

Foraging and feeding behaviour of chacma baboons in a
woodland habitat

by

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Preface

This thesis is the result of my own research, and contains no work done in collaboration, except where otherwise stated. No part of this thesis has been submitted to any other university in application for a higher degree.

Summary

Savannah baboons (*Papio cynocephalus*) have been studied in numerous sites throughout Africa. They have been found to display a wide variety of foraging and feeding behaviours. The aim of this study was to describe and quantify these for a troop in a southern woodland habitat and to determine what factors influence these in order to understand the choices made by baboons. This was done within an optimal foraging framework. The study included the development of random walk and optimal foraging simulation models of day journeys and a comparison of feeding and foraging before and after the troop divided into two daughter troops. The troop lived in a complex mosaic of habitat types with a high tree density. The troop's foraging strategies were found to be consistent with being time minimizers. Distance from the centre of the home range and distance from the nearest sleeping site had the most significant effect on utilisation of the home range. The effect of food availability on habitat use could only be distinguished by the use of simulation models. Comparison of food encountered by the troop and that encountered in the simulations demonstrated that the troop did better than could be expected if the day journey routes were random. The troop's results approximated those of a stochastic short-term optimisation model. The troop's diet consisted of a higher proportion of fruit than previous studies. The troop distinguished between commonly utilised foods and those only occasionally used on the basis of protein/fibre ratio, however food preference between main foods was not correlated with protein/fibre ratio. Any combination of the main foods would fulfil their protein requirement. Evidence is given that, without protein being limiting, the troop's selection amongst the main foods is based on carbohydrate content. After troop fission the daughter troops had shorter day journeys, spent less time walking, more time socialising resting. They also spent more time in food-rich habitats and were more selective in their diet. These results reinforce the important influence in group size and suggest that troop fission may be seen as a time-minimising strategy.

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Chapter 1

Introduction

1.1 Introduction

Savannah baboons (*Papio cynocephalus*) are extreme generalists occurring widely throughout Sub-Saharan Africa. Their only requirements are a constant source of water (baboons generally drink every day, Altmann and Altmann 1970, but see Brain 1988) and suitable cliffs or groves of trees for sleeping sites. They live in troops ranging from 10 to more than 200 individuals (Sharman and Dunbar 1982). These troops generally forage together (but see Anderson 1981) returning together to a safe sleeping site every evening. Their diet is extremely diverse. They feed on fruits, flowers, leaves, roots, exudate of plants, various invertebrates, and occasionally on mammals and birds (nestlings and eggs). The proportions of these food types eaten differ significantly between sites (Whiten *et al.* 1992).

Mkuzi Game reserve was initially chosen as a long-term study site as it represented a typical southern woodland habitat of baboons (Henzi *et al.* in press). The reserve consists of a complex of woodland habitat types many dominated by *Acacia* species. The occurrence of the different vegetation types appears to be determined by the interaction between soil types and water retention. This results in a complex mosaic of vegetation types, which often merge into each other (Goodman 1990). The reserve has a higher density of trees than the typical east African savannah study sites (e.g. Amboseli, Cholo, Gilgil), where much of baboon research has been carried out. Mkuzi appears to be intermediate between these sites and forest study sites such as Gombe in Tanzania and Ishasha, in Uganda. Figure 1.1 shows the location of major baboon study sites in Africa.

Within southern Africa many of the baboon studies have taken place in atypical habitats. They have been studied in: the south-western Cape at a Cape Point Nature reserve (Hall 1962; 1963; Davidge 1977; 1978), which consists of fynbos and coastal vegetation; the Mountain Zebra National park (R. Seyfarth, pers. comm. in Dunbar 1992), a dry, arid fynbos habitat; in the largely treeless Drakensburg mountains (Whiten *et al.* 1987; Byrne *et al.* 1989; Henzi *et al.* 1990; Whiten *et al.* 1992); in the arid Kuiseb canyon in the Namib desert (Hamilton *et al.* 1976; , Hamilton 1985, Hamilton 1986; Brain 1988), Suikerbosrand (Anderson 1981, 1987), a temperate highveld region and in the highly productive Okavango swamps in Botswana

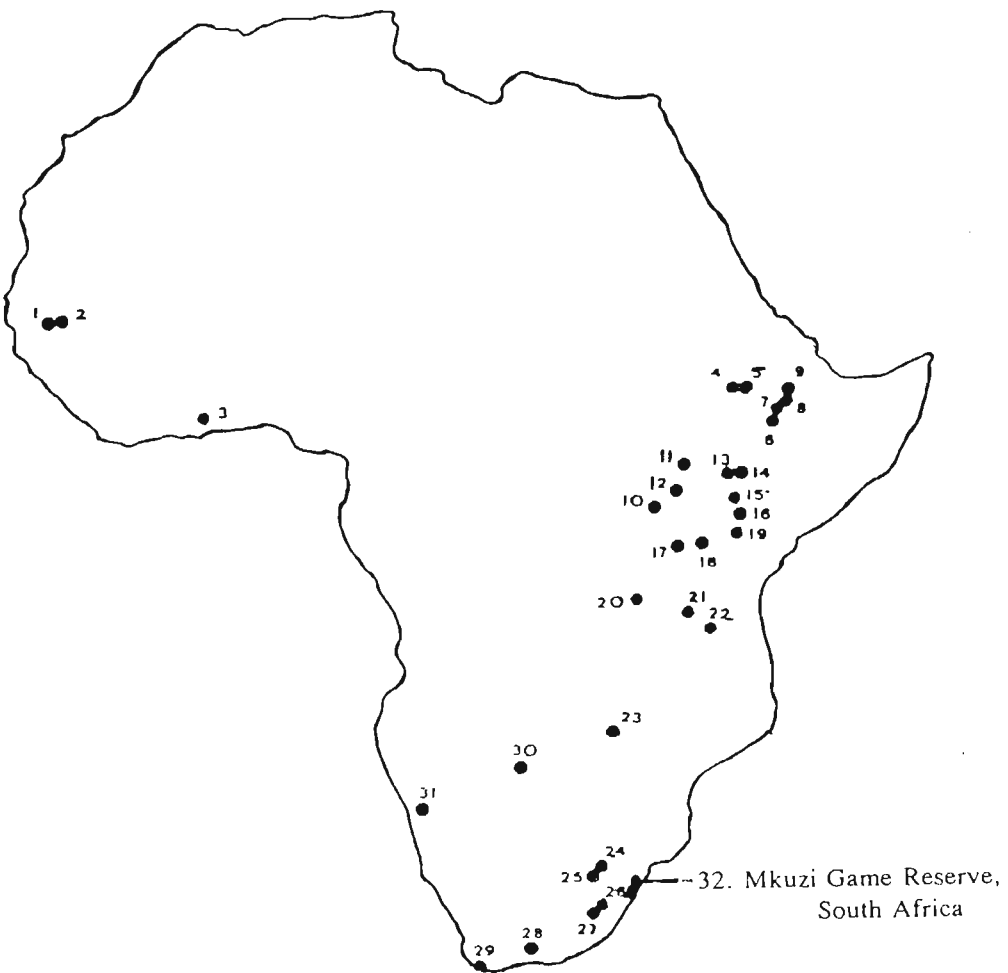


Figure 1.1: Map of Africa showing the location of Mkuzi and the other 31 major baboon study sites. Modified from Dunbar (1992).

Papio cynocephalus papio

1. Badi, Senegal
2. Mt. Assirik, Senegal
3. Shai Hills, Ghana
4. Bole Valley, Ethiopia
5. Mulu, Ethiopia
6. Metahara, Ethiopia
7. Awash Falls, Ethiopia
10. Ishasha, Uganda
11. Murchison, Uganda
12. Budongo Forest, Uganda
13. Chololo, Kenya
14. Laikipia, Kenya
15. Gilgil, Kenya
16. Nairobi NP, Kenya
17. Manyara, Tanzania
18. Serengeti NP, Tanzania

P. hamadryas

8. Awash Station, Ethiopia
9. Erer Gota, Ethiopia

P. cynocephalus cynocephalus

19. Amboseli, Kenya
20. Gombe, Tanzania
21. Ruaha, Tanzania
22. Mikumi, Tanzania
23. Kariba, Zimbabwe

P. cynocephalus ursinus

24. Honnet, South Africa
25. Suikerbosrand, South Africa
26. Giant's Castle, South Africa
27. Drakensburg, South Africa
28. Mt. Zebra NP, South Africa
29. Cape Point, South Africa
30. Okavango, Botswana
31. Kuiseb, Namibia
32. Mkuzi Game Reserve, South Africa

(Hamilton *et al.* 1976; 1978; Bulger and Hamilton 1987) . There have also been studies in more typical warm, woodland habitats, at Kariba in Zimbabwe (Hall 1963), and Honnet in the Transvaal (Stoltz and Saayman 1970) however these have been relatively short term studies. Thus the choice of Mkuzi was of interest both because of its intermediate nature, between typical savannah and forest, as well as an interest in providing complementary data to the studies in atypical habitats in southern Africa.

1.2 Aims of study

The objective of this study was to examine the habitat utilisation, foraging and feeding behaviour of chacma baboons in a typical southern woodland habitat. This was done within the broad framework of optimal foraging theory in order to see if this theory could successfully be applied to an omnivorous generalist. The aim was not to test whether the members of the Mtshopi troop were optimal foragers *per se*, but to see whether this approach could be successfully used to develop a better understanding of baboon responses to foraging in a relatively complex environment.

1.3 Subjects

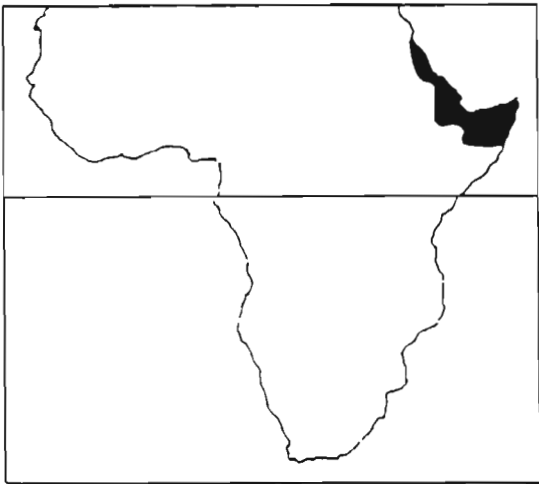
The study troop (Mtshopi troop) of chacma baboons (*Papio cynocephalus ursinus*) was studied at Mkuzi Game Reserve in Zululand, South Africa. The distribution of these baboons includes most of the southern third of Africa, from the southern regions of Angola, Zambia and Mozambique to Cape point (Figure 1.2). The Mtshopi troop consisted of 59 individuals at the start of this study (count- March 1989) and had grown to 76 individuals by March 1990. In April 1990 the troop split into two daughter troops, Darth's troop and Flash's troop. Darth's troop consisted of 43 individuals and Flash's troop consisted of 28 individuals.

1.4 Note on the taxonomy of the chacma baboon

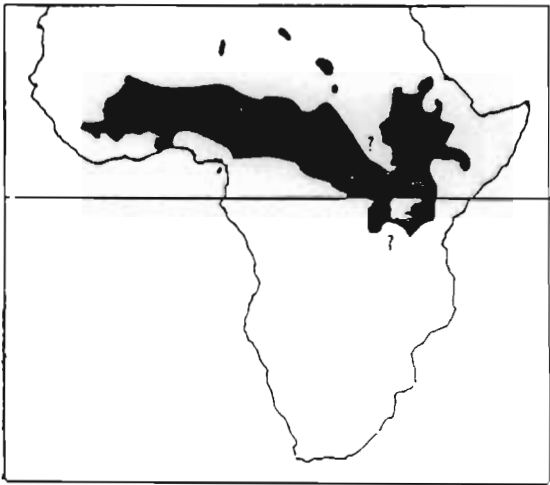
The chacma baboon is widely referred to as *Papio ursinus*, one of five nominal species of the genus *Papio*. However, this thesis follows the consensus of the taxonomists and primatologists who argue that these species are better considered as subspecies, both on the basis of their apparent behavioural continuum (Smuts *et al.* 1987; Dunbar 1992) as well as on genetic evidence (Shotake *et al.* 1977; Kawomuto *et al.* 1982). Thus the nominal species, *Papio cynocephalus* (yellow baboon), *P. anubis* (olive baboon), *P. papio* (guinea baboon) and *P. hamadryas* (hamadryas baboon) are referred to as subspecies of *P. cynocephalus* (e.g. *P. cynocephalus anubis*) in this thesis.

1.5 Optimal foraging theory

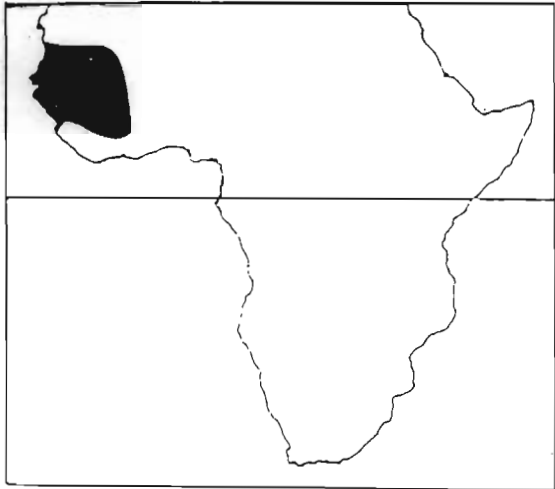
Optimal foraging theory is based on the premise that animals adjust their behaviour in



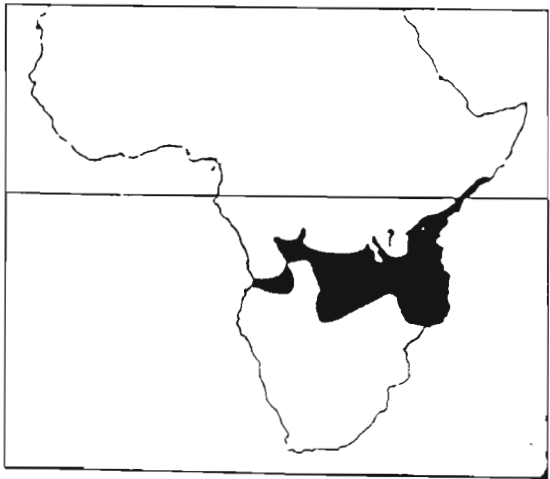
Hamadryas baboon, *P. cynocephalus hamadryas*



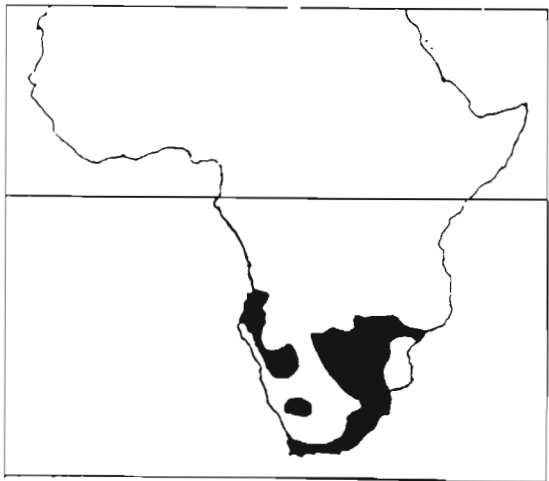
Olive baboon, *P. cynocephalus anubis*



Guinea baboon, *P. cynocephalus papio*



Yellow baboon, *P. cynocephalus cynocephalus*



Chacma baboon, *P. cynocephalus ursinus*

Figure 1.2: Distribution of the five sub-species of *Papio cynocephalus*. After Dorst and Dandelot (1976).

searching for and exploiting food in such a way as to maximise their rate of energy intake. It attempts to predict what methods animals should use to search for food, which food items they should choose to eat and how long to spend searching and feeding. Testing and developing models are not done in order to decide whether animals are optimal foragers or not. Evaluation and modification of the models serves an heuristic function, in terms of understanding the adaptations animals must make in response to differing constraints, abundances and distribution of foods (see Schoener 1987 for discussion of the validity and reasons for the optimal foraging approach).

Despite the potentially broad application of this theory, it has been used generally to "solve relatively tractable problems of single-resource exploitation in fairly simple field situations when only short-term optimisation is being considered" (Barton *et al.* 1992). Primate studies are normally interested in the long term consequences of foraging decisions and, in general, lack quantitative estimates of food availability and distribution (but see Hladik 1977 and Watts 1991). Consequently, there have been few optimal foraging studies of primates. Those that have been done have concentrated on the choice of food items (Milton 1980; Waterman and Choo 1981; Whiten *et al.* 1992) rather than on foraging strategies related to movement.

Baboons are interesting in terms of optimal foraging since they occupy habitats that differ greatly in availability, composition and distribution of food. They have the potential to offer insight to how a single species is able to adjust its behaviour to exploit very different circumstances of food distribution and abundance. At the same time their group living, large home range sizes and large number of different food items mean that studies of optimal foraging are logistically difficult. Consequently, it is only recently that studies have addressed questions of optimal foraging in relation to actual food availability (Barton *et al.* 1992; Henzi *et al.* 1992).

These and other studies of baboon ranging behaviour (Post 1978; Rasmussen 1979; Sigg and Stolba 1981) suggest that the ranging behaviour of baboons cannot be explained only in terms of optimisation of a single resource such as food. Altmann and Altmann (1970), Post (1978) and Barton *et al.* (1992) have all demonstrated that the distribution of water sources and sleeping sites play a major role in habitat use of baboons. Consequently, optimal foraging must be viewed within the constraints of the needs of having to access water and to leave from, and return to, sleeping sites every day. In addition there is evidence for both predation risk (Byrne 1981; Rasmussen 1983) and thermal costs (Stelzner and Hausfater 1986; Stelzner 1988) further constraining troop movement. Thus foraging behaviour is likely to represent a

compromise between these various constraints and the maximisation of the rate of food intake.

Optimal foraging has many aspects ranging from choice of home range, choice of day journey route, choice of food items, allocation of time both temporally and spatially, and size of foraging group. This thesis attempts to address these aspects. Chapter 2 starts with a description of the home range that emphasises the availability and distribution of food. It also examines whether day journey length is determined by food availability and whether the members of the Mtshopi troop are time minimizers or energy maximisers. Chapter 3 aims to define the constraints on the troop's pattern of home range use. In chapter 4 I determine whether the choice of day journey routes and allocation of time along them represent an optimal strategy. During this study the study troop split into two daughter troops, offering the rare opportunity for quantitative investigation of the effects of troop fission. Chapter six examines the consequences of the split in terms of habitat utilisation and foraging and more generally the costs and benefits of group living.

Chapter 2

Ranging and foraging effort of baboons in relation to food availability in a woodland habitat

2.1 Introduction

Descriptions of home range use have been made for almost every long-term study of baboons (Amboseli: Altmann and Altmann 1970; Post 1978, Kuiseb canyon: Hamilton *et al.* 1976, Hamilton 1986, Okavango: Hamilton *et al.* 1976, Gilgil: Harding 1976, Cape Point: Davidge 1978, Mikumi: Rasmussen 1979, 1983, Mt. Assirik: Sharman 1981, Suikerbosrand: Anderson 1981, Drakensburg: Henzi *et al.* 1992, Laikipia: Barton *et al.* 1992). Consequently a large body of data exists on the basic dimensions of range use. Comparative studies of these data have been made especially with respect to home range size (Sharman 1981; Dunbar 1988 and Barton *et al.* 1992) and day journey length (Sharman and Dunbar 1982; Dunbar 1988 and Barton *et al.* 1992).

Current understanding suggests that for primates the type of diet, nutritional quality of food, distribution of food, foraging group size, species' body weight and density of neighbouring troops all interact to affect home range size (Dunbar 1988). Since the home range is determined by the sum of day journeys, day journey length is also a function of these factors.

Within a species, diet and body weight is to a large extent held constant. Therefore home range size and day journey length at different study sites is assumed to be a function of food availability once the effects of group size have been partialled out (Dunbar 1988). Similarly, seasonal changes of home range size and day journey length of a troop are assumed to mirror changes in food availability within the home range (Davidge 1978; Anderson 1981; Dunbar 1988). Field studies support the assumption of a relationship between home range size, day journey length and food availability between sites. Baboons show a decrease in the median size of home range per animal and day journey length per animal when roughly grouped into habitat types of increasing food availability (Dunbar 1988). Barton *et al.* (1992) also found a significant negative correlation between annual rainfall (an estimate of food availability) and day journey length, although they found no similar correlation with home range size and annual rainfall. According to the authors this lack of correlation may be due to different methods that were employed in calculating home range size

(Barton *et al.* 1992) or to the lack of more refined methods for comparing habitat quality and, in particular, food availability (see Dunbar 1988 p.45).

Evidence for the relationship between monthly/seasonal changes in day journey and changes in food availability within the home range are not apparent at all study sites. While Anderson (1981) found that baboons at Suikerbosrand ranged further in the dry season than in the wet season, Sharman (1981); Altmann and Altmann (1970) and Post (1978) found no significant seasonal difference in day journey length of baboon troops. Implicit in these studies is the assumption that food is in short supply in the dry season. However, with no direct assessment of food availability in the different seasons, the conclusion that food availability does not affect day journey length is inconclusive. In a study that measured actual food availability Henzi *et al.* (1992) did find that day journey lengths were longer when food was scarce. Alternative evidence further suggests that food availability does have an effect on day journey length: for example Altmann and Maruthi (1988) showed that a semi-provisioned wild troop of baboons had a smaller home range and shorter day journey lengths than a neighbouring troop of similar size.

While some trends are apparent from the available data it is clear that further understanding of the determinants of home range use depends on quantitative data being made available on the actual habitats in which study troops live, particularly data relating to the density and distribution of trees and shrubs (Dunbar 1988) and direct measures of food availability (Barton *et al.* 1992). Consequently the first part of this chapter is given to a quantitative description of the study troop's (Mtshopi troop) home range and the amount and pattern of food availability within it.

The second part of the chapter addresses the relationship between home range size, day journey length and food availability, both from a comparative basis and in relation to changes in food availability through the year. Two questions are emphasised: (i) Do patterns reflect a strategy of time minimising or energy maximising as defined by Schoener (1971) and (ii) Does the troop conform to the prediction of longer average quadrat residency during periods of scarcity as predicted on the basis of optimal foraging theory (Rozenzweig 1985, also see Krebs and McCleery 1984; Stephens and Krebs 1986; Melton 1987).

The third part of the chapter examines whether the Mtshopi troop conforms to the predictions of home range use put forward by Hamilton and Watt (1970) in their refuging model. This model suggests that home ranges are differentiated into two

zones: (i) biodeterioration zones which are near sleeping sites and where animals visit often for short periods and (ii) areas of resource acquisition which are further from sleeping sites and are visited for longer periods. Sigg and Stolba (1981) found support for this model from a troop of hamadryas baboons which used a single sleeping site. They also presented some evidence that savannah baboons using more than one sleeping site (Altmann and Altmann 1970) did not differ in this pattern of differential home range utilisation. Consequently this chapter aims to investigate if this model, which was originally developed to explain habitat utilisation in groups using a single refuge, could be applied to the Mtshopi troop which used several sleeping sites.

Analysis of more detailed patterns of home range use by the Mtshopi troop in relation to food are undertaken in Chapter 3 on the correlates of home range use and in Chapter 4 which concentrates on day journey routes and the allocation of time on them.

2.2 Materials and methods

2.2.1 Study site and animals

The study troop (Mtshopi troop) consisted of 59 individuals at the beginning of the study (March 1989). By March 1990 the troop had increased to 76 individuals. In April 1990 the troop split into two daughter troops. Although the study continued after the split (see chapter 6) the behavioural data in this chapter is restricted to the Mtshopi troop before the split.

The study troop occupies a home range in the south western section of Mkuzi Game Reserve (latitude 32°38'S longitude 32°08'E) in north eastern Zululand, South Africa (Figure 2.1). The troop's home range is situated in the foothills of the hilly Lebombo mountains (480m asl) and the adjacent coastal plain of Cretaceous sediments and Quaternary dunes (100-150m asl) (Goodman 1990). The climate is warm and arid with a mean annual temperature of 22.40°C and a mean annual rainfall of 630mm most of which falls in the wet season (October to March). This period is hot with temperatures above 40°C. The winters are dry and warm (April to September) and are characterised by a water deficit (Goodman 1990). This study formed part of a long-term study of a habituated troop of baboons, *Papio cynocephalus ursinus*, inhabiting a mixed woodland habitat (see Henzi *et al.* in press). The reserve is representative of three veld types: Coastal forest and thornveld, Lowveld, and Zululand thornveld (Acocks 1975). The long-term study started in 1986. The field work for the present study took place from January 1989 till December 1990, though data on troop

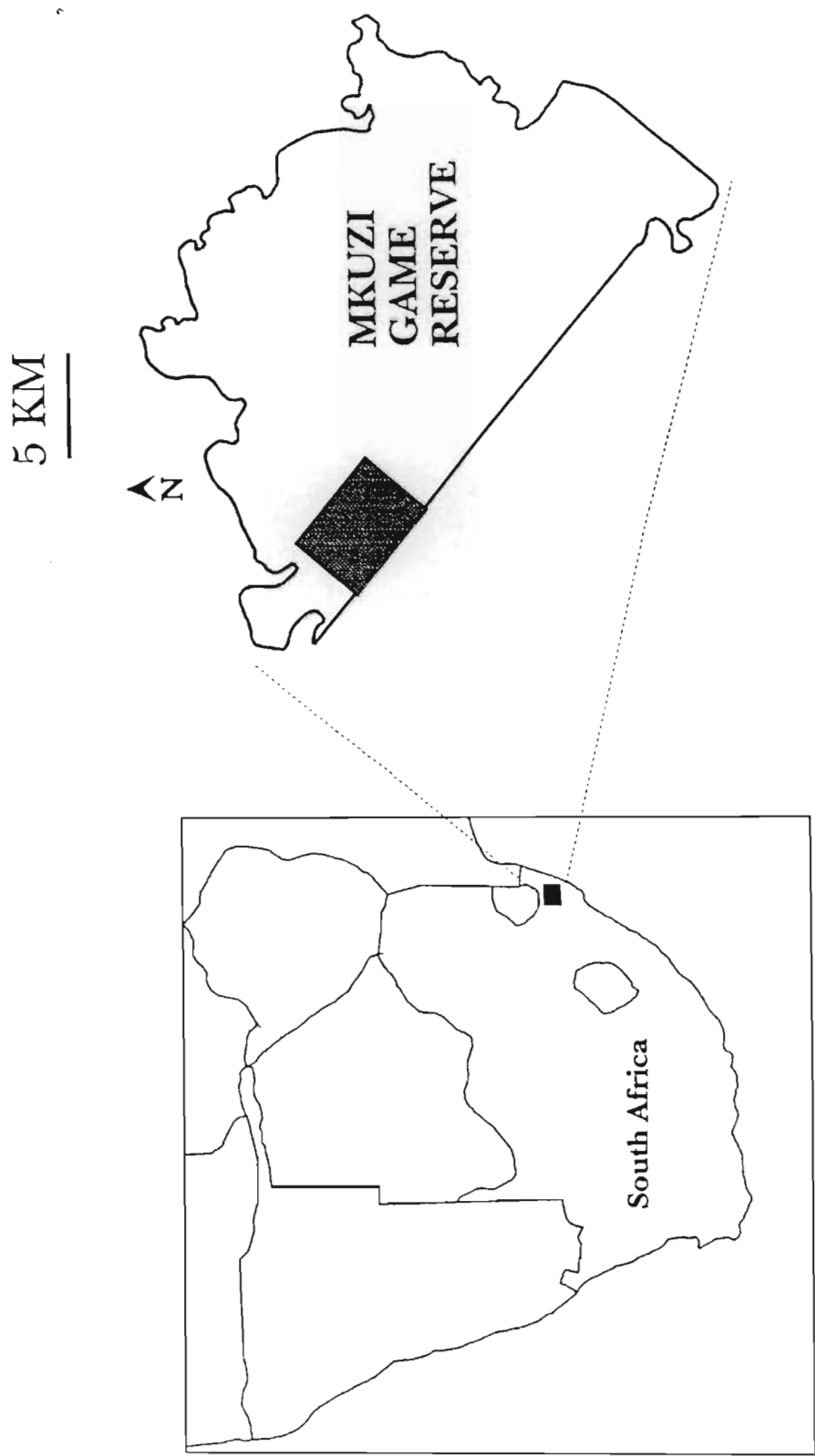


Figure 2.1: Location of Mkuzi game reserve in relation to Southern Africa (from Henzi *et al.* in press).

movement presented here is based on 70 full day follows over the period May 1989 to April 1990 after which the troop split into two new troops. During this period the rainfall was higher than normal (rainfall 1989 = 932mm; mean annual rainfall = 600mm).

2.2.2 Habitat description and vegetation sampling

Initial examination of the home range led to the subjective classification of the home range into seven habitat types, based on the dominant plant species, density of trees, and vegetation structure. The habitat descriptions were based on stratified random vegetation sampling at 1300 points throughout the home range. These comprised 200 samples in each habitat except hilly *Combretum* rocky outcrops (HCR) where only 100 points were sampled due to the small amount of area covered by this habitat type. The sampling was carried out according to the point centred quadrat (PCQ) method (Pielou 1959). Transects consisted of 5 sampling points. These were located randomly within the different habitats. At each point the distance to the nearest tree, shrub, forb and grass in the four quadrats aligned about the axis of the transect line were selected. The species, distance from the point, and the size of the species was measured. For trees and shrubs determination of size involved measuring or estimating (if over 2m in height) the height and canopy diameter. For forbs and grasses only height was measured. The densities of the different species (for method see Pielou 1959) and the median height of the trees and shrubs were then calculated for each habitat type as well as the median height of the trees and shrubs. These data were used in the quantitative description of the habitat types and in calculating the density and size structure of food species in different habitat types.

2.2.3 Mapping of habitat types

A map of the distribution of habitat types in the home range was drawn by tracing the borders of habitat types from a series of low level colour aerial photographs of the home range. It was possible to distinguish the different habitat types on the photographs by the different size, density and colour of the trees in the different habitats. Where there were any uncertainties as to habitat type or the exact borders, these were determined by reconnaissance of the area on foot.

2.2.4 Calculation of food availability

Estimation of food availability was carried out for all food items that constituted 80% of the feeding time in any month (32 species). Exceptions were grass leaves, *Cyperus* spp. corms and invertebrates. These only accounted for 6.48% of the total time spent feeding and 2.08% of the troops estimate of food intake by mass. All the remaining

food items were obtained from trees and shrubs.

The proportion of food trees with food on them, and the mean percentage of food items each tree contained was determined by the following method. A minimum of 20 trees of each food species were visited each month and the percentage of food items on each tree was recorded. This was a subjective assessment based on a scale where 100% represented the maximum amount of food items and 0% no food items. Since all the monitoring was carried out by the author the estimates are reasonably standardised.

Together with the data on density and height structure of food species obtained from the initial vegetation survey, the monthly surveys enabled me to calculate the number of individual trees of each food species which had food items per hectare, for each habitat type. The mean percentage of food items per tree was also calculated.

Estimation of dry mass of baboon food was measured and calculated using the following method: food items from several trees of each baboon food species were collected. For each tree sampled, the percentage of food items present, and the height was estimated. All food items were removed from an individual tree or when this was not feasible a tree was sub-sampled by removing 1/2 or 1/4 of the food items. These were then processed as would a feeding baboon in order to use only the food that was ingested by baboons. For example; hard shells were discarded (e.g. cover of *Strychnos madagascariensis* fruit) or flesh scraped off the pip (e.g. flesh of *Sclerocarya caffra*). The samples were then dried at 37°C until they reached a constant mass (see Hladik 1977 for methods). They were weighed in order to determine the production of that tree in terms of dry mass of baboon food yielded by the tree or shrub. When trees were sub-sampled, the total dry mass of baboon food yielded by the tree was extrapolated according to the proportion of the tree sub-sampled.

At this stage the production of a tree of a specific height and containing a certain percentage of food items for each food species was known. This yield had to be extrapolated to trees of different heights which contained various percentages of food items. To do so I made the assumption, that the production of food items increases linearly with tree volume. Equations expressing volume as a function of individual height were used to determine a tree's volume by extrapolation of height data. The dry mass of baboon food yield for any tree could then be extrapolated from the yield of the sampled trees by the use of the volume equations. Appendix A shows species

specific tree shapes and the volumetric equations used.

The production of each species of tree in each habitat for every month was calculated using the following equation:

$$TP_{ij} = med(H_{ij}) \times fV_{ij} \times \frac{EP_{ij}}{100} \times d_{ij} \times PP_i$$

where:

TP_{ij} is the total production of edible parts by species i in vegetation zone j .

$med(H_{ij})$ is the median height of species i in vegetation zone j .

fV_{ij} is the function describing the volume of species i in terms of tree height.

EP_{ij} is the mean estimate of the percentage of production of food parts for species i in habitat j for month k .

d_{ij} is the density of species i in habitat j .

PP_i is the projected production in grams dry mass of edible parts by species i .

Calculation of this for each food item resulted in a monthly estimate of baboon food availability. This was expressed in kilograms of dry weight per hectare for each food item in the different habitat types. The estimates of mass of baboon food per hectare for each species was then summed for all the habitat types to produce total production estimates in each habitat for each month.

2.2.5 Ranging data

The ranging data was collected during 70 full day follows. The troop was followed on foot from the time it left the sleeping site until it moved onto a sleeping site in the evening. The troop's position was marked at ten minute intervals on a 1:20,000 contour map and the route between the current and previous point drawn in.

The troop's home range size for the 12 months of the study was estimated by counting the 4 ha quadrats entered by the troop during the study together with any quadrats enclosed by them. A plot of cumulative estimates of home range size was used to see if it reached an asymptote and was therefore a realistic estimate of home range size for the period (Appendix B). The day journey length was calculated by digitising the day journey routes drawn onto the 1:20,000 map.

Quadrat residency was calculated by recording at 10 minute intervals the identity of

the quadrat in which the troop was. From these data the total time spent in a quadrat was calculated by summing the number of times the troop was recorded in that quadrat. The duration of stay was also calculated by counting the number of 10 minute time periods the troop remained in a quadrat. From this the mean duration of stay in a quadrat could be calculated.

2.3 Results

2.3.1 Home range size

The troop's home range size over the 12 month period was 24.42 km².

2.3.2 Habitat description

Seven habitat types were recognised. Illustrated summaries of the seven habitat types in the home range are given in Figure 2.2. The aim of this figure is to combine quantitative data with a representation of habitat structure. The number of trees in the habitat drawings reflect the mean density of trees in the different habitats. The species drawn are the most abundant species in each habitat. The number of trees in each diagram reflect the relative abundance of each tree species. The number of species in each diagram represent the relative diversity of species in each habitat. The trees are drawn to scale representing the growth form and median height for that species in each habitat type. The density of woody species above 2m in height (D), the index of diversity (NI-Hill's diversity index) (Ludwig and Reynolds 1988 pg. 90) and the clumping index (CI-index of clumping) (Ludwig and Reynolds 1988 pg. 38)for each habitat type are given at the top of the diagrams.

Acacia mixed woodland (ACW)

Acacia mixed woodland in the troop's home range forms a matrix within which other habitat types occur. It is open woodland dominated by several *Acacia* spp., mainly *A. karroo*, *A. nilotica*, *A. nigrescens*, *A. tortilis* and *A. gerardii*. These occur in conjunction with trees such as *Sclerocarya caffra*, *Dombeya rotundifolia*, *Combretum apiculatum* and *Ziziphus mucronata*. The dominant grass in the open areas is *Themeda triandra* with several species of *Panicum* dominant in shady areas.

Acacia karroo forest (AK)

Acacia karroo forest occurs on hill slopes of thuyolitic soils where drainage is poor and consists of nearly monospecific stands of *A. karroo* 2-4m in height. Consequently this

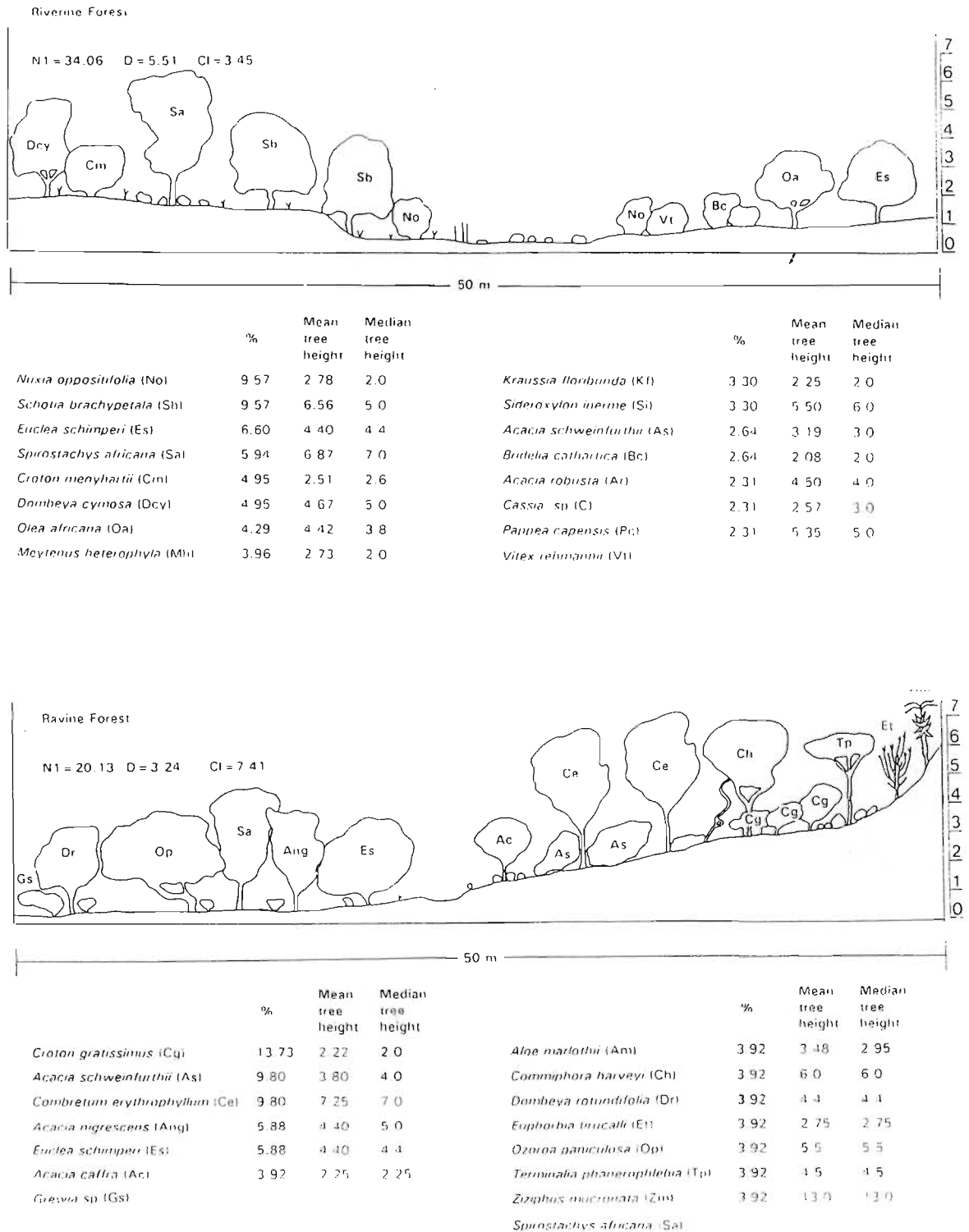
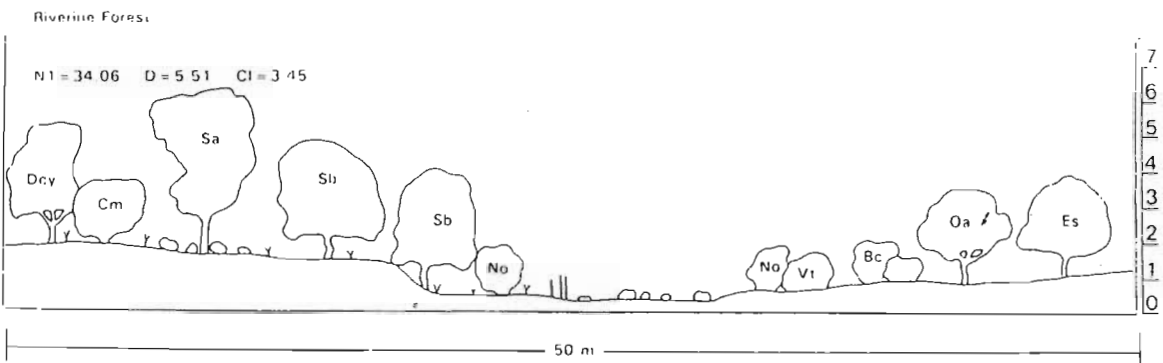
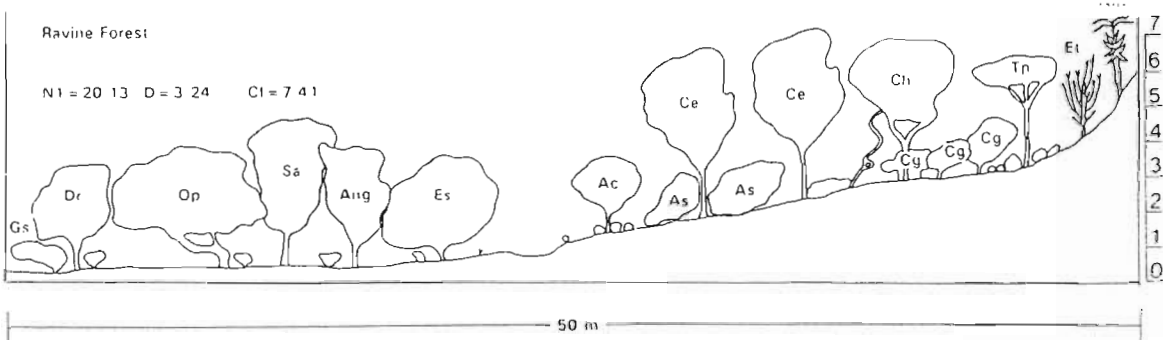


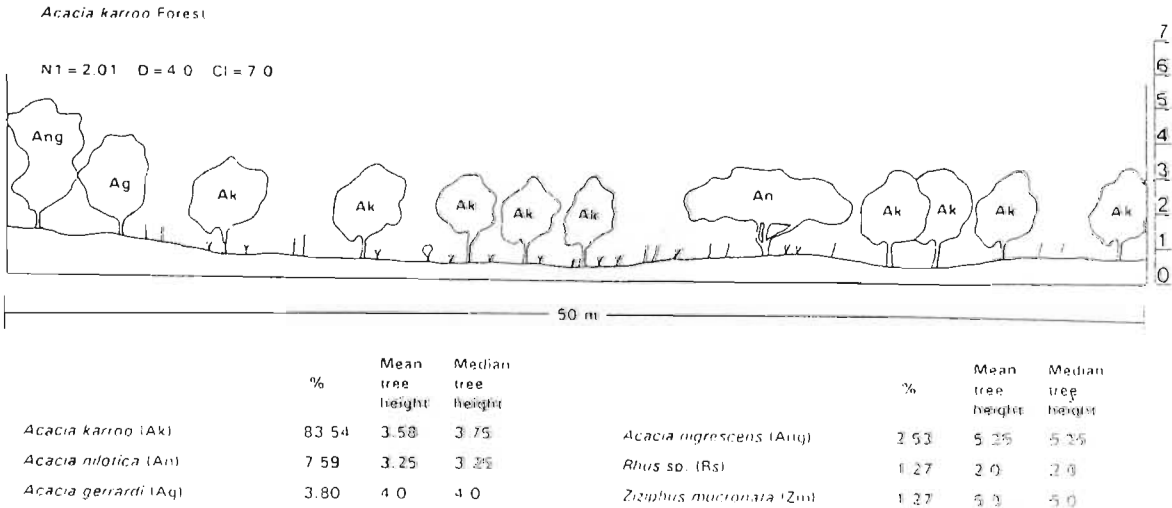
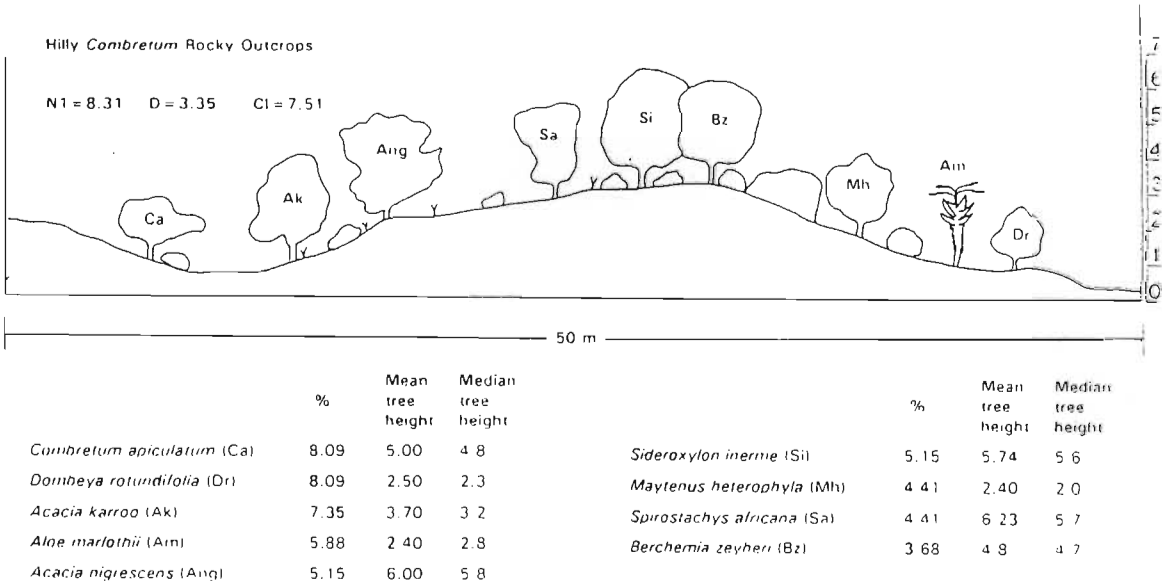
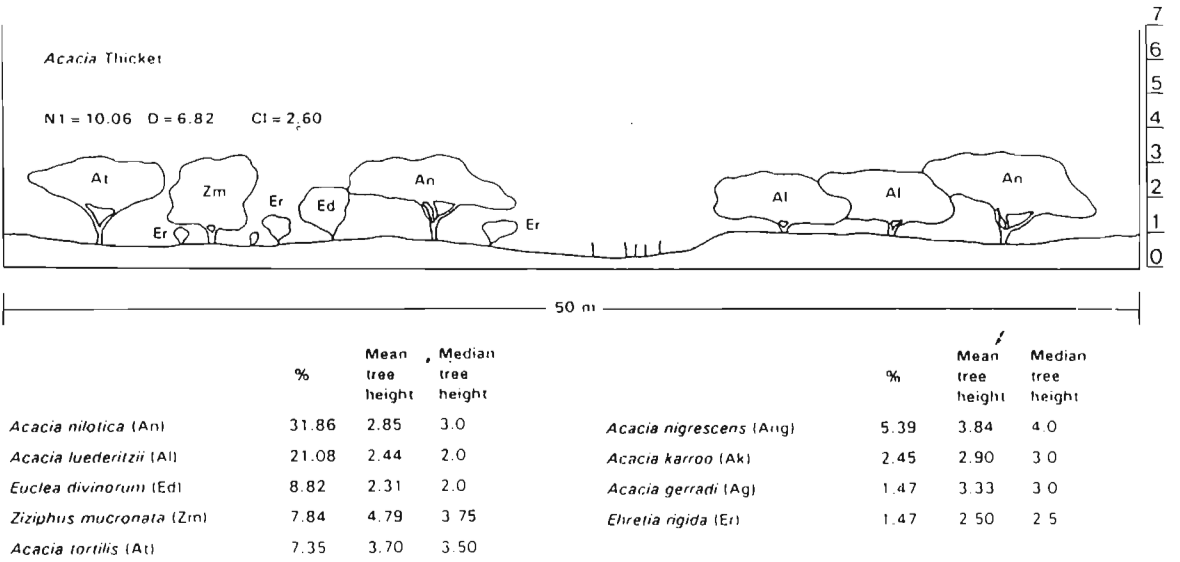
Figure 2.2: Diagrams of the 7 habitat types in Mtshopi troop's home range. $N1$ is the diversity index, D is the mean density of trees in the habitat, CI is the clumping index. The percentage column (%) gives the proportion of the trees in the habitat consisting of each species. The mean tree height and median tree height for each species is also shown. The y axis shows the median height in metres of each species. For more details see text.



	%	Mean tree height	Median tree height		%	Mean tree height	Median tree height
<i>Nuxia oppositifolia</i> (No)	9.57	2.78	2.0	<i>Kraussia floribunda</i> (KI)	3.30	2.25	2.0
<i>Schotia brachypetala</i> (Sh)	9.57	6.56	5.0	<i>Sideroxylon inerme</i> (Si)	3.30	5.50	6.0
<i>Euclea schimperi</i> (Es)	6.60	4.40	4.4	<i>Acacia schweinfurthii</i> (As)	2.64	3.19	3.0
<i>Spirastachys africana</i> (Sa)	5.94	6.87	7.0	<i>Bridelia cathartica</i> (Bc)	2.64	2.08	2.0
<i>Croton menyanthi</i> (Cm)	4.95	2.51	2.6	<i>Acacia robusta</i> (Ar)	2.31	4.50	4.0
<i>Dombeya cymosa</i> (Dcy)	4.95	4.67	5.0	<i>Cassia</i> sp. (C)	2.31	2.57	3.0
<i>Olea africana</i> (Oa)	4.29	4.42	3.8	<i>Pappaea capensis</i> (Pc)	2.31	5.35	5.0
<i>Meytenus heterophylla</i> (Mt)	3.96	2.73	2.0	<i>Vitex rehmannii</i> (Vt)			



	%	Mean tree height	Median tree height		%	Mean tree height	Median tree height
<i>Croton griffithianus</i> (Cg)	13.73	2.22	2.0	<i>Aloe marlothii</i> (Am)	3.92	3.48	2.95
<i>Acacia schweinfurthii</i> (As)	9.80	3.80	4.0	<i>Commiphora harveyi</i> (Ch)	3.92	6.0	6.0
<i>Combretum erythrophyllum</i> (Ce)	9.80	7.25	7.0	<i>Dombeya rotundifolia</i> (Dr)	3.92	4.4	4.4
<i>Acacia nigrescens</i> (Ang)	5.88	4.40	5.0	<i>Euphorbia tirucalli</i> (Et)	3.92	2.75	2.75
<i>Euclea schimperi</i> (Es)	5.88	4.40	4.4	<i>Ozoroa paniculosa</i> (Op)	3.92	5.5	5.5
<i>Acacia caffra</i> (Ac)	3.92	2.25	2.25	<i>Terminalia phanerophyllous</i> (Tn)	3.92	4.5	4.5
<i>Grewia</i> sp. (Gs)				<i>Ziziphus mucronata</i> (Zm)	3.92	13.0	13.0
				<i>Spirastachys africana</i> (Sa)			



habitat had the lowest index of diversity. Interspersed in these stands are other species of *A. nilotica*, *A. gerrardii*, *A. nigrescens* and *Z. mucronata*.

Acacia leuderitzii thicket (AT)

A. leuderitzii thickets are dense thickets typically 2-3m high occurring on poorly drained clay soils. The three dominant woody species are *A. leuderitzii*, *A. nilotica* and *Euclea divinorum*. Grasses are sparse, mainly consisting of *Dactyloctenium australe* and *Entereopogon monostachys*.

Combretum woodland (CW)

Combretum woodland occurs mainly in the foothills. It is an open woodland where the dominant tree is *Combretum apiculatum* occurring with other tree species such as *Aloe marlothi*, *A. gerrardii*, *A. karroo*, *Dombeya rotundifolia* and *Ozoroa paniculosa*. The dominant grass is *T. triandra*. CW is more open than ACW having a lower density of trees. The dominance of the single species *C. apiculatum* in CW results in a lower species diversity (NI) than ACW.

Hilly *Combretum* rocky outcrops (HCR)

Hilly *Combretum* rocky outcrops occur in the foothills where rock formations project above the soil on hill sides. This forms a catchment for moisture which supports a unique vegetation consisting of a closed canopy bush/tree clump. The centre contains relatively large trees such as *Sideroxylon inerme*, *Spirostachys africana*, and *Berchemia zeyheri*. The periphery of these clumps consists of trees more common in open woodland such as *C. apiculatum* and *D. rotundifolia*.

Ravine forest(RA)

This habitat occurs wherever there is a steep rocky slope leading down to a river bed. It is a closed canopy forest with a wide diversity of tall trees such as; *Commiphora harveyi*, *Combretum erythrophylum*, *Strychnos usambarensis*, *Cladostemon kirkii*, and *Euphorbia tirucalli*. It has a fairly well developed understorey consisting of *Croton gratissimus* and *A. schweinfurthii*. It is the most dense habitat type in the home range.

Riverine forest (RI)

Riverine forest varies from well developed forest to an open woodland of tall trees. This is the most diverse habitat type with common tree species being *Schotia brachypetala*, *Nuxia oppositifolia*, *Euclea schimperii*, *Olea africana*, *Spirostachys africana* and *A. robusta*.

The average density of trees (>2m) throughout the home range was calculated by multiplying the mean density of trees in the different habitat types by the proportion of the home range covered by the particular habitat types. This gave 283.54 trees/ha.

2.3.3 Distribution of habitat types in home range

The home range consists of a mosaic of habitat types within a matrix of *Acacia* mixed woodland over most of the area (Figure 2.3). The only extensive habitat type confined to a single area is *Acacia luederitzii* thickets which occur on the relatively flat coastal plain towards the north eastern boundary of the home range. The numerous rivers and streams ensure that patches of riverine woodland/forest occur throughout the home range. The constantly changing topography provides enough diversity of aspect and drainage to ensure conditions for the establishment of areas of the other habitat types throughout the home range.

2.3.4 Seasonal changes in food availability

Figure 2.4 summarises monthly changes in food availability estimates, monthly rainfall and mean monthly day journey lengths. Food availability was lowest in November. It increased consistently, peaking in May before decreasing consistently till it reached its lowest level in November. This pattern did not coincide with the monthly rainfall. There was no correlation between estimates of food availability and rainfall for the corresponding months (Spearman-rank $P=0.347$, $n=12$). There was however a significant correlation when using the sum of the previous 3 months rainfall (Spearman-rank $P=0.020$, $n=12$). There was also a significant regression of food availability with the sum of the previous 3 months rainfall ($r=0.37$, $P=0.0355$, $n=12$). Thus baboon food availability lagged 3 months behind the rainfall: food increased only in December while the monthly rainfall had already risen in September. Rainfall peaked in February while food availability only increased in May when the rainfall had already declined significantly.

Figure 2.5 shows changes in food availability in the different habitats within the home range for different months. When each habitat type is considered separately, it appears the food varied considerably in amount and in availability over time. From November to January ACW was the most productive habitat (in terms of baboon food), while from February to April ATH was more productive. From May to October AKF was the most productive. When the total amounts of food in all months for each habitat type are compared (Figure 2.6), AKF and ATH are the most productive followed by CHR, ACW, RAV, RIV and lastly CH. What is clear is the large changes in food

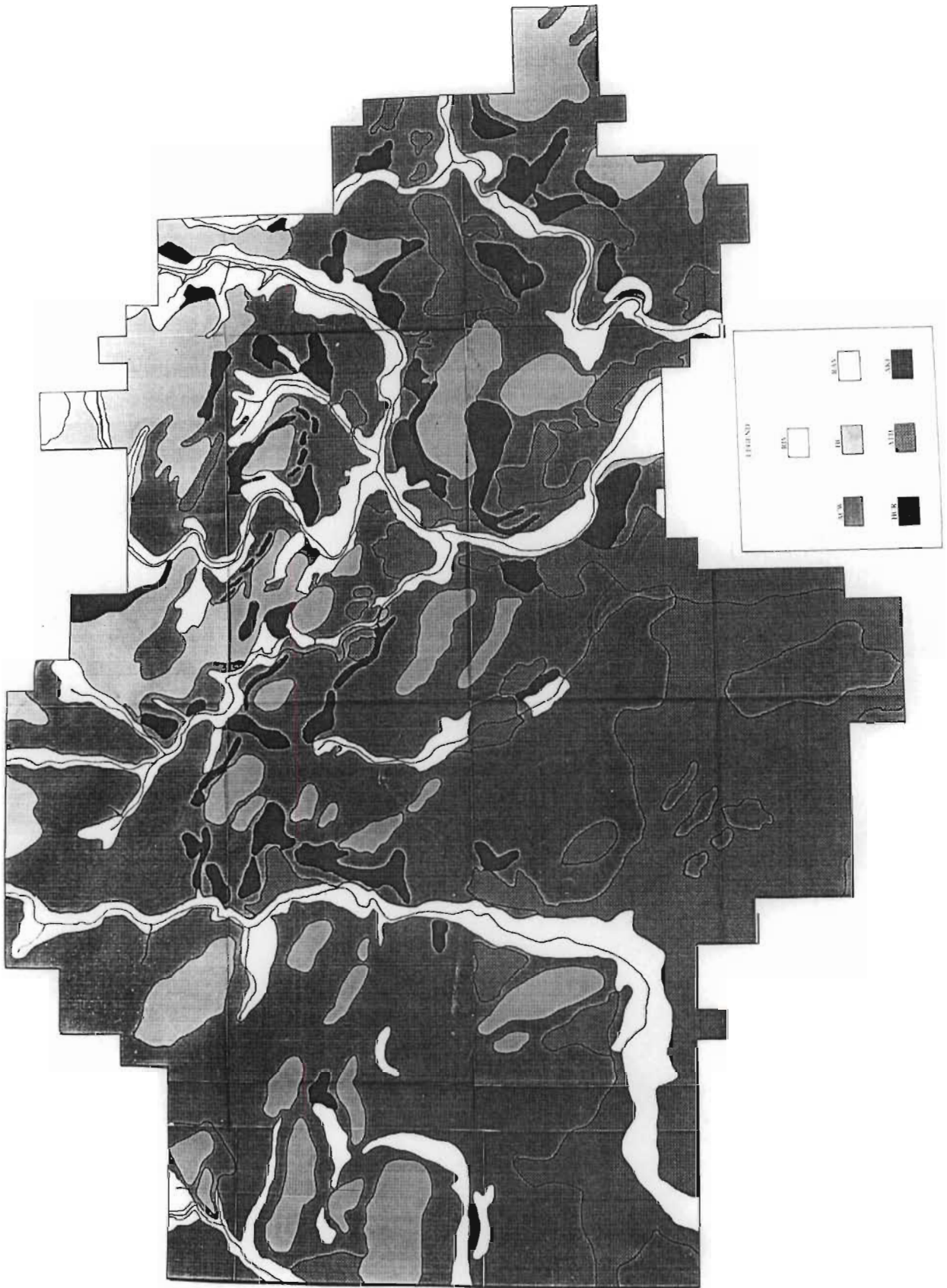


Figure 2.3: Vegetation map of Mtshopi troop's home range showing distribution of habitat types within the home range. For abbreviations of habitat types see text.

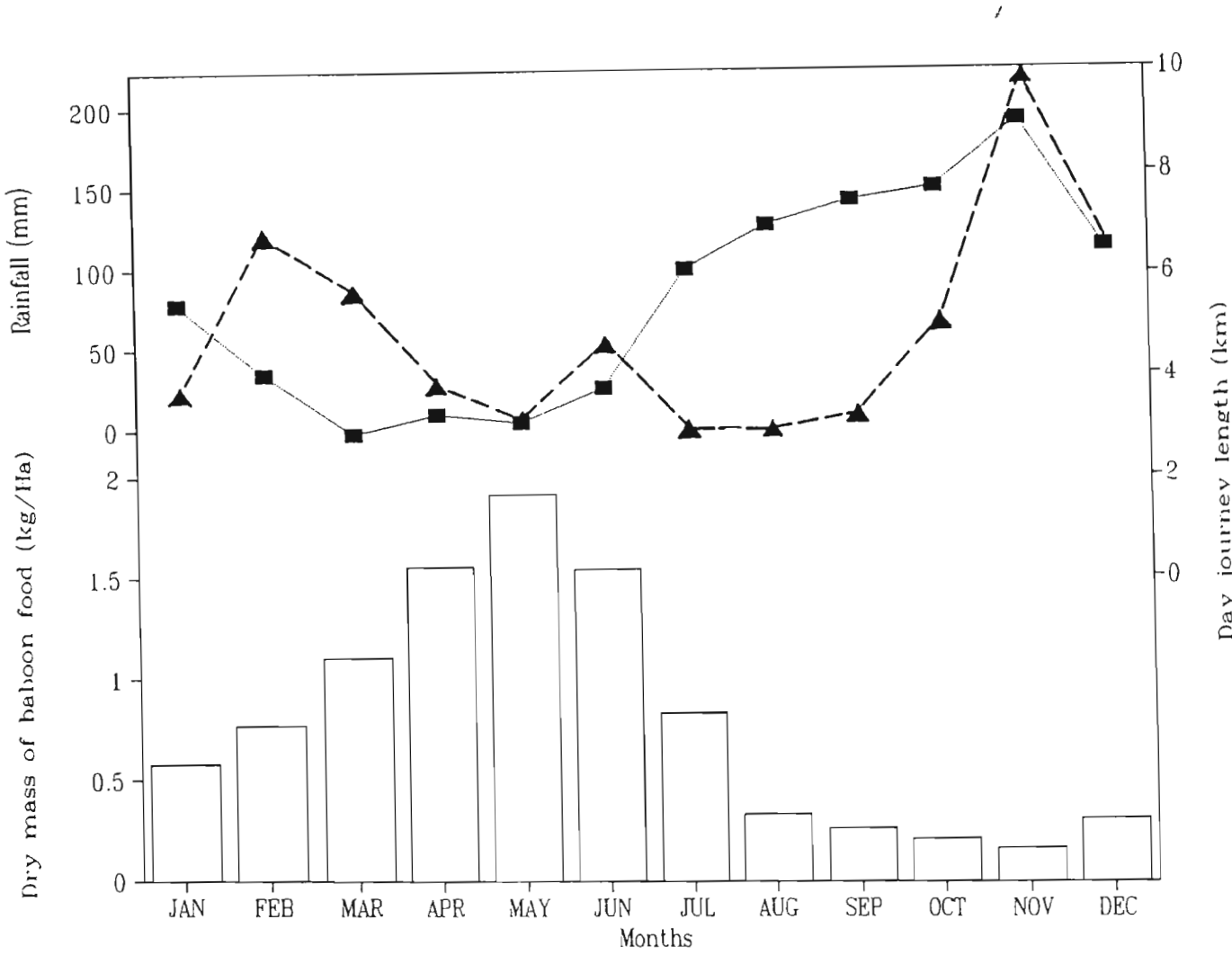


Figure. 2.4: Comparison of monthly changes in food availability (kg/hectare - bar graph), monthly rainfall (mm - triangles) and mean monthly day journey lengths (m - squares).

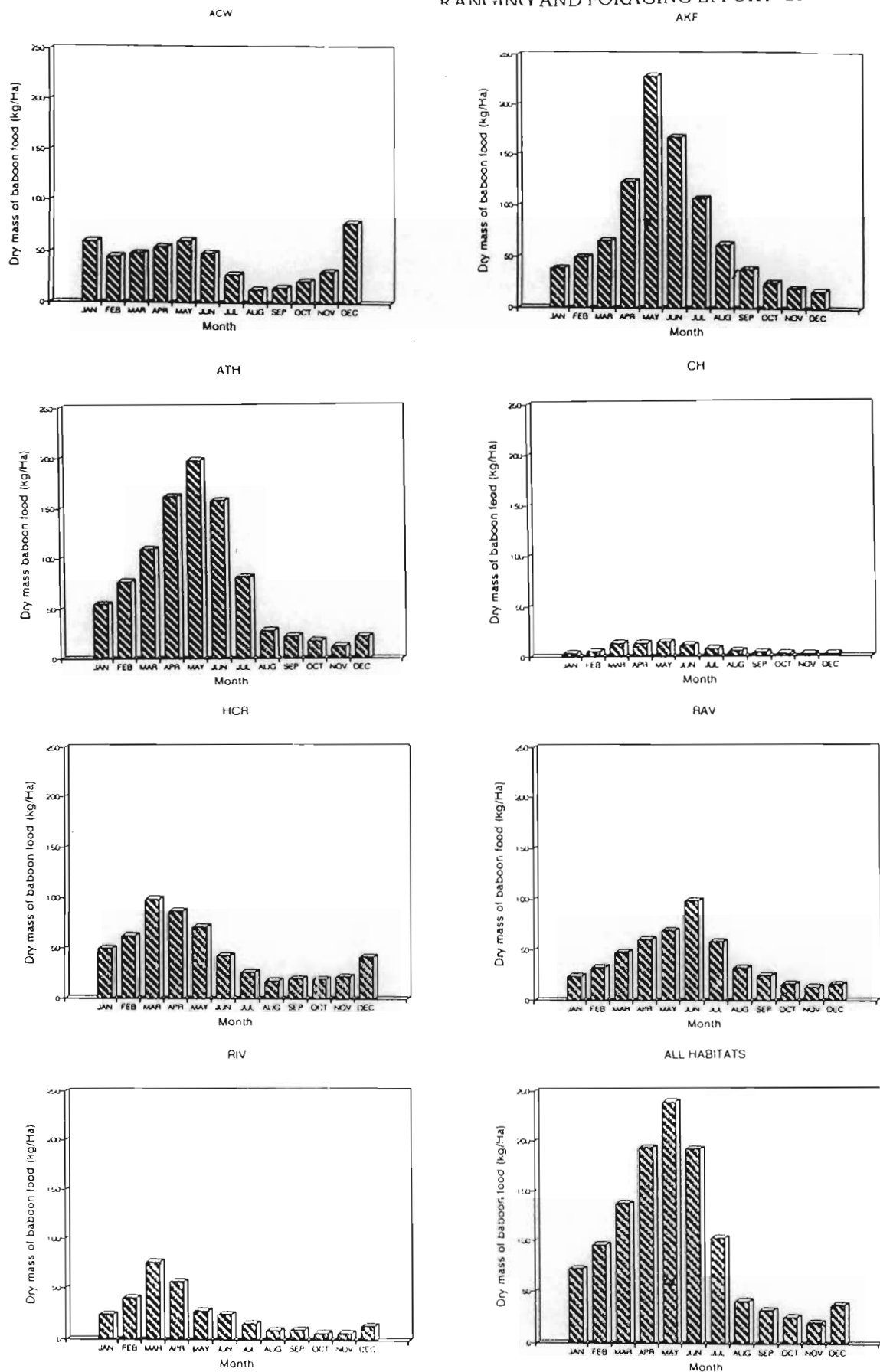


Figure 2.5: Monthly changes in food availability (kg/hectare) for different habitat types during the study period. For abbreviations of habitat type see text.

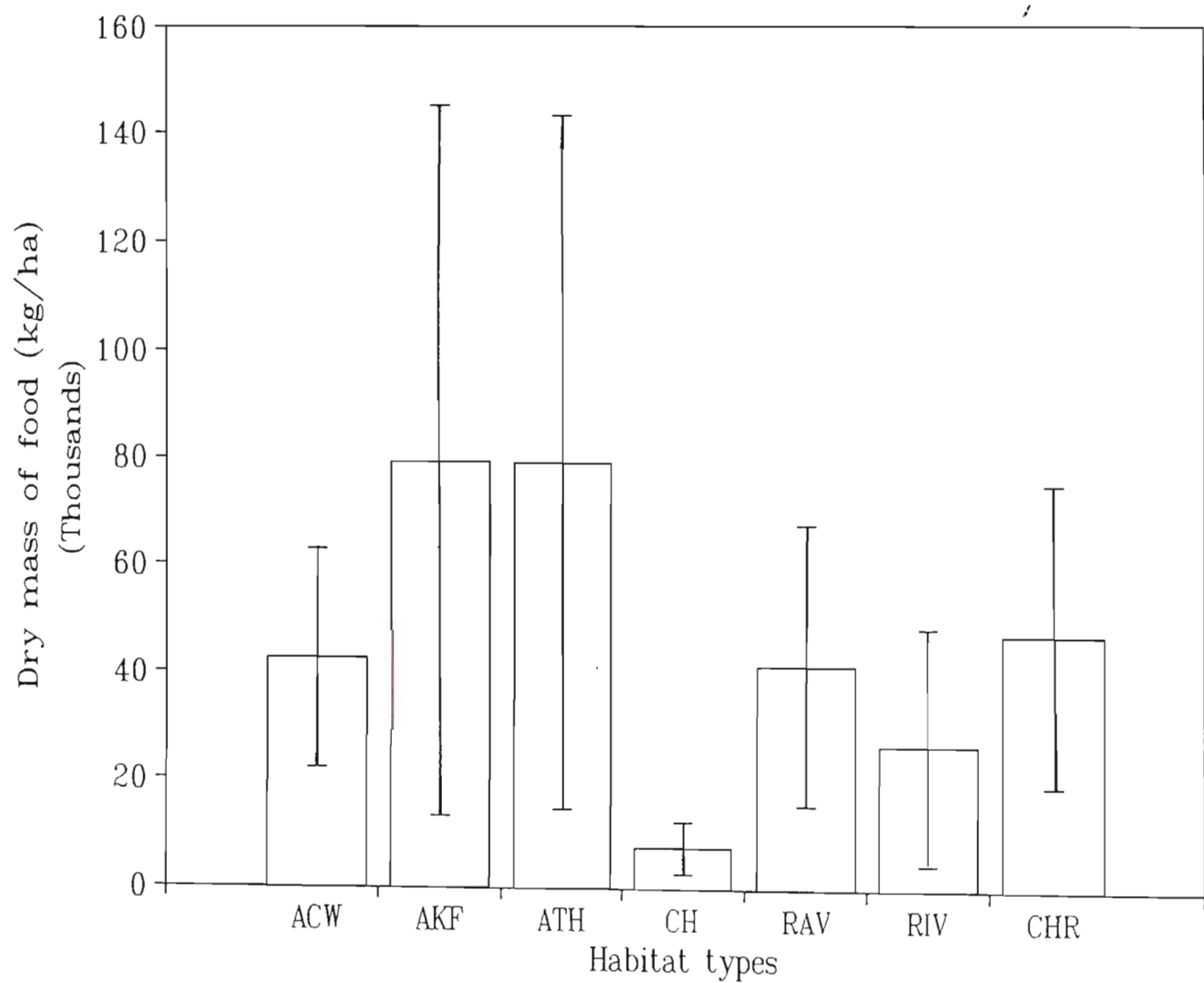


Figure 2.6: Comparison of mean \pm SD amount of food available (kg/hectare) over 12 months for each habitat type. For habitat type abbreviations see text.

availability, particularly in the two most productive habitats (as indicated by large SDs). This results in the rankings of habitats in terms of food availability constantly changing through the year.

Despite large differences in the density of trees (the major source of baboon food) there was no correlation between the density of trees in the different habitat types and the mean food available over the 12 months in those habitats ($r^2=0.163$, $P=0.0369$, $n=7$).

2.3.5 Day journey length

A plot of mean day journey length is given in Figure 2.4. The mean day journey length for the 12 months was 4.87km. Monthly variation in day journey length was significant (Kruskal-Wallis $H=44.62$, $df=11$, $P<0.001$, $n=12$). The overall difference between wet months and dry months was not significant ($Z=-0.624$, $P=0.532$, n Wet=22, n Dry=39), though the significance level increased as the test was repeated using data for the wet and dry seasons shifted forward a month at a time. A significant difference was found when the seasons were shifted forward by 2, 3 and 4 months. The level of significance was greatest when season was shifted 3 months forward ($Z=6.284$, $P<0.0001$, n Wet=34, n Dry=37), suggesting a 3 month lag between rainfall and its affect on baboon foraging. Similar to the 3 month lag between rainfall and food availability.

Day journey length was positively correlated with cumulative rainfall for the previous three months ($r^2=0.671$, $P=0.017$, $n=12$), while there was no correlation between day journey length and monthly rainfall.

There was a significant negative correlation between mean monthly day journey length and food availability ($r^2=0.889$, $P<0.001$, $n=12$).

2.3.6 Quadrat residency

Foraging theory predicts 3 options when food is relatively scarce: (i) animals should remain in patches for longer periods or (ii) travel times should be longer or (iii) both (i) and (ii) (Charnov 1976; Stephens and Krebs 1986). Barton *et al.* (1992) have refined these predictions for quadrat residency data, stating that long durations should make up a greater proportion of the total quadrat residency in the dry season than in the wet. Since at Mkuzi the dry/wet season dichotomy does not reflect food availability or day journey length I tested the prediction (method as in Barton *et al.*

1992) using the months of high food availability and short day journeys (February to July) and low food availability and long day journeys (August to January). Like Barton *et al.* (1992) the data confirmed the prediction. There was a significant difference in the residency distributions (based on how long the baboons spent at a time in a quadrat) between the high food months and the low food months (Kolmogorov-Smirnov $D_N=0.532$, $P<0.001$). The distribution of quadrat residency was skewed to stays of longer duration when food was scarce.

Optimal foraging also predicts spatial changes in patch residency in addition to temporal changes. It predicts that as travelling costs increase so animals should spend longer in food patches. This means that quadrat residency times should increase with distance from the sleeping site sites. Since travelling costs increase linearly there should be a straight line increase in duration of stay in quadrats with increasing distance from the nearest sleeping sites.

Hamilton and Watt's (1970) Refuging model also predicts changes in duration of stay with distance from sleeping site. Their model proposes that adjacent to the sleeping sites (the core area) there is a biodeterioration zone where resources will be soon be depleted resulting in animals moving through this area quickly. While further out from this there is a zone, the arena or resource acquisition zone, where resources are relatively unexploited and consequently animals spend more time in this zone.

The result for the mean duration of stay in quadrats against distance of quadrats from the nearest sleeping sites for the whole year are plotted in Figure 2.7. The data does not show a consistent increase in duration time with distance from sleeping site as predicted on the basis of foraging costs. However it does show a pattern where adjacent to the troop's sleeping sites, from 600 to 1600m, the duration of stay was short and then the duration of stays increased between 1800m and 2200m before decreasing again. Although the pattern appears weak given the high standard deviations, the same pattern was consistent when the analysis was repeated for the dry and wet seasons and the high and low food periods. This suggest that the pattern is not just an artefact of the high variation in the data.

Comparison of the durations of stay for those quadrats between 1800m and 2200m ($n=112$) from the nearest sleeping site with quadrats closer ($n=218$) and further from the nearest sleeping ($n=68$) sites show significant differences (Mann-Whitney: close: $Z=3.244$, $P=0.0012$, far: $Z=2.829$, $P=0.004$, two tailed).

The lack of a consistent increase in duration of stay in quadrats does not support the predictions of the foraging cost argument. In fact when a linear regression analysis is done on the data the slope is found to be negative (slope=-0.0015), rather than positive as predicted. The data appears to show that travel costs alone can't explain differences in duration of stay. The data appears to be more consistent with the Refuging model which predicts a zone of short duration stays adjacent to the core area (biodeterioration zone) and a second more distant zone of longer durations (resource acquisition zone).

Hamilton and Watt (1970) did not consider how far this resource acquisition zone would extend but it is reasonable to believe that as a troop gets to the edge of their home range unfamiliarity and the risk of potential encounters with other troops would result in a decreasing in durations of stay similar to that seen in Figure 2.7.

The frequency of quadrat use with distance from the sleeping site is given in Figure 2.8 (block symbols). Assuming that no other factors influenced quadrat use, frequency of visits per quadrat should decrease with increasing distance from the sleeping site (Sigg and Stolba 1981). This is because the number of potential quadrats to enter increases with distance from sleeping site and consequently the probability of entering a quadrat decreases with it's distance from the sleeping site. The number of potential quadrats increases according to the formula $Y=(X+2)^2$, where Y is the number of potential quadrats and X is the distance from the sleeping site. It was therefore possible to calculate the predicted frequencies of quadrat entry. These points are plotted in Figure 2.8. (cross symbols) together with the troop's data.

In general the troop's data follows the that of the predicted values. There are however notable deviations from the predicted values at zero and 200m from the nearest sleeping site and at 1800, 2000 and 2200m. The first two points are well below the predicted values. These could be explained by the fact that the day journeys were mapped only once the troop had started down from their sleeping cliffs, and then only on the quarter hour. Consequently there were days where the troop had already moved off more than 200m before mapping commenced resulting in the under-recording of the use of the quadrats within 200m of the sleeping sites.

At 1800, 2000 and 2200m the frequencies of quadrat entry are well above the predicted values. This corresponds with the increase in duration of stay in quadrats showing that this area was intensily used by the troop both in terms frequency of entering quadrats and in terms of longer durations of stays in these quadrats.

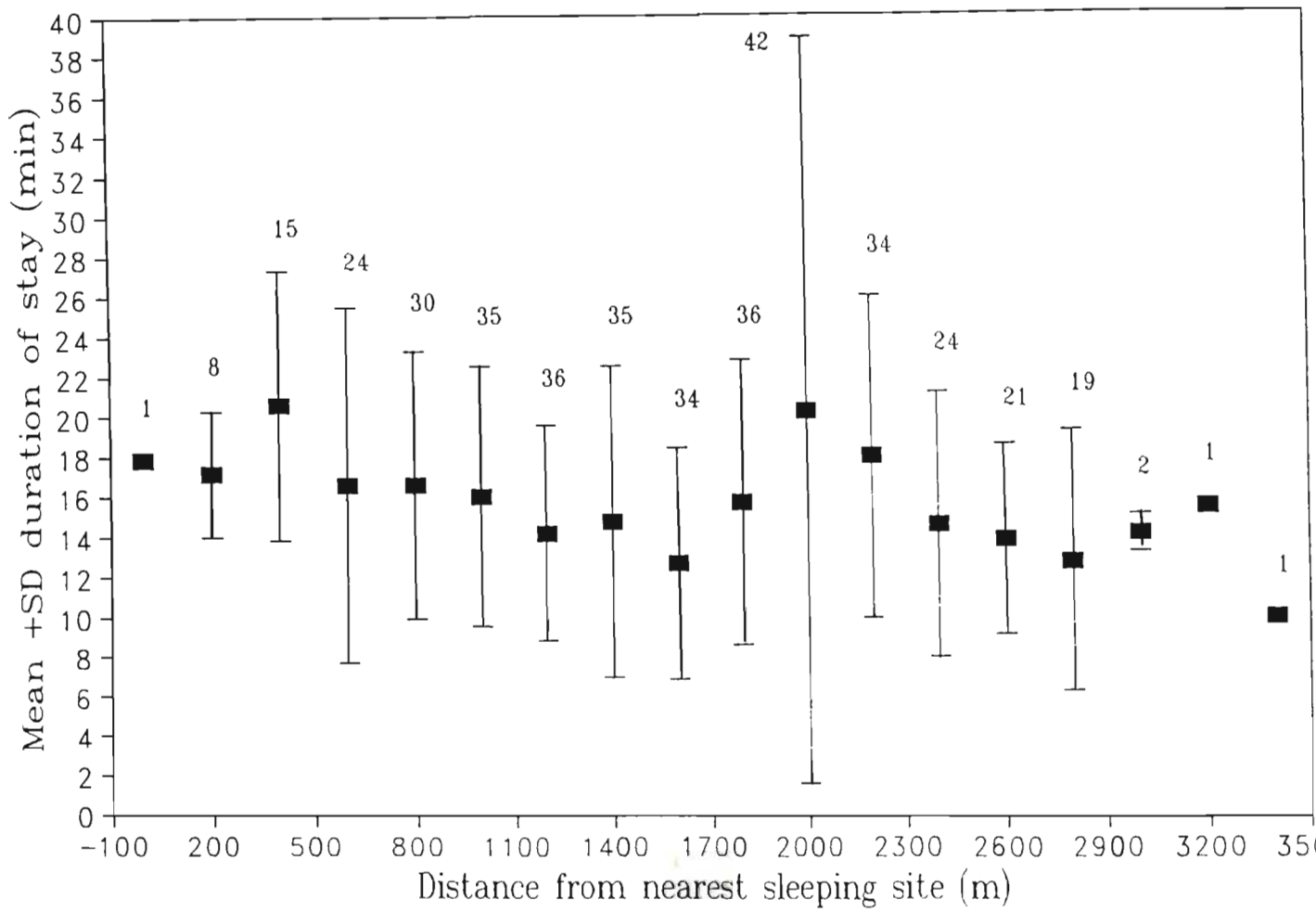


Figure 2.7: Mean and Standard deviation (SD) duration of stay in quadrats plotted against distance of quadrats from the nearest sleeping sites (metres) for the whole year. Numbers above indicate the sample size.

2.3.7 Variation in food encountered

All being things equal one would expect the total amount of food encountered on a day journey to increase with the number of quadrats entered. Figure 2.9 plots the amount of food encountered on a day journey against the number of quadrats entered on the day journey. There was no significant correlation between the amount of food encountered by the troop and the number of quadrats entered (Spearman rank-order correlation coefficient=0.2107, $P=0.1085$).

Figure 2.10 shows mean monthly number of quadrats entered plotted against mean monthly total food encountered on a day journey. This graph followed a similar pattern to the graph of day journey length against food availability (see Figure 2.4). Food increased from May to September but the total amount of food over that period actually decreased. This was presumably related to the decrease in overall productivity. The troop thus adjusted its day journey length and consequently the number of quadrats entered according to the amount of food available.

2.4 Discussion

Mkuzi represents a complex although characteristic habitat for baboons in southern Africa. The species requirement for safe sleeping sites often means that baboon home ranges are in areas where rivers have cut steep gorges. These areas invariably consist of a mosaic of several varieties of woodland, ravine forest and riverine forest. I have observed baboons in these type of habitat combinations in the foothills of the Zambezi valley escarpment of lake Kariba in Zimbabwe, the Waterberg and Soutspanberg in the Northern Transvaal, South Africa. Of the studies of baboons that have looked at patterns of habitat use in detail: Amboseli: Post 1978; Laikipia: Barton *et al.* 1992; Drakensberg: Henzi *et al.* 1992; Ere-Gota: Sigg and Stolba 1981; Mikumi: Rasmussen 1983, Mkuzi appears to be the most structurally complex in terms of the number and distribution of habitat types and differences between habitat types were less clear cut. Mkuzi is therefore important both as being a typical habitat of baboons in southern Africa and in terms of adding to the understanding of the spectrum of adaptability of baboons, especially their strategies for coping with complex environments.

The overall (all habitats combined) monthly pattern of food availability at Mkuzi is typical for a climate consisting of a single summer rainy season and a dry winter. There is a constant increase in food availability after the first rains in November. This peaks in May and then food availability decreases gradually during June-July until it

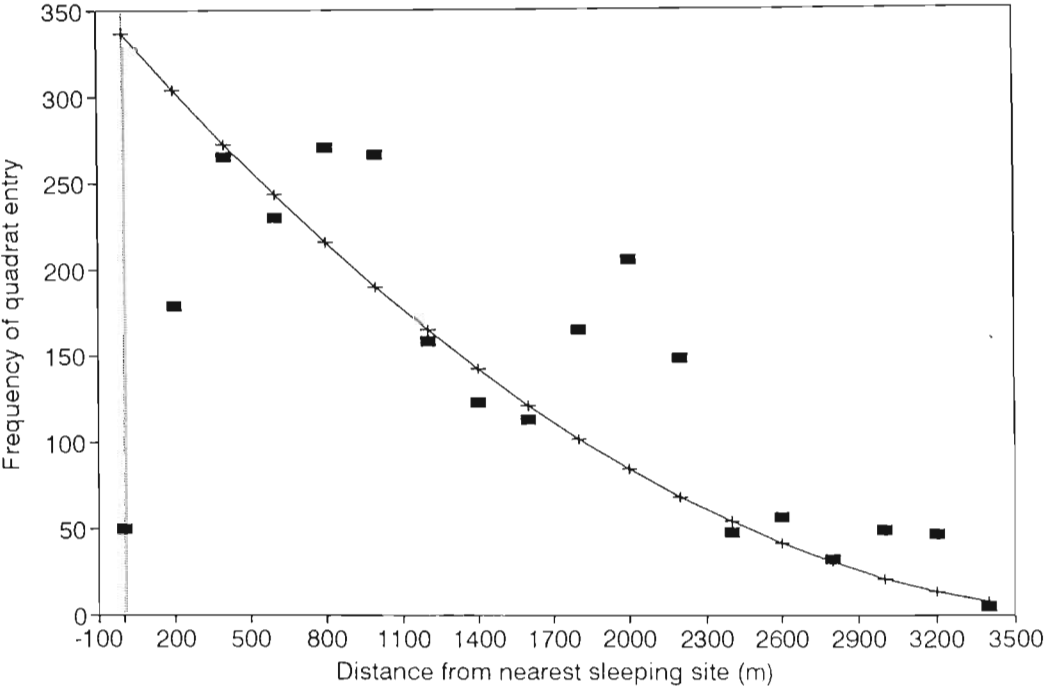


Figure. 2.8: Frequency of quadrat entry plotted against distances from nearest sleeping site: for the troop (block symbol) and as predicted on the basis of the decreasing chances of entering a quadrat further from the nearest sleeping site (see text for details)

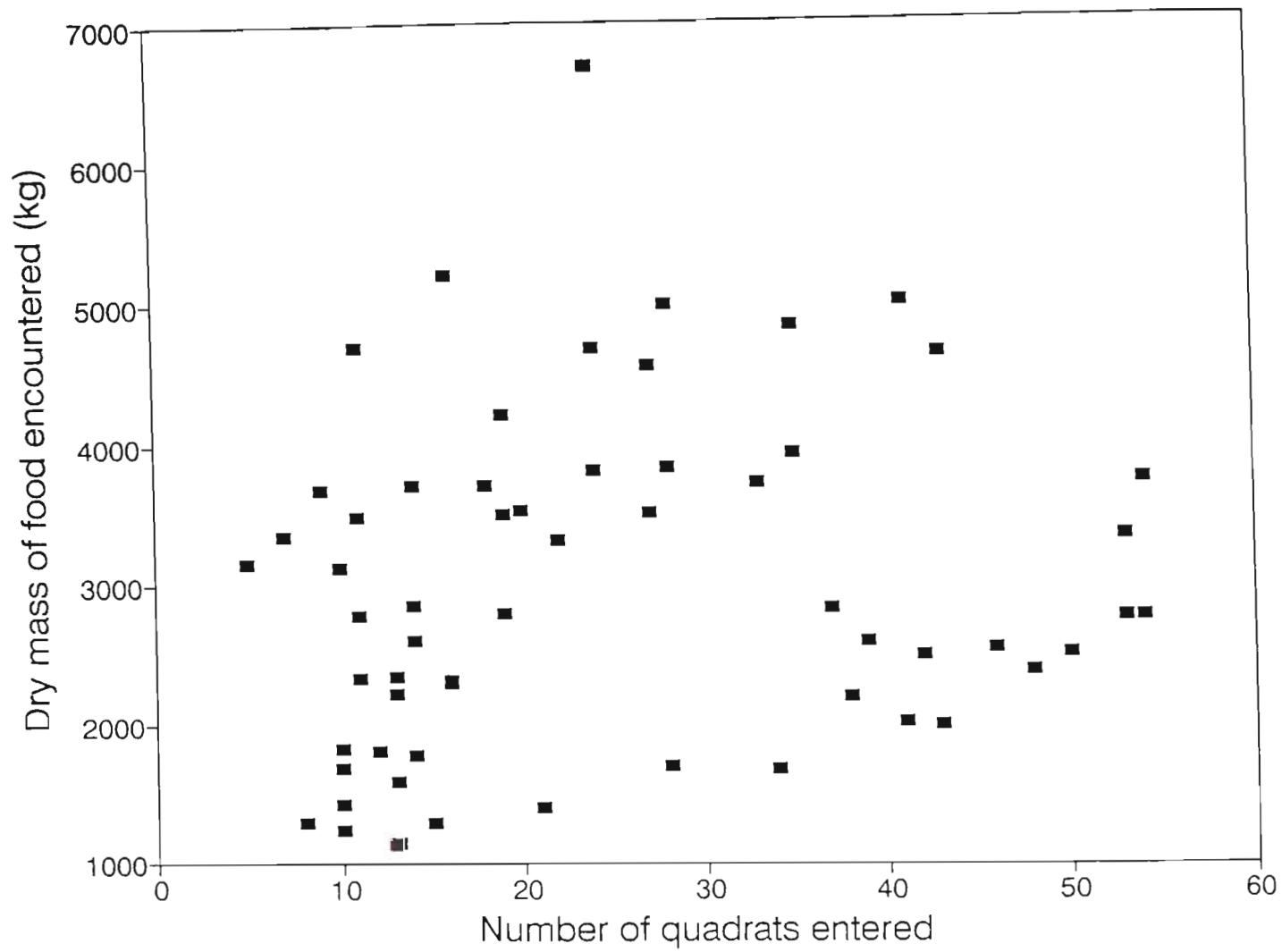


Figure 2.9: Plot of the amount of food encountered on a day journey (kg/hectare) against the number of quadrats entered on a day journey. Spearman rank-order correlation coefficient=0.2107, $P=0.1085$

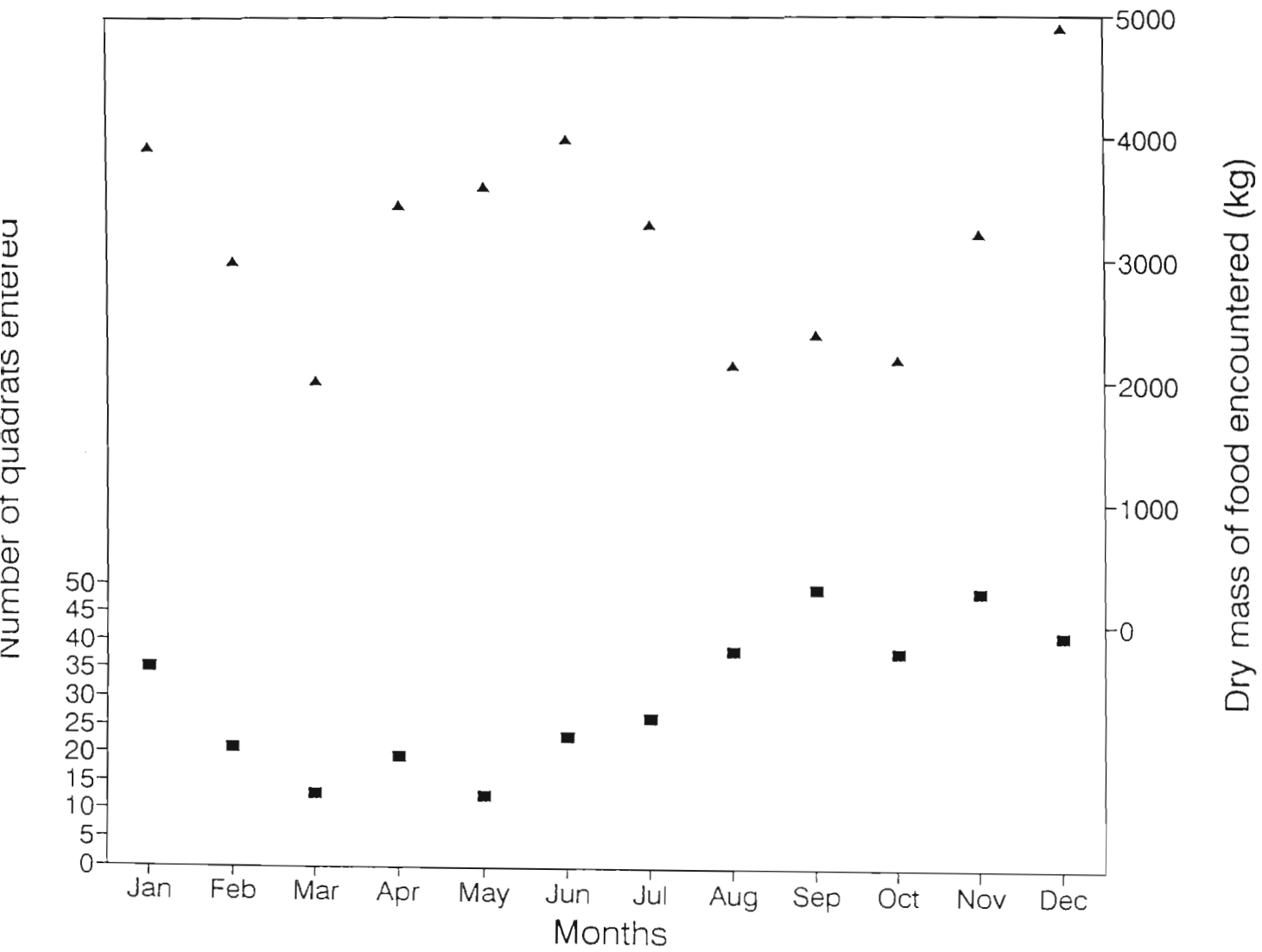


Figure 2.10: Mean number of quadrats entered during day journeys for each month plotted against the mean dry mass of food encountered on day journeys during the corresponding month (kg).

abruptly declines from August to November.

The lag between the pattern of rainfall and food availability reflects the time taken for vegetation to respond to rainfall. This may take from 2 months (Barton *et al.* 1992) to 3 months (Mkuzi). The longer response time at Mkuzi may be due to the high percentage of fruit in the diet of Mtshopi troop (see Chapter 5) which takes longer to develop than leaves or flowers. This lag also causes the period of high food availability to overlap both the dry and wet season. It is not surprising therefore that many studies found no differences in day journey lengths between wet and dry seasons (Altmann and Altmann 1970; Post 1978; Sharman 1981).

Troop size is the primary determinant of home range size (Milton and May 1976; Clutton-Brock and Harvey 1977; Harvey and Clutton-Brock 1981) and day journey length. Mtshopi troop had an average troop size (57.8) when compared with other baboon studies (67.5 from 23 study sites reviewed in Dunbar 1992). Consequently, one would expect home range size and day journey length to also be average. Mtshopi troops home range size (24.42 km^2) and mean day journey length (4.87 km) were both close to the average for a wide range of baboon studies (20.37 km, 5.16 km data from Sharman and Dunbar 1982) thus confirming this relationship. However, the per capita home range size ($0.42 \text{ km}^2/\text{animal}$) is larger than average while the per capita day journey length ($0.084 \text{ km}/\text{animal}$) is shorter than average. Since both these measures are assumed to reflect habitat quality the results appear to be anomalous. This could be explained by the distribution of fruits which constitute primary food resources of the troop (see Chapter 5). Fruit trees are widely and patchily distributed through the home range with each species fruiting at different times. This would require a large home range to encompass enough trees to support the troop through a year. On the other hand, food density and quality is high within a tree and would require only short individual day journeys. In addition, the low density of neighbouring troops (Henzi *et al.* in press) would further contribute to larger home range size by allowing unchallenged expansion of the home range.

The troop appears to follow the pattern of habitat use predicted by Hamilton and Watt's (1970) model. However, the results suggest a refinement of the model to take into account the decrease in durations of stay at the extremes of the home range. More time spent close to sleeping sites is probably due to early arrival and late departures from sleeping sites while short time spent in quadrats at the extremes of the home range is probably a result of unfamiliarity of the area and fear of an intertroop encounter. Taking these two effects into account the model would predict

a sigmoid pattern of duration of stay from the centre of the home range.

Hamilton and Watts theory was originally based on animals with a single refuge. Thus it was surprising to find a similar pattern for the Mtshopi troop which had 7 sleeping sites. This is at least partly due to a large proportion (76%) of the day journeys beginning or ending at Camp cliff which was located close to the geometrical centre of the home range, though I believe the results still suggest that multiple sleeping site home ranges are best described as multiple central place foraging systems rather than evenly utilised home ranges as suggested by Altmann and Altmann (1970).

Schoener's (1969; 1971) classification of foraging strategies into time minimising and energy maximising strategies has been the discussion of many foraging studies (hummingbirds: Hixon and Carpenter 1988; fish: Herbers 1981; Hoffman 1983; Hixon 1987; baboons: Barton *et al.* 1992). Pyke *et al.* (1977) showed that both energy maximisers and time minimizers should maximise the rate of energy intake, but time minimizers should spend as little time as possible foraging (only until their metabolic requirements are met) while energy maximisers should spend the maximum amount of time foraging (within the constraints imposed by the minimum time required for other activities). In terms of foraging effort, time minimizers should decrease their foraging effort as food supplies increase since they would be able to meet their metabolic requirements more easily, while energy maximisers should maintain a similar foraging effort independent of changes in food supplies. From the negative correlation between day journey length and food availability it is apparent that the troop is minimising its foraging effort and therefore conforming to a time minimising strategy. This pattern whereby the troop adjusted its foraging effort according to food availability is confirmed by the lack of a positive correlation between the number of quadrats entered and the total amount of energy encountered on the day journey.

These results have several implications. Firstly, they together with those of Barton *et al.* (1992) bring into question the assumption that the dry seasons in Africa are necessarily periods of food scarcity for baboons. The 1992 data from Barton *et al.* suggests that there is a two month lag between rainfall and the maximum biomass estimates. This study shows that at Mkuzi there was a three month lag between rainfall and the peak in food availability. These results suggest that seasonal comparisons based on rainfall are not likely to be a true reflection of the effects of food scarcity as is often assumed (e.g. Altmann and Altmann 1970; Anderson 1981; Sharman 1981).

The second implication of the results is the importance of diet in determining a troop's pattern of home range use. This point has been made before for primates as a whole. Mace and Harvey (1983) showed that frugivorous species require larger ranging areas than folivores, and Clutton-Brock and Harvey (1977) found that day journey length is positively correlated with foraging group biomass in frugivorous species, but not in folivorous ones. If the troops' larger than average per capita home range size and smaller than average per capita day journeys are correctly attributed to it being predominantly frugivorous, then diet must also be taken into account when comparing patterns of home range use within a single species.

The third implication that the results suggest is the potential importance of the depletion of food supplies by the troop itself in determining patterns of home range movement. The pattern of short durations of stays in a zone adjacent to the sleeping site suggests that these are areas of resource depletion around the sleeping sites (biodeterioration zones) and that the baboons alter their foraging in relation to this resource depletion.

The fourth implication arises from the ability to interpret the troop's foraging patterns in terms of models (for example Sigg and Stolba's (1981) exponential model and Hamilton and Watt's (1970) Refuging model) based on central place foraging from a single sleeping site. Altmann and Altmann (1970) suggested that savannah baboons gained an advantage from using several sleeping sites by being able to utilise their home range evenly. This is no doubt the case to some extent but the results suggest that troops utilising several sleeping sites in a home range are acting as multiple central place foragers, rather than achieving an even utilisation of their home range.

Finally the results of changes in day journey length and their relationship to changes in food availability show that the Mtshopi troop are time minimizers. Monthly changes in the troop's activity budgets also support this (Gaynor in prep.). Barton *et al.* (1992) also found that their study troop at Laikipia were time minimizers. These results suggest that baboons in non-marginal habitats are likely to be time minimizers. These findings appear to be at odds with the overwhelming evidence that food is a limiting factor in most populations (Hamilton 1986; Altmann and Alberts 1987; Eley *et al.* 1989; Altmann 1991; Samuels and Altmann 1991). This is because time minimising strategies imply that animals are able to meet their nutritional requirements through the year by changing the amount of time spent foraging, and therefore should not be nutritionally stressed. A more feasible explanation is that baboons are overall time minimizers, but become energy maximisers during periods of food scarcity and it is

these periods that are important in determining mortality. A second possible explanation of this apparent paradox is related to the fact that these analyses were derived from the observations of the whole troop. Since most baboon mortality occurs before the age of 4 years (Rhine *et al.* 1988, Bulger and Hamilton 1987) it would be informative to pursue this topic comparing age and sex classes, particularly those susceptible to mortality. Investigation of foraging strategies of these age groups during periods of food scarcity is undoubtedly important in understanding the evolutionary (stochastic?) environment under which baboons evolved and continue to evolve.

Chapter 3

Environmental correlates of differential home range use in a troop of woodland baboons

3.1 Introduction

Many studies of home range use by nonhuman primates have attempted to examine the relationship between area occupation densities and spatial and temporal variability in food distribution (yellow baboon: *Papio cynocephalus cynocephalus* Altmann and Altmann 1970; mountain gorilla: *Gorilla gorilla berengei* Watts 1991; Tana river red colobus: *Colobus badius rufomitratus* Marsh 1981; chacma baboon *Papio cynocephalus ursinus* Henzi *et al.* 1992; yellow baboon *Papio cynocephalus cynocephalus* Post 1978; olive baboon *Papio cynocephalus anubis* Barton *et al.* 1992; red colobus *Colobus badius tephrosceles* Clutton-Brock 1975; siamangs *Symphalangus syndactylus* Chivers 1974). Some of these have demonstrated a relationship between the intensity of home range use and food availability. Chivers (1974) found a strong relationship for siamangs (*S. syndactylus*) between the amount of time spent feeding in quadrats and the number of food trees in those quadrats. Clutton-Brock (1975) found the amount of time spent in quadrats by a group of red colobus (*C. badius tephrosceles*) was correlated with the abundance of food in those quadrats. Total quadrat occupation time was positively correlated with food biomass per quadrat for mountain gorillas (*G. gorilla berengei*) (Watts 1991). Henzi *et al.* (1992) demonstrated that the area of the home range utilised by baboons in the Drakensburg mountains (*P. cynocephalus ursinus*) followed the spatial distribution of food.

In many cases though, the relationship between food availability and utilisation of areas is not a simple one. Other factors affect the utilisation of areas. Altmann and Altmann (1970), Post (1978) and Barton *et al.* (1992) found utilisation of quadrats to be strongly negatively correlated with the distance of quadrats from sleeping sites and water sources. The closer quadrats were to the nearest sleeping site or source of water the more heavily utilised that quadrat was. Sigg and Stolba (1981) found the duration of stay in quadrats to increase with increasing distance from a central sleeping site, while the number of visits to quadrats decreased.

Although they were not able to compare actual measures of total baboon food availability in different quadrats in the home range, both Post (1978) and Barton *et al.*

(1992) were able to provide evidence for the relationship between food availability and differential home range use. Post (1978) correlated preference for different habitat types (expressed as selection ratios) with the density of important food species, suggesting that habitat preferences were based on food availability in those habitats. Barton *et al.* (1992) correlated the monthly productivity of important food species with the proportion of time spent in zones containing those species, suggesting that seasonal patterns in the selection of habitats was based on the difference in their profitability. However, since the analysis of environmental variables and food were done separately, it is difficult to compare the relative food availability and other environmental influences on quadrat use. The selection of a few important food species as a measure of food abundance does not address the question of the effect of food availability. As Post (1978 p.154) pointed out, a certain circularity in argument cannot be avoided. "Important" species may be just that because the animals are spending more time in areas where they occur for reasons possibly having nothing to do with total food availability. Therefore the demonstration that animals tend to occupy areas of the home range which are relatively abundant in these "important" species does not infer a causal relationship. This study therefore attempted to use a more objective basis by including as many food species as possible and using measures of dry mass of edible portion of foods as a measure of food availability. In practice I was able to base this estimate of food availability on 32 foods comprising most of the troop's diet. By choosing foods that fell in the top 80% of the troop's diet in any month, the problem of circularity was minimised, but not totally circumvented.

The aims of this chapter were therefore: (i) to determine what factors influence the intensity of quadrat use for the Mtshopi troop; (ii) ascertain the relative strength of these factors and; (iii) examine the seasonal differences of these influences on troop movement. This approach differed from previous studies in that I was able to estimate the dry mass of baboon food available per quadrat. Consequently, the effect of food could be directly assessed and compared with the effect of environmental factors

3.2 Materials and methods

3.2.1 Study site

This study was conducted on the Mtshopi troop of chacma baboons (*P. cynocephalus ursinus*) in Mkuzi Game Reserve. This reserve presents a complex but not unusual baboon habitat consisting of several habitat types ranging from ravine forest to open woodland and dense *Acacia* thickets. It is situated in the foothills of the Lebombo

mountains and part of the adjacent coastal plain (see Chapter 2 for detailed description of the study site). The troop's home range size was calculated as 24.42 km² for the period May 1989 to April 1990 (Figure 3.1). The data presented in this chapter were collected over the same period. The troop used seven sleeping sites, four of which were on cliffs adjacent to rivers flowing through the foothills and three in tall groves of trees in riverine forest towards the coastal plain. Numerous streams and rivers flow through the foothills and drinking water was abundant throughout the home range (Figure 3.1). During the study the reserve had a higher than average rainfall (see Chapter 2). Consequently even during the driest period there were 16 places where drinking water was available (mainly as pools in the now dry river beds)(Figure 3.1). A detailed description of the home range and habitat types is given in Chapter 2.

3.2.2 Estimates of food availability

These data are presented in Chapter 2.

3.2.3 Utilisation of home range

Utilisation of the home range by the troop was quantified from 70 dawn to dusk follows of the habituated baboon troop. During each day journey the position of the troop was recorded on a 1:20,000 contour map every 10 minutes. These data were subsequently read off as x and y co-ordinates of 4 hectare quadrats that were laid over the maps of the day journey routes and entered onto computer. These corresponded to those for which food availability had been calculated.

A graphic representation of the home range was obtained by entering the frequency of quadrat use for the whole year onto a commercial software package, SURFER. The program produced a topographical plot of the intensity of home range use where the intensity of use is represented by the height of the Z axis.

3.2.4 Analysis

The aim of the analysis was to determine the correlates of quadrat use and to compare the relative strengths of these correlates. Linear regression analysis was performed to determine which environmental variables were linearly correlated with the study variables. Stepwise multiple regression was then performed in order to see if variables could be combined in a linear model to describe significant variation in the study variables. The statistics package used (Statgraphics) does an internal check for multiple co-linearities between variables before including them in the model. This avoided problems that could arise when using variables that might not be strictly independent (see Barton *et al.* 1992). In practice none of the variables was rejected

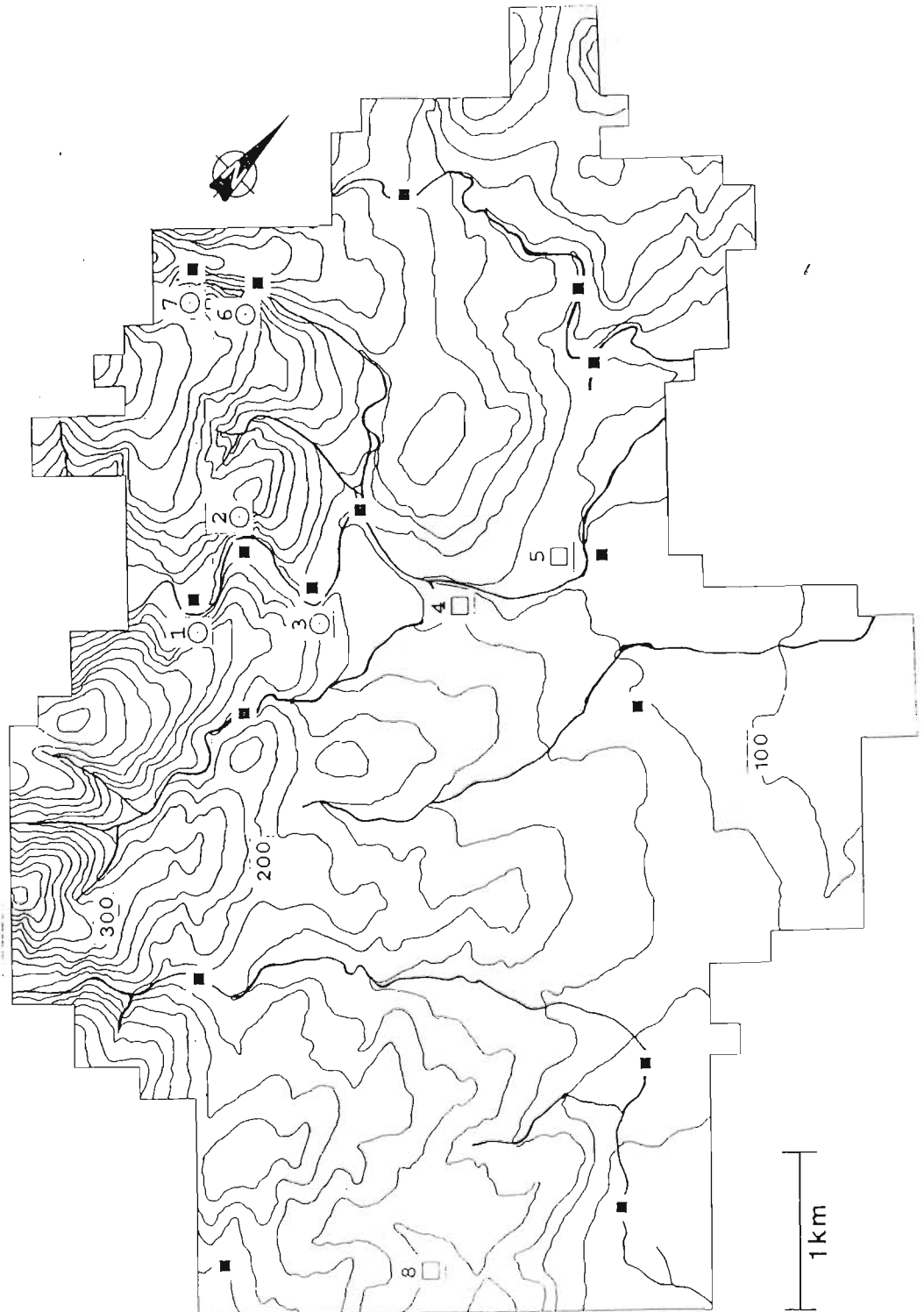


Figure 3.1: Topographic map of Mtshopi troop's home range. Numbers with circles indicate cliff sleeping sites, numbers with squares indicate tree sleeping sites. 1-West cliff, 2-Big cliff, 3-Camp cliff, 4-Tree site 1, 5-Trees site 2, 6-Gorge site 1, 7-Gorge site 2, 8-Fever forest. Squares indicate permanent water sites.

during the analysis.

The following variables were used in the analyses:

Dependant variables

- 1) Total time spent in quadrats - calculated as the total number of scans recorded in each quadrat.
- 2) Mean duration of time spent in quadrats - each time a quadrat was entered the number of consecutive scans spent in that quadrat was recorded. The mean amount of time spent in each quadrat was then calculated.

Both these measures were used since first variable does not differentiate between the frequency with which quadrats are entered and how long is spent in a quadrat. A baboon might need to pass through a quadrat to get to another area (and thus will be recorded as entering it) but time spent in a quadrat is a better reflection of the animals choice of habitat.

Independent variables

- 1) Proportions of the seven habitat types in each quadrat, this was calculated from the vegetation map (see above). These proportions were arcsin transformed.
- 2) Dry mass of baboon food per quadrat (see Chapter 2).
- 3) Number of trees per quadrat, calculated by multiplying the mean density of trees per hectare for each habitat type (as determined in Chapter 2) by the proportion of habitat types in the quadrat and multiplying the sum of these values by four (quadrat size=4 hectares).
- 4) Distance from nearest sleeping site, measured from the centre of the quadrat to the position of the sleeping site on 1:20,000 map (see Figure 3.1).
- 5) Distance from nearest permanent water source, measured from the centre of the quadrat to the position of the water source on a 1:20,000 map (see Figure 3.1).
- 6) Distance from the geographic centre of the home range, measured from the centre of the quadrat to the centre of the home range on a 1:20,000 map.

3.2.5 Seasonal analyses

In an attempt to separate effects related to food abundance and distribution, and purely climatic affects of ambient temperature and humidity, two seasonal analyses were carried out. The first based on the wet season/dry season dichotomy and the second on a high food/low food dichotomy. The wet season included the months October to March and consisted of months where there was a moisture surplus as determined by the relationship between precipitation and evaporation. The dry season

lasted from April to September, consisting of months where there was a moisture deficit (see Chapter 2 and Goodman 1990). The season of high food availability consisted of the months February to July where food availability was higher than the mean for the whole year. Conversely the period of low food availability consisted of the months where food availability was lower than the mean for the year and lasted from August to January. Conveniently the high food/low food seasons lagged 3 months behind the dry/wet season cycle. Each food season therefore had 3 months of moisture surplus and 3 months of moisture deficit which to some extent controlled for seasonal climatic differences between the two.

3.3 Results

3.3.1 Spearman rank-order correlations within environmental variables

Co-correlations between variables can influence the interpretation of relationships between the individual variables and the dependant variable when interpreting regression analysis. Consequently, Spearman rank-order correlation analyses were performed for all the variables in order to determine if there were correlations within the independent variables. These results are summarised as a correlation matrix in Table 3.1. Since food availability differs between seasons the correlation analysis between this variable and the others were repeated for the different seasons (Table 3.2).

Fifty-seven percent (12/21) of the correlations among the different habitat types were significant. This was predictable since it is likely that some habitats should occur together while others will seldom occur in conjunction with each other. For example, ATH which occurs towards the flat coastal plain was significantly negatively correlated with CH which occurs in the foothills (Table 3.1). The high number of correlations suggests that the distribution of habitats is not random.

TDEN was significantly correlated with all habitat types (Table 3.1). This could be expected since habitats have different tree densities (see Chapter 2). TDEN was also negatively correlated with DISSS, DISW and GEOM. RAV was positively correlated with TDEN and also negatively correlated with DISSS, DISW and GEOM. (Table 3.1). This could be explained due to the fact that the highest tree densities occurred in RAV which also was present at most of the sleeping sites, streams and had the general tendency to occur towards the centre of the home range.

	CH	ATH	AKF	RIV	HCR	RAV	TDEN	DISSS	DISW	GEOM
ACW	-0.376 (0)***	0.244 (0)***	-0.135 (0.006)**	-0.150 (0.002)**	-0.030 (0.540)	-0.290 (0)***	-0.682 (0)***	0.187 (0)***	0.211 (0)***	0.098 (0.047)*
CH		-0.332 (0)***	-0.103 (0.037)*	-0.297 (0)***	0.106 (0.032)*	0.189 (0)***	0.126 (0.012)*	-0.214 (0)***	-0.095 (0.052)	-0.229 (0)***
ATH			-0.148 (0.003)**	-0.026 (0.592)	-0.087 (0.077)	-0.245 (0)***	-0.111 (0.02)*	0.103 (0.037)*	-0.057 (0.234)	0.120 (0.015)*
AKF				-0.073 (0.139)	0.010 (0.845)	0.008 (0.874)	0.471 (0)***	0.013 (0.787)	-0.054 (0.276)	-0.120 (0.022)*
RIV					-0.016 (0.739)	0.016 (0.750)	0.334 (0)***	-0.017 (0.727)	-0.029 (0.562)	-0.074 (0.134)
HCR						0.057 (0.247)	0.205 (0)***	-0.164 (0)***	-0.050 (0.310)	-0.277 (0)***
RAV							0.549 (0)***	-0.467 (0)***	-0.286 (0)***	-0.195 (0)***
TDEN								-0.282 (0)***	-0.239 (0)***	-0.210 (0)***
DISSS									0.687 (0)***	0.596 (0)***
DISW										0.269 (0)***
GEOM										

Table 3.1: Spearman rank-order correlation matrix for environmental variables. Habitat types: ACW-*Acacia* mixed woodland, CH-*Combretum* woodland, ATH-*Acacia* thicket, AKF-*Acacia* karroo forest, RIV-riverine forest, HCR-hilly *Combretum* woodland, RAV-ravine. TDEN-tree density in each quadrat, DISSS-distance from nearest sleeping site, DISW-distance from nearest water other than that at a sleeping site, GEOM-mean distance from the geometrical centre of the home range. Top values are correlation coefficients. Values in brackets are significance levels. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	ALL	FOOD			
		DRY	WET	HIGH	LOW
ACW	0.1715 (0)***	0.0605 (0.3272)	0.3639 (0)***	0.1021 (0.1137)	0.8074 (0)***
CH	-0.7163 (0)***	-0.6608 (0)***	-0.6895 (0)***	-0.7186 (0)***	-0.5611 (0)***
ATH	0.5581 (0)***	0.4077 (0)***	0.5561 (0)***	0.4667 (0)***	-0.0437 (0.4597)
AKF	0.3539 (0)***	0.5401 (0)***	-0.0760 (0.2230)	0.4661 (0)***	0.1259 (0.033)*
RIV	-0.1743 (0)***	-0.018 (0.7712)	-0.3351 (0)***	0.0498 (0.4405)	-0.3531 (0)***
HCR	-0.0647 (0.1878)	-0.0451 (0.4659)	-0.0829 (0.1837)	-0.0372 (0.5647)	-0.0391 (0.5087)
RAV	-0.1889 (0)***	0.0861 (0.1635)	-0.3339 (0)***	0.0146 (0.821)	-0.2071 (0)***
TDEN	-0.0712 (0.1476)	0.3025 (0)***	-0.0894 (0.1516)	0.2222 (0)***	-0.5074 (0)***
DISSS	0.2028 (0)***	0.0209 (0.7356)	0.2069 (0)***	0.0896 (0.1649)	0.1397 (0.018)*
DISW	0.0757 (0.1237)	-0.1526 (0.0135*)	0.0824 (0.1867)	-0.1237 (0.0552)	0.1118 (0.0587)
GEOM	0.1546 (0.002)**	-0.0369 (0.5505)	0.1946 (0.002)**	0.0097 (0.8803)	0.0053 (0.0511)

Table 3.2: Spearman rank-order correlation matrix between environmental variables and food availability in different seasons (DRY, WET, HIGH, LOW) and when all seasons (ALL) were combined. See Table 3.1 for abbreviations of variables. Top values are correlation coefficients. Values in brackets are significance levels. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

TDEN was positively correlated with FOOD in the DRY and HIGH food seasons and negatively correlated with FOOD in the LOW food seasons. This could be due to fruits, which were the baboons most common foods (see Chapter 5), being less available in the low food season and those that were eaten (*Acacia* seeds & dry *Ziziphus mucronata* fruit) occurred in areas of lower tree density.

GEOM was negatively correlated with CH, AKF, HCR and RAV and positively correlated with DISSS. This demonstrates that these habitats and sleeping sites were concentrated at the centre of the home range (also see Figure 2.3, Chapter 2).

3.3.2 Frequency of use of home range

Total time spent in quadrats was used to produce a topographical plot of intensity of home range use (Figure 3.2). The vertical axis represents the intensity of use. It is clear that home range use is non-random and not uniform, with peaks and troughs occurring in specific areas. Most use is concentrated in one core area centred on the central sleeping sites. It extends in a north-east, south-west direction with smaller concentrations of use centred on the gorge areas, fever forest and *Acacia* thickets.

3.3.3 Linear regressions - Total time spent in quadrats

The results of linear regressions between total time spent in quadrats as the dependant variable and the environmental variables as separate independent variables are summarised in Table 3.3. Since the probability of reaching statistical significance increases with the number of tests carried out caution should be exercised in interpreting results that are significant for only a single season.

The only consistent significant regressions with habitat types were: (i) a significant negative correlation between total time spent in quadrats and proportion of ACW during both the dry season and the period of high food availability (Table 3.3) and; (ii) a significant positive correlation between total time spent in quadrats and proportions of RAV for both the wet season and period of low food availability (Table 3.3).

Food availability could explain the negative correlation in (i). During both these periods ACW never ranked higher than fourth in food availability (Table 3.4) whereas during the wet season and low food period it ranked highest in food availability for three of these months. The change in food availability in ACW through the year would explain why no relationship existed for the year as a whole.

A possible reason for the positive correlation in (ii) is that there was a period of overlap between the dry season and the period of high food (May-July). These

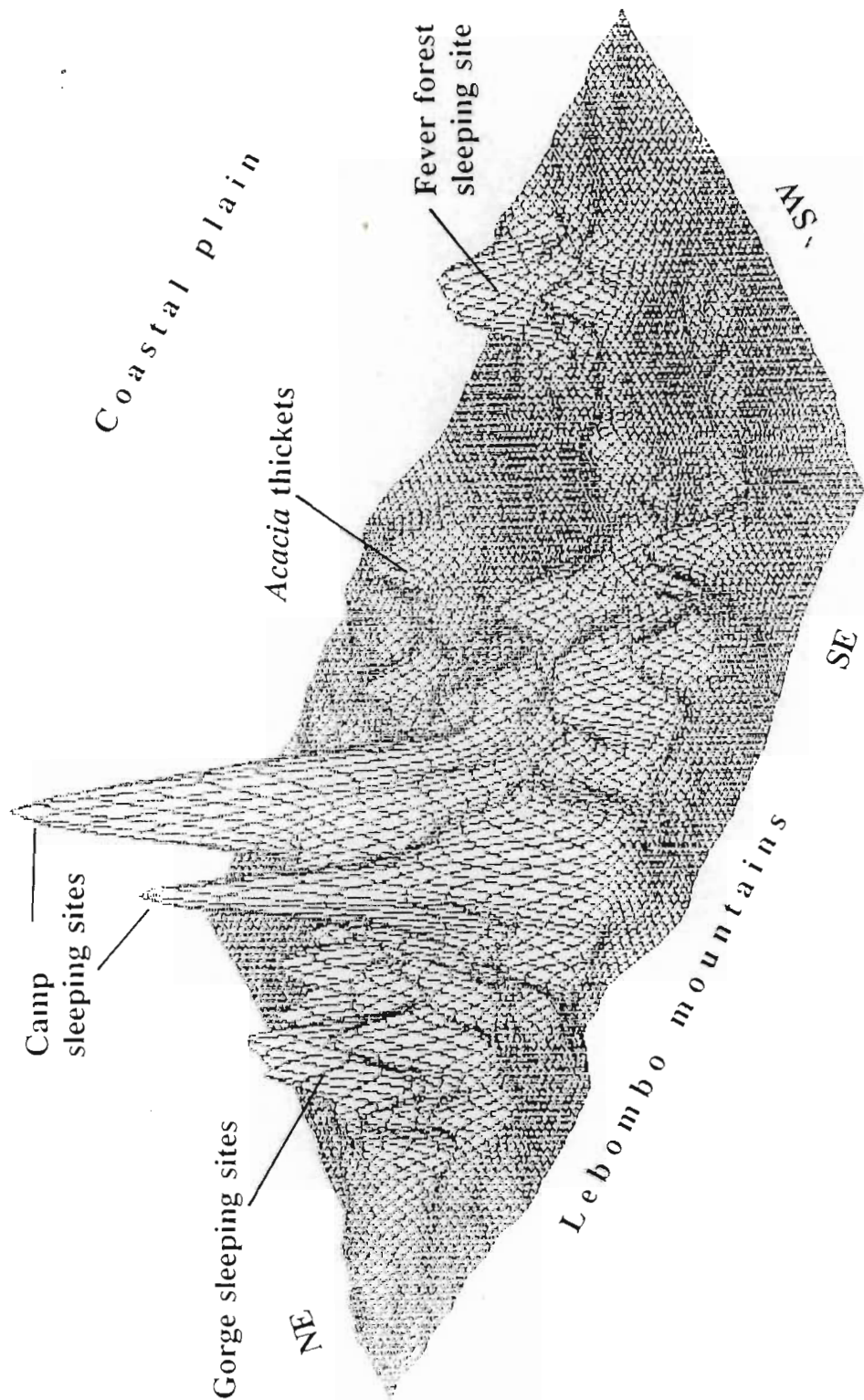


Figure 3.2: Graphic representation of quadrat use in Mtshopi troop's home range. generated from the computer program SURFER (see text for more details).

	ALL	DRY	WET	HIGH	LOW
ACW	-0.1458 0.0213 (0.0030)***	-0.2148 0.0461 (0.0005)***	0.0210 0.0004 (0.7365)	-0.2442 0.0596 (0)***	-0.0126 0.0002 (0.8317)
CH	0.0688 0.0005 (0.1619)	-0.0038 0 (0.9511)	0.0166 0.0003 (0.7913)	0.0131 0.0002 (0.8403)	0.0419 0.0018 (0.4793)
ATH	-0.1307 0.000 (0.9980)	0.0034 0 (0.9555)	-0.0237 0.0006 (0.7054)	-0.0256 0.0007 (0.6928)	-0.0917 0.0084 (0.1213)
AKF	-0.0001 0.0000 (0.9980)	-0.0267 0.0007 (0.6663)	-0.0590 0.0031 (0.3709)	-0.0596 0.0036 (0.3566)	-0.0110 0.0001 (0.8524)
RIV	0.0227 0.0005 (0.6453)	0.0283 0.0008 (0.6474)	0.0178 0.0003 (0.7755)	0.0854 0.0073 (0.1863)	0.0472 0.0022 (0.4256)
HCR	0.1204 0.0145 (0.0142)*	0.0840 0.0071 (0.1745)	0.0054 0 (0.9315)	0.0723 0.0052 (0.2643)	0.0028 0 (0.9619)
RAV	0.2367 0.0560 (0)***	0.2835 0.0804 (0)***	0.0046 0 (0.9414)	0.3153 0.0994 (0)***	-0.0114 0.0001 (0.8471)
FOOD	-0.1434 0.0206 (0.0034)**	0.0238 0.0006 (0.7004)	-0.0176 0.0003 (0.7784)	-0.0396 0.0016 (0.5409)	-0.0647 0.0042 (0.2745)
TDEN	0.2512 0.0630 (0)***	0.2936 0.0862 (0)***	-0.0289 0.0008 (0.6436)	0.3169 0.1004 (0)***	0.0041 0 (0.9447)
DISSS	-0.3616 0.1307 (0)***	-0.4075 0.1660 (0)***	-0.2388 0.0570 (0.0001)***	-0.4350 0.1892 (0)***	-0.0326 0.0544 (0)***
DISW	-0.0776 0.060 (0.1146)	-0.1073 0.0115 (0.0826)	-0.1494 0.0223 (0.1631)	-0.0314 0.0010 (0.6268)	-0.1628 0.0265 (0.0957)
GEOM	-0.4623 0.2137 (0)***	-0.3380 0.1143 (0)***	-0.2689 0.0723 (0)***	-0.3291 0.1083 (0)***	-0.3599 0.1295 (0)***

Table 3.3: Linear regression analysis for seasons (DRY, WET, HIGH, LOW) where the dependent variable is total time spent in quadrats and the independent variables are the environmental variables: habitat types, FOOD, TDEN, DISSS, DISW, and GEOM. See text for more details and Table 3.1 for abbreviations of variables. Top values are correlation coefficients, middle numbers are r^2 values and numbers in brackets are significance levels. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Habitats ranked according to food availability												
Rank	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	ACW	ATH	ATH	ATH	AKF	AKF	AKF	AKF	AKF	AKF	ACW	ACW
2	ATH	HCR	HCR	AKF	ATH	ATH	ATH	RAV	RAV	ACW	HCR	HCR
3	HCR	AKF	RIV	HCR	HCR	RAV	RAV	ATH	ATH	HCR	AKF	ATH
4	AKF	ACW	AKF	RAV	RAV	ACW	ACW	HCR	HCR	RAV	RAV	AKF
5	RAV	RIV	ACW	RIV	ACW	HCR	HCR	ACW	ACW	ATH	ATH	RAV
6	RIV	RAV	RIV	ACW	RIV	RIV	RIV	RIV	RIV	RIV	RIV	RIV
7	CH	CH	CH	CH	CH	CH	CH	CH	CH	CH	CH	CH

Table 3.4: Habitat types ranked in order of decreasing food availability for the months of the study period. See Table 3.1 for abbreviations of habitat types.

months also coincided with the peak in food availability in RAV (Table 3.4).

The proportion of habitat types in quadrats however never accounted for more than 11% of the variability in quadrat residency during all the seasons (Table 3.3). Thus on the whole the proportion of habitat types had little effect on the total time spent in quadrats.

Distance from nearest sleeping site (DISSS) and distance from geometric centre of home range (GEOM) showed consistent significant negative correlations with the total time spent in quadrats for all seasons (Table 3.3). They accounted on average for 10-15% of the variability. Thus the troop spent more time in a quadrat the closer they were to a sleeping site or to the geometric centre of the home range,

Distance from the nearest permanent water source (DISW) was not significantly correlated with total time spent in a quadrat for any of the seasons (Table 3.3). This was contrary to the expectation that it should be more influential in the dry than the wet season. These correlations only accounted for 2-3% of the variability in quadrat use.

Food availability (FOOD) was negatively correlated with total time spent in a quadrat for all the seasons but this was not significant (Table 3.3). A positive correlation would have been more plausible since one would expect baboons to spend more time in quadrats with more food rather than with less food.

3.3.4 Stepwise multiple regressions

Total time spent in quadrats

Stepwise multiple regressions were carried out for all seasons in order to see if a combination of variables could account for more of the variation in total time spent in quadrats than for each independent variable considered separately. This method combines the environmental variables (independent variables) in such a way as to explain the maximum amount of variability in total time spent in quadrats (dependant variable). The results are shown in Table 3.5. Although all the correlations were significant the adjusted r^2 values accounted for little additional variation in total time spent in quadrats (between 9% and 20% only) than was accounted for by single variables in the simple regressions.

The results of the multiple regression when all seasons are combined are given in

	HIGH	LOW	DRY	WET
Total time	0.2582 (4)	0.14731 (4)	0.22452 (6)	0.09995 (3)
x Duration	0.13568 (7)	0.005625 (5)		

Table 3.5: Adjusted r^2 values for stepwise multiple regression analysis for the different seasons, for total time spent in quadrats as well as mean duration of stay in quadrats. Top values are the significance levels and figures in brackets are number of environmental variables included in the analysis.

Adjusted $r^2 = 0.2577$

Variables	β -coefficient	std error	t-value	sig. level
Constant	12.610942	1.052558	11.9812	0
RIV	0.014288	0.014298	0.9993	0.3182
HCR	0.11109	0.100888	1.1011	0.2715
RAV	0.090093	0.018814	4.7886	0
FOOD	-0.006728	0.005675	-1.1856	0.2365
DISSS	0.108823	0.180451	0.6031	0.5468
DISW	-0.19835	0.190208	-1.0428	0.2977
GEOM	-0.860969	0.114025	-7.5507	0

Table 3.6: Stepwise multiple regression analysis for all seasons combined using total time spent in quadrats as the independent variable.

Table 3.6. The adjusted r^2 accounted for 25% of the variability when the model included RIV, HCR, RAV, FOOD, DISSS, DISW and GEOM. This was only 4% more than that accounted for by GEOM (see linear regression Table 3.3) despite the inclusion of six other variables in the model. The multiple regression models were therefore largely unsuccessful at predicting the intensity of quadrat use.

3.3.5 Linear regressions

Mean duration of stay in quadrats

The more frequent entry of quadrats nearer the sleeping sites could be explained on the basis of day journeys having to start and end at a sleeping site. The more frequent entry into quadrats at the centre of the home range could be explained due to day journeys having a high probability of passing through the centre of the home range. However, these reasons would not predict longer stays in those quadrats. In order to distinguish between the effects of more frequent entries or longer stays the analyses were repeated using the mean duration of stay in quadrats. The results are given in Table 3.7.

There was a consistent negative correlation between mean duration of stay and distance from the nearest sleeping site (DISSS) (Table 3.7). However, these regressions had lower r^2 values than those for total time spent in quadrats for both high and low food seasons (Table 3.3).

The correlation of GEOM with mean duration in quadrats in the low food season accounts for only 1.88% of the variation (Table 3.7) while it accounts for 13% of the variation when correlated with total time spent in quadrats (Table 3.3). This pattern is even stronger during the high food season (Tables 3.3 and 3.7).

When the seasons are combined (ALL) there was no significant correlation between GEOM and mean duration of stay (Table 3.7) despite accounting for 21% of the variability when correlated with total time spent in quadrats (Table 3.3).

Distance from the nearest permanent water source (DISW) was also not correlated in any season with mean duration of stay.

3.4 Discussion

3.4.1 Factors determining the intensity of quadrat use

Food availability is generally assumed to have a major role in determining the patterns of home range use by animals (Primates: Clutton-Brock 1975; Chivers 1974, Birds:

	ALL	HIGH	LOW
ACW	-0.0413 0.0017 (0.4014)	-0.2171 0.0471 (0.0007)***	0.0291 0.0008 (0.6091)
CH	-0.0449 0.0020 (0.3616)	0.0053 0 (0.9343)	-0.0925 0.0086 (0.1029)
ATH	-0.0959 0.0092 (0.0510)	0.0133 0.0002 (0.8371)	-0.0949 0.0090 (0.0094)**
AKF	0.0270 0.0007 (0.5838)	-0.0229 0.0005 (0.7234)	0.0596 0.0036 (0.2939)
RIV	0.1203 0.0145 (0.0142)*	0.1011 0.0102 (0.1175)	0.1215 0.0148 (0.0319)*
HCR	0.0008 0 (0.9864)	-0.0154 0.0002 (0.8116)	0.0090 0.0001 (0.8743)
RAV	0.1607 0.0258 (0.0010)***	0.2630 0.0692 (0.0004)***	0.0682 0.0046 (0.2299)
FOOD	0.0514 0.0026 (0.2961)	0.0076 0.0001 (0.9067)	0.0197 0.0004 (0.7296)
TDEN	0.1682 0.0283 (0.0006)***	0.2600 0.0676 (0.0004)***	0.0909 0.0083 (0.1091)
DISSS	-0.1960 0.0384 (0)***	-0.2391 0.0572 (0.0002)***	-0.1742 0.0304 (0.0002)***
DISW	0.0078 0.0001 (0.9856)	0.5422 0.0029 (0.4021)	0.0432 0.0019 (0.4464)
GEOM	-0.0680 0.0046 (0.1665)	0.0458 0.0021 (0.4789)	-0.1370 0.0188 (0.0154)*

Table 3.7: Linear regression analysis for seasons (HIGH, LOW) where the dependent variable is mean duration of time spent in quadrats and the independent variables are the environmental variables: habitat types, FOOD, TDEN, DISSS, DISW, and GEOM. See text for more details and Table 3.1 for abbreviations of variables. Top values are correlation coefficients, middle numbers are r^2 values and numbers in brackets are significance levels. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Houston 1975; Davis 1982). This assumption is central to most optimal foraging theories (Charnov 1976; Krebs 1978; Stephens and Krebs 1986) although many recent theories take into account other constraints (Pulliam 1975; Belovsky 1978; Heller and Malinsky 1979; Mangel and Clark 1986; Houston and Carbone 1992). Within this context it was surprising to find that food availability appeared to be not important in determination of quadrat use by Mtshopi troop.

This study differed from other studies in its ability to assign estimates of dry mass of baboon food to each quadrat in order to determine the effect of food availability on quadrat use. Although other studies of correlates of habitat use for baboons have been done (Post 1978; Barton *et al.* 1992), neither of these were able to assess the effect of food availability on the use of quadrats. Where this has been done for other primates (red colobus, Clutton-Brock 1975; siamang, Chivers 1974; chimpanzees, Watts 1991), a correlation between quadrat use and food availability has consistently been found. The overall negative correlation between food availability and total time spent in quadrats is therefore somewhat of an anomaly, suggesting that for Mtshopi troop other factors might have overridden the influence of food availability.

Two differences between baboons and forest dwelling primates suggest that quadrat utilisation may be particularly constrained for baboons: (i) baboons rely on a limited number of sleeping sites in their home range from which they must leave and to which they must return every day, while forest primate species are capable of sleeping throughout their habitat; (ii) baboons inhabit areas of greater structural diversity in terms of habitat types than relatively uniform forests. The consequences of these differences are that while quadrats in forests are only likely to differ (from a primates point of view) in the amount of food available, quadrats in baboon habitat could differ in distance from sleeping sites, predation risk, thermoregulatory load and proximity to other habitat types. These factors are all likely to interact with each other and food availability to determine the intensity of quadrat use, making it difficult to determine the role of food availability.

Of these factors, distance from sleeping site and distance from centre of home range appear to have had major effects on quadrat use for the Mtshopi troop, accounting for 13% and 21% of the variability in total time spent in quadrats. This was due to the troop having to leave and return to sleeping sites each day. Consequently, day journey routes diverge from and converge on sleeping sites, increasing the use of quadrats adjacent to them. The strength of the correlation with the centre of the home range could be ascribed to the more or less central location of the three major sleeping sites

(these sleeping sites accounted for 76% of all sleeping site use) as well as an increased probability of passing through areas nearer the centre of a proscribed range than areas towards the edge.

The general tendency of the troop to spend more time in quadrats with higher tree densities might be due to several different factors since tree density itself is correlated with several environmental variables. Tree density is positively correlated with food availability in the dry and high seasons and negatively correlated in the low food season. It is negatively correlated with distance from the nearest sleeping site and distance from the centre of the home range i.e. tree density is higher towards the centre of the home range and closer to sleeping sites. It is also strongly positively correlated with the proportion of RAV in a quadrat. The correlation with tree density could therefore be due to food availability. It could be merely a function of tree density being highest near the intensely utilised centre of the home range or due to the four most used sleeping sites occurring in RAV habitat type.

The positive correlations between tree density and total time spent in quadrats and between food availability and tree density in the dry and low food seasons suggests that food availability does play some role. However this is not likely to be the only factor since a significant negative correlation between tree density and food availability in the low season did not result in a corresponding negative correlation between tree density and time spent in quadrats for the same period. A more likely explanation is that the correlation with tree density is a result of an interaction between food availability and the tendency to spend more time in quadrats near sleeping sites and the centre of the home range.

Correlations with proportion of habitat types in quadrats also coincides with the patterns of food availability in those quadrats. The proportion of RAV in quadrats is positively correlated with quadrat use in those seasons where food availability is positively correlated with the proportion of this habitat type in quadrats. Similarly the negative correlations between ACW and total time spent in quadrats coincides with those seasons where there is a negative correlation between the proportion of ACW and food availability. While seasonal changes in use of some specific habitat types can be explained by the food availability in those habitat types, and correlations with tree density can be linked with food availability, these are of little value in addressing whether the use of quadrats can be explained by food availability. Within the limits of this analysis there was an overall negative correlation between food availability and total time spent in quadrats.

Predation risk has been shown to influence patterns of movement in baboons (Altmann and Altmann 1970; Rasmussen 1983; Byrne 1981). Byrne (1981) and Dunbar (1988) argued that the availability of trees in which to escape from predators are important in determining the predation risk, especially for terrestrial primates such as baboons. Consequently, the preference of the Mtshopi troop for entering and spending time in areas of high tree density might partly be due to the reduced predation risk in these areas. This preference would be overridden in the wet and low seasons due to the lack of food in areas of high tree density, thereby resulting in the lack of correlation between total time spent and tree density in those seasons as shown in the results. There is no direct evidence for the Mtshopi troop that this is the case. However, the scenario does demonstrate the possible interactions between factors that would influence habitat use and which are difficult to account for in this type of analysis.

3.4.2 Duration of stay in quadrats

In general the results of the correlations with mean duration of stay in quadrats mirror those obtained for the total amount of time spent in quadrats. This is not surprising since total time spent in quadrats is a function of the frequency of quadrats entered as well as the mean duration of stay. Differences between the results of the two analyses therefore represent differences in strategy between the frequency with which quadrats are entered and the duration of stay in those quadrats. While the frequency of quadrat entry is largely dependent on the constraints of day journey length and the position of quadrats, the mean duration of stay is less restricted and more likely to be related to the intrinsic characteristics of quadrats. The results for duration of stay differ from those of frequency of quadrat entry in three aspects: (i) there are significant positive correlations with the proportion of RIV in quadrats for the low season and all seasons combined; (ii) the effect of distance from nearest sleeping site and centre of the home range are reduced for mean duration of stay as compared with total time spent in quadrats; (iii) the correlation coefficients between food and total time spent in quadrats were negative but were positive for mean duration of stay. This last change suggests that duration of stay in quadrats was less constrained by factors related to the relative position of quadrats since there were more positive correlations with food availability. This suggests that the lack of correlation between quadrat utilisation and food availability might largely be due to the constraint to start and end day journeys at sleeping sites.

3.4.3 Seasonal differences in quadrat utilisation

Quadrat utilisation refers to both total time spent in quadrats and mean duration of

stay in quadrats.

Distance from sleeping sites was most strongly correlated with quadrat use in the high food season when day journeys were shortest. This was because short day journeys during the high food season were more strongly centred on the area adjacent to sleeping sites. Quadrat use was less strongly correlated with distance from sleeping sites in the low food season because day journeys were long and the troop left the vicinity of the sleeping site shortly after waking.

Correlations between distance from the centre of the home range and quadrat use were strongest in the low food season when day journeys were longest. This was probably due to day journeys being long enough for the probability of crossing through the centre of the home range to be high.

There were no significant correlations between quadrat utilisation and distance from the nearest water source. In fact the correlation was stronger in the wet season than the dry season. This is in contrast to expectation because correlations in the dry season would reflect scarcity of water. This suggests that in the Mtshopi troop's home range water was not limiting even in the dry season.

One would expect a stronger correlation between food availability and quadrat use when food is scarce. Baboons should spend more time in quadrats with more food in the low food season than in the high food season. For total time spent in quadrats the correlation was weaker in the low food season than in the high food season. This suggest that in the low food season they entered poor quality quadrats more often. However, when mean duration of time spent in quadrats is considered, food availability was more positively correlated in the low food season than in the high food season supporting the prediction above.

These differences suggest that there was a tendency to remain longer in quadrats containing more food when food was scarce, despite entering poor quality quadrats more often. The increased in frequency of entering poor quality habitats may be a function of the longer day journeys that the troop took when food was scarce.

3.4.4 Comparisons with other studies

In contrast to other studies of correlates of quadrat use in baboons (Post 1978; Barton *et al.* 1992) environmental variables accounted for only a small percentage of the variability in Mtshopi troops quadrat use. At Laikipia, Barton *et al.* were able to

account for 60% of the variability in total quadrat occupancy when they used distance to nearest sleeping site, distance to nearest water hole and proportions of habitat types in quadrats. At Mkuzi multiple regression analysis accounted for only 25% of the variability in total time spent in quadrats. Like the baboons at Laikipia (Barton *et al.* 1992) and Amboseli (Altmann and Altmann 1970; Post 1978) distance from sleeping sites played a significant role in determining the intensity of quadrat use. However, unlike the two previous studies, distance from a water source never had a significant effect on food availability. Mtshopi troop had constant access, even in the driest month of the study, to at least 13 sources of water throughout the home range. The study troops at Laikipia and Amboseli had access to only a few man made water holes in the dry months. At Mkuzi the troop were never further than 2km away from the nearest source of water. Thus in contrast to the other troops, encountering a water source was not a major goal during the day journey of Mtshopi troop.

Although Barton *et al.* (1992) and Post (1978) did not have a direct estimate of food availability in each quadrat they both argued for food availability playing a role in the determination of quadrat use. This was done indirectly by comparing the seasonal changes in production of some important species with the proportion of total time spent in different habitat types. Their troops were found to track food availability in certain habitats by increasing the proportion of time they spent in those habitats. However, they used an indirect estimate of food availability based on changes in the productivity of a food species that they regarded important. The food's importance was not determined independently. They may have been major items in the diet only because it occurs in a habitat that the troop frequents, possibly for reasons unrelated to food availability. Without knowing what the total amount of food is available in all quadrats of the home range it is not possible to determine the real choice of foods (see Post 1978). This study used a more independent and direct measure of food availability. The results showed that although some of the significant correlations could be explained by food availability (e.g. preference for RAV and areas of high tree density), overall food availability did not correlate with quadrat use. This suggests caution in assuming that correlations between food and particular habitat types mean that food availability is a major correlate of quadrat use. For the Mtshopi troop it appears that although food might play an important role, correlations with other factors introduced complications which detracted from possible correlations with food.

An additional factor could be the complex distribution of habitat types, and thus food, at Mkuzi compared with the two other study sites. This may explain the less than

clear cut results at Mkuzi. The mosaic nature of the habitat types at Mkuzi precludes any exclusive use of a single area during a day journey, since travelling a distance in any direction involves moving through a range of habitat types. Therefore quadrat residency is not only a result of habitat choice only but is also a result of the different habitat types that were encountered on movements between preferred habitats.

3.4.5 Limits of analyses in this chapter

Although useful in identifying possible constraints in habitat use, this type of correlation analysis must be treated with caution when interpreting correlations of quadrat use with food availability and habitat use. These analyses do not take into account the relative proportions of different habitat types within quadrats neither the spatial relationships between habitat types. Consequently, correlations with habitat types might simply reflect the relative proportions of these in the home range, or more specifically, within the range of the day journey length. Thus in seasons where food is plentiful and sufficient nutrients can be obtained by moving only a short distance the proportions of habitats available to troops might be very different to periods of food scarcity where longer day journeys make more distant habitat types more available. To realistically assess whether food availability does influence troop movement the constraints of day journey length and the need to leave from and return to a sleeping site should be taken into account. This is attempted in the following chapter.

Chapter 4

Baboon day journey routes: modelling optimal paths through complex habitats

4.1 Introduction

The use of space is important to a baboon troop because movement within the habitat will determine how resources are used. The direction and sequence of movements between habitats or within a nutrient gradient should determine whether a species is in fact able to optimise the resources available to it. Consequently it is often assumed that patterns of movement and habitat selection are designed to maximise the rate of food intake in relation to time and energy costs (Krebs *et al.* 1974; Charnov 1976), particularly when food is limiting.

Limited food availability is found in many baboon populations (Hamilton 1986; Altmann and Alberts 1987; Eley *et al.* 1989; Altmann 1991; Samuels and Altmann 1991) and food shortage can account for many causes of mortality (Dunbar 1988). Thus the ability to move through a habitat in such a way as to maximise the rate of energy intake should be under strong selection pressure. Despite this, the relationship between nutrient availability and the use of space is obscure (Barton *et al.* 1992) although there have been some attempts to link habitat use with the availability of specific food resources (Post 1978). The reason for this is because there are many constraints on the paths taken on day journeys such as inter-troop interactions, predation, and access to essential resources (Altmann 1979). Of the essential resources water and sleeping sites appear to be the most limiting. Altmann (1979), Post (1978) and Barton *et al.* (1992) found that apparent preferences for particular vegetation zones occurred as a result of the spatial coincidence of these with sleeping sites and water holes. Sigg and Stolba (1981) found that utilisation of an area depended on its distance from the sleeping site.

While these studies have distinguished some of the variables affecting habitat selection they have not yet addressed how to control for these variables in order to deal with the more central ecological question which is: what effect do food resources have on determining day journey routes? Stated from the animals point of view: Are baboons choosing daily routes on the basis of food? To solve this problem, the experimental approach should involve determining what variables affect the behaviour in question and controlling for them in order to detect the effect of the study variable (food availability in this case). This approach is impractical in most field situations, but it is

possible to model within the constraints imposed by the confounding variables (thereby controlling for them), while varying the study variable and comparing the results with those obtained in the field. This is the approach developed in this chapter.

The need to leave from and get to a safe sleeping site is the most consistent constraint determining the path taken on a day journey. This has made it difficult to determine what influence food availability has on choice of day journey routes for two reasons: (i) not all areas are equally available to the baboons because of differing distances from sleeping sites (ii) the probability of encountering a habitat type is not independent of the previous part of the day journey. The problem of dealing with the spatial distribution of resources is not unique to studies of primates. It has had a major effect on the direction optimal foraging theory has taken. The assumption of random encounter rate for patches has been a major theoretical problem in the analysis of optimal patch choice (MacArthur and Pianka 1966; Schoener 1974, Schoener 1987) and the analysis of habitat selectivity. Patches are not encountered randomly because they are not independent of the distribution of other patches in space. Failure to account for the non-random distribution of patches has led to theory concentrating on diet and how long to stay in a patch rather than movements between patches. This is evidenced by the lack of any quantitative study of optimal foraging routes in the literature.

A common approach to the study of the spatial distribution of resources has been to determine habitat choice using indices based on the deviation of observed habitat occupancy from that expected on the basis of habitat abundance (Post, 1978; Barton *et al.* 1992). This approach is questionable because of the assumption of equal accessibility to all habitat types. Post (1978) has noted, "Ideally one would like to examine a series of randomly constructed day-journeys, complete with a series of generated zone occupancy times, to use as the null zone (habitat type) occupancy distribution". Although Post wrote that work in that direction was under way (1978) nothing of this nature has yet been published.

Assumptions of random encounter of habitat types and equal accessibility of habitat types do not hold for many species since most species have one or more refuges in their home range which means unless habitat types are symmetrically arranged in equal proportions about these then they will not encounter habitat types in a random manner. In most cases some habitat types are going to be distributed further from a refuge than others thereby making it less likely to be encountered than would be expected on the basis of the proportion the home range it occupies. This problem is particularly acute

for baboons since they arrive and depart from particular sleeping sites and have particularly large (in relation to the distance they can cover during a day journey) and usually heterogeneous home ranges. I therefore set out to build a random walk model which was constrained by the need to start and end day journeys from particular sleeping sites while covering the same distance as the study troop within the known home range. This would enable an understanding of how 'optimally' (in terms of making effective use of the distribution of food resources) the study troop was able to use their environment. It would also allow development of a methodology for determining habitat availability given the above constraints. This type of model I believe represents a solution to the problem created by a non-random distribution of habitat types or patches. It provides a legitimate null hypothesis for habitat selection that takes into account the reality of the non-random juxtaposition of habitat types and the relationship of these to refuges or sleeping sites. It was used as a tool against which to test hypotheses with regards to habitat choice. This could be achieved by comparing quadrat utilisation, habitat preference and energy encountered between the study troop and the simulation model. This allowed the question: Is the troop making choices which are different to a random walk? to be addressed.

Two models were developed; a constrained **random walk model** and a similar stochastic short term **optimal model**. Both models had identical constraints. The two models tested whether there was a simple **optimal** solution (i.e. one using realistically simple rules) to foraging in the study troop's complex home range. The optimal model may also be used to gauge the level of complexity of the troops foraging strategy.

4.1.1 Availability vs. accessibility of habitats

In analyses of habitat utilisation, availability of habitat types is estimated by determining the percentage cover of the different habitat types in the home range. Use - either time spent in the different habitat types or the number of times different habitat types are entered - is then compared with the relative availability of the different habitat types. This is normally followed by attempts to correlate preferences for different habitats with some measure of resources, predation pressure, or parasites that might explain these preferences. This type of analysis does not take into account that not all habitat types are necessarily equally accessible. For example, a habitat's position on the periphery of the home range means that it is less accessible than others that occur in the centre of the home range. Equally important in affecting accessibility is the juxtaposition of habitats. To take an extreme but common example the occurrence of a high quality habitat type/patch surrounded by a low quality patch means that entering a high quality habitat/patch is contingent on entering the low

quality habitat/patch therefore affecting the relative accessibilities. Using relative proportions of habitat types as a measure ignores these effects rendering the analyses insensitive to all but very clear cut cases of habitat choice. Therefore, when examining what decision rules an animal uses in determining whether or not to enter a habitat type, or how long to spend in a habitat type, accessibility rather than availability should be the baseline against which to measure habitat choice. In order to determine whether baboons encountered the same proportion of habitat types when on a random walk as the proportion of habitats available to them in their home range, the following hypothesis was tested:

1. There is no difference between the proportion of habitats encountered during a random walk (accessibility) and the proportion of habitat types in the home range (availability).

4.1.2 Sleeping sites and habitat choice

For animals using several sleeping sites within a home range where habitat types occur in a non-uniform pattern, choice of foraging area is possible at two levels. At the gross level there is the choice of sleeping sites which affects the areas of the home range accessible during a day journey. At the finer scale there is the decision of where to go during the day. To examine whether the choice of sleeping sites had a significant effect on the accessibility of the habitat types, the following hypothesis was tested:

2. There is no significant difference in the proportion of habitat types encountered when departing from and returning to different sleeping sites.

4.1.3 Energy encountered during day journey routes

Optimising the use of food resources is dependent on choosing a route through areas of high productivity. However, choice of day journey route and allocation of time along the route is unlikely to be determined solely by a single resource such as food availability. Instead what baboons are likely to be optimising in a proximate sense is a trade off between nutrients, safety from predators, and energy expenditure (Partridge 1978; Belovsky 1984; Post 1984; Barton *et al.* 1992). Thus one cannot expect day journey routes to encounter the maximum (and thus optimal) amount of baboon food. In order to determine if the baboons were tending towards optimisation of food in relation to its availability, the following hypotheses were tested:

3. The baboons do not encounter more food during a day journey route than would a random model route.
4. The baboons do not encounter more food during a day journey route than would an optimal model route.

Initially the amount of energy encountered on a day journey route was calculated on

the basis of what quadrats were entered during the journey i.e. irrespective of the amount of time spent in each quadrat. This was then repeated again, but this time taking into account how long (how many scans) the troop had spent in the different quadrats. When allocation of time to the different quadrats entered during a day journey is taken into account, hypotheses 1 and 2 were tested again (hypotheses 5 and 6).

4.1.4 Food availability and habitat selection

The basis of any optimisation of food resources must lie in the selection of more profitable habitats. In order to determine the relationship between habitat selectivity and food availability, the following hypothesis was tested:

7. There is no correlation between the selectivity index (SI) in different habitat types and food availability in different habitat types.

4.2 Materials and methods

4.2.1 Study area

Field work was carried out in Mkuzi Game Reserve (latitude 32°38'S longitude 32°08'E) in north eastern Zululand, South Africa on a troop of approximately 68 baboons (March 1989 count - 59 individuals, March 1990 count 76 individuals). The baboons home range of 24.42 km² (home range size during the duration of this study) is situated on the eastern slopes of the Lebombo Mountains about 40 km from the coast and at an altitude of 100-300 metres above sea level. The habitat consists of a complex mosaic of mixed bushveld/woodland vegetation types dominated mainly by various species of *Acacia* (Goodman 1990). This is dissected by numerous seasonal streams for the most part flanked by riverine forest and woodland. Some of these have cut steep gorges consisting of rocky cliffs and ravine forest. These cliffs account for five of the study troop's sleeping sites. The other three sleeping sites are tall groves of tree in riverine forest (Figure 4.1).

The home range is a hilly woodland-savannah combination consisting of the following habitat types: *Acacia* mixed woodland (ACW); Hilly *Combretum* woodland (HC); *Acacia karroo* forest (AKF); Hilly *Combretum* rocky outcrops (HCR), *Acacia luederitzii* thicket (AT); Riverine forest (RIV) and Ravine forest (RAV) (see Chapter 2 for a detailed description of the habitat types).

The climate is warm to hot, humid subtropical (Schulze 1965) with a hot humid summer (mid-September to the end of March) which includes the rainy season

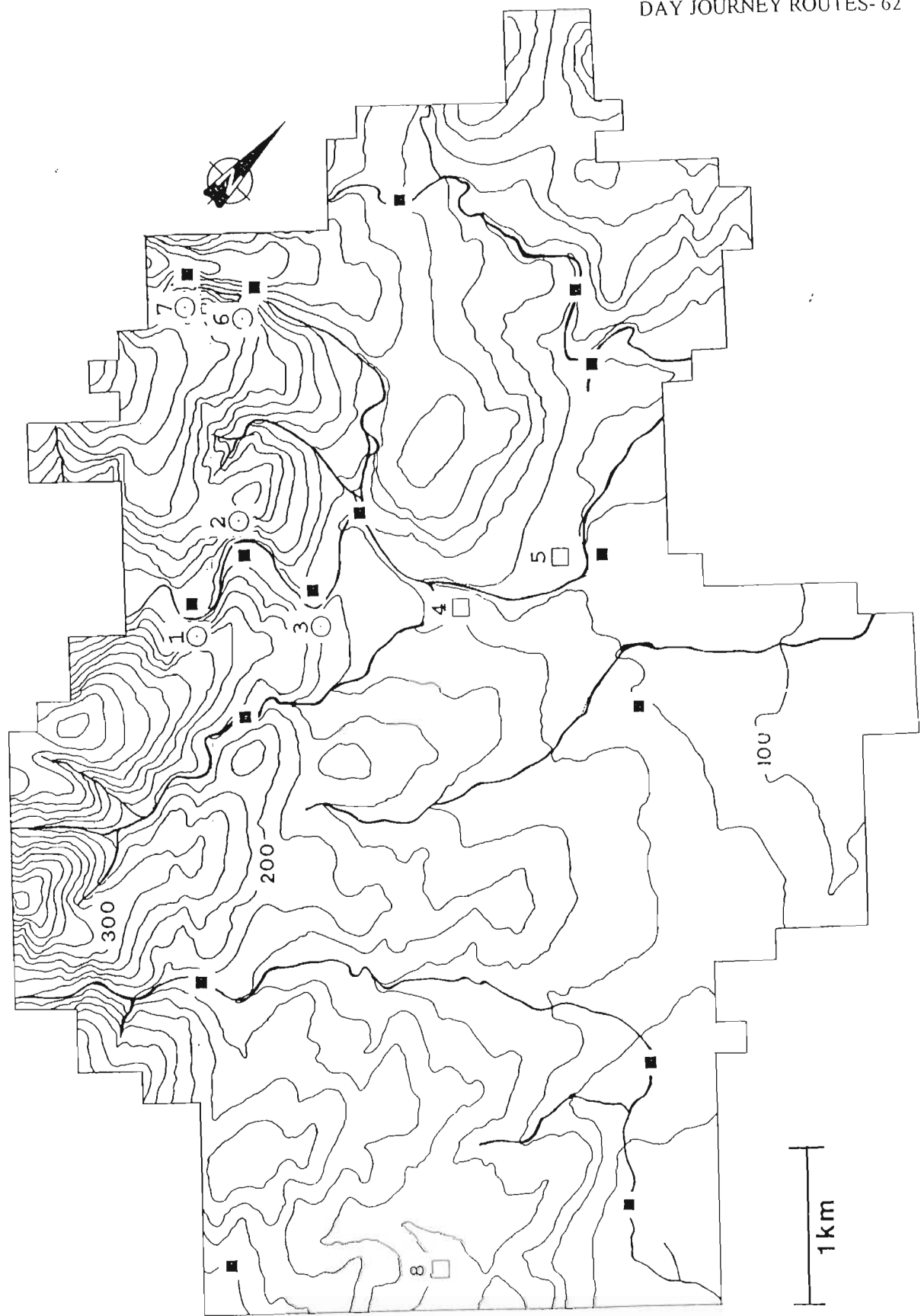


Figure 4.1: Topographic map of Mtshopi troop's home range. Numbers with circles indicate cliff sleeping sites, numbers with squares indicate tree sleeping sites. 1-West cliff, 2-Big cliff, 3-Camp cliff, 4-Tree site 1, 5-Tree site 2, 6-Gorge site 1, 7-Gorge site 2, 8-Fever forest. Squares indicate permanent water sites.

(October to March) and a warm arid winter (April to mid-September; Goodman 1990). The mean annual rainfall is generally about 600mm with 824mm recorded during the period of the study (May 1989-April 1990). The mean annual temperature in Mkuzi is 23.2 °C, the highest temperatures being in summer with the mean maximum temperature in January being 32.5 °C. The winters are cooler with a mean daily temperature of 18.8 °C in July, the coldest month.

4.2.2 Vegetation Sampling Methods

The seven habitat types were classified on the basis of the dominant species, density and structure of plant communities. These were then mapped in the field with the aid of series of colour aerial photographs of the home range (see Chapter 2 Figure 2.3).

4.2.3 Estimation of food availability

The available dry mass of edible food was calculated by collecting food from representative trees and shrubs. This food was then processed as baboons would prior to eating and then dried. This yielded the dry mass of foodstuff for trees/shrubs of known height from which the dry mass yield of other size trees could be extrapolated. Using these data and the densities, height structure and phenology of food species collected each month, the dry mass of food per hectare was calculated. This was done for all species that comprised 80% of the feeding observations in any month. Estimation of food availability is described in detail in Chapter 2.

4.2.3 Behavioural Data

The study began in February 1989 but the data set used in these analyses was based on 70 dawn-to-dusk follows of the habituated troop from May 1989 to April 1990. This allowed a period to become accustomed to the baboons and data collecting techniques. The position of the troop was located and recorded on a 1:20 000 map every 10 minutes. The troop's locations on the maps of the day journeys were then converted to the x and y co-ordinates and entered into a computer for analysis.

4.2.4 The models

The Random Walk Model

Stochastic simulations can be represented as a board game (Starfield & Beloch 1986). Using this analogy, the random walk model takes place on a board consisting of squares representing the quadrats of the home range. Four constraints are built into the model:

1. No moves are allowed out of the home range.
2. The first and last quadrats of the random walk are specified and correspond to

sleeping sites.

3. Only a specified number of moves are allowed. These represents the number of consecutive quadrats entered on a real day journey (essentially a rough measure of the day journey length).
4. Associated with the third constraint is that no move is allowed that makes it impossible to reach the destination in the amount of moves left (as specified by the total number of moves allowed minus the number of moves already used).

Initially these were the only constraints built into the model. The moves into adjacent quadrats were random with equal probability of moving into any of the quadrats. When the simulation was run, however, the "model troop" often oscillated between two quadrats which is a situation common in random walk models subject to stringent constraints. This was not consistent with natural foraging behaviour of the troop. Oscillations between quadrats never occurred during the day journeys of the study troop. Ecologically, oscillating between quadrats is not a viable strategy because as the troop moves through a quadrat it partially depletes the resources in that quadrat making it uneconomic to return to immediately as well as being energetically expensive. It is likely that baboons and other animals have a behavioural propensity to move forward rather than move in other directions in order to circumvent entering previously exploited areas. This was confirmed by counting (from the day journey maps) the number of times quadrats were entered: a) in line with the direction of movement (determined from the previous move), b) diagonally left and right of the direction of movement, c) at right angles to the left and right of the direction of movement, d) diagonally backward (left and right) to the direction of movement and e) directly backward from the direction of movement. The results indicated that the probability of moving into a quadrat decreases with an increase in the angle of deviation from the direction of movement (Figure 4.2). These probabilities were therefore built into the model. Since differences in the probability to move left or right were negligible (and likely due to sampling errors) the probabilities were assumed to be symmetrical. The average of the left and right probabilities were used in the model. This addition changed the nature of the model from a constrained random walk model (Markovian Type I process) where the direction of movement depends only on the current state or location to a Markov chain process where the probability of the direction of movement is dependent on the direction of movement in the previous time interval (Keen and Spain 1992).

The Optimal Model

An optimal model is any model that solves a problem of maximising a cost-benefit

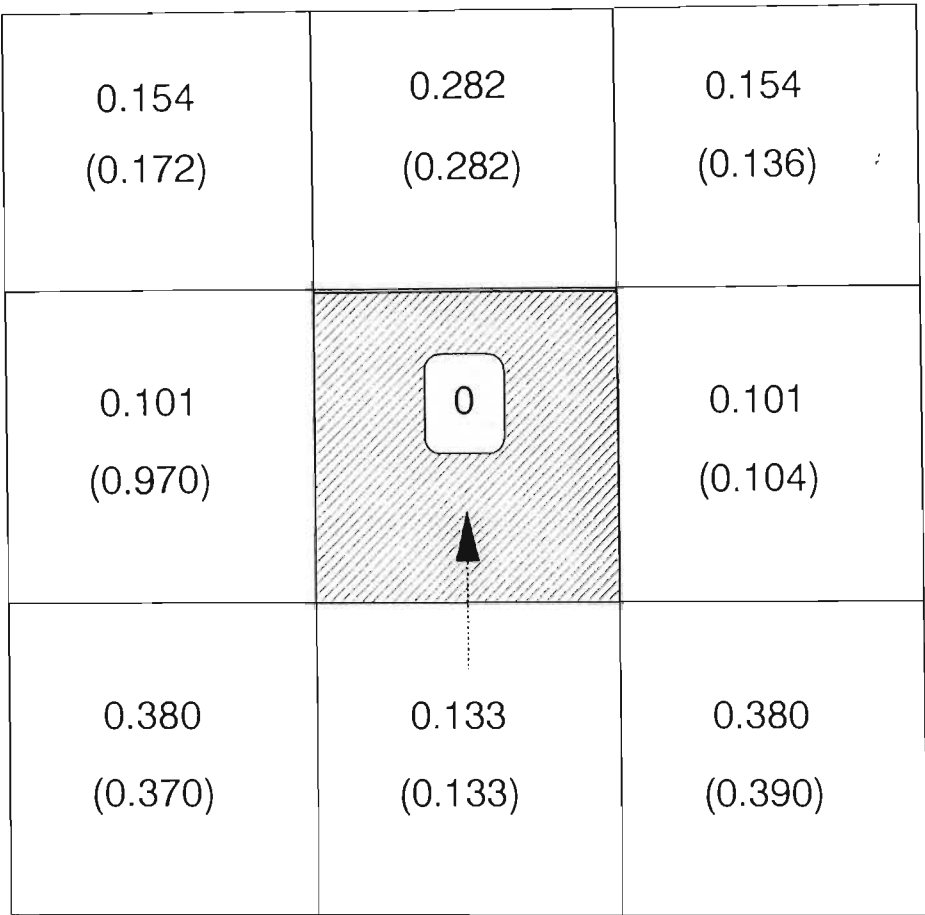


Figure 4.2: Frequency of occupation of quadrats that were: a) in line with the direction of movement (determined from the previous move), b) diagonally left and right of the direction of movement, c) at right angles to the left and right of the direction of movement, d) diagonally backward (left and right) to the direction of movement and e) directly opposite to the direction of movement. The centre quadrat represents the troops current position. The cell below represents the quadrat from which the troop moved to the current position. The arrow indicates the direction of movement. Data was used from day journey maps. Values in brackets are the probabilities while values on top are mean probabilities of moving in the 5 directions mentioned above.

relationship. How well it is able to maximise the cost benefit relationship depends on the constraints and rules within which it operates. Comparison between the results generated by an optimal model and results derived from a study animal give insights as to whether the model makes reasonable assumptions of the constraints faced by an animal and if the decision rules are similar to the ones the animal is using. The model, as in this case need not be the "ultimate" optimal solution that the foragers are trying to approximate but may represent a degree of optimisation that may be realistically achieved given the constraints faced by animals and using simple decision rules that might be available to the animal. The model might not result in a very good approximation of "ultimate" solution but if it produces similar values to those generated by the study animal it is a lot more useful in understanding the behaviour of the study animal.

The optimal model developed is a stochastic simulation model identical in all its constraints to the random model. However the probabilities of moving into the adjacent quadrats are weighted according to the relative estimated food availability in the quadrats. This represents a simple decision rule whereby the model troop chooses the next move on the basis of the food availability in the next quadrat. It is a form of short-term optimisation, ("thinking only one quadrat ahead") as opposed to long-term optimisation where the food availability of all the consecutive quadrats of a day journey are taken into account in choosing a journey. The choice of quadrat to which to move is stochastic being based on probabilities. This is analogous to the animal having an imperfect knowledge of productivity of the adjacent quadrats. The main features of both programs are shown in Appendix C.

4.2.5 Rationale behind models

The rationale behind the simulation models was to develop models with identical constraints to those found in the field. I matched simulations to individual day journeys of the study troop using the same two sleeping sites and number of quadrats entered. As the models were stochastic the simulations were run 20 times for each day. The number of simulations run for each day was based on plots of the cumulative standard deviations of the results of 100 simulations. In all cases the standard deviations evened out at or below 20 samples suggesting that this was an adequate number of iterations. In order to test the null hypothesis that there is no difference between results obtained for a day journey and the average of the results obtained from 20 iterations of the simulation model, paired t-tests were used. The simulations were programmed in GWBASIC.

4.2.6 Accessibility of habitat types

The accessibility of habitat types in the study troop's home range was determined from the frequency of encounter of the different habitat types during the random models day journeys. The random model estimate of accessibility for each habitat type is the sum of the percentage cover of that habitat for all the quadrats entered multiplied by the amount of times the quadrats were entered. All 1400 (70days X 20simulations) random simulations for the 12 month period were used for the calculations.

4.2.7 Availability of habitat types

Availability of habitat types for the troops home range was calculated from the percentage cover of each habitat types in the home range.

4.2.8 Effect of sleeping sites on habitat choice

The eight sleeping sites were clumped in 4 distinct areas of the home range. The sleeping sites within an area were at the farthest 900m apart (Figure 4.1). For the sake of simplicity I decided to group the sleeping sites together into four groups as follows: Camp group (C) sleeping sites (1, 2 and 3), Tree group (T) sleeping sites (4 and 5), Gorge group (G) sleeping sites (6 and 7) and the Fever (F) tree site (9). This was done since little would be gained from comparisons of sleeping sites in close proximity to each other. One hundred random simulations of day journeys were performed starting and ending at one of the four areas. Only combinations of day journeys which were recorded by the troop were used in the analysis (C-C,C-T,C-G,C-F,T-T,T-G,G-G). The geographic centre of all the sleeping sites in an area was used as the starting and end point of each simulation. All the simulations were 30 quadrats in length which is the mean number of quadrats that the study troop entered a day during the study. The χ^2 test was used to compare the proportion of habitats encountered during each route.

4.2.9 Energy encountered on day journeys

To calculate the amount of energy encountered during each day journey, the mean dry food mass in each quadrat was estimated. This was done by calculating the proportion of habitat types in each quadrat, multiplied by the mass of food available in each habitat type (corrected to represent a yield for four hectares - the size of a quadrat) as calculated on a monthly basis (see Chapter 2). These figures were summed to produce an estimate of dry food mass available in each quadrat. Food encountered during a baboon day journey was compared with food encountered during a random and an optimal day journey using chi square tests.

The amount of food encountered in each quadrat if time spent in each quadrat is taken

into account was also estimated. This was calculated by multiplying the dry mass of food in each quadrat by the number of observations (scans) which the baboons spent in each quadrat. Chi-square tests were also used to compare food encountered during a baboon day journey with food encountered during a random and an optimal day journey.

4.2.10 Habitat selection and food availability

To determine habitat selection a selectivity index was devised for each habitat type for each month. The index was calculated by dividing the proportion of habitats encountered during a baboon day journey route and during an optimal model day journey route, with the accessibility of each habitat as determined by the random model.

$$SI = \frac{FT_i}{\sum_i^j FT_{i \cdot \cdot j}} \div \frac{FR_i}{\sum_i^j FR_{i \cdot \cdot j}}$$

where: FT_i is the sum of the percentage cover of habitat i for each of the quadrats entered by the troop and the optimal simulation during day journeys for that month multiplied by the amount of times each quadrat was entered in that month; FR_i is the sum of the percentage cover of habitat i for each of the quadrats entered during the random simulation of the day journeys for that month multiplied by the amount of times that each quadrat was entered in that month. To investigate the relationship between food availability and selection of habitat types, food availability was plotted against selectivity index for both the troop, and the optimal simulation.

4.3 Results

4.3.1 Comparison of habitat choice between troop home range and the random walk model

Table 4.1 compares the availability of habitat types for the study troop's home range with the accessibility of the habitat type generated by the random model and the actual use of habitat types by the troop.

There was no significant difference between the two estimates ($P=0.223$, $\chi^2=6.96$,

Habitat type	% Availability	% Accessibility	% Disparity
ACW	49.7	49.8	0.2
AKF	8.3	5.1	38.6
ATH	6.8	11.0	38.2
CH	21.4	15.6	27.1
HCR	0.8	0.7	12.5
RAV	6.3	5.6	11.1
RIV	7.7	11.2	31.3

Table 4.1: Comparison between estimation of availability of habitat types for the study troop's home range with accessibility of habitat type generated by the random model. Habitat types: ACW-*Acacia* mixed woodland, AKF-*Acacia* *karroo* forest, ATH-*Acacia* thicket, CH-*Combretum* woodland, HCR-hilly *Combretum* woodland, RAV-ravine forest, RIV-riverine forest.

N=7). It is clear though that there are fairly large deviations between the two estimates for individual habitat types, with the exception of ACW and RAV. In the case of ATH the estimate of availability by area is a third larger than that determined by the random simulation. These differences are large enough to be important when comparing the time spent in a habitat type with the accessibility as opposed to the availability of that habitat type. Even small differences between availability and accessibility might mean the difference between a result showing a positive selection for a habitat as opposed to an avoidance of that habitat.

This can be demonstrated by comparing the habitat selectivity indices based on habitat accessibility (see Table 4.4) with the same indices based on estimates of habitat availability. There was a significant difference between the two habitat selectivity indices calculated for the troop ($P < 0.001$, $\chi^2 = 905.03$, $df = 83$). When analysed monthly there was a significant difference for 6 of the 12 months.

4.3.2 Sleeping sites and habitat choice

There was a significant difference in the ratios of habitat types encountered when departing and returning to different sleeping sites. Table 4.2 summarises these results. The study troop was therefore capable of altering the habitats available to them by their choice of sleeping sites. Habitat choice for the troop is therefore likely to involve an interaction between patterns of sleeping site use as well as the choice of day journey route.

4.3.3 Energy encountered on day journeys

Table 4.3 shows comparisons between total amount of energy encountered during day journeys for the random simulation model, the optimal model and the study troop for both number of quadrats entered and time spent in quadrats. One can see that for both analyses the optimal model simulations encounter more food than the random model (Quadrats entered: random=2922.47 Kg/day, optimal=3239 Kg/day, $t = 4.750$ $P < 0.005$; time spent in quadrats: $t = 4.672$ $P < 0.005$). This demonstrates that a level of optimisation is possible.

There is strong evidence that the troop does attain some level of optimisation. The troop appears to move through quadrats that have a higher mean dry mass of baboon food (3013.76 Kg/day) than does the random model simulations (2922.47 Kg/day) ($t = 1.477$ $P < 0.1$). Taking into consideration how tightly constrained the model is to conform to the study troop (same starting point, same destination, same number of quadrats entered, same propensity to move in the direction of movement, staying within the troops home range) 90% confidence that the troop encounters more food

Habitat	Habitat availability expressed as a percentage							χ^2 †
	C-C	C-T	C-G	C-F	T-T	T-G	G-G	
Acw	35.24	37.38	30.93	49.20	46.10	35.31	17.20	18.33 [*]
Akf	6.95	7.39	5.33	2.04	8.79	12.15	4.36	9.48
Ath	1.52	4.78	1.87	14.40	19.73	12.59	0.88	42.72 ^{**}
Ch	31.43	25.16	35.81	16.57	8.98	18.23	43.62	34.07 ^{**}
Hcr	1.35	0.88	0.89	0.42	0.26	0.56	0.35	1.34
Rav	15.44	10.63	15.40	1.83	0.09	5.90	27.82	50.04 ^{**}
Riv	8.08	12.24	7.65	13.54	15.70	11.95	5.10	7.96

$\chi^2 = 163.26^{**}$ with 36 degrees of freedom for the whole data set

† 6 degrees of freedom * $P < 0.01$ ** $P < 0.005$

Table 4.2: Ratios of habitat types encountered when departing and returning to different sleeping sites. For habitat type abbreviations see Table 4.1. Sleeping sites (see also Figure 3.1, Chapter 3): C-camp, T-tree, G-gorge, F-fever forest. The χ^2 statistics were calculated from the raw data and not the percentage data in the table.

	t Statistic and significance level		
	Troop-Random	Troop-Optimal	Optimal-Random
Quadrats entered ^δ	t=1.477*	t=1.258	t=4.750 ^{***}
Time spent in quadrats [†]	t=2.181 ^{***}	t=0.870	t=4.672 ^{***}

^δ Degrees of freedom=62 [†] Degrees of freedom=60 *P<0.1 **P<0.05 ***P<0.005

Table 4.3: Comparisons using paired t-tests between total amount of energy encountered during day journeys for the random simulation model, the optimal model and the study troop. Comparisons are for number of quadrats entered and time spent in quadrats.

than the random model should probably be regarded as statistically significant. Indeed in many modelling applications a probability of 0.1 is taken as statistically significant (Verner *et al.* 1986) Thus it appears that the study troop's day journey routes encounter more food than if they were chosen randomly.

When allocation of time to different quadrats is taken into account the troop encounters significantly more food than the random model ($t=2.181$ $P<0.005$). The troop is therefore spending more time in quadrats with greater food availability.

Comparison between the troop and the optimal simulations shows no significant difference in the amount of food encountered between the troop and the optimal model for both number of quadrats entered (troop=3013.76 Kg/day, optimal=3239.0 Kg/day $t=1.258$ $P>0.1$; and time spent in quadrats ($t=0.870$ $P>0.1$). These results suggest that the troop displays a similar level of optimisation as that displayed by the model.

A comparison of the amount of food encountered shows that the difference between that encountered by the troop and the random simulation is on average 92 kilograms while the difference between troop and the optimal simulation is 208 kilograms. This is despite the difference between the troop and the random simulation being significant, while the difference between the troop and optimal simulation is not significant. While it might seem that a difference of 208 kilograms should indicate that the difference between the troop and optimal simulation should be more significant rather than less significant than between the troop and random simulation, this is not the case given the nature of the paired t-test. The t-test does not test for the difference between means, but rather tests whether the troop did better than the simulations on more days than it did worse, and whether this result was significantly different. Therefore it is possible to have a smaller discrepancy between the mean amount of food encountered and a larger significant difference. This in fact makes the test more applicable to this study's needs, where food encountered on a day journey (simulated or real) varies greatly, thus allowing particularly large or small values to have a big effect on determining the mean. This is an especially risky situation when dealing with food encountered rather than food eaten, since during certain periods or on particular days the baboons might fulfil their nutritional requirements in a short time and spend most of the day in particularly food poor habitats, these days will then have an effect on the mean out of proportion to their biological importance. In such cases it is better to know if the troop is doing better than the better or worse a significant number of times more than the simulations.

Month	Habitat	% Frequency of use			Selectivity index		Food
		Troop	Random	Optimal	Troop	Optima	
1	ACW	36.19	39.67	36.49	0.91	0.93	23.51
1	AKF	8.67	7.51	6.06	1.15	0.81	15.16
1	ATH	3.00	4.13	3.10	0.72	0.76	21.46
1	CH	26.11	20.76	24.06	1.25	1.13	1.42
1	HCR	1.11	1.29	0.79	0.86	0.59	19.49
1	RAV	10.42	13.86	17.97	0.75	1.24	9.38
1	RIV	14.50	12.37	10.00	1.17	0.79	9.57
2	ACW	51.10	53.97	54.37	0.97	1.00	14.44
2	AKF	4.92	5.16	6.28	0.97	1.20	15.97
2	ATH	14.67	11.74	12.35	1.28	1.05	24.62
2	CH	10.91	10.71	10.22	1.04	0.93	1.69
2	HCR	0.34	0.75	0.68	0.47	0.90	19.95
2	RAV	4.36	4.40	4.22	1.01	0.95	10.34
2	RIV	9.80	11.53	10.86	0.87	0.94	12.99
3	ACW	36.64	38.60	40.25	0.95	1.05	10.57
3	AKF	10.50	6.47	6.48	1.63	1.02	14.28
3	ATH	3.83	3.66	5.66	1.05	1.53	23.62
3	CH	22.19	23.03	20.54	0.97	0.91	2.93
3	HCR	1.60	1.37	1.26	1.17	0.96	21.52
3	RAV	13.10	12.77	11.10	1.03	0.90	10.38
3	RIV	11.81	14.00	14.20	0.85	1.03	16.70
4	ACW	46.40	44.52	44.28	1.04	1.00	9.84
4	AKF	4.35	6.26	6.36	0.69	1.12	22.18
4	ATH	4.27	6.56	5.98	0.65	1.08	28.91
4	CH	24.58	18.97	19.57	1.29	1.21	2.38
4	HCR	1.10	1.06	1.05	1.03	1.07	15.59
4	RAV	10.60	9.61	11.20	1.10	1.26	10.90
4	RIV	7.81	11.51	9.41	0.67	0.88	10.21
5	ACW	36.08	62.05	45.69	0.61	0.73	9.13
5	AKF	5.34	3.43	5.70	1.62	1.49	33.99
5	ATH	26.68	11.64	17.19	2.39	1.54	29.41
5	CH	14.12	11.11	11.93	1.32	1.07	2.18
5	HCR	0.88	0.11	0.78	3.39	6.61	10.68
5	RAV	5.84	0.01	9.35	559.8	835.30	10.37
5	RIV	6.60	11.20	8.63	0.61	0.71	4.24
6	ACW	55.03	62.05	45.95	0.89	0.74	8.88

Table 4.4: Frequency of usage of different habitat types expressed as percentages for study troop, random model and optimal model. Columns 6 and 7 show selectivity indices expressing habitat type preferences, a score above 1 indicating a positive preference A score of below 1 indicates under-utilisation of a habitat type. Column 8 shows food availability (kg dry mass food per hectare) of the different habitats for the corresponding months. For habitat type abbreviations see Table 4.1.

6	AKF	1.71	3.43	2.70	0.50	0.82	30.34
6	ATH	21.20	11.64	32.68	1.83	2.36	28.49
6	CH	11.63	11.11	7.27	1.05	0.58	2.13
6	HCR	1.57	0.11	0.45	14.57	4.20	7.76
6	RAV	1.24	0.01	0.95	114.4	88.87	17.82
6	RIV	6.49	11.20	9.07	0.58	0.82	4.57
7	ACW	55.35	59.03	55.14	1.05	0.94	8.64
7	AKF	4.66	3.43	5.09	1.51	1.57	32.88
7	ATH	16.53	17.36	16.99	1.06	1.00	24.96
7	CH	5.36	7.36	9.29	0.81	1.32	2.42
7	HCR	0.76	0.10	0.56	8.77	5.91	8.21
7	RAV	0.45	0.08	2.49	6.21	31.36	17.96
7	RIV	6.34	12.38	9.78	0.57	0.82	4.93
8	ACW	52.36	56.52	48.64	1.04	0.86	7.81
8	AKF	6.01	3.94	7.07	1.71	1.77	36.77
8	ATH	9.46	17.94	13.77	0.59	0.77	16.78
8	CH	11.81	9.27	13.67	1.43	1.48	3.21
8	HCR	0.59	0.29	0.68	2.28	2.44	10.70
8	RAV	1.92	0.49	5.61	4.42	11.99	19.05
8	RIV	6.05	10.29	9.48	0.66	0.92	5.69
9	ACW	52.60	50.26	42.05	1.10	0.85	11.53
9	AKF	4.66	6.02	7.64	0.81	1.34	28.08
9	ATH	10.32	6.82	4.22	1.59	0.51	16.81
9	CH	15.17	15.63	19.85	1.02	1.12	3.02
9	HCR	0.37	0.76	0.78	0.51	1.00	14.74
9	RAV	1.18	7.51	15.15	0.17	1.95	18.32
9	RIV	10.68	12.62	8.91	0.89	0.75	7.49
10	ACW	38.76	46.94	52.13	0.85	1.08	19.54
10	AKF	4.20	1.71	6.06	2.51	2.97	22.79
10	ATH	29.47	33.31	6.78	0.91	0.22	16.25
10	CH	5.60	6.17	15.58	0.93	2.37	2.65
10	HCR	0.70	0.11	0.85	6.85	7.63	17.54
10	RAV	0.90	0.29	7.64	3.18	25.09	14.97
10	RIV	12.94	6.50	8.96	2.04	1.23	6.26
11	ACW	51.59	45.61	53.96	1.25	1.19	28.62
11	AKF	3.62	6.75	5.43	0.59	0.83	18.54
11	ATH	2.80	5.20	3.95	0.60	0.79	11.40
11	CH	20.60	22.95	16.73	0.99	0.72	2.36

11	HCR	0.67	0.70	0.93	1.06	1.35	20.27
11	RAV	3.03	6.62	8.19	0.51	1.27	12.55
11	RIV	7.29	11.28	8.94	0.71	0.83	6.28
12	ACW	49.57	37.89	48.21	1.30	1.35	40.62
12	AKF	13.38	7.63	4.82	1.75	0.75	8.95
12	ATH	2.21	1.95	1.73	1.14	1.04	11.70
12	CH	25.79	30.55	19.14	0.84	0.85	1.40
12	HCR	0.60	1.26	0.81	0.47	0.77	21.69
12	RAV	1.67	11.08	9.52	0.15	1.00	8.29
12	RIV	6.79	9.35	9.70	0.72	1.12	7.36

4.3.4 Food availability and habitat selection

Table 4.4 shows the frequency of usage of the different habitat types, expressed as percentage, for the study troop, random model and optimal model together with the food availability (kg dry mass food per hectare) of the different habitats for the corresponding months (column 8).

A correlation between proportional food availability and selectivity index was expected at least for the optimal model which was stochastically selecting quadrats on the basis of proportional food availability. There was a slight trend of increased selectivity with increasing food availability for the troop and optimal correlations (Figure 4.3a & 4.3b) although these were not statistically significant (Troop $r^2=0.00031$ $P>0.1$, Optimal simulation $r^2=0.0268$ $P>0.1$). While the lack of correlation between food availability and the selectivity indices for a model that chooses what quadrat to enter on the basis of food availability seems contradictory, it demonstrates how constrained habitat choice can become in a complex environment.

There was a significant linear regression between selectivity indices of the troop and those obtained from the optimal simulations (Figure 4.4. $r^2=0.288$, $P<0.0001$). This indicates a similar basis of selection between the troop and the optimal simulation.

4.4 Discussion

The results demonstrate that the troop is choosing its daily routes on the basis of food availability. This is based both on the comparison of the troop with the random walk model (which showed 90% confidence in the results) and in the comparison between the troop and the optimal model (which showed no significant difference despite the significant difference between the optimal model and the random walk model).

There has been some qualitative evidence for choosing routes on the basis of food availability. Sigg and Stolba (1981) noticed that foraging parties converged on particularly rich feeding sites and ignored other potential feeding sites; Post (1978) linked intensive utilisation of several habitat zones to the occurrence of favoured food species in these habitats; Henzi *et al.* (1992), Kummer (1968) and Dunbar and Dunbar (1974), showed that baboons changed their day journey routes seasonally to cope with changes in food availability. However, the present study is the first to show quantitative evidence for route choice on the basis of food availability. The problem has not previously been resolved because of the lack of quantitative data on food availability, as well as the inability to take into account effects of spatial distribution of habitat types and sleeping sites through the home range (Post 1978). Quantifying food

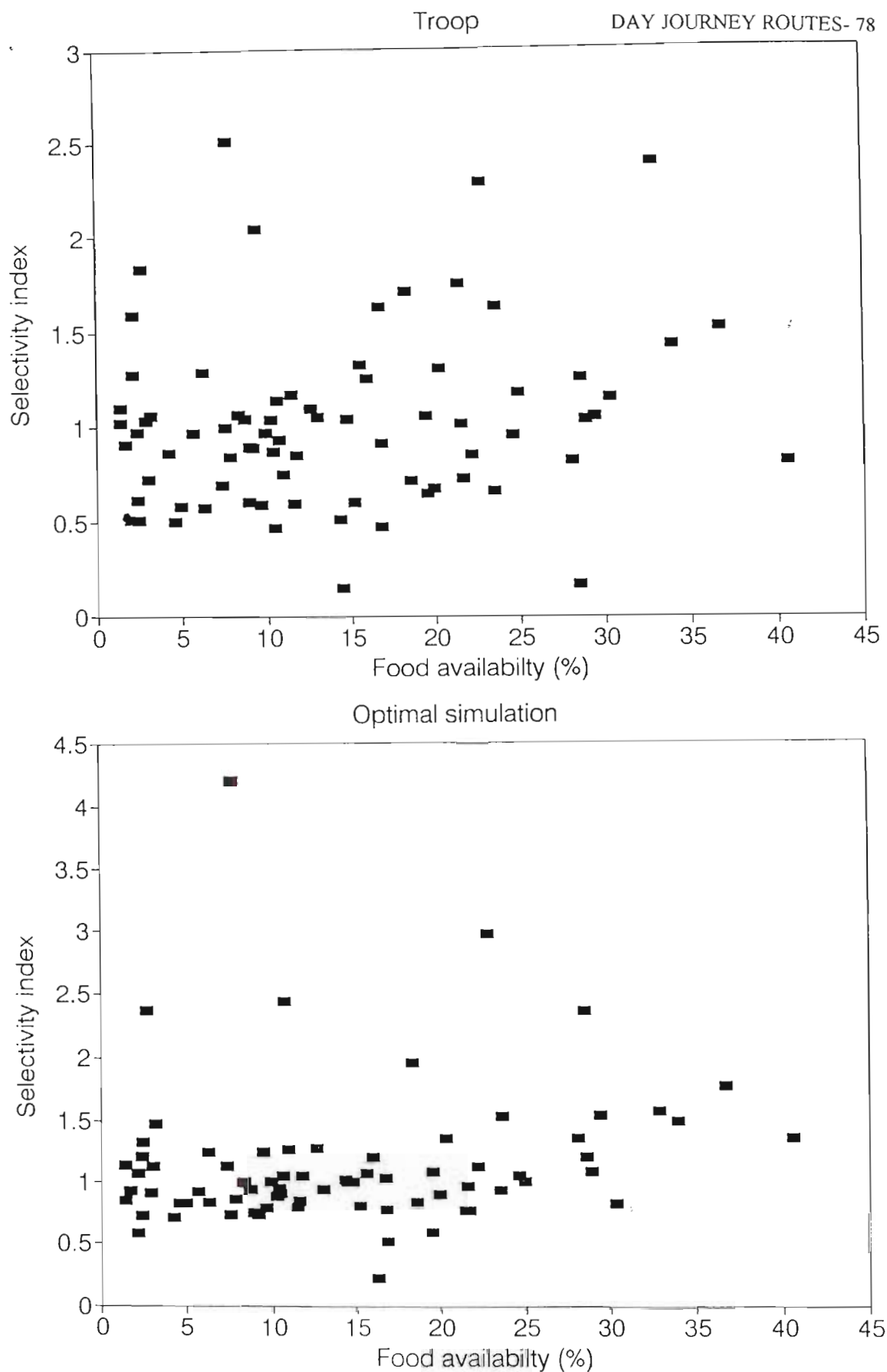


Figure 4.3: Plot of proportional food availability against selectivity index for the troop (a) and the optimal model (b). Data from Table 4.4 was used. Troop - $r^2=0.00031$ $P>0.1$. Optimal simulation - $r^2=0.0268$, $P>0.1$.

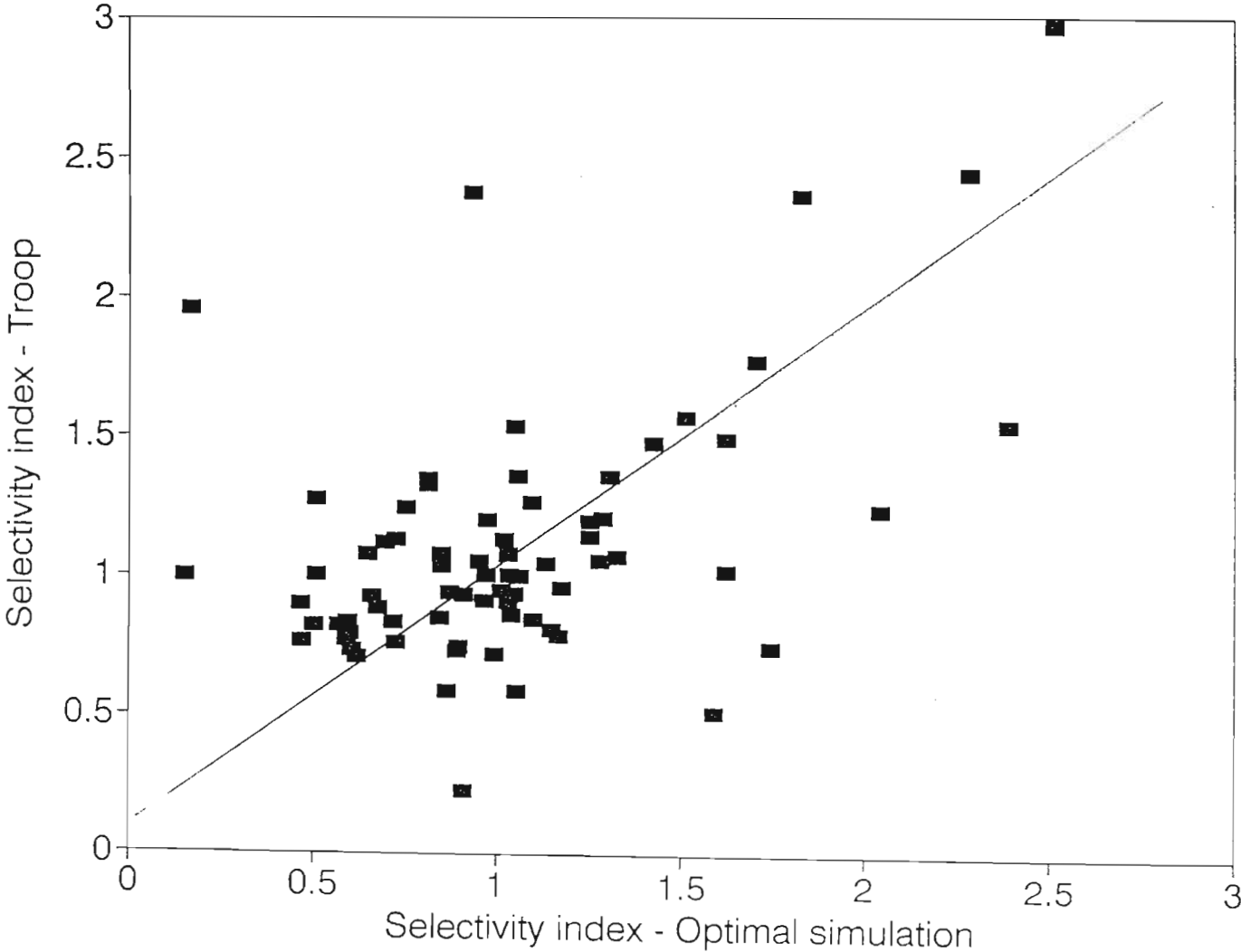


Figure 4.4: Regression between selectivity indices of the troop with those obtained from the optimal simulations. $r^2=0.288$, $P<0.0001$.

availability and comparing the results of the troop with a model and optimal foraging model overcame these problems.

The troop appeared to show a level of optimisation similar to, but not above that achieved by a simple stochastic optimisation model, thinking only one quadrat ahead. This short term optimisation appears to be contradictory to evidence that baboons have a well developed mental map of their entire home range and essential resources in it (Altmann and Altmann 1970; Sigg and Stolba 1981). Utilisation of food resources means that they get depleted and this would force the troop to utilise other food patches (Dunbar 1988). In addition the availability of different foods is constantly changing, often not displaying consistency in timing or amount between years (pers obs; Dunham 1990; Norton *et al.* 1987). Consequently baboons face a broad but uncertain daily foraging potential (Hamilton *et al.* 1978) in which long-term optimisation may not be viable. This is especially true in a mosaic of habitats, all of which contain potential foods such as found in the troop's home range (see Chapter 1).

In addition to optimisation of choice of day journey route, Mtshopi troop showed a greater degree of optimisation in allocation of time along the day journey route. The troop favoured quadrats with higher food availability, on average allocating more time to them than predicted by the random walk model. Taking allocation of time into account increased the significance of the difference between the mean dry mass of food encountered by the troop compared with that encountered by the random walk model from $P < 0.1$ to $P < 0.005$. This is probably due to allocation of time being less constrained than choice of day journey route.

Both the troop and optimal model showed no significant correlation between habitat preference and relative food availability. This was despite choice of quadrats on the basis of food availability being built into the optimal model, and despite both the troop and optimal model encountering more food than the random model. This shows that constraints such as spatial distribution of habitats and sleeping sites may have a large effect on "apparent habitat choice". The lack of correlation between habitat preference and food availability does also not prove that an animal does not take food availability into account when choosing where to go.

The strong correlation between habitat selection indices and food availability in the different habitats for both the troop and the optimal model suggests that they both had a similar basis for choosing habitats. This further strengthens the contention that the optimal model is a realistic representation of the process of optimisation used by the

troop.

These results have several implications. They demonstrate a practical solution to the problem of non-random encounter of habitat types and in doing this they emphasise the important influence that the spatial distribution of refuges and sleeping sites have on the ability of an animal to conform to expectations of what is optimal. The results also suggest that two levels of foraging strategies are possible. On one level, choice of sleeping sites within a home range can significantly influence the encounter rate of different habitat types; and on another level, the troop is able to alter its encounter rate through the choice of the day journey route between sleeping sites. What remains to be done is to apply this type of simulation model more widely for generating null hypotheses for encounter rates of food patches or habitat types. An obvious extension of the model for the Mtshopi troop is to extend the analysis from a comparison of dry mass of food encountered to nutrients encountered or range of food encountered.

Chapter 5

Diet selection of a troop of baboons (*Papio cynocephalus ursinus*) in a mixed woodland habitat

5.1 Introduction

Optimal foraging theory proposes that animals should forage so as to maximise the rate of nutrient intake (Schoener 1971; Schoener 1987; Krebs and Davies 1991; Lemon and Barth 1992). One aspect of this is the choice of habitats and foraging paths which maximise the rate of food intake. This has been addressed in previous chapters. The second aspect is choice of food types. Of all primates, omnivores such as baboons and vervets have the most diverse diets (Harding 1981). Norton *et al.* (1987) recorded 185 food species at Mikumi, Tanzania over five years. More typically 50 to 100 food species have been recorded at baboon study sites (Hall 1963; Post 1978; Sharman 1981). The large number and diversity of dietary items include underground stems, roots, seeds, flowers, gums, fruits and leaves. This is probably a function of a generalised digestive system, an intermediate body size, (baboons are not so small as to require a high energy diet, and not large enough to require a bulk feeding strategy), an ability to exploit both arboreal and terrestrial compartments of the habitat, and a manipulative ability that allows digging and handling food parts so as to discard inedible parts and extract edible parts. As a result of this diversity, any attempt to forage optimally requires that baboons may need to choose between dietary items with very different nutritional profiles.

Optimal foraging was developed initially to account for the dietary choices of predators (Schoener 1987). Predators face choices between prey items which differ in mass, abundance and handling time, but are relatively similar in terms of nutritional value per mass. In addition consumption of animal prey results in less chances of micronutrient and vitamin deficiencies since these have to a large extent been overcome by the prey. Omnivores, and especially extreme generalists such as baboons pose additional problems for optimal foraging theory since their diet differs greatly with respect to nutrient content (Barton *et al.* 1992). Consequently omnivores not only have to maximise energy intake, but balance their diet with respect to several nutritional components, most notably amino acids needed for maintenance and growth. Additionally because the digestion of plant matter is slower than animal matter digestive capacity and the rate of digestion becomes more of a constraining factor. Thus omnivores also need to select food on the basis of fibre content and

secondary compounds that inhibit digestion (Waterman 1984; Oftedal 1991).

Baboons have been characterised as eclectic/selective feeders (Norton *et al.* 1987). This describes the combination of feeding on a wide range of foods while being selective in light of the array of foods available to them. The ability to utilise foods from many compartments of the environment (Harding 1981) is to a large part responsible for the ability of baboons to survive in such diverse habitats as deserts, swamps, forests and montane regions (Whiten *et al.* 1987, Norton *et al.* 1987). Whiten *et al.* (1992) have shown that despite wide variation in baboon diets at different study sites, diets converge in terms of nutrient composition. This suggests that baboons have the ability to combine different dietary components in order to achieve a balanced and relatively constant nutrient profile.

There are several bases upon which diet can be determined, the most simple being encounter rate of different food types. In this scenario baboons feed on the first and subsequent species that have a suitable nutrient profile. Using this strategy, the diet would then approximate the relative densities of food species encountered. Selection in this case would be limited to the discrimination between food and non-food items and time spent feeding would be dependent on satiation rather than the abundance of the food. Other studies of baboons suggest that this is not the case. Whiten *et al.* (1992) have shown that although selection of food is grossly related to food availability, at a finer scale it is related to levels of protein, lipid, fibre, phenolic and alkaloid content. Hamilton *et al.* (1978) demonstrated a similar choice for high protein and low fibre levels when they compared food and non-food parts.

The aims of this chapter are: (i) to describe monthly variation in the study troop's diet; (ii) to test whether the troop's diet differs from that expected purely on the rate of encounter of different habitat types; (iii) to test whether the troop shares the same principles of dietary choice as described for the troops studied by Whiten *et al.* (1992); (iv) to test whether the study troop had a similar nutrient profile to those from other populations and (v) to test the prediction, from broader optimal foraging principles, that there will be an increase in diet breadth in periods of food scarcity (Rozenzweig 1985; also see Wrangham 1977; Melton 1987).

5.2 Methods

5.2.1 Study animals

The subjects of this study were members of the Mtshopi troop at Mkuzi Game Reserve in Northern Zululand, South Africa. The troop has been part of a long-term study which began in February 1986 (see Henzi *et al.* in press). The data presented here were collected from May 1989 to April 1990. During the entire long-term study the troop had been in a phase of growth (see Henzi *et al.* in press), which terminated with the split of the troop into two daughter troops in late April 1990. The troop consisted of approximately 59 individuals at the start of the 12 month study period and consisted of 76 individuals at the time of fission. The troop was well habituated, at times allowing approaches to within 3 metres without any visible effect on behaviour. This allowed accurate identification of foods eaten throughout the period.

The troop's home range occupied the foothills of the Lebombo mountains and part of the adjacent coastal plain in the north western part of the Mkuzi Game Reserve (27°30'S; 32°05'E). The reserve, 290km² in extent, is located on the coastal plain east of the Lebombo mountains in north-eastern Natal/Kwazulu province, South Africa. The troops home range is a complex mosaic of vegetation types, predominantly consisting of variations of *Acacia* woodland and thickets. These are intersected by ravine and riverine forest/woodlands bordering the numerous rivers and streams that course through the foothills down to the coastal plain. A complete description of the home range and vegetation types are given in Chapter 3.

5.2.2 Determination of diet

The dietary data were based on 70 dawn to dusk follows. The troop's diet was determined from instantaneous scan samples (*sensu* Altmann 1974) taken every 10 minutes during the day journey. The data therefore represent the proportion of time spent feeding on different food items. Although sampling every ten minutes might undermine the independence of each data point, it would tend towards a more accurate estimate of the time spent feeding on the different food items than would a longer interval between sampling. It also increased the probability of picking up rare food items. None of the analyses in this chapter are reliant on the statistical independence of individual feeding records.

5.2.3 Determination of food availability

Food availability was calculated for all foods that comprised the top 80% of the troops feeding time in any month, with the exception of grass leaves, mushrooms, invertebrates and cyperus corms. The contribution of grass leaves to the dry mass of baboon food could not be accurately assessed because of difficulties in determining the mean amount of grass ingested per sward (this varied greatly, and was partly determined by the length of new growth on swards), and the availability of grass

swards with green shoots (the troop only consumed young leaves). Mushrooms, invertebrates and *Cyperus* corms were too stochastically and patchily distributed to provide a meaningful estimate of their availability using the methods and sampling intensity employed in this study. These exceptions however, only accounted for 7.3% of the total feeding time of the troop. The 37 food items for which availability was calculated therefore remained representative of the diet, despite the exclusion of these four items.

A detailed description of the methods used to calculate food species density and food availability are given in Chapter 3. What follows is a brief description of the method. Between 100 and 230 locations within each of the seven habitat types were sampled using the point centred quadrat method (Pielou 1959). This enabled the composition, density and size structure of food species to be calculated for each habitat. The number and dry mass of food items for the different species was then determined by physically sampling and weighing food items from individual trees and shrubs. Food availability was calculated on the basis of the number of trees and shrubs with food items and the mean percentage of food items that they contained. This was determined from monthly censuses of the phenology of all food species. The amount of dry food available for each species was calculated by multiplying the density of food species by the proportion of individuals with food. This in turn was multiplied by the dry mass yield of food items adjusted for by the size structure and mean percentage of food items present for the specific month. This resulted in the dry mass of food available per hectare for each habitat. The total available mass of food for each species was adjusted according to the percentage of time the troop spent in each habitat. These data are presented in Chapter 3.

5.2.4 Seasonal analyses

For the purpose of analyses in this chapter the year was divided into two seasons on the basis of food availability. The high food season consisted of the months February-July with more than 80kg/ha dry mass of baboon food. The low food season consisted of months August-January with less than 80kg/ha (see Chapter 2, Figure 2.4). These seasons did not coincide with the dry/wet season dichotomy but rather overlapped each by three months (see also Chapter 3).

5.2.5 Nutritional analyses

Samples were analysed at Cedara Agricultural College feed analysis unit. The samples of food items represented the parts that the baboons ingested in the field as well as samples of non-food items and whole fruits. The latter were collected for comparison between the nutrient content of the whole fruits as opposed to the specific part of the

fruit that the baboons ingested. The non-food items were collected for comparison with food items. All samples were air dried at 37°C till they attained a constant mass. The analysis included acid detergent analysis of fibre, ether extraction of lipids and micro-Kjeldahl analysis of nitrogen. The proportion of protein was determined by N X 6.5. The major micro-nutrients and trace elements were also determined. No secondary compounds were analysed due to the lack of facilities.

5.3 Results

5.3.1 Diet

The troop was recorded eating up to 3 different parts of 92 plant species. A list of all foods that the baboons were observed eating, their index of availability, amount eaten and months in which they were eaten is given in Appendix D. The wide variety of food species eaten demonstrates the characteristic ability of baboons to utilise all parts of their environment especially those not available to potential ungulate competitors. The foods included roots, underground storage organs of *Cyperus* spp., exudate of *Acacia* and other species, leaves, fruits, seeds, flowers, fleshy stems, mushrooms, lizards and a variety of insects such as termites, ants and beetles. On two occasions during the study, mountain reedbuck (*Redunca fulvorufula*) calves were attacked and caught by males but they abandoned their prey due to the approach of game guards who chased the baboons off their prey. Animals formed a negligible part of the troops diet, at the most accounting for two and three percent of the diet in July and September. Most of the diet was plant based.

Table 5.1 shows the foraging profile of the study troop in relation to those recorded elsewhere (from Whiten *et al.* 1992). The diet of the study troop was dominated by fruit (both flesh and seeds). The troop's diet contained the highest proportion (90%) of fruit of all the study sites. Correspondingly there were low proportions of the other food types: underground items, leaves, flowers and animals. Of the fruit, 35% constituted consumption of only the seeds, the rest of the fruit being discarded. In the case of *Acacia* species not only the fibrous pod was discarded, but also the testae covering the embryos. These were wedged in the cheek pouches and spat out.

The diet varied markedly between months. Figure 5.1 summarises the proportions of foods that compromised 80% of monthly diets for nine months of the study. These are based on the number of feeding observations derived from scan samples. To control for the effect of different numbers of observations on the number of species included in the diet, the observations for all months were standardised at 200 by randomly

food type	percentage of time feeding at different study sites (1-12)												range (%)	mean (%)
	Mkuzi	1	2	3	4	5	6	7	8	9	10	11		
fruits	90	74	49	43	43	42	41	27	23	16	10	3	1-90	38
underground items	1	3	7	39	12	16	1	33	15	52	27	53	1-53	22
leaves	6	9	14	8	14	25	41	15	27	19	53	26	6-53	21
flowers	3	9	2	7	20	12	12	5	21	1	3	14	1-20	9
animals	1	1	13	3	?	3	4	1	1	9	2	4	1-13	4

Table 5.1: Foraging profile of the study troop in comparison with those at other study sites. Sites are ranked by % fruit in diet (the most common food type overall). 1. Mt Assirik, Senegal (*Papio cynocephalus papio*); 2. Gombe, Tanzania (*P. cynocephalus anubis*); 3. Suikerbosrand, South Africa (*P. cynocephalus ursinus*); 4. Mikumi, Tanzania (*P. cynocephalus cynocephalus*); 5. Cape Point, South Africa (*P. cynocephalus ursinus*); 6. Bole, Ethiopia (*P. cynocephalus anubis*); 7. Amboseli, Kenya (*P. cynocephalus anubis*); 8. Laikipia, Kenya (*P. cynocephalus anubis*); 9. Ruaha, Tanzania (*P. cynocephalus cynocephalus*); 10. Gilgil, Kenya (*P. cynocephalus anubis*); 11. Drakensberg, South Africa (*P. cynocephalus ursinus*). All data for other study sites from Whiten *et al.* (1992).

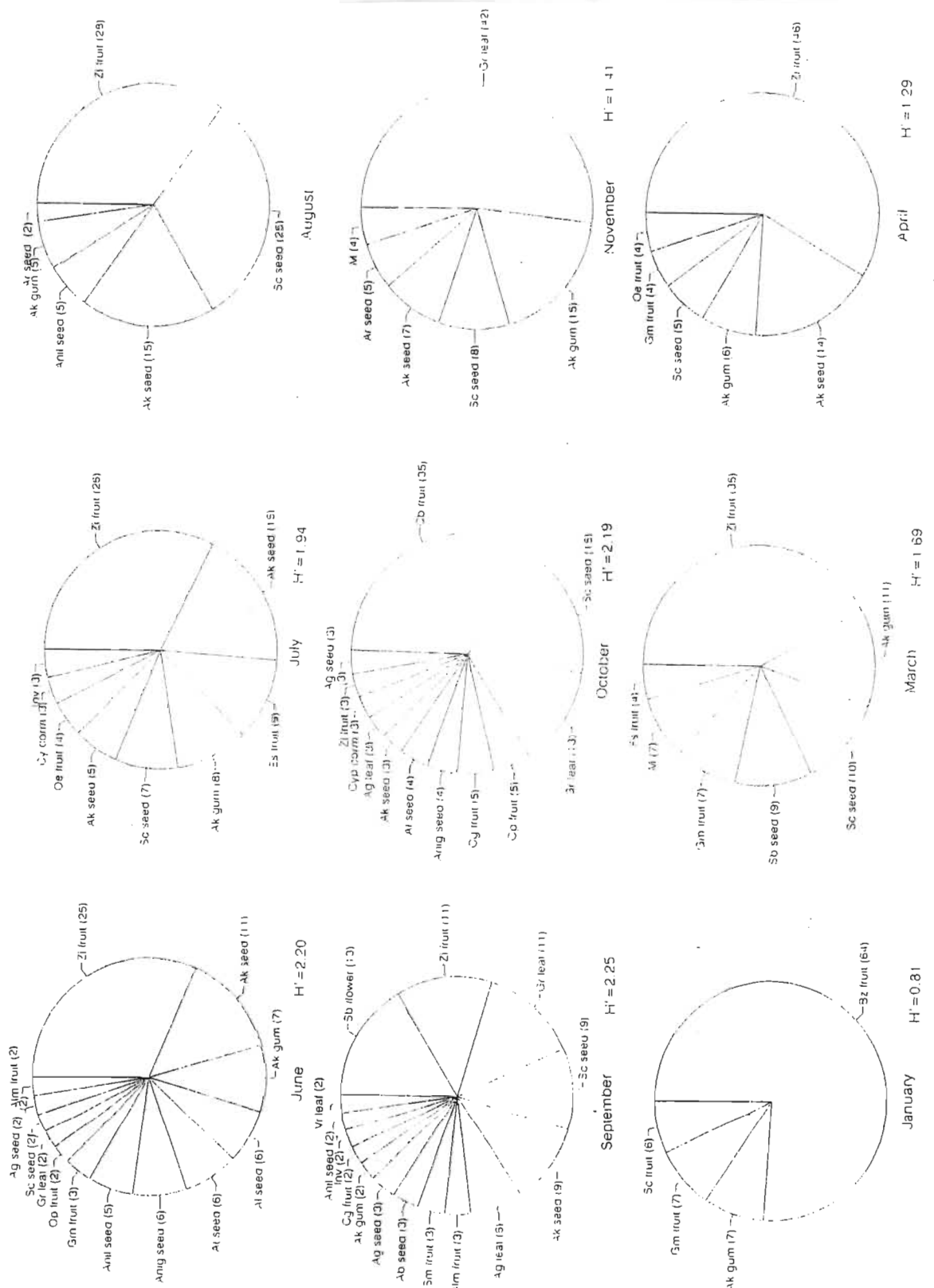


Figure 5.1: Main diet (foods comprising top 80% of diet for each month) and diversity index (Shanons H' index) for June 1989 to April 1990. The figures in brackets are the percentage of the monthly diet. December, February and May's data were not used since they consisted of fewer than 200 observations. All months are based on 200 randomly chosen feeding observations (see text). Ab=*Acacia burkeri*; Ag=*Acacia gerrardii*; Ak=*Acacia karroo*; Al=*Acacia luederitzii*; Alm=*Aloe marlothii*; Anil=*Acacia nilotica*; Anig=*Acacia nigrescens*; Ar=*Acacia robusta*; At=*Acacia tortilis*; Bz=*Berchemia zeyheri*; Cb=*Capparis brassia*; Cg=*Croton gratissimus*; Ct=*Cassine transvaalensis*; Cyp=*Cyperus* spp.; Es=*Euclea shimperi*; Fs=*Ficus soldanella*; Gm=*Grewia monticola*; Gr=grass spp.; Inv=invertebrates; M=mushrooms; Oe=*Olea europaea*; Op=*Ozoroa paniculosa*; Sb=*Schocia brachypetala*;

deleting excess observations. The most consistently utilised food over the year was *Ziziphus mucronata* fruit which was consumed from March to October and accounted for 28% of the total number of feeding observations. This was followed by *Sclerocarya caffra* and *Acacia karroo* seeds both accounting for about 11% of all feeding observations.

Concurrent with changes in the number of species were differences in the food parts used. Figure 5.2 shows the monthly changes in the proportions of food types. In all months except November fruit (seeds and flesh) comprised the major part of the diet (47-77%). During November, the month with the lowest food availability (see Chapter 2) the baboons spent most time (42% of scans) feeding on the new grass shoots emerging after the winter burns. The preceding two months showed a smaller diversification of diet to include post-burn grass shoots, *Acacia gerrardii* young leaves and *Schotia brachypetala* leaves. The months August to December are the months of greatest food scarcity at Mkuzi (see Chapter 2). Apart from this diversification in food type there was no difference between the diversity of species in the troop's diet (using Shannon's H' index of species diversity, Ludwig and Reynolds, 1988) between the low food season (August-January) and high food season (February-July) ($Z=-0.61$; $P=0.54$). There was also no difference in the proportion of available foods utilised between these two periods ($Z=0.37$, $P=0.71$). This is contrary to the optimal foraging prediction of broadening of diet during periods of food scarcity.

5.3.2 Food selection in relation to proportion of food species encountered

To test whether Mtshopi troop's diet differed from proportions of food species relative to non-food species encountered during their day journeys, densities of food species encountered were calculated. This was done by calculating proportions of habitat types entered (see Chapter 3). These proportions were multiplied by the habitat specific densities (Chapter 2) of the different food species. When expressed as proportions these figures represent the relative encounter rate of the different species for the troop. The density of each food species in each habitat type was calculated in Chapter 2 and from this the density of each food species in each quadrat entered during a day journey was calculated.

A χ^2 test was done to see if there was a difference between the proportion of food items in the diet and the proportion of food species encountered. A significant difference would indicate selection of specific food items rather than foods in proportion to which they encountered them. There was a significant difference

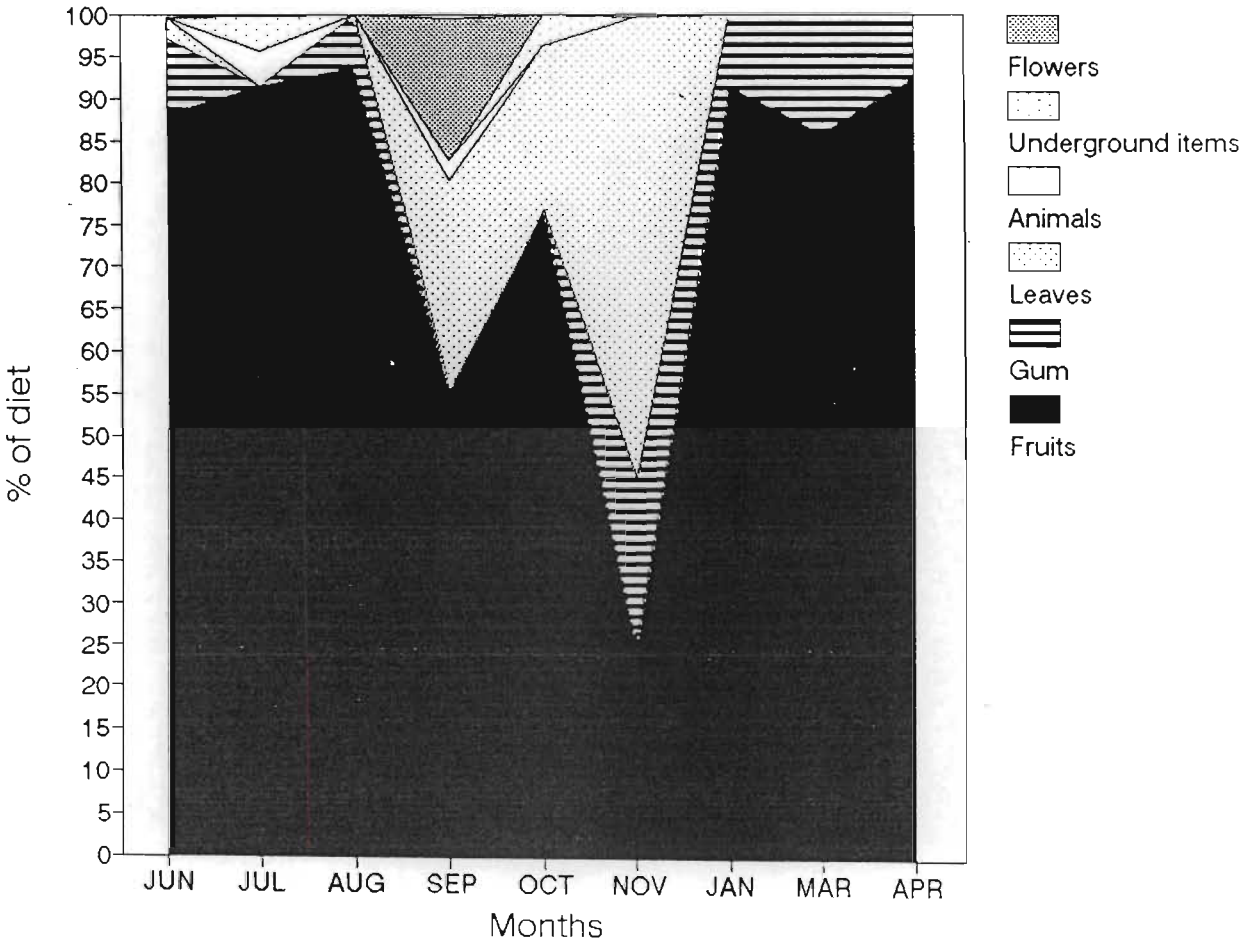


Figure 5.2: Monthly changes in proportion of food types contributing to the diet, based on 200 feeding observations each month.

between the proportional densities of food species and their occurrence in the troop's diet ($\chi^2=633.0$, $df=9$, $P<0.001$, $n=10$). This is a stringent test as the diet might not necessarily reflect the proportional densities but rather simply be correlated with them. While there was a positive correlation between the relative density of food species and their proportion in the diet, this was not significant ($r^2=0.0375$, $P=0.078$, $n=57$). Diet selection therefore appears to be only weakly based on the encounter rate of food species if at all.

5.3.3 Food selection in relation to number and mass of food items encountered

Further refinement of resource optimisation requires taking into account, not only the relative occurrence of food species, but also the number and mass of the food items at each encounter. To do this the available dry mass of the different food types was calculated (taking into account the proportions of the different habitat types entered) for each month (see Chapter 3). This gives better estimates of the relative value of the different food types than densities of the food species. Despite this there was no significant correlation between the available dry mass of food items and their proportion in the diet ($r^2=0.963$, $P=0.4713$, $N=57$). In fact the correlation was lower and less significant than obtained for the densities of food species alone.

The lack of correlation between the proportions of food items in the diet and their abundance could, within the optimal foraging paradigm, be accounted for by differences in nutritional content of the foods. This could lead to foods of the greatest nutritional value being sought out and fed on well in excess of that predicted by their availability.

5.3.4 Diet selectivity

I calculated a selectivity index (SI) in order to express the discrepancy between relative availability of foods and their proportion in the diet. This was calculated for the main food items in the troops diet as follows:

$$SI = \frac{(D_p - F_p)}{F_p}$$

where D_p = the proportion of the monthly diet that a food item comprises.

Calculated from feeding observations during scans.

F_p = the proportion of the available dry mass of baboon food that a food item

accounts for in the corresponding month (based on the percentage of habitat types the troop entered during that month).

A negative SI value indicates that the occurrence of that food in the diet is less than it would have been encountered in the home range while a positive value indicates the strength of a preference for that food. The SIs for the main foods in the troop's diet for each month are given in Table 5.2. Several foods have particularly large SIs. These would explain the lack of correlation between food availability and diet.

5.3.5 Diet choice and nutritional quality

In order to test whether the differences in preference (SI) for foods can be explained in nutritional terms, correlation analysis was performed between SIs and various measures of nutritional composition for the corresponding foods. These measures included the proportion of protein, lipid, fibre, carbohydrate and protein/fibre ratio and are shown in Table 5.3.

There were no significant correlations between food preference and any of these measures. Inspection revealed that five of the eight food items with SIs over 50 were relatively rare foods restricted to single habitat types: *Berchemia zeyheri* fruit (SI=251) restricted to riverine woodland/forest; *Olea europaeae* fruits (SI=94.3) restricted to riverine woodland/forest; *Ozoroa paniculosa* fruit (SI=56) restricted to *Combretum* woodland; *Capparis brassi* fruit (SI=219) restricted to *Acacia luederitzii* thickets and *Cassine transvaalensis* restricted to *Acacia* mixed woodland adjacent to the *Acacia luederitzii* thickets. These factors make the data sensitive to sampling errors or chance events.

Consequently it was decided to repeat the analyses of food availability and proportion in diet as well as food preference (SI) in relation to nutritional content without including the eight outliers (food items with SI's over 50). Spearman rank-order correlation analysis was unable to detect any correlation between SI's and the proportion of protein, lipid, fibre, carbohydrate and the protein/fibre ratio (protein: $r_s = -0.552$, $P = 0.098$, lipid: $r_s = -0.164$, $P = 0.624$, fibre: $r_s = 0.200$, $P = 0.549$, carbohydrate: $r_s = 0.188$, $P = 0.575$; protein/fibre $r_s = -0.249$, $P = 0.456$ $n = 12$ for all analyses).

There were however correlations when the analyses were repeated using only the eight *Acacia* species. These are relatively common as well as being widespread

food	selection indices									
	Jan	Mar	Apr	Jun	Jul	Aug	Sep	Oct	Nov	mean
<i>Acacia burkei</i> seeds	-	-	-	-	-	-	1.95	-	-	1.95
<i>A. gerrardii</i> seeds	-	-	-	0.49	-	-	0.24	2.58	-	1.10
<i>A. karroo</i> seeds	-	-	2.61	1.04	0.21	-0.44	-0.31	-0.49	0.51	0.45
<i>A. karroo</i> gum	250.27	482.26	496.33	-	456.77	-	-	-	502.70	427.27
<i>A. luederitzii</i> seeds	-	-	-	9.77	-	-	-	6.61	-	8.19
<i>A. nigrescens</i> seeds	-	-	-	1.25	-	-	-	1.09	-	1.17
<i>A. nilotica</i> seeds	-	-	-	-0.94	-	-0.87	-0.94	-	-	-0.92
<i>A. robusta</i> seeds	-	-	-	0.43	-	-0.74	-	-	4.53	1.41
<i>A. tortilis</i> seeds	-	-	-	-	-	-	-	-	-	-
<i>Aloe marlothii</i> fruits	-	-	-	-	-	-	210.73	-	-	210.73
<i>Berchemia zeyheri</i> fruits	251.90	-	-	-	-	-	-	-	-	251.9
<i>Capparis brassi</i> fruits	-	-	-	-	-	-	-	219.01	-	219.01
<i>Cassine transvaalensis</i> fruits	-	-	-	-	-	-	-	479.78	-	479.78
<i>Euclea schimperi</i> fruits	-	-	-	-	1008.63	-	-	-	-	1008.63
<i>Ficus soldanella</i> fruits	-	24.35	-	-	-	-	-	-	-	24.35
<i>Grewia monticola</i> fruits	-	-	-	919.97	-	-	-	-	-	919.7
<i>Olea europaea</i> fruits	-	465.97	54.11	-	94.32	-	-	-	-	204.8
<i>Ozornia paniculosa</i> fruit	-	-	-	56.47	-	-	-	111.38	-	83.93
<i>Schotia brachypetala</i> flowers	-	-0.59	-	-	-	-	2.66	-	-	1.04
<i>S. brachypetala</i> seeds	-	-	-	-	-	-	-	-	-	-
<i>Sclerocarya caffra</i> fruits	-0.88	-0.35	-	-	0.28	2.25	-	-	-	0.33
<i>S. caffra</i> seeds	-	-	-0.53	-0.49	-	-	0.79	-	-	0.08
<i>Strychnos madagascariensis</i> fruits	-	-	-	-	-	-	-	-	-	-
<i>Strychnos usumbaresis</i> fruits	-	-	-	-	-	-	-	-	-	-
<i>Vitex rehmanni</i> leaves	-	-	-	-	-	-	-	-	-	-
<i>Ziziphus mucronata</i> fruits	-	17.14	33.97	21.00	10.40	3.50	1.41	0.26	-	12.53

Table 5.2: Selection indices for foods comprising the top 80% of diet in each month (based on percentage time feeding on items). A score of above 1 indicates a preference for a food, while a score of below 1 indicates under-utilisation of a food

		% dry mass												ppm. dry mass					
rank	species	part	lipid	fibre	ash	pr	pr/fi	cho	N	Ca	Mg	K	Na	P	Zn	Cu	Mn		
5	Acacia karoo	gum	6.30	3.20	2.76	10.42	3.26	77.32	1.62	0.19	0.13	0.76	0.16	0.10	6	6	14		
30	Acacia robusta	seeds	5.79	15.02	4.99	24.52	1.63	49.68	3.92	0.95	0.26	0.74	0.07	0.37	46	18	23		
1	Sclerocarya caffra	seeds	8.20	12.20	4.90	17.20	1.41	57.50	2.01	0.54	0.12	0.68	0.12	0.10	10	6	22		
12	Acacia gerrardii	seeds	2.67	20.63	5.50	28.84	1.40	42.36	4.61	0.64	0.31	0.88	0.10	0.37	37	8	17		
2	Ziziphus mucronata	fruits	3.83	16.62	6.11	20.82	1.25	52.62	3.35	0.31	0.26	1.75	0.26	0.32	36	12	25		
3	Acacia karoo	seeds	6.40	23.91	4.88	28.90	1.21	35.91	4.62	0.39	0.34	0.88	0.16	0.39	43	7	25		
13	Acacia nigrescens	fruits	2.00	18.00	6.20	21.50	1.19	52.30	1.20	0.26	0.80	0.21	0.12	0.09	23	5	7		
16	Schotia brachypetala	seeds	2.10	9.39	2.44	11.12	1.18	74.95	1.78	0.19	0.13	0.56	0.14	0.15	30	12	14		
11	Acacia luederitzii	seeds	1.45	16.96	2.92	19.90	1.17	58.77	3.18	0.14	0.18	0.97	0.10	0.24	25	8	36		
14	Acacia gerrardii	leaves	3.80	20.20	8.70	22.40	1.11	44.90	0.57	1.20	0.30	1.00	0.14	0.20	6	11	6		
28	Acacia burkei	seeds	2.30	17.80	6.40	17.50	0.98	56.00	0.21	0.18	0.35	1.15	0.17	0.19	7	8	9		
9	Acacia nilotica	seeds	5.15	24.61	4.19	22.36	0.91	43.69	3.58	0.62	0.28	0.64	0.13	0.37	39	7	32		
10	Schotia brachypetala	flowers	4.10	14.70	5.50	12.50	0.85	63.20	3.41	0.58	0.14	1.12	0.30	0.10	16	7	5		
22	Acacia tortilis	seeds	1.35	35.07	4.78	28.78	0.82	30.02	4.60	0.31	0.31	1.24	0.16	0.43	47	6	27		
24	Sclerocarya caffra	fruits	6.60	9.20	8.80	6.90	0.75	68.50	2.00	0.80	0.21	1.35	0.32	0.20	8	4	18		
	Ekbolium amplexicaule	seeds	19.00	32.66		21.52	0.66	26.82	3.44	0.05	0.10	0.44	0.05	0.19	23	10	6		
8	Grewia monticola	fruits	1.51	15.91	4.23	10.37	0.65	67.98	1.66	0.45	0.15	1.19	0.15	0.18	23	6	16		
	Acacia nigrescen	flowers	3.18	32.83	5.50	18.62	0.57	39.87	2.98	0.27	0.32	1.10	0.15	0.19	22	3	28		
7	Capparis brassii	fruits	4.20	22.12	6.20	8.30	0.38	59.18	0.78	0.67	0.23	1.68	0.30	0.00	10	5	21		

Table 5.3: Nutritional analyses of food items in decreasing order of protein/fibre ratio. All foods were processed so as to represent only the parts that the baboons ingested. All foods were air dried at 35°C to a constant mass. Rank refers to the rank of the foods according to their contribution to the diet. This was calculated using time spent feeding on the different foods. Those foods without rank did not occur within the top 80% of the diet in any month. (pr=protein; cho=carbohydrates; pr/fi=protein/fibre ratio). Techniques: lipid-ether extraction; fibre-acid detergent; nitrogen-micro-keijeldahl; protein-Nx6.5.

15	<i>Euclea shimperii</i>	fruits	7.00	14.89	3.04	5.03	0.34	70.04	0.80	0.07	0.08	1.18	0.10	0.10	30	6	31
32	<i>Vitex rehmannii</i>	leaves	3.05	45.73	7.19	15.31	0.33	28.72	2.45	0.51	0.27	1.82	0.52	0.23	45	10	41
18	<i>Olea africana</i>	fruits	3.74	14.52	5.21	4.25	0.29	72.28	0.68	0.19	0.06	2.63	0.17	0.07	15	8	9
	<i>Dovyalis caffra</i>	fruits	5.75	14.02	2.91	3.84	0.27	73.48	0.61	0.08	0.07	1.22	0.12	0.10	35	7	35
29	<i>Strychnos madagascariensis</i>	fruits	2.68	18.36	2.39	4.73	0.26	71.84	0.76	0.08	0.11	1.32	0.11	0.11	11	6	33
31	<i>Strychnos usambarensis</i>	fruits	2.82	31.66	3.75	8.06	0.25	53.71	1.29	0.28	0.13	1.36	0.16	0.09	12	6	37
27	<i>Ficus soldanella</i>	fruits	14.27	58.77	10.79	13.41	0.23	2.76	2.15	0.96	0.31	3.70	0.25	0.32	38	12	26
	<i>Mimusops obovata</i>	seeds	9.21	19.10	2.00	4.30	0.23	65.39	0.69	0.09	0.05	0.73	0.09	0.06	7	2	4
19	<i>Cassine</i> sp. yellow fruit	fruits	0.73	24.44	6.14	5.07	0.21	63.62	0.81	0.72	0.19	1.78	0.28	0.07	7	4	102
	<i>Ficus glumosa</i>	fruits	1.89	40.80	3.22	7.62	0.19	46.47	1.22	0.17	0.17	1.25	0.19	0.14	19	31	30
	<i>Sideroxylon inerme</i>	fruits	24.11	44.43	5.76	8.29	0.19	17.41	1.33	0.41	0.24	1.60	0.65	0.09	17	7	16
	<i>Bridelia cathartica</i>	fruits	1.31	40.24	5.97	6.03	0.15	46.45	0.96	0.93	0.31	1.33	0.19	0.10	17	6	31
	<i>Cladostemon kirkii</i>	fruits	3.79	46.80	6.15	6.79	0.15	36.47	1.09	0.14	0.17	2.49	0.12	0.18	10	6	6
	<i>Mimusops obovata</i>	fruits	4.52	50.79	4.11	5.45	0.11	35.13	0.87	0.21	0.11	1.49	0.22	0.09	9	3	7
	<i>Ficus sycamorus</i>	fruits	9.24	55.59	4.96	5.75	0.10	24.46	0.92	0.34	0.29	1.41	0.28	0.16	21	7	15
	<i>Ficus ingens</i>	fruits	7.40	57.19	8.71	5.70	0.10	21.00	0.91	0.56	0.26	2.34	0.16	0.18	52	12	29
	<i>Vangueria esculenta</i>	fruits	1.39	44.21	3.11	3.10	0.07	48.19	0.50	0.09	0.09	1.29	0.15	0.08	6	4	14

throughout the home range. To further control for complicating factors only the use of seeds of these species was included in the analyses. The results show a significant correlation ($r_s=0.6244$ $P<0.01$, $n=8$) between density of the eight different *Acacia* species and the proportion of their seeds in the troop's diet, but no correlation with available dry mass of the different seeds ($r_s=0.1874$, $P=0.414$, $n=8$). This confirmed the pattern of a closer and stronger correlation with density than with food availability shown for all the main foods.

There were also significant correlations between food preference (SI's) and two of the nutritional components of the items. Food preference was positively correlated with the proportion of carbohydrates in seeds ($r_s=0.8095$, $P=0.0322$) and negatively correlated with proportion of fibre ($r_s=0.08810$, $P=0.0198$).

5.3.6 Nutritional values of foods

Table 5.3 shows results of nutritional analyses for a range of food items at Mkuzi. The table is arranged in decreasing order of protein/fibre ratio. The protein/fibre ratio has in many cases been found to be an effective estimate of food value (Van Soest 1977; Hendrickson *et al.* 1981). Nutritional analyses were carried out for 21 of the 24 food items comprising 80% of the diet in any month as well as 12 foods which were observed to have been eaten, but did not fall into the top 80% of the time spent feeding in any month. Loss of samples in a fire at the research camp meant that no analyses were carried out for *Berchemia zeyheri* fruit, *Aloe marlothi* flowers and *Ozoroa paniculosa* fruit. Foods were ranked according to their contribution to the diet. This was calculated using time spent feeding on the different foods. The overall rank of food items in the diet is given in column one of Table 5.3. Those without a rank represent foods that were eaten but did not account for the top 80% of time spent feeding in any month. Two trends from Table 5.3 are obvious: seeds tend to have the highest protein/fibre ratios and *Acacia* seeds account for the bulk of the high quality food items at Mkuzi.

5.3.7 Nutritional basis of diet selection

Since there was no correlation between preferences for foods and their nutritional content within the main foods, it appears that there was little discrimination on the basis of nutritional content. However, discrimination can take place at two other levels: 1) The crudest level of food choice is distinguishing between edible and non-edible items. Table 5.4 gives a comparison between the nutritional composition of food and non-food items as well as selectively processed food parts. *Acacia nigrescens* flowers were frequently eaten by the baboons while the very similar and

		Water	Protein	Lipid	Starch	Fibre	Pr/Fi
<i>Acacia nigrescens</i>	flower**	70.9	18.62	3.18	39.79	32.83	0.567
<i>Acacia robusta</i>	flower	68.2	5.07	1.98	26.83	58.89	0.086
<i>Dombeya rotundifolia</i>	flower	52.2	13.69	2.11	29.66	49.04	0.279
<i>Ficus soldanella</i>	fruit**	75.2	13.41	14.27	2.76	58.77	0.228
<i>Ficus ingens</i>	fruit*	80.3	5.7	7.45	21.00	57.19	0.0997
<i>Ficus glumosa</i>	fruit*	78.32	5.75	9.24	24.64	55.59	0.103
<i>Ziziphus mucronata</i>	flesh***	71.15	20.82	3.83	52.62	16.62	1.252
	whole fruit	65.72	6.63	2.82	40.89	45.12	0.147
<i>Acacia karroo</i>	seed***	77.00	28.9	6.4	35.91	23.91	1.209
	whole fruit	85.00	18.06	1.42	24.06	51.8	0.349
<i>Cassine transvaalensis</i>	Flesh**	88.20	0.73	5.07	63.62	24.44	0.030
	whole fruit	80.02	10.71	3.36	29.92	53.49	0.200

Table 5.4: Selection between food and non-food items, as well as between unprocessed foods and the parts consumed after processing. *** indicates a frequently eaten food, ** indicates a commonly eaten food and * indicates a rarely eaten food item.

equally common *A. robusta* flowers were never seen to be eaten. Similarly *Dombeya rotundifolia* flowers although common and plentiful were never eaten. Comparison of nutrient composition between these three flowers showed *A. nigrescens* flowers to have a higher protein, starch, water, and lipid content and a lower fibre content than the non-utilised flowers.

Of the three different species of fig fruit analysed *Ficus soldanella* was a frequent food, while *F. ingens* and *F. glumosa* were very rarely eaten despite being relatively abundant throughout the home range. *F. soldanella*'s proportion of protein was twice as high as the two other less infrequently eaten species. Its lipid content was also higher. Although it had a slightly higher fibre content, its protein/fibre ratio was higher than for the other two species.

Only *Ziziphus mucronata* fruit flesh was eaten. Comparison between nutrients of the whole fruit with only the flesh showed the flesh to have a much higher protein content as well as higher lipid, water and starch content. The fibre content of flesh was much lower than for the whole fruit.

The troop only ate the seeds of mature *Acacia karroo* fruits, discarding the pods. Analysis of the seeds revealed a higher protein, lipid and starch content as opposed to the whole fruit, while the fibre content was lower.

For *Cassine transvaalensis* the flesh, which was ingested by the baboons, had a lower protein content than the whole fruit, though the water lipid and starch levels were higher. The proportion of fibre was half that of the whole fruit.

Thus all food items had a higher protein content and protein/fibre ratio than comparable non-food/discarded items with the exception of *Cassine transvaalensis*. In general these results confirm those of Hamilton *et al.* (1978), Milton (1979), and Whiten *et al.* (1992) showing trends of lower levels of protein and higher levels of fibre, thus distinguishing non-foods from food items. Barton *et al.* (1992) used discriminant function analysis to distinguish food and non-food items on the basis of nutrients and secondary plant compounds. Their method was repeated in this study, but was not successful for this study since the analysis only identified a single discriminant function. The inability to separate foods and non-foods using this multivariate method is probably due to different foods being chosen for different specific nutrients, rather than a single set of criteria (although based on the assessment of several nutrients) being utilised in the choice of foods.

2) At a finer scale food choice may be detected on the basis of nutrient composition between staple foods and foods eaten occasionally. This appeared to be the case for this study troop. Comparison between nutritional contents of main foods ($n=21$) and those not comprising the top 80% of the diet in any month ($n=15$) showed significant differences. The proportions of protein, carbohydrate and the protein/fibre ratios of the main foods were significantly higher than for foods only occasionally utilised (Protein $Z=-2.63$, $P=0.008$; Carbohydrate $Z=-2.30$, $P=0.02$; Protein/Fibre $Z=4.08$, $P=0.0001$), while the proportion of fibre was significantly lower ($Z=3.20$, $P=0.001$).

Further evidence for maintenance of a balanced diet can be seen when comparing diet composition of a number of troops (Table 5.5). The coefficient of variation across the five samples (Mkuzi, Laikipia, Mikumi, Drakensberg and Aboseli) in the table of nutrient composition (coefficient of variation=0.185) is four times less than the coefficient of variation across the same 5 samples in the foraging profiles (Table 5.1; coefficient of variation=0.735). This demonstrates that while the foraging profiles between study sites differ considerably, the actual intake of nutrients is remarkably similar. This confirms Whiten *et al.*'s (1992) suggestion that different foraging routes can lead to similar nutritional ends.

5.4 Discussion

5.4.1 Diet composition

The Mtshopi troop displayed a broad diet, with a similar number of species being eaten over a period of a year as found at other study sites (Hall 1963; Post 1978; Davidge 1978; Sharman 1981). The troop's diet however had a higher proportion of fruit (90%)(seeds and flesh) than recorded for any of the 11 study sites given in Whiten *et al.* (1992). This preponderance of fruit resulted in low proportions of other food items in their diet. These low proportions were not obligatory since there was an abundance of other food types in the home range which were only occasionally utilised by individuals. These included many underground items, such as roots of grass species, corms of *Cyperus* species, roots of *Commiphora neglecta*, and flowers and young leaves of numerous species such as *Vitex rehmannii*. *Vitex rehmannii* had young leaves all year round and has a low fibre/high protein content. The young leaves were always available due to continual grazing by ungulates which resulted in regeneration of leaves. Despite this *Vitex rehmannii* leaves only formed a significant part of the diet in September when the availability of other baboon food was low. Other non-fruit items utilised during times of food scarcity (August to December)

	Mkuzi	Laikipia	Mikumi	Drakensburg	Amboseli	mean
water	65.1	70.9	-	63.8	57.6	64.3
protein	15.3	21.2	13.7	8.44	14.4	14.6
lipid	5.4	6.3	5.3	6.3	4.4	5.5
fibre	21.0	20.9	26.3	21.5	22.1	22.4

Table 5.5: Diet composition of study troop and four other baboon populations (from Whiten *et al.* 1992). Figures are means for: foods accounting for 68% of feeding time at Laikipia, Drakensburg and Amboseli; 80% of feeding time at Mkuzi and for all plants at Mikumi

were: underground corms of several species of *Cyperus*, post burn grass shoots, new flush of *Acacia gerrardii* leaves and *Schotia brachypetala* flowers. During this period non-fruit food items accounted for 11.5% of diet, a ten-fold increase compared to the rest of the year.

Fruit therefore appears to be the preferred food item with other food types being eaten during periods of food shortage. The same pattern has been recorded for other primates (Japanese macaques *Macaca fuscata*, Iwamoto 1982; Chimpanzees *Pan troglodytes* Wrangham *et al.* 1991).

5.4.2 Diversity of diet

The ability of baboons to diversify diets as a response to scarcity of preferred food items has been an important survival strategy for baboons who seldom migrate in periods of food shortage (Hamilton *et al.* 1978). Diversification from a predominantly frugivorous diet seems to be a method for coping with poor habitats or extreme intra-specific and inter-specific food competition (Hamilton *et al.* 1978). For example the successful incursion into such marginal habitats as the Drakensberg mountains (Whiten *et al.* 1987) and the Kuiseb canyon (Hamilton *et al.* 1978) (Namib desert) have been accompanied by diversification into other food types in particular underground items and insects. Judging from the proportion of fruit in the diet, Mkuzi appears to be a high quality baboon habitat in terms of baboon food, possibly representing a model baboon habitat. (Although, Mkuzi had a low population density of baboons, compared with other study sites, suggesting a poor quality habitat, I believe that this was a result of a previous population crash, possibly in the droughts of the early 1980's. The Mtshopi troops rapid and unconstrained growth seems to suggest that current population densities are not a true reflection of the carrying capacity for the baboon population.)

5.4.3 Preference for fruit

There are many good reasons for preference of fruit items. (i) They are a good source of carbohydrates and protein in the case of seeds of *Acacia* spp. (Table 5.3). (ii) Since they occur in trees they are not depleted by competition with other mammalian competitors (at Mkuzi these would include bushpig, warthog, and numerous ungulates). (iii) Fruits usually require minimal search and handling time (for example, the Mtshopi troop could feed on *Ziziphus mucronata* at a rate of 40 fruits per minute while the highest feeding rate for similarly sized *Cyperus* corms was at maximum seven per minute). (iv) Feeding in trees can reduce the risk of predation.

The high proportion of fruit in the diet appears to be related to the high number of

available fruits at Mkuzi, rather than a lack of other food types. It is surprising that this troop and those studied at Mt Assirik (Sharman 1981), both mixed woodland habitats, had higher levels of fruit in their diet compared with the fruit rich rain forest habitat at Gombe (Ransom 1981; Oliver in Whiten *et al.* 1992). These data support the contention that baboons' preferred foods occur in woodland habitats (Dunbar 1992) and that the amount of woodland species in a home range is a determinant of the quality of baboon habitat. This together with competition with other forest primates might explain why baboons are generally absent from large forests in Africa.

5.4.4 Nature of frugivory

The study troop's reliance on fruit helps to explain the apparent paradox that the troop had a larger than predicted home range and shorter than predicted day journey lengths (see Chapter 2). Frugivores in general require larger ranging areas for a given group size than folivores (Mace and Harvey 1983). The concentrated but widely dispersed nature of fruit would explain the necessity of a large home range (Dunbar 1988), while the relatively high nutritional return per tree would explain shorter day journeys. The day journeys however would have to be more diverse (in terms of foraging in different areas on consecutive days) to cover the large home range.

The reliance on fruits at Mkuzi is largely due to the nature of the troop's three staple fruits. These are available over a longer period than most other fruits enabling baboons to span the crucial months of August to December when other fruits are scarce. These staple foods were: *Ziziphus mucronata* flesh, (28% of the total diet); *Acacia* spp. (19.4%) and *Sclerocarya caffra* seeds (11.4%). *Ziziphus mucronata* retains fruit on the tree as they dry out till the beginning of the next fruiting season. The fruits occur in high densities and being fibrous rather than fleshy, dry on the tree without rotting. *Acacia* seeds do not either rot and dry on the tree. *Sclerocarya caffra* produces fleshy fruits from December to February during which only the fleshy exocarp is eaten by baboons. After a month or two of desiccating on the ground the embryos inside the nuts are eaten by cracking the tightly sealed cap that covers each embryo and extracting the embryo with a fingernail or canine. No other animal in the reserve is able to do this, consequently embryos are exclusively exploited by baboons. All these foods can survive up to a year, maintaining their nutritional quality. The winter burns expose numerous *Acacia* spp. and *Sclerocarya caffra* seeds that are hidden for up to eight months under thick grass. This exposure of seeds offsets the general decreasing availability of seeds.

5.4.5 Eclectic/selective nature of baboon diets

Norton *et al.* (1987) succinctly described baboons' diet as being eclectic/selective.

Eclectic in terms of the large number of species utilised and the broad range of the diet, but selective in terms of the proportion of potential species used and the careful selection and processing of parts that are consumed. This pattern was clearly shown by the study troop. The troop's diet, although consisting of 92 plant species represented only 10-15% of the estimated 700 to 900 plant species in the home range (estimate of plant species based on plant list collected during the study and list of herbarium specimens available for the quarter degree grid square within which the troops home range occurred). This is lower but broadly comparable to the estimate of about 25% of available species by yellow baboons at Mikumi (Norton *et al.* 1987).

5.4.6 Diet selection

The main body of these results stand in contrast to those obtained by Whiten *et al.* (1992) who demonstrated a fairly close approximation to optimal diet choice in baboons. At a gross level they showed a correlation between composition of diet and the relative availability of food items at Laikipia. They then provided evidence for a finer level of discrimination within main foods where protein/fibre ratios predicted food selection ratios.

The current study was unable to demonstrate any significant correlation between proportion of food in diet and its availability, except for a small subset of common widely-distributed species (*Acacia* spp.). In this case the correlation between selection ratios and density of food species encountered was significant while the correlation with available dry mass of foods encountered was not, despite the former being a cruder measure of potential food value. This study did not find any significant correlations between food preference and the nutritional composition of the top 80% of foods. Again however, when only *Acacia* seeds were considered, there were significant correlations. Preference was positively correlated with carbohydrate proportions and negatively correlated with seed fibre content. There was no correlation with protein proportions or protein/fibre ratio.

Protein/fibre ratios are widely recognised as a good estimate of food quality (Van Soest 1977; Hendrikson *et al.* 1981). Field studies have shown protein/fibre ratios to be related to food preferences (African ruminants: Field 1975, 1976; Black colobus: McKey *et al.* 1981; Mantled Howler monkeys: Glander 1981; Milton 1979). However protein/fibre ratios are only an approximation of what is in biological terms being optimised. Diet is certainly not a case of simple optimisation of a single resource. It is rather a process of simultaneous optimisation of acquisition rate of several resources so as to result in a balanced diet. What particular items are being

optimised is dependent on how limiting the different components of the diet are i.e. the levels of their availability relative to requirements (see Pulliam 1975; Belovsky 1978; 1981).

5.4.7 Levels of selection at Mkuzi

The level of selection by Mkuzi baboons appears to be in choosing between food and non-food items, selecting those rich in protein. Frequently eaten food parts also appear to be selected on the basis of a high protein/fibre ratio over those food items only occasionally eaten. Why then didn't the study troop extend these preferences to discriminate amongst the main food items?

Comparison of the mean percentage of protein for the main foods (representing the top 80% of the diet in any month) (15.34%), with the estimated protein requirement (10-14% in the diet) for wild adult primates (including reproductive requirements; Oftedal 1991)) demonstrates that the study troop was able to meet its protein requirements without selecting for the highest protein levels in main foods. How then was the troop able to meet its protein requirements?

At Mkuzi *Acacia* seeds constituted the major dry mass of baboon food available throughout the year (80.55%). The mean proportion of protein for *Acacia* seeds was 24.4% and this is above their estimated requirement of 10-14% (Oftedal 1991). The preponderance of *Acacia* spp. within the home range meant that this was a protein rich environment. The predominance of fruit in the diet also ensured that protein intake was high, particularly in comparison to other study troops which fed on more leaves which have only 10-16% protein; (Oftedal 1991).

5.4.8 Selection within main foods

Since the troop was able to meet its protein requirements by discrimination between frequently eaten foods and occasional foods, it was free to select between main foods on the basis of other requirements. If any specific nutrients are not limited, one would expect the troop to optimise energy gain (i.e. carbohydrates). This might explain the selection for carbohydrate levels amongst *Acacia* seed. Carbohydrates are a readily available energy source as opposed to proteins that require deamination (Schmidt-Nielsen 1983). Since all *Acacia* seeds have high levels of protein, it is not surprising that selection was based on carbohydrates rather than protein. Since carbohydrate levels were only crudely estimated by subtraction it was not possible to distinguish between the different types of carbohydrates. Because of differences in digestibility between structural polysaccharides, storage polysaccharides and simple sugar fractions of carbohydrate it was difficult to compare the value of different foods on

the basis of total carbohydrate. However, the proportions of different carbohydrate fractions are likely to be similar for similar food parts. Thus comparisons within *Acacia* seeds would represent true differences in nutritive value of carbohydrates, while other foods would not be comparable because they would differ in proportions of the different carbohydrate fractions. This might be the reason for no correlation between food preferences and carbohydrates amongst other main foods.

5.4.9 Selection of micro nutrients

Micro-nutrients such as vitamins, minerals and trace elements are required in small amounts and can be supplied by a single food type high in that specific element. Several of the foods at Mkuzi with high selection indices (SI) and no correspondingly high levels of protein, carbohydrates or lipids did have particularly high levels of specific nutrients and trace elements. *Olea europaea* with a mean SI of 74 had the highest level of potassium of all foods analysed and, *Grewia monticola* (mean SI=688) and *Cassine transvaalensis* (SI= 487) fruits had the highest and second highest levels of manganese, both about five times the average level of manganese for the combined food and non-food parts analysed.

While high preferences for some main foods may reflect selection for specific nutrients or trace elements, the general lack of correlation between selection indices and nutritional composition of food may be due to an inability to estimate the proportion of metabolizable energy available in form of carbohydrates and to a lesser extent lipids (which only form a small proportion of the foods that comprise the diet).

5.4.10 Why was there no correlation between proportion of main foods in the diet and their availability?

Optimal foraging models suggest that the most likely mechanism by which animals can adjust their food intake to correspond with food availability is by foraging in a patch until the rate of nutrient capture falls to what on average could be expected from the entire environment (Marginal value theorem, Charnov 1976). In this case patches are exploited in relation to the dry mass of their food availability and thus the proportions represented in the diet are correlated to food availability. There are two reasons why this might not occur in a primarily frugivorous troop such as in this study. Fruit and seeds are by nature locally abundant on or at the base of trees. In this case trees represent rich patches that might not show a significant decrease in nutrient capture rates before individuals reach satiation. Consequently time spent foraging in a patch (tree) would be determined by the constraint of digestion rate, rather than food availability. In this situation food proportion in the diet would mirror the density of

food species rather than food availability. Evidence based on limited data on feeding rates in *Ziziphus mucronata* trees suggests that this may be the case. There was no significant difference in feeding rate in the last minute of feeding bout compared to the first minute of feeding bout (mean rate 1st min.=13.95 fruits/min.; mean rate last min.=15.26 fruits/min.; $z=1.12$; $P=0.26$, $n=25$).

In addition, the average feeding rate in the last minute was slightly higher than the first minute, suggesting that an additional confounding factor was the necessity of individuals to stay with the troop. Individuals were not able to feed till there was a decrease in capture rate or till satiation before the troop moved on. Consequently the last minute of a feeding bout, more often than not, consisted of a frantic rush to fill cheekpouches with food before joining the departing troop. These effects would presumably be less marked for food items that are rarer but more uniformly (less clumped) distributed such as underground items, and insects.

5.4.11 Conclusion

The study troop had a broad but selected diet, similar in number of species and variety to other African troops. They did however have a higher proportion of fruit in their diet. Since fruit is preferred by baboons in general it appears that Mkuzi is a high quality habitat, at least in terms of food. This is supported by the troop's unconstrained growth (Henzi *et al.* in press) and lower than predicted day journey lengths (Chapter 2). The troop coped with seasonal scarcity of fruit in August to December by broadening the scope of its diet to include invertebrates, leaves and flowers, rather than increasing the number of species utilised.

The predominantly frugivorous nature of the study troop's diet, especially the abundance of *Acacia* seeds affected the basis of optimisation, in terms of nutrient availability, when compared with that shown for baboons by Whiten *et al.* (1992). Consequently the study troop needed only the most simple discrimination to meet its protein requirements. On meeting this it appears that selection was based on maximising rate of energy intake, subject to: digestibility of foods and constraints imposed by rate of digestion. The latter is particularly important with regards to fruit because of their short within patch handling and search time which results in intake rate exceeding digestion rate. This is compounded by the need of individuals to remain with the troop which further restricts individual abilities to optimise patch use according to food availability. Consequently, it is not surprising, even within the optimal foraging paradigm, that the proportion of an animal's diet, which

predominantly relies on fruits, reflects relative food species densities rather than food availability. This ability of baboons to adapt their patterns of optimisation so as to maintain a balanced diet under very different situations is the cornerstone of their ability to utilise such varied environments.

Chapter 6

Ecological consequences of troop fission in chacma baboons (*Papio cynocephalus ursinus*).

6.1 Introduction

Costs and benefits of living in different group sizes has been a topic of much debate in behavioural ecology (see reviews Alexander 1974; Betram 1978; van Schaik 1983; Pulliam and Caraco 1984; Terbough and Janson 1986, Dunbar 1992). The potential cost of larger group sizes is increasing foraging effort. This can take the form of direct interference competition or resource depletion (Alexander 1974). Possible benefits derived from larger group size are: (i) increased foraging efficiency, through information sharing about location and quality of food (Ward and Zahavi 1973; De Groot 1980), through group defence of scarce resources, or displacement of smaller groups from better quality habitats (Wrangham 1980)); (ii) reduced predation risk, through co-operative defence against predators (Crook 1972; Altmann 1970), dilution of risk to the individual (Pulliam and Caraco 1984) or early detection of predators (Kenward 1978; Lazarus 1979).

Troop fission provides an opportunity to compare costs and benefits of living in different sized groups. Troop fission in primates has been widely documented (Chepko-Sade and Sade 1979; Malik *et al.* 1985; Dittus 1988; Dunbar 1988; Oi 1988; Hohmann 1990; Prud'Homme 1991; Cords and Rowell 1986; Hamilton and Bulger 1993) however, there is much speculation about its causes and little agreement on the relative importance of social/demographic factors versus ecological factors. Some researchers have attributed little or no importance to ecological factors (e.g. Sugiyama 1960, Chagnon 1975, Malik *et al.* 1985) while some have suggested that fission is completely determined by ecological factors (e.g. Furuya 1969). More recently fission has been ascribed to a combination of both social and environmental factors (Dittus 1988; Dunbar 1988) but in general there has been no quantitative assessment of the ecological consequences of fission. Comparisons between the original troop and daughter troops enables the determination ecological costs and benefits resulting from troop fission. If no benefits result from the fission, troop fission must be regarded as a response to social or demographic costs of living in a large group (see Carpenter 1942; Furuya 1969; Chagnon 1975; Malik *et al.* 1985).

In the case of baboons (*Papio* spp.) only two studies have looked at social and

demographic consequences of fission (Nash 1976; Hamilton and Bulger 1993). In neither of these have the ecological consequences been recorded in any detail.

The purpose of this chapter was to compare the ecology of a baboon troop prior to fission with that of the two daughter troops formed as a result of fission. This was done in order to determine the costs and benefits associated with living in different sized groups and to examine the possible basis of troop fission.

The specific aims were to compare: 1) the size and quality of the three home ranges; 2) the foraging effort in terms of the distance travelled by the three groups; 3) the diet of the troops; 4) the habitat use by the different troops; 5) the differences in time budgets of different troops and 6) their behaviours associated with predator avoidance or detection.

6.2 Materials and methods

6.2.1 History of study troops

Mtshopi troop has been studied since 1987. The data on which this chapter is based were collected from February 1989 till December 1990. Mtshopi troop inhabited the foothills of the Lebombo Mountain range and part of the adjacent low lying coastal plain in Mkuzi Game Reserve in Northern Kwazulu/Natal, South Africa (latitude 32°38'S longitude 32°08'E). The 24.42km² home range was dissected regularly by streams which have cut steeply in the foothills resulting in gorges which open up downstream into riverine woodlands. This arrangement of alternating hills and valleys resulted in a rich mosaic of vegetation types ranging from hilly *Combretum* woodland through *Acacia* mixed woodland, stands of various almost monospecific *Acacia* forests, ravine forests, riverine scrub-woodland to dense low-lying *Acacia leuderitzii* thickets (these are described in Chapter 2). Since the beginning of the study the baboon population was in a demographic growth phase (Henzi et al. in press). The troop consistently increased in size from 44 in 1978 to 76 in March 1990. The troop experienced a low incidence of inter-troop encounters and the population density was low compared to other study sites (Henzi *et al.* in press).

In April 1990, two thirds of the way through this study, the troop split into two daughter troops. Flash's troop consisted of 28 individuals of which 5 were males, 9 females and 14 juveniles and infants. The ratio of males:females:juveniles was 1:1.8:2.8. Darth's troop consisted of 43 members - 4 males, 8 females and 31 juveniles and infants. The ratio of males:females:juveniles was 1:2.7:7.8. Social

aspects associated with the split are dealt with by Ron (1994) and Ron *et al.* (in press).

6.2.2 Data collection

Data for this chapter from the original Mtshopi troop were collected during June - September 1989, and for the two daughter troops, (Flash's and Darth's) during the corresponding period in 1990. There were 71 individuals in the Mtshopi troop at this time (by the time the troop split in April there were 76 individuals). The troops were followed for full days during which instantaneous scan samples (Altmann 1974) of as many individuals as possible were taken at 10 minute intervals. During each scan the position of the troop as well as the exact path between consecutive positions was plotted on a 1:20 000 map. The habitat type in which the scanned animals were was also recorded.

6.2.3 Home range utilisation

The extent of area utilised by the different troops and the degree of overlap of areas utilised was determined by overlaying a grid of 4ha quadrats and recording the quadrats entered during each full day journey. The number of full days used in the analyses was adjusted by the random elimination of days to ensure equal size of the data sets of all three troops. The topographical plots of home range use are based on the number of times the troops were recorded in the different quadrats as determined every 10 minutes.

6.2.4 Habitat types

The seven habitat types in the troops home range were identified during an initial period of vegetation sampling and are described in detail in Chapter 2. They consist of *Acacia* mixed woodland (ACW), *Acacia* karroo forest (AKF), *Acacia* *huederitzii* thickets (ATH), *Combretum* woodland (CH), hilly *Combretum* rocky outcrops (HCR), ravine forest (RA) and riverine forest/woodland (RIV).

6.2.5 Food availability

The monthly changes in the amount of baboon food (kg dry mass per hectare) in the different habitat types are also given in Chapter 2.

6.2.6 Habitat type accessibility

The relative accessibility of habitat types was calculated for the Mtshopi troop in Chapter 5. These figures are used for both the Mtshopi and daughter troops in this chapter. The relative accessibility was calculated from 1400 simulated random walks through the troop's home range in which the encounter rate with different habitat

types was calculated. The troops' utilisation of habitat types was determined from what habitat types the baboons were recorded in during each scan. The amount of different habitat types in the three troops home ranges was calculated by overlaying each troops home range on the habitat map (see Chapter 2) and measuring the area of the different habitat types in the home ranges.

6.2.7 Habitat selectivity

If proportion of time spent in a habitat exceeded the accessibility of that habitat, then habitat selectivity was calculated by dividing the proportion of time spent in a habitat by the accessibility of the habitat (expressed as a proportion). However, if accessibility of a habitat exceeded the proportion of time spent in that habitat then accessibility of the habitat was divided by the proportion of time spent in the habitat and this was expressed as a negative value, since it represents avoidance of the habitat.

6.3 Results

6.3.1 Home range size

Home range size increased with the size of the troops (Figure 6.1). Over the period of June to September 1990 Flash's troop (28 individuals) had a home range size of 4.72km^2 . DARTH's troop (43 individuals) had a home range of 6.88km^2 . The Mtshopi troop maintained a home range of 11.76km^2 over the corresponding period the previous year. Home range size increased monotonically with group size. The per capita home range sizes for the three troops were very similar. Flash's troop had a per capita home range size of 0.1686km^2 per individual, DARTH's troop: 0.1600km^2 per individual and Mtshopi troop: 0.1657km^2 per individual.

The home ranges of DARTH and Flash's troop are shown in relation to the home range of the Mtshopi troop in Figure 6.2. Forty percent of Flash's troop's home range overlapped with DARTH's troop's while this overlap accounted for 27% of Flash's home range. Thus the smaller troop's home range had a relatively larger area of overlap than the larger troop.

6.3.2 Home range utilisation

Both daughter troops utilised the three centre sleeping sites (1,2,3) but only DARTH's troop used the Gorge sleeping sites (6,7) (see Figure 2.1 Chapter 2).

The patterns of home range use for the three troops are shown in Figure 6.3. The

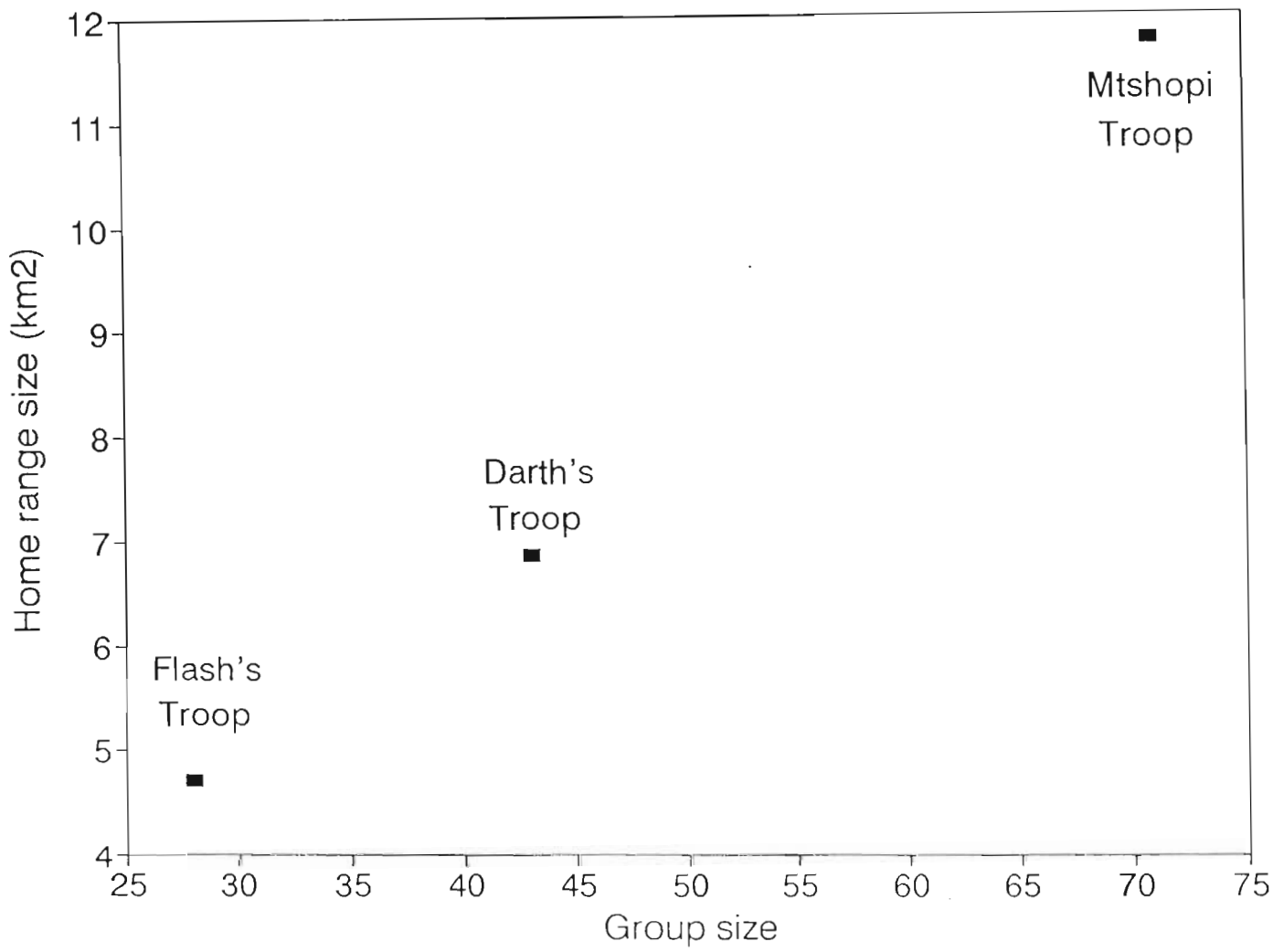


Figure 6.1: Home range sizes of the three troops Mtshopi, Flash's and Darth's troop.



Figure 6.2: Home range overlap of Darth and Flash's troops in relation to home range of Mtshopi troop. The dark area indicates the area of overlap between Darth and Flash's troop. Flash's home range occurs to the left of the dark area while Darth's home range occurred to the right of the dark area.

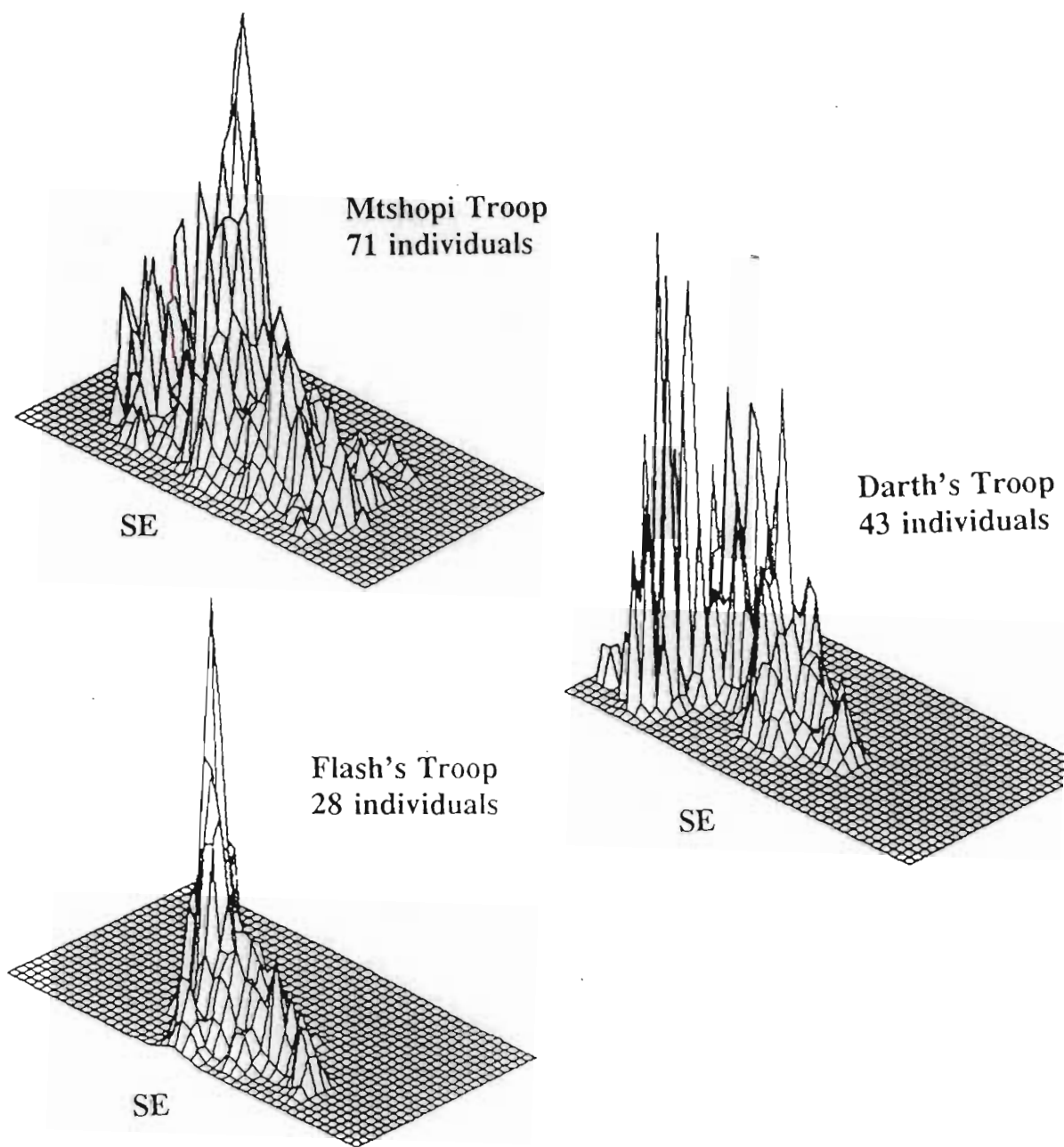


Figure 6.3: Patterns of home range use for the three troops. Y axis represents intensity of quadrat use.

plots of home range utilisation indicate that the core area of Flash's home range was centred on the central sleeping sites (1,2,3), while the core area of Darth's troop was centred on the Gorge sleeping sites (6,7). Flash's troop ranged towards the south-west of the home range while Darth's troop ranged north-east. Most of the area used by the two daughter troops (83%) was within the original home range (Mtshopi troop's home range). Ninety three percent of the area outside the initial home range was an extension to the north east of the gorge sleeping site. This was probably due to more extensive use (compared to the original Mtshopi troop) of Gorge sleeping sites by Darth's troop (see Figure 6.3).

6.3.3 Home range quality

Proportions of areas covered by different habitat types in the home ranges of the three troops are given in Figure 6.4. There was no significant difference in the proportions of habitat types between the daughter troops home ranges ($\chi^2=3.29$, $df=3$, $P=0.183$) and no difference between all three troops ($\chi^2=10.12$, $df=12$, $P=0.606$). Using the productivity of dry mass of baboon food per hectare in the different habitat types calculated in Chapter 2 it was possible to determine the mean food availability in the different habitats. This was done by multiplying the proportion of the habitat types making up the different home ranges by the mean food availability for each habitat type (see Chapter 2). These figures were summed, resulting in an estimate of food availability per hectare for the three home ranges. The mean food availability was similar in all the home ranges. The mean for Mtshopi troop (71 individuals) was 32.38kg/ha; for Darth's troop (43 individuals) 32.78kg/ha and for Flash's troop (28 individuals) 35.62kg/ha.

6.3.4 Day journey length

The day journey length for the daughter troops ($n=19$) were significantly shorter than the day journey lengths for the original Mtshopi troop ($n=20$) (Mtshopi-Darth, $t=3.012$, $P<0.01$; Mtshopi-Flash, $t=3.328$, $P<0.01$). There was no significant difference between day journey lengths of the two daughter troops ($t=0.345$, $P=0.734$).

Mean day journey length increased with group size (Flash's troop (28 individuals) - 3.63km, Darth's troop (43 individuals) 3.86km and Mtshopi troop (71 individuals) 6.036km (Figure 6.5).

6.3.5 Diet

Comparisons were made between diets of the three troops using 128 feeding observations for each study troop. The sample sizes were standardised by randomly

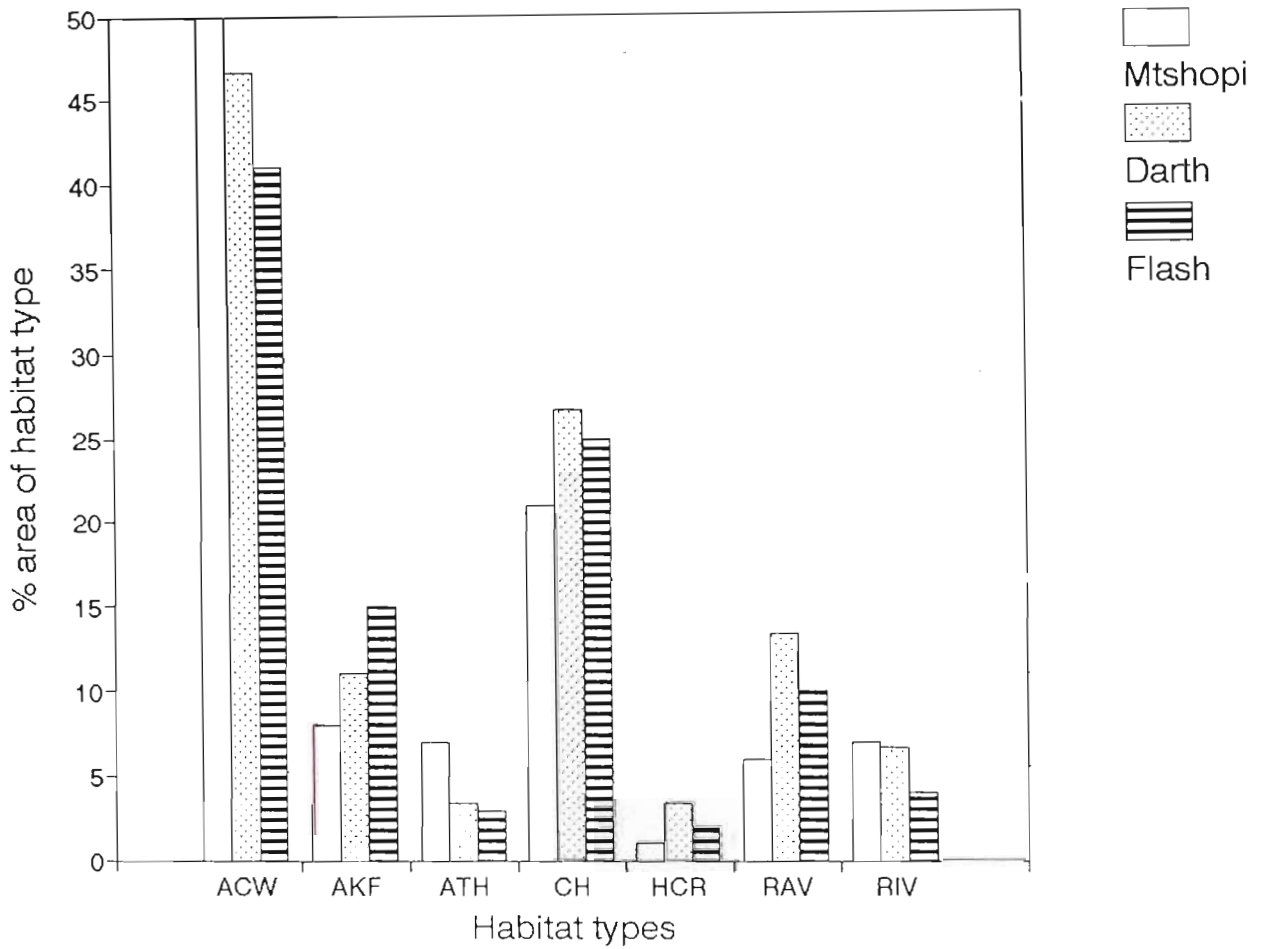


Figure 6.4: Proportions of areas covered by different habitat types in the home ranges of the three troops. There was no significant difference in the proportions of habitat types between all three troops ($\chi^2=10.12$, $df=12$, $P=0.606$) or between the daughter troops home ranges ($\chi^2=3.29$, $df=3$, $P=0.183$).

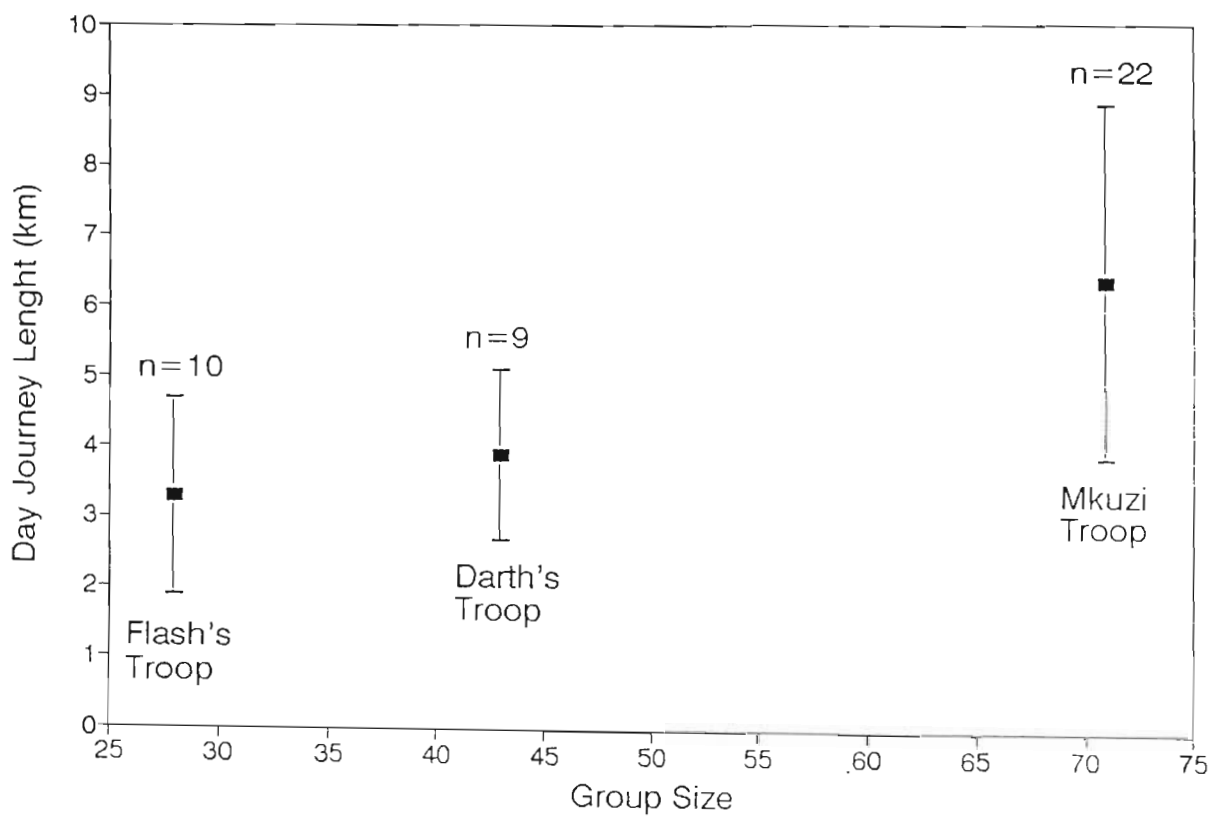


Figure 6.5: Mean day journey length of the three troops Mtshopi, Darth and Flash.

removing feeding records for DARTH's troop and Mtshopi troop until they had the same number of feeding records (128) as were recorded for Flash's troop. The diets of the three troops, as determined by proportion of time allocated to different foods are given in Figure 6.6. All grass species were grouped together as a single food, as were all invertebrates. For all three troops *Ziziphus mucronata* fruit and *Acacia karroo* seeds were the top two foods, accounting for 34% of Mtshopi troop's feeding records, 59% of DARTH's troop's feeding records and 62% of Flash's feeding records.

Feeding records for Mtshopi troop contained 19 different food items while both daughter troops only contained 14 food items each. Given that the sample sizes were identical, number of food items is the best measure of diet breadth (Ludwig and Reynolds 1988). The two daughter troops had a narrower diet than Mtshopi troop. Both the diversity indices used, (Hill's N1 and N2) are higher for the Mtshopi troop than for Flash and DARTH's troop (Table 6.1). N1 can be interpreted as a measure of number of abundant food items in the diet (Hill 1973). N2 can be interpreted as the number of **very** abundant items in the diet. Using these interpretations, the Mtshopi troop's diet had 13 abundant species and 11 very abundant species, DARTH's troops' had seven abundant foods and five very abundant food's, and Flash's troop's diet consists of eight abundant foods and six very abundant foods. Mtshopi troop's (71 troop members) diet appeared to be the most diverse, followed by Flash's (28 troop members), and then DARTH's troop which exhibited the least diverse diet.

6.3.6 Habitat utilisation

Time spent in habitat types for the three troops is given in Figure 6.7. There were significant differences in the proportion of time spent in different habitats between Mtshopi troop and the two daughter troops (Mtshopi-DARTH, $\chi^2=124.3$, $df=4$, $P<0.001$; Mtshopi-Flash, $\chi^2=222.6$, $df=4$, $P<0.001$), but no significant difference between DARTH and Flash's troops ($\chi^2=8.23$, $df=5$, $P=0.144$).

Mtshopi troop's use of habitat was more diverse (Hill's N1=4.25), than DARTH's troop's (N1=3.81), or Flash's troop's (N1=3.87).

The degree of habitat selectivity displayed by the different troops was examined by using the selectivity index SI. The selectivity indices for the different habitat types by the three troops are summarised in Figure 6.8. The sum of absolute values of these figures divided by number of habitat types is a measure of overall selectivity (positive or negative) by different troops. Mtshopi troop was the most selective with a selectivity index (SI) of 6.39, followed by Flash's troop (SI=-3.50) and DARTH's troop

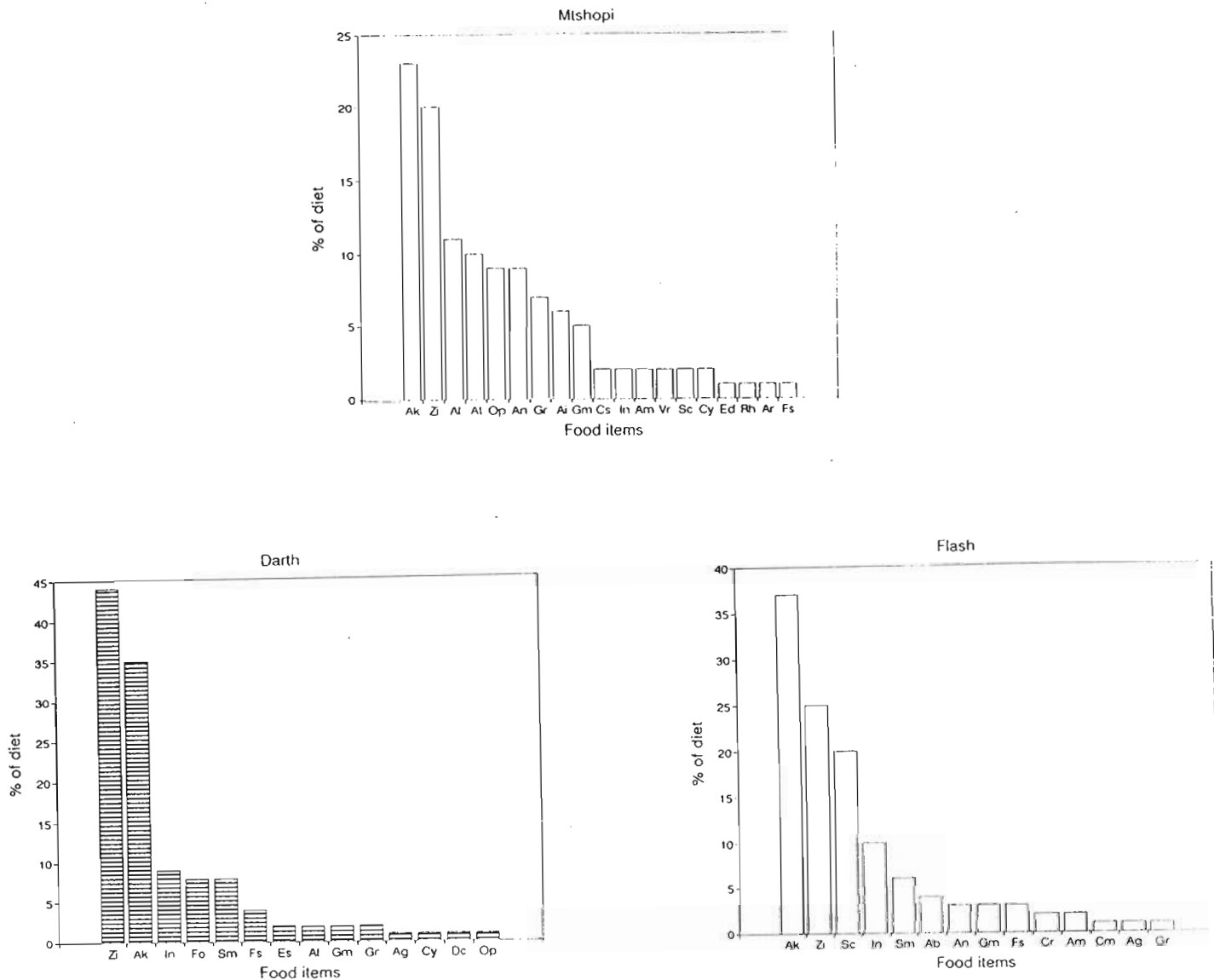


Figure 6.6: Diets of the three troops, as determined by proportion of time allocated to different foods. Ab=*Acacia burkei*; Ag=*Acacia gerrardii*; Ak=*Acacia karroo*; Al=*Acacia luederitzii*; Alm=*Aloe marlothii*; Anil=*Acacia nilotica*; Anig=*Acacia nigrescens*; Ar=*Acacia robusta*; At=*Acacia tortilis*; Bz=*Berchemia zeyheri*; Cb=*Capparis brassii*; Cg=*Croton gratissimus*; Ct=*Cassine transvaalensis*; Cyp=*Cyperus* spp.; Es=*Euclea shimperi*; Fs=*Ficus soldanella*; Gm=*Grewia monticola*; Gr=grass spp.; Inv=invertebrates; M=mushrooms; Oe=*Olea europaea*; Op=*Ozoroa paniculosa*; Sb=*Schotia brachypetala*; Sc=*Sclerocarya caffra*; Sm=*Strychnos madagascariensis*; Su=*Strychnos usambarensis*; Vr=*Vitex rehmanii*; Zi=*Ziziphus mucronata*.

	Mtshopi	Flash	Darth
No. of species	20	15	15
N1- No. abundant species	13.1	8.4	7.0
N2- No. very abundant species	11.1	6.4	4.9
E5- Evenness index	0.83	0.73	0.64

Table 6.1: Diet diversity indices for the three troops. N1 is a measure of number of abundant food items in the diet, N2 is the number of **very** abundant items in the diet and E5 is a modified Hill's ratio $(N2-1)/(N1-1)$ expressing evenness of diet.

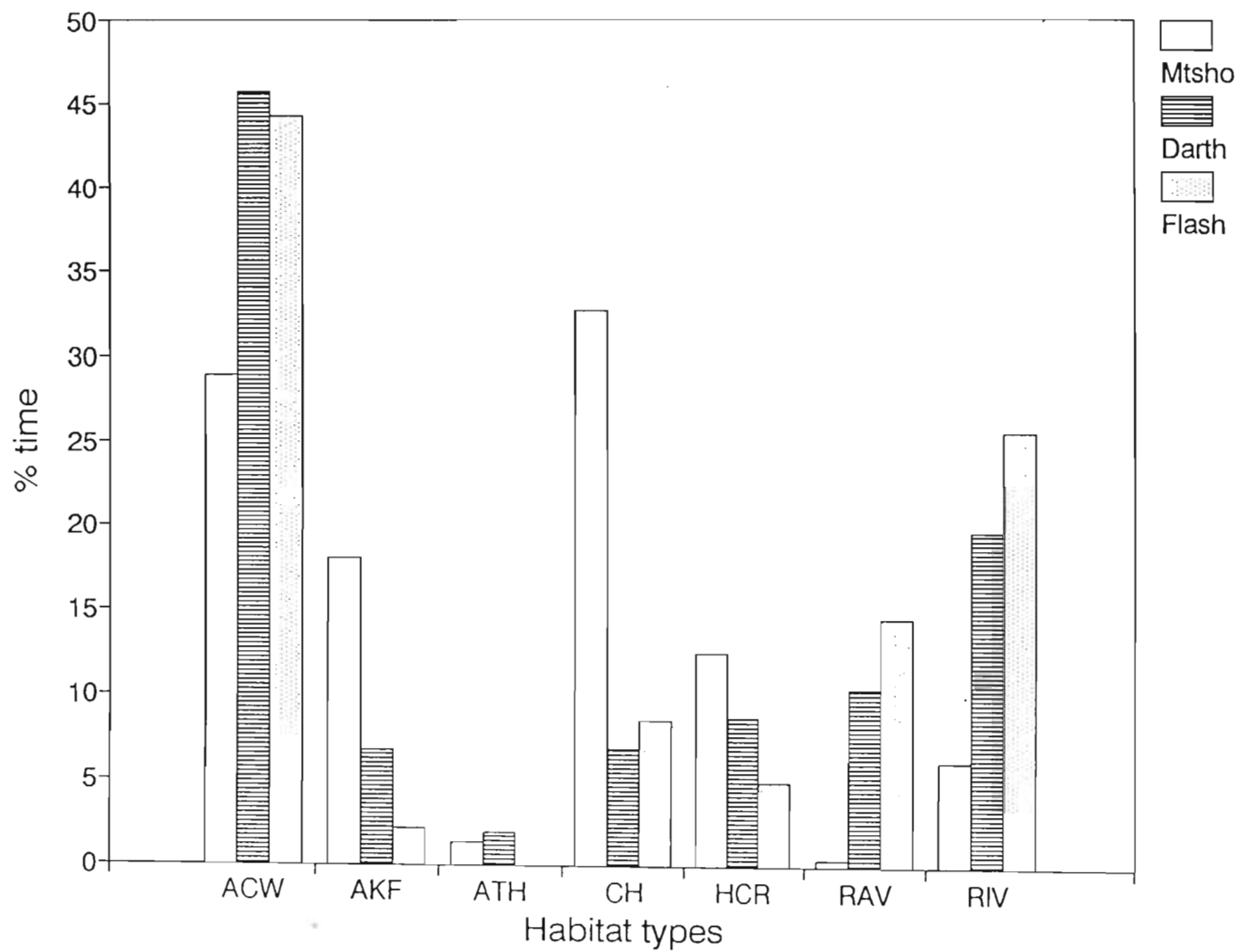


Figure 6.7: Time spent in habitat types for the three troops. Habitat types. ACW-*Acacia* mixed woodland, CH-*Combretum* woodland, ATH-*Acacia* thicket, AKF-*A. karroo* forest, RIV-riverine forest, HCR-hilly *Combretum* woodland, RAV-ravine.

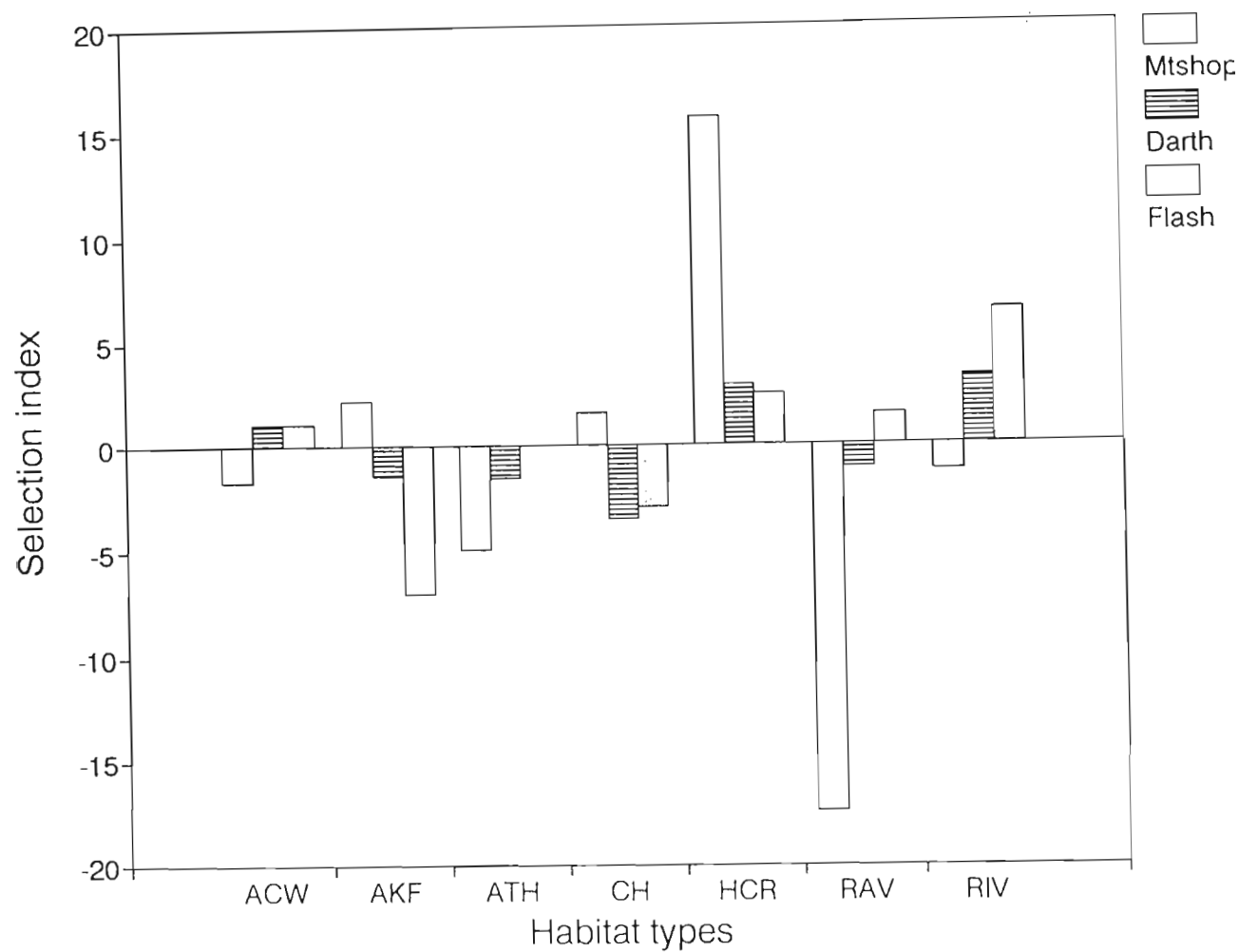


Figure 6.8: Selectivity indices for the different habitat types by the three troops. A negative value indicates avoidance of a habitat while a positive value indicates habitat preference. Habitat types: ACW-*Acacia* mixed woodland, CH-*Combretum* woodland, ATH-*Acacia* thicket, AKF-*A. karroo* forest, RIV-riverine forest, HCR-hilly *Combretum* woodland, RAV-ravine.

(SI= 2.15). Since these SIs were a measure of habitat choice in relation to habitat availability, the time spent in habitats differed from the accessibility of the corresponding habitats by a factor of 6.39 for the Mtshopi troop, 3.50 for Darth's troop and 2.15 for Flash's troop.

The mean amount of food encountered per hectare was calculated on the basis of time spent in different habitats. Mtshopi troop encountered 32.64kg/ha, Darth's troop 31.40 kg/ha and Flash's troop 27.52kg/ha. This contrasted with the mean amount of food per hectare calculated for the three home ranges. This increased with decreasing home range size (and troop size) while the figures based on time spent in the different habitat types increased with increasing home range size. These results showed that Mtshopi troop spent more time in quadrats of higher than average food availability, while the two daughter troops spent less time in quadrats of high food availability.

The time spent in the seven habitat types differed significantly from the proportion of habitat types found in the home ranges for all the troops (Mtshopi- $\chi^2=41.13$, $df=4$, $P<0.001$; Darth- $\chi^2=53.89$, $df=5$, $P<0.001$, Flash- $\chi^2=119.34$, $df=3$, $P<0.001$).

6.3.7 Activity budgets

Both Darth's and Flash's troop's activity budgets differed significantly from Mtshopi troop's: Mtshopi-Darth, $\chi^2=9.23$, $df=3$, $P<0.05$; Mtshopi-Flash, $\chi^2=11.48$, $df=3$, $P<0.01$, (see Figure 6.9). There was however, no significant difference between the activity budgets of the two daughter troops (Darth-Flash, $\chi^2=5.07$, $df=3$, $P=0.167$).

Mtshopi troop spent a greater proportion of its time walking than Darth or Flash's troops. The proportion of the activity budget used in social activities, resting and foraging appeared to increase with decreasing group size, with Mtshopi troop spending the least time socialising, resting and foraging. Darth's troop spent the most time foraging followed by the Mtshopi troop and Flash's troop

6.3.8 Predation pressure

The effect of predation pressure was examined by comparing: i) the time individuals spent in vigilance, ii) the time spent in relative safety in trees or on cliffs and iii) the mean distance between individuals. Individuals in Darth's troop spent 2.13% (33 records) of the total number of scans in vigilant behaviour (i.e. sitting or standing in an upright position scanning an area), followed by Flash's troop - 1.25% (18 records), and Mtshopi troop - 0.73% (10 records).

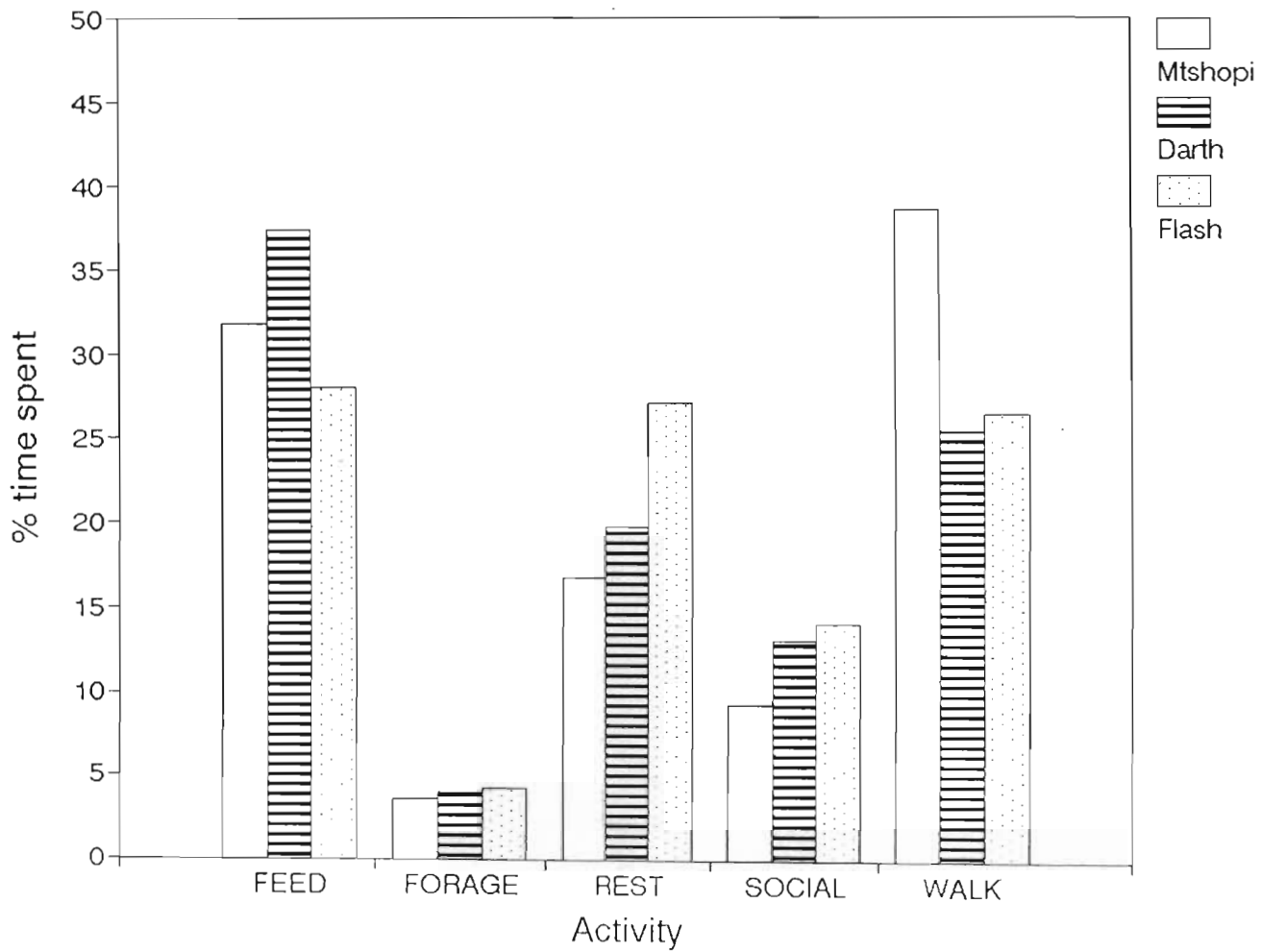


Figure 6.9: Activity budgets for the three troops. DARTH and Flash's troop's activity budgets were significantly different from Mtshopi troop's (Mtshopi-DARTH, $\chi^2=9.23$, $df=3$, $P<0.05$; Mtshopi-Flash, $\chi^2=11.48$, $df=3$, $P<0.01$). There was no significant difference between DARTH and Flash's troops (DARTH-Flash, $\chi^2=5.07$, $df=3$, $P=0.167$).

There was no significant difference in the percentage of scans per day that individuals were recorded in trees for the three troops ($F\text{-ratio}=0.262$, $P=0.771$, $df=40$). The time spent in trees per day was similar for all the troops: Mtshopi troop - 20.3% ($n=22$), DARTH's troop - 21.6% ($n=9$) and Flash's troop -20.3% ($n=10$)

There was no significant difference in the daily mean distance between nearest neighbours for the three troops ($F\text{-ratio}=1.916$, $P=0.1612$, $df=40$) The nearest neighbour distance was smallest for Mtshopi troop (3.74m), followed by Flash (4.51m) and DARTH (4.71m).

6.4 Discussion

The analyses indicate differences in home range size, habitat quality, day journey length, diet, habitat utilisation and predator detection behaviour between Mtshopi troop and the two daughter troops. These changes could be attributed to changes in troop size as a result of fission, though it must be borne in mind that the comparison was also between two consecutive years and differences due to differences in food availability could not be ruled out. Smaller home range sizes and day journey lengths, in addition to more favourable activity budgets and diets for the daughter troops might suggest 1990 was simply a more productive year in terms of food. However, mean annual rainfall in 1990 was lower (707mm) than 1989 (1080mm) (240mm during study period (June to September) and three months prior to it, as opposed to 268mm for the same period the previous year). Thus the results should be interpreted as being a result of changes in group size rather than higher food availability after the troop split.

6.4.1 Home range size

The increase in home range size with increasing troop size in this study concurred with results for primates in general (Milton and May 1976; Clutton-Brock and Harvey 1977; Iwamoto and Dunbar 1983) as well as for other studies of baboons (*Papio* spp.). When comparing troops in similar areas, both Stacey (1986) and Davidge (1978) found home ranges to increase with troop size. Barton *et al.* (1992) found 36% of variation in group size between different study sites could be accounted for by troop size. In this study, per capita home range size was almost identical for all three troops indicating that the home range sizes were modified so as to maintain a constant density (see also Henzi *et al.* in press) of baboons. This was not found in other studies (Stacey 1986; Davidge 1978) where slight differences in habitats between different sized troops might have resulted in different carrying capacities and consequently

different densities of baboons.

6.4.2 Day journey length

This study confirms Dunbar's (1992) analysis for baboons which found an increase in day journey length with group size. The longer day journey routes for Mtshopi troop represents the necessity of having to travel further to meet feeding requirements of a larger troop. The reason being due to indirect competition through resource depletion by members of the troop (see Wrangham *et al.* 1993). Since all individuals travel together the added distance increases the costs to individuals in large troops.

Unlike per capita home range size, per capita day journey length was similar only for Mtshopi troop and Darth's troops. Flash's troop, the smallest troop was a third longer, despite having a higher mean density of food. This could be a result of the high overlap (40%) between this troop's home range with Darth's troop, resulting in additional resource depletion in the home range, necessitating longer day journeys.

6.4.3 Food availability

If resource defence is an advantage of group living (Wrangham 1980) then larger troops should be able to displace smaller troops from prime areas and therefore establish their home range in higher quality areas. Since the smaller daughter troop (Flash's troop) occupied a home range with a higher mean density of food than Darth's troop, it did not appear that Flash's troop was displaced, rather the troops tended to concentrate their habitat utilisation in different areas.

6.4.4 Diet

Foraging theory predicts that as intra-specific competition increases diet breadth should increase, as animals become less selective in what foods they feed on (Krebs 1978). Since the density of animals remained essentially the same before and after the split, diet breadth was a measure of intensity of competition between individuals in different sized groups. The small troops had a less diverse diet than Mtshopi troop, suggesting that they were more selective in their diet. It therefore appears that the level of competition decreased after fission. This provides evidence against theories that argue for a feeding advantage from group living (Wrangham 1980), as this should increase, at least to some extent, with group size. These results support the existence of a foraging cost associated with group size.

6.4.5 Habitat use

Like diet, the breadth of habitat use was wider for Mtshopi troop than the daughter troops. However, this might not necessarily reflect more competition in the large

troop but rather was a function of smaller home range size and possibly restricted choice of habitats for the smaller troops. All habitat types were available in the three home ranges but time spent in habitat types was significantly different from the proportion of habitats available to the three troops. This suggests that the decreased habitat breadth for the smaller troops did indeed reflect decreased competition by individuals in the smaller troops.

The results showed that Mtshopi troop spent more time in areas of high food availability than the mean for the home range while the two daughter troops spent their time in areas with lower than average food availability. This is contradictory to maximising rate of food intake. Explanations for this can be found when looking at activity budgets and predation risk. The smaller troops spent 25% more time resting and socialising. These activities do not require being in food rich areas and would allow habitat choice on the basis of low predation risk.

6.4.6 Activity budgets

Comparison of activity budgets of the three troops showed that activity budgets of the daughter troops were more favourable than that of the original Mtshopi troop. Time spent walking was on average reduced by 12 percent in the daughter troops suggesting that they spent less energy obtaining food as a result of higher foraging efficiency. These results are in contrast to those obtained by Stacey (1986) who compared three neighbouring troops of yellow baboons (*Papio cynocephalus cynocephalus*). He found that the smallest troop spent only half the time feeding than the larger troops, but there was no significant difference in time spent moving. Either way, an increase in time spent feeding, or an increase in time spent walking, with group size reflects increased net costs of obtaining food. While time spent feeding represents only a lost opportunity cost, increased time spent walking represents a lost opportunity cost in addition to increased energy requirements.

Reduction in time spent walking resulted in increases in time spent resting and socialising in the daughter troops. Socialising increased with decreasing group size despite the number of potential social interactions being less, suggesting that before fission the Mtshopi troop might not have been able to spend enough time socialising. This would have been primarily due to long day journeys and consequent increases in time spent walking.

6.4.7 Predation pressure

Predation pressure has often been suggested as being the main reason for group living (DeVore 1965; Hamilton 1971; Crook 1972; Eisenberg *et al.* 1972; Rowell 1979; van

Schaik 1983). This advantage is probably due either one or any combination of the following: i) detection of predators facilitating escape or ii) the dilution effect or iii) group defence against predators. At Mkuzi both leopards (*Panthero leo*) and spotted hyenas (*Crocutta crocutta*) are common within the troops' home range, however no successful predation attempts were observed during the course of the study. Consequently predation risk in the different sized troops could not be directly assessed. Behaviours that reflected the susceptibility to predation however were assessed.

Stacey (1986) found vigilance and time spent in elevated positions where individuals would have a wider view of potential attacks to be significantly higher in smaller troops than large troops. Altmann (1974) also found that baboons stayed closer together in areas of high predation risk. This study found an increase in the incidence of vigilant behaviour in smaller troops, but no major differences in the distance to nearest neighbours or in the time in trees (when not feeding). This may be because the higher tree density in the home ranges of the smaller troops resulted in some protection in the form of a higher density of refuges meant that the smaller troops were never far from trees large enough to escape to in the event of an attack by a predator.

6.4.8 Group size

Home range size, day journey length and mean food density in home range increased with increasing group size while proportion of time spent foraging, resting, socialising and mean food encountered decreased. Although Mtshopi troop (71 individuals) was less selective of food and habitats than the daughter troops this pattern was not consistent when comparing daughter troops. DARTH's troop (43 individuals) was less selective of both food and habitats than FLASH's troop (28 individuals). This reversal may be due to the overlap of DARTH's home range with 40% of FLASH's home range. This would result in increased resource depletion, forcing FLASH's troop to have longer per capita day journey lengths and be more selective of their foods and habitats. In general though, the results are consistent with theories that predict a foraging advantage in smaller groups, allowing shorter day journey lengths, more selective choice of habitats and foods and more favourable time budgets, with extra time allocated to resting and foraging.

Although, only indirect evidence of increased foraging risk in smaller sized troops is available (small troops spent on average two times more time vigilant than Mtshopi troop), predation seems to be the only other possible advantage for living in large

groups. This conforms with van Schaik's (1983) predation - intra-group feeding competition theory where group size is determined by the interaction between a reduction of predation risk with increasing group size and increased foraging costs with increasing group size.

6.4.9 Troop fission

The results of this study suggest that troop fission produces significant advantages in smaller troops. This is through an increase in nett foraging efficiency, and a better energy budget with more time for socialising and resting. Demonstration of ecological advantages that arise from troop fission does not necessarily imply that social factors do not play an important role in the occurrence of troop fission. However, it appears that advantages of this fission event were large, suggesting that it was probable that the increased ecological costs associated with a larger troop size was the precursor for fission in Mtshopi troop, with social factors acting mainly to modifying the timing.

Chapter 7

Summary and Conclusion

This thesis has been an investigation of how baboons in a woodland habitat make a living; how they interact with their environment in order to obtain enough food and water for survival. In the study area water was available throughout the home range even in the driest months of the study, consequently, the emphasis has been on food acquisition. The general premise has been that range use is primarily determined by the need to acquire sufficient food. That the acquisition of food is the main motivation for movement of animals should require little elaboration. All but a few sessile animals are unable to obtain their nutritional requirements without moving, thus movement becomes essential to survival. What this thesis investigated was the strategies used by the troop, and the constraints faced by it while collecting food in this particular habitat. This was done within the general frame of optimal foraging theory. What follows is a summary of the findings of each chapter and emphasising the links between the different chapters.

7.1 Chapter 2

This chapter described habitat types that made up the study troop's home range and their distribution. From these descriptions it emerged that the home range consisted of a broad variety of habitat types distributed in a complex mosaic. Although the mean tree density in the home range was calculated no similar measures were available for any other baboon study sites. Consequently, no quantitative comparisons were possible, although according to qualitative descriptions of habitats this troop's home range appeared to have had a higher tree density than other sites with the exception of Gombe, Tanzania (Ransom 1981) and Ishasha, Uganda (Rowell 1966) where baboons live on forest edges.

Quantitative measures of food availability, in terms of dry mass of baboon food, were also presented. Although the overall pattern (all habitats combined) showed a consistent pattern of increasing food availability from December to May followed by a steep decline till November, a separate analysis of habitats showed a lot of individual variation in timing of food availability. Consequently, habitat ranks in terms of food availability only remained constant between June-July and August-September. This meant that the troop faced a constantly changing environment in terms of food distribution. Decisions on habitat use (based on food availability) in one month were therefore seldom valid for following months. Both changes in food availability and the

complex arrangement of habitat types made for a complicated foraging environment (see Chapters 3 and 4).

The rest of the chapter dealt with the baboons movements within the home range and whether the baboons were following a strategy of energy maximising or time minimising.

At a coarse level the troop was found to have both an average home range size and day journey lengths as compared with other baboon studies. Since group size is the major determinant of both home range size and day journey length (Barton *et al.* 1992) the typical home range size and day journey length could be largely accounted for by the troop's size. This was close to the overall average for study sites throughout Africa. Since in all populations there is a wide variation in group size (Dunbar 1992) individual troop size is not necessarily indicative of habitat quality (though modal group sizes for a population would be, with richer habitats being able to maintain higher group sizes (see Wrangham *et al.* 1993)).

With the effect of group size accounted for, Mtshopi troop had a larger than predicted per capita home range , but a smaller than predicted day journey length. This is an apparent contradiction since both home range size and day journey length are assumed to decrease with increasing habitat quality (when comparing troops of the same size, Dunbar 1988). However, both food distribution and it's mean density are important to animals (Krebs and Davies 1991). Differences in distribution are likely to alter the relationship between home range size and day journey length. Essentially, home range size reflects the area required to support a troop through the whole year, while day journey length reflects the distance animals need to move in a day to meet their energy requirements. If food distribution is such that food patches are widely dispersed but relatively rich then day journeys should be relatively short, while the area required to contain enough patches to supply the troop through the whole year would be large. This has been used to explain the large home ranges of frugivorous primates compared with foliovores (Clutton-Brock and Harvey 1977). Mtshopi troop was the most frugivorous (including the use of seeds in this definition) of 11 baboon study troops (see Chapter 5). The majority of fruits and seeds that the troop relied on occurred profusely in widely distributed trees scattered throughout the home range. Thus the high proportion of fruit eaten might explain the apparent contradiction between a large per capita home range and small per capita day journey length. From this it appears that day journey length is likely to be a better predictor of habitat quality than home

range size. This is partly because day journey length is a direct measure of a decrease in the quality of time budgets (see Chapter 6).

More specific aspects of home range use addressed in the chapter were temporal and spatial differences in quadrat use and residency. The troop exhibited both a seasonal difference in quadrat use and a difference with distance from sleeping sites. They had a long duration of stay in more quadrats during the low food season when food was scarce then in the high food season. This conformed to optimal foraging predictions. The second analysis only showed partial agreement with optimal foraging predictions, suggesting that travel cost foraging theory could not be applied directly to animals such as baboons, without modifications.

Optimal foraging theory predicted that as travel costs increase, time spent foraging in a patch should increase. It predicted a linear increase with distance. This study found that time spent in quadrats did not increase linearly with distance from sleeping sites, although there was an increase in time spent 1.8 to 2km from the nearest sleeping site. The results were found to be in better agreement with Hamilton and Watt's (1970) Refuging model where the area around a sleeping site becomes degraded through consistent exploitation, therefore animals pass through this area relatively quickly and move to more distant, less exploited "resource acquisition zones" where they spent longer in quadrats. The results for the Mtshopi troop confirmed this prediction, but also suggested that the relationship with time spent in quadrats was a sigmoidal function with the troop having longest duration of stay immediately adjacent to the home range before dropping some distance from the sleeping site (Hamilton and Watt's biodeterioration zone), increasing in the area of resource acquisition and tailing off again towards the edge of the home range.

This pattern of use takes into account the reality of troops arriving early and leaving late from sleeping sites which results in long mean duration of stay in the immediate vicinity of sleeping sites. It also takes into account troop behaviour at the edge of its home range, where unfamiliarity and inter-troop encounter risks preclude long stays (see Sigg and Stolba 1981).

The results showed that not only was this pattern true for mean duration of stay in quadrats but also for frequency of entry of quadrats once the natural exponential decrease in probability of entering a quadrat (with distance from sleeping site) is taken into account. It was interesting that Mtshopi troop conformed to Hamilton and Watts' model since the model was developed for central place foragers. This suggested that baboons using several sleeping sites conformed to multiple central place foragers,

rather than use several sleeping sites in order to use their home ranges more evenly as suggested by Altmann and Altmann (1970). The results of a comparison between a central place foraging troop and a troop using many sleeping site by Sigg and Stolba (1981) also seemed to suggest little difference in the evenness of home range use.

The occurrence of consistent patterns of spatial differences in quadrat use were surprising since these analyses were made independently of food distribution. They perhaps provide some additional reasons for why there was no apparent correlation between quadrat use and food availability (see Chapter 3) since the analyses of food availability did not take into account the differences in food availability suggested by these results.

Analysis of food encountered showed that Mtshopi troop were time minimizers. The amount of food encountered did not correlate significantly with the amount of food available. As food became scarce the troop's day journey became longer, compensating for the decrease in food availability. Evidence of a time minimising strategy was not restricted to these analyses. Reduced time spent walking after fission did not lead to a commensurate increase in time spent feeding, rather in Darth's troop time spent feeding actually decreased (Chapter 6). The two troops rather increased time spent resting and socialising, a strategy incompatible with energy maximising, where relaxation in time budgets should result in an increase in time spent resting (Hixon and Carpenter 1988).

The implications of Mtshopi troop using a time minimising strategy are important in interpreting the results of the rest of the study. Time minimising implies that an animal is able to meet its nutritional requirement within the constraints of its time budget and is able to devote time to activities other than feeding. It suggests that feeding is important only until the nutrient requirements of the troop are met, after this other activities take precedence, such as socialising or minimising predation risk. Thus it becomes harder to distinguish whether animals are tending towards an optimal solution since the analyses include periods where the troop is fulfilling other needs. The problem of looking at foraging in primates and especially baboons is their ability to feed at any opportunity and the difficulty associated with teasing out behaviours directed at finding food or occurring for other reasons. Thus often when looking at strategies as a whole, such as the choice of a day journey route optimisation in terms of food might be difficult to detect (see Chapter 4).

7.2 Chapter 3

Chapter three analysed what factors determine quadrat use. The lack of multiple regression to explain a significant amount of variation in habitat use, while the same techniques had a strong explanatory power for the baboons at Laikipia (Barton *et al.* 1992) may be due to the complex nature of Mtshopi troop's habitat and food availability (Chapter 1). Despite failure of the stepwise multiple regressions to combine environmental variables in a linear model so as to explain a meaningful amount of variability in quadrat use, individual environmental factors were found to be significantly correlated with quadrat use.

Despite being able to calculate the dry mass of baboon food available in each quadrat, the amount of food was not correlated with quadrat use. Of the variables tested distance from the centre of the home range and distance from the nearest sleeping site were the most important in determining quadrat use. A positive correlation with tree density suggested a possible preference (in terms of total time spent in quadrats) for safer (in terms of predation risk) quadrats (a high density of trees indicating the number of possible refuges from predator attack). That this correlation became non-significant in the low food season, when food was scarce, could be explained by the need to be in food rich quadrats outweighing the need to be in safer quadrats at this time. When the results were analysed in terms of mean duration of stay in quadrats, rather than total time spent in quadrats the constraints of distance from the centre of the home range and from the nearest sleeping site seemed to relax. In general the results concurred with Barton *et al.*'s (1992) findings that suggested a need to leave from and return to a sleeping site was a major influence on quadrat use that traditional foraging theory could not take into account. Barton also found the distance from a water resource was a major correlate of quadrat use for his study troop, that relied on a few man-made water holes. This was not the case at Mkuzi where water resources were numerous even in the driest month of the study.

These analyses seemed to emphasise the importance of spatial relationships of quadrats to resources and quadrat position in the home range. Consequently in the next chapter a simulation model was built that would take into account the spatial arrangement of the home range in terms of habitat type and consequently food distribution. It was clear from the analyses in this chapter that the need to leave from and return to a sleeping site would also have to be built into a model that would take into account the spatial arrangement of habitat type in the home range and its effect on food distribution. It was clear from the analyses in this chapter that the need to leave from and return to a sleeping site would also have to be included in any simulation model.

7.3 Chapter 4

This chapter attempted to come to terms with developing, what Post (1978) has called an "appropriate null hypothesis for habitat residency", one that predicts habitat utilisation for an area assuming that animals moved randomly with respect to food availability. While discussing the problems associated with determining habitat preference of baboons he wrote:

"Ideally one would like to examine a series of randomly constructed day-journeys, complete with a series of generated zone (habitat type) occupancy times, to use as the null zone occupancy distribution, examining the deviations of observed from simulated zone (habitat type) utilisation for significant departures..."

While Post envisaged using this for examining habitat choice the ability to estimate food availability in the different habitat types, meant that this study could address the question of the affect of food availability directly, by comparing the amount of food encountered by the troop on a day journey with that encountered by a simulated random walk day journey.

The development of the random walk model enabled the determination of **accessibility** of habitat types-the proportions in which different habitat types would be encountered if the troop was walking randomly with regard to food availability, as opposed to habitat **availability**-the proportions of the home range covered by different habitat types.

There was a significant difference when habitat preference was calculated using the relative area of different habitat types available (availability) as opposed to habitat preferences calculated on the basis of proportions of habitats one could expect a troop to encounter if it were walking randomly (accessibility). While the measure of difference between habitat availability and actual proportion of time spent in different habitats might be a useful description of habitat use it does not necessarily demonstrate a behavioural preference, or otherwise, for the different habitat types. Only comparison with the encounter rate of a simulated random walk model would demonstrate behavioural preferences for different habitat types.

Apart from the methodological purposes of this chapter, the major aim was to determine whether Mtshopi troop chose it's day journey routes on the basis of food availability. The results of comparisons between food encountered by the random

model and the troop showed that the troop did indeed encounter more energy than the random simulation. Results of the troop were very similar to those obtained by the stochastic optimal model and the troop appeared to be using a similar level of short-term optimisation. This suggested that the troop's day journey route was a response to the amount of food it was encountering on day journeys as opposed to deciding on a route prior to setting off for the day journey. The latter would require both a capability of forming a mental map of the home range (Altmann and Altmann 1970), and having an enormous amount of information about potential foraging returns at that particular time throughout the home range. While it is almost certain that baboons have a mental map of their home range (see Sigg and Stolba 1981) it is questionable whether baboons would have comprehensive enough information about food availability to construct a long-term optimal day journey route in all but the simplest habitats.

Baboon troops have large home ranges. In most populations only a small fraction of the home range could be covered by a troop, even given their longest day journey lengths. This restricts the amount of information that a troop has about the distribution of food in the home range as well as putting a premium on sampling different areas of the home range in order to gain information on variability of food availability. In addition the number of food items that baboons eat and the differences in timing of their appearance and abundance make relative assessment of the relative abundance of food throughout the home range even more difficult. A final impediment to maintaining sufficient information about relative food availability through the home range is the constant depletion of food resources both by the troop, as well as other troops and animals. This can only act to make assessment of relative food availability even harder. Consequently, given the information constraints and the need to sample different areas while still fulfilling daily nutritional requirements, short-term optimal foraging might be the only feasible strategy for baboons. Certainly, for the study troop whose home range was complex, and where the relative food availability between the different habitat types differed constantly throughout the year, it appeared unlikely that the troop could acquire enough information on which to base an *a priori* choice of day journey route that maximised the rate of nutrient intake.

A consequence of long-term optimisation of day journey route would be relatively constant day journey lengths and energy intakes on consecutive days. The data from this study show remarkably variable day journey lengths, with the troop walking 1km one day and 7km on the next. The variance in day journey length was very high for every month of the study (see Chapter 2). Likewise Stacey (1986) found substantial daily variation in food and energy intake for all animals in the three baboon troops he

studied. Thus the evidence seems to suggest that day journey routes in other populations may also be chosen on the basis of short-term optimisation.

The analysis that took into account the amount of time spent in quadrats along the day journey demonstrated how allocation of time on a day journey was influenced by food availability in quadrats encountered on the day journey. When time spent on the day journey was taken into account it was found that the troop spent longer in quadrats with a higher food availability. Again, like in the previous chapter where mean duration of stay in quadrats was less constrained than frequency of entry into quadrats, it appears that duration of stay is likely to follow the pattern of food availability while choice of which quadrats to enter on a day journey were more constrained.

The analysis in this chapter has wider implications than for the study of baboons. It demonstrates a method to control for the effect of non-random spatial arrangement of habitat types, essential resources, and food patches in home ranges. Early on in the development of optimal foraging theory it was realised that the general formulation of optimal diet choice models could not be applied to habitat or patch choice, because the assumption of random encounter of habitat types or patches was untenable. Using simulation modelling within a home range where the spatial distribution of patches or habitat types are specified the encounter rate can be estimated, allowing analysis of optimal use of the home range. Simulation modelling therefore opens opportunities for studying optimal foraging in relation to actual distribution of habitat types or food patches.

7.4 Chapter 5

Chapter 5 represented a change from looking at the optimisation of troop movement to optimisation in terms of the choice of foods. It examined whether the troop was choosing what to include in its diet according to optimal foraging principles. Both food density (in terms of dry mass) and food quality was taken into account. The proportion of food in the troop's diet was found to be a closer approximation of food species than total food item mass. This could be explained by the constraints of passage rate, where individuals reach satiation before having significantly depleted a foraging patch.

If most foraging patches consist of so many food items that animals reach satiation before significantly depleting the patch, the items of food in their diet would represent relative species density rather than their productivity. For example, if species A produces 5000 food items per tree and species B only 3000, and an animal's satiation is

reached at 500 fruits per sitting, then both species A and B would be equally represented in the diet if they occurred at equal densities. However if they occurred at different densities they would be represented in the diet in the same proportion as their densities.

The study provides some evidence that this occurred. The feeding bouts in *Ziziphus mucronata* ended before there was a significant decrease in the rate of fruit intake and the general impression in the field was that this was true for all other food items occurring in trees above the size of 2m. The troop had a diet mainly consisting of fruit. Trees containing numerous fruit fulfil the description of food distributed in a patch containing food items in quantities where animals reach satiation before a significant decrease in their feeding rate. This might explain why Mtshopi troop's diet was closer to the density of food species while the diet of Barton *et al.*'s (1992) study troop at Laikipia was significantly correlated with the actual availability of food items. At Laikipia fruits only accounted for 23% of the diet with other food types such as underground items being represented in fairly large proportions.

Diet would represent the density of food species more closely than the availability of food items in relatively food rich areas where most of the food species produced a lot of food items per tree. This description appears to be apt for Mkuzi. Of the troops main foods a large percentage occurred on common medium sized trees distributed widely through the home range. Therefore it may not be surprising that the Mtshopi troop's diet reflected food species density rather than food availability.

The question never-the-less arises as to why should the baboon troop should move on after reaching satiation and not remain in the feeding patch until passage rate constraints were eased so that they could continue to feed in the same patch? There are three possible reasons: 1)the value of the information gathered by moving on and sampling other areas outweighs any advantage achieved by staying in a single patch 2)continuous moving reduces the risk of predation by increasing the uncertainty of a predator locating the troop 3)this may also be a passive mechanism whereby the troop is insured of getting a balanced diet. By moving into another area the probability of the next food being different to the one just fed on (till satiation) no doubt increases. Any of these or all three working together should provide a significant stimulus for moving on.

The latter part of the chapter compared preferences for different food items with their nutritional content. From, 1)the difference in nutrient content between food and non-

food items and 2) the difference between the parts of food item selectively consumed compared with the whole food items it was clear that the troop was choosing between food and non-food items and selecting what parts to ingest on the basis of higher nutrient content, in particular on the basis of a high protein/fibre ratio. This selection for a high protein/fibre ratio was also present at the level of distinguishing between frequently eaten food items and only occasionally eaten food items. It was however not evident in the preferences for the different main food items. There was no correlation between the preference shown for foods and either the protein or fibre content. This was surprising given the widespread evidence for the importance of maximising the protein/fibre ratio (see Oftedal 1991).

However, analysis of the main foods demonstrated that the protein requirement could be met by any combination of the troop's main foods. Without protein being limited the troop would be free to concentrate on maximising energy intake. Carbohydrates were the most available nutrient and most likely to be used for energy maximisation. Unfortunately, the analysis of carbohydrates was not detailed enough to test whether digestible carbohydrates were the basis of selection between the troop's main foods, but comparison amongst *Acacia* seeds suggested that this was a feasible model.

The major reason for the selection for high protein/fibre ratios not affecting preferences between the main foods was that the troop lived in a protein rich environment. This was due in particular to the high density of edible protein rich *Acacia* species in Mkuzi (see Chapter 2). The selection pattern of the Mkuzi troop reinforces the principle that selection for protein will only occur when it is limiting, otherwise barring any other major limiting nutrients animals should maximise the rate of energy intake (Oftedal 1991).

Exceptionally high selection ratios for a few species in the troop's diet appear to be related to high levels of micro nutrient in those species and may have been a response to periodic shortages in specific micro nutrients. These micro nutrients are needed in only trace amounts and are likely to be met by the selection of just single food species high in that micro nutrients and thus would not affect selection for the large proportion of the diet.

This chapter demonstrated the advantages of pursuing an optimal foraging approach. Both the lack of correlation between preference in the main foods with protein or fibre and the lack of correlation between diet and food availability in their home range suggested, not that the troop was not complying to optimal foraging theory, but that

different models were needed, and the original assumptions needed to be re-evaluated. In both instances this led to a deeper understanding of foraging in the Mtshopi troop. In the first case it led to an understanding of how the distribution of food and processing constraints may affect our expectations of what represents an optimal strategy, and in the second case it led to an understanding that the troop lived in a protein rich environment and therefore might be able to select among the main foods on an energetic criteria rather than on the basis of the protein/fibre ratio.

The analyses also demonstrated that despite the complications involved in examining the diet of a generalist omnivore, it is possible to apply optimal foraging methodology in order to understand the foraging decisions faced by baboon troops.

7.5 Chapter 6

Chapter 6 examined ecological consequences of troop fission for Mtshopi troop. The advantages experienced by the smaller troops were, shorter day journey lengths, a more favourable time budget with less time spent walking and more time spent socialising and resting. The daughter troops appeared to be able to spend more time in food rich habitats. Smaller troops were also more selective in their diet and choice of habitat. The only apparent disadvantage appeared to be increased predation risk, though the evidence of this was indirect: daughter troops were more vigilant than the Mtshopi troop.

These results demonstrated that fission is a method of constantly adapting to environmental pressures. In a sense the fission of the Mtshopi troop can be considered as a time minimising strategy. Fission resulted in a more favourable time budget. The additional time resulting from the decrease in time spent walking was used in socialising and resting rather than for increasing time spent feeding as predicted by an energy maximising strategy.

The data suggested that within-group competition has a large effect on individuals in large troops. In the case of Mtshopi troop it's large size meant that time spent socialising decreased to a similar amount as found in marginal baboon habitats and time spent walking increased to a par with troops living under harsh conditions (see Dunbar 1992). This unfavourable time budget occurred despite the troop living in a relatively high quality habitat, within a low density population. Troop fission resulted in dramatic improvements without there being a change in food availability or density of baboons.

7.6 Conclusion

The main findings of this thesis have, perhaps not surprisingly, suggested that the foraging and dietary strategies of a troop of baboons are complex and hard fit to an into a simple single theoretical frame work. Such frameworks are necessarily a simplification of the real world, however, to fulfil their function they must explain a significant proportion of the variation in the real world. A general mathematical model of optimal foraging paths has been an example where a theory was still born because its main underlying assumption; that of a random encounter rate of habitat types or patches was untenable (Krebs *et al.* 1984) In the real world, animals are heavily constrained by the need to pass through other habitats to get into favourable ones and the distribution of these habitats are seldom if ever random. The problem in formulating a general model is that for each study the relationships between habitats is always unique. Consequently virtually no quantitative field work has been done on day journey routes. Simulation models played out on a map of the actual habitat types circumvents the problem of the non-random spatial relationships between habitat types. The simulation modelling approach used in this thesis was the first time that I am aware of, that this approach was used in context of day journey route optimisation.

The results not only emphasised the importance of non-random distribution of habitats types, but represented a way to deal with this. It showed that the question of optimal day journey routes can be tractable. Similar simulation modelling should result in more meaningful null models, when addressing questions involving movement of animals through different habitats.

One of the most important lessons learnt from the modelling exercise was that the complexity of spatial distribution can mask even an optimising strategy. There was no significant correlation between food availability and the utilisation of quadrats for the model that was actually stochastically choosing which quadrat to go to on the basis of food availability. This should be a warning of how optimisation strategies in animals might be masked. If the results of the model came from an animal study it would be easy to suggest that no optimisation strategy lay behind the results. However, the optimising procedure was intrinsic to the model.

The troop's home range proved to be a good example of complex spatial and temporal pattern of resources. The baboon troops response to this was to use a short-term form of optimisation. Despite a well developed memory and an ability to form mental maps (see Altmann 1974, and Sigg and Stolba 1981) the troops response was only at the level of short-term optimisation, possibly following a "rule of thumb" This probably reflects the constraints of collecting information and predicting food availability in a complex environment.

Like movement through the home range the choice of diet in the troop's home range proved to site specific. The general model of food choice was one of maximising the rate of intake of protein, but this study suggested that in the absence of a protein shortage, it is likely that animals will maximise their rate of carbohydrate intake. This scenario is likely to happen when any random choice of foods is likely to fulfil the animals daily requirements. This situation is probably more quite common when

dealing with animals that eat fruits and seeds in Africa, because of the preponderance of *Acacia* species, which, as this study demonstrated, are generally rich in protein.

For food choice the results again suggested the re-evaluation of optimality models taking into account further constraints. The constraint imposed by food passage rates, interacting with the pattern of food dispersion, where food in trees is concentrated in rich patches resulted in diet choice reflecting the density of food species rather than the dry weight measure of food availability. An additional factor might be the information constraints mentioned earlier.

Foraging and diet choice was not only affected by the nature and distribution of the habitat types and abundance of food but as comparison between the different size troops showed it is to a large extent determined by the size of the troop itself. Despite being located in a food rich habitat the Original troop had a mean day journey length similar to study troops in low quality habitats (Dunbar 1988), however this was only a function of troop size. When the troop split, the day journey lengths almost halved. The effect of the troop itself was not restricted to day journey length. The short durations of stay in quadrats around the sleeping sites was due to the modification of food availability due to intensive use by the troop in those areas close to the sleeping sites.

Given the complexity of baboons' diet, the constraints involved in returning to sleeping sites every night and the interaction between group size and foraging patterns and diet choice it is not surprising that these complex interactions are not predicted by simple optimal foraging models. Rather the study demonstrated that optimal foraging theory when applied to particular questions was successful in understanding the constraints faced by a generalist omnivore and this led to a deeper understanding of the basis of foraging and diet choice by baboons.

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Appendix A: Tree shapes and derved equations for calculating the relationship between tree height and volume.

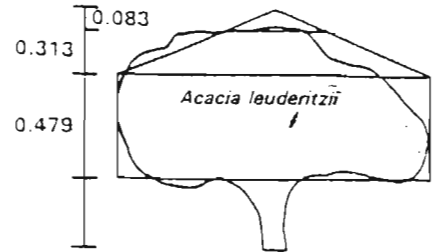
Acacia leuderitzii

$$\text{Cylinder} = 0.479Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.313Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.083Ht \times \pi (r_2)^2}{2}$$

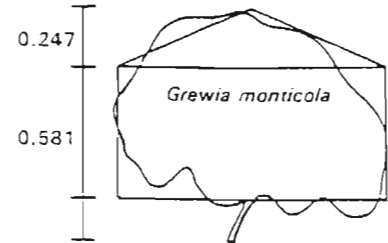
$$r_2 = \sqrt{[0.267 \times (\sqrt{0.313Ht^2 - \left(\frac{d}{2}\right)^2})^2 - 0.083Ht^2]}$$



Grewia monticola

$$\text{Cylinder} = 0.581Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.247Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

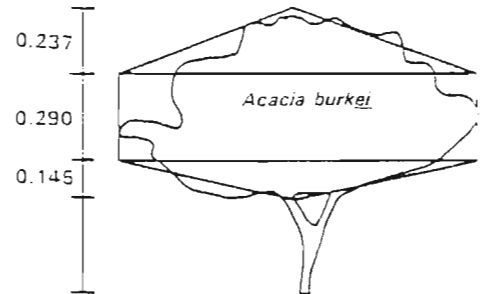


Acacia burkei

$$\text{Cylinder} = 0.290Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.237Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Bottom cone} = \frac{0.145Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

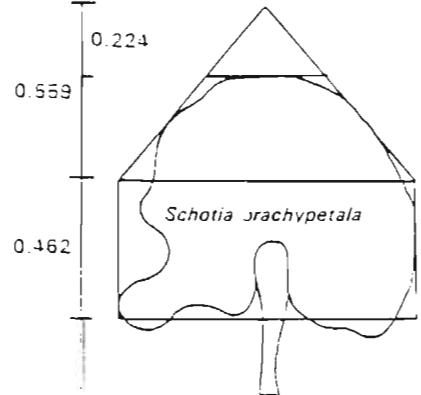


Schotia brachypetala

$$\text{Top cone} = \frac{0.559Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.224Ht \times \pi (r_2)^2}{2}$$

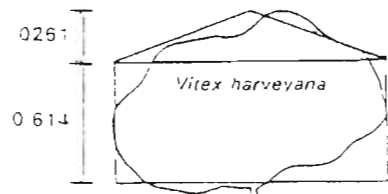
$$r_2 = \sqrt{[0.401 \times (\sqrt{0.559Ht^2 - \left(\frac{d}{2}\right)^2})^2 - 0.224Ht^2]}$$



Vitex harveyana

$$\text{Cylinder} = 0.614Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.261Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$



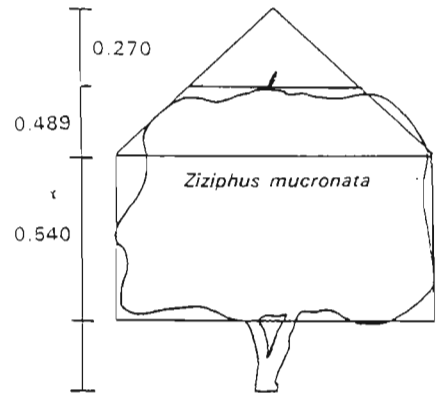
Ziziphus mucronata

$$\text{Cylinder} = 0.540Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.489Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

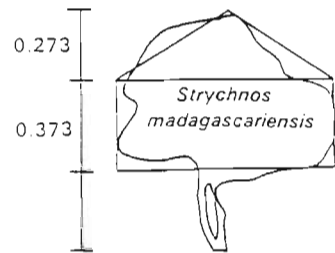
$$\text{Excess cone} = \frac{0.270Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{\left[1.233 \times \left(\sqrt{0.489Ht^2 - \left(\frac{d}{2}\right)^2}\right)^2 - 0.270Ht^2\right]}$$

Strychnos madagascariensis

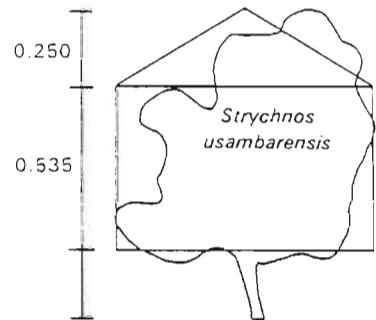
$$\text{Cylinder} = 0.373Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.273Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

Strychnos usambarensis

$$\text{Cylinder} = 0.535Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.250Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

Sclerocarya caffra

$$\text{Cylinder} = 0.355Ht \times \pi \left(\frac{d}{2}\right)^2$$

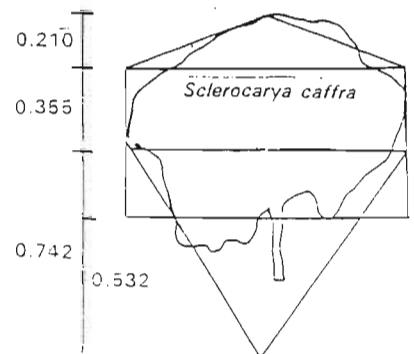
$$\text{Top cone} = \frac{0.210Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Bottom cone} = \frac{0.742Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.532Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{\left[0.717 \times \left(\sqrt{0.742Ht^2 - \left(\frac{d}{2}\right)^2}\right)^2 - 0.532Ht^2\right]}$$

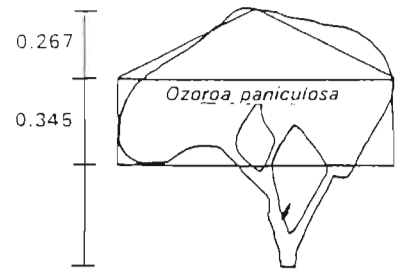
$$\text{Cylinder} = 0.355Ht \times \pi \left(\frac{d}{2}\right)^2$$



Ozoroa paniculosa

$$\text{Cylinder} = 0.345Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.267Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

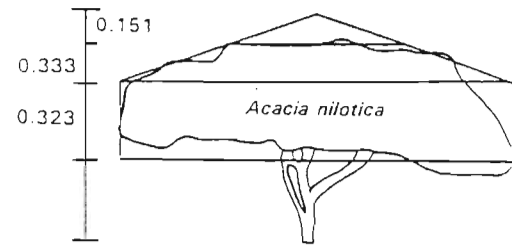
Acacia nilotica

$$\text{Cylinder} = 0.323Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.333Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.151Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.453 \times (\sqrt{0.333Ht^2 - (\frac{d}{2})^2})]^2 - 0.151Ht^2}$$

Berchemia zeyheri

$$\text{Cylinder} = 0.229Ht \times \pi \left(\frac{d}{2}\right)^2$$

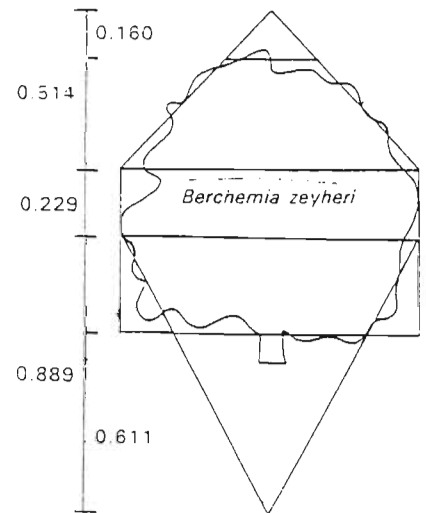
$$\text{Top cone} = \frac{0.514Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.160Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.311 \times (\sqrt{0.514Ht^2 - (\frac{d}{2})^2})]^2 - 0.160Ht^2}$$

$$\text{Bottom cone} = \frac{0.889Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.611Ht \times \pi (r_3)^2}{2}$$

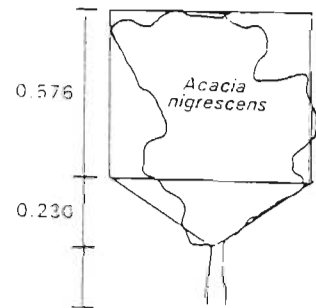


$$r_3 = \sqrt{[0.687 \times (\sqrt{0.889Ht^2 - (\frac{d}{2})^2})]^2 - 0.611Ht^2}$$

Acacia nigrescens

$$\text{Cylinder} = 0.576Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Bottom cone} = \frac{0.230Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$



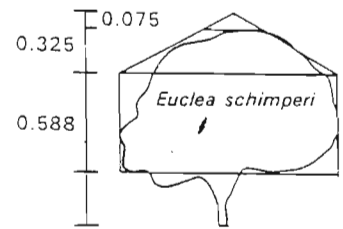
Euclea schimperi

$$\text{Cylinder} = 0.588 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.325 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

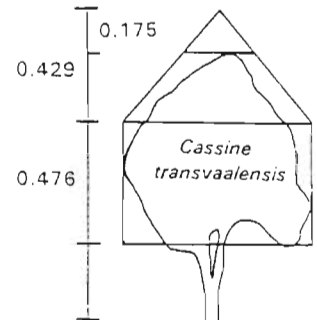
$$\text{Excess cone} = \frac{0.075 H t \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.230 \times (\sqrt{0.325 H t^2 - \left(\frac{d}{2} \right)^2})^2 - 0.075 H t^2}$$

Cassine transvaalensis

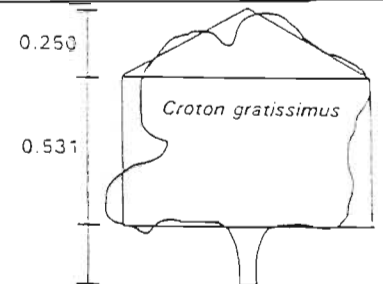
$$\text{Cylinder} = 0.476 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = 0.429 H t \times \pi \left(\frac{d}{2} \right)^2$$

Croton gratissimus

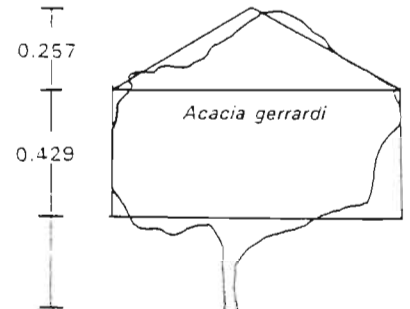
$$\text{Cylinder} = 0.531 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.250 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

Acacia gerrardi

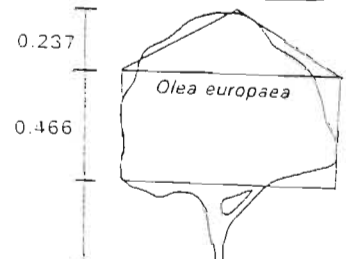
$$\text{Cylinder} = 0.429 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.257 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

Olea europaea

$$\text{Cylinder} = 0.466 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.237 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$



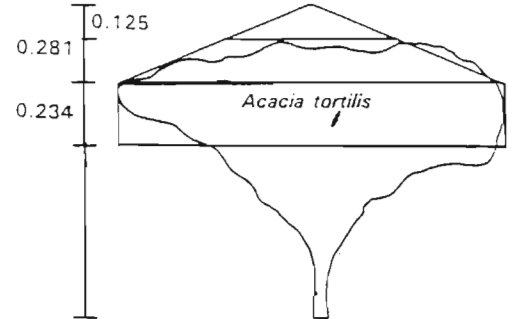
Acacia tortilis

$$\text{Cylinder} = 0.234 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.281 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

$$\text{Excess cone} = \frac{0.125 H t \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.445 \times (\sqrt{0.281 H t^2 - \left(\frac{d}{2} \right)^2})^2 - 0.125 H t^2]}$$

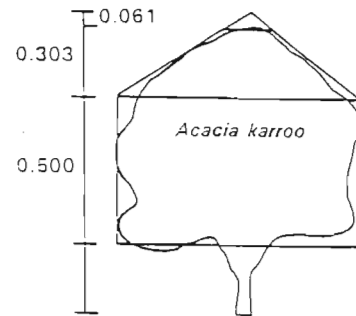
Acacia karroo

$$\text{Cylinder} = 0.500 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.303 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

$$\text{Excess cone} = \frac{0.061 H t \times \pi (r_1)^2}{2}$$

$$r_1 = \sqrt{[0.201 \times (\sqrt{0.303 H t^2 - \left(\frac{d}{2} \right)^2})^2 - 0.061 H t^2]}$$

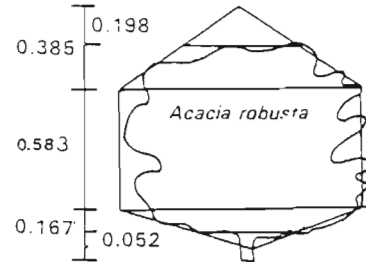
Acacia robusta

$$\text{Cylinder} = 0.583 H t \times \pi \left(\frac{d}{2} \right)^2$$

$$\text{Top cone} = \frac{0.385 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

$$\text{Excess cone} = \frac{0.198 H t \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.514 \times (\sqrt{0.385 H t^2 - \left(\frac{d}{2} \right)^2})^2 - 0.198 H t^2]}$$



$$\text{Bottom cone} = \frac{0.167 H t \times \pi \left(\frac{d}{2} \right)^2}{2}$$

$$\text{Excess cone} = \frac{0.052 H t \times \pi (r_1)^2}{2}$$

$$r_1 = \sqrt{[0.311 \times (\sqrt{0.167 H t^2 - \left(\frac{d}{2} \right)^2})^2 - 0.052 H t^2]}$$

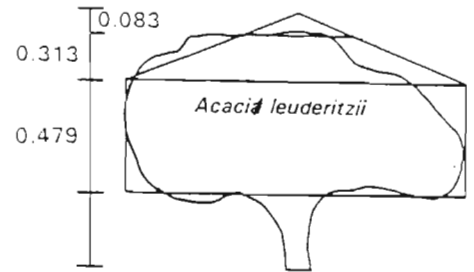
Acacia leuderitzii

$$\text{Cylinder} = 0.479 Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.313 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

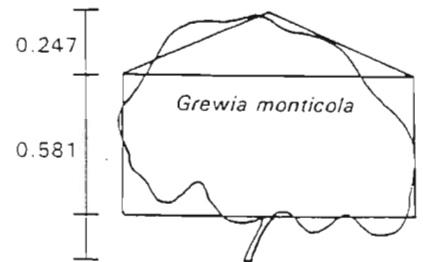
$$\text{Excess cone} = \frac{0.083 Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.267 \times (\sqrt{0.313 Ht^2 + \left(\frac{d}{2}\right)^2})^2 - 0.083 Ht^2]}$$

Grewia monticola

$$\text{Cylinder} = 0.581 Ht \times \pi \left(\frac{d}{2}\right)^2$$

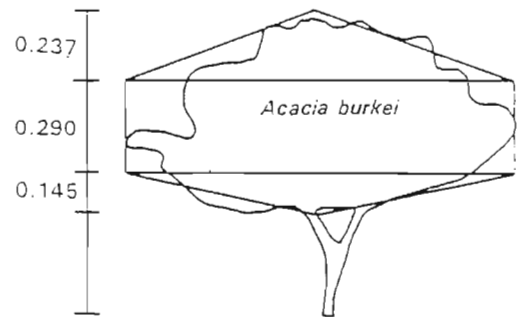
$$\text{Top cone} = \frac{0.247 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

Acacia burkei

$$\text{Cylinder} = 0.290 Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.237 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

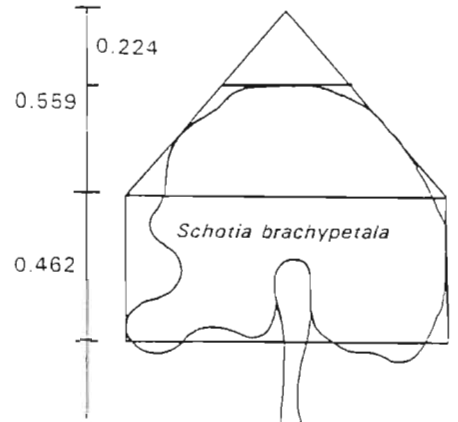
$$\text{Bottom cone} = \frac{0.145 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

Schotia brachypetala

$$\text{Top cone} = \frac{0.559 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.224 Ht \times \pi (r_2)^2}{2}$$

$$r_2 = \sqrt{[0.401 \times (\sqrt{0.559 Ht^2 + \left(\frac{d}{2}\right)^2})^2 - 0.224 Ht^2]}$$

Vitex harveyi

$$\text{Cylinder} = 0.614 Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.261 Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$



Appendix A: Tree shapes and derived equations for calculating the relationship between tree height and volume.

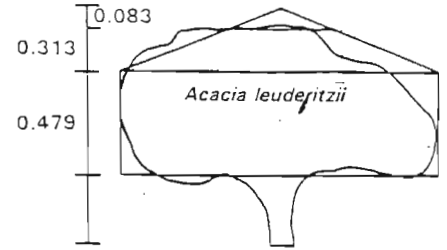
Acacia leucoxantha

$$\text{Cylinder} = 0.479Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.313Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.083Ht \times \pi (r_2)^2}{2}$$

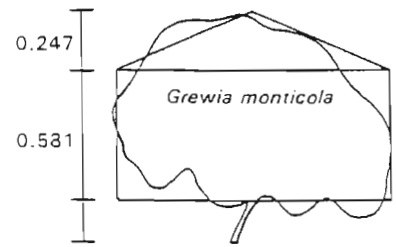
$$r_2 = \sqrt{[0.267 \times (\sqrt{0.313Ht^2 - \left(\frac{d}{2}\right)^2})^2 - 0.083Ht^2]}$$



Grewia monticola

$$\text{Cylinder} = 0.581Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.247Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

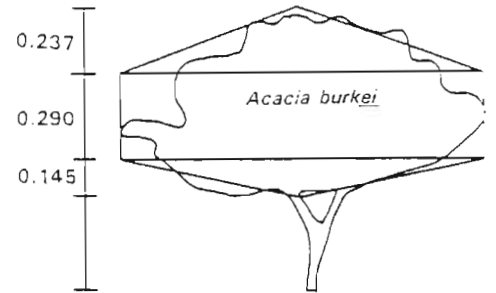


Acacia burkei

$$\text{Cylinder} = 0.290Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.237Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Bottom cone} = \frac{0.145Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

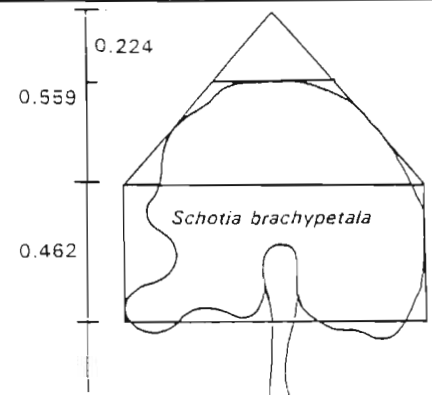


Schotia brachypetala

$$\text{Top cone} = \frac{0.559Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$

$$\text{Excess cone} = \frac{0.224Ht \times \pi (r_2)^2}{2}$$

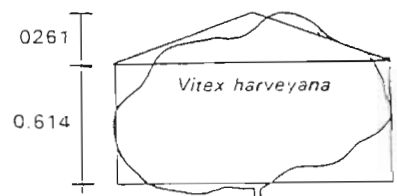
$$r_2 = \sqrt{[0.401 \times (\sqrt{0.559Ht^2 - \left(\frac{d}{2}\right)^2})^2 - 0.224Ht^2]}$$



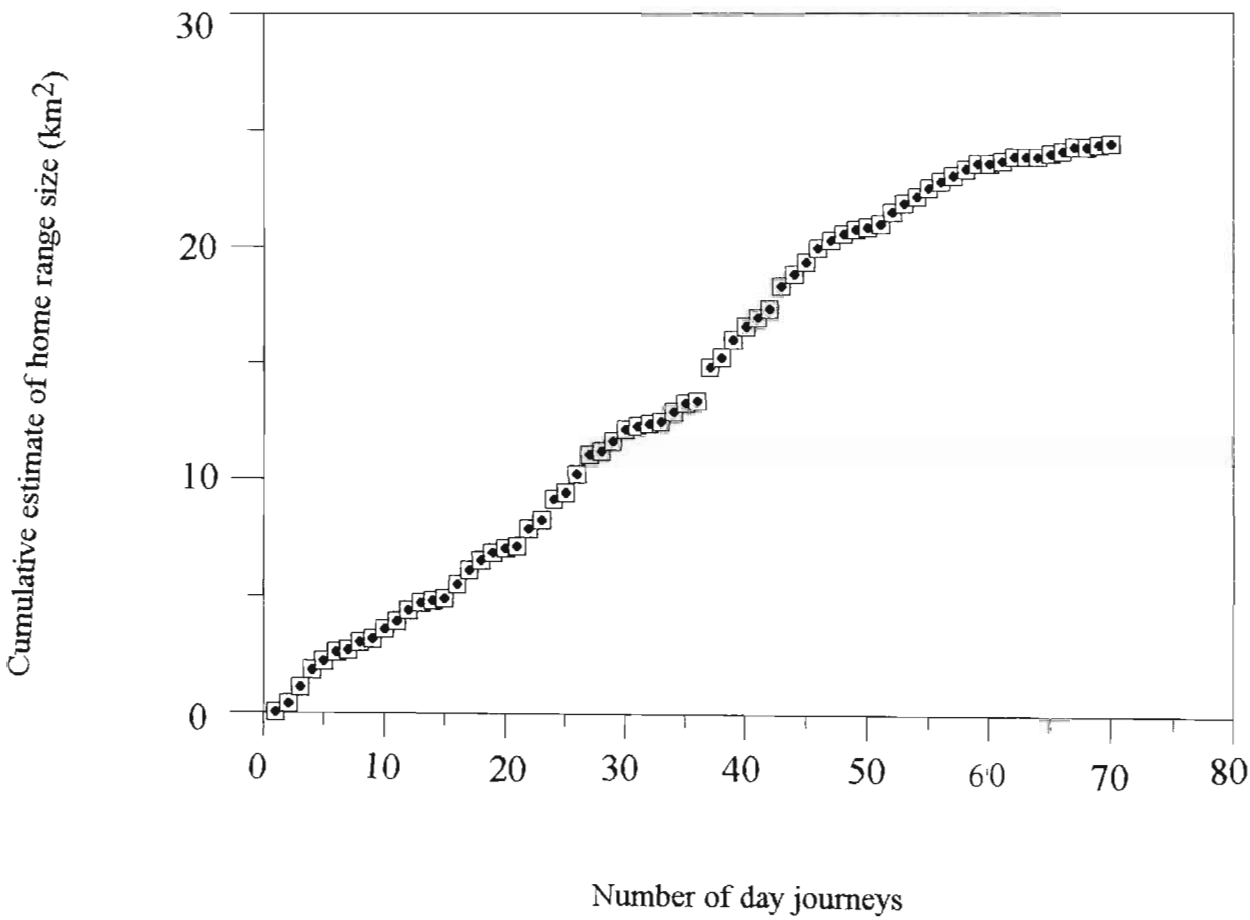
Vitex harveyana

$$\text{Cylinder} = 0.614Ht \times \pi \left(\frac{d}{2}\right)^2$$

$$\text{Top cone} = \frac{0.261Ht \times \pi \left(\frac{d}{2}\right)^2}{2}$$



Appendix B: Plot of cumulative estimates of home range size for the Mtshopi troop (February 1989-March 1990).



Appendix C: Main feature of the random walk and optimal foraging simulation programs in BASIC.

Random simulation model program

```

10 INPUT "NAME OF FILE TO SAVE DATA TO";F$
11 INPUT "X COORD OF SLEEPING SITE=";X
12 INPUT "Y COORD OF SLEEPING SITE=";Y
13 INPUT "X COORD OF DESTINATION=";P
14 INPUT "Y COORD OF DESTINATION=";Q
15 INPUT "LENGTH OF DAY JOURNEY IN QUADRATS=";L
20 INPUT "NUMBER OF ITERATIONS ";Z
16 OPEN "A" ,#1, F$
17 DIM QUADRAT(48,30)
40 I=X
60 J=Y
115 GOTO 3110
120 FOR V=1 TO Z
130 PRINT "TOTAL ENERGY-";TE
140 IF V>1 THEN X=I
150 IF V>1 THEN Y=J
160 IF V>1 THEN C=0
170 TE=0
180 PRINT "XY COORD OF DESTINATION";X,Y "NO OF QUADRATS";L
190 PRINT #1 ,"XY COORD OF DESTINATION";P,Q "NO OF
QUADRATS";L
200 C=1
210 N=VAL (MID$(TIME$,7,2))
220 RANDOMIZE N
230 R=INT((RND*3)-1)
240 S=R+X
250 N=VAL (MID$(TIME$,7,2))
260 RANDOMIZE N
270 R=INT((RND*3)-1)
280 T=R+Y
290 IF S=X AND T=Y GOTO 210
300 X=S
310 Y=T
320 PX=I
330 PY=J
335 IF X<0 THEN X=40+X
340 DE=QUADRAT(X,Y)
350 PRINT X,Y,DE
360 PRINT #1 ,X,Y,DE
370 TE=DE
380 C=C+1
390 CO=0
400 CO=CO+1
410 IF CO>100 GOTO 3050
420 N=VAL (MID$(TIME$,7,2))
430 RANDOMIZE N
440 R=INT(RND*100)
450 IF X-PX=-1 AND Y-PY=-1 GOTO 1110
460 IF X-PX=0 AND Y-PY=-1 GOTO 1200
470 IF X-PX=1 AND Y-PY=-1 GOTO 1290
480 IF X-PX=1 AND Y-PY=0 GOTO 1380
490 IF X-PX=1 AND Y-PY=1 GOTO 1470
500 IF X-PX=0 AND Y-PY=1 GOTO 1560
510 IF X-PX=-1 AND Y-PY=1 GOTO 1650
520 IF X-PX=-1 AND Y-PY=0 GOTO 1740
530 S=XR+X
540 IF S<2 OR S>34 GOTO 400
550 T=YR+Y
560 IF T<4 OR T>26 GOTO 400
570 IF S=X AND T=Y GOTO 400
580 IF T=1 GOTO 1840
590
PROCEDURE TO READ ILLEGAL QUADRATS IE QUADRATS OUTSIDE
HOME RANGE IF ILLEGAL GO TO 400 IF NOT GOTO 880

```

Data input.

Read quadrat energies into the 2 dimensional array - QUADRAT.

Generate random values for the X and Y coordinates to move to for first move. First move is strictly random.

DE becomes the energy of the quadrat moved to.
Print to file quadrat co-ordinates of quadrat moved to and the the energy of that quadrat (DE).

Generate a random number for subsequent moves.

Dependant on position relative to previous quadrat (ie. direction of movement) goto subroutines specifying the chances of moving into the adjacent quadrats.

If out of home range generate random number again.
If out of home range generate random number again.

Determine if the move will be out of the home range if so regenerate random number again.

```
880 IF ABS(S-P) < ABS(T-Q) GOTO 1070
```

```
890 IF ABS(S-P) > ABS(T-Q) GOTO 1090
```

```
900 D = ABS(S-P)
```

```
910 E = L-C
```

```
920 IF E-D < 0 GOTO 400
```

```
930 PX = X
```

```
940 PY = Y
```

```
950 X = S:Y = T
```

```
960 IF X < 0 GOTO 3090
```

```
970 DE = QUADRAT(X,Y)
```

```
980 TE = TE + DE
```

```
990 PRINT X,Y,DE
```

```
1000 PRINT #1 ,X,Y,DE
```

```
1010 IF L-C = 0 GOTO 1030
```

```
1020 GOTO 380
```

```
1030 PRINT #1 , "TOTAL ENERGY-";TE
```

```
1035 NEXT
```

```
1040 PRINT #1 , "TOTAL ENERGY-";TE
```

```
1045 CLOSE #1
```

```
1050 PRINT "TOTAL ENERGY-";TE
```

```
1055 CLOSE #2
```

```
1060 END
```

```
1070 D = ABS(S-P) + (ABS(T-Q)-ABS(S-P))
```

```
1080 GOTO 910
```

```
1090 D = ABS(T-Q) + (ABS(S-P)-ABS(T-Q))
```

```
1100 GOTO 910
```

```
1110 IF R >= 0 AND R < 17.55 GOTO 3020
```

```
1120 IF R >= 17.55 AND R < 49.72 GOTO 2810
```

```
1130 IF R >= 49.72 AND R < 62.27 GOTO 2840
```

```
1140 IF R >= 62.72 AND R < 78.62 GOTO 2870
```

```
1150 IF R >= 78.62 AND R < 82.765 GOTO 2900
```

```
1160 IF R >= 82.765 AND R < 84.245 GOTO 2930
```

```
1170 IF R >= 84.245 AND R < 88.39 GOTO 2960
```

```
1180 IF R >= 88.39 AND R < 100 GOTO 2990
```

```
1190 GOTO 530
```

```
1200 IF R >= 0 AND R < 17.55 GOTO 2810
```

```
1210 IF R >= 17.55 AND R < 49.72 GOTO 2840
```

```
1220 IF R >= 49.72 AND R < 62.27 GOTO 2870
```

```
1230 IF R >= 62.72 AND R < 78.62 GOTO 2900
```

```
1240 IF R >= 78.62 AND R < 82.765 GOTO 2930
```

```
1250 IF R >= 82.765 AND R < 84.245 GOTO 2960
```

```
1260 IF R >= 84.245 AND R < 88.39 GOTO 2990
```

```
1270 IF R >= 88.39 AND R < 100 GOTO 3020
```

```
1280 GOTO 530
```

```
1290 IF R >= 0 AND R < 17.55 GOTO 2840
```

```
1300 IF R >= 17.55 AND R < 49.72 GOTO 2870
```

```
1310 IF R >= 49.72 AND R < 62.27 GOTO 2900
```

```
1320 IF R >= 62.72 AND R < 78.62 GOTO 2930
```

```
1330 IF R >= 78.62 AND R < 82.765 GOTO 2960
```

```
1340 IF R >= 82.765 AND R < 84.245 GOTO 2990
```

```
1350 IF R >= 84.245 AND R < 88.39 GOTO 3020
```

```
1360 IF R >= 88.39 AND R < 100 GOTO 2810
```

```
1370 GOTO 530
```

```
1380 IF R >= 0 AND R < 17.55 GOTO 2870
```

```
1390 IF R >= 17.55 AND R < 49.72 GOTO 2900
```

```
1400 IF R >= 49.72 AND R < 62.27 GOTO 2930
```

```
1410 IF R >= 62.72 AND R < 78.62 GOTO 2960
```

```
1420 IF R >= 78.62 AND R < 82.765 GOTO 2990
```

```
1430 IF R >= 82.765 AND R < 84.245 GOTO 3020
```

```
1440 IF R >= 84.245 AND R < 88.39 GOTO 2810
```

```
1450 IF R >= 88.39 AND R < 100 GOTO 2840
```

```
1460 GOTO 530
```

```
1470 IF R >= 0 AND R < 17.55 GOTO 2900
```

```
1480 IF R >= 17.55 AND R < 49.72 GOTO 2930
```

```
1490 IF R >= 49.72 AND R < 62.27 GOTO 2960
```

```
1500 IF R >= 62.72 AND R < 78.62 GOTO 2990
```

```
1510 IF R >= 78.62 AND R < 82.765 GOTO 3020
```

```
1520 IF R >= 82.765 AND R < 84.245 GOTO 2810
```

```
1530 IF R >= 84.245 AND R < 88.39 GOTO 2840
```

viable, in terms of whether it's possible to reach the destination in the number of moves left over, else generate random number again.

DE becomes the energy of the quadrat moved to.

Print to file quadrat co-ordinates of quadrat moved to and the the energy of that quadrat (DE).

Routines for determining number of moves from destination.

Specify direction dependant probabilities.

..

..

..

..

```

1550 GOTO 530
1560 IF R>=0 AND R<17.55 GOTO 2930
1570 IF R>=17.55 AND R<49.72 GOTO 2960
1580 IF R>=49.72 AND R<62.27 GOTO 2990
1590 IF R>=62.72 AND R<78.62 GOTO 3020
1600 IF R>=78.62 AND R<82.765 GOTO 2810
1610 IF R>=82.765 AND R<84.245 GOTO 2840
1620 IF R>=84.245 AND R<88.39 GOTO 2870
1630 IF R>=88.39 AND R<100 GOTO 2900
1640 GOTO 530
1650 IF R>=0 AND R<17.55 GOTO 2960
1660 IF R>=17.55 AND R<49.72 GOTO 2990
1670 IF R>=49.72 AND R<62.27 GOTO 3020
1680 IF R>=62.72 AND R<78.62 GOTO 2810
1690 IF R>=78.62 AND R<82.765 GOTO 2840
1700 IF R>=82.765 AND R<84.245 GOTO 2870
1710 IF R>=84.245 AND R<88.39 GOTO 2900
1720 IF R>=88.39 AND R<100 GOTO 2930
1730 GOTO 530
1740 IF R>=0 AND R<17.55 GOTO 2990
1750 IF R>=17.55 AND R<49.72 GOTO 3020
1760 IF R>=49.72 AND R<62.27 GOTO 2810
1770 IF R>=62.72 AND R<78.62 GOTO 2840
1780 IF R>=78.62 AND R<82.765 GOTO 2870
1790 IF R>=82.765 AND R<84.245 GOTO 2900
1800 IF R>=84.245 AND R<88.39 GOTO 2930
1810 IF R>=88.39 AND R<100 GOTO 2960
1820 GOTO 530
1830 END
CHECK FOR ILLEGAL MOVES RETURN TO 400 OR 880
2810 XR=-1
2820 YR=1
2830 GOTO 530
2840 XR=0
2850 YR=1
2860 GOTO 530
2870 XR=1
2880 YR=1
2890 GOTO 530
2900 XR=1
2910 YR=0
2920 GOTO 530
2930 XR=1
2940 YR=-1
2950 GOTO 530
2960 XR=0
2970 YR=-1
2980 GOTO 530
2990 XR=-1
3000 YR=-1
3010 GOTO 530
3020 XR=-1
3030 YR=0
3040 GOTO 530
3050 PRINT#1, "impossible route!!!!!!!"
3060 PRINT, "impossible route!!!!!!!"
3070 GOTO 140
3090 DE=QUADRAT(X*-1+40,Y)
3100 GOTO 980
3110
READ FOOD DRY MASS VALUES INTO QUADRAT() THEN RETURN

```

Specify increment for X and Y co-ordinate.

Print impossible route to file if after 100 tries there is no viable solution for the next move, then start day journey again.

Read dry mass values for the quadrats into the 2-dimensional array QUADRAT, then return to main part of the program.

Optimal simulation model program

```

420 N=VAL (MID$(TIME$,7,2))
430 RANDOMIZE N
440 R=INT(RND*100)
441 RTOT=QUADRAT(X-1,Y+1)+QUADRAT(X,Y+1)+
QUADRAT(X+1,Y+1)+QUADRAT(X-1,Y)+QUADRAT(X+1,Y)+
QUADRAT(X-1,Y-1)+QUADRAT(X,Y-1)+QUADRAT(X+1,Y-1)
442 R1=QUADRAT(X-1,Y+1)/RTOT
443 R2=QUADRAT(X,Y+1)/RTOT
444 R3=QUADRAT(X+1,Y+1)/RTOT
445 R8=QUADRAT(X-1,Y)/RTOT
446 R4=QUADRAT(X+1,Y)/RTOT
447 R7=QUADRAT(X-1,Y-1)/RTOT
448 R6=QUADRAT(X,Y-1)/RTOT
449 R5=QUADRAT(X+1,Y-1)/RTOT
450 IF X-PX=-1 AND Y-PY=-1 GOTO 1110
460 IF X-PX=0 AND Y-PY=-1 GOTO 1200
470 IF X-PX=1 AND Y-PY=-1 GOTO 1290
480 IF X-PX=1 AND Y-PY=0 GOTO 1380
490 IF X-PX=1 AND Y-PY=1 GOTO 1470
500 IF X-PX=0 AND Y-PY=1 GOTO 1560
510 IF X-PX=-1 AND Y-PY=1 GOTO 1650
520 IF X-PX=-1 AND Y-PY=0 GOTO 1740
530 S=XR+X
535 SUM=0
540 IF S<2 OR S>34 GOTO 400
550 T=YR+Y
560 IF T<4 OR T>26 GOTO 400
570 IF S=X AND T=Y GOTO 400
580 IF T=1 GOTO 1840
880 IF ABS(S-P)<ABS(T-Q) GOTO 1070
890 IF ABS(S-P)>ABS(T-Q) GOTO 1090
900 D=ABS(S-P)
910 E=L-C
920 IF E-D<0 GOTO 400
930 PX=X
940 PY=Y
950 X=S:Y=T
970 DE=QUADRAT(X,Y)
980 TE=TE+DE
990 PRINT X,Y,DE
1000 PRINT #1 ,X,Y,DE
1010 IF L-C=0 GOTO 1030
1020 GOTO 380
1030 PRINT #1 ,"TOTAL ENERGY-";TE
1034 TOT=TOT+TE
1035 NEXT
1040 PRINT #1 ,"TOTAL ENERGY-";TE
1042 GOTO 32
1045 CLOSE #1
1050 PRINT "TOTAL ENERGY-";TE
1055 CLOSE #2
1060 END
1070 D=ABS(S-P)+(ABS(T-Q)-ABS(S-P))
1080 GOTO 910
1090 D=ABS(T-Q)+(ABS(S-P)-ABS(T-Q))
1100 GOTO 910
1110 RMTOT=R8*.1755+R1*.3217+R2*.1155+
R3*.1735+R4*.04145+R5*.0148+R6*.04145+R7*.1161
1115 IF R>=SUM AND R<SUM+((R8*.1755)/RMTOT)*100 GOTO 3020
1117 SUM=SUM+((R8*.1755)/RMTOT)*100
1120 IF R>=SUM AND R<SUM+((R1*.3217)/RMTOT)*100 GOTO 2810
1125 SUM=SUM+((R1*.3217)/RMTOT)*100
1130 IF R>=SUM AND R<SUM+((R2*.1155)/RMTOT)*100 GOTO 2840
1135 SUM=SUM+((R2*.1155)/RMTOT)*100
1140 IF R>=SUM AND R<SUM+((R3*.1735)/RMTOT)*100 GOTO 2870

```

Generate random number.

Determine probability of entering adjacent quadrats based on dry food mass.

Dependant on position relative to previous quadrat (ie. direction of movement) go to sub-routines specify the probabilities of moving into adjacent quadrats based on the direction of movement.

Procedure to calculate the probabilities of moving into adjacent quadrats, combining the direction dependant probability and the

```

1145 SUM=SUM+((R3*.1735)/RMTOT)*100
1150 IF R>=SUM AND R<SUM+((R4*.04145)/RMTOT)*100 GOTO 2900
1155 SUM=SUM+((R4*.04145)/RMTOT)*100
1160 IF R>=SUM AND R<SUM+((R5*.0148)/RMTOT)*100 GOTO 2930
1165 SUM=SUM+((R5*.0148)/RMTOT)*100
1170 IF R>=SUM AND R<SUM+((R6*.04145)/RMTOT)*100 GOTO 2960
1175 SUM=SUM+((R6*.04145)/RMTOT)*100
1180 IF R>=SUM AND R<SUM+((R7*.1161)/RMTOT)*100 GOTO 2990
1190 GOTO 530
1200 RMTOT=R1*.1755+R2*.3217+R3*.1155+
R4*.1735+R5*.04145+R6*.0148+R7*.04145+R7*.1161
1205 IF R>=SUM AND R<SUM+((R1*.1755)/RMTOT)*100 GOTO 2810
1207 SUM=SUM+((R1*.1755)/RMTOT)*100
1210 IF R>=SUM AND R<SUM+((R2*.3217)/RMTOT)*100 GOTO 2840
1215 SUM=SUM+((R2*.3217)/RMTOT)*100
1220 IF R>=SUM AND R<SUM+((R3*.1155)/RMTOT)*100 GOTO 2870
1225 SUM=SUM+((R3*.1155)/RMTOT)*100
1230 IF R>=SUM AND R<SUM+((R4*.1735)/RMTOT)*100 GOTO 2900
1235 SUM=SUM+((R4*.1735)/RMTOT)*100
1240 IF R>=SUM AND R<SUM+((R5*.04145)/RMTOT)*100 GOTO 2930
1245 SUM=SUM+((R5*.04145)/RMTOT)*100
1250 IF R>=SUM AND R<SUM+((R6*.0148)/RMTOT)*100 GOTO 2960
1255 SUM=SUM+((R6*.0148)/RMTOT)*100
1260 IF R>=SUM AND R<SUM+((R7*.04145)/RMTOT)*100 GOTO 2990
1265 SUM=SUM+((R7*.04145)/RMTOT)*100
1270 IF R>=SUM AND R<SUM+((R8*.1161)/RMTOT)*100 GOTO 3020
1280 GOTO 530
1290 RMTOT=R2*.1755+R3*.3217+R4*.1155+
R5*.1735+R6*.04145+R7*.0148+R8*.04145+R1*.1161
1295 IF R>=SUM AND R<SUM+((R2*.1755)/RMTOT)*100 GOTO 2840
1297 SUM=SUM+((R2*.1755)/RMTOT)*100
1300 IF R>=SUM AND R<SUM+((R3*.3217)/RMTOT)*100 GOTO 2870
1305 SUM=SUM+((R3*.3217)/RMTOT)*100
1310 IF R>=SUM AND R<SUM+((R4*.1155)/RMTOT)*100 GOTO 2900
1315 SUM=SUM+((R4*.1155)/RMTOT)*100
1320 IF R>=SUM AND R<SUM+((R5*.1735)/RMTOT)*100 GOTO 2930
1325 SUM=SUM+((R5*.1735)/RMTOT)*100
1330 IF R>=SUM AND R<SUM+((R6*.04145)/RMTOT)*100 GOTO 2960
1335 SUM=SUM+((R6*.04145)/RMTOT)*100
1340 IF R>=SUM AND R<SUM+((R7*.0148)/RMTOT)*100 GOTO 2990
1345 SUM=SUM+((R7*.0148)/RMTOT)*100
1350 IF R>=SUM AND R<SUM+((R8*.04145)/RMTOT)*100 GOTO 3020
1355 SUM=SUM+((R8*.04145)/RMTOT)*100
1360 IF R>=SUM AND R<SUM+((R1*.1161)/RMTOT)*100 GOTO 2810
1370 GOTO 530
1380 RMTOT=R3*.1755+R4*.3217+R5*.1155+
R6*.1735+R7*.04145+R8*.0148+R1*.04146+R2*.1161
1385 IF R>=SUM AND R<SUM+((R3*.1755)/RMTOT)*100 GOTO 2870
1387 SUM=SUM+((R3*.1755)/RMTOT)*100
1390 IF R>=SUM AND R<SUM+((R4*.3217)/RMTOT)*100 GOTO 2900
1395 SUM=SUM+((R4*.3217)/RMTOT)*100
1400 IF R>=SUM AND R<SUM+((R5*.1155)/RMTOT)*100 GOTO 2930
1405 SUM=SUM+((R5*.1155)/RMTOT)*100
1410 IF R>=SUM AND R<SUM+((R6*.1735)/RMTOT)*100 GOTO 2960
1415 SUM=SUM+((R6*.1735)/RMTOT)*100
1420 IF R>=SUM AND R<SUM+((R7*.04145)/RMTOT)*100 GOTO 2990
1425 SUM=SUM+((R7*.04145)/RMTOT)*100
1430 IF R>=SUM AND R<SUM+((R8*.0148)/RMTOT)*100 GOTO 3020
1435 SUM=SUM+((R8*.0148)/RMTOT)*100
1440 IF R>=SUM AND R<SUM+((R1*.04145)/RMTOT)*100 GOTO 2810
1445 SUM=SUM+((R1*.04145)/RMTOT)*100
1450 IF R>=SUM AND R<SUM+((R2*.1161)/RMTOT)*100 GOTO 2840
1465 GOTO 530
1470 RMTOT=R4*.1755+R5*.3217+R6*.1155+
R7*.1735+R8*.04145+R1*.0148+R2*.04146+R3*.1161
1475 IF R>=SUM AND R<SUM+((R4*.1755)/RMTOT)*100 GOTO 2900
1477 SUM=SUM+((R4*.1755)/RMTOT)*100
1480 IF R>=SUM AND R<SUM+((R5*.3217)/RMTOT)*100 GOTO 2930
1485 SUM=SUM+((R5*.3217)/RMTOT)*100

```

probability based on relative food abundance.

”

”

”

```

1495 SUM=SUM+((R6*.1155)/RMTOT)*100
1500 IF R>=SUM AND R<SUM+((R7*.1735)/RMTOT)*100 GOTO 2990
1505 SUM=SUM+((R7*.1735)/RMTOT)*100
1510 IF R>=SUM AND R<SUM+((R8*.04145)/RMTOT)*100 GOTO 3020
1515 SUM=SUM+((R8*.04145)/RMTOT)*100
1520 IF R>=SUM AND R<SUM+((R1*.0148)/RMTOT)*100 GOTO 2810
1525 SUM=SUM+((R1*.0148)/RMTOT)*100
1530 IF R>=SUM AND R<SUM+((R2*.04145)/RMTOT)*100 GOTO 2840
1535 SUM=SUM+((R2*.04145)/RMTOT)*100
1540 IF R>=SUM AND R<SUM+((R3*.1161)/RMTOT)*100 GOTO 2870
1550 GOTO 530
1560 RMTOT=R5*.1755+R6*.3217+R7*.1155
+R8*.1735+R1*.04145+R2*.0148+R3*.04146+R4*.1161
1565 IF R>=SUM AND R<SUM+((R5*.1755)/RMTOT)*100 GOTO 2930
1567 SUM=SUM+((R5*.1755)/RMTOT)*100
1570 IF R>=SUM AND R<SUM+((R6*.3217)/RMTOT)*100 GOTO 2960
1575 SUM=SUM+((R6*.3217)/RMTOT)*100
1580 IF R>=SUM AND R<SUM+((R7*.1155)/RMTOT)*100 GOTO 2990
1585 SUM=SUM+((R7*.1155)/RMTOT)*100
1590 IF R>=SUM AND R<SUM+((R7*.1735)/RMTOT)*100 GOTO 3020
1595 SUM=SUM+((R8*.1735)/RMTOT)*100
1600 IF R>=SUM AND R<SUM+((R1*.04145)/RMTOT)*100 GOTO 2810
1605 SUM=SUM+((R1*.04145)/RMTOT)*100
1610 IF R>=SUM AND R<SUM+((R2*.0148)/RMTOT)*100 GOTO 2840
1615 SUM=SUM+((R2*.0148)/RMTOT)*100
1620 IF R>=SUM AND R<SUM+((R3*.04145)/RMTOT)*100 GOTO 2870
1625 SUM=SUM+((R3*.04145)/RMTOT)*100
1630 IF R>=SUM AND R<SUM+((R4*.1161)/RMTOT)*100 GOTO 2900
1640 GOTO 530
1650 RMTOT=R6*.1755+R7*.3217+R8*.1155
+R1*.1735+R2*.04145+R3*.0148+R4*.04146+R5*.1161
1655 IF R>=SUM AND R<SUM+((R6*.1755)/RMTOT)*100 GOTO 2960
1657 SUM=SUM+((R6*.1755)/RMTOT)*100
1660 IF R>=SUM AND R<SUM+((R7*.3217)/RMTOT)*100 GOTO 2990
1665 SUM=SUM+((R7*.3217)/RMTOT)*100
1670 IF R>=SUM AND R<SUM+((R8*.1155)/RMTOT)*100 GOTO 3020
1675 SUM=SUM+((R8*.1155)/RMTOT)*100
1680 IF R>=SUM AND R<SUM+((R1*.1735)/RMTOT)*100 GOTO 2810
1685 SUM=SUM+((R1*.1735)/RMTOT)*100
1690 IF R>=SUM AND R<SUM+((R2*.04145)/RMTOT)*100 GOTO 2840
1695 SUM=SUM+((R2*.04145)/RMTOT)*100
1700 IF R>=SUM AND R<SUM+((R3*.0148)/RMTOT)*100 GOTO 2870
1705 SUM=SUM+((R3*.0148)/RMTOT)*100
1710 IF R>=SUM AND R<SUM+((R4*.04145)/RMTOT)*100 GOTO 2900
1715 SUM=SUM+((R4*.04145)/RMTOT)*100
1720 IF R>=SUM AND R<SUM+((R5*.1161)/RMTOT)*100 GOTO 2930
1730 GOTO 530
1740 RMTOT=R7*.1755+R8*.3217+R1*.1155
+R2*.1735+R3*.04145+R4*.0148+R5*.04146+R6*.1161
1745 IF R>=SUM AND R<SUM+((R7*.1755)/RMTOT)*100 GOTO 2990
1747 SUM=SUM+((R7*.1755)/RMTOT)*100
1750 IF R>=SUM AND R<SUM+((R8*.3217)/RMTOT)*100 GOTO 3020
1755 SUM=SUM+((R8*.3217)/RMTOT)*100
1760 IF R>=SUM AND R<SUM+((R1*.1155)/RMTOT)*100 GOTO 2810
1765 SUM=SUM+((R1*.1155)/RMTOT)*100
1770 IF R>=SUM AND R<SUM+((R2*.1735)/RMTOT)*100 GOTO 2840
1775 SUM=SUM+((R2*.1735)/RMTOT)*100
1780 IF R>=SUM AND R<SUM+((R3*.04145)/RMTOT)*100 GOTO 2870
1785 SUM=SUM+((R3*.04145)/RMTOT)*100
1790 IF R>=SUM AND R<SUM+((R4*.0148)/RMTOT)*100 GOTO 2900
1795 SUM=SUM+((R4*.0148)/RMTOT)*100
1800 IF R>=SUM AND R<SUM+((R5*.04145)/RMTOT)*100 GOTO 2930
1805 SUM=SUM+((R5*.04145)/RMTOT)*100
1810 IF R>=SUM AND R<SUM+((R6*.1161)/RMTOT)*100 GOTO 2960
1820 GOTO 530
1830 END
1840
PROCEDURE TO READ ILLEGAL QUADRATS IE. QUADRATS OUTSIDE
HOME RANGE IF ILLEGAL GO TO 400 IF NOT GOTO 880

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2810 XR=-1
2820 YR=1
2830 GOTO 530
2840 XR=0
2850 YR=1
2860 GOTO 530
2870 XR=1
2880 YR=1
2890 GOTO 530
2900 XR=1
2910 YR=0
2920 GOTO 530
2930 XR=1
2940 YR=-1
2950 GOTO 530
2960 XR=0
2970 YR=-1
2980 GOTO 530
2990 XR=-1
3000 YR=-1
3010 GOTO 530
3020 XR=-1
3030 YR=0
3040 GOTO 530

Appendix D: Plant foods of the study troop ordered alphabetically by genus and species. Appended is a list of the non-plant foods, also in alphabetical order. Availability ranges from 1 (commonly available food species) to 4 (rarely available). Amount eaten ranges from 1 (staple food species) to 6 (rarely eaten).

Family	Species	Part eaten	Month	Availability	Amount eaten
Malvaceae	<i>Abutilon austroafricanum</i> Hochr.	seed	6	1	1
Leguminales	<i>Acacia burkei</i> Benth.	pod	7-9,3	2	3
Leguminales	<i>Acacia burkei</i> Benth.	gum	8,10,1	2	1
Leguminales	<i>Acacia caffra</i> (Thunb.) Willd.	flower		1	1
Leguminales	<i>Acacia gerrardii</i> Benth. var <i>gerrardii</i>	seed	10	1	1
Leguminales	<i>Acacia gerrardii</i> Benth. var <i>gerrardii</i>	gum	8,10,11,1,3,4,5	2	3
Leguminales	<i>Acacia gerrardii</i> Benth. var <i>gerrardii</i>	leaf	7-12,3	4	5
Leguminales	<i>Acacia gerrardii</i> Benth. var <i>gerrardii</i>	pod	5,6 8-11	4	6
Leguminales	<i>Acacia karroo</i> Hayne	sprouts			
Leguminales	<i>Acacia karroo</i> Hayne	bark			
Leguminales	<i>Acacia karroo</i> Hayne	gum	1-12	4	6
Leguminales	<i>Acacia karroo</i> Hayne	leaf	9-11	4	3
Leguminales	<i>Acacia karroo</i> Hayne	pod	4-12	4	6
Leguminales	<i>Acacia karroo</i> Hayne	sprouts			
Leguminales	<i>Acacia luederitzii</i> Engl. var <i>retinens</i> (Sim) J.H.Ross & Brennan	gum	11	3	1
Leguminales	<i>Acacia luederitzii</i> Engl. var <i>retinens</i> (Sim) J.H.Ross & Brennan	pod	5-11	4	3
Leguminales	<i>Acacia nigrescens</i> Oliv.	flower	7,8	3	3
Leguminales	<i>Acacia nigrescens</i> Oliv.	gum	9-12,3	2	1
Leguminales	<i>Acacia nigrescens</i> Oliv.	leaf		7 4	1

Fabaceae	<i>Acacia nigrescens</i> Oliv.	pod	4-11,1	3	3
Fabaceae	<i>Acacia nigrescens</i> Oliv.	sprout			
Fabaceae	<i>Acacia nilotica</i> (L.) Willd. ex Del. subsp. <i>kraussiana</i> (Benth.) Brenan	gum	8,9		
Fabaceae	<i>Acacia nilotica</i> (L.) Willd. ex Del. subsp. <i>kraussiana</i> (Benth.) Brenan	pod	5-11	3	5
Fabaceae	<i>Acacia nilotica</i> (L.) Willd. ex Del. subsp. <i>kraussiana</i> (Benth.) Brenan	sprout			
Fabaceae	<i>Acacia robusta</i> Burch. subsp. <i>clavigera</i> (E.Mey.) Brenan	pod	5-12	2	2
Fabaceae	<i>Acacia robusta</i> Burch. subsp. <i>clavigera</i> (E.Mey.) Brenan	gum	6	2	1
Fabaceae	<i>Acacia robusta</i> Burch. subsp. <i>clavigera</i> (E.Mey.) Brenan	leaf	11	2	1
Fabaceae	<i>Acacia schweinfurthii</i> Brenan & Exell var <i>schweinfurthii</i>	Pods		4	1
Fabaceae	<i>Acacia senegal</i> (L.) Willd.	gum	3	1	1
Fabaceae	<i>Acacia senegal</i> (L.) Willd.	pod	9	1	1
Fabaceae	<i>Acacia tortilis</i> (Forsk.) Hayne subsp. <i>heterocantha</i>	leaf	10	4	1
Fabaceae	<i>Acacia tortilis</i> (Forsk.) Hayne subsp. <i>heterocantha</i>	pod	5-10	4	2
Fabaceae	<i>Acacia tortilis</i> (Forsk.) Hayne subsp. <i>heterocantha</i>	gum	6-8,10	4	1
Fabaceae	<i>Acacia xanthophloea</i> Benth.	gum	10	1	1
Liliaceae	<i>Aloe marlothii</i> Berger	seed	9	3	2
Liliaceae	<i>Aloe marlothii</i> Berger	fruit	9	3	2
Liliaceae	<i>Aloe marlothii</i> Berger	flower stem	6,9,10	3	1
Liliaceae	<i>Aloe sessiflora</i> Pole Evans	flower			
Liliaceae	<i>Antherecium galpinii</i> Bak.	flower	11,12	2	1
Rhamnaceae	<i>Berchemia zeyheri</i> (Sond.) Grubov	fruit	12,1,2	3	5
Rhamnaceae	<i>Berchemia zeyheri</i> (Sond.) Grubov	flower	10	3	1
Capparaceae	<i>Capparis brassii</i> L.	fruit	10	3	5
Apocynaceae	<i>Carrissa bispinosa</i> (L.) Desf. ex Brenan	fruit			
Fabaceae	<i>Cassia floribunda</i> Cav.	Pods	12	1	1
Celastraceae	<i>Cassine aethiopica</i> Thunb.	fruit	7-9	1	1
Celastraceae	<i>Cassine transvaalensis</i> (Burt Davy) Codd	fruit	9,10	2	3
Capparaceae	<i>Cladostemon kirkii</i> (Oliv.) Pax & Gilg	fruit	10,11	1	1

Burseraceae	<i>Commiphora harveyi</i> (Engl.) Engl.	fruit			
Burseraceae	<i>Commiphora neglecta</i> Verdoorn	root			
Burseraceae	<i>Commiphora neglecta</i> Verdoorn	fruit			
Burseraceae	<i>Commiphora schimperi</i> (O. Berg) Engl.	fruit			
Fabaceae	<i>Crotalaria macrocarpa</i> E.Mey.	Pods	12	1	1
Euphorbiaceae	<i>Croton gratissimus</i> Burch. var. <i>gratissimus</i>	fr			
Euphorbiaceae	<i>Croton megalobotoris</i> Muell. Arg.	leaf			
Euphorbiaceae	<i>Croton megalobotoris</i> Muell. Arg.	seed	1	3	2
Cyperaceae	<i>Cyperus fastigiatus</i> Rottb.	stem			
Cyperaceae	<i>Cyperus obtusiflorus</i> Vahl. var. <i>obtusiflorus</i>	corm	6-11,3		
Liliaceae	<i>Cyrtanthus galpinii</i> Bak.	root	9	1	1
Fabaceae	<i>Dichrostachys cinerea</i> (L.) Wight & Arn. subsp. <i>africana</i> Brenan & Brum	Pods	8,9	4	1
Flacourtiaceae	<i>Dovyalis caffra</i> (Hook.f. & Harv.) Hook.f.	fruit			
Flacourtiaceae	<i>Dovyalis longispina</i> (Harv.) Warb.	fruit		1 1	1
Acanthaceae	<i>Ecbolium amplexicaule</i> S. Moore	seed	1,2,4	2	2
Boraginaceae	<i>Ehretia rigida</i> (Thunb.) Druce	fruit	9	1	1
Zamiaceae	<i>Encephalartos natalensis</i> R.A.Dyer & Verdoorn	fruit			
Ebenaceae	<i>Euclea divinorum</i> Hiern	fruit	6,10,12	3	1
Ebenaceae	<i>Euclea schimperi</i> (A.DC.) Dandy subsp. <i>schimperi</i>	fruit	7-9	1	2
Euphorbiaceae	<i>Euphorbia grandidens</i> Haw.	stem	4,7,9	2	1
Euphorbiaceae	<i>Euphorbia ingens</i> E.May. ex Boiss.	stem	4	1	1
Euphorbiaceae	<i>Euphorbia tirucalli</i> L.	stem	6	3	1
Moraceae	<i>Ficus abutilifolia</i> (Miq.) Miq.	fruit			
Moraceae	<i>Ficus glumosa</i> (Miq.) Del	fruit	9	1	1
Moraceae	<i>Ficus ingens</i> (Miq.) Miq.	fruit	6,9	2	1
Moraceae	<i>Ficus natalensis</i> Hochst.	fruit	9	1	1
Moraceae	<i>Ficus sycamorus</i> L.	fruit	9	1	1
Lythraceae	<i>Galpinia transvaalica</i> N.E.Br.	fruit			

Tiliaceae	Grewia flavescens Juss. var. olukondae (Schinz) Wild	fruit	3-6	2	2
Tiliaceae	Grewia microthrysa K.Schum. ex Burret	fruit	4-6,9,10	1	1
Tiliaceae	Grewia monticola Sond.	fruit	4,5	1	1
Anacardiaceae	Harpephyllum caffrum Bernh.	fruit	8	1	1
Rubiaceae	Hypercanthus amoenus E. Mey. Ex Bridson	fruit			
Verbenaceae	Lantana rugosa Thunb.	fruit			
Liliaceae	Ledebouria sp.	bulb	9,10	3	2
Sapotaceae	Manilkara concolor (Harv. ex C.H.Wr.) Gerstn.	fruit			
Celastraceae	Maytenus heterophylla (Eckl. & Zeyh.) N.K.B. Robson	flower			
Celastraceae	Maytenus heterophylla (Eckl. & Zeyh.) N.K.B. Robson	fruit			
Stereuliaceae	Melhania forbesii Planch. ex Mast.	seed	1-4	2	2
Loganiaceae	Nuxia floribunda Benth.	fruit			
Oleaceae	Olea europaea L. subsp. (Mill.) P.S.Green	seed	4-6,8	2	2
Oleaceae	Olea europaea L. subsp. (Mill.) P.S.Green	fruit	4-6,8	2	2
Fabaceae	Ormocarpum trichocarpum (Taub.) Engl.	flower	3	1	1
Fabaceae	Ormocarpum trichocarpum (Taub.) Engl.	fruit	3	1	1
Anacardiaceae	Ozoroa paniculosa (Sond.) R. & A. Fernandes	fruit	6,9,10		
Poaceae	Panicum deustum Thunb.	leaf	9-11,6,1	3	1
Poaceae	Panicum maximum Jacq.	seed	9,1,3,4	3	1
Sapindaceae	Pappea capensis Eckl. & Zehy.	fruit	1-5	1	2
Rubiaceae	Pavetta edentula Sond.	fruit			
Arecaceae	Phoenix reclinata Jacq.	fruit			
Rubiaceae	Plectroniella armata (K. Schum.) Robyns	fruit			
Portulacaceae	Portulacaria afra Jacq.	leaf			
Liliaceae	Protasparagus falcatus (L.) Oberm.	shoot	5	1	1
Liliaceae	Protasparagus subulatus (Thunb.) Oberm.	leaf	4	1	1
Vitaceae	Rhoicissus tridentata (L.f.) Wildd & Drummond	fruit	3	2	1
Anacardiaceae	Rhus engleri Britt.	fruit			

Anacardiaceae	<i>Rhus guenzii</i> Sond.	fruit			
Fabaceae	<i>Rhyncosia nervosa</i>	Pods	7,8	1	1
Fabaceae	<i>Schotia brachypetala</i> Sond.	flower	8,9	3	5
Fabaceae	<i>Schotia brachypetala</i> Sond.	leaf	9	3	1
Fabaceae	<i>Schotia brachypetala</i> Sond.	pod	9,2,3		
Fabaceae	<i>Schotia capitata</i> Bolle	Pods		1	1
Fabaceae	<i>Schotia capitata</i> Bolle	flower		1	1
Anacardiaceae	<i>Sclerocarya birrea</i> (A.Rich.) Hochst. subsp. <i>caffra</i> (Sond.)	seed	1-12	3	6
Anacardiaceae	<i>Sclerocarya birrea</i> (A.Rich.) Hochst. subsp. <i>caffra</i> (Sond.)	gum	4	3	6
Anacardiaceae	<i>Sclerocarya birrea</i> (A.Rich.) Hochst. subsp. <i>caffra</i> (Sond.)	bark		3	6
Anacardiaceae	<i>Sclerocarya birrea</i> (A.Rich.) Hochst. subsp. <i>caffra</i> (Sond.)	fruit	9-2	3	6
Sapotaceae	<i>Sideroxylon inerme</i> L.	fruit			
Euphorbiaceae	<i>Spirostachys africana</i> Sond.	bark			
Loganiaceae	<i>Strychnos madagascariensis</i> Poir.	fruit	7,9	3	5
Loganiaceae	<i>Strychnos usumbariensis</i> Gilg	fruit	9	2	3
Fabaceae	<i>Tephrosia longipes</i> Meisn.	pod	3	1	1
Poaceae	<i>Themeda triandra</i> Forssk.	leaf	1-12		
Malvaceae	<i>Thespesia acutiloba</i> (Bak.F) Excell. & Mendonca	fruit	3	1	1
Liliaceae	<i>Trachyandra</i> sp.	flower	11	1	1
Liliaceae	<i>Trachyandra</i> sp.	bulb	11	1	1
Liliaceae	<i>Trachyandra</i> sp.	stem	11	1	1
Rubiaceae	<i>Vangueria esculenta</i> S.Moore	fruit			
Verbenaceae	<i>Vitex harveyana</i> H. Pearson	leaf	1,6,8-10	1	2
Velloziaceae	<i>Xerophyta retinervis</i> Bak.	leaf	6,9,3	1	2
Oleaceae	<i>Ximenia africana</i> Sond.	fruit	11		
Oleaceae	<i>Ximenia caffra</i> Sond. var. <i>caffra</i>	fruit	10		
Rhamnaceae	<i>Ziziphus mucronata</i> Willd. subsp. <i>mucronata</i>	fruit	3-12		
	Ant	eggs			

Beetle	larva
Cacoons?	
Grass	leaves
Grass	roots
Grass	seeds
Grasshopper	whole
Lizard	whole
Mulberry	fruits
Mushrooms	whole
Praying mantis	egg case
Slug	whole
Termite	eggs
Termites	whole
Zea mays	cob
