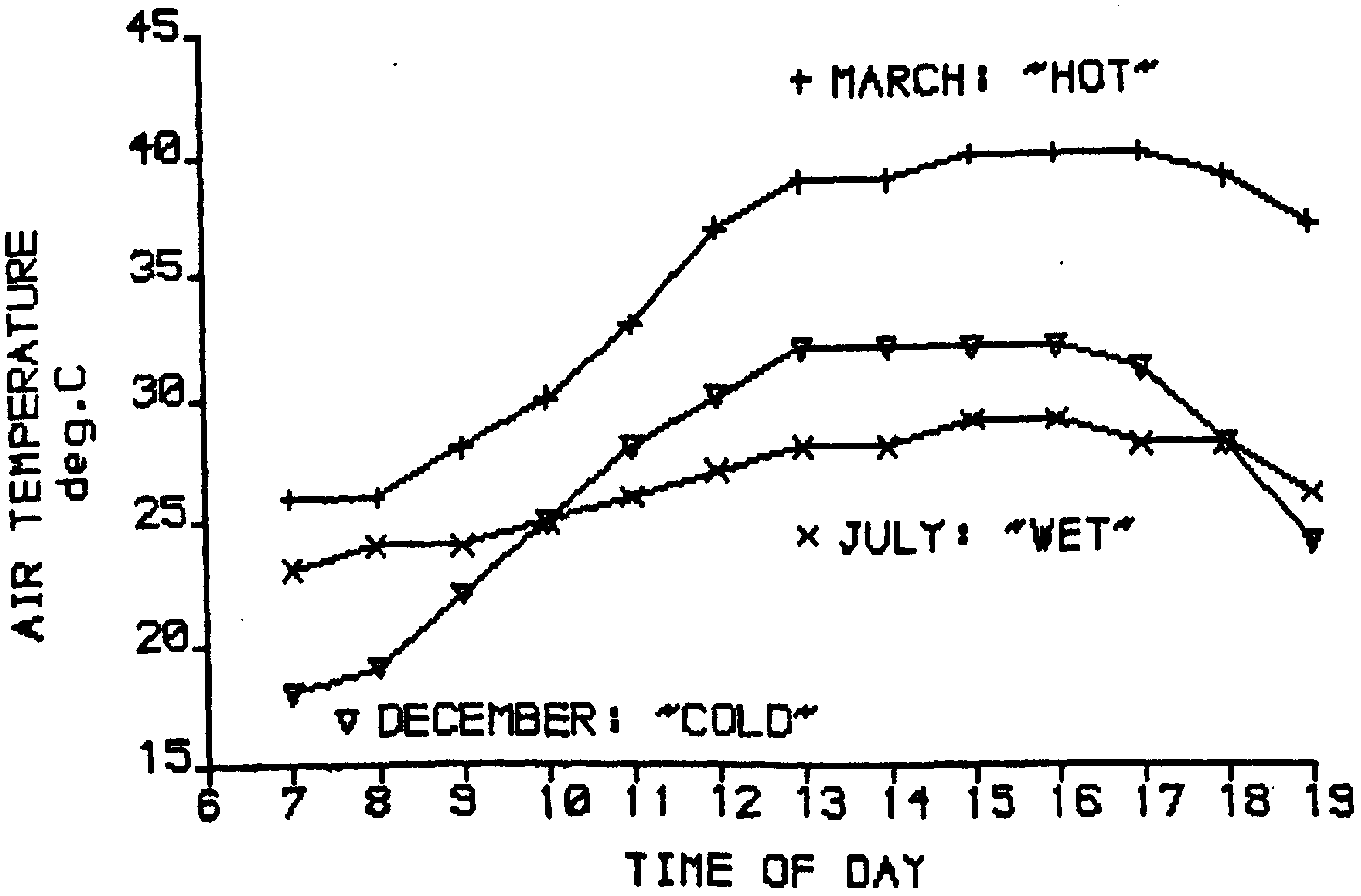


Figure 7.3. Comparison of diurnal temperature rhythms between three sample months.

start to approach those of the later dry season, the annual fires do not arrive until several months after the rains finish (this year burning took place after the December 5-day sample). Hence, not only are November and December cooler months in terms of the winter solstice, but also all the grass and foliage still remain to trap the morning dew, which cools the air as it evaporates in the rising sun. Figure 7.4 shows evaporation, and mean temperatures during each month's 5-day sample - November and December stood out as having "wet season" mean temperatures, combined with "dry season" levels of evaporation.

In conclusion then, seasonal influences of temperature on diurnal feeding rhythms can be divided into three different effects:

i) 'Cold months': early dry season, before the annual grass fires, when hourly feeding activity and temperature were positively correlated - the monkeys did not feed during the relatively cold mornings and evenings, but began to feed as the day warmed up.

ii) 'Hot months': late dry season, from January to May, when the hourly feeding/temperature relationship was inverse - the monkeys fed primarily in the relative cool of the mornings and evenings, and stopped feeding during the mid-afternoon temperature peak.

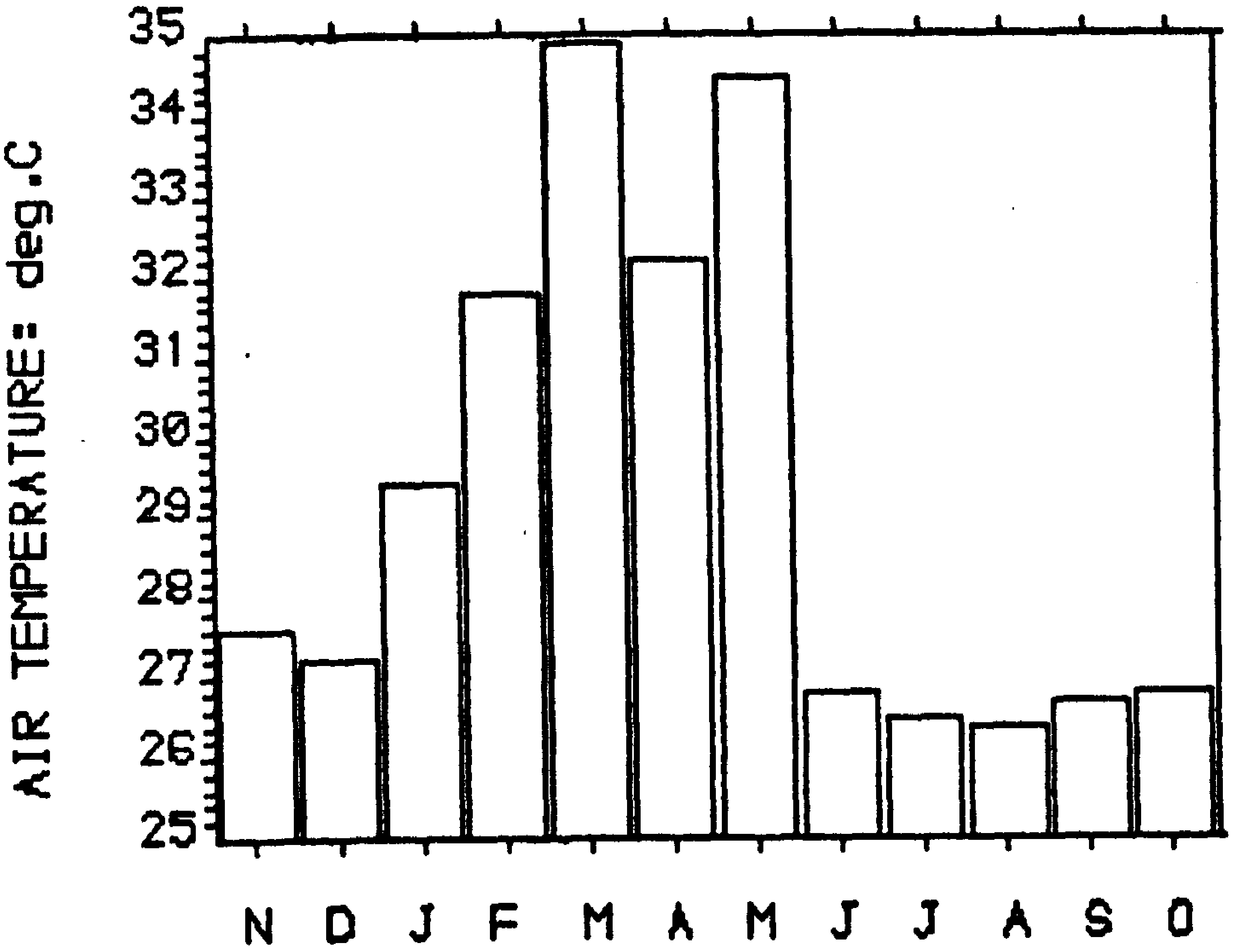


Figure 7.4. a) mean monthly air temperature during 5-day samples.

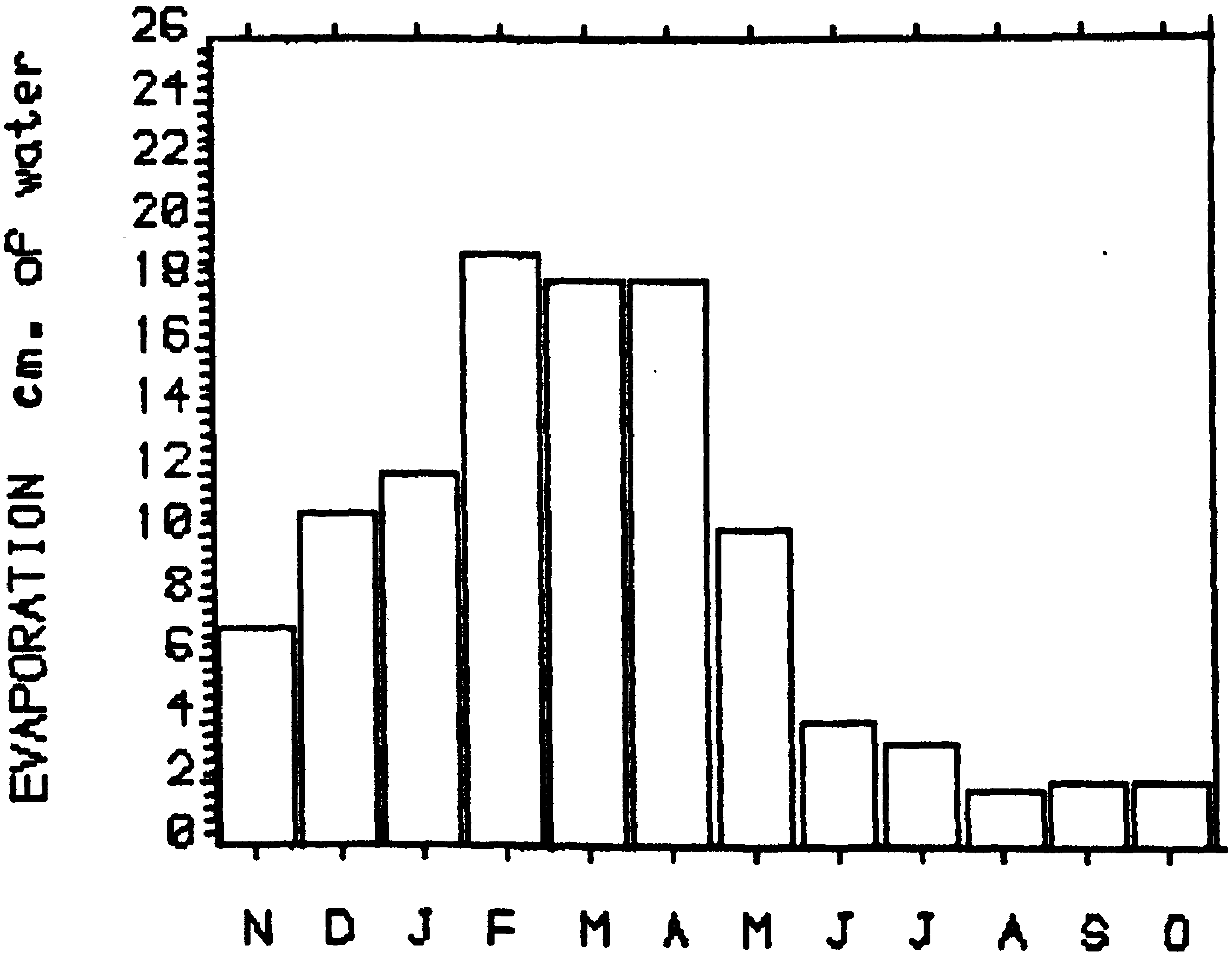


Figure 7.4. b) mean daily evaporation during monthly 5-day samples.

iii) wet season months: June to October, when the monthly temperatures were all approximately the same (and well within the annual extremes of temperature), and there was no pattern in the relationship between diurnal feeding and temperature cycles. Thus, temperature had no predictable effect on wet season feeding activity.

7.3.2 Feeding Peaks.

Before discussing reasons for the ways in which the green monkeys responded to seasonal changes in temperature, criticism may be voiced at using 5-day means for each hourly activity measure. During most months, the percentage of time spent feeding at any particular hour varied considerably from day to day, within a month. Some reliability in the consistency of feeding cycles from day to day within each month is needed before accepting comparisons between months. It would be particularly difficult to demonstrate consistency between such cycles statistically: the tools of curvilinear regression would help, if polynomial equations to fit the data could be found easily. However, the complexity of such techniques seems unnecessary here, and an alternative method is used.

Firstly, one would not expect monkeys to synchronize their activities by the hour on consecutive days, since feeding at any particular time depends on a variety of immediate factors, such as where they are, how much food is there, when they last ate, etc. Since a bout of feeding is generally followed by a rest or by movement in search of more food, the "curve" of the diurnal feeding rhythm will be very erratic, and it is unlikely that the many peaks and troughs in the level of activity will be in phase on consecutive days. This explains why the hourly means from five consecutive days have large standard deviations.

Secondly, as regards temperature correlations, one would not expect the monkeys to be so sensitive to temperature changes that the latter would precisely determine each hour´s level of feeding activity. Rather, in certain seasons temperature might influence the likelihood of particular activities occurring at certain points throughout the day.

Thus, in examining the determinants of diurnal feeding rhythms, it is worth distinguishing between each month´s overall rhythm and whether or not it shows a broad relationship to diurnal temperature changes, as opposed to each day´s detailed pattern which would be subject to proximate, hourly regulation, for example by the exact location of food, its ripeness or local abundance, time since the last feeding bout, etc. In support of this distinction, when a single day´s hourly feeding percentages were correlated with that day´s hourly temperatures, poor or variable coefficients were generally produced within a month: as a random example, in March the overall correlation was r= -.42, but correlations for individual days ranged from r= -.19 (day 5) to r= -.60 (day 4). So, to establish confidence in monthly means, despite variation from day to day, an analysis was carried out to show whether each day´s erratic feeding curve did tend broadly towards the rhythm predicted by the previous temperature analysis. This involved examining the trend of daily feeding peaks, and thus avoided having to take mean hourly values over five days.

The method was as follows: a feeding peak was arbitrarily defined as a feeding percentage greater than one standard deviation above the mean percentage for all hours of the month. For example, in January a feeding peak was scored at any hour for which the percentage feeding time exceeded 70.1% (mean= 52.4% + std.dev.=17.7%). Some hours on some days had few or no scan records; thus a criterion for inclusion in this analysis was set, such that at least 10 records for any hour were required for that hour to be scored, otherwise it was omitted. All peaks for each hour throughout the day were summed over the five days each month, and to account for missing hours, the number of peaks per hourly period was scored as a percentage of the number of hours for which there were data (i.e. maximum 5 per hourly period).

These data are plotted in Figure 7.5. This provides a general picture of the consistency of timing of daily feeding peaks, for each month's five days. Next to each month's graph is the correlation coefficient previously calculated between mean hourly feeding, and temperature. By inspection, these rhythms of feeding peaks are consistent with the predictions from the earlier analysis of seasonal temperature influences.

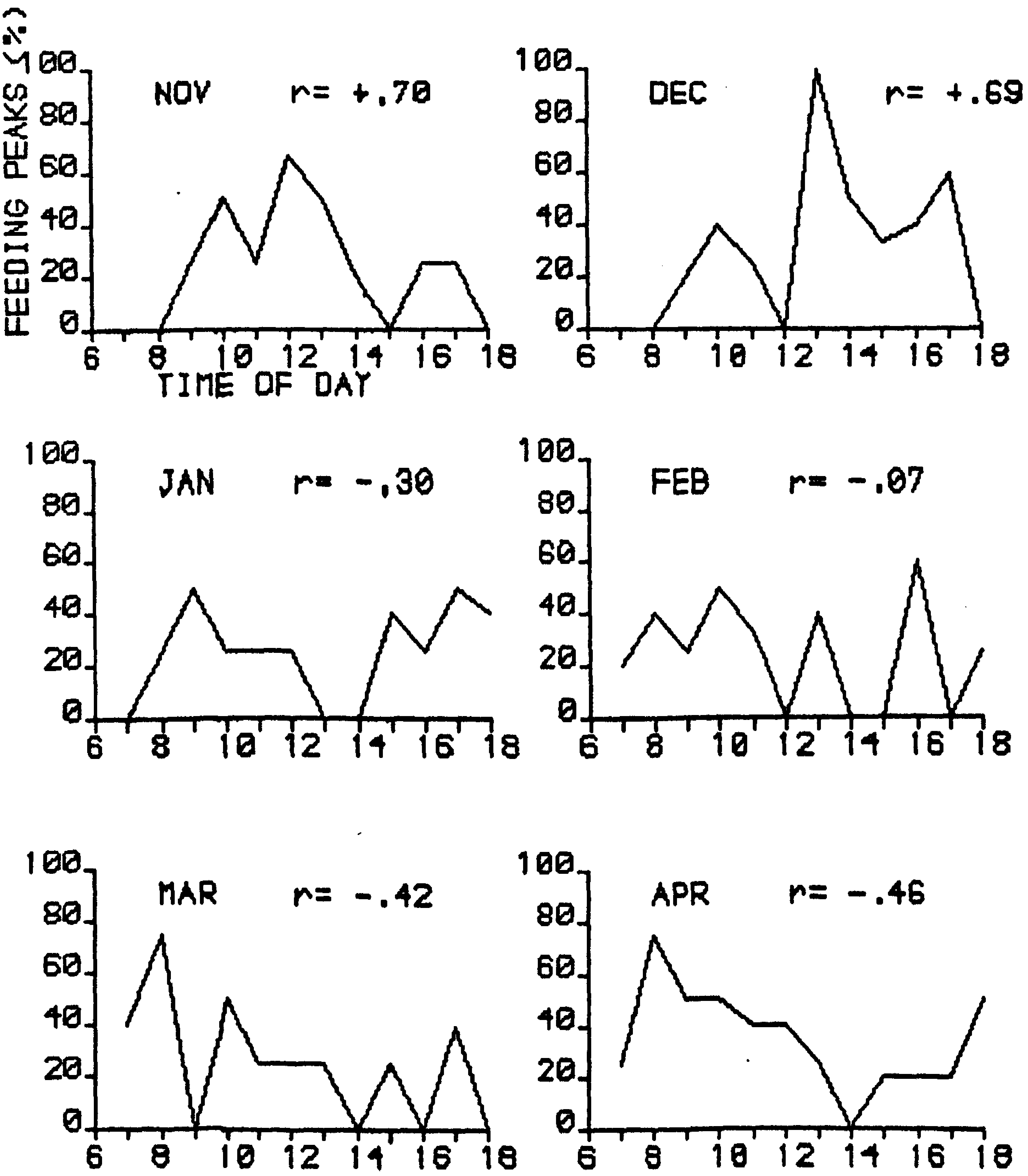


Figure 7.5. Hourly feeding peaks (see text) for each month's 5-day sample. Correlation coefficients show the relationship between hourly feeding activity and temperature.

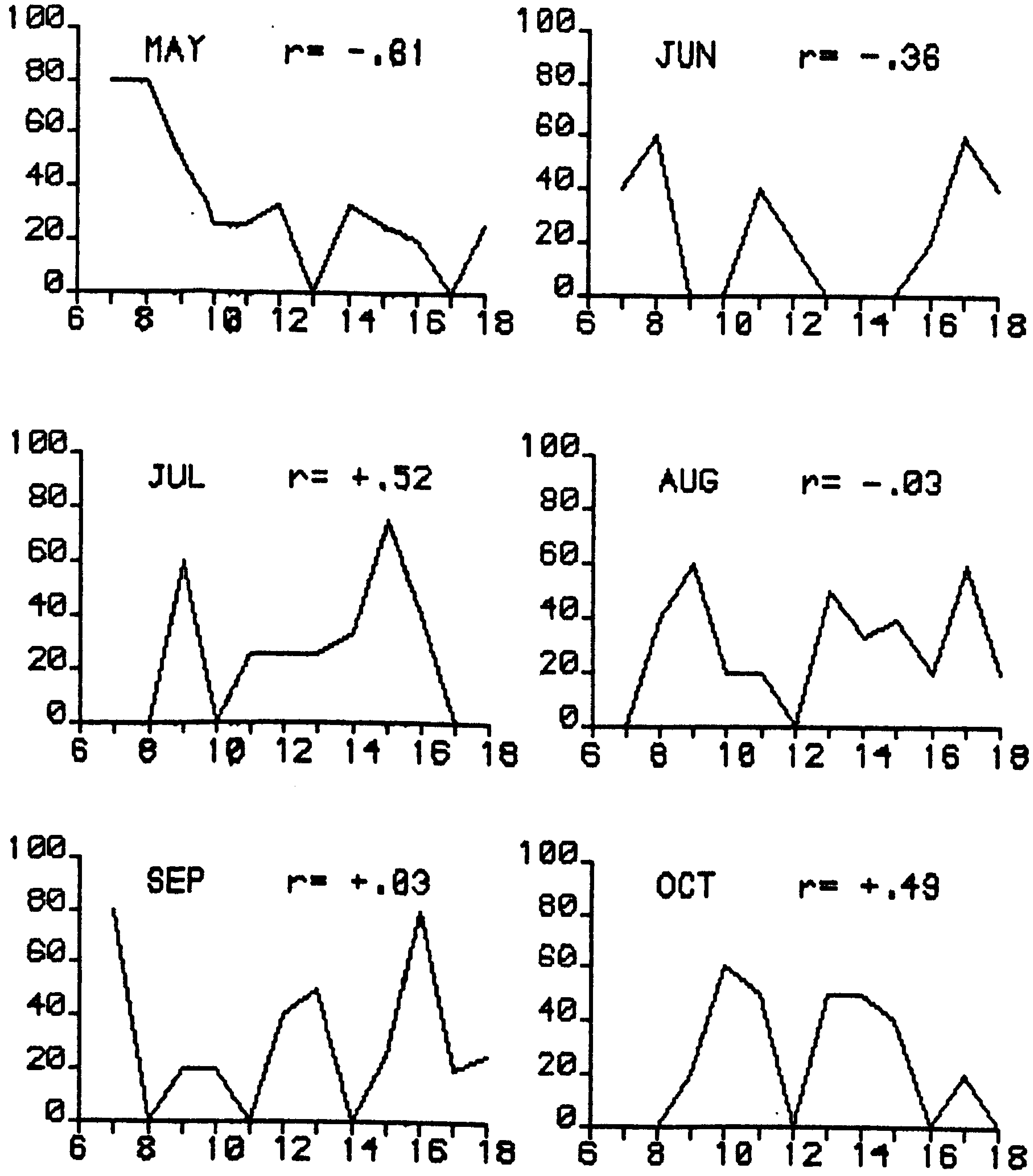


Figure 7.5. (cont.)

7.3.3 Diurnal Rhythms In Ranging.

I have considered only diurnal variation in feeding activity. Patterns of ranging are also important in the monkeys' strategy for dealing with the influences of temperature, rainfall, and humidity. Diurnal variation in hourly distance travelled is depicted in Figure 7.6. In an analysis similar to that for feeding rhythms, I calculated correlation coefficients, for each month, for the relationship between mean hourly distance travelled during the day and the corresponding mean hourly temperatures. The results are as follows:

Nov: r= .33
Dec: r= .72
Jan: r= -.34
Feb: r= -.10
Mar: r= -.77
Apr: r= -.84
May: r= -.55
Jun: r= -.36
Jul: r= .30
Aug: r= -.17
Sep: r= -.05
Oct: r= .56

As with the coefficients calculated for feeding rhythms, these coefficients are also related to the overall mean monthly temperature: r= -.71 ($p<.01$). Distances travelled at each hour during the day were related to temperature changes in the same way as feeding cycles, that is, in the hottest months, hourly distances travelled were inversely related to temperature, and as months got cooler, temperature exerted less and less influence on travelling, and in the coldest months, diurnal changes in distance travelled became positively related with temperature (see Figure 7.2).

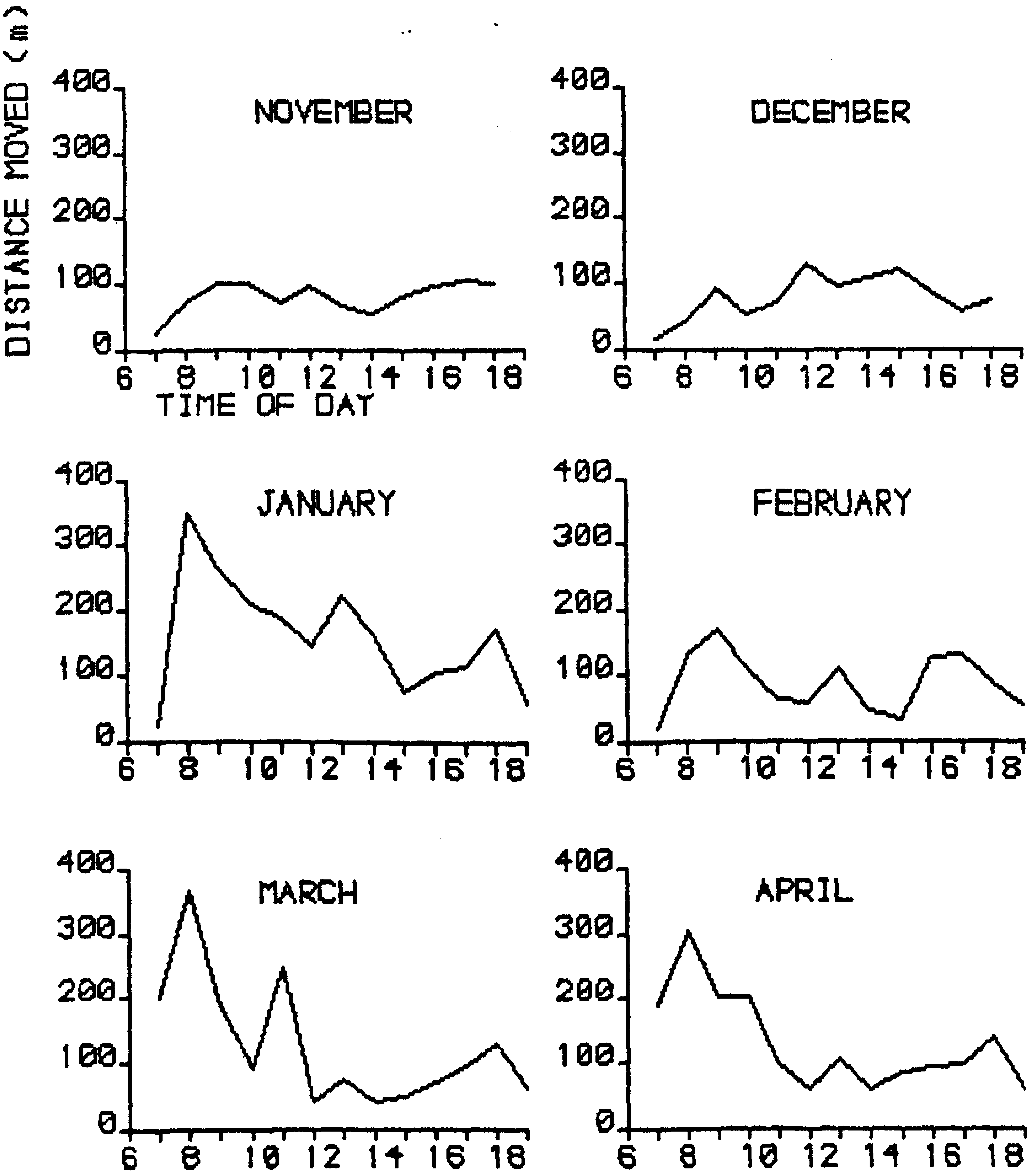


Figure 7.6. Diurnal variation in distance travelled each hour, for each month of the year.

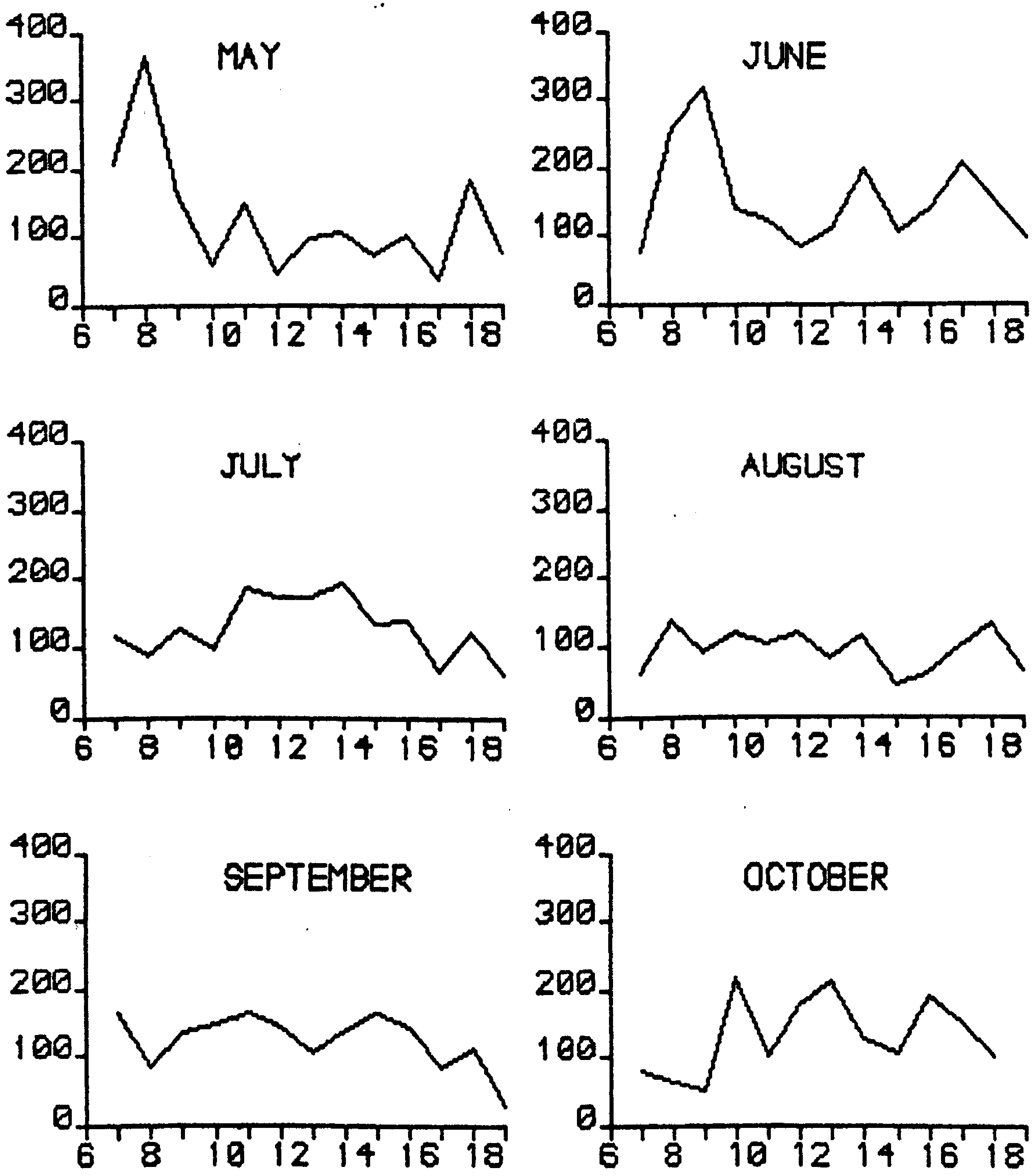


Figure 7.6. (cont.)

7.3.4 Leaving And Entering Sleeping Sites.

Another aspect of ranging behaviour that has important consequences for diurnal activity rhythms is the time at which the monkeys leave their sleeping trees in the morning, and enter sleeping trees at night. From ranging maps for the 5-day samples, I tabulated on a daily basis whether the monkeys left the area of their sleeping site during the first, second, third etc. half-hour period after dawn, and whether they arrived at their next sleeping site in the last, second from last, third from last etc. half-hour period before dusk. Data were analysed in three seasons, wet, early dry, and late dry, for compatability with the previous analysis of feeding cycles.

There were significant seasonal differences in times of leaving and entering sleeping areas (Kruskal-Wallis Anova: for times of leaving (a.m.), H=11.38, df=2, p<.01; for times of arriving (p.m.), H=9.01, df=2, p<.02) (see Table 7.1). Comparison of each pair of seasons revealed where the differences lay (using Mann-Whitney U): The green monkeys left the area of their sleeping sites later in the morning during the 'cold', early dry season than in either the wet or dry season (p<.01); and they entered areas of sleeping sites earlier in the evening during the wet season than during the dry season (p<.01). These seasonal patterns of leaving and entering sleeping areas were consistent with the patterns of diurnal feeding rhythms through the seasons.

7.3.5 Discussion.

Why do the green monkeys respond to seasonal changes in diurnal temperatures in these ways? During November and December, the monkeys rested during the cold early mornings, mostly huddled in small subgroups, and began to feed only when the temperature rose later on. As a method of behavioural thermoregulation, huddling can decrease the rate of heat loss of animals at low environmental temperatures (Kleiber, 1961). Probably the monkeys suffered less net energy loss in keeping warm by huddling than by moving around in search of food.

During the hot dry season, from January to May, the diurnal activity rhythm was centred around the early afternoon temperature peak, when the monkeys rested in the relative cool of the gallery forest. At this time, the humidity frequently

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Table 7.1. Times of leaving and entering sleeping-areas: frequency (f) of arrival or departure during n.th 1/2-hour period after dawn or before dusk.

	Departure (a.m.)		Arrival (p.m.)	
	n.	f	n.	f
Early dry season (Nov-Dec):	1	3	1	7
	2	4	2	3
	3	3		
median=	2		1	
Dry season (Jan-May) :	1	17	1	21
	2	7	2	3
	3	1	3	1
median=	1		1	
Wet season (Jun-Oct) :	1	21	1	11
	2	4	2	10
			3	4
median=	1		2	

Comparisons: a.m.: "early dry" later than "wet", $p<.01$
"early dry" later than "dry", $p<.05$
p.m.: "wet" earlier than "dry", $p<.01$

fell below 10-20%, with temperatures between 35 and 40 oC: these are measures from the woodland met. station - early afternoon ´sunshine´ temperatures on the open plateaux often reached 45-50 oC. Activity during this period of intense heat could overtax the monkeys´ cooling mechanisms and lead to heat stress: Kleiber(1961) states that if environmental temperature rises above a critical limit, metabolic rate no longer decreases and animals cannot get rid of the heat they produce, which can lead to dangerously uncontrolled cellular processes as both body temperature and metabolic rate increase. The green monkeys almost always headed for the streambed in the valley, to areas of gallery forest with dense cover and water, to drink and rest (see chapter 8). On particularly hot days, this rest period lasted up to three hours, during which time there was no movement at all and the monkeys appeared to sleep (eyes closed, bodies draped over branches). It was at this time of year that there was the greatest difference in temperature between the streambed (forest met. station) and outside the valley (plateau and woodland met. station): the mean hourly woodland/valley temperature difference for the dry season was 6.0 oC, whereas the mean difference for the wet season was 1.2 oC. Thus the valley provided a relatively cool refuge from the intense ´outside´ heat, although even valley temperatures were frequently 30-35 oC on these dry season afternoons.

In response to this necessity for an early afternoon allocation of time to resting, the green monkeys' time-budget was adjusted such that intensive feeding began at dawn, and continued while the relative cool of the morning lasted. Likewise, evening feeding and distance travelled increased after the afternoon inactivity, as the temperatures dropped again. The pattern of very early feeding and ranging was particularly marked towards the end of the dry season, when the monkeys began moving out of their sleeping trees with barely enough light to see, and headed for the first feeding-sites.

As in other cases (e.g. selectivity and diversity of diet, chapter 6; group spread, chapter 8), the data for February do not fit predictions closely. February was probably the hardest month of the year for the monkeys, in terms of dryness and the low quality and sparseness of food, which for adult females was added to the burdens of pregnancy. However, although the correlations between diurnal temperature changes and feeding (r= -.07), and distance travelled (r= -.10) are at odds with the higher negative coefficients for other months in the dry season, the predicted decrease in both feeding and travelling during the afternoon temperature peak was present (see Figure 7.5). The low correlations are due to the greater fluctuations in the level of activity at other times of day, which were probably related to the lack of predictability of food sources: if food was scarce and poor in quality, the constraints of high temperatures on feeding and ranging may have become less important than searching continuously for unpredictable food. Such causal influences in the diurnal feeding rhythm will be considered again in the following section on feeding synchrony and time of day.

After the ´cold´ and the ´hot´ months, the third seasonal change in the effects of temperature on diurnal rhythms concerns the wet season months, June to October. Diurnal correlations showed that the daily cycle of temperature had no simple effect on feeding and ranging during these months. Temperature variation in these months was far less than during the dry season, as well as these temperatures being cooler: compare wet season 5-day samples, mean temperatures from 22-30 oC = 8 oC difference; dry season, from 22-40 oC = 18 oC difference. Early afternoon temperatures of 27-30 oC in the wet season would not be enough to overheat an active monkey, and thus placed no limits on the activity-budget for this period. Hence, the main influences on feeding rhythms in the wet season were likely to be, for example, the distribution of food sources, the timing of rainstorms (during which feeding stopped), or the degree of feeding synchrony between individuals.

7.4 FEEDING SYNCHRONY.

The previous section showed predictable effects of temperature on rhythms of activity in certain seasons - i.e. feeding within the group was synchronised broadly with temperature. Here, I examine whether feeding was synchronized between individuals on a finer time-scale, irrespective of time of day. One might expect less need for synchrony when feeding on abundant or evenly distributed foods, whereas at a clumped resource, it might be to an individual's advantage to join other monkeys in feeding, despite the cost of increased competition, before the group moved away from that food source. Similarly, a monkey that did not feed with others at a limited resource might risk losing its share. Thus food-related synchrony may call for more immediate decision-taking than does temperature-related synchrony.

Two hypotheses are tested: that feeding synchrony occurs irrespective of time of day, and that the degree of synchrony is related to the availability of food.

7.4.1 Methods.

Feeding synchrony must be examined within each scan: to what extent are scans made up of all feeding or of all non-feeding records? For each day during a 5-day sample, each scan that fell on alternate hours was selected. Even hours, from 0800-1800, were arbitrarily chosen. Two-hour, rather than one-hour, intervals increase the independence between scans. Three factors were then tabulated: frequency of feeding vs. non-feeding monkeys, at six time periods per day, over five days. A three-way G-test (Sokal and Rohlf, 1969) was applied to each month's data. This test indicates the significance of clustering (synchrony) of the feeding vs. non-feeding records in each scan, accounting for time of day and day of the month. What is being tested is intra-scan dependence, such that a significant result means that frequencies are more clumped (towards feeding or non-feeding) than expected if the probability of feeding vs. non-feeding is independent, irrespective of time of day.

To test for a relationship between feeding synchrony and the availability and distribution of food, a measure of the feeding synchrony associated with each major species of fruit and flowers was calculated. From scan records, the proportion of each scan made up by the various food species was calculated, and for each species, the mean proportion was calculated over all scans in which it occurred. For example, in December there were 29 scans in which the flowers of _Ceiba pentandra_ were recorded, with a mean of 46.1% of the monkeys per scan eating these flowers. Since each scan is taken to be a sample of the activities of all monkeys in the group, this implies that on average 46.1% of the group fed on _C.pentandra_ flowers whenever these flowers were eaten; in other words 46.1% were synchronized. Measures of the overall availability of food, food available per quadrat, and the measure of food distribution, are as used elsewhere (see chapter 4).

7.4.2 Results.

The outcome of the G-tests (Table 7.2) shows that in every month there was significant synchrony of feeding between monkeys, which was independent of the time of day and of temperature influences. The strength of the synchrony, as measured by the value of G, varied from month to month.

The degree of synchrony associated with each food species is shown in Table 7.3. This was inversely related to the overall amount of food available in the home range (with ln-ln transformations, $r= -.49$, $p<.001$): the more food of a particular species there was available throughout the monkeys' range, the less synchrony there was when feeding on that species.

There was no relationship between the synchrony associated with a species and the distribution of that species, as measured by CI, the index of clumpedness ($r= -.02$,ns). It seems that overall availability was the crucial factor, since CI takes no account of the amount of food in quadrats, and even the availability of food per species quadrat (Av) just fails to show a significant relationship with degree of synchrony ($r= -.25$, $.05<p<.1$). This supports the hypothesis that for commonly available foods there was no advantage to any monkey to synchronize feeding with other monkeys, since

Table 7.2 Results of 3-way G-tests (activity by time by day).

Month	Chi-squared value (G)	Signif.(df=20)*
Nov	47.8 *	p<.001
Dec	137.2	"
Jan	104.8	"
Feb	77.5	"
Mar	60.4	"
Apr	98.8	"
May	99.3	"
Jun	75.0	"
Jul	65.4	"
Aug	110.4	"
Sep	106.0	"
Oct	64.2	"

* In November, df=15: only 4 day's data were used as one day was lost due to tape-recorder malfunction.

Table 7.3. Degree of synchrony (%) associated with each major food species each month. Also, number of scans that include each species (n).

	%	n.
Nov:Herbs	40.0	39
F.lecardii	70.1	2
Z.mauritiana	51.7	11
Grasses	29.6	14
Dec:*C.pentandra*	46.1	29
D.mespiliformis	38.2	24
P.erinaceus	50.7	12
Herbs	23.0	25
Jan:*P.erinaceus*	52.2	75
D.mespiliformis	63.0	15
Z.mucronata	75.4	6
D.oliveri	54.4	11
Feb:*F.umbellata*	48.7	25
P.erinaceus	49.8	18
D.mespiliformis	62.1	13
Mar:*P.microcarpa*	47.1	40
L.acida	66.8	15
F.umbellata	41.0	17
Cassia sp.	28.2	21
Ficus sp.	42.0	9
Apr:*P.microcarpa*	46.5	45
S.juglandifolia	44.0	31
F.umbellata	31.1	23
L.acida	49.2	13

	%	n.
May:*S.senegalensis*	34.7	41
F.umbellata	30.6	19
L.microcarpa	41.4	35
Jun:*S.senegalensis*	40.3	79
P.lucens	53.2	9
F.umbellata	43.2	13
L.heudelotii	31.9	51
Jul:*L.heudelotii*	52.6	70
F.umbellata	70.4	26
Herbs	30.5	22
Aug:*C.lanata*	64.3	37
Herbs	27.6	37
Grasses	32.5	29
N.latifolia	35.8	43
A.digitata	40.5	9
S.mombin	49.5	9
Sep:*S.mombin*	52.0	68
N.latifolia	36.0	40
Herbs	25.4	22
Oct:Herbs	44.4	54
F.umbellata	67.3	12
N.latifolia	27.2	14
S.mombin	48.8	10
V.madiensis	29.0	16
C.populnea	30.8	11

there was a high likelihood of these species occurring in most areas the monkeys would visit. On the other hand, for foods with more restricted availability, a monkey that did not feed when others were feeding was at a disadvantage, since it was less likely to encounter these foods again in other areas of the range, or might have lost out because these foods quickly became depleted. Further support for this hypothesis comes from a negative correlation between synchrony and the proportion of time spent in species-quadrats ($r= -.28$, $p<.05$): the more time that was spent in areas containing a particular species, the less synchronized the monkeys were when feeding on that species. In other words, there was more need for a monkey to feed with others when the group passed through an area quickly, so as not to miss feeding opportunities, whereas if more time was spent there, synchrony was less important.

At a descriptive level, other variation in the synchrony associated with various food-species can be accounted for by several factors. Species which grow in very open areas, away from dense tree cover, elicited feeding synchrony despite being very abundant; for example, the flowers of P.erinaceus were common and widely distributed in January, but showed high feeding synchrony. The monkeys often had to cross open ground to reach these trees, many of which were leafless and exposed. The risk to any individual, particularly from aerial predation, would be reduced if many monkeys were feeding in the tree at the same time (Hamilton, 1971), which was frequently the case. There were also species which, particularly at the end of the fruiting cycle, were too few for any synchrony to be possible; for example, the fruits of N.latifolia were so rare and dispersed by October that the predicted synchrony was impossible.

In conclusion, there were two factors influencing whether or not the monkeys synchronised their feeding activities: on a broad time-scale over each day, changes in temperature determined when peaks of resting and feeding occurred, while on a finer time-scale, the degree to which feeding was synchronised was influenced by the availability of each food-species.

7.5 AGE AND SEX DIFFERENCES IN TIME-BUDGETS.

As in diet, age/sex differences in time-budgeting might occur through different nutritional requirements, or through intraspecific competition (see chapter 6). In this section I shall see if such differences occur. The following five age/sex categories are used: adult and subadult males, adult females, immature males, immature females, and infants up to nine months old.

7.5.1 Age/sex Differences In Feeding: Annual.

Using the proportion of time over the whole year that each monkey spent feeding, resting, or socializing, mean figures for each age/sex class were calculated (Figure 7.7). There were marked age/sex differences in each activity (Anova: %time feeding, F= 82.7, p<.001; %time resting, F= 58.9, p<.001; %time socializing, F=23.0, p<.001). Subsets of means that are significantly different (all p<.05, using Least Significant Differences test for post-hoc comparison of means) are shown with symbols on each histogram (Figure 7.7). For infants, the very low score for feeding represents solid foods, i.e. other than mother's milk, since suckling could not be reliably distinguished from clinging in scan sampling of very young infants (see chapter 3). This also explains the very high scores for infants resting, which included 'clinging'. The high scores for infants' socializing reflect the amount of time that older monkeys, mostly mothers and other females, spent grooming, handling, or playing with the infant (separate study, in prep).

The high proportion of time spent feeding by immature males and females runs contrary to expectations from their small body-size, and may be related to their eating less weight of food per unit of feeding-time, and thus having to feed for longer to get enough food. Possibly, juveniles as growing organisms need more food than their body-size suggests. Immature monkeys also spent significantly less time resting than adults of both sexes, presumably due to their levels of feeding combined with time spent in social activity (i.e.playing instead of resting). There were no sex differences in activity-budgets between the young monkeys. Adult males spent significantly less time socializing than did adult females or young. This reflects the extent to which adult and subadult males were more socially peripheral to the group, at least in terms of observable affiliative bonds with other group members (separate study, in prep.).

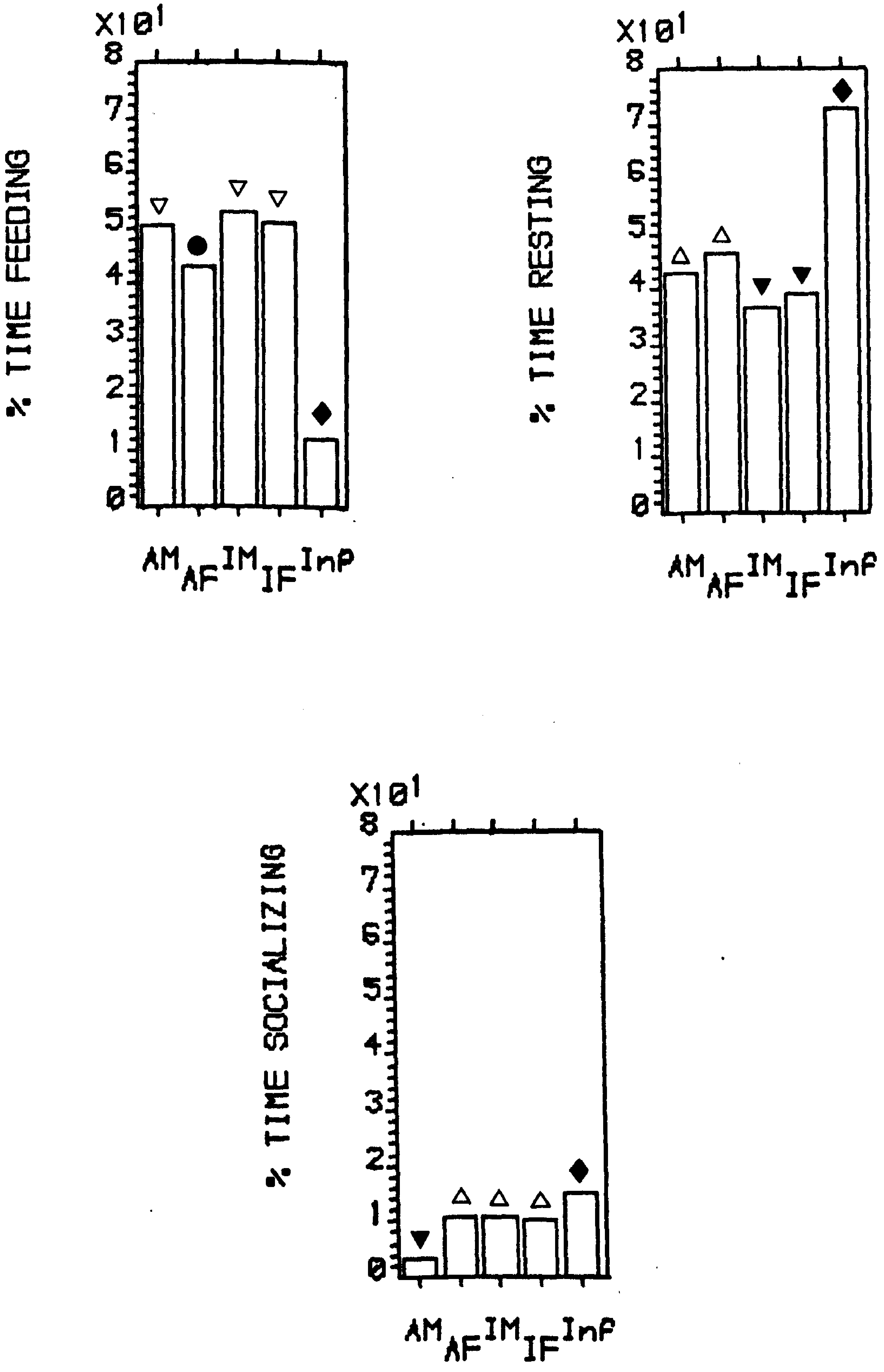


Figure 7.7. Mean annual proportions of time spent feeding, resting, and socializing by each age/sex class. Age/sex classes and symbols as for Figure 6.9.

Adult females spent significantly less time feeding than did adult males or young. This difference between adults may have been related to sexual dimorphism. From various estimates of adult body-weight for C.aethiops (Clutton-Brock and Harvey, 1977; Haltenorth and Diller, 1977; Johnson et al., 1973), I calculated means as follows: males 5.1 kg., females 3.5 kg. (i.e. females approximately 70% of male body-weight). Since metabolic rate varies with the 0.75 power of body-weight (Kleiber, 1961), relative 'metabolic body-size' was calculated from these weights: males 3.4, females 2.6 (i.e. females require approximately 76% of the calories required by males - slightly less dimorphism than suggested by body-weight alone). If the proportion of time spent feeding by males is corrected by 76%, to account for their increased metabolic needs, comparative figures become: females 43.2% of time feeding, males 38.3% of time feeding (50.2 x 0.76). In other words, per unit of metabolic body-size, females fed for slightly longer than males. (Without individual body-weights, no statistical comparison can be made).

7.5.2 Age/sex Differences In Feeding: Seasonal.

One might expect such sex differences due to the greater energetic and nutritional needs of females during pregnancy and lactation (Sadleir, 1969a). To test for this, I divided the females into those with and without infants, and compared them over times of year when different reproductive or developmental stages occurred. The females without infants were two subadult females and two females who were pregnant but lost their infants at or prior to birth, early in the dry season (n=4). There were five females who gave birth successfully (n=5), and eight adult and subadult males were included in the analysis (n=8). Data from the first two months of the study, November and December, were omitted from the seasonal analysis since these early data were not completely reliable as regards individual recognition of the monkeys.

Throughout the year, there was no difference between the proportion of time spent feeding by adult females with and without infants (44.2% vs. 43.7%, Mann-Whitney U=9, p>.4). To assess seasonal variation, perhaps due to different stages of infant development, the mean proportions of time spent feeding each month by three types of individuals (adult males, and females with and without infants) were plotted (Figure 7.8). Inspection of this plot suggests that sex differences were minimal in the wet season (June to October) - although perhaps there was a tendency for females with infants to feed more, in the early part of the season - and that the overall difference between males and females in time spent feeding was largely due to variation within the dry season. Statistical analysis confirmed these impressions: there were no significant differences in time spent feeding between adult males, females with infants, or females without infants over the five months of the wet season (Friedman Anova, chi2= 5.2, df= 2, p=.09) - although this is close to significance; there were differences in the five months of the dry season, January to May (chi2= 7.6, df= 2, p<.05), and the mean percentages for

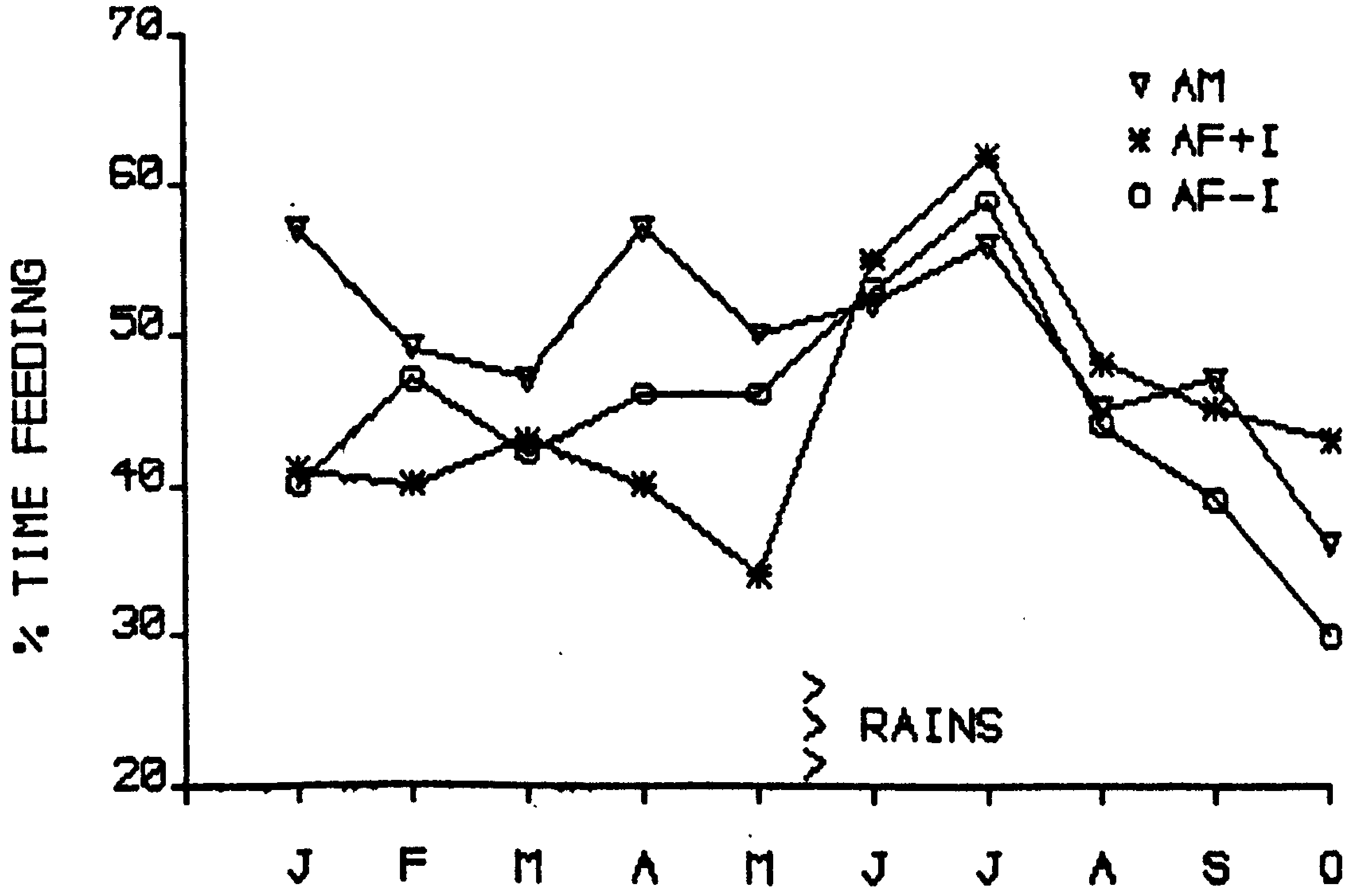


Figure 7.8. Mean monthly proportions of time spent feeding by adult males (AM), adult females with infants (AF+I), and adult females without infants (AF-I).

these months (Table 7.4) show that the difference lay between the adult males and both sets of females, regardless of whether they were carrying infants.

To determine whether this difference was related to the foods that individuals were eating, I tabulated the proportion of the diet made up by fruit, flowers, invertebrates, and 'other' vegetable food parts (mainly foliage, but including grasses, leaves, herbs, gum, fungus, and seeds), for each of the three groups of monkeys, in the wet season and dry season (Table 7.5).

Analyses of variance showed no differences between the diets of males and females with and without infants. However, combining data for females showed that in the dry season the diet of males had a higher proportion of flowers than did the diet of females (16% vs. 11%, Mann-Whitney U= 5.5, p<.01),

Table 7.4 Mean proportions of time spent feeding by adult males, and adult females with and without infants, in the wet and dry seasons.

	dry season	wet season
AM :	50%	47
AF+I :	42	51
AF-I :	44	45

Table 7.5. Mean proportions of the diet of adult males, and adult females with and without infants, made up by fruit, flowers, 'other', and invertebrates, in the wet and dry seasons.

	Fruit			Flowers			'Other'			Invertebrates		
	AM	AF +I	AF -I	AM	AF +I	AF -I	AM	AF +I	AF -I	AM	AF +I	AF -I
Dry sn:	62%	63	59	16	11	10	13	16	18	9	10	11
Wet sn:	61	57	61	2	1	2	23	30	25	14	13	13

while females ate a higher proportion of ´other´ foods (17% vs. 13%, U= 15, $p<.05$).

A more precise measure of food-intake is given by calculating the percentage of total time spent feeding on particular foods (e.g. % of diet made up by fruit multiplied by % of time spent feeding: see Table 7.6).
This shows that males spent more time eating both fruit and flowers in the dry season (Kruskal-Wallis H= 6.8, df=2, $p<.05$; H= 10.1, df=2, $p<.01$, respectively), while females with infants tended to spend more time feeding on foliage, herbs, grasses etc. in the wet season (H= 5.3, df=2, $.05<p<.1$). At this point it may be worth recalling Hladik´s (1977b) cautionary note concerning the discrepancy between temporal measures of feeding, and weight of food eaten (see chapter 3). This may be particularly relevant to sex differences in feeding: a slight increase in time spent feeding on fruits implies a substantial increase in weight of food eaten, while a slight increase in time spent feeding on foliage implies a comparatively lower increase in food-weight. In this case, the higher fruit content of the diet of males may be important for their greater metabolic needs than females. However,

Table 7.6. Proportion of total time spent feeding on fruit, flowers, ´other´, and invertebrates, by adult males, and adult females with and without infants, in the wet and dry seasons.

	Fruit			Flowers			´Other´			Invertebrates		
	AM	AF +I	AF -I	AM	AF +I	AF -I	AM	AF +I	AF -I	AM	AF +I	AF -I
Dry sn:	31%	26	26	8	5	4	7	7	8	5	4	5
Wet sn:	29	29	27	1	1	1	11	15	11	7	7	6

nutritional considerations (such as the higher level of protein in foliage) are likely to be as important as food weight per se.

The reason that males fed for longer than females in the dry season might have been due to their priority of access to certain foods under competition (see chapter 6): Fruit and flowers, both ´primary choice´ foods, formed a large part of the diet in the dry season, but were of lower importance in the wet season owing to the abundance of herbs, grasses, leaves etc. Evidence for food competition in the dry season was seen in males spending more time than females eating fruit and flowers, and in the case of flowers, these formed a higher proportion of the adult male diet. Perhaps because of their brief appearance, flowers were under more intense competition between monkeys than were other foods. On the other hand, adult females ate higher proportions of ´secondary choice´ foods such as leaves, grasses and herbs etc. in the dry season (see chapter 6 for details of diet selection). If differences in metabolic body-size were to account for higher levels of fruit and flower feeding by males, it is puzzling why this difference is only seen in the dry season. This may be the time of greater environmental stress, causing more food competition within the group, which is relieved in the wet season by the abundance of water, grass, shoots, herbs, and invertebrates.

7.5.3 Age/sex Differences In Feeding: Pregnancy & Lactation.

Activity-budgets of females with and without infants warrant further examination with regard to stages of infant development, since the dry season covers both pregnancy and lactation. Altmann (1980) makes the simplifying assumption that a female in late pregnancy has the same energetic requirements as a nonpregnant, nonlactating female of the same weight. The increased energetic demands on a mother come with lactation, when she has to feed her infant as well as herself. In particular, females may have increased protein requirements during this period (Sadleir, 1969a). If this is the case with green monkeys, we may expect any change in maternal time budgets to occur from March-April, after infants were born, until weaning. (Portman (1970) gives figures for the metabolic rates of pregnant females as increased by a factor of 1.25 over non-pregnant females, and of lactating females as increased by a factor of 1.5).

Green monkeys at Mt.Assirik had a marked birth season, in March and April. Examination of Figure 7.8 shows a marked drop in the proportion of time spent feeding by mothers with new infants, during April and particularly during May. The mean percentages for May were 34% for females with infants, and 46% for females without infants, a significant difference (Mann-Whitney $U= 0.5$, $p<.01$). With the onset of the rains in June, new mothers showed a dramatic boost in their amount of feeding (from 34% of time in May, to 55% in June). This period at the beginning of the rains also corresponded with the peak of weaning activity between mothers and their infants (separate study, in prep). Thus, the period of peak lactational demand on mothers was clearly reflected in their time-budgets. However, the response by green monkey mothers was the opposite of that predicted (and shown) by Altmann (1980) for baboons (*Papio cynocephalus*), who increased feeding time to make up for the additional energetic demands of lactation. The evidence suggests that the green monkey mothers were conserving bodily resources, minimizing energy expenditure, for example by resting where possible, avoiding heat stress, and avoiding exessive activity in competition with others over food: time not feeding was spent resting (62% of time in May, the highest monthly figure of the year) and not socializing (4% of time in May, the lowest monthly figure), (see Plate 7.1). The new mothers may have been using fat reserves: evidence from laboratory and domestic mammals suggests that females will drain their own body reserves to a remarkable degree before any decrease in milk quality or quantity is observed (Sadleir, 1969a). Such losses could be rapidly replaced with the onset of the rains - as evidenced by the great increase in feeding time by new mothers in June, July, and August, to levels higher than males or females without infants (see Figure 7.8). (Riopelle *et al.*(1974) showed that in captive rhesus monkeys weight-loss due to a low-protein diet was regained within 6 weeks of the resumption of a normal diet). Table 7.5 shows that the females with infants also tended to eat higher proportions of leaves, herbs, grasses, etc. in the wet season than did males or females without infants. Such a diet is rich in protein (A.Hladik, 1978; C.Hladik, 1977b, 1978).

Plate 7.1. An adult female with her newborn infant and yearling daughter, resting in the relative cool of the gallery forest.

During April and May, mothers faced severe environmental demands, such as high temperatures and restricted water availability, in addition to lactation and protection of their infants. It seems likely that weight-loss could have been severe if these conditions were prolonged; women maintain a steady body-weight during lactation only with a 32% increase in caloric intake, and lose weight even with a 23% increase (Whitchelow, 1976, cited in Altmann, 1980). Clearly the reduction in feeding time by green monkey mothers can only be a suitable energetic strategy because the period of heavy lactational demand is relatively short compared to humans or baboons (weaning activity in the green monkeys started at 2 months: separate study, in prep), and because the onset of the rains and resultant exuberant vegetation is predictable enough at Mt.Assirik that an abundant source of easily available food is more or less guaranteed, and weight-loss or protein-deficiency can be rectified immediately. In addition, infants can move on to solid foods at the same time, and very quickly reduce lactational demands on their mothers. This strategy of low food-intake combined with a reduction in energy expenditure has been demonstrated elsewhere in the green monkeys, i.e. in their overall feeding strategy for dealing with fluctuations in food-availability (see chapter 10).

In summary, there were no sex differences in time-budgets among immature monkeys, who spent over 50% of their time feeding. In terms of body weight, adults of both sexes spent less time feeding than young, but between adults, females spent more time feeding per unit-body-weight. Females fed less on choice foods during the dry season, possibly because of competition from males. Females with new infants adopted a low energy strategy during lactation, and reduced their feeding until the rains had started and weaning was under way. Adult females and young spent more time socializing than did adult males, which in the case of the young may have resulted in their having least time for resting.

7.6 VERTICAL DISTRIBUTION OF ACTIVITIES.

Over the whole year, the green monkeys spent 33.4% of their time on the ground (Figure 7.9). This was not due simply to feeding at ground level, since equivalent proportions of time resting and socializing were also spent on the ground (Figure 7.10). Figure 7.10 shows the proportions of time spent in each activity to be distributed amongst all the height-levels in a similar manner, with one exception: there were a comparative lack of feeding records from height level 0-5m. Examinating the distribution of heights of a sample of 418 important food-trees reveals a corresponding lack in number of trees in this height range (Figure 7.11). Comparing feeding heights (excluding ground feeding) with the heights of important food-trees suggests that feeding heights were randomly chosen according to where food was available: the distributions are similar, but that for feeding heights is positively skewed (i.e. towards lower height-levels), while the distribution of tree heights tails off more slowly at higher heights - as expected, since feeding monkeys move

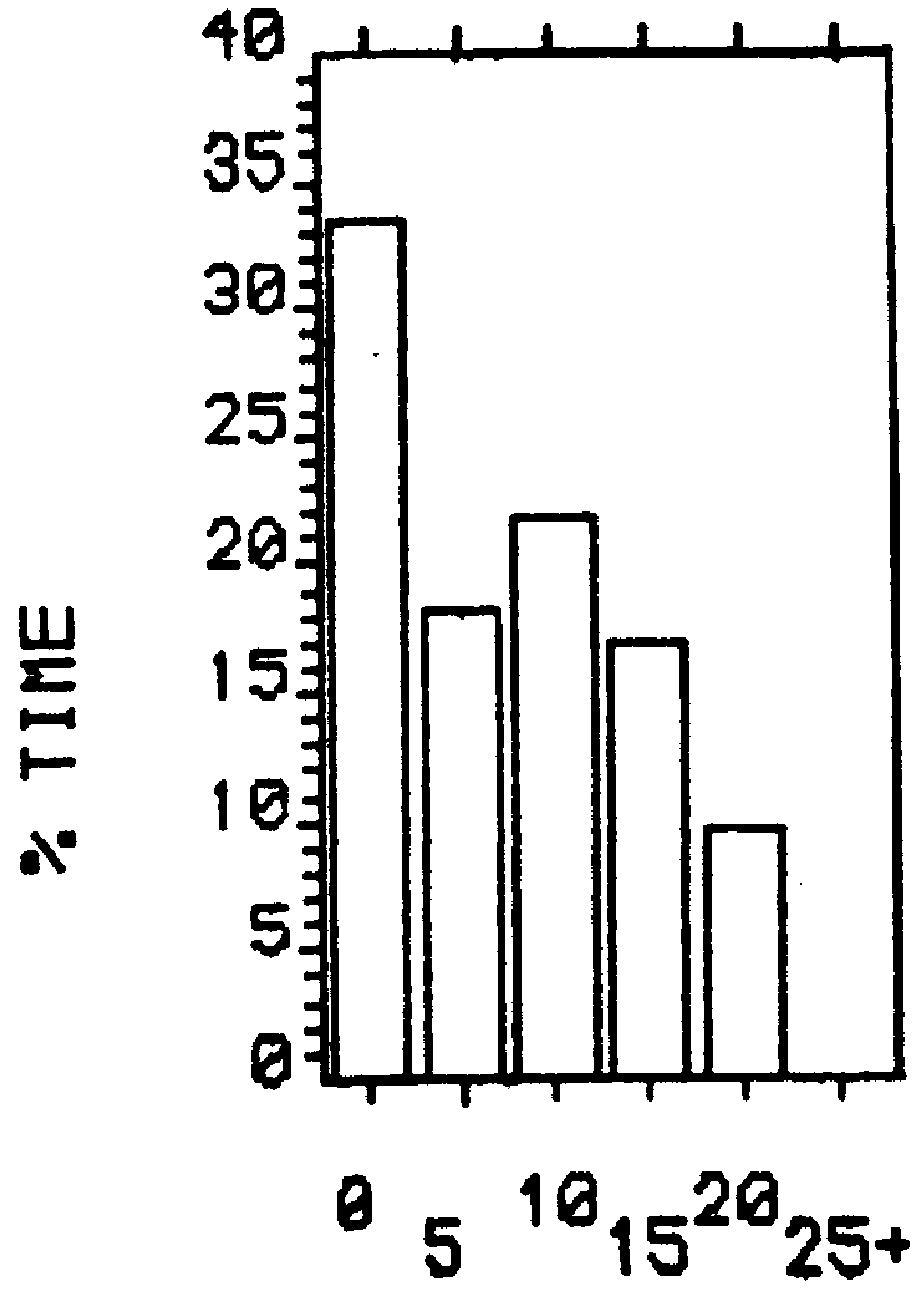
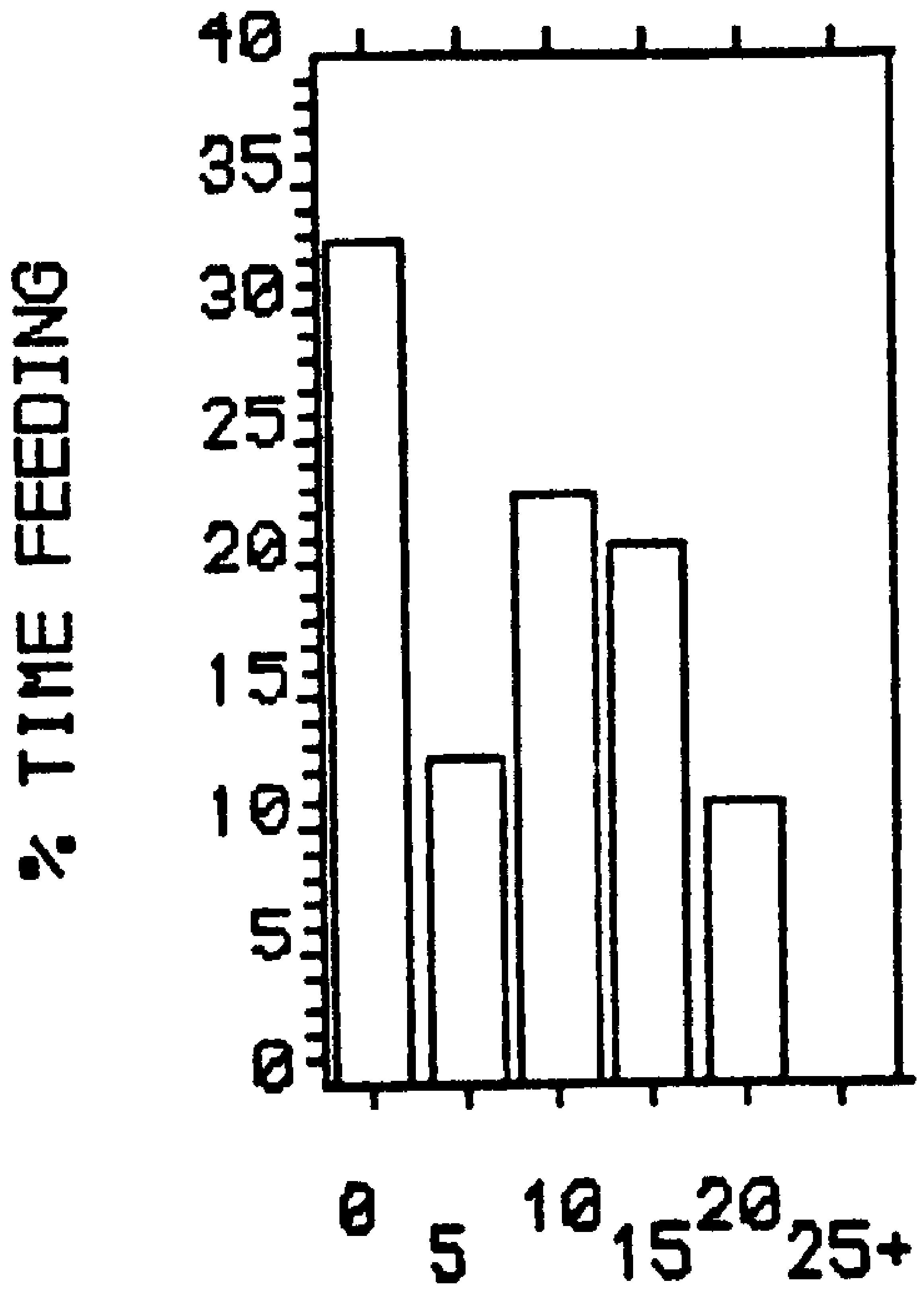


Figure 7.9. (see below)



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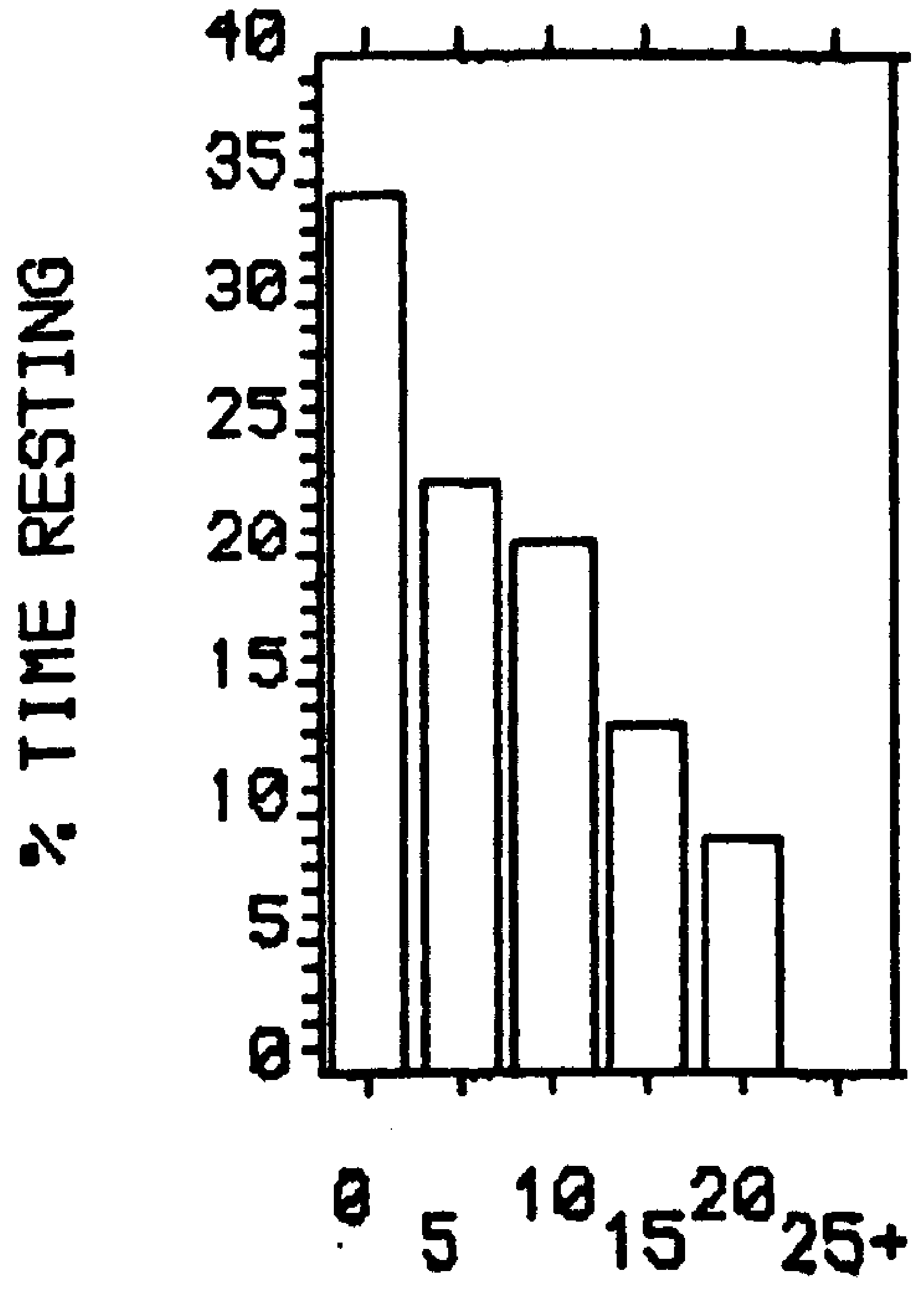

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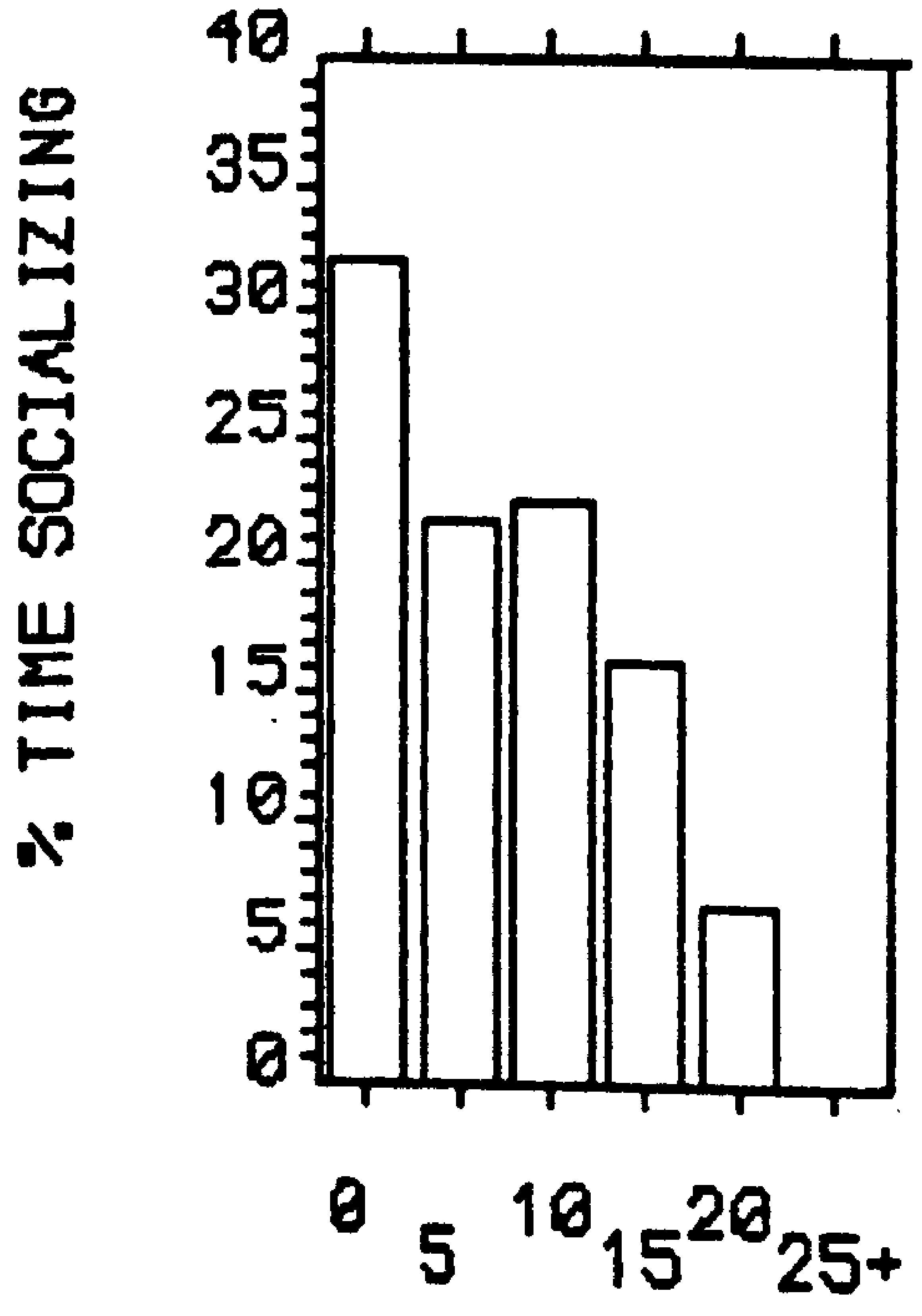

Figure 7.10.

Figure 7.9. Annual proportions of time spent in different 5-metre height-bands. (0 = ground; 5 = 0-5m; 10 = 5-10m etc.).

Figure 7.10. Annual proportions of time spent feeding, resting, and socializing in different 5-m height-bands.

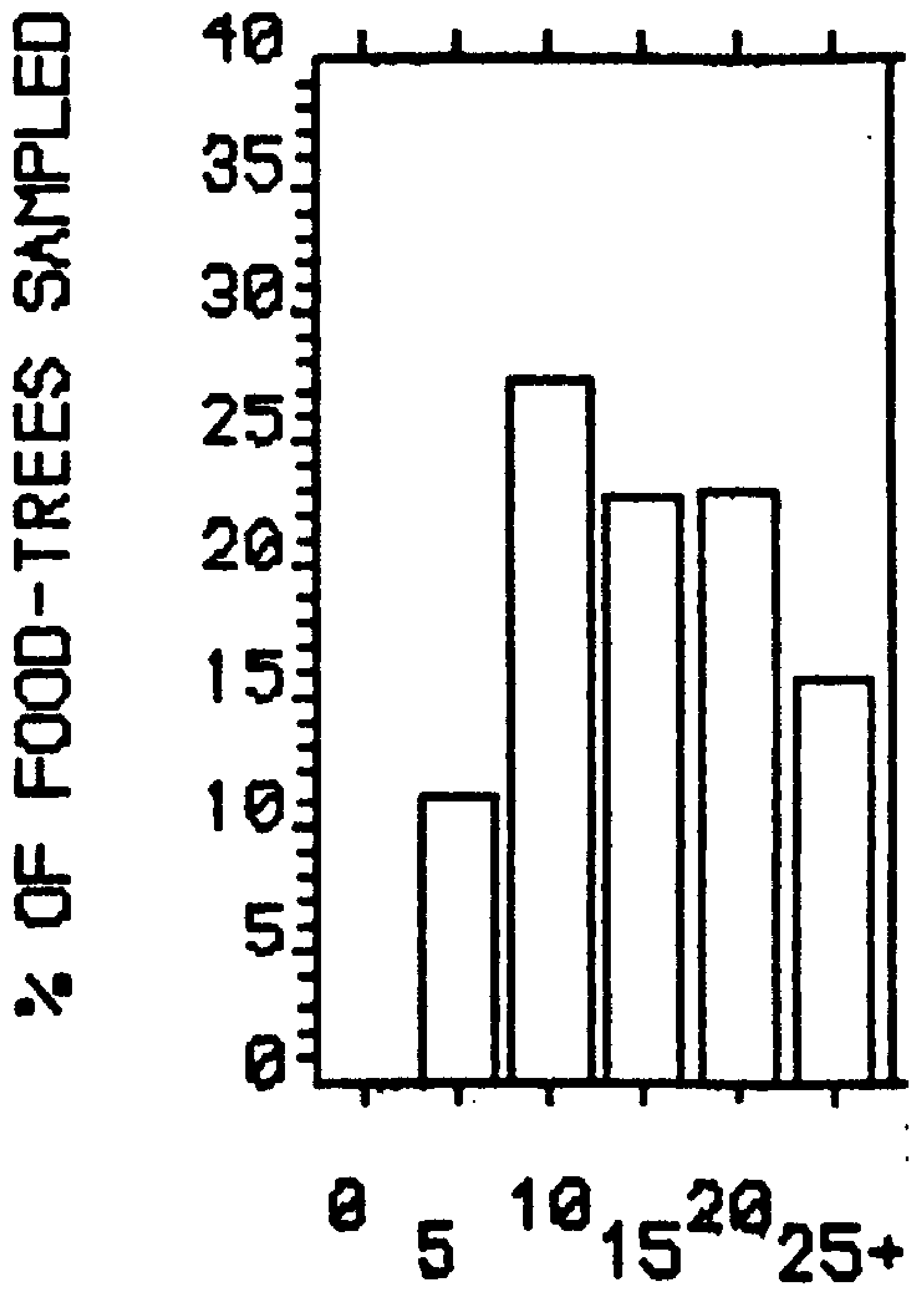

Figure 7.11. The distribution of heights of major food-trees, within 5-m bands.

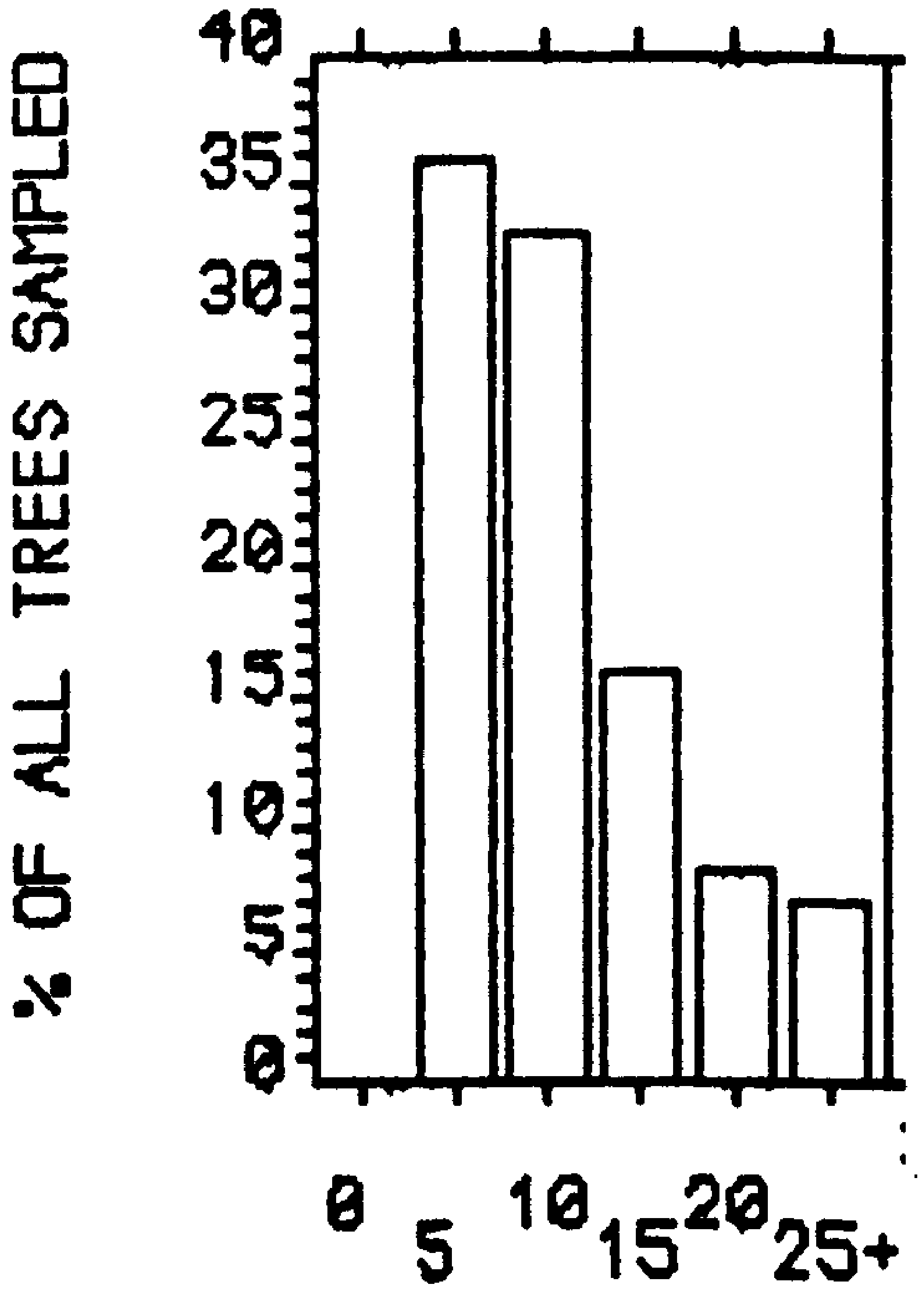

Figure 7.12. The distribution of heights of all trees, within 5-m bands.

throughout any tree canopy, and not just at the top of the crown. A similar comparison, between the distribution of heights of all trees in the S.A.P.P. vegetation transects (479 food and non-food trees, Figure 7.12) with the distribution of heights of resting and socializing suggests that these activities also occurred at random heights. One exception was heights over 20m: while 7.1% of the sampled trees were over 20m high, almost no activity was recorded at this height. The monkeys probably avoided these heights since escape routes from very tall or emergent trees were more limited than through the thicker, lower canopy.

Despite the generally non-selective use of heights for different activities, and thus the absence of any particular height niche used by the monkeys, it is worth testing for age/sex differences in heights used, i.e. a form of niche-differentiation within trees that could arise from competition between individuals. A series of Anova tests showed no age/sex differences in heights used, except for young monkeys and infants using height 0-5m more than adults (0-5m: $F= 4.01$, $p<.05$; all other heights: $F< 1.00$, n.s.).

7.7 DISCUSSION.

Comments and discussion of the data have been made after each analysis and presentation of results. Further analysis and discussion of seasonal variation in various measures of activity will be carried out in chapter 10, with reference to models in optimal foraging theory.

7.7.1 Comparative Discussion.

Comparing activity-budgets between different populations of the same species, in different habitats, can provide important clues to adaptive differences in behaviour, but the exercise is frought with methodological difficulties. Marsh (1981) points out some of the ways in which the measurement of population differences in time-budgets is sensitive to the methods used to detect them. He distinguishes particularly between ´instantaneous´ (i.e. at the instant the target is spotted) and ´sustained´ (i.e. first activity sustained for 5 secs) scan-sampling of activity. Homewood (1978) distinguishes between eating and foraging in her activity records, perhaps a more serious methodological point because the mangabeys (Cercocebus galeritus) that she studied spent 35% of their time eating, but 49% of the time if foraging was included. A further problem involves equating feeding time with the rate or weight of food-intake in different populations (see Hladik, 1977b).

Studies of C.aethiops from which comparative data on time-budgets are available include Kavanagh (1977, 1978), Dunbar and Dunbar (1974), Galat and Galat-Luong (1976, 1977, 1978), and Wrangham and Waterman (1981). Both Kavanagh and Galat and Galat-Luong specify that they used instantaneous scan-sampling, and that they included foraging (manipulation, turning debris etc.) in their feeding records. Dunbar and Dunbar, and Wrangham and Waterman used instantaneous scan-sampling, and the Dunbars did not include foraging (pers.comm.to Homewood, 1978). Data on the proportion of time spent feeding are available from seven populations (Table 7.7), although the last two listed will not be considered as they were of very short duration, and the present study indicates a large variation in activity-budgets throughout a year.

Comparative studies of feeding time-budgets have proposed several variables that could account for differences: environmental temperature, since animals require less energy to maintain body temperature in hotter environments (Marsh, 1981; Oates, 1977); and differences in the diversity of the diet, such that if a monotonous diet is slower to digest than a varied diet, then less time is available for feeding (Marsh, 1981; Struhsaker and Oates, 1975). Inspection of the above table immediately suggests rejecting both of these hypotheses as being too simplistic in the case of *C.aethiops*. The green monkeys at Mt.Assirik showed the highest proportion of time spent feeding, and yet it is amongst the hottest of these sites. Vervet monkeys at Amboseli also showed very high feeding times, and yet the lowest diversity of food-species.

Table 7.7 Time-budgets from 7 populations of *C.aethiops*.

%F = % of time spent feeding: mean (range)
Temp= mean temperature range or (seasonal maxima)
Nsp = number of food-species eaten
Dur = duration of study, months

Site	%F	range	Temp	Nsp	Dur	Author
Mt.A,Senegal	44.8	(35-55)	(30-40)	67	12	this study
Kal,Cameroon	20.0	(17-23)	(30-40)	41	4	Kavanagh
B.N.,Cameroon	24.5	(17-36)	(31-40)	26	4	Kavanagh
Amboseli,Kenya	-	(21-51)	9-33	9	9	Wrangham
R.Sen.,Senegal	-	(23-32)	26-36	17	18	Galat
Saloum,Senegal	8	(70 hours obs. over 7 months)				Galat
Bole,Ethiopia	27.4	(58 hours obs. over 6 months)				Dunbar

Many differences in feeding behaviour between populations, including time-budgets, are more likely to be related to differing floristic compositions of the habitats concerned (e.g. Struhsaker, 1975), and different calorific and nutritive content of foods at each site (Marsh, 1978). This was discussed in chapter 6. Both Marsh (1981) and Oates (1977), for Colobus badius and Colobus guereza respectively, have shown that groups living in poorer, marginal habitats spent less time feeding, a finding that concurs with my conclusions about seasonal variation in feeding time by the green monkeys: at times of lower food-availability, less time was spent feeding (chapter 10). This principle may be a strong element in primate feeding strategies, if it is consistent both within and between groups, and between species. This study, and the two examples given above, demonstrate consistency within and between populations. Several other species were cited in chapter 8 as showing a similar pattern: increased activity (ranging and time spent feeding) with increased food-availability (e.g. Chivers, 1977; Clutton-Brock, 1975b; Raemakers, 1980; Richard, 1977). Notably, baboons consistently show the opposite trend: with decreased food-availability, more time is spent feeding (Altmann and Altmann, 1970; Dunbar, 1977; Kummer, 1968; Nagel, 1973; Oliver and Lee, 1978; Sharman, 1981).

Unfortunately, little attention has been paid to quantifying food-availability in many field-studies, and from the seven sites of C.aethiops considered above, only two provide such data: the present study, and Wrangham and Waterman (1981).

It is clear that Amboseli has a relatively simple habitat compared to Mt.Assirik, which has a far greater variety of species, and a much higher density of trees (see chapter 4). In addition, the green monkeys had a much bigger annual home range than any recorded at Amboseli. These three criteria suggest a much higher overall availability of food at Mt.Assirik; and consistent with expectation, the green monkeys fed for longer than the vervets (35-55% at Mt.Assirik vs. 21-51% at Amboseli).

Energetics are unlikely to account for all variation between populations, since the effect of differences in the nutritive values of foods at various sites may conflict with an energetic strategy: for example, the very low proportion of time spent feeding by the green monkeys in the Sine-Saloum in Senegal (8%) is likely to be accounted for by the very high nutritive value of their diet (primarily crabs and mangrove roots): in addition, this rich diet was available with minimal travelling costs, since the food was abundant, and densely and evenly distributed. This was a very short study (although not seasonally biased), and probably subject to greater observational bias than most (because of its open beaches and inaccessible mangroves). However, it strongly suggests that food-availability is not necessarily the only important variable in determining time-budgets, but that the nature of the diet and its nutritive value may also greatly affect time-budgets.

Evidence of temperature regulating diurnal cycles in the level of activity is given for several species and study sites, where midday resting peaks are more regular in hotter seasons (Lindburg, 1977; Kummer, 1968; Richard, 1977). The present study has quantified this relationship in detail, showing that the green monkeys did not feed either when it was too hot or too cold, and that in the wet season, temperature had no effect on activity patterns. These effects were explained in terms of optimal energetic strategies in the face of physiological responses to changes in temperature. Dunbar and Dunbar (1974), Hall and Gartlan (1965), and Kavanagh (1977) all found diurnal variation in the activities of C.aethiops. The Dunbars found that feeding increased throughout the day, while the other authors found some tendencies for morning and evening peaks of feeding, but all of these studies were either short or did not cover all seasons representatively. Clutton-Brock (1974) reported no correlation between temperature and feeding rhythms for red colobus (Colobus badius) at Gombe, but here the highest monthly mean temperature was only 29 oC - only slightly warmer than the wet season at Mt.Assirik, and well below the dry season temperatures that strongly influenced the green monkeys.

Synchrony of feeding on a finer time-scale, and irrespective of time of day (i.e. temperature), has been demonstrated amongst tantalus monkeys by Kavanagh (1978). He gives descriptive evidence for the significance of this, for example at clumped trees in open woodland, or when termites swarmed for a limited period. Data from Mt.Assirik have quantified this relationship, demonstrating that feeding synchrony became more marked when feeding on rarer foods.

Data on sex differences in time spent feeding by other populations of C.aethiops are available only from Kavanagh (1977). He found no differences at Kalamaloue (males= 25% vs. females= 22%), but at Buffle Noir adult females spent more time feeding than adult males (22% vs. 28%), the opposite to green monkeys at Mt.Assirik. A number of studies have shown females to spend more time feeding than males in other species, for example Marsh (1981: Colobus badius, 28%:35%); Smith (1977: Alouatta palliata, 14%:18%); Cluttton-Brock (1974: Colobus badius, 22%:31%); Waser (1977: Cercocebus albigena, 41%:49%). One reason proposed by Clutton-Brock (1977) for this difference might be that males have dominant access to areas of maximal food-availability, and thus could feed less often: however, in the green monkeys it seems that this was precisely the reason why males fed more than females on such foods (fruit and flowers). In addition, Smith (1977) demonstrated that adult females carrying young infants fed for longer than females without infants, and Altmann (1980) showed that female baboons (Papio cynocephalus) spent increasing amounts of time feeding as their unweaned infants grew. This evidence strongly suggests that lactation placed heavier energetic demands on these females, who responded with increased feeding time. However, the green monkeys responded by decreasing feeding time, which was arguably an equally successful alternative strategy, minimizing energy expenditure under conditions of intense heat, food competition, and the demands of lactation and infant care, despite reducing food-intake.

One major problem with optimality principles and invoking "optimal strategies" is that if data do not fit predictions, it is simple to create an alternative model around the data, and assume this also to be optimal. However, in the above case, there are justifiable grounds for assuming that several strategies may be operating, each one consistently used by the animals concerned. The green monkeys adopt a "high-cost,high-yield/low-cost,low-yield" strategy in their feeding, increasing time spent feeding as food-availability increases, and vice versa (see chapter 10); it follows that a similar strategy may be used by lactating females, who do not attempt to feed for longer to compensate for their increased energy demands, but rather take the low-cost, low-yield alternative, in keeping with their general feeding strategy. (This might also explain why adult males fed for longer than females, given that they had access to more and better food through their dominant status). Baboons, in contrast, adopt a feeding strategy where decreasing food-availability is compensated for by increasing time spent feeding (see refs. above); it follows that lactating females should also use the same strategy, meeting their increased energy demands by increasing feeding time. In the case of howler monkeys (Alouatta palliata), Milton (1980) did not find seasonal variation in feeding time, but rather a change in dietary focus (from fruits to leaves) as food-availability decreased.

In other words, as with the baboons, the howlers did not adopt an energetic strategy similar to the green monkeys, and this was also reflected in the response of lactating females, who fed for longer than non-lactating females (Smith, 1977). This hypothesis needs to be examined further, by testing to see if the predictions are met in other species: that is, that the feeding strategy of lactating females matches the overall feeding strategy of the population, as regards costs and benefits.

The degree of terrestriality reported amongst populations of C.aethiops is very consistent. About one-third of the time spent on the ground is the figure given by Dunbar and Dunbar (1974), Galat and Galat-Luong (1976), Gartlan (1966), Kavanagh (1978), and this study. The green monkeys on the River Senegal provide one exception, as they spent 70-75% of their time on the ground (Galat and Galat-Loung, 1976). This may reflect the very high proportion of graminaceous leaves in their diet (Galat and Galat-Luong, 1977), which require intensive use of the ground level to exploit. Kavanagh (1978) states that at his two savanna sites in Cameroon, the tantalus monkeys spent 85% and 90% of their feeding time between the ground and a height of 10m. The comparable figure for Mt.Assirik was 68%, which reflects the greater proportion of tall trees at Mt.Assirik, especially in the forest (see chapter 4). Thus, C.aethiops have no restriction on the height-niche they occupy, and they exploit the understory and various height-levels according to the foods they contain.

CHAPTER 8.

RANGING.

8.1 INTRODUCTION.

There are several reasons why the study of ranging behaviour is interesting: firstly, a knowledge of range-size and spatial overlap among neighbouring groups is needed for estimates of population densities and biomass, important factors in the ecology of a region; secondly, although much is descriptive, there is a growing body of quantitative evidence demonstrating the various environmental and social variables that determine patterns of range-use, both in space and time (Clutton-Brock, 1977; Gautier-Hion *et al.*, 1981; Milton, 1980; Rasmussen, 1979).

In this chapter, I shall examine several aspects of the green monkeys' ranging, laying heavy emphasis on the seasonality of the variables measured, and using monthly differences to test hypotheses concerning the relationship between feeding and ranging, and the seasonally changing composition of resources in the home-range. The ranging parameters investigated include patterns of movement about the range (distance, speed, area covered, grouping), and differential use of various areas within the annual range.

8.2 DAY-RANGE LENGTH.

The length of a single day's travel varied between 665m and 2670m, and monthly means ranged from 943m in December to 2087m in January (Figure 8.1). Despite considerable variation within each month, differences between monthly mean day-range lengths were significant (Kruskall-Wallis H= 31.95, df= 11, p<.001). These differences were not attributable to gross seasonal effects: there was no difference between wet and dry season mean monthly day-range lengths (Mann-Whitney U= 17, p=.50); nor were day-range lengths more variable in one season (wet vs. dry season monthly standard deviations, U= 7, p=.053 - although this is close to significance). However, if the two 'cold' months in the early dry season (November and December) are removed from the dry season scores, there was a significant difference between wet and later dry season standard deviations (U= 2, p=.016). Justification for dividing the dry season into early and late months was given in chapter 7, in terms of temperature differences.

Thus, the only gross seasonal effect on day-range lengths was that in the wet season there was less variability in daily distance travelled. This effect was most likely related to the influence of temperature on diurnal rhythms of activity (chapter 7): in the heat of a dry season day, the monkeys moved to the relative cool of the gallery forest in the valley, to drink and rest. Thus if they ranged away from the valley in the morning, they had a long return journey after noon, but if they fed in the valley, the forest was never far: hence the greater variation in day-range lengths in the dry

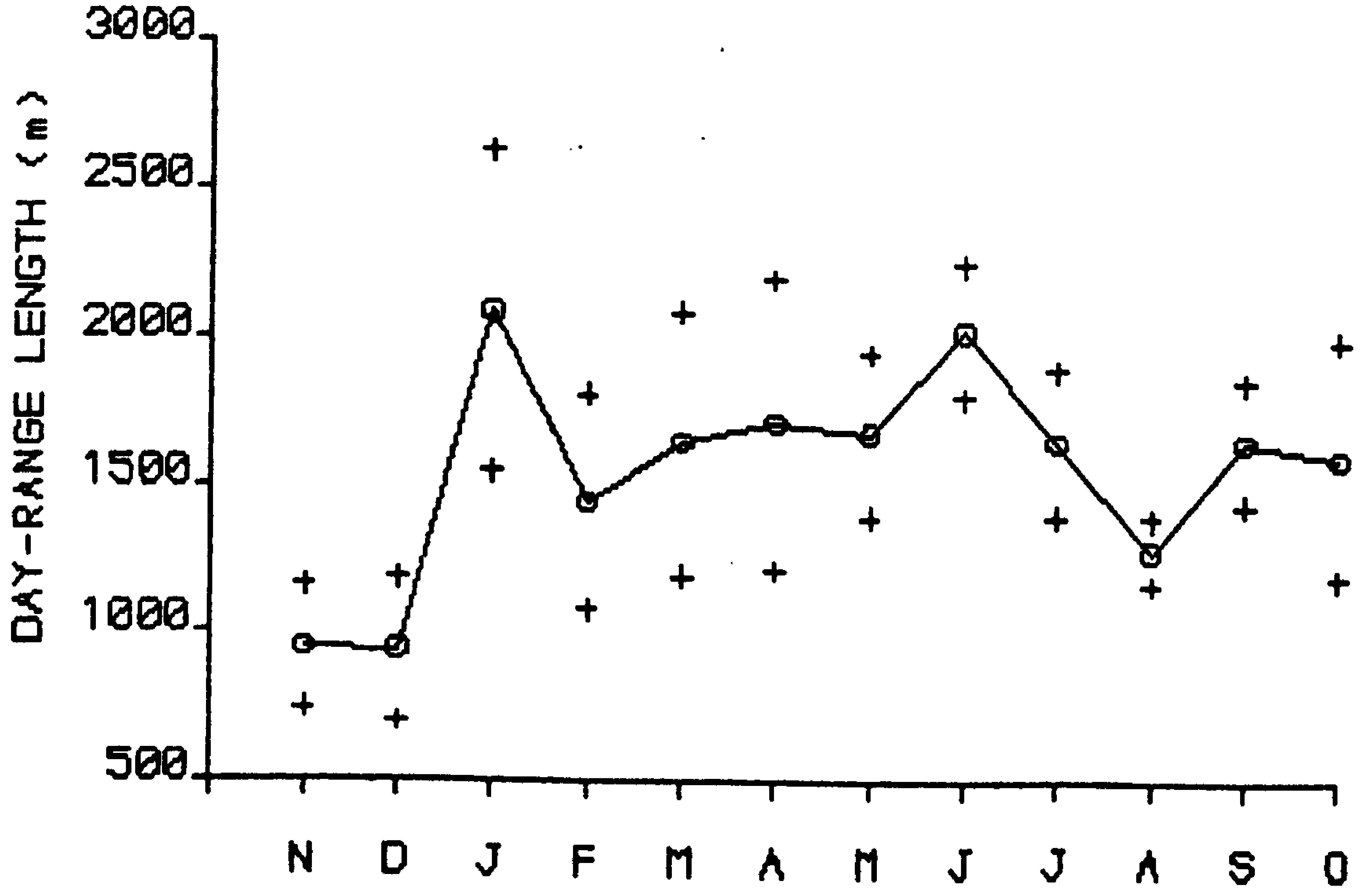

Figure 8.1. Mean day-range lengths (in metres), with standard deviations, for each month's 5-day sample.

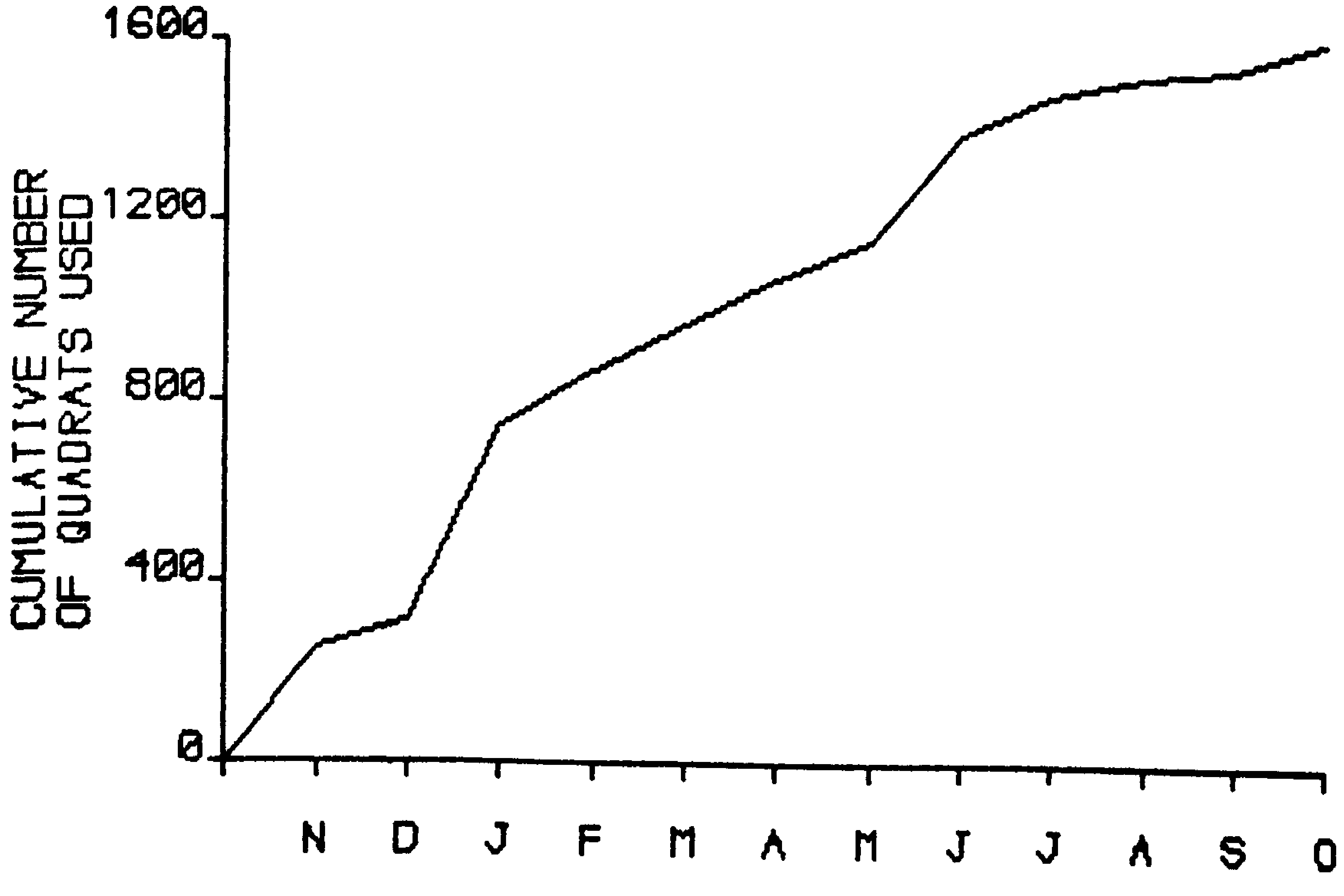

Figure 8.2. Cumulative number of new quadrats entered during 5-day samples.

season. In the wet season, these constraints were absent, and daily travel distances were more consistent.

The question of why mean day-range lengths differed from month to month will be considered in chapter 10, in the light of data on feeding patterns and food-availability. To anticipate, day-range lengths increased as food-availability increased.

8.3 SPEED OF MOVEMENT.

The 5-day means of distance travelled at each hour during the day were presented, by month, in Figure 7.6 (chapter 7). Inspection of the data suggests two things: that in most months there was a diurnal rhythm of speeds of movement, and that the extent and patterning of the rhythm varied between months. This aspect of ranging was analysed in chapter 7, together with diurnal rhythms in the time-budgeting of the monkeys' maintenance activities.

8.3.1 Speed Of Travel And Habitat-type.

Habitat-type did affect the speed of movement of the monkeys. However, the data were collected in such a way that the average speeds of movement in each habitat-type cannot be considered in isolation from the effects of the monkeys' predominant activities: for example, since open woodland was used mainly for feeding rather than resting, the average speed of movement would be higher than for forest.

Nevertheless, habitat-type did affect speed of movement in certain ways, irrespective of the monkeys´ activities. Cover was probably the most important factor: the monkeys moved more slowly in the forest and closed woodland, and in open woodland in the wet season when the grass was tall and all trees were in full leaf, than in open woodland in the dry season, when the grass was burnt and the trees leafless. And on most occasions when the monkeys ranged out across the open plateaux, they either ran or walked briskly and alert. On these occasions mothers carried their infants ventrally, even beyond the age of normal ventral carrying. These effects were probably exaggerated by my own presence: in open woodland in the dry season not only did the monkeys move faster between feeding sites, but their flight distance from me increased to over 50m, compared with about 20m in the wet season in open woodland. When crossing open plateaux, adult females were especially reluctant to move away from cover if I was too near, and when they did, they often ran at full speed.

It was evident that the green monkeys relied on hiding in the security of vegetational cover as a strategy for protection from predators, generally only moving away from cover to feed, or gain access to feeding areas. This is in marked contrast to the strategies used by the patas monkeys (long distance flight, Henty in prep) and the baboons (loud barking, Byrne, 1981), both of whom probably exploited open vegetation more intensively than the green monkeys. In addition, green monkeys may be more vulnerable to aerial predators than either of the other two species.

8.4 SIZE OF HOME-RANGE.

8.4.1 Total Range-size.

During the monthly five-day samples the monkeys used a total of 1598 quadrats, representing an area of 99.9 hectares. Figure 8.2 shows a cumulative graph of the number of new quadrats used in successive months thoughout the annual cycle of 5-day samples. By the end of the year's study, the cumulative area used by the monkeys was still increasing, but more and more slowly, indicating that not all of the quadrats in their home-range had been recorded. Indeed, the total number of quadrats visited at any time during 15 months of observation was 2854. Despite this big discrepancy, between known and sampled home-range, the decreasing slope in Figure 8.2 indicates that most of the quadrats that were used with any regularity were recorded during 5-day samples, and many of the additional 1256 quadrats were visited extremely rarely. These quadrats consisted mainly of treeless plateau (see below, Table 8.6), on which the green monkeys foraged only at special times, such as when searching for baked or roasted invertebrates after the annual grass fires (Plate 8.1), or chasing insects brought in with the first rains and new growth of plateau grass in the wet season (Plate 8.2). When these areas are included, the total known home-range was 178.4 hectares (Figure 8.3).

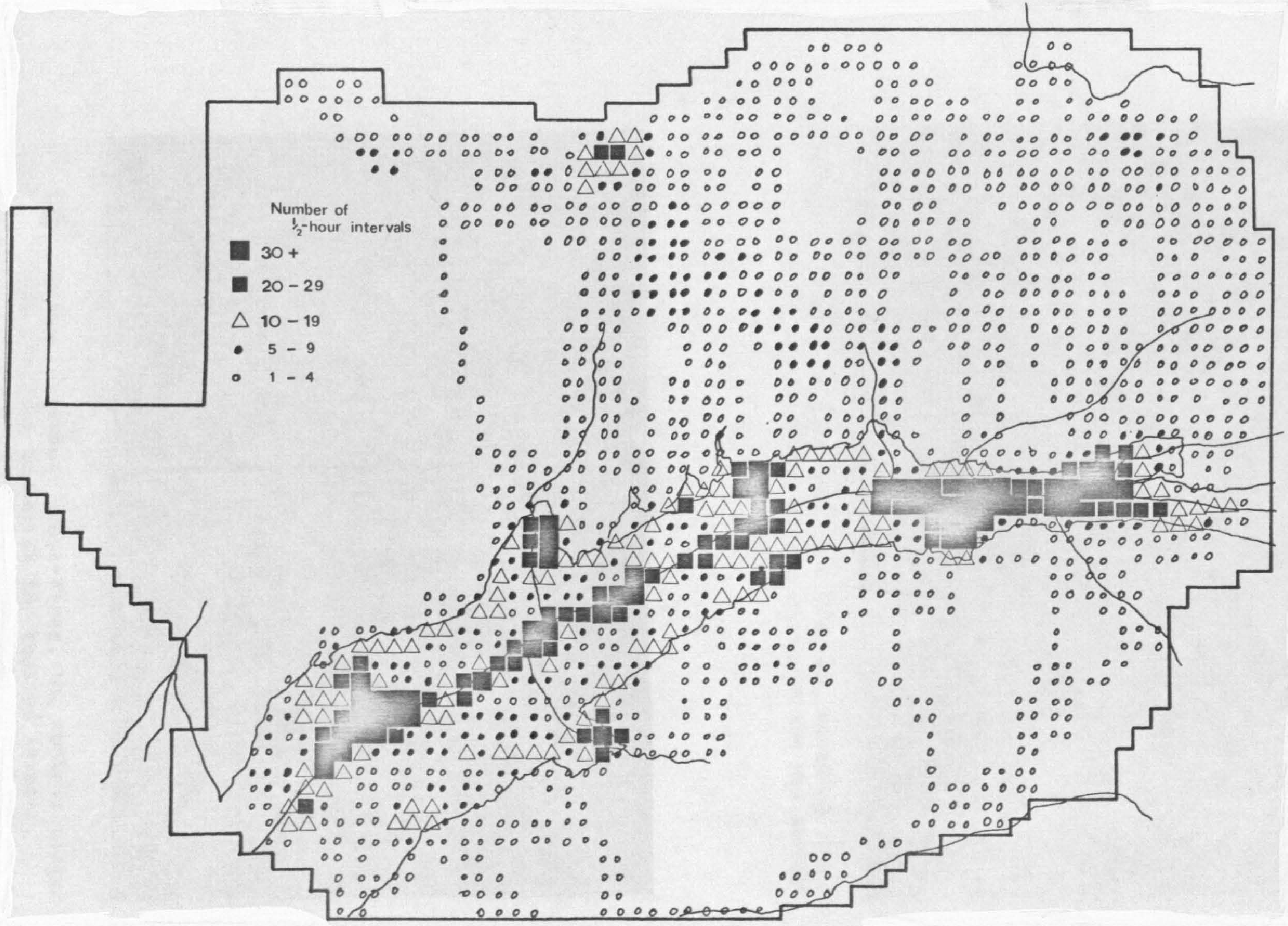

Figure 8.3. The complete known home-range of Camp Group, showing also the differential use of this area during 5-day samples, as measured by the number of ½-hour intervals that monkeys occupied each quadrat.

Plate 8.1. Monkeys on the edge of a plateau, scraping insects from the softened earth, early in the wet season.

Plate 8.2. After the annual grass-fires, the monkeys ranged onto the plateaux to search for roasted insects.

8.4.2 Monthly Range-size.

The green monkeys used different parts and varying amounts of their annual home-range at different times of the year (Figure 8.4). A monthly ´home-range´ is defined as the area used during a 5-day sample. As with day-range lengths, differences in monthly range-sizes were marked, varying from 215 quadrats in December to 640 in January. Monthly day-range lengths and range-sizes were highly correlated ($r = .94$, $p < .001$). This correlation implies that the further the monkeys travelled in a day, the more ´new´ quadrats were visited. Inspection of the daily ranging maps showed that re-use of quadrats on the same day was negligable, and was generally restricted to crossing an earlier foraging path, or returning to the same sleeping site. To examine re-use of quadrats on consecutive days, monthly graphs were plotted showing, for each successive day in a 5-day sample, the proportion of the day´s quadrats that were ´new´, i.e. visited for the first time during that 5-day sample (Figure 8.5). Evidently, the size of quadrat will affect the results: larger quadrats would lose detail and might reduce these percentages.

In all months, the decline in the proportion of ´new´ quadrats being used was relatively slow, indicating that the monkeys were selecting new areas in which to forage on consecutive days. Even on the fifth day, in all but two months (July and September), over 50% of the quadrats used had not been visited during the previous four days. It seems that the green monkeys covered their monthly range (that is, the

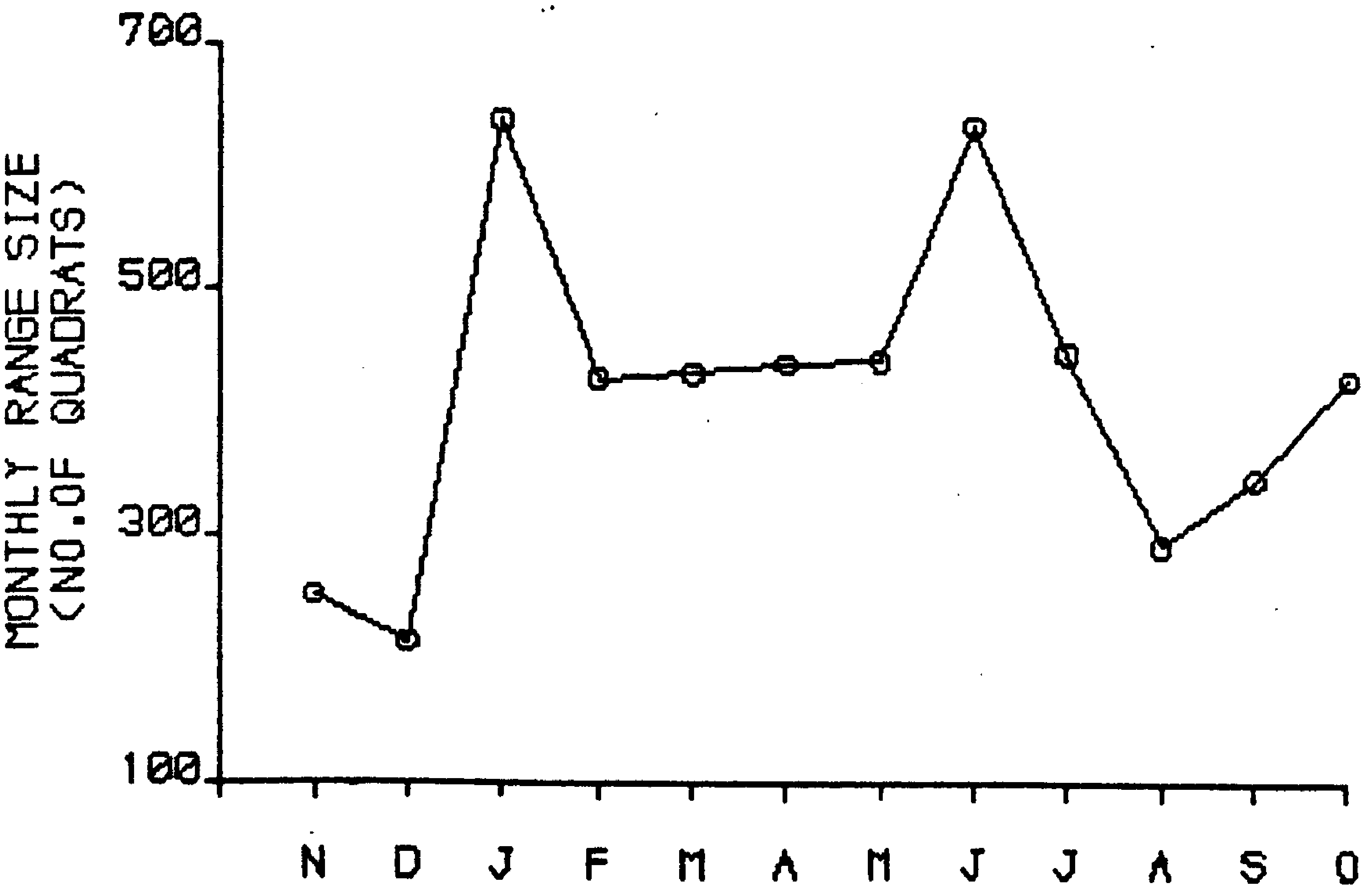

Figure 8.4. Monthly variation in the number of quadrats visited.

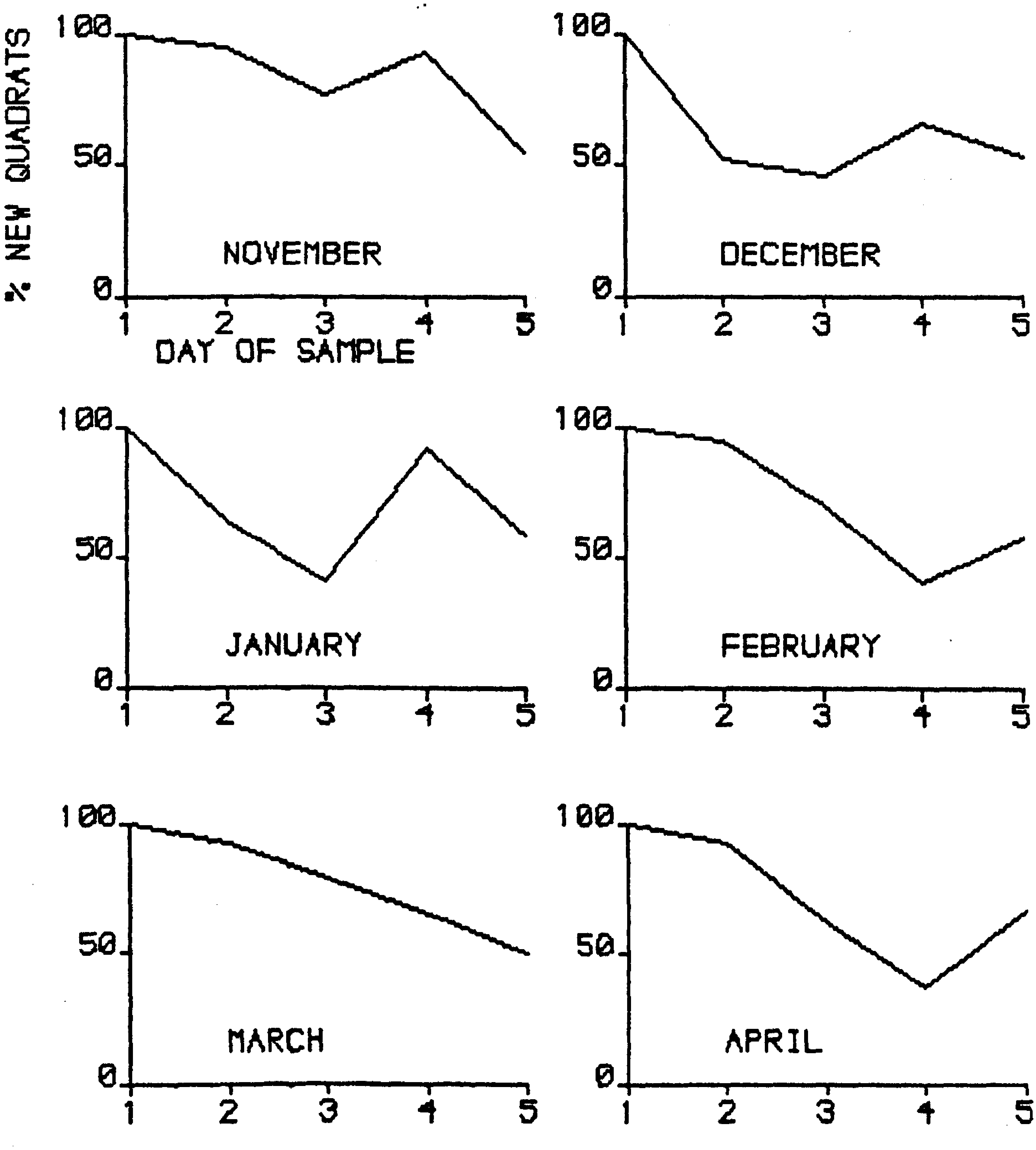

Figure 8.5. Proportions of 'new' quadrats entered during successive days of 5-day samples. (see text).

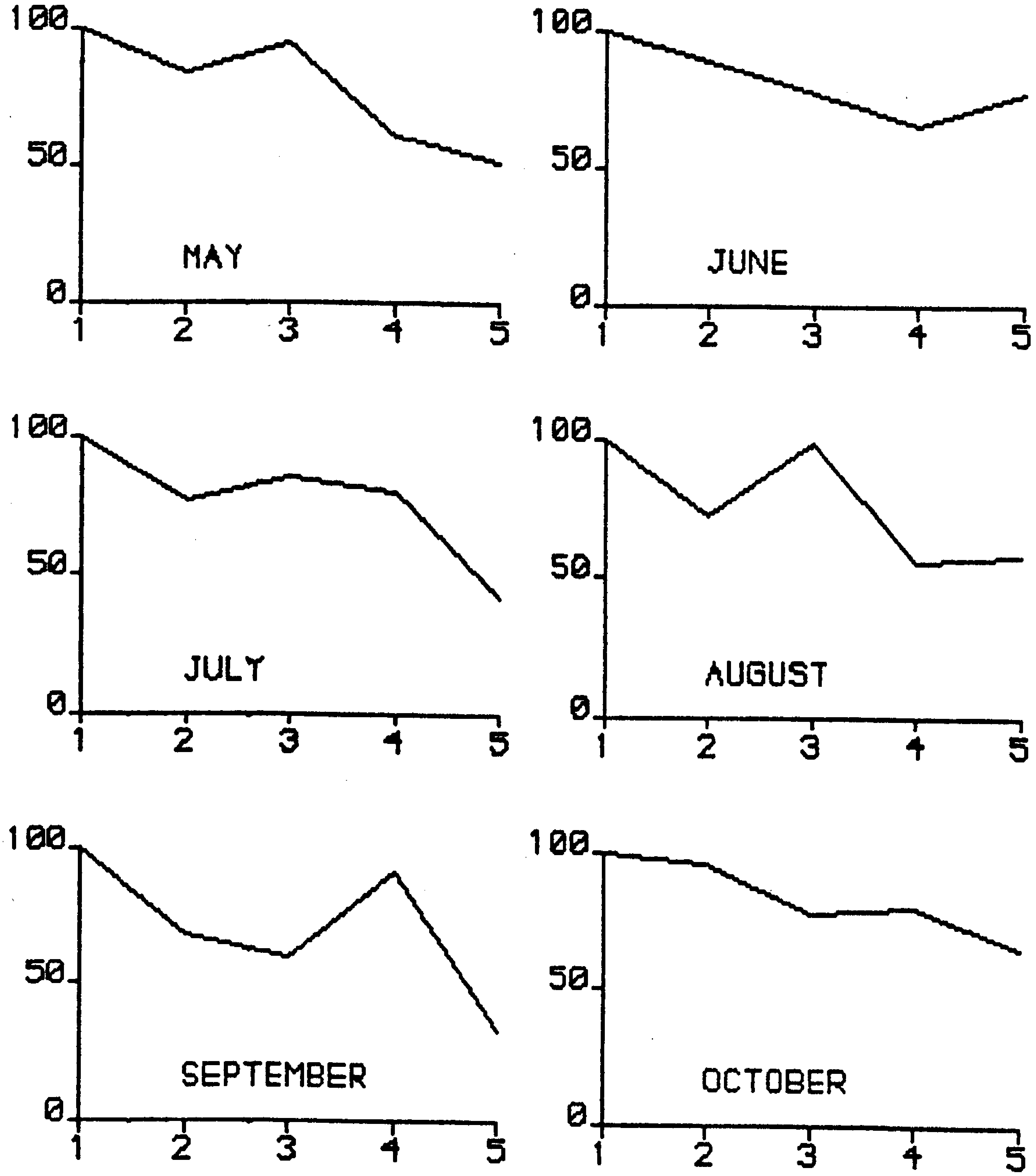

Figure 8.5. (cont.)

areas suitable for exploitation in any month, containing food, unripe food being monitored, water, sleeping sites, territorial boundaries - see below) in cycles of five or more days. Figure 8.6 provides a few examples of travel routes during 5-day samples. Areas that were re-used during five consecutive days generally contained good food resources, sleeping trees, or in the late dry season, water - three variables that were important in determining patterns of range-use (see below).

Clutton-Brock (1975b) showed that for Colobus badius at Gombe, a 5-day sample of ranging would have provided a poor indication of a troop's monthly use of their range. However, the high correlations found between the green monkeys' range-use and other environmental and social variables (this chapter) show that a 5-day sample is sufficient to ascertain certain principles underlying patterns of range-use, although five days will obviously not give complete coverage of each month's ranging.

These data on the low re-use of quadrats on consecutive days explain the high correlation between day-range length and monthly range-size: the further the group travelled (into 'new' quadrats) each day, the greater the 5-day total of quadrats visited. An explanation of monthly differences in day-range length (and thus range-size) is given in chapter 10. To anticipate, longer day-range lengths were associated with increased food-availability, since under these food conditions it was an optimal strategy to range further and feed more, despite increased ranging costs. Given also the heterogeneous

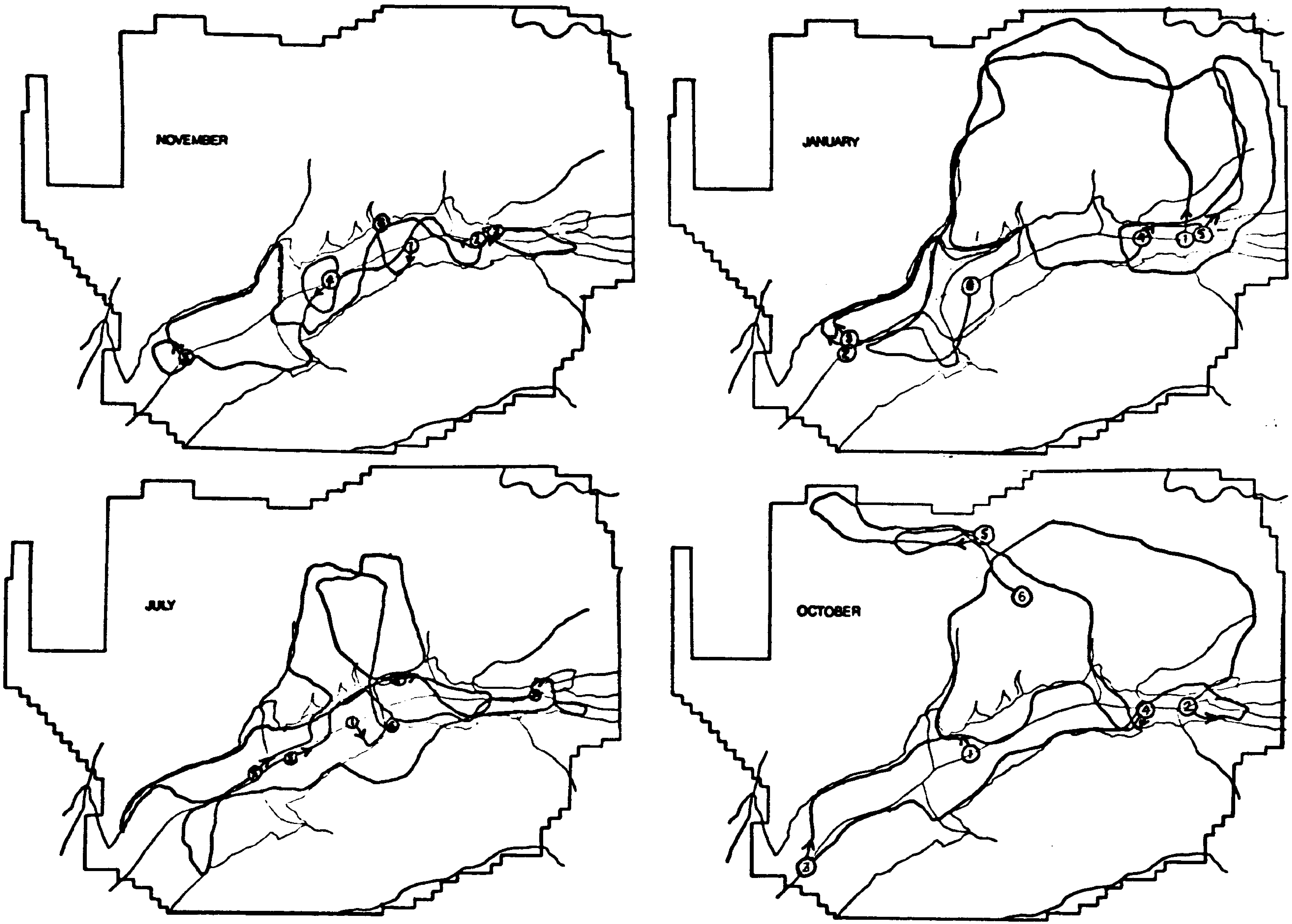

Figure 8.6. A sample of travel routes used during 5-day samples.

nature of the vegetation (clumped sources of fruit and flowers distributed widely throughout the habitat), increased time spent feeding resulted in a very large annual home-range, given other limitations on the population density of the green monkeys around Mt.Assirik (chapter 5).

8.5 GROUP SPREAD.

The monkeys travelled throughout their range as a group (with the rare exception of migrating adult males). Seldom did the group become split and rejoin later in the day, and only once after a split did the two subgroups sleep at different sites. However, even though normally a cohesive social unit, the spread of the group as they foraged or rested varied considerably. Several hypotheses concerning this variation will be tested:

i) If animals live in groups to reduce individual risk of being preyed upon (Hamilton, 1971), one might expect a more compact group in more open vegetation, where risks are possibly greater (especially from aerial predation), and protective cover is less available.

ii) Particular activities may affect the spread of the group: for example, resting or socializing monkeys may be more cohesively grouped than when feeding; feeding monkeys may disperse to reduce food competition, or to improve their food-searching success.

iii) Given that the monkeys spread out to feed, one might expect greater dispersion to be associated with higher food-availability, since the amount of food has been shown to determine time spent feeding (chapter 10).

8.5.1 Methods.

The mean group spread for each month was calculated from ranging maps as follows: the whole group was rarely visible at one time, but even so I moved about enough to be able to note fairly accurately where all the monkeys were at the end of each 1/2 hour interval. Thus, the area encircled on the range maps (see chapter 3) represented the group's spread and was unlikely to be biased by differential visibility across habitat-types. The spread of the group nearly always covered several quadrats, each of which would therefore have a 1/2 hour time-entry. Thus the total number of time-entries for all quadrats used exceeds the actual number of time-intervals that passed. Dividing each month's total number of time-entries for all quadrats used, by the number of 1/2 hour intervals in the 5-day sample, gives the mean number of quadrats over which the group was spread during that month. This will be overestimated, since not all of a quadrat need be used for that quadrat to be scored. However, this bias will be consistent for all months.

8.5.2 Results.

Mean group spread ranged from 3.9 quadrats in November (less than 2500 m2) to 8.6 quadrats in January (less than 5400 m2)(Figure 8.7). There was no correlation between group spread and the proportion of time spent in open habitat - defined as plateau and open woodland (r= .25, n.s.), but there

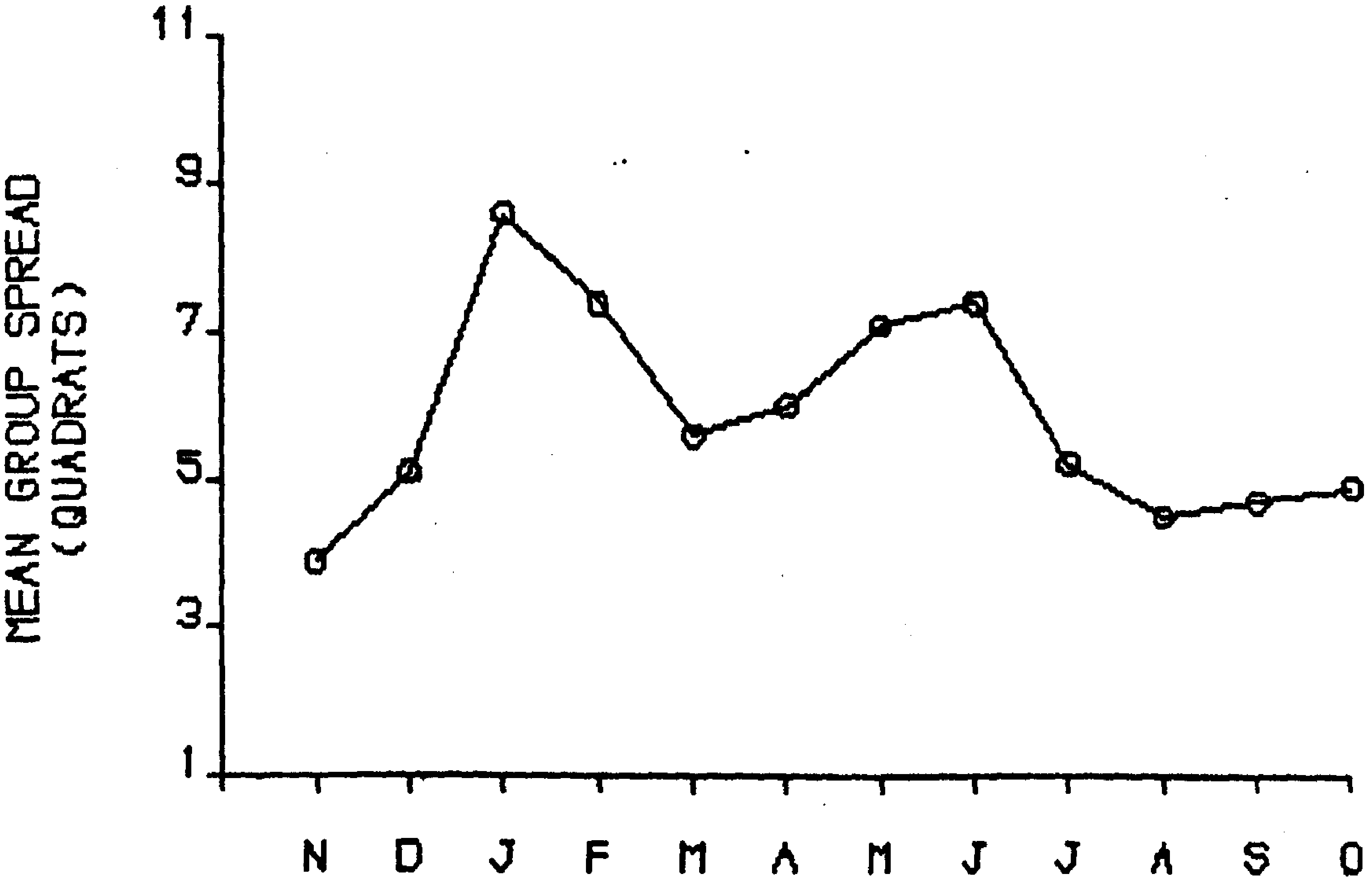

Figure 8.7. The mean number of quadrats occupied by the group at any one time, during each month's 5-day sample.

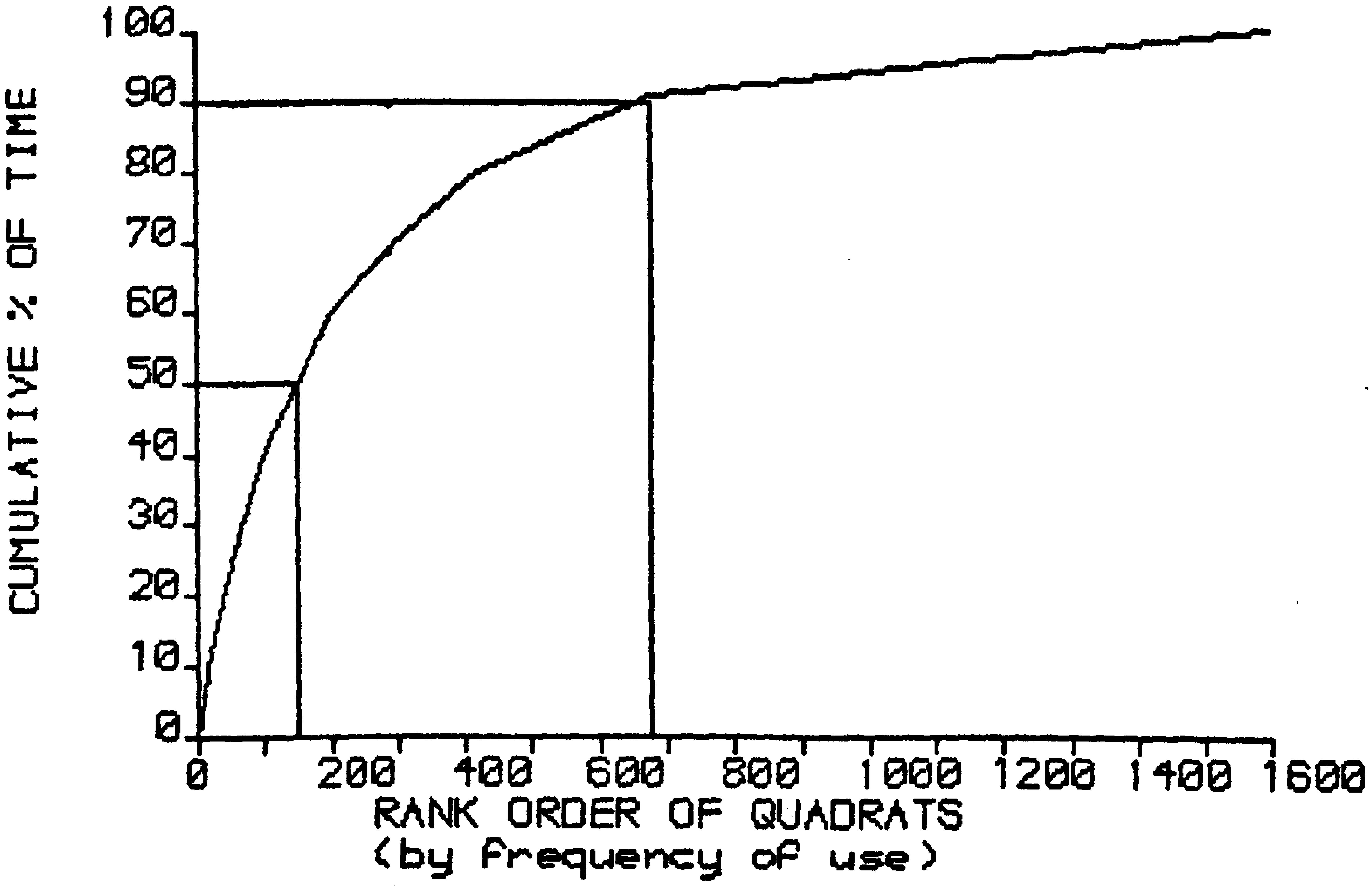

Figure 8.8. The cumulative proportion of time spent in quadrats ranked from most to least frequently used over the year.

was a positive correlation between group spread and the proportion of the monthly range made up by open vegetation (r= .62, p<.05): the more open habitat that was visited during a month's ranging, the bigger was the group spread. This contradicts the first hypothesis, that the group would be compact where there was less protective cover from predators. It may have been that the green monkeys moved into open woodland specifically to forage, and thus spread out more, consistent with the second hypothesis: indeed, there was the predicted trend in correlation between group spread and the proportion of time spent feeding, but this just fails to reach significance (r= .48, p=.056). Non-significant but predicted trends were also seen in the relationship between group spread and proportions of time spent resting (r= -.29, n.s.) and socializing (r= -.36, n.s.): these trends were consistent with the hypothesis that monkeys were more compact when resting and socializing, and more spread out when feeding. Possibly correlations are weak because these data are not amenable to examining the group spread directly associated with each activity.

Finally, group spread and food-availability were correlated (r= .76, p<.01). If the monkeys had to spread out when feeding, to reduce food competition and/or improve their foraging success, it was predictable that the amount of food available would affect group spread, since the former also determined the amount of time spent feeding (chapter 10). Since food availability also predicted day-range length and monthly range-size (this chapter and chapter 10), the positive association between group spread and day-range length ($r= .71$, $p<01$) and range-size ($r= .82$, $p<.001$) were also expected.

In conclusion, if indeed there was an increased risk of predation in open vegetation, the monkeys did not respond to this by moving in a more compact group. Since in general they selected denser, closed vegetation in preference to open vegetation (this chapter, below), it seems likely that they moved into open habitat mainly to feed, and thus would be more alert to danger than when resting or socializing. Presumably the benefits, by spreading out, of reduced feeding competition and improved chances of finding food, outweighed any increased risk of predation.

8.6 RANGE-USE.

The patterns of range-use by the green monkeys were variable throughout the year. Differential use of the annual home-range, in both space and time, has been shown amongst primates to be related to environmental factors such as the abundance and distribution of resources (Altmann and Altmann, 1970; Chivers, 1977; Clutton-Brock, 1975b; Gautier-Hion _et al._, 1981; Richard, 1977), disease control (Freeland, 1979), habitat structure (Gautier-Hion _et al._, 1981), and predators (Altmann and Altmann, 1970), and to social factors such as mates and conspecific competitors (Rasmussen, 1979; Struhsaker, 1974).

In this section, I shall test a series of hypotheses derived from previous studies, concerning the main influences on patterns of range-use by the green monkeys: to what extent were monthly variations in ranging patterns determined by the availability and distribution of food, water, habitat-type, sleeping sites, and by intergroup relations?

8.6.1 Influence Of The Availability And Distribution Of Food.

Intuitively, the availability and distribution of food might be expected to exert a strong influence on patterns of range-use. Several studies have shown some measures of ranging to be correlated with food-availability, such that reductions in movement and activity were associated with a reduction in available food (Chivers, 1977; Clutton-Brock, 1975b; Raemaekers, 1980; Richard, 1977). Studies of baboons show an opposite trend, where more time feeding and travelling were associated with a reduction in food-availability (Altmann and Altmann, 1970; Dunbar, 1977; Kummer, 1968; Oliver and Lee, 1978; Sharman, 1981). Still other studies showed no apparent relationship between patterns of range-use and food-availability (Oates, 1977; Struhsaker, 1974; Waser, 1977). In some of these studies availability could not be measured in detail, so that conclusions are tenuous.

8.6.1.1 Diversity Of Range-use. -

Over the whole year, the distribution of the green monkeys' time amongst the quadrats in their range was very uneven: 50% of their time was spent in only 9% (148) of the 1598 sampled home-range quadrats, and the least visited 58% (922 of 1598) of quadrats accounted for only 10% of their time (Figure 8.8).

One way of quantifying patterns of ranging is to measure the diversity of range-use each month. The Shannon and Weaver formula ($H= -\sum pi \log pi$; Pielou, 1966) was used to calculate indices of diversity of quadrat use each month (Table 8.1). For a month when the monkeys' time is distributed evenly amongst the quadrats they use, the index of diversity (H) will be high; whereas if most of the time is concentrated in relatively few of the quadrats visited, H will be low. I used Shannon's formula to be consistent with other authors who use this index (e.g.Oates, 1977; Raemaekers, 1980; Struhsaker, 1974, 1975). However, as Rasmussen (1980) points out, this index is sensitive to the number of quadrats on which it is calculated. Thus, as expected, the monthly indices correlate highly with day-range length ($r= .82$, $p<.001$) and monthly range-size ($r= .87$, $p<.001$). The influence of the number of quadrats can be controlled by dividing the value of H by its maximum value for a given number of quadrats, H(max), where $H(max)= \log N$, and N= number of quadrats (Rasmussen, 1980) (Table 8.1).

These corrected indices do not correlate with day-range length ($r=.14$, n.s.) or monthly range-size ($r= .21$, n.s.).

Several hypotheses regarding the likely determinants of variation in ranging diversity have been tested for other primates (Clutton-Brock, 1975b; Oates, 1977; Struhsaker, 1974). I tested ranging diversity against the same variables, but no relationships were found: between H/H(max) and rainfall (wet vs. dry season, Mann-Whitney U=12, n.s.); overall monthly availability of important fruits and flowers (r= .12, n.s.); monthly diversity of time spent on the top-ranking 5 food items (r= -.40, n.s.); diversity of time spent on different food parts (r= .09, n.s.); and number of intergroup encounters during the monthly 5-day sample (r= -.40, n.s.). Similar correlations were calculated between these variables and the uncorrected values of H, for consistency with other authors, and again no relationships were found, except between H and monthly food-availability (r= .65, p<.05) - this relationship is spurious since H is heavily influenced by the number of quadrats used, and monthly range-size (i.e. the number of quadrats used) was determined by food-availability (see chapter 10).

Table 8.1. Indices of diversity of range-use (see text).

	H	H(max)	H/H(max)
Nov:	5.318	5.513	.965
Dec:	4.915	5.288	.929
Jan:	5.988	6.229	.961
Feb:	5.530	5.864	.943
Mar:	5.371	5.659	.949
Apr:	5.496	5.844	.941
May:	5.308	5.872	.904
Jun:	5.784	6.122	.945
Jul:	5.761	5.958	.967
Aug:	5.121	5.549	.923
Sep:	5.457	5.743	.950
Oct:	5.626	5.829	.965

Both Struhsaker (1974) and Oates (1977) found no relationship between ranging diversity (H) and rainfall, availability of major food species, or various measures of dietary diversity. One weakness with an index of diversity is that it measures differential distribution of time over various quadrats, but it fails to account for the location of these quadrats. Thus Shannon's equation is an insufficient index of patterns of range-use, and may not be expected to correlate well with environmental variables or patterns in the diet.

8.6.1.2 Food And Range-use: A Correlational Approach. -

A direct correlational approach may prove more fruitful in explaining variation in range-use in terms of food-availability and distribution. Clutton-Brock (1975b) made no use of an index of diversity of range-use; he used this second approach, and found that quadrat-use was correlated with the frequency of the 3 top-ranking food species in those quadrats, but as more species were included in the analysis, the coefficient dropped. My data on various measures of the availability and distribution of food throughout the green monkeys' range, and their temporal and spatial use of the range, are particularly suited to a correlational analysis.

This analysis is restricted to fruiting and flowering species, the class of foods most selected by the monkeys, and thus most likely to reveal influences on patterns of range-use. Hereafter I shall refer to a quadrat that contains a particular food species as a ´species-quadrat´. Measures of food-availability are:

- N, the number of species-quadrats.
- Av, the area of fruiting or flowering canopy available per species-quadrat, accounting for phenological variation.

The measure of food distribution is:

- CI, the index of clumpedness, measuring the average number of the 8 quadrats surrounding a species-quadrat that also contain that particular species. (This index measures both local clumping and the wider distribution characteristics of each species, see chapter 3).

These are three independent variables. The dependent variables used in this analysis are:

- %time, the proportion of time spent in species-quadrats.
- %f, the proportion of feeding time spent on a species in the monthly diet.

- N(used), the number of species-quadrats that were visited during the monthly 5-day sample of ranging.

- %(used), the proportion of species-quadrats that were visited (=N(used)/N x 100).

- HR, the monthly range-size (number of quadrats).

Each of 41 food-species has a value on all of these variables. In a regression analysis, I sought to answer the following questions:

1. Did the availability and distribution of food influence patterns of range-use in space and time?

Multiple regression coefficients show that the three measures of food-availability and distribution (N, Av, CI) together account for a very large proportion of the variance in the three measures of patterns of range-use:

on N(used) R= .87, r2= 76%
on %(used) R= .73, r2= 53%
on %time R= .82, r2= 67%

The overall regression measures can be broken down to ask:

2a. How did food-availability influence range-use in space?

Of the independent variables, N accounts for 68% of the variance in N(used): r= .85, $p<.001$. The influence of N on N(used) was irrespective of Av - controlling for Av in a partial regression does not alter the coefficient. Also, N strongly predicts the proportion of the home-range that is made up by N(used): $r = .94$, $p < .001$. Thus, the more quadrats containing fruit or flowers there were during any month, the more of these quadrats were visited, regardless of how much food was in them, and the higher the proportion of the monthly home-range these visited quadrats made up.

Although this would not be the prediction if, for example, the monkeys selected a standard number of species quadrats each month, it may be argued that the above relationship would be predicted even if the monkeys sampled their annual range randomly each month, since the probability of visiting one of the more abundant species-quadrats is higher than that of visiting a rare species-quadrat. However, this would be true only if an equal number of quadrats from the annual range were sampled each month, but this was not the case: monthly range-size varied, and is shown in chapter 10 to have been determined by overall food-availability. Thus the case for random use of the range must be rejected. The relationship between N and N(used) predicts more extensive range-use with more commonly occurring species.

The second finding as regards the influence of food-availability on range-use (in space) concerns Av. Av accounts for 28% of the variance in %(used): $r = .53$, $p < .001$. With reference to the previous finding, the more species-quadrats there were available during a 5-day sample, the more were visited, regardless of the amount of food in them; and here, the more food that was in these quadrats, the higher was the proportion of N(used) to N. Several concrete examples may help to clarify this (see Table 8.2).

In other words, with more N, there were more N(used), but with higher Av, there were proportionally still more N(used). This is consistent with the findings that with increased overall food-availability, the proportion of time spent feeding and travel distance both increased (see chapter 10) - a correlation which is also seen if simply Av, the amount of food per individual species-quadrat, is considered rather than overall availability (i.e. the summed availability of several species for one month): the correlation between Av and %f is r= .38, p<.01.

2b. How did food-availability influence range-use in time?

N and %time are highly correlated (r= .68, p<.001): perhaps not surprisingly, the more species-quadrats there were (and thus the more that were visited), the more of each month's time was accounted for by these quadrats. Concerning Av, the simple regression of %time on Av at first shows no relationship (r= .09, n.s.), but partial regression reveals that the relationship between N and %time (see above) is

Table 8.2. Examples to illustrate the relationship between range-use and food-availability (see text).

Species	Month	N	N(used)	%(used)	Av
		-quadrats-			-m2/qu-
Pterocarpus erinaceus	Jan	995	399	40	44
" "	Dec	995	101	10	1
Lannea acida	Mar	304	82	27	13
" "	Apr	304	71	23	4
Spondias mombin	Sep	50	29	58	56
Ficus umbellata	Apr	46	41	89	67
" "	Jun	46	33	72	63

obscuring the correlation between Av and %time: controlling for N, the coefficient becomes $r= .37$ ($p<.01$). In other words, although higher N accounted for more time, the proportion of time spent per quadrat was reduced (correlation of N with %time per species quadrat: $r= -.32$, $p<.05$), but if this effect is controlled, it is revealed that the monkeys did spend more time in quadrats containing more food.

3a. How did the distribution of food influence patterns of range-use in space?

CI accounts for 61% of the variance in N(used) ($r= .78$, $p<.001$): species-quadrats that were more evenly distributed were visited more than those species occurring in widely dispersed quadrats.

3b. How did the distribution of food influence patterns of range-use in time?

CI accounts for 66% of variation in %time ($r= .81$, $p<.001$): similar to the previous finding, more time was spent in species-quadrats that were evenly distributed than those that were dispersed, or clumped. With reference to both of these findings, CI and N are in fact related in nature ($r=.79$, $p<.001$): i.e. the more species-quadrats there are, the more likely they are to be neighbouring quadrats, and thus more evenly distributed. This effect should be controlled before making conclusions about range-use and the distribution characteristics of food. Partialling out N reduces, but does not eliminate, the above correlations, which remain statistically significant (between CI and N(used), $r= .33$,

$p<.05$; between CI and %time, $r= .61$, $p<.001$).

This fact that, after controlling for the effects of N, the higher of these two coefficients is between CI and %time, suggests the following conclusions:

a) that the degree of clumping in the distribution of food species accounted mostly for the distribution of time about the monthly range (CI: %time, controlling for N, $r=.61$, $r2= 37\%$ of the variance), whereas

b) the spatial distribution of quadrats used in the monthly range was mostly accounted for by the location of species which occurred in larger numbers of quadrats (N: N(used), $r= .85$, $r2= 72\%$ of the variance), and to a much lesser extent by the clumpedness of the species concerned (CI: N(used), controlling for N, $r= .33$, $r2= 11\%$ of variance).

In conclusion, the availability and distribution of individual species of fruit and flowers did strongly influence differential patterns of range-use, in both space and time. A summary of the major regression coefficients is given in Table 8.3. Chapter 10 shows how each month's combined availability of all foods determined monthly range-size.

8.6.2 Influence Of Availability And Distribution Of Water.

Although drinking is rare in some, notably forest, primates (e.g. Rudran, 1978; Struhsaker, 1975), in others, water sources are commonly reported to influence ranging patterns (Altmann and Altmann, 1970; Hamilton _et al._, 1976; Lindburg, 1977; Struhsaker, 1967e; Struhsaker and Gartlan, 1970;

Wrangham, 1981).

The green monkeys were rarely seen to drink during the wet season, but probably drank daily during the dry season: drinking was not observed during 25 all-day observations in the wet season, and was recorded on 29 out of 35 days during the dry season. Table 8.4 shows monthly patterns of drinking, and Figure 8.9 shows the diurnal pattern.

The monkeys started drinking on a regular basis after the annual fires, in January when temperatures were high and humidities low (see chapter 2). The diurnal pattern shows that drinking occured predominantly during the afternoon. This period corresponds with other findings for the later dry season, when temperatures exerted an increasingly strong influence on diurnal activity rhythms (chapter 7).

Table 8.3. Summary of the main regression coefficients in the analysis of the influence of availability and distribution of food on patterns of range-use.

Overall: multiple regression of N, Av, and CI
(independent variables) on N(used): R= .87, r2=76%
on %(used): R= .73, r2=53%
on %time : R= .82, r2=82%

Availability: N / N(used): r= .85, p<.001.
Av / %(used): r= .53, p<.001.
N / %time : r= .68, p<.001.

Distribution: CI / N(used): r= .78, p<.001.
CI / %time : r= .81. p<.001.

Table 8.4. Number of days that drinking was observed during 5-day samples.

	Dry season							Wet season				
Month:	N	D	J	F	M	A	M	J	J	A	S	O
No. of days:	3	3	4	5	4	5	5	0	0	0	0	0

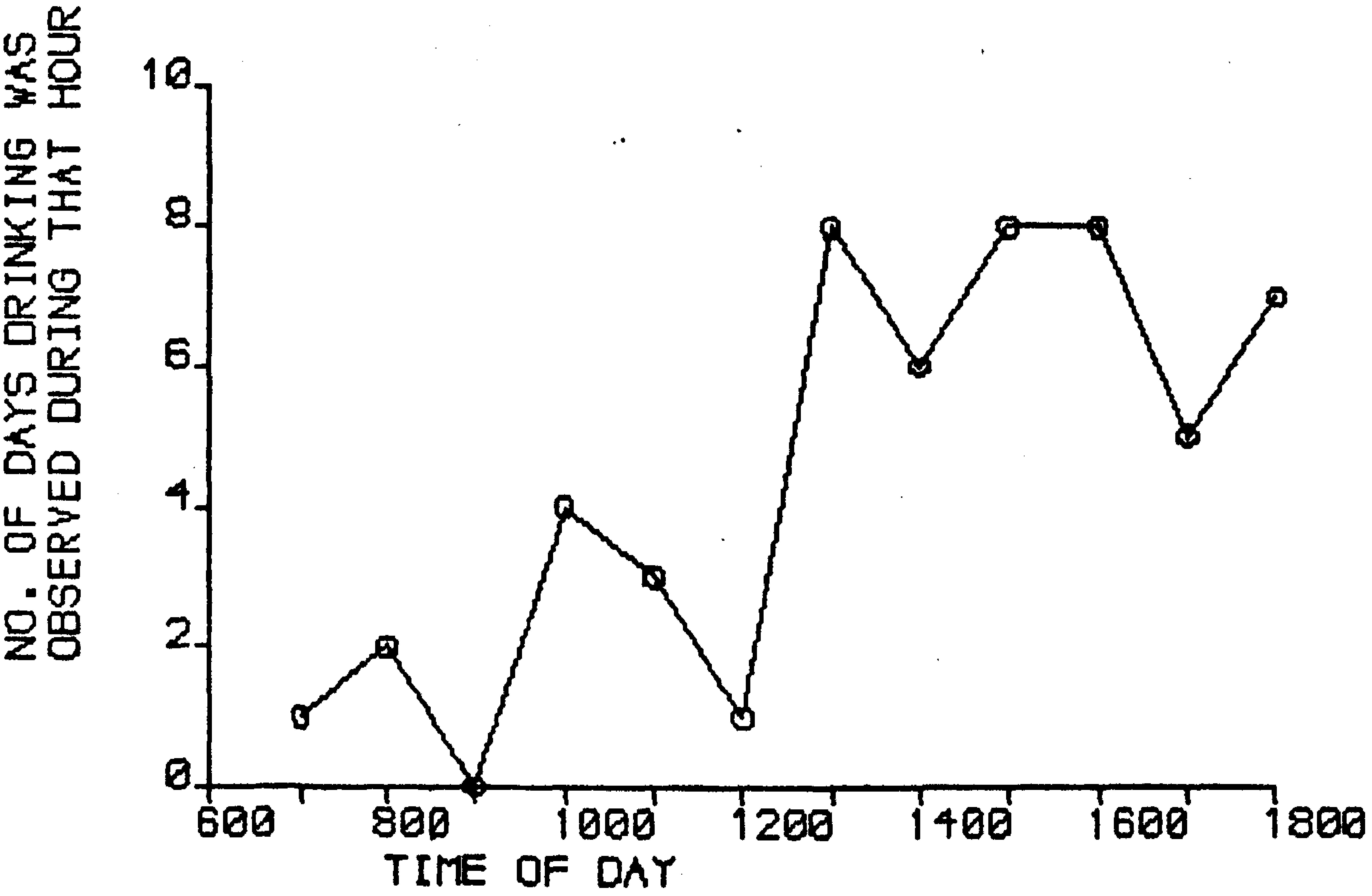

Figure 8.9. The diurnal rhythm of drinking, measured by the number of days during 5-day samples that drinking was observed, for each hour of the day.

Water demands were probably highest during February, when there was little fruit in the diet, and the dessicating Harmattan wind blew persistently. During this period the monkeys drank from the dwindling water sources in long bouts (up to 30 secs continuous drinking). Later in the season, when water was in even shorter supply, but the humidity was rising and more fruit was available, the monkeys still drank regularly, but in shorter bouts (5-10 secs). They usually drank in turn, rarely more than four drinking simultaneously, while others waited or rested nearby. Because of the importance of water to the monkeys, and its restricted distribution in the dry season, it seems likely that water exerted an important influence on ranging.

8.6.2.1 Methods. -

To examine the extent of influence of the distribution and availability of water on ranging patterns, I mapped the location of all quadrats containing water each month during the dry season (see Figure 8.10). Subsequently I extracted, from ranging maps, data on the amount of time (number of 1/2 hour intervals) that the monkeys spent in these quadrats - hereafter named water-quadrats. Since the number of water-quadrats declined through the dry season, these data were also expressed as the amount of time spent per water-quadrat (Table 8.5).

Time spent in a water-quadrat does not imply that drinking occurred, just as time spent in a quadrat containing a particular food species does not mean that that food was

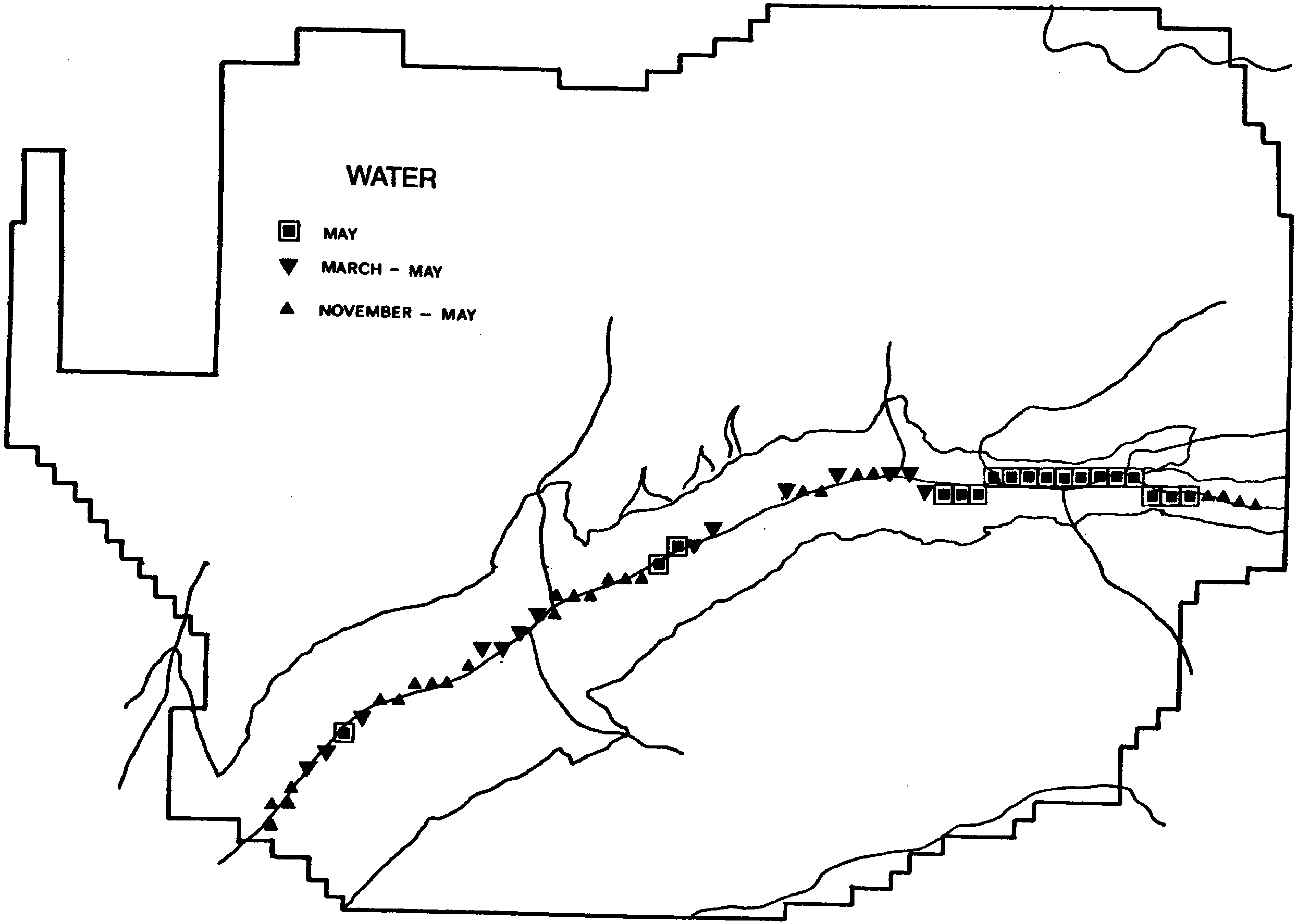

Figure 8.10. The distribution of quadrats containing water in successive months of the dry season.

necessarily eaten. Whilst in these quadrats, although it is likely that in general the monkeys would be eating or drinking the relevant resource, they may also be monitoring phenological changes, assessing resource availability, or defending resources from neighbouring groups. They may even be there for reasons unrelated to food or water, such as resting in suitable vegetation, or sleeping. However, for both food- and water-quadrats, when comparisons between quadrats or between months are made, the above measure does indicate the degree to which the monkeys allotted their time to particular quadrats, and thus also the degree to which their ranging was constrained by the location of these quadrats.

8.6.2.2 Results. -

The green monkeys showed a steady increase in time spent per water-quadrat throughout the later dry season, from January when 57 water-quadrats were available, to May when only 18 quadrats contained water (Table 8.5). This indicates more and more concentration on a decreasing number of water-quadrats,

Table 8.5. Use of "water-quadrats" in the later dry season (Jan-May).

	Total no. of 1/2-hours spent in water-qds.	% total time	N water-quadrats	1/2-hours per water-quadrat
Jan:	102	10	57	1.8
Feb:	154	17	57	2.7
Mar:	108	16	32	3.4
Apr:	121	16	32	3.8
May:	99	11	18	5.5

rather than simply a case of spending more time at water as the dry season pregressed. As mentioned above, the weather and diet in February probably left the monkeys more dehydrated than during other months, while May probably made least demands because of the rising humidity and high fruit content of the diet: this impression is supported by data for proportions of total time spent in water-quadrats (17% of time in February, as opposed to only 11% in May).

In conclusion, the location of water-quadrats did exert an increasingly strong influence on ranging patterns in the dry season, but no influence in the wet season. Further, this influence would not be restricted just to the areas containing water, since the location of water would also constrain distances and travel routes through the rest of the range.

The influence of water was predictable enough that whenever I had to find the green monkeys in the dry season, I was virtually sure of success if I searched areas near water-quadrats in the early afternoon; this was in marked contrast to the wet season, when locating the group before a 5-day sample was often very difficult - in one month I searched for six days without success.

8.6.3 Influence Of Habitat On Patterns Of Range-use.

While it may be difficult to separate habitat-type from food- or water-availability as causal influences on ranging behaviour, it is worth investigating whether habitat-structure alone - its density, visibility, foliage cover, or canopy height - has predictable effects on patterns of range-use. Preferences for particular habitat-types may be an important element in the strategy for defense against predators: Gautier-Hion *et al.* (1981) showed that vegetation structure was the main factor determining range-use by *Cercopithecus cephus* during periods of inactivity during the day, and at night, which was interpreted as minimizing the chance of detection by predators.

8.6.3.1 Methods. -

I analysed the monkeys' monthly use of different habitat-types (in space and time) for comparison with the use expected from random choice of habitat-type (i.e according to the proportions in which each habitat occurs in the known home-range). Spatial selection ratios were calculated as the proportion of quadrats in a month's range made up by each habitat-type, divided by the proportion of the total range made up by that habitat (s.r.= %observed / %expected). Temporal selection ratios were calculated as the proportion of time spent in a habitat-type, divided by its proportional abundance in the total range.

8.6.3.2 Results. -

Spatial and temporal selection of particular habitat-types was very marked (Tables 8.6 and 8.7).

Differences in selection ratios between habitat-types were significant and consistent from month to month (Kruskal-Wallis Anova; for spatial ratios, $H = 59.97$, $df = 5$, $p < .001$; for temporal ratios, H= 56.84, df= 5, p<.001). By inspection of the data, gallery forest, closed woodland, and scrub were selected more than expected on the basis of their availability in the home-range, and plateau and bamboo were consistently selected against. Open woodland was used more closely in proportion to its abundance: i.e. it was not selected, although in absolute terms, it was the habitat visited the most. For gallery forest the monkeys showed even greater

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Table 8.6. Annual use of habitat types, in space and time, during 5-day samples.

	Space:(quadrats)			Time:(1/2-hour periods)		
Habitat	N in range	N used during sampling	%	N	% of time	Selection ratio
Gallery	185	182	98.4%	4287	49.3	7.6
Closed wood.	54	53	98.1	574	6.6	3.5
Open wood.	1022	844	82.6	3075	35.3	1.0
Bamboo	114	72	63.2	182	2.1	0.5
Scrub	24	19	79.2	226	2.6	3.3
Plateau	1455	428	29.4	356	4.1	0.1

Table 8.7. Monthly selection ratios for use of different habitat-types, in space (sp) and time (tm).

	Gallery forest		Closed wood.		Open wood.		Bamboo		Scrub		Plateau	
	sp	tm	sp	tm	sp	tm	sp	tm	sp	tm	sp	tm
Nov:	7.8	9.3	4.2	3.8	1.0	0.8	0.0	0.0	4.5	4.0	0.0	0.0
Dec:	8.0	10.3	3.2	5.5	1.0	0.6	0.0	0.0	3.5	2.4	0.0	0.0
Jan:	2.6	4.8	2.4	2.1	1.7	1.5	1.9	1.7	2.5	2.8	0.2	0.1
Feb:	5.0	7.9	2.6	2.0	1.5	1.0	0.4	0.2	2.9	9.5	0.1	0.0
Mar:	3.6	8.4	2.2	2.9	1.6	1.0	0.8	0.3	4.4	4.3	0.2	0.0
Apr:	4.9	10.0	2.1	2.2	1.4	0.7	0.7	0.3	1.8	1.2	0.2	0.1
May:	4.1	8.1	4.3	6.9	1.4	0.7	0.5	1.2	3.6	1.4	0.2	0.0
Jun:	3.2	7.6	2.3	3.2	1.0	0.8	0.4	0.4	2.4	3.0	0.7	0.3
Jul:	4.6	6.7	1.7	1.4	1.3	1.2	0.0	0.0	2.3	2.4	0.4	0.2
Aug:	5.8	8.4	3.4	2.5	1.1	0.8	0.0	0.0	4.3	2.8	0.2	0.2
Sep:	4.2	6.6	3.6	3.9	1.7	1.3	0.0	0.0	2.1	1.8	0.1	0.0
Oct:	3.4	4.2	2.9	6.3	1.7	1.5	1.5	1.3	4.1	1.8	0.0	0.0
mean=	4.8/7.7		2.9/3.6		1.4/1.0		0.5/0.5		3.2/3.2		0.2/0.1	

temporal than spatial selectivity (s.r.(time) vs. s.r.(space): sign test, p<.001).

It appears that the green monkeys were selecting habitats that provided dense tree cover (forest, closed woodland, scrub) and selecting against habitats with little or no cover (plateau, bamboo) - chapter 4 presents data on vegetational ground cover at grass, shrub, and tree level for each habitat-type, and evidence is also given for the close negative relationship between vegetational cover and visibility. These findings are consistent with the hypothesis that green monkeys rely on cover (to hide or escape) and reduced visibility (to reduce chances of detection) as protection from predators. Similarly, they rarely use very open vegetation, to avoid unnecessary exposure to danger. This is especially so when resting (when vigilance is probably decreased), since feeding sites must be determined more by the location of food than by specific habitat types. However, the locations of food and habitat-types are not factors that are easily separated when considering their influences on ranging patterns, and both are likely to be important in the green monkeys' decisions about where to go and how long to stay.

8.6.4 Influence Of Sleeping Sites On Patterns Of Range-use.

Since such a substantial proportion of the monkeys' time was spent sleeping, patterns of use of sleeping sites are an important aspect of range-use. The location of sleeping sites has implications for diurnal patterns of range-use, such as the consistency of use of particular sites and how these relate to daily ranging. Rasmussen (1979) found a relationship between time of departure from sleeping trees and various ranging parameters: yellow baboons (Papio cynocephalus) left sleeping trees earliest when range-use was least clumped, and when home-range (area used during specific sample periods) was largest. The influence of seasonal changes in temperature on times of arrival and departure from sleeping areas, and thus on patterns of range-use, has already been discussed in chapter 7.

8.6.4.1 Methods And Results. -

Each month's 5-day sample provided data on 6 sleeping sites, giving a total of 72 nights system atically recorded during the year. Each night the monkeys slept spread over several quadrats, so the total number of 'quadrat-nights' exceeds 72 (Figure 8.11).

120 different quadrats were used on 299 quadrat-nights. The number of quadrat-nights divided by the actual number of nights gives a mean of 4.2 quadrats used per night (299 / 72 = 4.2); this implies an average spread of the sleeping monkeys of just over 2500 m2.

90% (108 / 120) of the quadrats were in gallery forest, the remaining 10% (12 / 120) were in closed woodland. These 12 quadrats were only used once as a sleeping site, and were recorded on the last two nights of the year's study, the only two nights when the monkeys were recorded as sleeping outside the gallery forest in the valley during the entire field

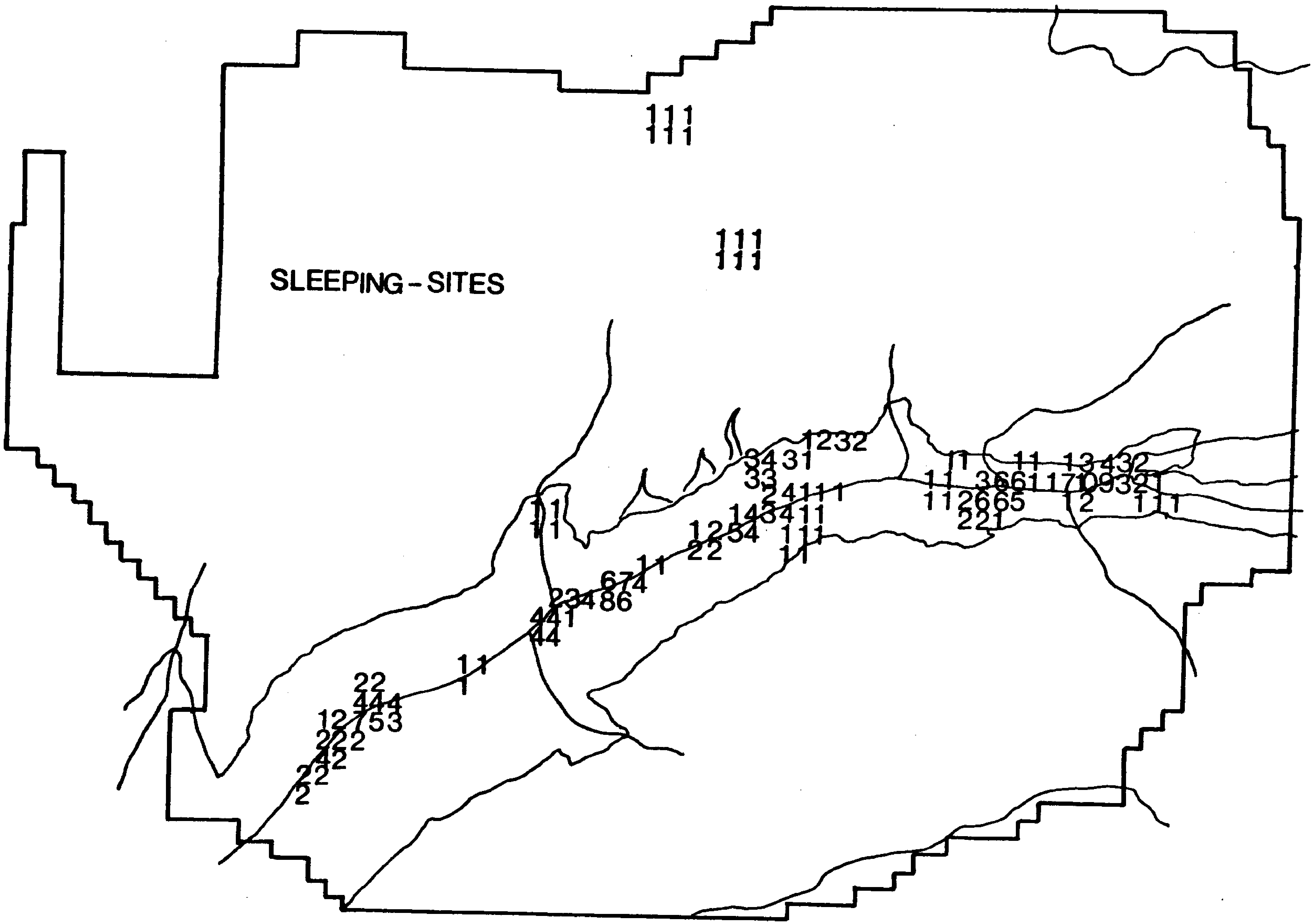

Figure 8.11. The distribution of quadrats containing sleeping-sites, and the number of nights that each was used over the year, during 5-day samples.

study. This indicates the extreme rarity of the monkeys selecting a site other than in forest; in any case, the two closed woodland sites were composed of thick vine tangles and dense tree canopy. This description fits all of the forest sites, where the monkeys selected areas of dense foliage in the high canopy, often where no single tree was distinguishable in the thick tangle of branches and lianas. This provided excellent cover from above and below, from being seen and from being approached, since any approach would be warned through the springy branches or heard in the rustle of foliage.

The trees commonly used as sleeping sites (e.g. *Erythrophloem suaveolens*, *Manilkara multinervis*, *Pseudospondias microcarpa*, *Treculia africana*) occurred mostly in gallery forest, especially where found in combination with thick vine tangles. Presumably it was for this reason that the monkeys selected gallery forest as opposed to other habitat-types, but even within the forest there was strong selectivity: 33% of all quadrat-nights were spent in only 13% of the sleeping quadrats (15 / 120), and 67% of quadrat-nights were spent in 36% of quadrats (43 / 120) (Figure 8.12). From Figure 8.11 one can see that the highly selected areas were centred on 5 main clusters of sleeping quadrats, spread out down the valley from the ´top´ to the ´bottom´ of the range. Earlier in this chapter I showed that re-use of the same quadrats over several consecutive days was generally low, and that the green monkeys covered new areas of their monthly range on successive days, possibly in cycles of 5 days or

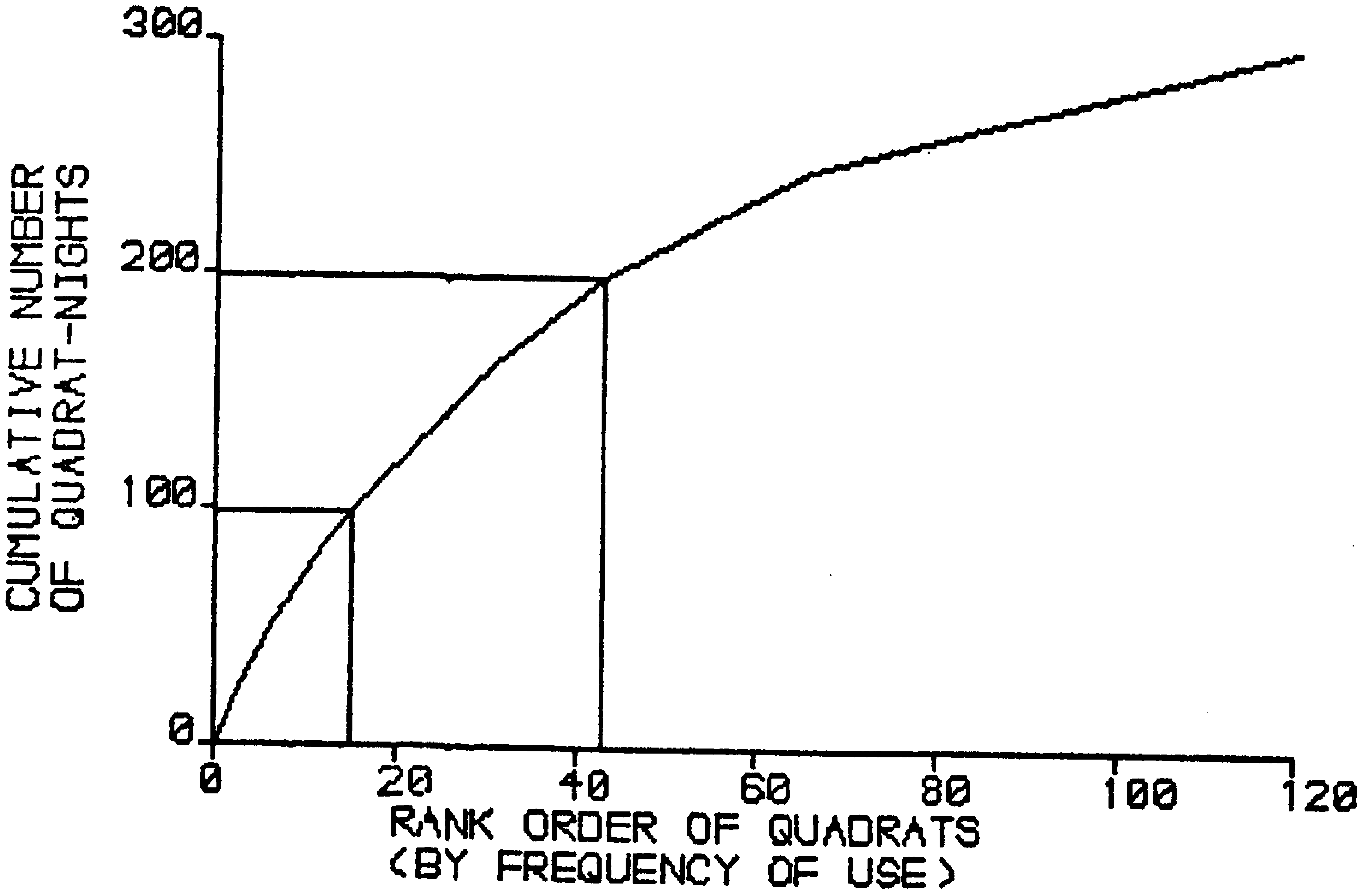

Figure 8.12. The cumulative number of quadrat-nights (see text) spent in quadrats ranked from most to least frequently used over the year.

more. Having 5 preferred sleeping areas distributed throughout the gallery forest meant that finding a particular location at night was not a large constraint on ranging patterns. However, the fact that sleeping sites were mostly restricted to the forest did provide a constraint on a broader level: a day's foraging must end in gallery forest, but was not restricted to one specific place within the forest.

8.6.5 Influences Of Intergroup Relations On Range-use.

The possibility that intergroup relationships influence patterns of range-use is intuitively appealing, and has been demostrated amoung red colobus (Colobus badius) by Struhsaker (1974): he found that the monthly index of diversity of range-use was positively correlated with the number of intergroup encounters each month. Rasmussen (1979) also found in baboons (Papio cynocephalus) that the chances of intergroup encounters were highest when range-use was most even, and when the home-range was largest. No such correlation was found with the green monkeys (H with frequency of intergroup encounters, $r= -.21$, n.s.), but as discussed earlier, the index of diversity (H) is sensitive to range-size. The corrected index (H / H(max)) does show a non-significant trend, but in the opposite direction to that found by Struhsaker and Rasmussen ($r= -.40$, $p<.2$): more intergroup encounters tended to occur when ranging was less diverse (more clumped in time).

Intergroup relations are examined more thoroughly in chapter 9, but I shall present a few relevant data here, within the context of patterns of range-use: there was a significant positive correlation between time spent in quadrats in the area of overlap between neighbouring groups (hereafter named overlap-quadrats), and frequency of intergroup encounters ($r= .61$, $p<.05$); there was also a non-significant positive correlation between the number of overlap-quadrats used and frequency of intergroup encounters ($r= .48$, $.05<p<.10$). Thus, more encounters were associated with more intensive use of overlap-quadrats.

In chapter 9 data on seasonal variation in intergroup encounters are presented, as well as evidence of the expansion and contraction of the monthly range according to the availability and distribution of specific resources and intergroup competition for them. I argue that territorial behaviour was the result of seasonally variable competition between groups in their search for rare but important resources. Given that more intensive use of overlap-quadrats was associated with defending particular resources from neighbouring groups, and that ranges expanded and contracted seasonally, the implication is that at certain times of the year, intergroup relations did influence patterns of range-use.

8.6.6 Conclusions.

In conclusion, I have demonstrated that there are several important factors that determine patterns of range-use in space and time by the green monkeys. These are the availability and distribution of important species of fruit and flowers, and water in the dry season; the location of dense vegetation (providing tree cover) on the one hand, and open vegetation (providing no cover) on the other hand; the location of gallery forest for suitable sleeping sites; and the occurrence of neighbouring groups competing for limited supplies of important resources, which demand time to monitor and defend.

8.7 COMPARATIVE DISCUSSION.

Table 5.4 in chapter 5 provides a summary of home-range-sizes and daily travel distances in several populations of C.aethiops. The home-range-size of the green monkeys at Mt.Assirik is the largest recorded for any population. However, such comparison may be misleading if the monkeys' differential use of their home ranges is not considered. For example, 51% of the home-range of the green monkeys at Mt.Assirik consisted of plateau, a habitat that was distributed amongst preferred habitats, but which was used very little (only 4% of time). Gallery forest was used far more than expected from its availability, a finding that concurs with Kavanagh's (1977) data from both of his savannah populations in Cameroon. Kavanagh also gives a proportional breakdown of the habitat for two home-ranges, shown in Table

8.8.

Without the inclusion of plateau at Mt.Assirik, the difference in home-range-size between groups is reduced, although the green monkeys still had a greater area (and proportion) of the most preferred habitat - gallery forest. Kavanagh makes a qualitative note about the effects of food, water, sleeping sites and cover availability on patterns of range-use by the tantalus monkeys, which suggests similar principles governing their range-use to those demonstrated in this chapter for the green monkeys.

Comparisons of ranging behaviour between populations is particularly difficult without precise measurement of specific parameters. Apart from Kavanagh's, no other data are available. More general population differences in home-range-size and day-range lengths were discussed more fully in chapter 5. Seasonal variation in the extent of ranging in the green monkeys is considered in chapter 10, with reference to models in optimal foraging theory.

Table 8.8. Area and proportion of range made up by each habitat-type in three groups of *C.aethiops*.

	Mt.Assirik		Kalamaloue		Buffle Noir	
	ha.	%	ha.	%	ha.	%
Gallery :	11.6	6.5	2.0	3.6	2.8	2.7
Transition:					5.3	5.1
Woodland :	68.8	38.5	29.3	52.2	90.5	88.3
Bamboo :	7.1	4.0				
Plateau :	90.9	51.0				
Floodplain:			13.5	24.1		
"Open area":			11.5	20.5		
Riverbed :					4.0	3.9
Total:	178.4 ha.		56.3 ha.		102.5 ha.	

CHAPTER 9.

TERRITORIALITY.

9.1 INTRODUCTION.

With increasing numbers of field studies of primates, there is better scope for inter- and intraspecific comparison of territorial behaviour. Territoriality can best be understood using comparative data, especially data that includes relevant ecological detail, either comparing different populations or seasonal variation within one population. In this chapter, I shall examine the dynamics of territorial behaviour in the green monkeys at Mt.Assirik, and discuss this with reference to information on other populations of *C.aethiops*.

Several possible functions of territoriality can be postulated: to reduce competition for mates, to reduce risks of being preyed upon by dispersing the population, to protect local supplies of food. In this chapter, I shall consider the last of these in detail.

There are several factors concerned with ranging behaviour, and relationships between groups, that should be made clear. While ´home range´ covers any area that animals use (monthly, seasonally, annually - see chapter 8), and various grades of ´core area´ may be defined according to different levels of intensity of use, ´territory´ as originally defined by Burt (1943) refers to any area defended from others of the same species. Another concept is that of ´exclusive territory´, which refers to the area into which others are never allowed to enter (Jolly, 1972). In studying territorial behaviour, one must bear these distinctions in mind, but equally, as I shall show with the green monkeys, they may be arbitrary distinctions in what is really a flexible system of land and resource partitioning, with a variable set of costs and benefits to defending resources.

Territorial behaviour in the green monkeys will be considered in three sections: home-range overlap, intergroup encounters, and seasonal variability in resources.

9.2 METHODS.

Ranging patterns were recorded during 5-day samples. All intergroup encounters were recorded, with those occurring during 5-day samples giving an estimate of their frequency. At each encounter, as full a description as possible was made of the monkeys' behaviour and the prevailing ecological circumstances. All occurrences of the noisy displays of adult males, and the duration of each encounter could be scored reliably, as could the detailed mapping of locations and the group's movements. Durations of encounters were measured by the following criteria: an encounter started when each group became aware of the other's presence, as signalled by vigilance, vocalizations, or displays; an encounter ended if one group moved away, or if each group ceased to pay attention to the other. Individual identities of participants were noted whenever possible but are not analysed here, since the fast action and poor visibility at encounters gave unreliable data using such opportunistic sampling.

9.3 HOME-RANGE OVERLAP.

As described in chapter 8, Camp group's home-range centred on Middle Lion Valley. There were three neighbouring groups, with whom Camp group had aggressive encounters in areas where their ranges overlapped. The main competing neighbours were CMM group, whose range included the forest upstream of Camp group, and D group which ranged downstream. The third, AV group, was rarely encountered, since its range bordered that of Camp group in a less commonly used stretch of woodland (Figure 9.1).

These three groups used areas that overlapped Camp group's total home-range (2854 x 25m-square quadrats) by 74, 124, and 75 quadrats respectively. These 273 quadrats of home-range-overlap (which equal 17 ha.) represent 9.6% of Camp group's range, and are henceforth referred to as overlap-quadrats. Since neighbouring groups were not followed systemmatically, these figures may be underestimated.

9.3.1 Use Of Overlap-quadrats.

The use of overlap-quadrats by Camp group was calculated from ranging maps and scan data: 13.7% (219 / 1598) of quadrats used during 5-day samples were in the overlap-zone, while 17.3% (1508 / 8700 1/2-hour intervals) of time was spent in these quadrats. Temporal and spatial selection ratios may be calculated as measures of whether overlap-quadrats were

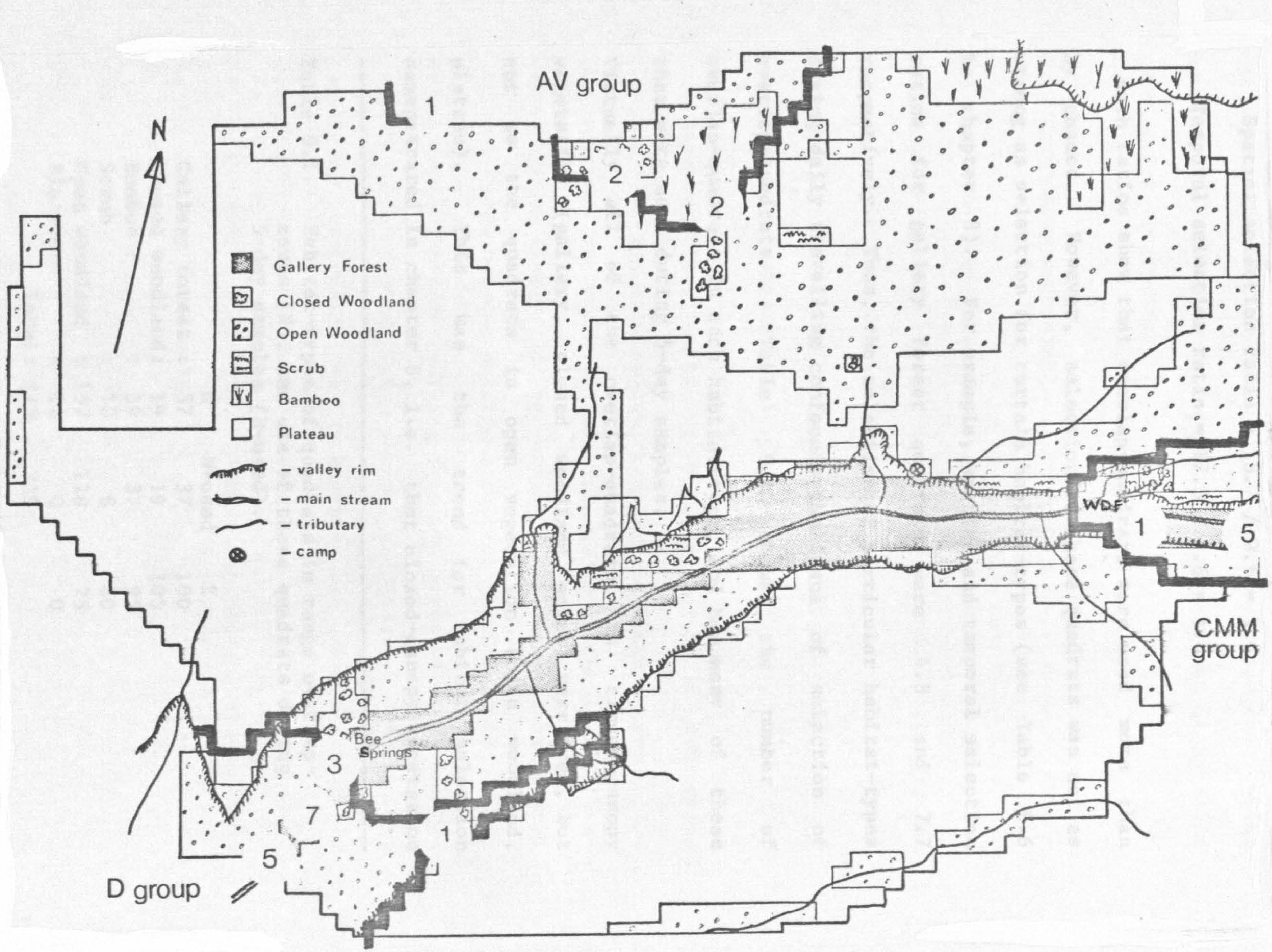

Figure 9.1. A map showing the areas of range-overlap (within the heavy black lines) between Camp Group and its neighbours; D, CMM, and AV groups. White circles show the location and frequency of intergroup encounters.

used more than expected by chance during 5-day samples (s.r.= %observed / %expected, in which a ratio of one is chance):

Spatial selection ratio = 13.7 / 9.6 = 1.4

Temporal selection ratio = 17.3 / 9.6 = 1.8

Both ratios show that overlap-quadrats were used more than by chance. However, selection of these quadrats was not as strong as selection for certain habitat-types (see Table 8.6 in chapter 8). For example, spatial and temporal selection ratios for gallery forest quadrats were 4.8 and 7.7 respectively. Thus, the selection of particular habitat-types during daily travelling confounds the issue of selection of overlap-quadrats. Table 9.1 shows the number of overlap-quadrats in each habitat-type, and how many of these that were used during 5-day samples.

Virtually all of the overlap-quadrats in closed-canopy vegetation (gallery, closed woodland, scrub) were used, but not so the quadrats in open vegetation (open woodland, plateau). This was the trend for habitat selection demonstrated in chapter 8, i.e. that closed-canopy vegetation

Table 9.1. Habitat-types of quadrats in range overlap-zones (N), and use of these quadrats during 5-day samples (N-used).

	N	N-used	%
Gallery forest :	37	37	100
Closed woodland:	19	19	100
Bamboo :	39	37	95
Scrub :	10	8	80
Open woodland :	157	118	75
Plateau :	11	0	0
Total:	273	219	

was chosen in preference to open vegetation. Thus, I conclude that over the year the monkeys were not using the overlap-quadrats more than expected from their preference for particular vegetation-types. In other words, the green monkeys did not engage in regular ´border patrols´ along their territorial boundaries.

9.4 INTERGROUP ENCOUNTERS.

I shall describe in some detail encounters between groups of green monkeys at Mt.Assirik, for two reasons: firstly, the types of encounters between the same groups of monkeys vary considerably; and secondly, other populations of C.aethiops show different patterns of intergroup behaviour.

On rare occasions, barking from adult males in one group elicited barking in response from the neighbouring group, but this was not recorded as an intergroup encounter. These seemed more likely to be warning calls taken up by several callers; even baboons sometimes started barking as well. On many more occasions, barking from one group of green monkeys brought no response from nearby neighbours. Thus, no intergroup encounter at Mt.Assirik was characterised by vocalizations alone. Further, since no encounters involved ´friendly´ mixing of groups, all meetings between groups could be described as territorial.

Intergroup encounters started in various ways: when approaching a boundary, adult males might move ahead of others in the group to investigate; or, upon sighting a neighbouring group, several females or immatures might give specific calls (long rrrr rrrr calls) which alerted other members of the group to the presence of neighbours; or the encounter might be a surprise when groups met in thick vegetation, in which case adult males started barking and females and young gave chutters, and most monkeys ran towards the commotion, to investigate but not necessarily to take part (see below).

Initiation of an intergroup encounter was followed by displays, and sometimes chases, by adult males. These displays involved mainly ritualized ´leaping and crashing´ through the canopy, ricocheting off branches while leaping from tree to tree, sometimes jumping to land heavily in dense foliage, which made much noise. These impressive bouts of ´leaping and crashing´ would be interspersed with vigilant males remaining high in trees, scanning the canopy in the direction of the opposing group. Males from each group might face each other and give silent, long-distance (5-40m) displays of their white chests and jerking penile erections, bounce off their hands onto their haunches, bob their heads, or give wide yawns to reveal their canines. These displays would often lead to further leaping and crashing chases. However, no physical contact between opposing males was observed during intergroup encounters.

Usually only adult males took part in intergroup encounters. As younger males grew up, they began to engage in the visual displays, but rarely in chases or ´leaping and crashing´. Apart from the initial calling, and occasionally running towards any commotion, the rest of the group stayed on the ground and took no further part. Generally the females and young were relaxed, often continuing to feed, groom, or play beneath the noisy arboreal displays of the males. All age/sex classes seemed to be aware of the focus of any intergroup commotion, even if they did not take part in it, so that they remained a cohesive group watching the proceedings. Given that encounters at different sites in different seasons varied in nature and intensity, it would be important that all members of a group were aware of the current status of the territorial boundary. This would determine if they were on ´safe´ ground or should retreat from a more intense defense by the neighbouring group.

The above description of the monkeys´ behaviour occurred in intergroup encounters in gallery forest or closed woodland. Ninety percent of the observed encounters (24 out of 27, see below) took place in these habitats. The other three were in open woodland or bamboo and took a different form. Most notably, all age/sex classes except infants took part: this involved skirmishes on the ground between opposing phalanxes of monkeys rushing and slapping out at each other, or adult males chasing each other on the ground. Throughout, the females and youngsters kept up a chorus of chuttering. Groups remained tightly bunched, and the encounters were brief, lasting no more than a minute before one group fled. The key factor in these encounters seemed to be the lack of continuous canopy in which males could carry out their ´leaping and crashing´ displays, as the ritualized expression of inter-group aggression. These intergroup encounters on the ground involving most group members were similar to those seen by Struhsaker (1967b) in the open habitat of Amboseli.

9.4.1 Frequency Of Encounters.

A total of 27 intergroup encounters were observed throughout this study, and these form the basis of this analysis (16 with D group, 6 with CMM group, and 5 with Assirik Valley group). As a measure of the frequency of territorial encounters, only those that occurred during 5-day samples are considered: 15 encounters during 60 all-day observations gives an average rate of one encounter with any of the three neighboring groups every four days; or, an encounter with the same group every 12 days. However, encounters tended to occur in bursts (i.e. on successive days) between longer lulls without encounters; the longest gap between observed encounters was two months. Although the group was not continually monitored during this gap, their feeding and ranging suggested that encounters were unlikely. This is in marked contrast to vervets in the open habitat at Amboseli, for example, where groups occupy small ranges, and the chances of at least visual contact daily between groups is high (Cheney, 1981; P.Lee, pers comm).

9.5 SEASONAL VARIATION IN TERRITORIALITY.

In this section I shall report on seasonal variation in territoriality at Mt.Assirik. This seasonal variation covers most of the patterns of intergroup behaviour seen in other populations, from rigid, ritualised encounters, through relaxed, mutual, intergroup tolerance, to intensely fierce defense of an area by aggressive supplantation. I shall show ecological correlates with these patterns, which suggest that the nature of territorial behaviour is related to the defense and defendability of certain resources, and that interpopulational differences in territoriality are related to the density and distribution of important resources.

During 5-day samples, 4 intergroup encounters occurred in the 7-month dry season, compared with 11 encounters in the 5-month wet season (i.e. on average, one encounter every 8.8 days in the dry season, and one every 2.3 days in the wet season) (Table 9.2). There was a corresponding seasonal difference in the monkeys' use of overlap-quadrats, both in space and time: in the dry season, a mean of 13% of the quadrats used each month were overlap-quadrats, compared with 17% of quadrats in the wet season; similarly, 16% of time each month in the dry season was spent in overlap-quadrats, compared with 22% of time in the wet season (Table 9.2).

The direction of these differences is suggestive, but in neither case are they significant (Mann-Whitney: spatial use, U= 11, n.s.; temporal use, U= 10, n.s.). However, if monthly figures are analysed individually, rather than as a gross seasonal comparison, there is a positive correlation between temporal use of overlap-quadrats and frequency of intergroup encounters ($r= .61$, $p<.05$). The same trend is seen for spatial use of overlap-quadrats, but this just fails to reach statistical significance ($r= .48$, $.05<p<.1$).

Thus, more intergroup encounters were associated with more intensive use of overlap-quadrats, which tended to occur more in the wet season. Were the monkeys making more use of these quadrats because they were involved in intergroup encounters or monitoring neighbouring groups, or were their chances of meeting another group increased because of the more intensive use of overlap-quadrats, for example in search of food? I shall try to answer this question in the following analysis of the ecological circumstances surrounding each intergroup encounter. To anticipate, I believe the latter to be the

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Table 9.2. Seasonal use of overlap-quadrats, in space and time, during 5-day samples.

		% of monthly quadrats	% of monthly time-periods	No. of encounters
Dry...	Nov:	12%	9%	0
	Dec:	16	13	1
	Jan:	14	13	0
	Feb:	15	31	0
	Mar:	13	13	0
	Apr:	7	11	1
	May:	11	22	2
Wet...	Jun:	11	15	2
	Jul:	11	13	1
	Aug:	25	30	3
	Sep:	19	30	4
	Oct:	18	22	1

	Overall means		Totals
Dry season:	13%	16%	4
Wet season:	17%	22%	11

case, that territorial behaviour amongst these green monkeys was not the rigid maintenance of boundaries, but a flexible response to seasonally variable competition for resources.

9.5.1 Ecological Context Of Intergroup Encounters.

Camp group's range expanded and contracted according to their needs, determined by food distribution and availability (see chapter 8). I identified three important aspects of resources which constrained the ranging strategies of the group, and thus affected intergroup relations: these were, whether a resource was clumped or even in distribution, whether it was abundant or rare, and the degree to which it could be depleted.

Four different types of intergroup encounter were distinguished, which depended upon the prevailing ecological circumstances. The distinctions are based on qualitative descriptions of these circumstances, and on the behaviour of the monkeys, but later in this chapter I shall present some quantitative support for the distinctions. The four categories of intergroup encounter were as follows:

i) chance
ii) ritual
iii) one-sided
iv) intense

A series of descriptive examples illustrate each type of encounter.

9.5.1.1 Chance Encounters. -

These were chance meetings between groups, at unexpected locations, with brief displays and mutual avoidance (n=5, 18% of encounters). The encounters were unpredictable in terms of their past history at these locations, where there were no specific resources to contest. Typically these encounters occurred in less frequently used areas of woodland, when the foraging paths of neighbouring groups happened to meet.

9.5.1.2 Ritual Encounters. -

These were ritual meetings between groups, on established territorial boundaries, near a limited but shared, non-depletable resource such as water (n=9, 33% of encounters). They involved brief and relaxed displays from adult males, and mutual tolerance either side of an accepted border. There were two periods during the year when this type of encounter occurred: one was in the mid- to late dry season, after a boundary had been established around a water spring (Bee Springs, see Figure 9.1) at the downstream end of Camp group's range, neighbouring D group. I describe 'establishing' a boundary to imply that the territorial boundaries were not fixed, but shifted during the year (up- or downstream in the case of D or CMM group), according to changing patterns of ranging and intergroup relations. (Under type iv encounters, I shall describe how these temporarily stable boundaries were established).

At the upstream end of Camp group's range (around Wild Dog Fork, see Figure 9.1), there was good drinking water throughout the dry season, and the series of water pools around Wild Dog Fork stretched up into the neighbouring CMM group's range, precluding competition for water between these two groups. However, the stream had dried up as far down as Bee Springs, more than half a kilometre downstream. Bee Springs was also the only water source in this area for Camp group's downstream neighbours, D group. D group had access to one other pool, 1 km from Bee Springs. Thus, the pool at Bee Springs was a limited resource that was important for both Camp and D groups, but a resource that would not be depleted by use from one group only. In other words, it was to neither group's advantage to fight for exclusive access to the pool, but rather to the advantage of both groups to have shared access to the water. A boundary running through Bee Springs was established, and maintained by brief, relaxed, ritual displays from adult males, without chases or loud calling, each time the groups met near the spring. Each group seemed to be revealing its presence and acknowledging the presence of the other. Each group drank in turn from the spring, and often they would rest for long periods within 50m from each other, without further interaction.

The other period when this type of encounter occurred was in September, in the late wet season. It followed a period of intense, aggressive encounters in August, in defense of an area with an important source of scarce Nauclea latifolia (see type 4 encounters). By September, the area (more than 100m downstream of Bee Springs) had lost most of its high resource-value, and both groups foraged there opportunistically for the few late-ripening fruits. With N.latifolia fruits being so rare, and Spondias mombin fruits becoming widely available, this area was no longer economically defendable, despite N.latifolia being a depletable resource. However, it would still have been disadvantageous for either group to completely relinquish access to the area. Thus, when the groups met, the previously established border was maintained by relaxed and ritual displays.

9.5.1.3 One-sided Encounters. -

One-sided encounters occurred in areas containing resources that were important for one group but relatively unimportant for the other (n=9, 33% of encounters). The encounters involved the former group aggressively supplanting the latter, whose members retreated into home territory without much resistance. Important resources in these cases were ones which were clumped, rare, and significantly depleted by use - such as prized fruit trees with limited distribution or which cropped badly - and which were therefore worth fighting for. Since the fruit in trees is depleted by use, full advantage can only be gained from such resources if the defending group can maintain exclusive access to them, unlike the case for a pool of water, which can be shared between groups without disadvantage.

The best example of the ecological circumstances producing these one-sided encounters occurred during the fruiting season of Pseudospondias microcarpa. This fruit was highly prized amongst the chimpanzees, baboons, and green monkeys, but had a very restricted distribution, growing only near permanent water (see distribution map, Figure 4.3 in chapter 4). Along the streambed in Camp group's range there were approximately 90 P.microcarpa trees, while in the exclusive territories of D and CMM groups there were three trees and one tree respectively. Thus, there was strong pressure for these neighbouring groups to expand their ranges and aggressively maintain exclusive access to the P.microcarpa trees in the areas of overlap with Camp group's range. In contrast, there was no pressure on the members of Camp group to defend these areas, or to prevent encroachment by their neighbours, since P.microcarpa was common elsewhere in their range (phenological samples in March showed that 58% of P.microcarpa trees were fruiting, giving approximately 55 trees containging ripe fruit in their range). Through February and early March, before the fruit had ripened, there was a series of one-sided intergroup encounters between Camp group and each of the neighbouring groups (n=4 observed). During each of these, Camp group retreated without resistance from the advancing, aggressive displays of adult males from D and CMM groups. During this period, there were no other important resources in these areas that could have been responsible for both neighbouring groups chasing Camp group into retreat, which suggests that the ripening crop of P.microcarpa fruit was their major concern. (Throughout this period, all groups regularly tested

P.microcarpa fruit for ripeness by feeling, smelling, and test-biting selected fruits. Camp group sometimes made clearly deliberate detours from their foraging path to test fruits).

By March, the range of Camp group had contracted, presumably as a result of the earlier encounters, and they made consistent use of only the middle section of the valley (although still using the woodland), rarely venturing to the up- and downstream ends of their range. The neighbours expanded their ranges, moving more consistently into the areas of range-overlap to feed on P.microcarpa fruits. Throughout the fruiting season (March-early April), no encounters were observed between Camp and either of the neighbouring groups.

Under the prevailing ecological circumstances, D and CMM groups were highly motivated to maintain exclusive access to certain areas of gallery forest, and Camp group temporarily withdrew from these areas (at little cost to themselves) to avoid unnecessary conflict. Later in April, after the fruiting season of P.microcarpa had ended, Camp group expanded its range again, and engaged in a new set of intergroup encounters with D group to establish another temporary boundary at the Bee Springs water source (see type ii encounters, above). This range expansion immediately after the end of the P.microcarpa crop provides further evidence for the resource-dependent nature of territorial boundaries and intergroup encounters in the green monkeys. These one-sided encounters were not the result of fixed dominance relationships between groups, in which one group might supplant a consistently subordinate group (as, for example, in *Colobus badius*, Struhsaker and Oates, 1975; and *Papio ursinus*, Hamilton *et al.*, 1975). In the above examples, Camp group was supplanted by CMM group which was only one third of its size, and contained only one adult male as opposed to the 5 adult and 2 subadult males in Camp group. On other occasions, Camp group successfully supplanted both of its neighbours.

9.5.1.4 Intense Encounters. -

Intense, mutually aggressive encounters occurred over resources that were important to both groups, such as scarce, depletable, fruit trees (n=4, 15% of encounters). Both groups gave intense displays and aggressive chases, and these encounters were long and noisy (both in terms of vocalizations and 'leaping and crashing' displays).

Two species of fruit tree were involved in these encounters, *Diospyros mespiliformis* once, and *Nauclea latifolia* twice. Both species were important in the green monkeys' diet, and both were few in number: *D.mespiliformis* occurred in 38 quadrats in Camp group's range (local density= 2.6 trees per quadrat, clumpedness index= 1.4 of surrounding 8 quadrats); *N.latifolia* occurred in 38 quadrats (local density= 1.3 trees per quadrat, clumpedness index= 1.6 of surrounding 8 quadrats). The site of the first encounter was at an isolated clump of *D.mespiliformis* trees in the area of range-overlap with CMM group. To exemplify this type of encounter, I shall give full details of those which occurred in the area of range-overlap with D group, involving N.latifolia, a large woody vine producing sweet fruit the size and shape of golfballs.

Although 38 quadrats in Camp group's range contained N.latifolia (see distribution map, Figure 4.3), fewer contained good specimens that bore heavy crops of fruit. In the overlap-zone between Camp and D groups, 9 quadrats contained good specimens: in other words, even if the quality of the resource were ignored, about 25% of all N.latifolia in Camp group's range was concentrated in the area of overlap with D group. Details of the availability of this species in the exclusive territory of D group were not recorded, but there were no more than three vines 1/2 km into their range from the Camp group border. Opportunistic surveys suggested that N.latifolia was rare throughout their range. Phenological samples in August showed 89% of vines bearing fruit. Thus, heavy use of the overlap-zone by both groups was expected, with both being keen to defend a certain proportion of this area for exclusive access, given that with shared access the fruits might be depleted by one group to the disadvantage of the other.

On the 17th August I observed the first intergroup encounter under these conditions. This occurred at the upstream side of the 124-quadrat overlap zone, at the edge of Camp group's exclusive territory (see Figure 9.1). The encounter was ritual and relaxed (type ii), and Camp group made no attempt to move further downstream. The following day there was another encounter, but this time Camp group had moved about

150m further downstream. On meeting, both groups erupted into violent chasing and fierce ´leaping and crashing´ displays - an intense, type iv encounter. This lasted for 2 hours and 20 minutes, before Camp group moved upstream. Three days later, another intense intergroup encounter took place, lasting 2 hours and 30 minutes. This encounter was less fierce, and took place mid-way between the previous two encounters, suggesting that a temporary boundary was emerging, to divide this crucial stand of N.latifolia between the groups.

So, within five days and under virtually identical ecological conditions, this difference in the type of intergroup encounter was produced solely by the different locations of the encounters. Following this, the monkeys from each group fed extensively from the N.latifolia on either side of the border that was established from these initial, intense encounters. In September, after this area had lost its high resource-value, there followed a series of ritual encounters. N.latifolia fruits were no longer as important in the diet, since the fruits of Spondias mombin had ripened and were more widely available to both groups; it was not economical to fight intensively to maintain exclusive access to the few late-ripening N.latifolia fruit, and both groups foraged opportunistically in the overlap-zone, engaging in ritual encounters when they met.

The fourth intense encounter I observed was prior to the series of ritual encounters at Bee Springs water, in the late dry season (see above, type ii encounters). Such an encounter may have signalled the preparedness of both groups to fight for the resource under competition, and in the case of a non-depletable resource, mutual tolerance was quickly established around the water pool. In conclusion, in certain ecological contexts long and intense intergroup encounters occurred when both groups were highly motivated to fight for a particular resource.

9.5.2 Absence Of Encounters.

A description of the ecological conditions under which no intergroup encounters occurred will further clarify the important qualities of resources that cause territoriality. The lack of encounters during the fruiting season of _Pseudospondias_ _microcarpa_, through March and early April, was discussed earlier: Camp group, with ample supplies of this resource, contracted its range under pressure from both neighbouring groups, which had very limited supplies of _P.microcarpa_. Camp group avoided encounters during this period by restricting its daily ranging patterns to the central part of the valley, and avoided moving up- or downstream to the range boundaries.

The longest period lacking observed encounters was from mid-December to mid-February: this period coincided with the cycle of flower buds and flowers of <u>Pterocarpus erinaceus</u>, the most widespread tree species in the region, which made up over 50% of the monkeys' diet in January. <u>P.erinaceus</u> occurred in 995 quadrats throughout Camp group's range (see distribution map, Figure 4.3), and the buds or flowers were evenly distributed (local density= 3.6 trees per quadrat; clumpedness index= 5.5 of surrounding 8 quadrats; phenology (January)= 56% of trees flowering). <u>P.erinaceus</u> flowers were equally abundant for neighbouring groups. Thus, there was no possible localized competition between groups for the major food source during this period, nor for any less important resources, and no intergroup encounters occurred.

It is not simply the overall availability of any food that determines whether or not it is a potentially competitive resource, but more particularly its distribution and relative importance to either competitor. There was no correlation between overall food availability and the number of intergroup encounters (r= -.17, n.s.).

9.5.3 Number Of Displays And Duration Of Encounters.

Two quantifiable measures were taken during intergroup encounters which lend support to the independently derived, qualitative distinctions between types of encounter. The mean number of displays and the mean durations for each type of encounter are plotted in Figures 9.2 and 9.3.

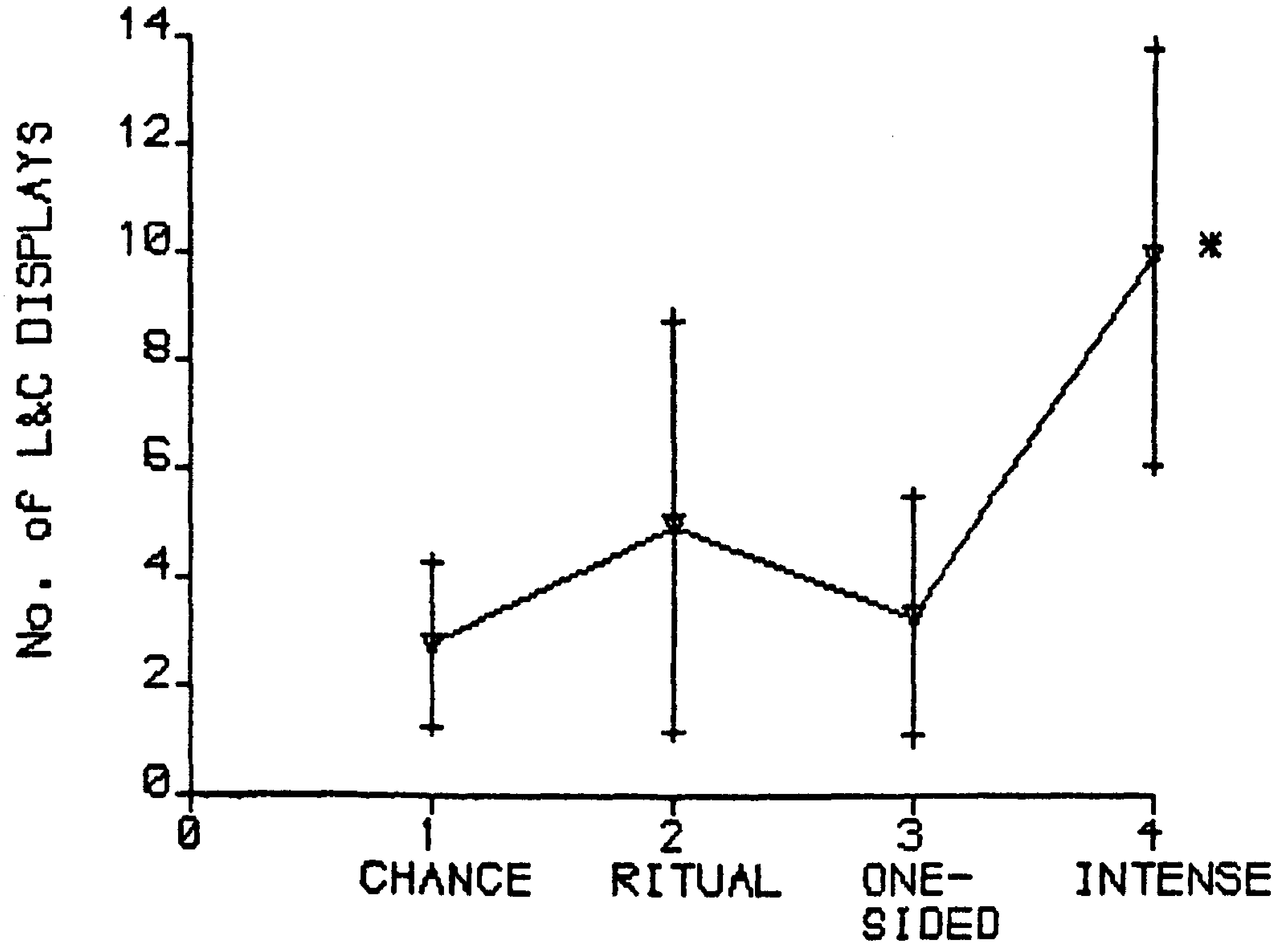

Figure 9.2. Mean number of 'Leaping and Crashing' displays during each type of intergroup encounter. The asterisk marks the statistically different mean (p<.05).

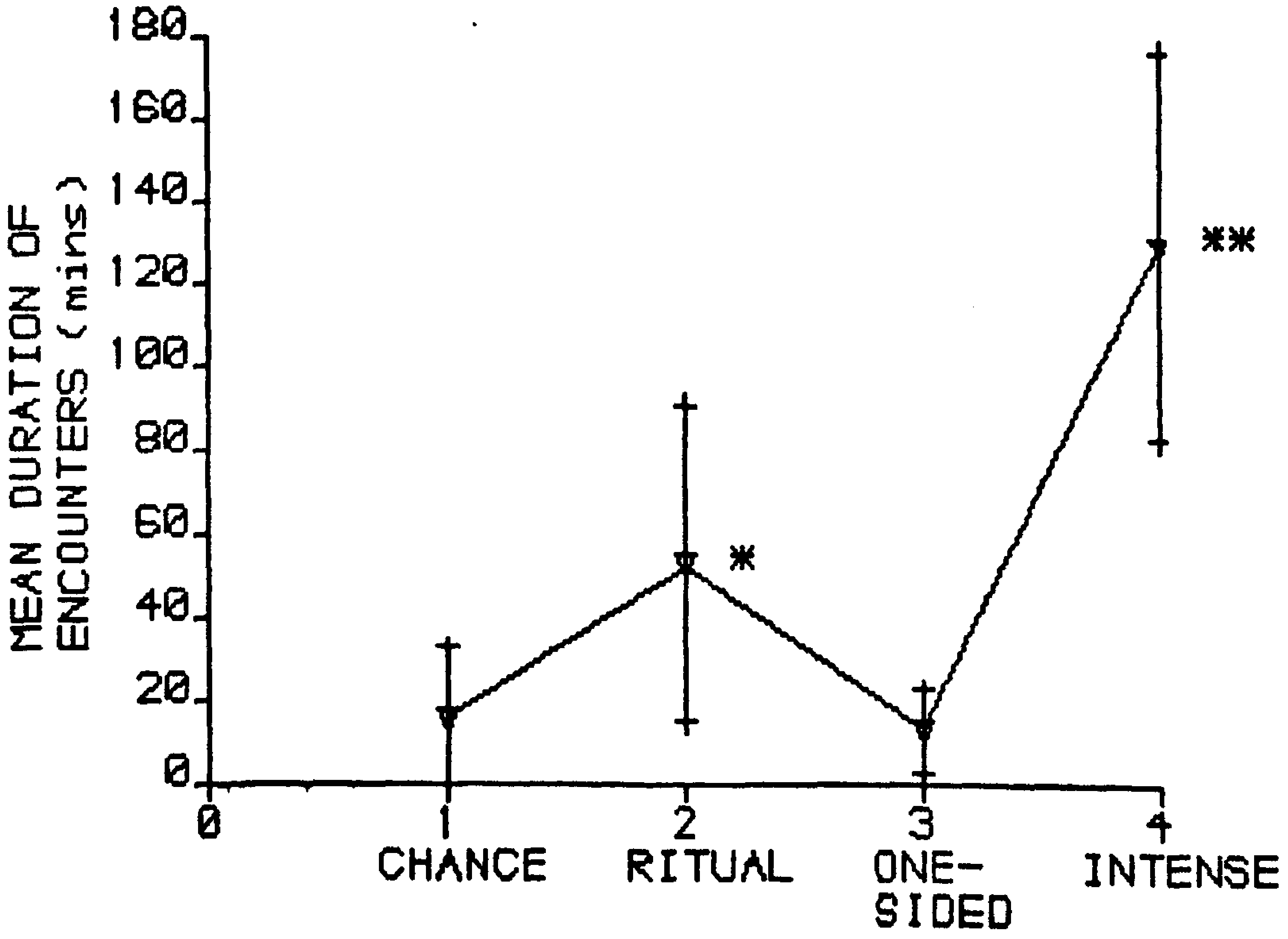

Figure 9.3. The mean duration (in minutes) of each type of intergroup encounter. Asterisks as in Figure 9.2.

Analyses of variance of the number of displays per encounter, and of the durations of encounters show significant differences (Anova: F= 5.0, p<.01; F= 14.4, p<.001, respectively). Post hoc comparisons of means (LSD, p<.05) show that intense encounters had significantly more displays and lasted longer than other types of encounter. Ritual encounters lasted longer than chance or one-sided encounters, although there were no differences in the number of displays between these three types.

In summary, chance encounters involved very few displays, and through mutual avoidance, ended quickly. One-sided encounters ended as quickly, and one group supplanted the other with as few displays. Ritual encounters lasted much longer, but also involved a small number of displays per encounter (although this represents far fewer displays per unit time, in keeping with their milder nature). Intense encounters involved most displays and lasted far longer than other encounters. However, I believe that this is a somewhat arbitrary imposition of categories onto a continuous scale of the monkeys' motivation to defend resources, or future access to them. If members of both groups have low motivation to defend a resource (determined by its current distribution and availability), then ritual encounters would be more likely when groups met; if members of one group were more motivated than the other, one-sided encounters would occur; and if members of both groups were highly motivated to fight for a resource because of its importance, rarity, location, and history of encounters, intense encounters would be most likely. Thus, each type of encounter may represent a grade of intensity according to each group´s level of motivation.

This more cognitive approach to the question of variability in territorial behaviour does not contradict the analysis of the ecological circumstances underlying this variability. Rather, the two approaches complement each other, indicating that territoriality is not a rigid phenomenon in these monkeys, but that decisions are involved and territorial boundaries are flexible according to the demands of the seasonally changing environment.

9.6 DISCUSSION.

In this section, I consider what seasonal and interpopulational differences in territorial behaviour may tell us about the mechanisms and function of territoriality.

9.6.1 Comparison With Amboseli.

Cheney (1981) provides the only directly comparable data on different aspects of territorial behaviour in C.aethiops, although her study primarily investigates the social factors involved in the segregation of groups, rather than the ecological variables investigated in the present study. Table 9.3 summarises and compares the salient features of territorial behaviour in vervets at Amboseli (after Cheney) and green monkeys at Mt.Assirik (this study).

There are several differences in territorial behaviour between these two populations. Intergroup encounters were far more frequent at Amboseli than at Mt.Assirik: the number of encounters observed between any pair of groups can be compared, e.g. Camp vs. D group at Mt.Assirik, n = 16; A vs. B group at Amboseli, n = 68. (Strictly, rates cannot be compared directly because Cheney does not report any systemmatic sampling at Amboseli). Over 50% of encounters at Amboseli involved vocalizations alone (intergroup ´chutter´ and ´aahr´), yet this did not occur at Mt.Assirik. Since visual contact was made between neighbouring groups at Amboseli every day, a higher proportion of vocal territorial interactions may be expected, since these are less energetically costly than physical displays. The herding of females by males of the same group was observed only once during intergroup encounters at Mt.Assirik, but was more common at Amboseli (see competition for mates, below). Friendly mixing between members of opposing groups was never

Table 9.3. Comparison of various aspects of territorial behaviour in two populations of C.aethiops.

	Mt.Assirik	Amboseli
Number of encounters observed :	27 *	234 **
Rate for one group per all-day-follow :	1 per 4 days	?
% of encounters with herding :	4%	20%
" " " " displays :	92%	38%
" " " only vocal :	0%	53%
" " " with intergrp mixing:	0%	4%
Non-AM participation in encountrs:	rare	common, but males more aggressive

* involving 4 groups:
Study group with D = 16
with CMM= 6
with AV = 5

** involving 10 groups:
Study groups A with B = 68
B with C = 51

seen at Mt.Assirik, but did occur at Amboseli (although rarely, see below). By contrast, virtually all encounters at Mt.Assirik involved aggressive arboreal displays from males, whereas this was much less common at Amboseli. The relative absence of suitable tree canopy at Amboseli may account for this difference. Active involvement in encounters by group members other than adult males was very rare at Mt.Assirik, but was common at Amboseli, although males were more aggressive towards other groups than were females or young, and aggression from both males and females was directed more towards opposing males than females or young.

No individual differences in behaviour at intergroup encounters could be recorded reliably at Mt.Assirik without systemmatic sampling. Cheney found that dominant males were more involved in displays, herding, and intergroup aggression. There were also differences in the nature of encounters according to the history of male-transfer between groups: there was more aggression from males at encounters between groups that had exchanged males, but more aggression from females at encounters between groups that had no common history of male-transfer. The only comparative evidence from Mt.Assirik suggests that such situations may not arise, as all males that transferred out of the study group (n=3) during this study did not join neighbouring groups, but travelled further afield. This in itself is an important populational difference, since males must transfer without knowledge of potential new groups. This may explain the consistent pattern of all males who attempted to leave the study group at some stage (n=5) returning between two and four weeks later with severe wounds. One such male was seen alone, back in the study group's territory, barely able to move due to back or leg injuries - he hid in a cave and was not seen again. Two males returned and remained with the group, and two others left the group for a second time, after their wounds had recovered, and did not return.

9.6.2 Comparisons With Other Populations.

Other studies of C.aethiops suggest a range of behavioural variation in patterns of intergroup encounter. Some variation stems from the extent to which each behavioural element is present in each conflict ('leaping and crashing' displays, penile erection, head- and body-bobbing, chasing, vigilance, advance of opposing groups in phalanx, etc), but several reported differences may be more significant: at Mt.Assirik, Buffle Noir (Cameroon: Kavanagh, 1981), and Lolui Island (Uganda: Gartlan, 1966) no non-agonistic mixing between groups was observed, and yet at Amboseli (Kenya) intergroup grooming and play was observed between low-ranking females and juvenile males (Cheney, 1981; Struhsaker, 1967b). On rare occasions at Kalamaloue (Cameroon: Kavanagh, 1981) groups were seen to mingle passively. It is possible that there was no peaceful mixing between groups at Mt.Assirik because neighbours met relatively rarely, leaving little chance for individual recognition to develop between group members, and therefore less chance of friendly interactions. However, even at Amboseli such mixing was rare (9 of 234 encounters), and possibly it may not have been seen in other populations simply because of small sample-sizes.

The incidence of intragroup aggression during intergroup encounters is reported as common at Buffle Noir as well as Amboseli. This is rarely seen elsewhere: there was only a single occasion at Mt.Assirik when, during a particularly dispersed yet intense intergroup encounter, an adult male from D group attacked an adult female from his own group, biting her in the neck and chasing her into home territory. It may be significant that this occurred in August, at the beginning of the mating season. Cheney (1981) reports transferred males herding females away from the group's periphery during intergroup encounters, and these males were involved in more copulations during the breeding season. The herding of females may reflect a function of territoriality separate from the protection of food-resources, namely to limit competition between males for access to breeding females.

Another major source of interpopulational variation in territoriality lies in the nature of territorial encounters: the degree of tolerance or intolerance between groups, the intensity of displays, the amount of range-overlap. On Lolui Island and at Bokassi (Cameroon: Kavanagh, 1977), where the monkeys have very small ranges, defense of their stable territories is fairly rigid, with little range-overlap. In other areas, such as Kalamaloue, encounters are more variable and relaxed, and home-range-overlap is more extensive. Kavanagh (1981) gives figures for areas of range-overlap: 10.3 ha at Kalamaloue (18.2% of the home-range); 5.8 ha at

Buffle Noir (5.6% of the home-range). The comparable figure for Camp group was 17 ha (9.6% of the home-range). Unfortunately, no comparative data are given for frequency of encounters at the two Cameroon sites. It may be that more rigid territoriality is accompanied by smaller areas of range-overlap. However, this takes no account of seasonal variation in the intensity of territorial interactions, which was clear at Mt. Assirik. Struhsaker (1967b) also reports seasonal variation in the degree of range-overlap and intensity of encounters, although he makes no mention of the ecological circumstances underlying such variability. As a deviation from the normally rigid territoriality, vervet groups showed considerable mutual tolerance in the vicinity of small water-holes. In contrast, Wrangham (1981) reports that female vervets at Amboseli were prevented from gaining access to a waterhole in a neighbouring group's range, through typical patterns of range defense.

One further populational difference is seen in the identity of participants in intergroup encounters. Only adult males took part in encounters at Mt.Assirik, except in the rare woodland encounters. A similar pattern seems to occur in Cameroon (Kavanagh, 1981). At Amboseli, however, it was common for females to be actively involved in encounters (Cheney, 1981). The reason for this difference is unclear. There is an interesting similarity between encounters at Amboseli, where the habitat is very open, and the few encounters in open woodland at Mt.Assirik, which did involve females and young, and occurred on the ground amidst much intergroup ´chutter´ calling.

9.6.3 Comparisons With Other Species.

In chacma baboons (Papio ursinus) Hamilton et al.(1976) described up- and downstream shifting of ranges very similar to that shown by the green monkeys. This occurred between three troops of baboons in the Kuiseb River canyon, in the Namib Desert, in response to the changing location of waterholes: through aggressive encounters, one group gained and retained access to water in an area of range-overlap with its neighbouring group. Other intergroup encounters occurred at favourable feeding areas in the overlap-zone. However, in these cases, one group was always dominant to the other, and the latter either retreated or was supplanted. At the Okavango Swamp, where food and water were freely and evenly available to all troops, Hamilton et al. reported that sleeping sites were the key resource that caused territotial encounters. In one case, encounters between two troops were frequent at roosting time at a frontier where there was only one grove of sleeping trees. In contrast, at another frontier with two sleeping groves only 300m apart, neighbours showed mutual tolerance as each troop slept in one grove.

Hamilton et al. also reported that equilibrium at spatially well-defined frontiers (within an overlap-zone) gradually became established as encounters developed, providing a further interesting similarity between the green monkeys and chacma baboons in the dynamics of territorial defense. Male chacma baboons also herd females belonging to their own troops during intergroup encounters (Hamilton et al., 1975). However, whereas a dominant troop of these baboons could supplant a subordinate troop, the same was not true for the green monkeys at Mt.Assirik. In general, the processes underlying the variability in territorial behaviour are consistent between these two populations.

9.6.4 Economic Defendability.

In discussing territoriality by individual birds, Brown (1964) emphasised that diversity in territorial systems depended on the influence of two primary variables, competition and economic defendability. In the examples above, similar types of ecological pressures seemed to be acting on both species of primate, at Mt.Assirik and Kuiseb River, and similar types of territorial responses were shown, marked by seasonal flexibility. In terms of Brown's view, each group was competing for resources in a highly seasonal habitat, in which resources were widely spread and thus not always economically defendable.

Brown also suggested that although competition was essential for the evolution of territoriality, different levels of economic defendability would lead to different territorial responses. Mitani and Rodman (1979) have attempted to quantify economic defendability in an analysis designed for cross-species comparisons of group-size, range-size, and territoriality in primates, but also usefulfor intraspecific comparisons. To maintain a territory, group members must encounter the perimeter of their range frequently enough to monitor potential intruders. Based on this proposal, Mitani and Rodman used as an index of defendability (D) the ratio of day-range length to home-range area: the higher the index, the more defendable is the territory. In their sample, all populations with indices of defendability of less than one are non-territorial. All territorial populations have indices of greater than one, although a few with such indices are non-territorial. Thus, a high index permits but does not ensure territoriality.

Given that a relationship between defendability and territoriality exists between species, one may expect that variation in defendability within species will also predict variation in territoriality. Mitani and Rodman cite two examples to support this: non-territorial langurs (*Presbytis entellus*) in northern India have an index D= 0.44 (Jay, 1963 quoted in Mitani and Rodman, 1979), while a southern population has an index of D= 1.44, and is territorial (Yoshiba, 1967). Comparison between two populations of black and white colobus (*Colobus guereza*) shows a similar relationship (Oates, 1977; Dunbar and Dunbar, 1974b). Although there are no reports of *C.aethiops* being non-territorial, it may be that variations in the degree of territoriality between populations is related to differences in defendability. Although indices may be calculated for several populations, only Cheney (1981) provides comparative data on frequency of intergroup encounters: at Amboseli, the frequency of encounters was high, and D= 1.65 (calculated from Struhsaker, 1967e); at Mt.Assirik the rate of encounters was low, and D= 1.03. This agrees with prediction, that vervet ranges at Amboseli are small enough to be highly defendable, whereas the large home-range of the green monkeys at Mt.Assirik is less economically defendable, and thus lower rates of intergroup encounter were found. Qualitative differences in the degree of territoriality in two savannah populations in Cameroon (Kavanagh, 1981) is also associated with the predicted difference in defendability (Buffle Noir, D= 1.8 - higher levels of territoriality; Kalamaloue, D= 1.4 - lower levels of territoriality).

In conclusion, defendability is determined by a combination of the ranging patterns and distribution of monkeys throughout a region, and these factors are ultimately influenced by patterns of resource distribution in space and time. The seasonal variation in the distribution and availability of resources at Mt.Assirik, and the different territorial responses shown by the green monkeys to these changes, clearly illustrate one aspect of the mechanisms and function of territoriality, and the possible sources of variation in territorial behaviour between populations.

CHAPTER 10.

OPTIMAL FORAGING.

10.1 INTRODUCTION.

In this chapter, I shall draw together some of the measures of feeding, ranging, and activity-budgets presented in previous chapters, in an attempt to find functional relationships between the parameters concerned, and provide a clearer, unified picture of green monkey behavioural ecology. In particular, as several parameters have 12 monthly data-points, some of these data are suited to a correlational analysis to test some of the models of optimal foraging theory (for a review, see Pyke, Pulliam, and Charnov, 1977).

Optimal foraging theory is based on the premise that as a result of natural selection an animal will optimise its foraging efficiency. Efficiency is measured in terms of some "currency" (Schoener, 1971), which is usually energy, and the basic hypothesis is that animals will maximise their net energy intake, given certain costs and benefits of feeding. This approach has been fruitful for many studies of the feeding strategies of birds in particular, studies that have applied themselves to the following questions: where do animals feed? (optimal patch choice); how do they get there? (optimal ranging patterns and speeds of movement); how long do they spend there? (optimal allocation of time to different patches); and what do they eat? (optimal choice of diet);see Pyke *et al.* (1977).

However, when many of these models are applied to herbivores, several problems have arisen, in particular the question of which currency is used - for example, risks of predation or nutritional requirements may be in conflict with increasing the net rate of energy intake. Westoby (1974) states that the objective of large generalist herbivores is to obtain an optimal mix of nutrients, rather than to maximise the energy yield per unit foraging time, since search time for food in unlikely to be a constraint. Freeland and Janzen (1974) suggest that plant secondary compounds will be the major constraint in the feeding strategies of herbivores.

Few studies of primates have specifically been placed within the framework of optimal foraging theory (exceptions include Glander, 1981; Hamilton _et al._, 1978; Milton, 1980). However, these and several other studies do report detailed data on the nutritive values (e.g. Hladik _et al._, 1971; Hladik, 1977a,b) and potentially toxic constituents (e.g. Oates, 1977; Oates _et al._, 1980; Wrangham and Waterman, 1981) of primate foods. What is clear from this research is that there are several currencies in use in optimal diets for these primates. These include the maximisation of energy, the balance of nutrients, the digestibility of protein (e.g. in leaves, according to their age, or secondary compounds that may inhibit protein breakdown), the balance in "quality" of food (e.g. fibre content), and the minimisation of plant secondary compounds.

* It is worth pointing out that although optimal foraging theory assumes exclusive use of resources, my measures of food-availability take no account of any reduction in the amount of food due to competition from other species of primate. The principle habitats used by the patas monkeys (grasslands and the ecotone between plateau and woodland; Henty, in prep) overlap little with areas used commonly by the green monkeys, and little competition exists between these two species. In contrast, the habitat-use and diet of chimpanzees and baboons overlaps to a large degree with green monkeys. However, direct competition for resources is greatly reduced by niche-differentiation between these species: although the baboons live at higher density, in terms of biomass,(8 per km2), they range much more widely than the green monkeys (up to 45 km2), and concentrate more of their time in woodland and open scrub areas (see Sharman, 1981); the chimpanzees have more similar habitat-preferences to green monkeys, avoiding open vegetation, using woodland extensively, and relying particularly on gallery forest in the dry season, but they live at such a low density (0.1 per km2) and range so widely (up to 300 km2) (see Baldwin, 1979), that little competition with individual groups of green monkeys exists.

The low levels of resource-competition by other primates may provide confounding variables that have not been incorporated into the models of optimal foraging being tested. Such variation may be no worse than that which already exists in my fairly crude measures of food-availability. However, as will be seen in this chapter, the data fit the models well, despite these potentially confounding variables, which tends to add weight to conclusions about foraging strategies in the green monkeys, and emphasises the robust nature of these strategies.

In the present study, no data were collected on the nutritional content of the green monkey diet, so I cannot test specifically for an optimal diet based on nutrient balance, but I shall discuss the feeding strategies used by the green monkeys with reference to these various dietary requirements. However, I can test certain models of optimal foraging which use energy as the currency being maximised within certain time constraints. *

10.2 OPTIMAL DIET.

The most efficient foraging strategy should be to obtain an optimum mix of energy and nutrients, given the constraints of a maximum bulk of food, certain costs of procurement (risks of predation, climatological stresses, food searching and processing, toxic plant compounds), and certain time limitations. Both New and Old World folivorous primates have digestive specialisations that enable them to exploit leaves as a major food source, for energy and nutrients. Although they often select highly seasonal foods, such as fruit and flowers, at times when such foods are scarce and their cost of procurement is high, these primates do concentrate on perennial and abundant mature leaves (Clutton-Brock, 1975; Glander, 1981; Hladik and Hladik, 1972; Milton, 1980). However, many primates do not have this ability and have adopted alternative strategies in their choice of diet.

10.2.1 The Green Monkey Diet.

The green monkeys selected fruit as the major item in their diet, and ate fruit according to its availability and without preference for particular species. Flowers too were an important item when available, whereas other food items (excepting invertebrates - see below) assumed a secondary importance in the diet, depending on the availability of fruit and flowers. Since fruit is composed primarily of soluble carbohydrates (e.g. Hladik, 1978), the major source of ready energy in food, this suggests that the monkeys were maximising their intake of ready energy. Flowers can also contain a substantial amount of carbohydrates (e.g. Milton, 1980). Thus, it seems that energy is an important currency for the green monkeys, and their choice of diet is optimal in maximising this currency, by being a generalist fruit-feeder in preference to feeding on other less energy-rich vegetable foods. The fact that there was no selection of particular species of fruit is evidence against taste or specific nutrients being major influences in this part of the diet.

However, fruits are highly seasonal items, subject to great spatial and temporal variability, and flowers are generally extremely short-lived. There must come a time, during fruit shortage, when it is energetically too costly to search for fruit (i.e. insufficient return on search time/energy expenditure), and some alternatives in the feeding strategy must be used. The green monkeys certainly showed flexibility, manifest in their change to a more diverse diet as fruit became scarce. This ability to adapt to a great diversity of "bits and pieces" in the diet during times of fruit-shortage or poor quality food is essentail for coping with the seasonally variable availability inherent in a frugivorous diet, and the possibility of crop-failure in major species of fruit.

Within the framework of optimal foraging theory, the above findings fit the predictions of MacArthur and Pianka's (1966) original model of the optimal use of a patchy environment (see also Pulliam, 1974; Schoener, 1971; Krebs and Davies, 1978). This model concerns the trade-off between profitability of food items (food value per unit handling time), and searching time: if the availability of high ranking food items (fruit, in this case) increases, the optimal diet includes fewer items, because the search-time for such food is shorter. If fruit is common, it does not pay the monkeys to stop and eat food of low profitability. The important predictions from this model are that the monkeys should:

i) prefer more profitable prey - in terms of ready energy value, fruit gives best value per unit handling time, and the green monkeys do select fruit over other less profitable vegetable items.

ii) be more selective when profitable prey are common - in chapter 6 I showed the predicted (but non-significant) trend that as fruit and flower availability increased, the diversity of food parts in the diet decreased ($r= -.443$, $p=.074$), as higher proportions of the diet were given over to fruits and flowers.

iii) ignore unprofitable foods which are outside the optimal set, regardless of how common they are - this did apply to certain items, such as leaves or grass, that were abundant but ignored when fruit was abundant.

The above analysis is concerned with energy as the currency being maximised by the green monkeys in their choice of diet. There is, however, an upper limit to the amount of fruit that can be consumed, since it is essential that the monkeys have a source of protein, which is generally only available in small quantities in fruit (e.g. Hladik, 1978). This introduces a second currency that is important in an optimal diet - nutritive balance. As green monkeys do not have the digestive specializations to deal with any substantial bulk of leaves as a source of protein, the monkeys nearly always included a consistent proportion of invertebrates in their diet, which provided them with a good source of protein (as well as fatty acids, which are as important as amino acids). In addition, animal protein is generally of higher quality than vegetable protein, which often has inadequate amounts of certain essential amino acids (Kerr, 1972). The importance of invertebrates in providing a nutrient balance in the diet is shown in the consistency of their intake from month to month (see chapter 6), irrespective of the amount of fruit available, and thus irrespective of the immediate maximisation of ready energy (in the form of soluble carbohydrates): there was no correlation between %fruit and %invertebrates in the monthly diet ($r= .040$, n.s.). Two exceptions to this consistent intake of invertebrates occurred during January and August, when only 2% of the diet was made up by invertebrates.

These two months also produced the highest proportions of flowers in the monthly diet. As well as some flowers being a good source of soluble carbohydrates, others also contain substantial amounts of protein (e.g. Milton, 1980), and it is possible that the flowers eaten in January and August provided sufficient protein for a balanced diet. The diet in August also contained the highest proportion of foliage for any month (herb leaves, grass, and bases of grass stems), a good source of vegetable protein. I can only speculate that during January and August, the abundance of flowers meant that it was more efficient, in terms of time invested, to exploit the flowers as a source of protein than to search for invertebrates. It seems very unlikely that there was a sudden decrease in the availability of invertebrates during these months.

Although green monkeys are unable to ingest leaves in large quantities, it was notable that even if in very small amounts, there was some foliage in each month's diet. This too may have been an important element in the nutrient balance of the green monkeys' diet: for example, Hladik _et al._(1971) gave several examples amongst folivorous primates of a balanced composition of leaf and fruit in the diet, each providing complementary amino acids. Hladik (1978) stated that domestic animals require at least 12% protein in their diet, and that 5-20% of a diet as insects would only provide 7.5-10% of total dry weight as protein; therefore, a complementary protein source is needed, and young leaves, shoots, and seeds provide the solution. This certainly seems the case with green monkeys, with their small but regular monthly consumption of some leaf material. In addition, leaves perhaps provide essential amino acids to balance the deficits in fruit.

An example of the difficulty green monkeys face in digesting leaf-material was seen in regurgitation. Individuals were seen to regurgitate food on 25 occasions, swallowing it again each time. This always occurred within an hour of dawn. The two peaks in the occurrence of regurgitation were during February (n=9) and August (n=6), the two months with the highest percentage of foliage in the diet. Most of the rest occurred in November and December (n=9), when herbs and leguminous seeds formed the bulk of the diet. This evidence suggests that the monkeys had difficulty in digesting the cellulose in foliage, or perhaps even that it was mildly toxic.

One problem that is particularly salient in the folivorous part of any diet is the presence of secondary compounds. This may provide another currency in any optimal diet, but in this case, a currency to be minimised. Oates (1977) and Oates _et al._(1980) demonstrated an inverse correlation between tannins and food choice in the selective, leaf-eating _Colobus guereza_ and _Presbytis johnii_; Wrangham and Waterman (1981) showed a similar pattern in the omnivorous _C.aethiops_. Toxic secondary compounds occur primarily in leaves, and increase in their strength as leaves mature. Thus, this problem is less likely to affect the green monkeys, who eat few leaves. However, immature fruits contain alkaloids, which are detoxified as the fruit ripens (McKey, 1974). Although baboons seem to be able to consume immature fruit without ill-effect (for example, *Papio ursinus*: Hamilton *et al.*, 1978), it was notable that green monkeys selected only ripe fruit; before fruits were picked, they were often tested by sniffing, mouthing, or manually squeezing, and if unripe, they were rejected. The fruits of *Saba senegalensis* provided a good example: in May, few of these prized fruits had ripened, and the monkeys' strong preference for such fruit showed itself in strong competition and much aggression between monkeys for the few ripe fruit available. The following month, with approximately the same volume of fruit available, but most of it ripe, the competitive aggression was virtually absent.

It seems, therefore, that the monkeys do minimise ingestion of toxic secondary compounds. Even in the small quantities of leaves eaten, it was evident that choice of species was not random or made simply according to availability (see chapter 6), since far fewer species were eaten than were available, and only flushing leaves and shoots were consumed. It is possible that they ate a variety of particular species, in small amounts, to avoid a build-up of toxins; i.e. they acquired doses of different toxins that were small enough to be neutralized (see Freeland and Janzen, 1974). For example, there was a high number of species of leaves eaten in February, the month with only poor quality fruit available, and with the highest intake of foliage in the diet (compare 10 species of leaves eaten of 12 species available in February, with 3 of 14 species eaten in March, and 1 of 17 eaten in April).

In conclusion, despite the gross and perhaps over-simplistic nature of my nutritional analysis, which takes little account of the variation in the nutritive content of plant parts of different ages, habitats, or species (Boyd and Goodyear, 1971), there are several ways in which the green monkeys meet the predictions of an optimal diet. It is clear that several currencies are in use in the process of optimisation: the monkeys do maximise their intake of ready energy, by selecting fruit as a primary choice in the diet, but while also maintaining a balance of nutrients independent of the availability of fruit. The green monkeys also avoid, or at least minimise, plant secondary compounds found in immature fruits or mature leaves.

10.3 OPTIMAL TIME-BUDGETING.

In the previous section I discussed selectivity and diversity in feeding as a strategy for maintaining an optimal diet under given circumstances; namely, as food density decreases, the diet becomes more diverse. This strategy concerns the contents of the diet - how feeding time should be distributed over various food parts. The great spatial and temporal variation in the availability of fruit over any year also poses a problem concerning the overall energetic costs and benefits of foraging, and how to allocate time to various activities. In other words, another strategy governing the energetics of maintaining an optimal diet should be expected, a strategy governing the time-budgeting of activities, and travelling costs while in search of patchily distributed foods.

Given the requirements of a nutrient balance in the diet, the monkeys' time-budget must allow for a regular intake of invertebrates and small amounts of foliage, but after that, the problem becomes one of maximising the net energy gain after the overall energetic costs and benefits of feeding are balanced out.

The constraints include a certain amount of food available, and a certain amount of time in which to feed. A mathematical model is discussed by Norberg (1977) and Krebs and Davies (1978), which predicts that if the density of food is low, the most efficient way to feed is to travel slowly or cover minimal distances (economising on energetic costs), since this strategy will optimise the net gain under these conditions, even though less time is available for feeding. This may be called a "low-cost, low-yield" strategy. As food density increases, animals should shift to progressively more costly feeding methods, i.e. travelling fast and far, which is energetically expensive , but which allows more time, within the constraints imposed, in which to feed. This can be called a "high-cost, high-yield" strategy.

The data needed to test this model are as follows:

i) a measure of the energetic cost of foraging. For this I used day-range length to represent the expenditure of energy in searching for food. Implicit in this is a measure of the average speed of movement over a whole day. [Monthly mean speeds of movement were calculated, in metres per hour, to account for seasonal differences in the length of daylight (11.5 - 13 hours). Even with this adjustment, mean speeds of movement correlated highly with day-range length ($r= .95$ $,p<.001$)].

ii) a measure of the energetic benefits of foraging. For this I used the amount of time spent feeding on fruits and flowers; in terms of the model being tested, the faster an animal travels, the more time there is available for feeding. This measure may have shortcomings for cases where the weight of food ingested is not represented by the amount of time spent feeding on it; the discrepancy is most likely to exist between food parts (e.g. fruits as opposed to flowers), rather than within fruits (the main subject of this analysis).

iii) a measure of food density. From data on tree size, local density, the number of quadrats containing each species, and phenology, I have for each species a measure of the total area of tree canopy with food available to the monkeys. The total for all important species in the diet during a month's 5-day sample gives a figure for the monthly food availability.

Two potential problems in this analysis are the lack of measures of availability of invertebrate foods, and the enormous figures involved in including areas of grass, herbs or leaves available. However, given that the model being tested concerns the maximisation of net energy intake, it seems justified to include only fruit and flowers in the analysis, since the soluble carbohydrates in these foods provide the primary source of ready energy for the monkeys, while invertebrates and foliage involve mainly protein intake (although lipids and proteins can be important sources of longer-term energy). Secondly, the monkeys did select fruit or flowers as the major component of their diet, and thus most of their foraging decisions relating to energy would be concerned with these foods. As I discussed earlier, the need for a nutritive balance in the diet may be satisfied independently from, or in parallel with, the energetic strategy that regulates day-range length and activity-budgets.

In this analysis, calculations of time spent feeding and total fruit and flower availability were made using data from important species only (as defined for other analyses, important species were those contributing to over 5% of the monthly diet). An alternative cut-off point, such as including the five top ranking species each month, produces very similar figures for time spent feeding and total food density.

10.3.1 Results.

As predicted from the model, day-range length and time spent feeding were closely correlated ($r = .66$, $p < .01$): the faster and farther the monkeys travelled, the more they fed (Table 10.1). The model also predicted that these two variables should covary with the density of food, from a "low-cost, low-yield" strategy at low food densities, to "high-cost, high-yield" when food was abundant. This prediction is also borne out: day-range length and food density were highly and positively correlated (r= .74 ,p<.01), as were time spent feeding and food density (r= .72 ,p<.01) (see Table 10.1). Both correlations appear to be logarithmic functions - log transformations on food density produce a better linear fit of the data (r= .77 ,p<.001; and r= .79 ,p<.001, respectively. See Figures 10.1 and 10.2). A logarithmic function may be expected as there will be an upper limit to the amount of food potential an animal can exploit - as the amount of food continues to increase, the curve for feeding time and travel distance must level off to an asymptote.

In conclusion, because of the strong seasonal variation in the density of food that is available at Mt. Assirik throughout the year, the green monkeys adopt a feeding strategy that optimises the balance of costs and benefits associated with any particular density of food. If food is sparce, they use a "cheap" strategy, economising on energy

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Table 10.1. Monthly values for time spent feeding on fruits and flowers (% time), daily distance travelled (metres), and food availability (area in m2).

Month	% Time	Day-range	Food-density
Nov	7.2	952	2,766
Dec	22.4	943	5,180
Jan	42.3	2087	44,844
Feb	14.9	1442	4,549
Mar	29.3	1640	14,184
Apr	25.2	1707	8,418
May	21.0	1670	12,717
Jun	28.7	2020	31,689
Jul	31.0	1639	11,028
Aug	28.2	1273	7,520
Sep	29.8	1639	4,396
Oct	14.2	1588	3,238

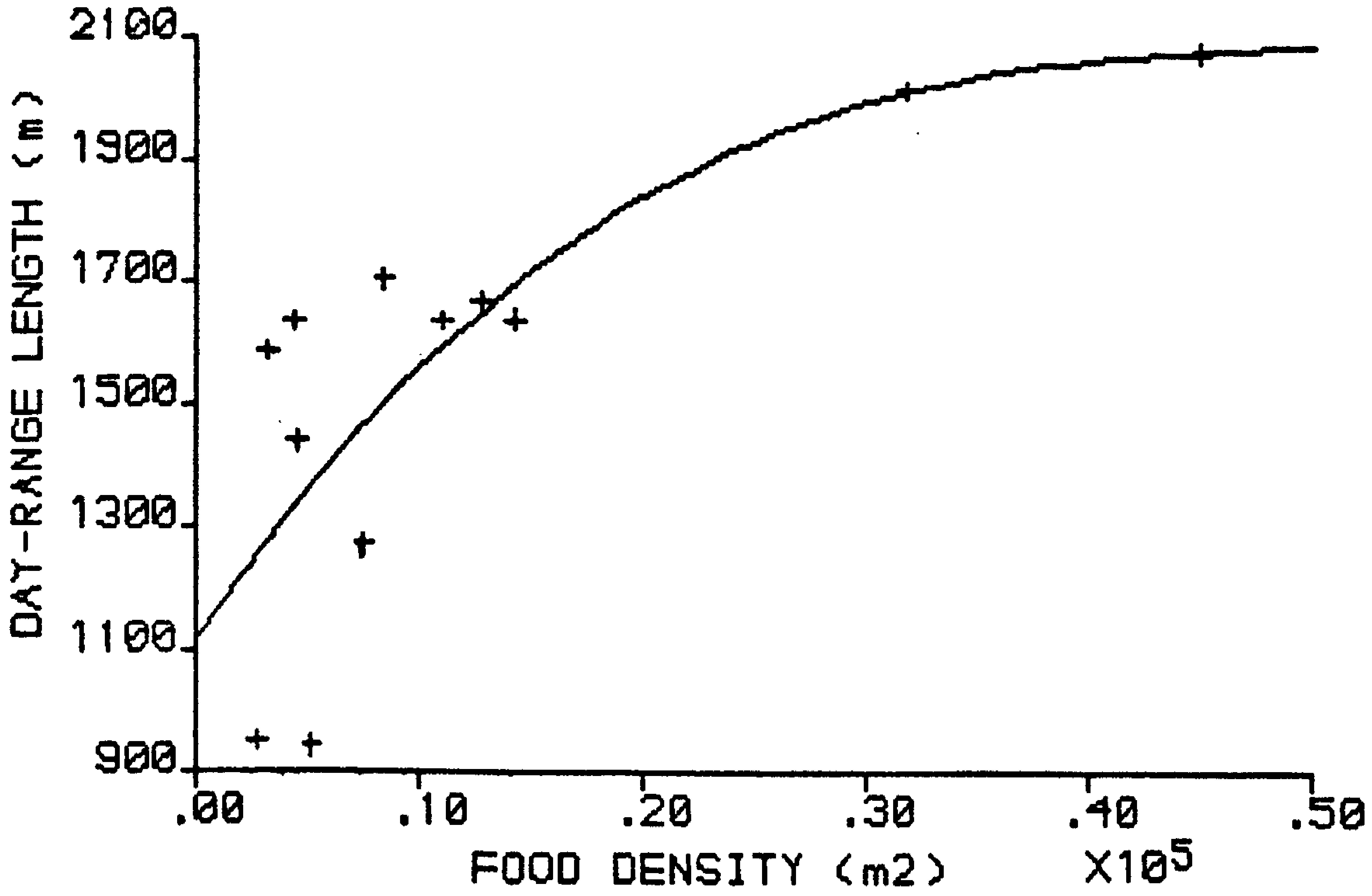

Figure 10.1. Mean monthly day-range lengths plotted against overall monthly food-availability.

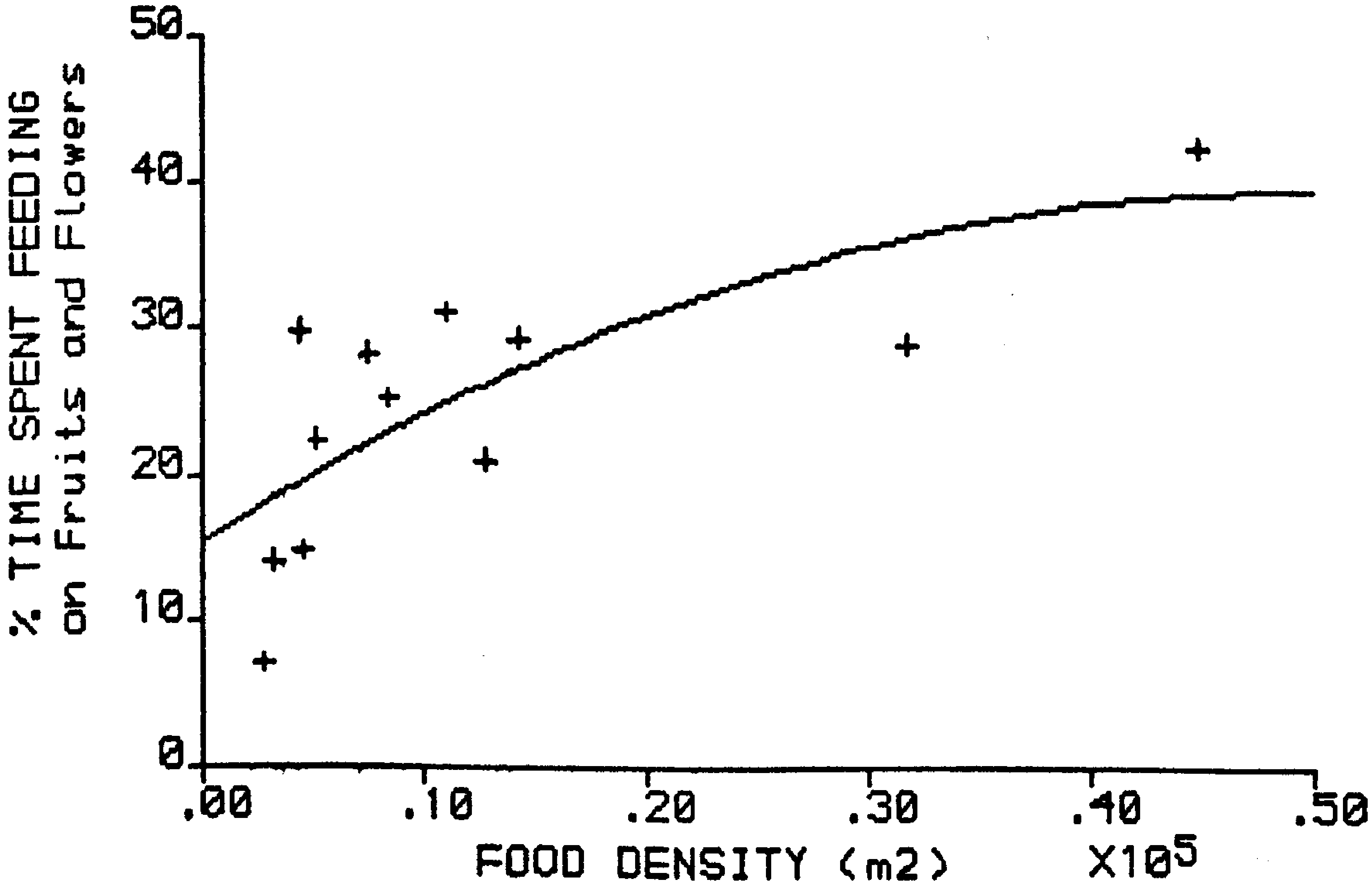

Figure 10.2. Proportions of the monthly diet as fruit or flowers plotted against overall monthly food-availability.

expenditure, and as food density increases, they switch to a gradually more "expensive" strategy, involving increased travel costs, but a higher net return on energy from their increased feeding time.

10.3.2 Time-scale.

Another question that has emerged in the literature on optimal foraging is that of the time scale over which animals are optimising energy, or any other currency (Katz, 1974). For example, foraging behaviour that maximises net energy obtained by an animal over a week or a month may be different to that which optimises over a single day.

In the previous analysis, day-range lengths and time spent feeding were mean figures taken over the monthly 5-day sample periods. There was considerable variation in these measures from day to day; for example, several randomly picked months were examined for daily correlations between the proportion of time spent feeding and day-range length, and no pattern of correlations emerged: January $r= -.15$, March $r= -.44$, June $r= .12$, October $r= -.60$ (all $n=5$, n.s.). Thus, the very high overall correlations shown in the previous analysis strongly suggest that the monkeys were balancing their foraging costs and benefits over a succession of days. There was no consistent pattern from one day to the next because the monkeys would often be feeding on different foods in different parts of their range; one day spent travelling little and feeding intensively in an area of rich fruit supply might be followed by a day of long travelling in search of invertebrates or more widely distributed fruits, or monitoring the state of ripeness or availability of new food sources. Nevertheless, these day to day feeding and ranging plans still remained within the optimal strategy governing "cheap" or "expensive" foraging, and the energetic costs and benefits were balanced over several days.

CHAPTER 11.

CONCLUSION.

11.1 INTRODUCTION.

The significance of findings on the feeding, ranging and activity-budgets of the green monkeys was discussed in detail in each of the relevant chapters, and comparisons with available data from other populations of C.aethiops were made. Chapter 10 provided a functional framework within which each of these aspects of behaviour was drawn together, and related to environmental details. In this concluding chapter, I shall provide an overview of the important elements of the behavioural ecology of the green monkeys at Mt.Assirik, and briefly discuss the important findings from comparisons between widely separated populations of the same super-species of monkey.

11.2 BEHAVIOURAL ECOLOGY.

One of the aims of this study was to go into sufficient detail in the measurement of behavioural and ecological variables that the ways in which environmental pressures shape behaviour could be stated as precisely as possible, and that conclusions should have predictive value. For example, several authors (e.g., see Clutton-Brock, 1977) have referred to the ways in which patterns of feeding and ranging respond to the seasonally changing environment, but few have quantified this relationship, with details of the availability of resources as well as the behaviour of the animals. However, limitations must be stated. Even a year's study of one group of monkeys, and the changes in vegetation and climate pertinent to them during this period, is only a slice out of a continuous, dynamic process, and a brief look into the long life-histories of individuals. For this reason, one must make careful use of any absolute values measured, for example, the size and composition of group or home-range, the amount of time spent feeding, the amount of food available, or the location of territorial boundaries. These variables are not static, with fixed values for one group or population.

However, the importance of using optimality principles and comparative methods to guide research in behavioural ecology is that they help us to understand adaptations. And the assumptions about adaptation in a wild population of monkeys lead us to believe that an adaptive equilibrium exists, at the time of study, between the many environmental forces impinging in any individual. Thinking in these terms leads to the consideration of strategies and principles underlying behaviour, and system atic research over even a single annual cycle allows the testing of hypotheses framed in such terms. Thus, one important theme to emerge from this study was the ways in which the green monkeys' time-budgets, feeding, ranging, and territorial behaviour involved strategies that were carried out according to specific principles.

Firstly, there was an energetic strategy that lay behind different feeding and ranging patterns, according to the amount of available food providing ready energy in the form of soluble carbohydrates. When there was much fruit and flowers, a high-cost ranging strategy provided the best net return of energy from feeding, while a more economic ranging strategy was optimal with lower densities of such resources. Differences in the feeding strategies of lactating mothers also followed such principles, incorporating the added constraints of supporting an unweaned infant.

Secondly, there was an adaptive strategy underlying the monkeys' choice of foods under different conditions. In a patchy environment, there is a trade-off between the profitability of consuming a food-item (in food-value per unit handling time), and its cost of procurement. The monkeys were more selective in their diet when profitable foods were common, while ignoring unprofitable foods, however abundant. Their decision-rules were based on the principles of choosing an optimal diet.

Thirdly, there was a 'nutritive' strategy governing food-choice as well. In parallel with the energetic principles determining ranging and time-budgets, the monkeys included a diet diverse enough to include a range of essential nutrients (for example, by consistent inclusion of insects and leaves, as well as the available fruit and flowers). They seemed also to be minimising their intake of plant secondary compounds, although this was not quantified.

Finally, the green monkeys variable patterns of territoriality were governed by the seasonally changing distribution and density of resources throughout their home-range and the ranges of their neighbours. Again, certain costs and benefits are associated with defending resources, and the balance of these between groups determined the presence or absence of territorial encounters, and the intensity of these encounters.

The precise patterns of range-use within these strategies governing feeding and ranging were determined by interactions of several environmental pressures, in predictable ways: these pressures were temperature, the distribution and density of food, the location of water and sleeping sites, and the occurrence of intergroup encounters.

11.3 DIFFERENCES BETWEEN POPULATIONS.

If these principles underlie seasonal variation in the behaviour of these green monkeys at one site, do they also help us to understand differences in behaviour between populations? In chapter 7, differences in the amount of time spent feeding by vervets in Amboseli were shown to follow this pattern: in general, less time was spent feeding by the vervets than by the green monkeys, in keeping with the relative poverty of their habitat, and their small ranges. Comparable patterns may exist in territoriality between different populations, in their ranging strategies, or in their choice of diet. Unfortunately, detailed measurements of the availability and distribution of food are the key data missing from other studies that are essential for such comparisons.

A semi-terrestrial way of life in a heterogeneous and seasonal habitat is central to the ecology of C.aethiops. Selective pressures have operated towards flexible responses to environmental factors; for example, an omnivorous diet is more adaptable than a specialist diet, allowing a range of strategies to cope with environmental variations in an optimal way. Omnivory does not imply lack of selectivity: the green monkeys were selective when possible, preferring fruits as the major part of the diet when available, or choosing a specific age or part of leaves and leaf species. Similarly, the monkeys chose specific sleeping sites, in the gallery forest: to say that the location of gallery forest is a constraint on where a day's foraging should end seems to imply that behaviour is restricted in some sense. However, in other populations, C.aethiops sleep in open habitats (e.g. Acacia trees in sparse woodland at Amboseli). Thus, at Mt.Assirik it is not that green monkeys cannot sleep in open areas, but that given the circumstances, they behave optimally in choosing dense forest to sleep in, to maximize protection from predators.

Finally, it is interesting to speculate about cognitive differences in monkeys from the same super-species that live in very different habitats. The feeding and ranging 'problems' faced by a green monkey in the complex mosaic of different vegetation-types in a large home-range at Mt.Assirik may be very different from those faced by vervets in the relatively simple, open habitat at Amboseli, where the monkeys cover most of their small ranges during each day's foraging, with good visibility of neighbouring groups, and a relatively narrow range of foods to choose from. A green monkey at Mt.Assirik is thus faced with many more environmentally-oriented decisions in daily life than a vervet at Amboseli. Similarly, because of the thick vegetation, large home-ranges, and varied topography at Mt.Assirik, an adult male that transfers between groups may have little knowledge of the terrain, the location and composition of other groups, and even of some of the vegetation, outside his home-range. Apart from having to locate a potential new group, and form new relationships as he joins, he will also have to learn about a new distribution of resources and possibly even new foods. In contrast, a vervet at Amboseli will see a variety of neighbouring groups each day, and can start forming relationships with members of other groups before transferring. The range of foods and their distribution will be similar to those that he has already experienced.

One way in which these differences are reflected is that social variables seem to be more pervasive through the lives of vervets at Amboseli. The frequency of social contact between mothers, infants and caretakers during infant development is higher at Amboseli than at Mt.Assirik, while physical contact between mothers and their infants alone is longer at Mt.Assirik (separate study, in prep). The frequency of intergroup encounters is far higher at Amoseli, together with greater active involvement by all group members (except infants) in encounters. Dominance relationships amongst adult males, and their level of participation in displays and the herding of females during encounters, also seem important: groups met more frequently around their small ranges at Amboseli, so that the possibility of a foreign male impregnating a female was higher than at Mt.Assirik. Thus, perhaps it is more important for dominant males to herd their own females during encounters. This seemed less significant at Mt.Assirik.

It remains for further research to quantify these variables precisely, and to determine whether other social interactions such as levels of play or grooming are higher at Amboseli than at Mt.Assirik. Milton (1981) has discussed the distribution patterns of foods as an evolutionary stimulus to mental development in different species of primates. If would be intriguing to assess whether any such cognitive differences exist between different populations of the same species, according to differences in the spatial and temporal distribution of plant foods, and their predictability in space and time.

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